HABITAT MODIFICATION AND LANDSCAPE FRAGMENTATION IN AGRICULTURAL ECOSYSTEMS: IMPLICATIONS FOR BIODIVERSITY AND LANDSCAPE MULTI-FUNCTIONALITY

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EDITORIAL
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Editorial: Habitat Modification and Landscape Fragmentation in Agricultural Ecosystems: Implications for Biodiversity and Landscape Multi-Functionality

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Editorial on the Research Topic

Habitat Modification and Landscape Fragmentation in Agricultural Ecosystems: Implications for Biodiversity and Landscape Multi-Functionality

INFLUENCE OF HABITAT LOSS AND FRAGMENTATION IN AGRICULTURAL ECOSYSTEMS

Biodiversity is the basis of several important ecosystem functions, which guarantee the provision of irreplaceable Nature's contribution to people, for example food production. Long-term maintenance of such functions and services in agricultural ecosystems thus depend on the maintenance of the biodiversity of agro-ecosystems (Foley et al., 2005; Tomlinson, 2013). Biodiversity loss is therefore a major global environmental problem, with habitat deterioration being one of the main drivers (Tilman, 2001; Brook et al., 2008). As habitat loss is one consequence of agricultural intensification (Benton et al., 2003), and agricultural ecosystems comprise 40% of Earth's land ecosystems (FAO, 2021), agriculture plays a critical role for biodiversity and ecosystem functioning at large.

However, the influence of habitat loss, fragmentation and modifications in agricultural ecosystems on biodiversity and ecosystem functions is still hard to disentangle from that of other mechanisms. For some taxa or ecosystem services (e.g., pollinators and pollination), landscape and habitat modification have been shown to be important, e.g., as increasing habitat fragmentation or crop isolation from natural areas decrease pollination services (Ricketts et al., 2008; Farwig et al., 2009; Garibaldi et al., 2009, 2011). For other groups or services (e.g., seed dispersal and predation) this has so far not been thoroughly investigated (but see Perrot et al.). Landscape and habitat changes can have different effects on biodiversity and ecosystem services depending on not only the taxon or function investigated, but also on landscape structure (Viana et al., 2012), local management (Holzschuh et al., 2008; Vergara and Badano, 2009; Batáry et al., 2012; Kennedy et al., 2013; Rundlöf et al., 2015; Hipólito et al., 2018) or the interaction between these factors (Concepción et al., 2012; Andersson et al., 2014; Faria and Morales, 2021; Tarjuelo et al., 2021).

This issue compiles studies from three continents on different aspects of fragmentation and habitat modification in agricultural ecosystems. Studies include a broad range of organisms: plants, arthropods, birds and bats, as well as multiple functions. We were able to bring together authors and reviewers from different countries around the world (Brazil, Chile, Argentina, Spain, Portugal, France, Sweden and Australia) to share some fresh and innovative approaches evidencing the critical role of biodiversity in the functioning of agricultural ecosystems and how this is modulated by landscape structure and human land-use across spatial and temporal scales. Under this conceptual framework, the reader of this special issue will learn about the significant value for ant conservation of even small and isolated habitat patches, which play several important ecological roles in agroecosystems (Azcárate et al.). This study highlights the need to rethink how small natural habitats inserted in an agricultural matrix can be protected and managed, and how the complex interactions between organisms and landscape factors result in the need to include multiple spatial scales in management and conservation planning. The effect of some management strategies may be particularly complex and depend on both the spatial scale and taxon investigated. For example, Nilsson et al. show that annual flower strips favored the abundance of hoverfly larvae and possibly solitary bees, but had no significant effects on either natural enemies or natural pest control. In the wider landscape, however, the abundance of bees was not affected by annual flower strips (but see Jönsson et al., 2015) and the authors conclude that permanent non-crop structures are likely more important for many organisms.

On one hand, results published in this special issue support the idea that both landscape heterogeneity and configuration contribute to explain the three properties of functional diversity, as shown for bees in Coutinho et al. However, differences can be found between taxonomic groups. For example, bird species richness and abundance did not show a significant response to the amount of neighboring native grassland in restored Brazilian grasslands (da Silva and Fontana), although small landscape elements can double the landscape connectivity compared to a theoretical baseline landscape containing no such elements, with riparian forests contributing the most to enhance landscape connectivity (Siqueira et al.). Although logged forests tend to recover their height after a decade, they do not recover the original forest cover, measured by the Normalized Difference Vegetation Index. Likewise, decade-long recovering stands continue to show lower avian species richness and abundance, and different community composition than unlogged forests (Ribeiro et al.).

Understanding and addressing the effect of spatial scales on agro-ecosystem structure and functioning are critical for conserving farmland biodiversity (Ekroos et al., 2016). Therefore, this is another topic central to this special issue. For example, resolution of the geographical data (land cover) used will affect the relationship found between landscape complexity and species richness and abundance. In this line of evidence, Carneiro et al., report a strong and positive influence of landscape heterogeneity in low thematic resolution land-use classifications (i.e., few cover classes on maps) on richness and rare species abundance. In a different approach to scale effects, Giralt et al. demonstrate a large-scale influence of irrigation expansion on bird community composition in non-irrigated habitats. An increase of irrigated tree orchards favored species richness up to 500 m away from the irrigated area. However, as specialists were replaced by generalist species, this land-transformation process had a negative effect on the dry cereal farmland bird community, which lost singular and threatened species. Such influence of surrounding habitats at large spatial scales and its implications for ecosystem function is also addressed by Perrot et al., who show that both seed and aphid predation levels in agricultural fields increased with the proportion of grassland in a 500 m radius buffer, regardless of the distance to the nearest grassland patch.

The effects of climate change on agro-ecosystem function, another hot topic of present day ecology, is here addressed by Díaz et al., who demonstrate that drought can have adverse effects on many ecosystem functions, in this case in dehesa silvo-pastoral systems. For example, seedling recruitment decreased, while abortion and predispersal seed predation increased, with higher drought intensity. Forest opening aimed at decreasing adult tree mortality under climate change scenarios will then have little or no effects on tree recruitment. Dehesas are savannah-like traditional systems created by man, but known to have high conservation value. However, the replacement of natural habitats, like true savannahs, with commercial tree plantations, like acacias, can result in loss of all biodiversity dimensions, either taxonomic, functional or phylogenetic, at regional scales. Something which was shown by Carvalho et al., who found that Amazonian bat communities were less diverse in acacia plantations than in native forests and the savannah matrix replaced by those plantations, and that this was mainly driven by greater abundance of generalist species in the latter habitat. Nevertheless, some artificial elements associated with agricultural areas can be used as complementary tools for biodiversity conservation in natural habitats. Such is the case of the water tanks studied by Lamelas-López et al., which were shown to work as biodiversity reservoirs for pristine natural ponds. Therefore, and in a broader perspective, in order to understand the true complexity of landscape fragmentation and habitat modification in agricultural systems, it is clear that we need to work with multiple dimensions, organisms and ecosystem services. The history of former land-use is very important in this context, as shown by Uribe et al. Land-use history can affect diversity of forest species in plantations replacing native forests. In particular, pine plantations that directly replaced native forests had a higher abundance of forest specialists and lower abundance of exotics and generalists than plantations on former agricultural land.

Call for Action

The current biodiversity and environmental crisis urges us to adopt more efficient and sustainable agricultural practices (Tilman, 1999) that take into account, not only increased productivity through environmental conservation (e.g., ecological intensification Bommarco et al., 2013), but also food security through socio-economic policies, and thus managing trade-offs between agriculture and environmental conservation (Foley et al., 2005; Brosi et al., 2008; Clough et al., 2011). The development of scientifically sound models that support sustainable landscape and land-use policies that reconcile the conservation of biodiversity and ecosystem services with agricultural productivity and guarantee the required amount and spatial distribution of habitat in the landscape, is a main challenge for research (Brosi et al., 2008; Clough et al., 2011; Martin et al., 2019; Garibaldi et al., 2021). The studies in this special issue provide not only new scientific insight into the ecological basis of such models, but also for their development and application. The speed of biodiversity decline and the strength of the environmental crisis calls for a shift in the way agricultural and other productive landscapes are treated. They must not only be seen as sources of food and other supplies for a human population in growing need and inequity, but also as functional ecological systems that allow us to obtain such supplies which, ultimately, depend on species and their interactions.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct, and intellectual contribution to the work and approved it for publication.

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Consequences of Replacing Native Savannahs With Acacia Plantations for the Taxonomic, Functional, and Phylogenetic α- and β-Diversity of Bats in the Northern Brazilian Amazon

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Across the globe, millions of hectares of native vegetation have been replaced by commercial plantations, with negative consequences for biodiversity. The effects of the replacement of native vegetation with commercial plantations on the functional and phylogenetic diversity of bat assemblages remain understudied, and most studies have focused exclusively on the taxonomic component of diversity. Here, we investigate how the replacement of natural savannahs by acacia plantations affects the α- and β-diversity of bat assemblages. We sampled bats, using mist-nets at ground level, in natural forest, savannah areas and acacia plantations, in the Lavrados de Roraima in the northern Brazilian Amazon. Our results show that, in general, acacia is less diverse than native forests in terms of taxonomic and functional diversity, and is also less taxonomically diverse than the savannah matrix which it substitutes. The observed patterns of α- and β-diversity found in the present study are in large part driven by the superabundance of one generalist and opportunistic species, *Carollia perspicillata*, in the acacia plantations. Taken together, our results show that the replacement of areas of natural savannah by acacia plantations causes a regional loss in diversity across all diversity dimensions: taxonomic, functional and phylogenetic. However, further studies are required to fully understand the ecological and conservation implications of this landscape change.

Keywords: Amazonian ecosystems, Amazonian savannahs, Chiroptera, landscape change, Lavrados de Roraima, non-forest habitats

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INTRODUCTION

Across the globe, millions of hectares of native vegetation have been replaced by commercial plantations, such as rice, soybean, corn, wheat, oil palm, eucalyptus, and acacia (Lepers et al., 2005; Phalan et al., 2013; Fernandes et al., 2016; Carvalho et al., 2019). In recent decades, most of these anthropogenic landscape changes have been concentrated in tropical regions, where increasing demand for land for commercial plantations and livestock production are the key drivers of habitat loss (Boucher et al., 2011; Carvalho et al., 2019; Colli et al., 2020; Rajão et al., 2020). Brazil is one of the countries in which deforestation and the conversion of natural landscapes into agricultural landscapes has been most pronounced (Curtis et al., 2018). For example, among Brazilian biomes, the Atlantic Forest retains just 28% of its original forest cover, of which most is secondary forest and highly fragmented (Rezende et al., 2018), the Cerrado retains less than 54% of its original cover (Strassburg et al., 2017), and the Brazilian Amazon has lost 20% of its original forest cover (Cruz et al., 2020). Beyond these 20%, in recent years increasing areas of savannah within the Brazilian Amazon have been transformed into soybean, corn, eucalyptus, and acacia plantations (Mustin et al., 2017; Carvalho et al., 2019). The conversion of natural to human-modified landscapes, together with the associated fragmentation of habitats, can have irreversible negative consequences for biodiversity.

Habitat loss and fragmentation have been shown to have negative effects on tropical vertebrates (Willig et al., 2007; Coelho et al., 2014; Meyer et al., 2016; Saccol et al., 2017; Ramos Pereira et al., 2018; Aninta et al., 2019; Palmeirim et al., 2020). For bats, habitat conversion leads to decreased availability of roosts and food resources, which will affect their presence, abundance, and behaviour (Jones et al., 2009; Meyer et al., 2016). The effects of habitat conversion also lead to a decrease in the genetic diversity of populations (Collevatti et al., 2020), and loss of richness, taxonomic, functional, and phylogenetic diversity (Ramos Pereira et al., 2018; Aninta et al., 2019). However, few studies have evaluated the effect of the conversion of natural vegetation to tree plantations, such as eucalyptus, on bat assemblages (see Meyer et al., 2016; Farneda et al., 2020; Mendes and Srbek-Araujo, 2020 for a review). Those studies carried out to date have found lower species richness and diversity of bats in eucalyptus plantations than in unlogged forests (Barlow et al., 2007) and natural forests (Pina et al., 2013). As these flying mammals play a key role in maintaining forests and non-forest ecosystems through seed dispersal and insect suppression, the loss of bat species has major consequences for the functioning of these ecosystems (Treitler et al., 2016; Laurindo et al., 2019). In general, studies carried out in the Neotropics, including Brazil, show that gleaning animalivorous bats are negatively affected by landscape changes such as habitat fragmentation, whereas frugivorous and nectarivorous bats may respond positively to such changes (Delaval and Charles-Dominique, 2006; Willig et al., 2007; Meyer and Kalko, 2008; Farneda et al., 2015, 2020; Meyer et al., 2016; Oliveira et al., 2017). These differential effects on different groups of bats have manifested as changes in species composition in human-modified landscapes, with losses of species, functions and lineages (Aninta et al., 2019; Farneda et al., 2020).

The consequences of changes in natural habitats can be even more detrimental to biodiversity and ecosystem services in savannahs and open-canopy woodlands (Veldman et al., 2015), such as the Amazonian savannahs, which are not as effectively protected as other Amazonian habitats (Overbeck et al., 2015; Carvalho et al., 2019). Amazonian savannahs are a natural mosaic of vegetation with forest patches, gallery forests and palm forests of different sizes and structures immersed in a matrix of savannah (Mustin et al., 2017). So far, at least 100 bat species have been recorded in these savannahs (Aguirre, 2002; Bernard and Fenton, 2002; Loayza and Loiselle, 2009; Silva et al., 2013; Carvalho et al., 2018; Lim and Lee, 2018), with studies showing that this ecosystem has the same species richness, but higher abundance of bats than continuous forest (Bernard and Fenton, 2002; Carvalho et al., 2018). In addition, in this natural mosaic of vegetation, bats have high mobility and readily traverse the savannah matrix (Bernard and Fenton, 2003; Loayza and Loiselle, 2009), which may reflect the long history of natural fragmentation in this landscape, such that species are adapted to the configuration of forest patches in a mosaic of savannahs (Bernard and Fenton, 2003). However, very little is known regarding the effects of landscape change on any taxa in the Amazonian savannahs, and those studies that have been carried out have focused exclusively on taxonomic diversity (e.g., Piña et al., 2019), despite the availability of tools to estimate the taxonomic, functional and phylogenetic dimensions of both α- and β-diversity (Moreno et al., 2018). Indeed, for vertebrates, studies have been limited to medium and large-sized mammals, and have shown that richness and diversity are not impacted (Coelho et al., 2014; Piña et al., 2019). To the best of our knowledge, the present study is the first to examine the impacts of landscape change on bat assemblages in the Amazonian savannahs.

Here, we investigate how the replacement of natural savannah by acacia plantations affects the α- and β-diversity of bat assemblages in the northern Brazilian Amazon. Specifically, we (i) compare bat species richness and the taxonomic, functional and phylogenetic diversity dimensions between natural areas of forest and savannah and acacia plantations. In addition, we (ii) assess between-habitat differences in bat assemblage structure and species composition, and (iii) estimate the contribution of the turnover and nestedness component of β-diversity for taxonomic (TβD), functional (FβD) and phylogenetic (PβD) β-diversity among the three habitat types. We expect acacia plantations to have lower taxonomic, functional and phylogenetic diversity than natural forest and savannah areas, due to the loss of species, functions and lineages, as has been previously shown with the replacement of natural vegetation by commercial plantations in the Cerrado (Pina et al., 2013; Ramos Pereira et al., 2018). Bats have high mobility and readily traverse the savannah matrix in Amazonian savannahs (Bernard and Fenton, 2003; Loayza and Loiselle, 2009), making forest patches and savannahs taxonomically similar (e.g., Bernard and Fenton, 2002). Thus, we expect that acacia plantations will change the permeability of the savannah matrix that they replace, and that as such bat assemblage composition will be altered in such a way that taxonomic, functional and phylogenetic β-diversity will be higher between acacia plantations and forest than between savannah and forest. Due to the loss of species, functions and lineages, regarding β-diversity we expect the species richness difference component to be of greater importance than species replacement when the landscape is changed from savannah to acacia plantations.

MATERIALS AND METHODS

Study Area

The study was carried out in the Serra da Lua region, municipality of Bonfim, state of Roraima, in the northern Brazilian Amazon (2°48’24.06′′N and 60°21’12.85′′W; 2°42’3.77′′N and 60°21’18.39′′W; **Supplementary Figure S1**). The average annual temperature in the region is 26°C, and precipitation ranges from 1,700 to 2,000 mm year^{-1} (Barbosa, 1997). The Serra da Lua region is part of the "Lavrados de Roraima" (also known as the Guyana savannahs), the second largest block of Amazonian savannah (Carvalho and Mustin, 2017). This region is currently threatened by the replacement of its natural habitats with commercial tree plantations, plantations of grains and pulses, pastures for domestic cattle, uncontrolled fires, and mining (Barbosa et al., 2007; Carvalho and Mustin, 2017; Carvalho et al., 2019). The study region is a mosaic of planted forests of *Acacia mangium*, remnants of "lavrado" (local name for savannah), forest patches and gallery forests (**Supplementary Figure S1**). Between the late 1980s and early 1990s, most of the natural savannahs in the area were cleared and converted to cattle pasture. However, after 8–10 years the areas were abandoned and monocultures of *A. mangium* were established to supply raw material to both the sawn products industry, and to energy and paper production (Toledo and Nascimento, 2019).

Our data were collected in permanent plots in four modules, established according to the RAPELD standard (Rapid Assessment Protocol for Long-term Ecological Studies; Magnusson et al., 2005) as part of the long-term ecological research of the Biodiversity Research Program (PPBio)[1]. Each module was comprised of two parallel trails of 5 km, 1 km apart from each other. Each trail contained five plots of 2 × 250 m (0.05 ha), totalling 10 plots per module. Out of the total of 40 permanent plots in our study area, we chose six plots in forest, four in savannah and six in acacia plantations (**Supplementary Figure S1**), based on maximum possible variation in age and vegetation structure within habitat types. Two additional plots in savannah were set up outside the modules, as there was no possibility of access to the savannah plots within the modules during the time this study was carried out, due to poor road and trail conditions. Therefore, a total of 18 plots were sampled, six in each habitat type: forest, savannah and acacia plantation. The age of planting in the plots in acacia plantations varied between 11 and 17 years (mean = 13.4 ± *SD* 2.30).

The forest is the most tree species rich habitat (286 species) in the study area and also the most complex in structure, with a high density of trees (∼3,500 stems > 1 cm diameter ha^{-1}), widely variable in stem size, from 1 to 96 cm (mean ∼6 cm), and canopy height around 20 m with large trees of several species (> 30 cm in diameter) reaching up to 40 m in height. The acacia plantations have around six times fewer tree species (48 species) than natural forests and are less heterogeneous, with tree density (∼1,550 stems ha^{-1}) half that of natural forests and stem diameter being less variable, ranging from 1 to 57 cm (mean ∼14 cm). The canopy is almost exclusively made up of *A. mangium* and is lower than the native forests (∼15 m), with few trees in the older plantations reaching 30 m in height. Forest pioneer species such as *Cecropia* spp. (Moraceae) and *Vismia* spp. (Hypericaceae) colonise the understorey of the plantations. The grassy stratum still remains in the understorey of plantations with an open canopy, but *Piper* spp. (Piperaceae) and several herbaceous species are abundant under more closed canopies. The savannah has a dominant grassy vegetation stratum interspersed with trees which are generally small in diameter (1–53 cm, mean ∼7 cm), short in stature (mean of ∼3 m and a few trees up to 10 m) and stem density is around 1,800 stems ha^{-1}. More detailed botanical data for the study plots used in this study are available in Toledo and Nascimento (2019).

Bat Capture

We captured bats during one night in each plot, between July and August 2017, using nine mist-nests (12 × 3 m; 14 mm mesh size) set in the understorey. This sampling period fell within the rainy season, the time of year with the highest bat capture rates in the northern Brazilian Amazon (Carvalho et al., 2018). The mist-nets were set up at dusk, around 18:00 h, and were kept open until 00:00 h. The total sampling effort, calculated according to Straube and Bianconi (2002), was 34,992 m2*h, being 11,664 m2*h for each of the three vegetation types sampled.

Captured bats were removed from the nests and placed in cotton bags for later identification. Bats were sexed, weighed and identified in the field according to Lim and Engstrom (2001); Gardner (2008), López-Baucells et al. (2016), and Reis et al. (2017). Species nomenclature follows Garbino et al. (2020). For the genus *Pteronotus*, we consider all individuals as *Pteronotus* spp. because we cannot be certain if the species are *P. alinotus* or *P. rubiginosus*, recently recognised for this region (Thoisy et al., 2014; Pavan et al., 2018). All applicable institutional and/or national guidelines for the care and use of animals were followed. Also, the fieldwork, handling, and processing of all captures followed the guidelines of the American Society of Mammalogists (Sikes et al., 2016).

Functional Traits

From our capture data and the literature, we compiled data on four functional traits to estimate α- and β-functional diversity: (1) body mass, (2) diet, (3) vertical stratification, and (4) wing morphology (**Supplementary Table S1**). Body mass was based on the average body mass of each species captured in each habitat, excluding pregnant females and juveniles. For species that had no more than 10 individuals, we supplemented the information with body mass data from bats captured in other locations in the northern Brazilian Amazon (William Carvalho, unpublished data). Body mass was log-transformed to normalise

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[1] http://ppbio.inpa.gov.br

values. Information on diet was obtained from the Ecological Register database (ecoregister.org; accessed on 15 January 2019—Alroy, 2017). Thus, we classified the species according to their specific diet as carnivores, frugivores, insectivores, nectarivores, omnivores, or sanguinivores. Vertical stratification was based on the use of vegetation stratum by bats within the forest, being divided into understorey or canopy species (Kalko and Handley, 2001; Ramos Pereira et al., 2010). Finally, for wing morphology, we used data from Tavares (2013) and Marinello and Bernard (2014) for measures of aspect ratio and relative wing loading.

Data Analysis

We restricted our analyses to phyllostomids and the mormoopid *Pteronotus* spp., which can be sampled adequately with understorey mist nets (Kalko et al., 1996). Firstly, we used Spearman's correlation to test if species richness, Shannon's and Simpson diversity and abundance varied with the age of the acacia plantations. All correlations were non-significant ($p > 0.05$; **Supplementary Table S2**), so we pooled the data of the acacia plots. Secondly, we performed a Partial Mantel test (Mantel, 1967) to assess the presence of spatial autocorrelation in the data, after accounting for the effect of habitat type on species composition. For this, we used Euclidean geographic distance, habitat type, and bat assemblage similarity among sites to test whether compositional similarity (using the Bray-Curtis index—Clarke, 1993) was explained by geographic distance. The result of the Mantel test showed no spatial autocorrelation in species composition after accounting for habitat type ($r = 0.128$; $p = 0.113$).

For all analyses, except for species richness, we considered only those species that had more than five captures (see **Supplementary Table S3**). We did this because species with few captures in our study, such as *Artibeus concolor*, *Glossophaga soricina,* and *Gardnerycteris crenulatum*, are relatively frequently captured in areas of Amazonian savannahs when higher sampling effort is employed (see Bernard and Fenton, 2002; Carvalho et al., 2018). Therefore, we cannot be sure that these species were well-sampled in our study, and as such removing them should avoid biasing our results due to our low sampling effort. After this filtering, we had to remove two plots that were sampled in the savannah, as they presented none or only one species with at least five captures. Thus, all analyses were performed using only four savannah plots.

Alpha Diversity

The α-diversity between the three habitats was compared using the estimated species richness, dominance (Simpson's Index D), taxonomic, functional, and phylogenetic diversity. For all indices, except for dominance, we used Hill numbers (Hill, 1973). Hill numbers are defined by the q parameter, which determines the sensitivity of the measure to relative species abundances and facilitates comparison of the data (Hill, 1973; Chiu and Chao, 2014). Thus, as q increases, the diversity values become more sensitive to common species (Chiu and Chao, 2014; Li, 2018a). For Hill numbers, $q = 0$ is equivalent to estimated species richness (species abundance is ignored), $q = 1$ is equivalent to Shannon's diversity (all species are weighted by their abundance), and $q = 2$ is equivalent to Simpson diversity (common species receive greater weight than rare species; Hill, 1973; Chiu and Chao, 2014; Li, 2018a). To estimate species richness ($q = 0$), interpolated and extrapolated species accumulation curves were constructed in the R package "iNEXT" (Hsieh et al., 2016). These curves were constructed for each plot and considering a sample size of twice the smallest sample (52 individuals—total number of individuals captured in the four analysed plots of savannah), as recommended by Chao et al. (2014). For taxonomic, functional and phylogenetic diversity, we used the R package "hillR" (Li, 2018b), considering only the values of q for Shannon's ($q = 1$) and Simpson's diversity ($q = 2$), as these two indices take into account species abundances. For functional diversity, Hill numbers incorporate species pairwise functional distances calculated from species traits (Chiu and Chao, 2014), while for phylogenetic diversity, Hill numbers incorporate a phylogenetic tree (Li, 2018b). For phylogenetic diversity, we used a phylogenetic tree based on the phylogeny of Jones et al. (2002). Subsequently, we used a Kruskal-Wallis test to compare species richness, taxonomic, functional, and phylogenetic diversity between the forest, savannahs and acacia plantations. Additionally, we used Dunn's test, with Bonferroni correction, as a *post hoc* test to assess pairwise between-habitat differences.

Bat Assemblage Structure and Species Composition

Differences in bat assemblage composition between habitats were visualised using a Non-Metric Multidimensional Scaling (NMDS) ordination. The significance of a grouping by habitat type was assessed using analysis of similarity (ANOSIM) with the Bray-Curtis index (Clarke, 1993), applying a Bonferroni correction. To calculate the contribution of each species to the observed differences in species composition between habitats, we used the similarity percentages breakdown (SIMPER) procedure with the Bray-Curtis index (Clarke, 1993). ANOSIM, SIMPER, NMDS, Kruskal-Wallis analyses, Dunn's test, and calculation of the Simpson's Index D were carried out in software Past (Hammer et al., 2008).

Taxonomic, Functional, and Phylogenetic Beta Diversity

We examined the variation in taxonomic (TβD), functional (FβD), and phylogenetic (PβD) β-diversity to elucidate the ecological processes behind the differences in bat assemblages of these habitats. For this purpose, we measured total β-diversity using the Jaccard index and partitioned it into turnover and nestedness components through the β^{-3} and βrich indexes (Carvalho et al., 2012) and applied this framework to TβD, FβD and PβD. For TβD, the two components were species replacement ($T\beta D_{Tur}$—species turnover) and species richness difference ($T\beta D_{Rich}$—due to loss or gain of bat species). For FβD, the two components were functional replacement ($F\beta D_{Tur}$—functional turnover) and functional richness difference ($F\beta D_{Rich}$—due to loss or gain of functional traits). For PβD, the two components were lineage replacement ($P\beta D_{Tur}$—lineage turnover) and lineage richness difference ($P\beta D_{Rich}$—due to loss or gain of bat lineages). The β-diversity components (i.e., $\beta_{Tur} + \beta_{Rich}$) were computed using rarefaction

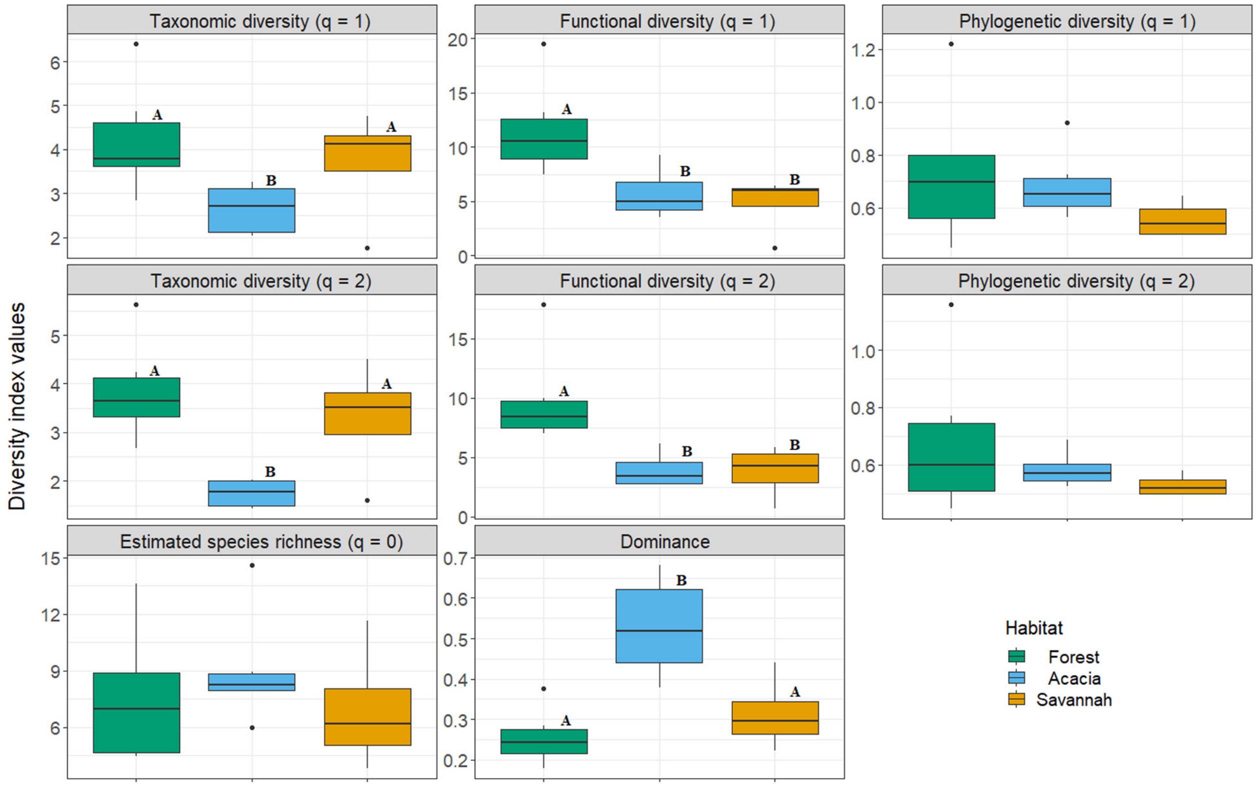

FIGURE 1 | Comparison of taxonomic, functional, and phylogenetic diversity, as well as species richness and dominance of bat assemblages sampled in the forest, savannah and acacia plantations in the northern Brazilian Amazon in 2017. Different letters indicate a significant difference for diversity indices between habitats.

(1,000 runs) of 104 individuals (as was done to estimate species richness—$q = 0$) for each plot. The analyses were conducted using the beta function of the R package "BAT" (Cardoso et al., 2015). For these estimates, we used the same functional traits (previously transformed into a functional tree) and the same phylogenetic tree mentioned above for α-diversity. Posteriorly, to visualise the similarity between habitats in terms of TβD, FβD, and PβD, we used Unweighted Pair Group Method with Arithmetic Mean (UPGMA) clustering. All necessary packages were run in R, version 4.0.2 (R Core Team, 2020).

RESULTS

Overview

We captured a total of 528 bats belonging to 29 species, 21 genera and two families (Phyllostomidae and Mormoopidae; **Supplementary Table S3**). *Carollia perspicillata* was the most captured species in all three habitats, followed by *Artibeus lituratus*, *Artibeus planirostris,* and *Artibeus cinereus* (**Supplementary Table S3**). Seven species were exclusively captured in the acacia plantations (*Chrotopterus auritus*, *Carollia brevicauda*, *Lophostoma brasiliense*, *Pteronotus* spp., *Sturnira lilium*, *Tonatia maresi,* and *Trinycteris nicefori*). The forest was the second habitat with the greatest number of unique species (*Artibeus concolor*, *Glossophaga soricina*, *Micronycteris hirsuta,* and *Vampyriscus bidens*). Only one species (*Lophostoma carrikeri*) was found exclusively in the savannah. The acacia plantations also had the greatest number of individuals captured (385), followed by forest (75), and savannah (68).

Alpha Diversity

There was no significant difference in estimated species richness between the forest (mean ± SD—7.56 ± 3.61), savannah (6.94 ± 3.38), and acacia plantations (8.99 ± 2.92; **Figure 1** and **Supplementary Table S4**). Taxonomic diversity was significantly lower in the acacia plantations than in forest and savannah, for both Shannon and Simpson diversity (**Figure 1**). Dominance was significantly higher in the acacia plantations compared to the forest and savannah (**Figure 1**). Additionally, functional diversity was higher for $q = 1$ (Shannon's diversity) and $q = 2$ (Simpson's diversity) in the forest than in the savannah and acacia plantations (**Figure 1**). For all other comparisons, including phylogenetic α-diversity, there were no significant differences (**Figure 1** and **Supplementary Table S4**).

Bat Assemblage Structure and Species Composition

Considering all three habitats together, species composition differed significantly (Global $R = 0.63$; $p < 0.01$). However, this was driven by the difference between the forest and acacia

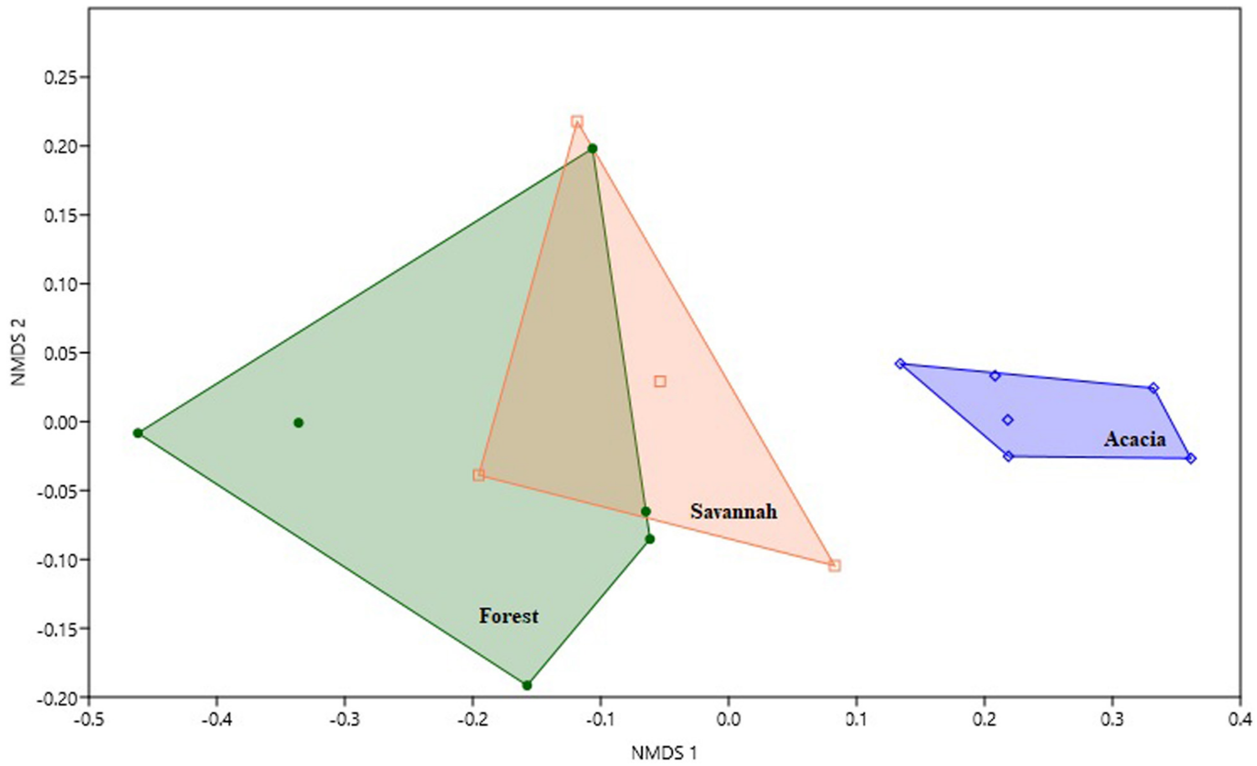

FIGURE 2 | Non-metric multidimensional scaling (NMDS) ordination plot displaying the differences in bat species composition between the forest, savannah, and acacia plantations in an area of Amazonian savannah in the northern Brazilian Amazon. The NMDS was performed on a Bray-Curtis similarity matrix.

plantations ($R = 0.62$, $p < 0.01$) and between the savannah and acacia plantations ($R = 0.40$, $p = 0.04$), and not between the forest and savannah, where species composition did not differ ($R = 0.01$, $p = 1.0$). These differences and similarities between species composition were further supported by the NMDS, which showed a clear separation between the acacia plantations and the other two habitats (**Figure 2**). Together, *C. perspicillata* (70%), *Mesophylla macconnelli* (5%), and *A. planirostris* (4%), contributed ~80% to the dissimilarity between the forest and acacia plantations. All three species had higher average abundance in the acacia plantations than in the other two habitats (**Figure 3**). *Carollia perspicillata* (70%), *M. macconnelli* (5%), and *A. lituratus* (6%) contributed ~80% to the dissimilarity between savannah and acacia plantations. Of these three species, only *A. lituratus* had a higher average abundance in the savannah than in the acacia plantations, with *C. perspicillata* and *M. macconnelli* having a higher average abundance in the acacia plantations (**Figure 3**).

Taxonomic, Functional, and Phylogenetic Beta Diversity

In terms of taxonomic diversity, the savannah and acacia plantations were slightly more similar than the savannah and forest, because the β-diversity between these two habitats was the lowest (TβD = 0.60; **Figures 4**, **5**). The highest value of β-diversity was found between the forest and the acacia plantations (TβD = 0.77), with forest and savannah falling in between (TβD = 0.64; **Figure 5**). Moreover, for functional and phylogenetic β-diversity, forest and savannah attained the lowest values for β-diversity (FβD = 0.30; PβD = 0.24; **Figure 5**), being more similar habitats (**Figure 4**). The savannah and acacia plantations had intermediate values of functional and phylogenetic β-diversity (FβD = 0.53; PβD = 0.37; **Figure 5**), and the forest and acacia plantations the highest values (FβD = 0.59; PβD = 0.46; **Figure 5**).

When we partitioned β-diversity, turnover (β_{Tur}) was the main component of taxonomic and functional β-diversity between the forest and the savannah, and between the forest and the acacia (**Figure 5**). The difference in species richness and functions (β_{Rich}) was the main component of taxonomic and functional β-diversity between the savannah and the acacia plantations (**Figure 4**). On the other hand, turnover was only the largest component of phylogenetic β-diversity when we compared the forest with the savannah. Between the forest and the acacia plantations, and between the savannah and the acacia plantations, the difference in lineage richness was the main component of phylogenetic β-diversity (**Figure 5**).

DISCUSSION

We found that, in general, acacia is less diverse than native forests in terms of taxonomic and functional diversity, and is

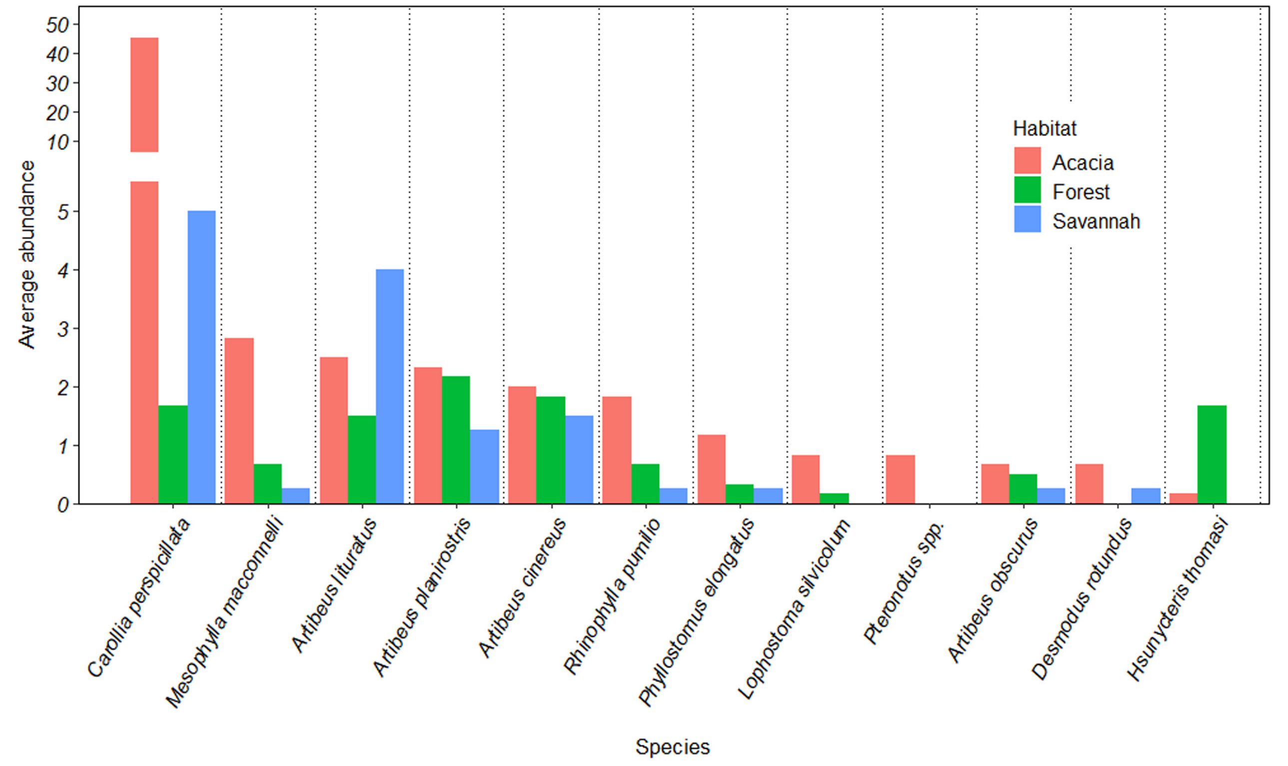

FIGURE 3 | Average abundance of the 12 most common bat species sampled in forest, savannah and acacia plantations in an Amazonian savannah in the northern Brazilian Amazon in 2017. The mean abundance values were estimated using the similarity percentages breakdown (SIMPER) procedure. For better visualisation of the data, the *y*-axis was expanded below the value of 10.

also less taxonomically diverse than the savannah matrix which it substitutes. This result is similar to those found in other studies that have shown lower taxonomic diversity in areas with eucalyptus plantations in the Cerrado (Brazilian savannah—Pina et al., 2013), and in the Amazon (Barlow et al., 2007), and with commercial tree plantations in other ecosystems (Phommexay et al., 2011; Syamsi, 2013). The observed patterns of α- and β-diversity found in the present study are in large part driven by the superabundance of one generalist and opportunistic species, *Carollia perspicillata*, in the acacia plantations, and overall the species composition in the acacia plantations differs significantly from that in both the forest and savannah habitats. Our results have direct implications for the ecology of bats in the Amazonian savannahs, as well as the conservation of these unique and threatened habitats.

The dominance of *C. perspicillata*, which is highly abundant in the acacia plantations, largely drives the lower taxonomic diversity of the acacia compared with the forest and savannah habitats. *Carollia perspicillata* is an opportunistic species that tends to consume more fruit of pioneer plant species (e.g., *Piper* spp. and *Vismia* spp.) when they are available (Fleming, 1986; Andrade et al., 2013; Cely-Gómez and Castillo-Figueroa, 2019). These pioneer plant species are found in early successional secondary forests and forest edges, and are also present in commercial forest plantations not subjected to understorey suppression (Bernhard-Reversat, 2001; Laurance et al., 2002; Toledo and Nascimento, 2019). The acacia plantations in our study area were not being managed and had a very dense undergrowth, in which pioneer plant species, such as *Piper* spp., *Cecropia* spp., *Anona* spp., and *Vismia* spp. are very abundant (see section "Materials and Methods"). Accordingly, *C. perspicillata*—a generalist species that can adapt very well to altered environments, using them for foraging and roosting (Fleming, 1986; Galindo-González, 2004; Castro-Luna et al., 2007; Cely-Gómez and Castillo-Figueroa, 2019)—was the most abundant species in this study, and the most common species in the acacia plantations. In the timber industry, understorey clearing is a common management practise in forest plantations. Forest plantations without understorey clearing, where management has ceased or for some other reason is less intensive than that which would usually be carried out, provide a less hostile habitat for bats and other mammals than do plantations that are managed more intensively and which have management regimes that include the suppression of understorey vegetation (Barlow et al., 2007; Pina et al., 2013, Piña et al., 2019). As such, we would expect that a comparison between native habitats and actively managed acacia plantations would show a greater difference in bat diversity, with acacia plantations being less taxonomically and functionally diverse than both forest and savannah habitats. Furthermore, the superabundance of generalist species in the acacia plantations in our study area has a series of implications for ecological

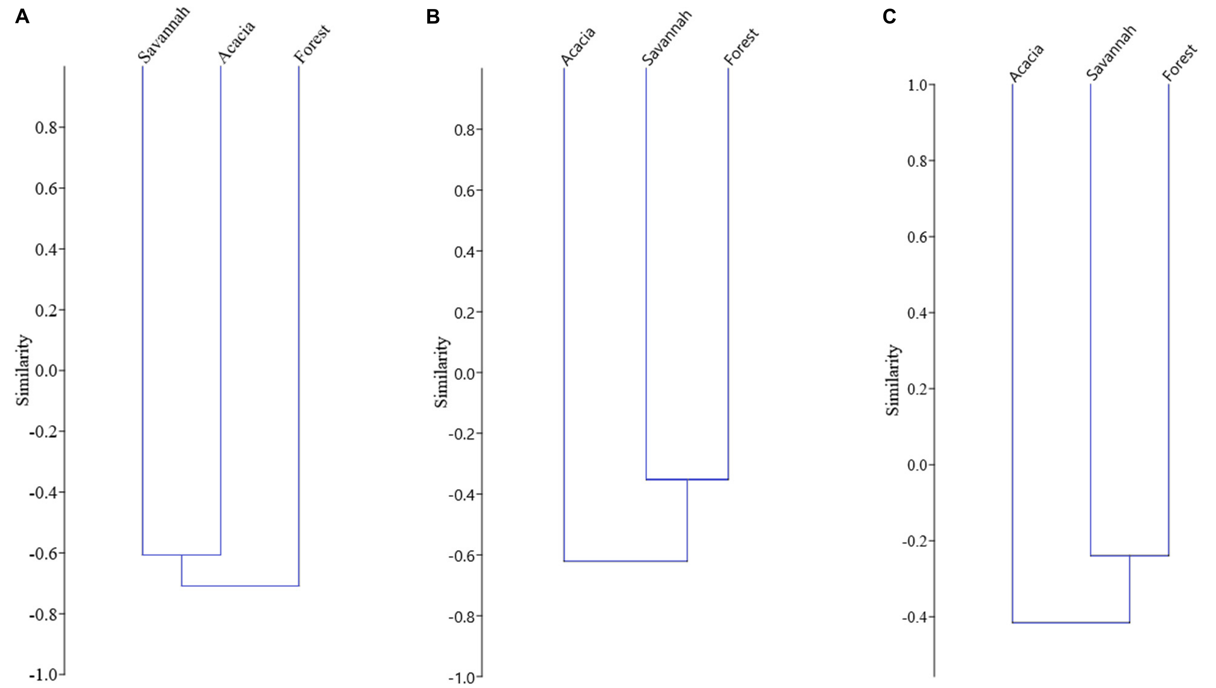

FIGURE 4 | Unweighted Pair Group Method with Arithmetic Mean (UPGMA) clustering of values of **(A)** taxonomic, **(B)** functional, and **(C)** phylogenetic β-diversity for bat assemblages sampled in the forest, savannah, and acacia plantations in an Amazonian savannah in the northern Brazilian Amazonia in 2017.

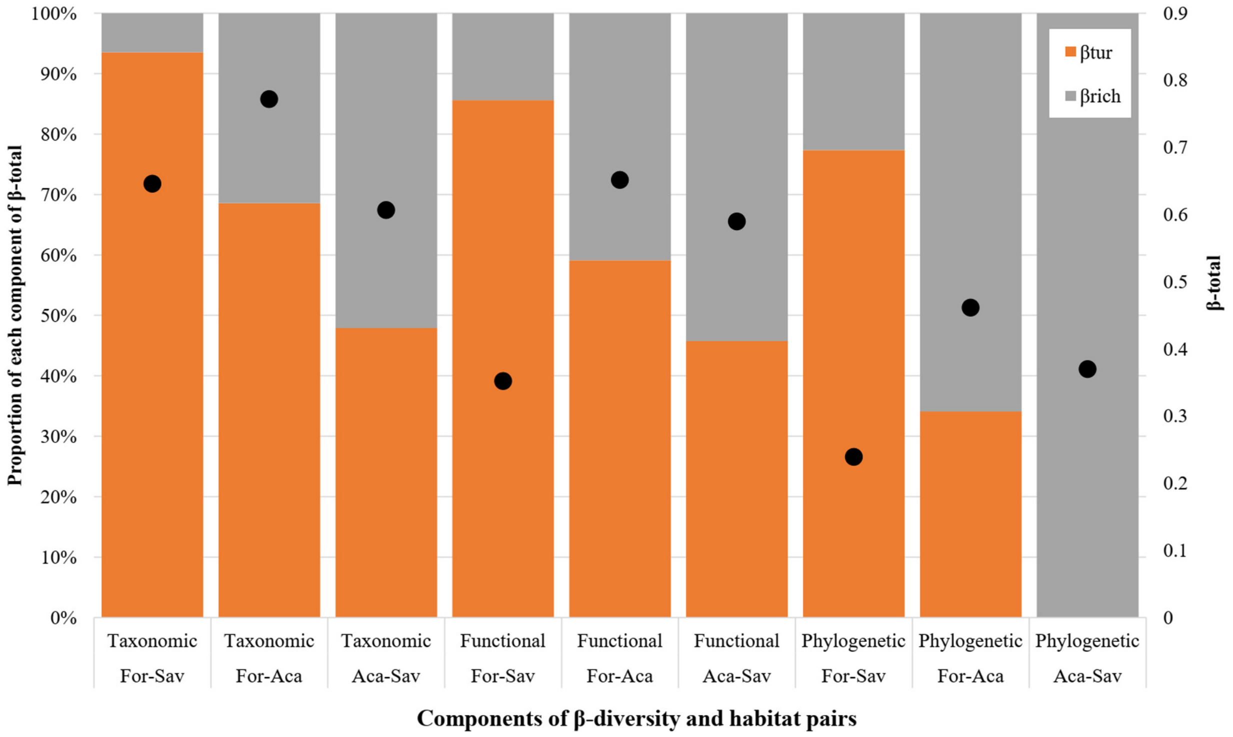

FIGURE 5 | Values of taxonomic (TβD), functional (FβD), and phylogenetic (PβD) β-diversity and percentage of each of the components (β_{Tur} and β_{Rich}) that make up the total β-diversity for the bat assemblages sampled in the forest, savannah and acacia plantations in an Amazonian savannah in the northern Brazilian Amazonia in 2017. The black dots inside the bars represent the total β-diversity values of each partition (*z*-axis). For, Forest; Sav, Savannah; Aca, Acacia.

interactions, seed rain, and subsequently for habitat quality for bats and other species.

Beyond the increase in abundance of generalist species such as *C. perspicillata*, our results also show that some more specialised species, such as gleaning animalivores *Chrotopterus auritus* and *Lophostoma brasiliense*, and the insectivorous *Pteronotus* spp. use the acacia plantations in the vicinity of Amazonian savannahs. These are species typically associated with intact forest environments (Fenton et al., 1992; Farneda et al., 2015), and were not captured in the natural savannah matrix. Preliminary data for the savannahs of the state of Amapá, northeastern Amazon, where the savannah matrix was replaced by eucalyptus plantations (William D. Carvalho—preliminary data) also show these gleaning animalivores using the plantations. This suggests that for some specialist, forest-associated species the substitution of savannah vegetation with commercial tree plantations may increase permeability. However, it is important to highlight that the Amazonian savannahs are a natural mosaic of vegetation with patches of forest, gallery forests and palm forests of different sizes and structures immersed in a matrix of savannah (Mustin et al., 2017), and bat species that occur in these areas are adapted to use these different types of habitats, easily traversing the landscape (Bernard and Fenton, 2003; Loayza and Loiselle, 2009). In contrast, a study in the Cerrado biome found that gleaning animalivores did not use the eucalyptus plantations (Pina et al., 2013). Further studies are required, focussing on landscape use by bats, in order to understand how the substitution of savannah vegetation with commercial tree plantations in the Amazonian savannahs affects matrix permeability and subsequently connectivity between forest patches.

Furthermore, despite the occurrence of some forest-dependent species in the acacia plantations (e.g., *Lophostoma silvicola* and *Pteronotus* spp.), assemblages in this habitat were less functionally diverse than the forest habitats for both Shannon ($q = 1$) and Simpson diversity ($q = 2$). This may again be largely driven by the superabundance of *C. perspicillata* in the acacia plantations, increasing the weight of shrub frugivores in the functional diversity index. This pattern, in which the acacia plantations are less functionally diverse than the forest, is also in part driven by the higher structural complexity of forests compared to acacia plantations, favouring the presence of a greater number of species with different functions, as in other Amazon regions (Farneda et al., 2018; Carrasco-Rueda and Loiselle, 2019).

Functional and phylogenetic β-diversity were always higher between the acacia and each of the natural habitats, than between the forest and the savannah. Thus, our results show that the replacement of savannah by acacia plantations increases the dissimilarity with forests. Functional β-diversity between the acacia and the forest areas is driven slightly more by turnover than richness, and phylogenetic β-diversity more by richness than turnover. However, it is the loss of functions and lineages, much more than turnover, that drives the erosion of functional and phylogenetic diversity when acacia plantations replace savannah areas. Other studies carried out in the Cerrado and Amazon biomes have already shown the loss of bat species, their functions and lineages in human-modified landscapes in comparison with areas of native vegetation (Ramos Pereira et al., 2018; Aninta et al., 2019; Farneda et al., 2020). As such, the multidimensional approach used here is powerful and goes beyond merely species richness and taxonomic diversity. By examining the functional and phylogenetic components of diversity, we are able to move away from exploring only the patterns of diversity, and can instead begin to understand how the substitution of native vegetation with plantations is impacting ecosystem processes. For example, the loss of a particular species does not necessarily have an impact on ecosystem functioning, but the loss of certain functions could have important implications for the ecosystem as a whole (Gitay et al., 1996). Similarly, while the loss of a particular species from an area may have conservation implications, when that species carries a unique evolutionary history and its loss represents the loss of a lineage, the implications for conservation are amplified (Aninta et al., 2019). In this study, by considering α- and β-taxonomic, functional, and phylogenetic diversity, we have been able to show that the replacement of areas of natural savannah by acacia plantations causes a regional loss in diversity across all diversity dimensions.

Despite the limited sampling in this study, and the use of mist nets only at ground level, our results are similar to those of other studies carried out throughout South America (Ramos Pereira et al., 2018; Farneda et al., 2020), particularly in the Amazon (Willig et al., 2007; Farneda et al., 2015; Aninta et al., 2019). Also, the sites sampled were spatially grouped by habitat, with the sites in forest very close to each other, compared with the sites in the savannah and those in acacia plantations. However, our initial spatial analysis, incorporating geographic distance, habitat type, and bat assemblage similarity, suggested that there was no influence of the sampling design on our results. We show that, although the acacia plantations partially retain the taxonomic, functional and phylogenetic diversity of the forest bat assemblages, they are significantly less taxonomically and functionally diverse than the forests themselves, and the diversity they retain may reflect their proximity to forest patches. In addition, the proximity of acacia plantations to forests can also have an indirect negative effect on forest bat assemblages, and this should be investigated by future studies. Acacia plantations seem permeable to some species of bats, providing increased availability of food for generalist species such as *C. perspicillata*, and potentially acting as corridors for forest-dependent species such as *L. silvicola*. However, the replacement of savannah by acacia plantations leads to the loss of species, functions and lineages in the bat assemblage. Furthermore, the superabundance of generalist species in our study area has a series of ecological and conservation implications. As such, taken together our results suggest that acacia plantations in the Amazon are not appropriate to use in offset programmes that aim to reforest or in forest compensation schemes. However, this type of plantation tends to be used by a wider range of species than other types of plantations, such as herbaceous crops, or pasture, and as such may be comparatively less negative for biodiversity (Barlow et al., 2007; Brockerhoff et al., 2013; Carrasco-Rueda and Loiselle, 2019). That being said, there is an alternative route for sustainable economic development in the Amazon savannahs and in the region as a whole. Given that the replacement of native savannah and forest vegetation with acacia plantations has negative impacts on bat diversity, we recommend that joint conservation and development initiatives such as The Amazon Third Way (Nobre and Nobre, 2018) should be supported and expanded. The Amazon Third Way proposes an innovative bioeconomy based on the aggregation of value to sustainably harvested non-timber forest products (NTFPs), building capacity in local communities and traditional populations, and combining traditional knowledge with state-of-the-art technology to generate jobs along the supply chain and develop the regional and national economy in a socially just and environmentally sustainable way (Nobre and Nobre, 2018). This idea is innovative, but is also based on a long history of projects that aim to support the aggregation of value to NTFPs and thus value the standing forest whilst providing sustainable and culturally appropriate livelihoods to local communities and traditional populations. In conclusion, further studies are required to fully understand the ecological and conservation implications of the conversion of native habitats to commercial tree plantations in the Amazon, but there is also a need to critically evaluate the local, regional and national social and economic impacts of this type of commercial activity and in particular to compare them to more socially, environmentally, and economically sustainable alternatives.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

ETHICS STATEMENT

The animal study was reviewed and approved by Comissão de Ética no Uso de Animais da Universidade Federal de Amapá—CEUA-UNIFAP.

AUTHOR CONTRIBUTIONS

WC and JT originally formulated the idea. WC, KM, SS, DP, UC, and JT conducted fieldwork. WC and CM performed statistical analyses. WC, CM, BX, and KM wrote the drafts of the main manuscript and the online resources. All authors contributed critically to the manuscript and gave final approval for publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.609214/full#supplementary-material

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Remnants of Native Vegetation Surrounding Do Not Affect the Diversity and Density of Birds in Brazilian Grassland-Restoration Sites

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Since in general the surrounding landscape influences the species diversity and abundance in fragments of native vegetation, an amount of native-vegetation cover nearby may also positively affect communities in restored areas, regardless of the sizes of individual habitat patches. We investigated for the first time whether the species richness, total abundance, and density of grassland birds in restoration sites are influenced by the amount of native grassland in the surrounding landscape in the Brazilian Pampa. We sampled birds by point counts in five restoration sites in the most representative area of grasslands in Brazil. We established an outer buffer zone with a 1 km-radius around the point-count areas in each site, and calculated the percentage of native grassland vegetation in the surrounding landscape. Bird species richness and abundance did not show a significant response to the amount of neighboring native grassland in restored areas. Individual analyses of the density of seven bird species associated to grassland also showed similar pattern. We believe the vegetation structure in these restoration sites may already been sufficiently re-established to provide necessary resources and a suitable habitat for the birds. Even so, we assume that previously existing landscape features were important for recovery of the vegetation structure, as continuous native grassland in the surroundings. Thus, we recommend consider the landscape context as an additional issue in studies dealing with conservation strategies for recovery of grasslands in Brazil.

Keywords: active restoration, grassland birds, landscape, passive restoration, SESA Grasslands

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INTRODUCTION

Global biodiversity has been continually impacted, with most species now living in fragmented patches resulting from land-use changes and habitat destruction (Haddad et al., 2015; Fletcher et al., 2018). The surrounding landscape influences the species abundance and diversity in fragments, since the landscape may include connecting corridors, influence dispersal between habitat fragments, and depending on the nature of land use, can alter conditions in habitat patches negatively or positively (Öckinger et al., 2012). Landscapes that retain substantial amounts of native vegetation cover should generate large positive ecological responses at the local scale (Kroll et al., 2014).

Community structure is influenced by the landscape configuration, and diversity within a patch depends on the structure of the surrounding landscape (Dauber et al., 2003), i.e., a community in a restored habitat may depend to some degree on the surroundings. Species richness can be shaped by the physical environment, which includes several characteristics of habitat patch area, e.g., quality, size, configuration, and connectivity (Aggemyr et al., 2018). In the case of birds, where individuals can occur across a variety of habitat patches (Whitaker and Warkentin, 2010; Lee and Carroll, 2014), the proportion of native-grassland patches remaining in the landscape can affect the presence of bird species in grasslands (Cerezo et al., 2011). The larger the amount of native grassland in the patches, the greater the richness and abundance of birds (Silva et al., 2015). Therefore, bird species distribution and occurrence can be strongly influenced by landscape characteristics (Lee and Carroll, 2014).

Grasslands have been replaced and fragmented due to changes in land use, mainly agricultural expansion (Pretelli et al., 2018). Restoration of degraded habitats, i.e., recovery of an ecosystem, is still not widely used for tropical and subtropical grasslands (Buisson et al., 2019). Conservation strategies to preserve and restore habitats should consider the quality of the landscape as a whole (Fahrig, 2001). In grassland restoration, spontaneous vegetation recovery depends on the persistence of seed banks and on input of seed from external sources such as native grasslands near the restoration sites (Favreto and de Medeiros, 2006; Andrade et al., 2015; Vieira et al., 2015). Hence, well-conserved landscape patches are important, since recovery is affected by the surrounding land-use matrix that serves as a vital source of propagules (Holl and Aide, 2011).

The total number of species in a given habitat type within a landscape increases with the total amount of that habitat in the landscape, regardless of the size of individual habitat patches (Fahrig, 2013). In view of this, and considering the high proportion of degraded grasslands in the Brazilian Pampa biome in southeastern South America (SESA Grasslands; Azpiroz et al., 2012), we have compared the structure of bird communities of restoration sites with those of native grasslands. We found similarity in the species richness and composition between sites under passive restoration and sites in native grassland (Silva et al., 2019), but these variables differed between sites under active restoration and sites in native grassland (Silva and Fontana, 2020). These findings suggested that the similarities might be due to effects from fragments of native grassland in the surroundings of grassland under restoration. Here, our objective was to examine whether the species richness, total abundance, and density of grassland birds in the same restoration sites are influenced by the amount of native grassland available in the landscape. We expected that restoration sites with large areas of native grassland vegetation nearby would have higher diversity and density of grassland bird species. The landscape matrix can facilitate the dispersal and movement of organisms between habitat patches, which can provide additional habitat for them (Haynes et al., 2007; Lindenmayer et al., 2010).

MATERIALS AND METHODS

Study Area

We carried out the study at five restoration sites located in the Brazilian Pampa grasslands, state of Rio Grande do Sul, southern Brazil, which have been used in previous studies (Silva et al., 2019; Silva and Fontana, 2020; **Supplementary Figure 1**). This was the maximum number of restoration sites found after more than 6 months of search during previous study design. The region is characterized by the presence of native grasslands used mainly for extensive livestock and grain cultivation, especially rice and soybeans (better description of the vegetation, fauna, soil characterization and use can be found in Roesch et al., 2009). Four of the studied sites were undergoing passive restoration, i.e., unassisted recovery following abandonment of fields that had been used to grow soybeans and/or rice for more than 10 years. The sizes of these sites ranged from 65 to 600 ha, and three of them were on private land. The fifth site, on the Brazilian Army reserve, has been undergoing active restoration since 2015 and was previously planted with soybeans for at least 10 years. Several restoration techniques have been used in this 400-hectare site, including fallowing, mechanical mowing, controlled cattle grazing, cattle-exclusion periods, and cattle as transport and dispersal agents for native-plant seeds. Most of the grasslands in this region have been converted to agriculture and afforestation, but few remnants of native grassland and forest persist. This study is part of the first university-government initiative to evaluate bird communities in restoration habitats in grasslands of South America. All five sites had similar relief, soil types, and climates, besides a low cattle stocking rate (≤1 animal unit per ha). They were at least 2.5 km apart, and had a restoration time ranging from 5 to 35 years (the location map and details of each study site are in Silva et al., 2019 and Silva and Fontana, 2020).

Bird Sampling

We sampled birds during the breeding season, i.e., between November and February, in 2015–2016 and 2016–2017, totaling two sampling in each site. We surveyed birds in point counts of 5 min and a 100-m radius, totaling 50 point counts for all sites, all completed by TWS. The sampling occurred soon after sunrise on days of favorable weather (see Silva et al., 2019 and Silva and Fontana, 2020 for details). The distance from the observer to the birds was measured with a rangefinder, and birds in flight were not considered. We recorded a total of 50 species. From that we considered 30 species of birds that are restricted to or that make extensive use of grassland habitats (*sensu* Azpiroz et al., 2012). For the analysis, we selected 11 species with five or more occurrences in point counts, i.e., observed in at least 10% of the point counts (Lockhart and Koper, 2018).

Landscape Data

We obtained satellite images of Bing Aerial Layer, using Quantum GIS 2.18 (Qgis Development Team, 2016). For each site, first we marked a 250-m inner buffer zone around the bird point counts (with a 100-m radius and 150 m from the edges). We then marked an outer buffer zone with a 1-km radius, surrounding the smaller buffer zone. We determined this buffer proportion because it encompasses the home ranges of most Neotropical songbirds (Lee and Carroll, 2014), and is sufficiently large for the birds to perceive as a landscape (Rodewald and Yahner, 2001), covering all environmental features (Alexandrino et al., 2019). We drew polygons of all land uses except native grassland inside the outer buffer zone for each site, using a 1:20,000-scale screen. Land-use types were monocultures, native forest, water bodies, and human-impacted areas. We calculated the percentages of land uses for each outer buffer zone and subtracted them from the total area of this buffer zone, to obtain the percentage of native grassland area (**Table 1**).

TABLE 1 | Relative number of grassland-bird species and individuals per point count, and area of native grassland in passive (PR) and active (AR) restoration sites in Brazilian Pampa grasslands.

Species	**Sites (number of point counts)**				
	PR1 (12)	**PR2 (12)**	**PR3 (10)**	**PR4 (6)**	**AR (10)**
Grassland Sparrow *Ammodramus humeralis*	0.08	1.92	2.60	3.00	2.50
Firewood-gatherer *Anumbius annumbi*	0.17	0	0.20	0.33	0
Wedge-tailed Grass Finch *Emberizoides herbicola*	0.50	0.83	0.10	0.67	0.10
Pampa Finch *Embernagra platensis*	0.33	0.25	0	0	1.20
Spotted Nothura *Nothura maculosa*	0	0	0.40	0.17	0
Red-winged Tinamou *Rhynchotus rufescens*	0	0.58	0	0	0.10
Grassland Yellow Finch *Sicalis luteola*	0	0.67	1.50	1.50	1.90
Rusty-collared Seedeater *Sporophila collaris* – NT (R)	0	0.58	0	0	0
Pearly-billied Seedeater *Sporophila pileata* – VU (R)	0.25	0	0.30	0.50	0.10
Fork-tailed Flycatcher *Tyrannus savana*	0.50	0.08	0.10	1.00	0.10
Blue-black Grassquit *Volatinia jacarina*	0.17	0.17	1.30	0	1.20
Relative number of species	0.58	0.67	0.80	1.17	0.80
Relative number of individuals	2.00	5.08	6.50	7.17	7.20
Point-count area (ha)	172	162	130	84	151
Total buffer-zone area (ha)	1275	1120	920	769	1007
Native grassland in surrounding area (ha)	510 (40%)	818 (73%)	534 (58%)	515 (67%)	856 (85%)

Regional conservation status (R; Rio Grande do Sul, 2014): VU, vulnerable; NT, near threatened. Geographical coordinates: PR1, 30°05′07″S, 51°40′37″W; PR2, 29°29′42″S, 55°38′39″W; PR3, 29°35′52″S, 54°54′32″W; PR4, 29°36′16″S, 54°54′37″W; AR, 30°04′32″S, 55°04′36″W.

Statistical Analysis

To determine if there was a relationship in species richness and abundance of grassland birds with the amount of native grassland habitat available in the landscape, we performed a Hierarchical Linear Model (HLM) using the function “lmer” in the “lmerTest” package in R software (Kuznetsova et al., 2017; R Core Team, 2020). Our models included the richness and abundance for each point-count (response variables), the percentage of native grassland (independent variable) and a null model, and site as random effect to control for non-independence of point-counts. Our full model was “x = lmer (response variable $\sim$ independent variable $+$ $(1|\text{site})$.” We selected the best model comparing the full and null model using ANOVA comands (Zuur et al., 2009). To density, we performed a Tweedie compound Poisson generalized linear model, since the Tweedie distribution accept non-integer and zeros values. We used the “cpglm” function of the “cplm” package in R (Zhang, 2013). We compared the full and null model using the second-order Akaike’s Information Criterion (AIC) corrected for small sample sizes (AICc). The model with the lowest AICc value was selected as the best model. The significance level was $\alpha = 0.05$.

We estimated the density for the seven most associated grassland species at each site using distance-sampling analysis of our point-count data and the multiple covariates distance sampling (MCDS) engine in Distance 7.1 Release 1 (Buckland et al., 2001; Thomas et al., 2010). Grassland species with >30 observations were analyzed individually (Grassland Sparrow *Ammodramus humeralis*, Grassland Yellow Finch *Sicalis luteola*, and Blue-black Grassquit *Volatinia jacarina*), and we post-stratified analysis by sample. For other four species, to reach the minimum number of observations required to produce a reliable detection function with Distance (Buckland et al., 2001), they were combined into a single group (Wedge-tailed Grass Finch *Emberizoides herbicola*, Pampa Finch *Embernagra platensis*, Rusty-collared Seedeater *Sporophila collaris*, and Pearly-billied Seedeater *Sporophila pileata*). We grouped these species according to their use of habitat for breeding and feeding in southern Brazil, e.g., similar types of vegetation structure, grass height and foraging strategy (Azpiroz et al., 2012; TWS and CSF, personal observation). For species analyzed as a group, we used the group detection probability function and post-stratified the model by species to obtain each species’ density in each site. We compared the following models for each species and group: half-normal and hazard-rate key functions with cosine, simple polynomial, and hermite polynomial series expansion adjustments. We chose the model based on the Kolmogorov–Smirnov probability test for goodness of fit and on Cramer–von-Mises uniform and cosine probability tests for plausibility, and then compared AIC values to select the model with the lowest AIC.

RESULTS

We found no significant difference among the species richness (HLM, t-value = 3.22, P = 0.06) and abundance (HLM, t-value = 2.20, P = 0.13) of grassland birds and the amount of native habitat in the landscape (**Figure 1**). We found the same

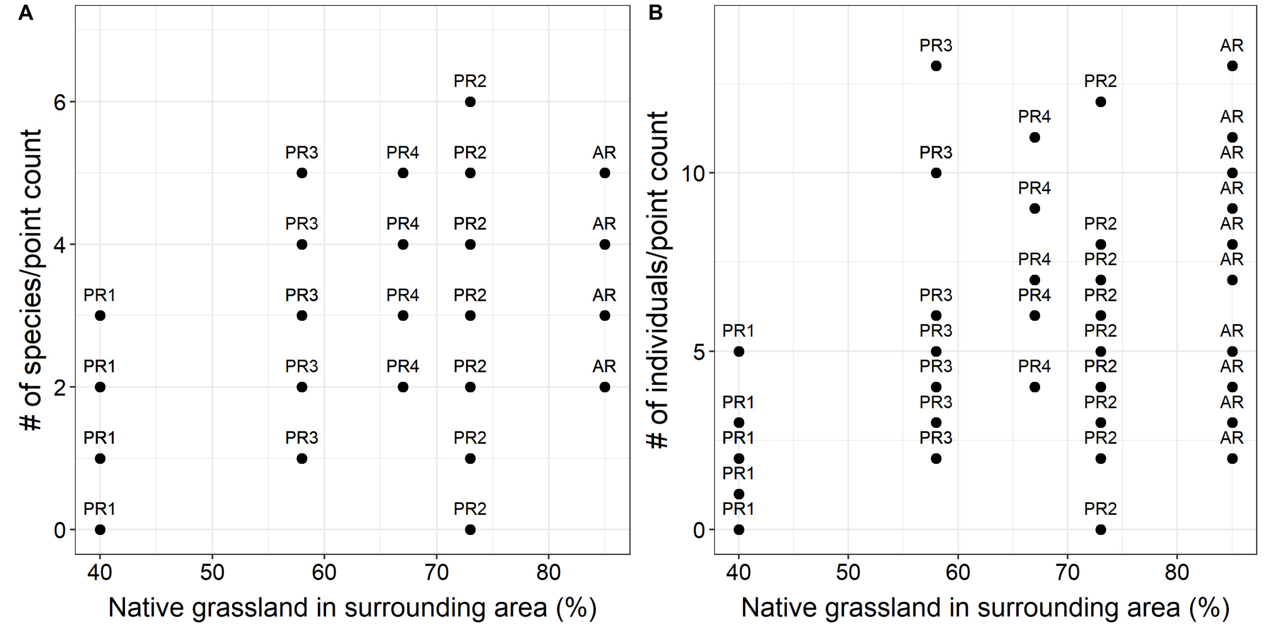

FIGURE 1 | Species richness **(A)** and abundance **(B)** of grassland birds relative to the amount of native grassland in the landscapes.

for the densities of seven grasslands bird species (**Figure 2**). For all species, the best model was null model, i.e., the amount of native grassland had not influence on grassland birds density in restoration areas. However, the density of Grassland Sparrow increased with the amount of native grassland, up to four individuals per hectare in the site with 67% native grassland, and for Grassland Yellow Finch up to three individuals per hectare in the site with 85% native grassland in the surroundings (**Figure 2**), showing a potential pattern to be explored in the light of additional data (more sample sites).

DISCUSSION

The surrounding landscape matrix influences the responses of species in habitat fragments (Pretelli et al., 2018), and responses to landscape attributes provide information about improvements in habitat management (Kroll et al., 2014). Increasing the amount of native vegetation may provide additional habitat and can be considered a key driver of species richness (Lindenmayer et al., 2010). Previous studies have found a significant positive relationship between bird species diversity and the amount of native vegetation in the landscape surrounding the patch of habitat where they occur (e.g., Haire et al., 2000; Lindenmayer et al., 2010; Wentworth et al., 2010). Landscapes with large areas of continuous grasslands significantly enhance the richness and abundance of grassland-specialist birds (Codesido et al., 2013; Pretelli et al., 2018). Therefore, the surrounding context has been considered a more important issue than assessing the patch size and degree of isolation (Collinge et al., 2003; Lindenmayer et al., 2010). However, we did not find a strong evidence of this association between the landscape and the species richness, total abundance, and density of grassland bird species. Similarly, a study in Canadian prairies found only weak effects of habitat amount on grassland-songbird relative abundance and richness, although the habitat configuration did strongly influence these parameters on the birds (Lockhart and Koper, 2018). However, our non-significance is weak and can be due to the small number of replicates. We believe that more replicates could provide more-robust information on the effect of the surroundings on birds in restoration areas of Brazilian grasslands. However, in these grasslands we encountered enormous difficulty in locating enough restoration areas and permissions for sampling, which limited our current study. Moreover, in our previous studies evaluating the bird species richness, abundance and composition in these same five restoration sites, we found a recovery potential of the bird community comparable to native grasslands (Silva et al., 2019; Silva and Fontana, 2020). The continuous native grassland surrounding the restoration sites may have influenced this similarity, i.e., the habitat configuration (Lockhart and Koper, 2018). Therefore, the response that we found does not preclude the existence of benefits from remnant grasslands, and there could have been reduction of habitat quality even though native vegetation covered over half of the surrounding landscape.

A high proportion of native grasslands in the landscape can further the recovery of grasslands in the process of restoration (Waldén et al., 2017). Therefore, the habitat structure (vegetation) of the restoration sites that we evaluated may already be sufficiently re-established to provide necessary resources and a suitable habitat for the birds. Furthermore, because at the sampling sites the areas of grassland under restoration were large, the amount of neighboring grassland may have little impact on grassland birds (Lockhart and Koper, 2018). In addition, when less than 30% of native habitat remains in the landscape (which

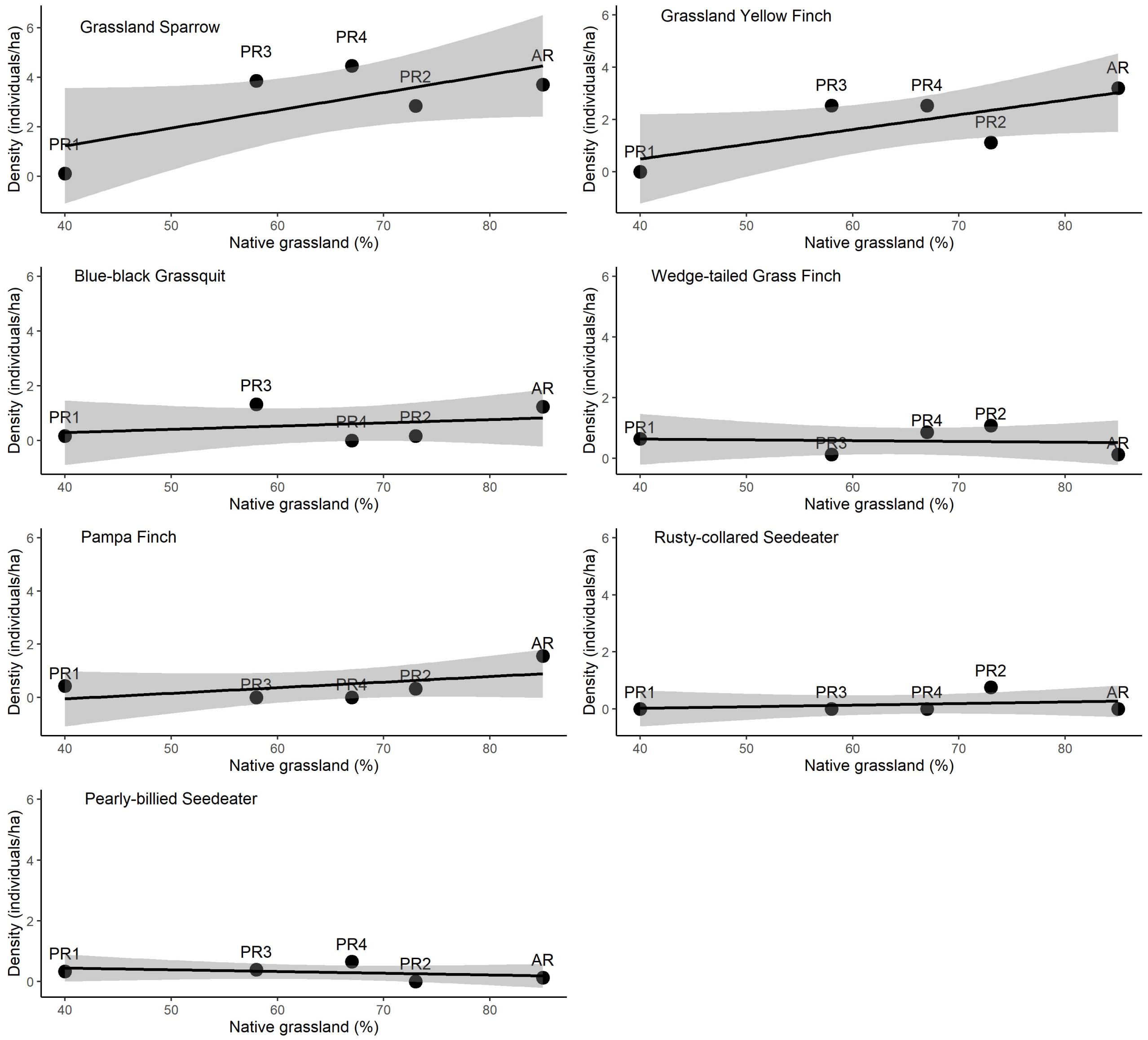

FIGURE 2 | Proportion of grassland-bird density (individuals/ha) per 6 to 12 point counts within each restoration site, to the amount of native grassland vegetation in the landscapes. Confidence intervals are in gray.

was not the case for our areas, which had at least 40% native grassland), the effects of fragmentation begin to be greater (With and Crist, 1995; Fahrig, 2003). This aspect may be another reason for the observed low influence of neighboring native grassland on the grassland birds. Moreover, our first results for restored grasslands agree with another study conducted in Brazilian remaining native grasslands (Camilotti, 2009), and this pattern may be specific for the Brazilian Pampa. Even so, further studies are needed to confirm if the native habitat of the surroundings does not influence the bird community of sites under restoration.

The lack of a significant correlation between the densities of the seven species evaluated and the amount of native grassland nearby may be associated with the factors described above. Each species may respond differently to habitat and landscape transformation, because of the nature of its particular specialization for foraging and reproduction (Manning et al., 2004; Fischer and Lindenmayer, 2007; Shahan et al., 2017). Species responses can also be influenced by dispersal, movement, and the spatial scale at which species-landscape interactions manifest (Shahan et al., 2017). Although Grassland Sparrow and Grassland Yellow Finch use alternative habitats and occupy a range of grass heights, both species make extensive use of grassland habitats and showed increases in density with increased percentages of neighboring native grassland, a pattern previously observed in Brazilian grasslands (Silva et al., 2015).

This is the first landscape-matrix analysis of birds in grassland habitats under restoration in South America. In view of the small number of study sites and the level of significant found, caution is needed in extrapolating these results. However, even though we failed to find a relationship between the surrounding landscape and the richness and abundance of grassland birds, the previously existing landscape features were important for recovery of the vegetation structure (Overbeck et al., 2013). In addition, it is known that the amount of native habitat in the surroundings can significantly influence the diversity of bird species. We stress the need to consider the landscape context as a complementary approach to guide future decision-making on habitat management in restoration projects and to determine conservation strategies.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because there was not collected and/or manipulation of birds, only observation in the wild.

AUTHOR CONTRIBUTIONS

TWS and CSF conceived and designed the research, discussed ideas, and improved all previous versions of this manuscript. TWS performed the experiments, conducted the analyses, and wrote the manuscript. CSF edited the manuscript. Both authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.576705/full#supplementary-material

Supplementary Figure 1 | Restoration sites studied in the Brazilian Pampa grasslands: PR1 to PR4 – passive restoration, AR – active restoration. Photos: TWS.

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Biodiversity Patterns of Macroinvertebrate Assemblages in Natural and Artificial Lentic Waters on an Oceanic Island

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The Azorean islands have been historically affected by human activities, mainly due to the combined effects of habitat degradation and fragmentation, and the introduction of exotic species. We here aim to analyze the role of environmental characteristics and spatial descriptors in supporting regional biodiversity of macroinvertebrates by considering natural ponds and artificial tanks. After the monthly variation of macroinvertebrate assemblages was assessed in three temporary and two permanent ponds in the Azorean island of Terceira during a complete inundation-desiccation annual cycle, the assemblage differences of 12 ponds (three temporary and nine permanent ponds) and 8 closely-located artificial tanks were analyzed across a range of landscape disturbances. Macroinvertebrate assemblages were found to differ according to hydroperiod and sampled months. Although the former explained the highest variance, macroinvertebrate differentiation by hydroperiod was also dependent on the study month. Our results also revealed a consistent monthly pattern of species replacement. However, the contribution of nestedness to the macroinvertebrate β-diversity was notable when temporary ponds were close to desiccation, probably indicating a deterministic loss of species due to the impoverished water conditions of the ponds facing desiccation. When the macroinvertebrate assemblages were analyzed in relation to physico-chemical variations and spatial descriptors, the artificial tanks were not clearly segregated from the natural ponds, and only differentiated by pH differences. In contrast, those natural ponds exhibiting high concentrations of total phosphorous (likely signs of anthropization) also discriminated the ordination of ponds in a distance-based redundancy analysis, and showed impoverished assemblages in comparison with well-preserved ponds. The macroinvertebrate assemblages of the natural ponds showed a significant spatial pattern, but this spatial influence was not significant when tanks and ponds were considered together. Our results suggest that tanks may act as possible reservoirs of biodiversity during the desiccation period of temporary ponds, but are unable to establish successful populations. These fishless permanent tanks can complement the conservation of a biodiversity that is largely maintained by the pristine high-altitude natural ponds. The establishment of a guideline for conservation management that also considers the artificial tanks is necessary to benefit the local and regional Azorean macroinvertebrate diversity.

Keywords: beta-diversity, farm ponds, hydroperiod, landscape transformation, conservation, oceanic islands, pond water quality, temporary ponds

INTRODUCTION

Freshwater ecosystems are currently highly vulnerable to external perturbations associated with anthropogenic changes, mainly due to the introduction of exotic species, landscape transformations and climate change (Sala et al., 2000; Pyšek et al., 2010). Indeed, landscape transformation (e.g., to urban or agricultural areas) has largely contributed to the global loss and degradation of freshwater habitats and is a major threat to freshwater organisms (McKinney, 2002). In contrast to the general negative role of human disturbance in shaping biodiversity, artificial ponds or tanks associated with agricultural systems have sometimes demonstrated that they are able to sustain biodiversity (Abellán et al., 2006; Declerck et al., 2006; Céréghino et al., 2008; Thiere et al., 2009). These human-made ponds usually have different environmental characteristics in comparison with natural ponds (e.g., Hill et al., 2016, but see Deacon et al., 2018, 2019 for similar chemical properties), given that these artificial systems usually have concrete sides and reduced vegetation cover, and possibly higher contaminant inputs compared to natural ponds (Hassall, 2014). Artificial ponds usually show reduced freshwater biodiversity, can support the occurrence of exotic species and may act as possible ecological traps (Oertli and Parris, 2019). However, artificial ponds that maintain good water quality (e.g., low concentrations of nutrient and other pollutants, vegetated bed/margins, low electrical conductivity) may provide habitat diversification, refuge and supplies for aquatic macroinvertebrates, amphibians, and terrestrial species (Mitsch and Gosselink, 2000; Oertli and Parris, 2019). Hence, artificial permanent waterbodies for cattle drinking-water have received increasing attention as regards conservation due to their secondary function as refuge habitat for macroinvertebrates (Ruggiero et al., 2008). In the current scenario of a changeable world, decisions regarding human-made ponds are essential for conservation programs. However, the particular environmental conditions that favor or deplete biodiversity in artificial ponds across different land-uses, and their positive or negative contribution to biodiversity in a natural pond network remain quite unexplored.

Temporary ponds are characterized by recurrent inundation and desiccation (Williams, 1997; Florencio et al., 2011; Céréghino et al., 2012), but they can usually persist for centuries in the same region, in addition to possessing a worldwide distribution (Williams, 1997; Williams et al., 2001). However, the high and valuable biodiversity (high species richness in relation with the size of the pond, rare taxa, and uniqueness) of temporary ponds contrasts with their sensitivity and vulnerability to external perturbation (Williams, 2006). Consequently, temporary ponds are considered priority habitats for conservation by the European Union (code 3170 of the Habitat Directive). The inundation of temporary ponds usually starts at the onset of the rainy season, whereas the duration of the recurrent dry period is less predictable (Williams, 1997). These temporary ponds support singular macroinvertebrate taxa that often cannot survive in other types of aquatic ecosystems (Collinson et al., 1995; Bilton et al., 2001; Williams, 2006). The macroinvertebrate species that inhabit these ponds must cope with pond desiccation by adjusting their life cycles to the water permanence (hydroperiod) and employing particular strategies to survive pond desiccation (Williams, 2006). Moreover, these macroinvertebrates usually cannot cope with the presence of fish, having evolved in the absence of these top predators, which in most occasions are restricted to permanent ponds (Wellborn et al., 1996). In addition, the heterogeneity of a pond network is reflected in its hydroperiod gradient (Florencio, 2010). Therefore, widely variable hydroperiods, together with good pond connectivity, are key factors that contribute to the conservation of a high diversity of macroinvertebrates (Urban, 2004; Jeffries, 2005).

The proper management and conservation of biodiversity against possible threats require the acquisition of a good understanding of the regional species diversity, and the measurement of β-diversity is a useful concept to assess that (Socolar et al., 2016) as it allows the proper assessment of seasonal and spatial changes in aquatic invertebrate assemblage compositions (Florencio et al., 2016a). In metacommunity ecology, β-diversity may be defined as the variation in species composition among sites in a geographical region (Legendre et al., 2005; but see e.g., Koleff et al., 2003; Tuomisto, 2010; Anderson et al., 2011). The observed differences in β-diversity values may be the result of the combination of species between sites (replacement), and of the loss (or gain) of species between sites (nestedness), which it is known as a form of β-diversity partitioning (Baselga, 2010; Baselga and Orme, 2012). Alternatively, Carvalho et al. (2012) also provide this partition of β-diversity, but incorporate a richness difference component instead of nestedness. In ponds, those systems with high species replacement would demand the conservation of several ponds with variable richness and environmental conditions, while systems with low species replacement and high nestedness contribution to the β-diversity would prioritize the conservation of those ponds with the highest richness (see Baselga, 2010).

The Azorean archipelago is an ideal model system to assess the impact of landscape alterations on biodiversity, given that the Azores has suffered intensive landscape transformations, as well as the introduction of exotic species (approximately 58% of the arthropods are exotic species; Borges et al., 2005). Such transformations from native to agricultural areas have drastically restricted the extent of the original native forests to high altitude areas, much less accessible to humans (Triantis et al., 2010; Borges et al., 2020). Natural freshwater ecosystems in Macaronesian archipelagos (Azores, Madeira, Selvagens, Canary Islands, and Cabo Verde, *sensu* Engler, 1914) are considered priority conservation areas by the EU Water Framework Directive (2000/60/EC) (WFD), and are mainly located in the high-altitude native forests. Although these ecosystems are essential for the conservation of a unique freshwater community, limited knowledge of their temporal and spatial dynamics hinders the establishment of proper conservation guidelines (Hughes and Malmqvist, 2005). The present study focuses on the landscape matrix of Terceira Island, Azores, where natural and artificial ponds are located, to analyze the role of environmental characteristics and human-made ponds in supporting regional biodiversity. The spatio-temporal variations in the natural temporary and permanent ponds in Azores were first determined by using monthly data of three well-preserved temporary and two permanent ponds that were sampled monthly, during a complete year of inundation-desiccation cycling. Secondly, changes in macroinvertebrate assemblages were addressed across a range of anthropogenic disturbance, using all accessible ponds within Terceira Island as a study case, encompassing 12 natural ponds (three temporary and nine permanent ponds), and eight closely-located artificial tanks constructed to supply water for cattle. We hypothesized that (i) pond differences and seasonal variations in macroinvertebrate assemblages would indicate different pre-dominant taxonomical groups during the hydrological year, and that such differences would be explained by the pond characteristics; (ii) artificial tanks could act as reservoirs of aquatic biodiversity, and be inhabited by similar macroinvertebrate assemblages as natural ponds. To explore the latter, we have disentangled the environmental characteristics that favored macroinvertebrate diversity in these artificial tanks.

MATERIALS AND METHODS

Study Site

The Azores is an archipelago located in the North Atlantic, about 1,600 km from the European coast and 3,900 km from North America, between latitudes 36° 55′-39°43′ N and longitudes 24°45′-31°17′ W (**Figure 1**). It comprises nine main islands and some islets, all of volcanic origin, which are organized in three groups: the western group (Corvo and Flores islands); the central group (Faial, Pico, São Jorge, Graciosa, and Terceira islands); and the Eastern group (São Miguel and Santa Maria islands). The climate is temperate oceanic, characterized by stable temperatures, substantial precipitation (mean annual precipitation of 740–2,400 mm; Bettencourt, 1979) and high relative atmospheric humidity, which can reach more than 95% in high-altitude native forests.

This study was carried out in Terceira Island which has an area of 402 km^2 and a maximum elevation of 1,023 meters above sea level. The Azorean archipelago, and specifically Terceira Island, was colonized by the Portuguese in the 15th century. Since the first settlements, the landscape was gradually transformed to accommodate agricultural activities and intensive pasturelands for cattle and crops after 1,950 (Triantis et al., 2010). Native forests were gradually destroyed as a consequence of these major land-use changes and currently the few remnants of the original forest or even secondary patches are located in the most inaccessible areas of the island (**Figure 1**), representing scarcely 6% of the Terceira Island surface area (Gaspar et al., 2008). Eight of the 12 studied ponds were located in natural and seminatural areas of Terceira Island, at between 387 and 912 m.a.s.l., including two protected areas with still pristine native forest, considered two of the most pristine areas in the Azores (Gaspar et al., 2011): "Caldeira de Santa Bárbara e Mistérios Negros" and "Terra Brava." These ponds are small (<7,000 m^2) and shallow. The dominant aquatic vegetation is formed by the genera *Juncus* (Juncaceae), *Eleocharis* (Cyperaceae), and *Sphagnum* (Sphagnaceae), and by the species *Littorella uniflora* (Plantaginaceae), *Hydrocotile vulgaris* (Apiaceae), and *Polytrichum commune* (Polytrichaceae). The surrounding area is dominated mainly by native and endemic plants (e.g., *Juniperus brevifolia*, *Laurus azorica*, *Ilex perado* subsp. *azorica*, and *Erica azorica*), with a dominance of two types of forests: "*Juniperus-Ilex* Montane Forests" and "*Juniperus* Montane Woodlands" (Elias et al., 2016) that also include bryophyte communities on all substrates (Gabriel and Bates, 2005). The other four ponds and the eight tanks were located in human-modified landscapes (**Figure 1**, see details below).

Our study period was from November 2013 to August 2014. First, to understand the variations in the macroinvertebrate assemblages of the natural ponds on Terceira Island, monthly samples were collected in three temporary ponds (VF1, VF3, VF5) and two permanent ponds (NEG, SER) between November 2013 and August 2014 (**Figure 1**, see also **Supplementary Figure 1**, ESM1 in the Supplementary Material) (hereafter referred to as "monthly sampling"). These ponds were selected based on their hydroperiod gradient and spatial location within the protected area "Caldeira de Santa Bárbara e Mistérios Negros." Secondly, we sampled almost all natural ponds (12 out of the 16 known ponds as four of them were inaccessible; local names included in **Supplementary Table 1**, ESM1 in the Supplementary Material), and eight artificial tanks in Terceira Island in May 2014 (hereafter referred to as "extensive sampling") to assess the environmental characteristics that would determine differences in the macroinvertebrate assemblages across a gradient of landscape disturbance (**Figure 1**, see also **Supplementary Figure 2**, ESM1 in the Supplementary Material). The artificial tanks were located in agricultural areas, and were selected as the closest sites to a natural pond in order to consider their role as possible reservoirs of the aquatic fauna. The tanks have an artificial substrate of cement, with a surface area of 4–6 m^2, and 0.4–1 m of maximum depth.

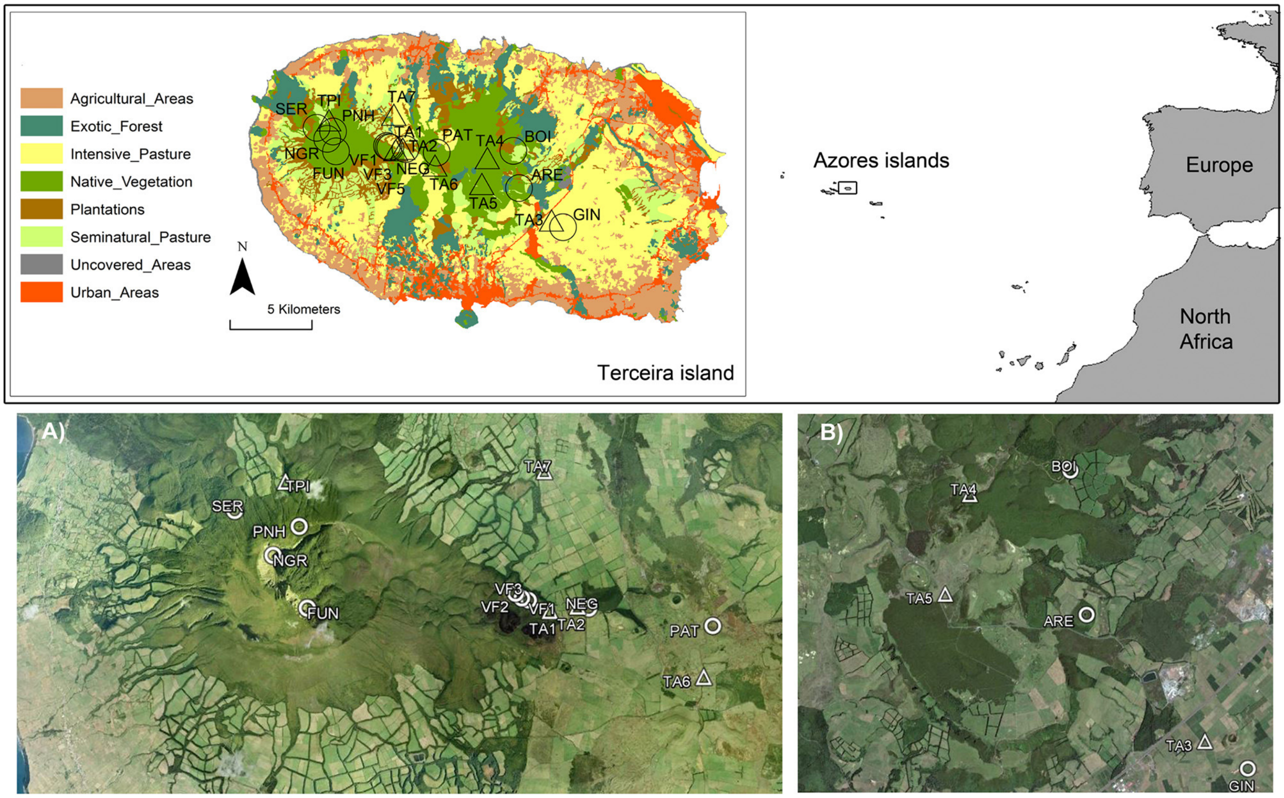

FIGURE 1 | Location of the Azores archipelago including Terceira Island (38°40′N–27°10′W). The location of the study ponds and tanks are also shown in Terceira Island (ARE, BOI, FUN, GIN, NEG, NGR, PAT, PNH, SER, VF1, VF3, and VF5 are ponds; TPI, TA1, TA2, TA3, TA4, TA5, TA6, and TA7 are tanks). A land-use map for Terceira Island was included and divided into eight categories: (1) urban and industrial areas; (2) agricultural areas, including arable lands, fruit orchards and permanent crops; (3) exotic forests dominated mainly by *Pittosporum undulatum*; (4) forestry plantations of *Cryptomeria japonica* and *Eucalyptus* spp.; (5) intensive managed pasturelands exposed to intensive cattle grazing throughout the whole year; (6) seminatural pasturelands, which were only managed with low cattle grazing activity and usually located in high elevation areas; (7) uncovered areas including rocky and open spaces without vegetation, and (8) native vegetation including native forests dominated by endemic plant species. At the bottom of the figure, we show a magnification of the location of natural ponds and artificial tanks embedded in **(A)** native vegetation, and **(B)** areas with some degree of disturbance.

Sampling Methods

Macroinvertebrates were sampled using a dip net of 40 × 25 cm with 1 mm mesh size. Approximately 1.5 m stretches of water were netted in each sampling unit, which encompassed three successive sweep nettings, collecting benthic, and open-water macroinvertebrates. Sampling was performed from the littoral zone to the deepest point of the pond when accessible, and considering different aquatic plant covers to include all the possible microhabitats. Because the dip netting efficiency seems to be better in small ponds (Heyer et al., 1994), the number of sampling units was proportional to the pond size (see Florencio et al., 2009). Hence, the number of samples per pond ranged from 5 to 19 sampling units. In total, 557 samples were obtained during the monthly sampling and 169 during the extensive sampling. Most individuals were sorted in the field, counted, and released, to minimize the researcher's impact in the field. Individuals of unidentified species were preserved in 70% ethanol for subsequent identification in the laboratory. Individuals were identified to species level, except for the genus *Dryops* which was identified to genus level, Culicidae to family level and Oligochaeta to Class level; adult and larval stages were considered separately given their different ecological requirements (hereafter referred to as "species" for simplicity). The Dipteran family Chironomidae was not considered because of sampling and mesh size limitations.

Physico-Chemical Characteristics and Land-Use Variables of Ponds

The following environmental variables were measured *in situ* to characterize the study ponds during monthly and extensive samplings: electrical conductivity (EC) standardized at 20°C (Multi-range Conductivity meter HANNA HI 98127), pH (pH meter HANNA HI 98311), dissolved oxygen concentration, and temperature (Oxi 315i WTW) in the water column. Two replicates were obtained for each measurement per pond and month, but given the homogeneity in the measurements, the two pond values per month were averaged before statistical analyses. We also collected 1,500 ml of the water column that was later filtered in the laboratory (Whatman GF/C filters, 47 mm diameter) to measure the concentrations of chlorophyll-a (spectrophotometric methods, Gonçalves, 2008), dissolved inorganic nitrogen (DIN) (following Golterman, 1991) and dissolved inorganic phosphate reactive to Mo (i-P) according to Murphy and Riley (1962). The concentration of total phosphorous in the water (TP) was also analyzed as i-P after acid digestion of the unfiltered water sample treated with $K_2S_2O_8$ (Golterman, 2004). DIN and i-P concentrations were only measured in the extensive sampling.

The land-use map of Terceira Island was constructed based on land-use cover classes of CORINE 2006 Land Cover (see Bossard et al., 2000) and DROTH (2008), at 30 × 30 meters resolution (**Figure 1**). The land-use map was divided into eight categories: (1) urban and industrial areas; (2) agricultural areas, including arable land, fruit orchards and permanent crops; (3) exotic forests dominated mainly by *Pittosporum undulatum*; (4) forestry plantations of *Cryptomeria japonica* and *Eucalyptus* spp.; (5) intensive managed pasturelands exposed to intensive cattle grazing throughout the whole year, characterized by common exotic grasses and leguminous forbs; (6) seminatural pasturelands, which were only managed with low cattle grazing activity and usually located in high altitude areas; (7) uncovered areas including rocky and open spaces without vegetation, and (8) native vegetation including native forests dominated by endemic plant species, but also including high-elevation anthropized pasturelands that have been abandoned and colonized by naturalized vegetation (native and exotic plants).

The percentage area occupied by the different land-uses in Terceira Island was calculated to quantify the impact of anthropogenic disturbance on the analyzed ponds and tanks. For this, each pond/tank center was established as the centroid of a 250-meter-radius buffer in order to estimate the local influence of the surrounding land-uses on the macroinvertebrate assemblages. Only intensively managed pasturelands, seminatural pasturelands and native vegetation surrounded the study ponds, and thus their percentage areas were considered as explanatory variables. The land-use map and the occupied percentage area calculation were performed using the GIS-based software ArcGIS 10 ArcMap v. 10.1.

Spatial Variables Based on Interpond Distances

Regarding the extensive sampling, we retained 11 orthonormal spatial descriptors of the 12 natural ponds and seven tanks ($N = 19$, one tank was excluded because no individuals were collected) using Principal Coordinates of Neighborhood Matrix (PCNMs) map distances. We used as truncation distance the longest distance among ponds to maintain pond connectivity (Borcard and Legendre, 2002). The extraction of these spatial descriptors was performed in R software 2.14.2, using the "pcnm" command in the "vegan" package (Oksanen et al., 2019).

Data Analyses

Temporal Biodiversity Patterns

For the monthly sampling data, abundance-based rarefaction, and sample-based rarefaction were used to determine the completeness of the natural pond inventories (see ESM2 in the **Supplementary Material**). Given that differences in sampling efforts were not observed among the 5 monthly-sampled ponds (ESM2 in the **Supplementary Material**), raw data were used to perform all statistical analyses. To analyze the differences in the macroinvertebrate assemblage compositions among the sampled ponds and months, we constructed a matrix of species (columns) and ponds (rows) including all the sampling months by averaging the number of individuals of each species per each pond and month. Then, triangular matrices were obtained using the Bray-Curtis index of similarity (the inverse of the Bray-Curtis index of dissimilarity). Assemblage similarity differences between ponds and months, as well as the possible interaction between these two factors (ponds × months), were analyzed using a two-way crossed permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001). This non-parametric procedure allowed us to analyze differences between ponds and months based on the Bray-Curtis similarity distance. Statistically significant differences were tested using permutations of group membership; 9,999 permutations were performed using the software PRIMER v.6 (Anderson et al., 2008).

Differences in macroinvertebrate β-diversity patterns were investigated across the sampled months and ponds using presence-absence matrices and pooling adult and larval stages for each independent taxon. Then, triangular matrices were calculated using the Sørensen index of dissimilarity on the incidence data. The β-diversity partitioning approach proposed by Baselga (2010) was used to calculate the β-diversity patterns. Because the temporary ponds were drying out during the summer months, the per-month matrices varied in matrix size. Therefore, to determine β-diversity partitioning between ponds and to obtain comparable values of β-diversity for different matrix sizes, a multiple-site dissimilarity procedure was used (Baselga, 2012). To calculate the multiple-site β-diversity partitioning, the minimum number of ponds sampled in a month (three) was used to resample the total number of ponds sampled per month (1,000 random samples). To determine multiple-site β-diversity partitioning, the command "beta.sample" (betapart package, Baselga and Orme, 2012) was used, implemented in R software 2.14.2. Multiple-site β-diversity (β_{SOR}) was partitioned into two additive components that accounted for dissimilarity due to species replacement (β_{SIM}) and dissimilarity due to nestedness (β_{SNE}), respectively, in accordance with the formula $\beta_{SOR} = \beta_{SIM} + \beta_{SNE}$ (Baselga, 2010).

Environmental and Land-Use Effects on Macroinvertebrate Assemblages

Using monthly data, an environmental matrix per pond and month was constructed. With this matrix, triangular matrices of similarity were calculated using the Euclidean distance between each pair of ponds for each environmental variable. In order to analyze the environmental variables that influenced the monthly pattern of β-diversity, the multiple-site β-diversity partitioning, β_{SIM} and β_{SNE}, were regressed against the average Euclidean distances of each environmental variables per month. A forward stepwise regression was performed following Blanchet et al. (2008), using the β_{SIM} and β_{SNE} per month as response-variables and the average Euclidean distances of the environmental variables per month ($N = 10$) as predictor variables. This complete procedure is considered to be an effective procedure for controlling Type I error (Peres-Neto and Legendre, 2010). These analyses were performed using the Statistica V.8 software.

Regarding the extensive sampling, environmental data and the land-use variables were used to construct a matrix including the 12 natural ponds and seven artificial tanks as cases. This matrix was used first to analyze the explanatory variables that determined the differences in macroinvertebrate assemblages of natural and artificial ponds. Secondly, a matrix was constructed that excluded the artificial tanks to analyze the explanatory variables that determined the differences in macroinvertebrate assemblages only among the natural ponds. The studied environmental variables were the concentration of TP, i-P, and DIN, electrical conductivity at 20°C, dissolved oxygen concentration, pH, and chlorophyll-a concentration in the water column. The studied land-use variables were the percentage area of native vegetation, seminatural pasturelands, and intensive pasturelands. All variables, with exception of pH and the land-use variables, were log (x+1) transformed to satisfy normality assumptions. Triangular matrices were constructed using Euclidean distances of the environmental variables to determine if the explanatory variables (environmental and land-use characteristics) of ponds and tanks differed. Then, an ANOSIM analysis was performed using the aquatic systems (pond or tank) as factor, and 9,999 permutations for the significance level. Moreover, each individual variable was analyzed using a Student *t*-test, and alternatively a Mann-Whitney test when the normality assumption was not satisfied, to determine whether it differed significantly between natural ponds and artificial tanks. Moreover, in order to detect if the macroinvertebrate assemblages differed between ponds and tanks, a matrix was constructed including the average number of individuals of each species (columns) per pond (rows). Then, a triangular similarity matrix was built using the Bray-Curtis index on the abundance matrix. Subsequently, an ANOSIM test was performed using pond and tank as grouping factor, and 9,999 permutations to assess the significance level. Finally, an exploratory SIMPER analysis was performed to detect the species mainly contributing to the differences between ponds and tanks.

Furthermore, to investigate the impact of the explanatory variables and the spatial descriptors driving the macroinvertebrate assemblages across the extensive sampling, the relationship between the biological Bray–Curtis similarity matrix, the aforementioned matrix of transformed explanatory variables and the spatial descriptors (PCNMs) was analyzed. To do that, a resemblance matrix was also constructed based on Bray–Curtis similarity that excluded the tanks to analyze the variables driving the differences among the assemblages of ponds. We first visualized the relationship between all biological data and the explanatory variables as principal component ordinations using a distance-based redundancy analysis (dbRDA) (McArdle and Anderson, 2001), which constrains to linear combinations of the predictor variables (Anderson et al., 2008). A Student *t*-test, or alternatively a Mann-Whitney test, was performed, using the scores of the axes 1 and 2 of the dbRDA (dbRDA1 and dbRDA2) to analyze if they discriminated natural ponds and artificial tanks. Secondly, a distance-based linear model (DistLM) was performed for data partitioning (analogous to linear multiple regression) using forward stepwise and Adjusted R^2 ($AdjR^2$) criteria for variable selection. This procedure was performed separately for the aforementioned explanatory variables and for the spatial descriptors, retaining the significant variables that contributed to the dissimilarities of the macroinvertebrate assemblages. This DistLM model only included predictor variables that improved the explained sum of squares that would be expected by adding some random variable, taking into account the number of variables in the model (Anderson et al., 2008). We thus estimated the sequential partial increase in explained variability using the $AdjR^2$. The DistLM analysis was performed, first to analyze the differences between the tanks and natural ponds, and secondly, among the natural ponds alone. All these multivariate analyses were performed using the Primer V.6. software, the DistLM and dbRDA analyses were performed using the add-on package PERMANOVA+ (Anderson et al., 2008), while *t*-test and Mann-Whitney' test were performed in R software 2.14.2. In order to explore the partial contribution of the significant explanatory variables and the significant spatial descriptors (PCNMs) retained in the DistLM analyses on the macroinvertebrate assemblages, multiple regression on distance matrices (MRM) was performed, an extension of Mantel test (Legendre et al., 1994). We considered Spearman correlations (r_s) and performed a forward-selection procedure to identify the significant variables (Legendre et al., 1994). The significance of the MRM models was assessed using 1,000 permutations using the "MRM" command ("ecodist" package, Goslee and Urban, 2007) in R software 2.14.2. Two successive models were constructed: (i) *the environmental model*, only using the significant explanatory variables to measure environmental influence on the macroinvertebrate assemblages, and (ii) *the environmental + spatial model*, using the significant PCNM spatial descriptors in addition to the explanatory variables to obtain partial effects. This procedure was performed for the considered tanks and natural ponds ($N = 19$), and among the natural ponds alone ($N = 12$).

RESULTS

General Diversity Patterns

A total of 4,247 individuals (3,295 individuals in the monthly study and 952 in the extensive study) were collected, belonging to 17 species; Basommatophora (1), Ephemeroptera (1), Odonata (3), Heteroptera (2), Coleoptera (9), and Trichoptera (1) (see ESM3 in the **Supplementary Material**). In the monthly sampling, temporary ponds had the highest species richness (temporary ponds = 13 species, permanent ponds = 9 species). In contrast, permanent ponds had the highest proportion of native individuals. Overall, temporary ponds had the highest occurrence of endemic species (represented by *Hydroporus guernei* Régimbart, 1891 - Dytiscidae and *Limnephilus atlanticu*s Nybom, 1948 - Limnephilidae), and exhibited the highest proportion of endemic individuals. Temporary and permanent ponds had a similar small proportion of exotic individuals (1 and 0.8%, respectively, **Figure 2A**). The seasonal pattern of macroinvertebrates revealed high abundance of the Fam. Dytiscidae, mainly consisting of the endemic *H. guernei* (61.3%), with both adults and larvae detected across three different periods (November, February and May, see **Figure 3**, and ESM5 in the **Supplementary Material**). Moreover, the Families Libellulidae and Corixidae were also abundant when most temporary ponds were close to the desiccation (April and May, **Figure 3**).

Notably, natural ponds harbored the highest proportion of individuals of native (84%) and endemic species (13%), in comparison with the artificial tanks (79% and 8%, respectively). Exotic species were more frequent in tanks (13%) in comparison with the natural ponds (3%, **Figure 2B**). The two types of systems shared three exotic species, i.e., *Helisoma trivolvis* (Say, 1817), *Helochares lividus* (Forster, 1771), and *Cercyon haemorrhoidalis* (Fabricius, 1775). Additionally, individuals of the gastropods Planorbidae and the coleopterans Hydrophilidae were mostly detected in tanks, where only Culicidae and Baetidae individuals were found. In contrast, the nymphs of the odonates Coenagrionidae, Libellulidae and the endemic *L. atlanticus* were only detected in natural ponds (**Figure 4**).

Temporal Biodiversity Patterns

Significant effects of both pond and month factors were detected in the macroinvertebrate assemblages, as well as a significant interaction between these two factors (PERMANOVA, Pond Factor: *Pseudo-F* = 3.801, *P-value* < 0.001; Month Factor: *Pseudo-F* = 12.623, *P-value* < 0.001; Month × Pond Factor: *Pseudo-F* = 2.548 *P-value* < 0.001). While pond explained a higher variance (14.47%) than the month factor (6.56%), the high explanatory variance of the interaction between the two factors, month and pond (13.38%), indicated that the macroinvertebrate differences between ponds were dependent on the study month. Analyzing the monthly β-diversity partitioning, the contribution of species replacement to the β-diversity was higher than the contribution of the nestedness component across almost the whole seasonal pattern. However, in August, when most temporary ponds had dried out and permanent ponds had notably reduced their surface area, the value of the nestedness contribution to β-diversity increased, while the value of species replacement notably decreased (**Figure 5**).

Environmental and Land-Use Effects on Macroinvertebrate Assemblages

In the monthly sampling, the dissolved oxygen concentration, the TP concentrations, the electrical conductivity and the pH significantly explained the monthly pattern of species

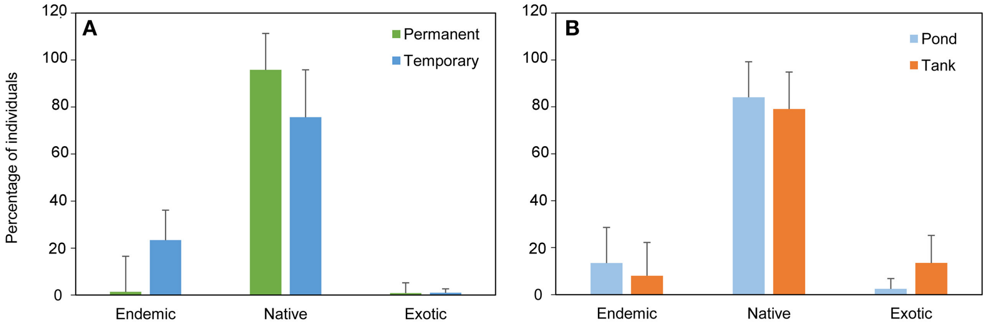

FIGURE 2 | Mean percentage of individuals of exotic, native and endemic species found **(A)** in the temporary and permanent ponds during the monthly sampling, and **(B)** in the natural ponds and artificial tanks during the extensive sampling.

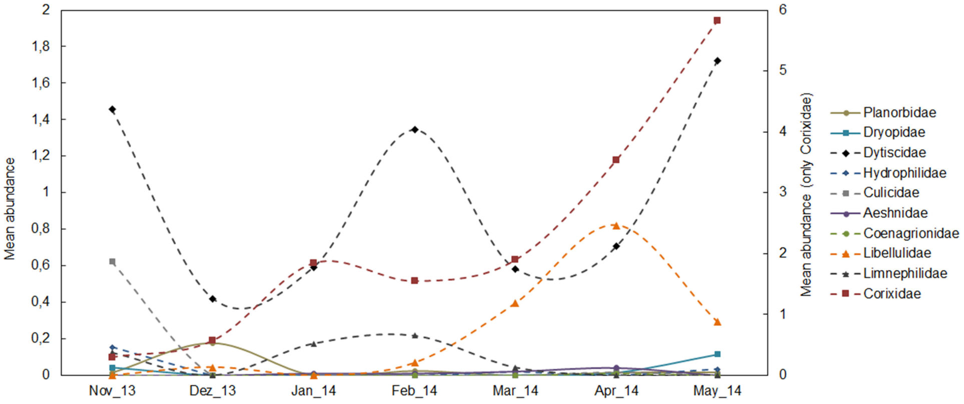

FIGURE 3 | Average number of individuals at the Family taxonomic level calculated per pond and month during the monthly sampling. Because of their high abundance, the Fam. Corixidae is indicated in an additional axis (see ESM4 in the **Supplementary Material** for details).

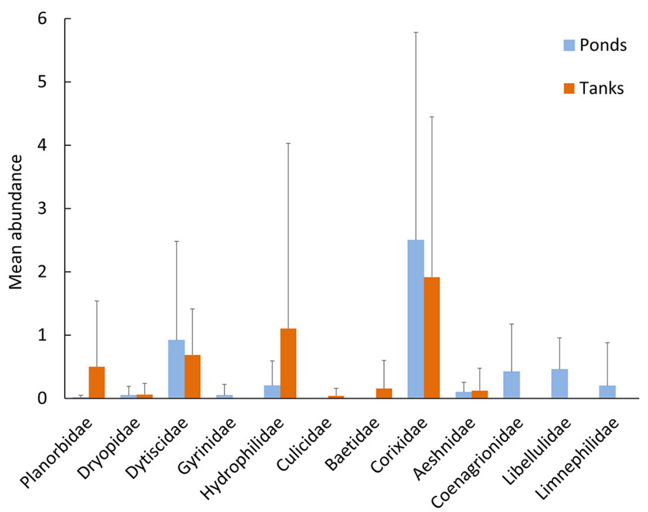

FIGURE 4 | Average number of individuals at the Family taxonomic level captured in the ponds (light blue) and tanks (dark orange) (Mean ± SD) across the extensive sampling (n = 12 ponds, n = 8 tanks).

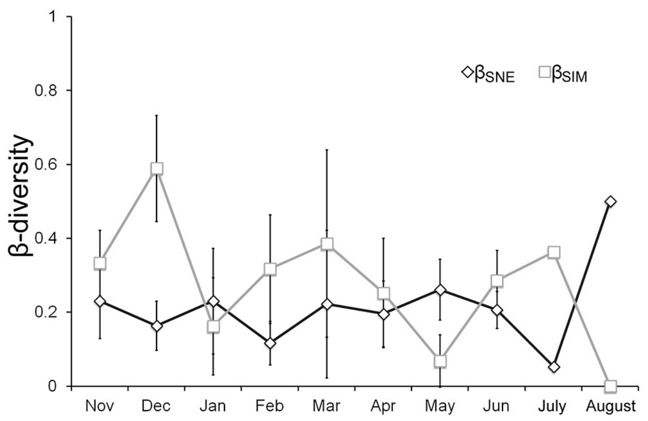

FIGURE 5 | Average values of the components of the macroinvertebrate β-diversity, the species replacement (β_{SIM}) and the contribution of the nestedness (β_{SNE}) to the β-diversity after β-diversity partitioning. Bars indicate the standard deviation (SD); July and August do not show SD because only a pair-wise comparison between the three ponds that maintained water by that time was performed.

TABLE 1 | Monthly effects of the averaged Euclidean distances of the environmental variables on the components of the macroinvertebrate β-diversity partitioning, β_{SIM} (species replacement) and β_{SNE} (nestedness component), through multiple linear regression analysis.

Environmental variables	*P*-value (β_{SIM})	Wald Stat.	*P*-value (β_{SNE})	Wald Stat.
Dissolved oxygen	0.001	1.700	0.192	9.770
pH	0.006	0.664	0.415	7.435
Electrical conductivity	0.082	0.053	0.816	3.020
Total phosphorous	0.001	0.036	0.849	11.010
Chlorophyll-a	0.474	4.586	0.032	0.511

The P-values and the Wald statistic (Wald Stat.) are indicated.

replacement, while only chlorophyll-a concentration significantly explained the monthly pattern of the contribution of nestedness to the observed β-diversity (**Table 1**).

In the extensive sampling, the environmental variables indicated very low mineralization water and low DIN concentrations ($\leq$0.35 mg L^{-1}) in all sites, while only a few of them showed TP concentrations above 100 µg L^{-1} (**Table 2**). Natural ponds and artificial tanks markedly varied in the water pH (pH$_{\text{tanks}}$ 9.1–10.7, pH$_{\text{ponds}}$ 4.3–7.0), while also showing significant differences in the concentration of dissolved oxygen (DO$_{\text{tanks}}$ 7.80–13.35 mg L^{-1}, DO$_{\text{ponds}}$ 4.20–8.33 mg L^{-1}), electrical conductivity (EC$_{\text{tanks}}$ 60.5–135.0 µS cm^{-1}, EC$_{\text{ponds}}$ 28.8–79.5 µS cm^{-1}), and the percentage area occupied by natural vegetation (Nat$_{\text{tanks}}$ 0–59%, Nat$_{\text{ponds}}$ 0–100%) (**Table 2**). In most of the natural ponds, more than 98% of the surrounding area comprised natural vegetation (FUN, NGR, PHN, and SER). However, GIN pond was located in a disturbed area only surrounded by intensive pasturelands (**Table 2**). Tanks were located in pasturelands, most of them contiguous to natural ponds located in areas of native vegetation (**Figure 1**). The surrounding area of TPI, TA4, and TA5 included ~50% of native vegetation, while some tanks (e.g., TA3, TA6, and TA7) were located in areas dominated by intensive pasturelands (**Table 2**). Hence, significant differences in the environmental explanatory variables were observed between these two groups of ponds and tanks (ANOSIM, Global R = 0.979, P-value < 0.001). In contrast, statistically significant but weak differences were observed between the macroinvertebrate assemblages of the natural ponds and artificial tanks (ANOSIM, Global R = 0.186, P-value < 0.05). The SIMPER analysis revealed that the only taxa with a contribution >10% to this dissimilarity were the larvae of *Corixa affinis* and the Oligochaeta, mainly occurring in the artificial tanks (see ESM5 in the **Supplementary Material**).

In the dbRDA ordination, we observed that pH was the main difference between the assemblage compositions of ponds and tanks (**Figure 6**). The scores of axes 1 and 2 of the dbRDA significantly differed between natural ponds and tanks (dbRDA1 t = 2.879, P-value < 0.01; dbRDA2 W = 38, P-value < 0.0001). Hence, the DistLM analysis revealed that pH was the only significant variable explaining the differences among the macroinvertebrate assemblages of ponds and tanks (5% of explained variability, **Table 3**). However, another four variables were also retained in the DistLM analysis, which explained 12% of the total variability (**Table 3**). Only using natural ponds, the dbRDA1 axis could also discriminate them into two groups: the ponds with relatively high concentrations of DIN and dissolved oxygen, and mostly surrounded by native vegetation (group 1: PHN, SER, FUN, NGR, NEG, VF1, VF3, and VF5 ponds), and those with high concentrations of TP and chlorophyll-a (group 2: GIN, PAT, BOI, and ARE ponds). When the DistLM analysis was performed only using these natural ponds, the concentration of TP in the water column was the single significant explanatory

TABLE 2 | Environmental variables of the water column of the study ponds and tanks during the extensive sampling, measured in May 2014.

	DO (mg L^{-1})	pH	EC (μS cm^{-1})	TP (μg L^{-1})	Chl. (μg L^{-1})	DIN (mg L^{-1})	i-P(μg L^{-1})	Nat (%)	Sem (%)	Int (%)
Ponds										
ARE	7.13	5.2	49.5	65.53	15.17	0.039	1.00	23	3	22
BOI	7.55	6.8	32.5	257.28	24.71	0.074	5.23	6	49	0
FUN	8.33	5.5	28.0	49.27	2.06	0.089	1.82	100	0	0
GIN	4.20	5.5	79.5	90.78	2.47	0.108	20.18	0	0	100
NEG	7.00	7.0	37.8	99.03	5.49	0.168	0.64	6	52	0
NGR	8.25	6.2	29.8	29.37	9.12	0.054	2.03	100	0	0
PAT	7.10	5.6	38.8	104.86	17.06	0.108	1.39	69	31	0
PNH	7.93	5.1	28.8	23.54	0.75	0.138	3.42	100	0	0
SER	7.58	5.5	47.8	29.13	1.7	0.177	1.17	98	0	0
VF1	8.25	5.1	36.8	36.41	4.36	0.192	1.71	76	1	8
VF3	6.85	4.9	41.0	25.49	0.74	0.103	1.50	83	0	5
VF5	7.93	4.3	68.5	26.94	22.12	0.350	3.63	83	0	5
Tanks										
TPI	10.70	9.9	60.5	153.64	64.36	0.237	2.24	46	31	0
TA1	9.95	10.0	87.0	28.64	21.42	0.034	1.60	32	47	1
TA2	7.80	9.2	51.5	44.42	2.06	0.069	2.03	9	71	0
TA3	9.75	10.0	135.0	90.53	2.06	0.074	22.53	0	0	100
TA4	8.60	9.1	97.5	48.30	2.88	0.030	1.28	57	43	0
TA5	11.20	10.3	112.5	35.68	31.58	0.079	6.09	59	41	0
TA6	10.00	10.2	103.5	123.79	5.88	0.000	5.55	41	0	53
TA7	13.35	10.7	106.5	55.83	2.88	0.000	5.98	0	18	59
Diff	-4.21^{***}	-14.86^{***}	-5.28^{***}	$-0.57_{n.s.}$	$-0.66_{n.s.}$	$1.95_{n.s.}$	$-1.16_{n.s.}$	2.16^{*}	$28_{n.s.}$	$41.5_{n.s.}$

*DO is dissolved oxygen concentration, EC is electrical conductivity, TP is total phosphorous concentration, Chl. is chlorophyll-a concentration, DIN is dissolved inorganic nitrogen concentration and i-P indicates dissolved inorganic phosphate concentration. The percentage areas of native vegetation (Nat), seminatural pasturelands (Sem), and intensive pasturelands (Int) are also indicated as land-use variables. A Student t-test was performed to analyze if the environmental variables were significantly different between natural ponds and artificial tanks, and a non-parametric Mann-Whitney test for Sem and Int, which did not satisfy normality assumption. Diff indicates the statistic values of these two parametric (t) and non-parametric (W) tests, respectively; the P-values are also indicated as * < 0.05,** < 0.01,*** < 0.001; all the non-significant differences were P-values > 0.06 (indicated as n.s.).*

variable (10% of explained variability, **Table 3**). However, another three variables were retained in the DistLM analysis, which explained 21% of the total variability (**Table 3**).

Environmental Variables vs. Spatial Descriptors

In the extensive sampling, seven out of the 11 spatial descriptors were retained in the DistLM analysis. Only the PCNM7 had a significant influence on the macroinvertebrate assemblages (**Table 3**). However, when the partial effect of the PCNM7 was analyzed taking into account the pH, the model revealed that only the pH was significant in explaining the dissimilarity of the macroinvertebrate assemblages (**Table 4**). When the DistLM analysis was repeated with only the natural ponds, two significant spatial descriptors (PCNM2 and PCNM5) were detected out of the five PCNMs retained. The partial effect of these two spatial descriptors, taking into account the concentration of TP in the water column, revealed the important effect of these two PCNMs on the dissimilarities in the macroinvertebrate assemblages, as they explained 34% of the total variability in *the environmental + spatial model* (**Table 4**).

DISCUSSION

In order to understand the extent of the anthropogenic influence on the unique freshwater ecosystems of Macaronesia, we have first investigated the ecological dynamic of these singular ecosystems and their macroinvertebrate assemblages. In the Azorean island of Terceira, a consistent seasonal pattern of macroinvertebrate species replacement has been detected across a hydroperiod gradient that disappeared when most temporary ponds were desiccated in summer. This desiccation period was thus observed to be an important factor for the community structure of the Azorean macroinvertebrates, as occurs in other sensitive regions of temporary pond networks, such as in Mediterranean-climate areas (Florencio et al., 2011). The role of artificial tanks as possible reservoirs for macroinvertebrates might be especially relevant as refuges during aestivation for those organisms inhabiting temporary ponds, which need to cope with pond desiccation in summer (see Deacon et al., 2019; Samways et al., 2020). Our results suggest that the studied artificial tanks maintain good water quality and are suitable for macroinvertebrate species, thus increasing the heterogeneity of habitats as permanent waterbodies in the peak of the hydroperiod gradient. This is even more important if we consider that

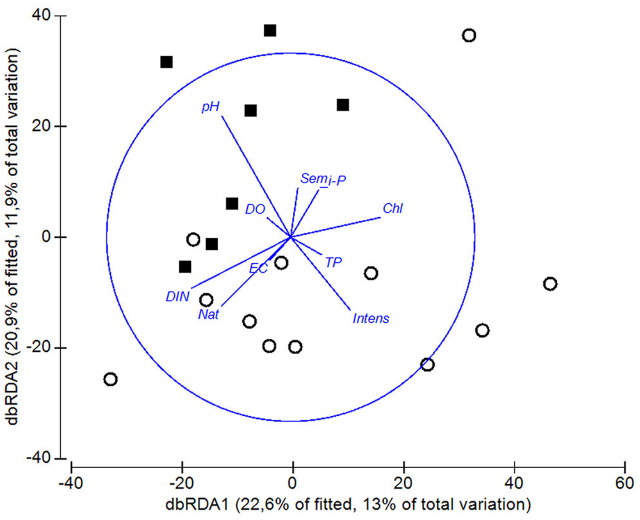

FIGURE 6 | Distance-based RDA ordination relating the explanatory variables with the macroinvertebrate assemblages, using the Bray-Curtis similarity index. The length and direction of the vectors represent the strength and direction of the relationship. DO is dissolved oxygen concentration, EC is electrical conductivity, TP is total phosphorous concentration, Chl is chlorophyll-a concentration, DIN is dissolved inorganic nitrogen concentration, i-P is dissolved inorganic phosphate concentration. For the land-use variables, Nat is the percentage area of native vegetation, Sem is the percentage area of seminatural pasturelands, and Intens is the percentage area of intensive pasturelands. Squares indicate the artificial tanks and open circles the natural ponds.

fishless permanent waterbodies are scarce in the Azorean islands (Florencio and Lamelas-López, 2016; Raposeiro et al., 2017).

Characteristics of The Azorean Natural Ponds

The natural ponds in Terceira Island were characterized by well-oxygenated and slightly acidic waters, with low values of conductivity, which indicates that the ponds are primarily flooded with rainwater (Florencio and Lamelas-López, 2016). Differences in macroinvertebrate composition among ponds were observed to be higher than seasonal differences (monthly), which can be associated with the limited fluctuations in temperatures throughout the year under a temperate oceanic climate. This result contrasts with the typical seasonal variations of European ponds, where changes in the environmental characteristics are reflected in seasonal variations of assemblage compositions (e.g., Jeffries, 2003). Seasonal differences among ponds in the macroinvertebrate assemblages reflected the desiccation of the temporary ponds and the reduction of the water level in the permanent ponds. Interestingly, the larvae and adults of the endemic beetle *H. guernei* peaked three times during the hydrological cycle of temporary ponds, i.e., November (after pond inundation), February, and May (close to pond desiccation). This result seems to indicate at least three successive periods of reproduction for this species, which is important for conservation regarding: (1) the Endangered category of this species in the IUCN Red List of Threatened Species (Borges et al., 2018), and (2) the protected character of these high-altitude natural ponds in the Azores. We acknowledge that a strong signal of seasonal variation in assemblage composition was detected though the number of ponds was low. It is likely, then, that the sampled ponds provided a good representation of the study area.

Seasonal β-diversity patterns revealed that the differences in assemblage compositions were mainly associated with species replacement, and that pond desiccation favored the contribution of nestedness to the observed β-diversity, a pattern that has also been found in other temporary pond networks (Florencio et al., 2011, 2016a). The seasonal variation of the dissolved oxygen and TP concentrations, electrical conductivity and pH determined the seasonal changes in species replacement, probably associated with the variation in the timing and amount of rainfall. However, the proximity to the dry-period increased the contribution of nestedness to the β-diversity and also reduced species replacement. Close to pond desiccation, high concentrations of TP and chlorophyll-a were reached in concordance with a reduction in the inundated surface area, which also seemed to influence the pH and electrical conductivity of the water. Pond desiccation is an asynchronous process within a temporary pond network, as it depends on the hydroperiod of each pond. In Mediterranean ponds, water depth and electrical conductivity have also been detected as key variables explaining changes in assemblage composition and β-diversity associated with species replacement (Florencio et al., 2014). In our results, most temporary ponds were desiccated in August, when the values of nestedness contribution to β-diversity were maximal, mainly influenced by a high chlorophyll-a concentration. Fish were detected in the only two permanent ponds that held water during August during the study period (Florencio and Lamelas-López, 2016), and these were the only ponds that were able to act as refuge for macroinvertebrates in summer.

Artificial Tanks as Reservoirs for Biodiversity

Fishless artificial tanks associated with agricultural systems acquire an important role in preserving the macroinvertebrate assemblages of Azorean ponds. This possibility is supported by the similar composition that has been detected in the macroinvertebrate assemblages of ponds and tanks, with only small variations explained by the notably higher pH of artificial tanks. This could be explained by the longer persistence of water, smaller rain catchment (i.e., smaller basin) and the construction materials of the tanks (basic materials; Hassall, 2014). Hence, the high pH values in tanks could have favored the gastropods of the Fam. Planorbidae (e.g., Şahin and Zeybek, 2016). The conservation of macroinvertebrates in artificial tanks was also supported by their low concentration of nutrients and chlorophyll-a, reflecting a low probability of eutrophication (see Campbell et al., 2009). Consequently, tanks can be considered potential suitable habitats for at least 10 species of macroinvertebrates (see ESM3 in the **Supplementary Material**). Notably, some native species were only captured in tanks, such as the beetles *Hygrotus confluens* (Fabricius, 1787) or the single species of the Ephemeroptera order known in Azores, *Cloeon*

TABLE 3 | Partial effects of the explanatory variables (*Environmental*) and the spatial descriptors based on PCNMs (*Spatial*) using distance-based linear models (DistLM), performing a forward stepwise process based on the *Adjusted* R^2 (*AdjR*^{2}).

Environmental	AdjR^2	Pseudo-F	*P*-value	Spatial	AdjR^2	Pseudo-F	*P*-value
Ponds vs. tanks							
pH	0.049	1.935	<0.05	PCNM7	0.042	1.789	<0.05
TP	0.084	1.634	0.085	PCNM11	0.080	1.711	0.064
Nat	0.094	1.191	0.292	PCNM4	0.094	1.244	0.289
Chl	0.101	1.103	0.356	PCNM5	0.105	1.188	0.290
DIN	0.117	1.257	0.260	PCNM3	0.116	1.174	0.324
				PCNM8	0.128	1.176	0.325
				PCNM6	0.144	1.224	0.281
Only ponds							
TP	0.099	2.205	<0.05	PCNM2	0.123	2.541	<0.05
Sem	0.163	1.768	0.077	PCNM5	0.215	2.169	<0.05
i-P	0.165	1.022	0.411	PCNM4	0.287	1.917	0.079
DO	0.210	1.454	0.182	PCNM6	0.290	1.029	0.417
				PCNM7	0.302	1.123	0.362

Environmental and Spatial DistLM analyses have been performed separately. The Pseudo-F and the P-values are also indicated. The AdjR^2 *indicates the explained variability that added the inclusion of each explanatory variable in a sequential order. These analyses were performed using the biological resemblance matrix (Bray-Curtis similarity index) and the environmental and land-use variables to analyze the explanatory variables that mainly contributed to the differences in the assemblage compositions between ponds and tanks (Ponds vs. tanks), but also among the ponds alone (Only ponds). DO is dissolved oxygen concentration, TP is total phosphorous concentration, Chl is chlorophyll-a concentration, DIN is dissolved inorganic nitrogen concentration, i-P is dissolved inorganic phosphate concentration. For the land-use variables, Nat is the percentage area of native vegetation and Sem is the percentage area of seminatural pasturelands.*

TABLE 4 | Multiple regression models (MRM) revealing the partial contribution of the spatial descriptors (PCNMs) and the explanatory variables to the dissimilarity in the macroinvertebrate assemblages, between ponds and tanks (Ponds *vs.* tanks), but also among the ponds alone (Only ponds).

Variable	r^2	r_s	*P*-value
Ponds vs. tanks			
Environmental	0.030		<0.05
pH		0.173	<0.05
Environmental + Spatial	0.046		0.170
pH		0.186	<0.05
PCNM7		0.128	0.382
Only ponds			
Environmental	0.199		<0.05
TP		0.446	<0.05
Environmental + Spatial	0.344		<0.01
TP		0.265	<0.05
PCNM7		0.422	<0.05

We only used those retained variables that were significant in the DistLM analyses (see ***Table 3****), including only the explanatory variables (Environmental) in the MRM model, and including the spatial descriptors in this model (Environmental + Spatial). TP is total phosphorous concentration in the water column,* r^2 *is the model explanatory capacity (ranged 0–1),* r_s *indicates the coefficients of Spearman correlations.*

dipterum (Linnaeus, 1761). This is possibly associated with the preference of these species for higher water temperature, as has been registered in tanks (see Stauder, 1991; McKee and Atkinson, 2000). In Azores, Ephemeroptera mainly occurs in human-made systems (Brinck and Scherer, 1957), contributing to increase the total biodiversity. We also found adults and larvae of the endemic species *Hydroporus guernei* and larvae of the *Limnephilus atlanticus* (Borges et al., 2010) in tanks, although these species were mainly recorded in natural temporary ponds. Other species can benefit from the long hydroperiod of artificial tanks, such as the dragonfly *Anax imperator* Leach, 1815 (Fam. Aeshnidae), which usually prefers permanent waters to develop its instars and complete metamorphosis (see Corbet, 1957). However, natural ponds harbored the highest proportion of individuals belonging to native non-endemic and endemic species, most of which (8 out of 13 species) were also detected in artificial tanks. Additionally, although exotic species were more frequently detected in tanks (13% of all the collected individuals in tanks belong to exotic species), these exotic species do not seem to have so far successfully colonized natural ponds, which are only harboring 3% of individuals belonging to exotic species. This is probably due to the pristine conditions of habitats surrounding the natural ponds. However, the artificial tanks had a higher proportion of exotic species than natural ponds despite the short distance between them (180–2,130 meters). It is possible that, due to their location in the pristine native forests, the natural ponds could be able to resist the invasion of exotic species (i) as well-preserved communities (biotic resistance to invasion, *sensu* Elton, 1958), (ii) because high-altitude native forests could act as physical barriers to the colonization of exotic species (Florencio et al., 2016b), (iii) and possibly also due to the temporary character of some natural ponds, which harbor a singular fauna adapted to pond desiccation (Williams, 2006). Hence, when comparing two distinct types of systems (natural vs. artificial), the macroinvertebrate dissimilarities between them seemed to be lower than those found between ponds located in well-preserved areas and those with signs of anthropogenic disturbance. The former group exhibited slightly higher concentrations of DIN and dissolved oxygen, which could be related to a different exposure to the wind, given that these ponds are generally located at higher altitude in the native forest. The latter group of ponds were associated with human activities, located at lower altitude where agricultural activities and cattle ranching are more common, which was reflected in the slightly higher concentrations of TP and chlorophyll-a. Nonetheless, both natural ponds and tanks exhibited a relatively low concentration of nutrients (DIN and TP) that fell within the range of other wetlands and ponds located in protected areas of comparable rainfall regimes (Plenzler and Michaels, 2015).

Natural ponds displayed a high degree of endemicity that was mainly associated with temporary ponds, and a low species richness of macroinvertebrates. These two phenomena of high endemicity and "disharmony" (impoverished biota in comparison with the adjacent mainland, even lacking entire taxonomical groups) are typical of the insular biota, and have been described for the freshwater invertebrates of the Azores (Raposeiro et al., 2012; Florencio and Lamelas-López, 2016). The macroinvertebrate assemblages of these natural ponds were spatially structured, but this spatial pattern was not detected when tanks and ponds were considered together. This result suggests that the aquatic organisms benefit from tanks as refuges (e.g., to cope with the desiccation of temporary ponds), though they are not suitable habitats to establish successful populations (but see Svensson, 1977).

CONCLUSIONS

Despite storing water for livestock farming, it has been shown that artificial tanks can play a beneficial role in preserving macroinvertebrate assemblages. These freshwater systems of anthropogenic origin can harbor a wide range of taxa (see Hassall, 2014; Hill et al., 2015), enhancing regional diversity without replacing the essential conservation value of natural ponds (Reyne et al., 2020). In the present study, the artificial tanks in Terceira Island provided permanent waters that were able to harbor endemic and native species, increasing the heterogeneity of habitats along the hydroperiod gradient. The good water quality of the study tanks has also been shown, as they exhibited low concentrations of nutrients and chlorophyll-a, and low conductivity. These tanks increased the regional biodiversity despite their concrete walls without aquatic vegetation, both considered possible disruptive elements for macroinvertebrate diversity in urban/rural ponds (Oertli and Parris, 2019). However, we suggest that these concrete walls could have prevented grazing cattle from entering the water, which can significantly affect water quality (Campbell et al., 2009). Nevertheless, the occurrence of submerged and littoral vegetation might provide food, refuge and structure (e.g. for reproduction) for some macroinvertebrates (Fuentes-Rodríguez et al., 2013) and amphibians (Swartz and Miller, 2019). In our study, the lack of aquatic vegetation in the tanks could have prevented the proper establishment of odonate species (see Foote and Hornung, 2005; Hykel et al., 2020), as well as the occurrence of other aquatic species (e.g., aquatic beetle and bug species, see Deacon et al., 2018). Additionally, it is not known if tanks located at greater distances from the protected areas would also act as refuge habitats of macroinvertebrate assemblages. Our study suggests some recommendations to preserve the macroinvertebrate diversity of the Azorean ponds. (1) Maintain optimal environmental conditions in tanks like those found in natural and non-disturbed ponds (except for the pH of the water, due to the nature and physical structure of the tanks). (2) Maintain a high level of conservation of the pristine areas that contain the natural ponds, which allow most species to develop their life cycles and sustain high biodiversity, and protect these ponds against the arrival of potential invaders (see Samways et al., 2020). (3) The identification of anthropogenic pressures on the most disturbed ponds is essential to establish management strategies for conservation, mainly in the agricultural areas. (4) Further studies should evaluate possible strategies for the management of the artificial tanks to establish suitable conservation guidelines at local and landscape scales, that integrates both artificial tanks and natural ponds. Some examples of these strategies may be the inclusion of aquatic vegetation in the artificial tanks, as well as building facilities in their concrete walls (e.g., ramps) to favor the entrance/exit of some aquatic organisms. (5) The design of corridors from high-altitude native forests to the coast (see Aparício et al., 2018), including some of the study ponds and close-located tanks, could promote the conservation of the aquatic macroinvertebrates of the Terceira Island. We also highlight the importance of conducting seasonal studies that cover complete inundation-desiccation periods of ponds to properly represent the entire macroinvertebrate community, and to establish appropriate guidelines for conservation regarding the whole community. The singularity and vulnerability of the Azorean ponds must be highlighted, mainly regarding the scarce number of temporary ponds in Terceira Island, and we recommend including them in conservation programs, such as the Ramsar Convention.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

MF and LL-L conceived the idea. LL-L performed the field sampling with the help of MF. VG and LS carried out some chemical determinations in the laboratory. LL-L and MF wrote the manuscript with significant contributions by PB, and all the authors revised the different versions of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.605176/full#supplementary-material

Supplementary Material 1 | Photographs of some of the study natural ponds (**Supplementary Figure 1**), some of the artificial tanks (**Supplementary Figure 2**), and a list of the local names of the study natural ponds (**Supplementary Table 1**).

Supplementary Material 2 | Completeness of the pond inventories through abundance- and sample-based rarefaction curves to assess if the pond inventories are comparable in sampling efforts.

Supplementary Material 3 | Check-list including the relative abundance of the taxa captured during the extensive sampling. The relative abundance was calculated as the average number of individuals captured, considering the number of sampling units per pond and tank.

Supplementary Material 4 | Check-list of the captured taxa, including the number of individuals per pond and month, during the monthly sampling ("monthly sampling" spreadsheet), and the environmental variables of these ponds per sampling month ("variables monthly sampling" spreadsheet). A indicates Adult, L Larva, - Not captured. DO is dissolved oxygen concentration, EC is electrical conductivity, TP is total phosphorous concentration, and Chl is chlorophyll-a concentration.

Supplementary Material 5 | Independent percentage of contribution of each species to the macroinvertebrate dissimilarities detected between natural ponds and artificial tanks after a SIMPER analysis.

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Landscape Structure Is a Major Driver of Bee Functional Diversity in Crops

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Land-use change is having a negative effect on pollinator communities, and these changes in community structure may have unexpected impacts on the functional composition of those communities. Such changes in functional composition may impact the capacity of these assemblages to deliver pollination services, affecting the reproduction of native and wild plants. However, elucidating those relationships requires studies in multiple spatial scales because effects and consequences are different considering biological groups and interactions. In that sense, by using a multi-trait approach, we evaluated whether the landscape structure and/or local environmental characteristics could explain the functional richness, divergence, and dispersion of bee communities in agroecosystems. In addition, we investigated to what extent this approach helps to predict effects on pollination services. This study was conducted in an agroecosystem situated in the Chapada Diamantina region, State of Bahia, Brazil. Bees were collected using two complementary techniques in 27 sample units. They were classified according to their response traits (e.g., body size, nesting location) and effect traits (e.g., means of pollen transportation, specialty in obtaining resources). The Akaike information criterion was used to select the best models created through the additive combination of landscape descriptors (landscape diversity, mean patch shape, and local vegetation structure) at the local, proximal, and broad landscape levels. Our results indicate that both landscape heterogeneity and configuration matter in explaining the three properties of bee functional diversity. We indicate that functional diversity is positively correlated with compositional and configurational heterogeneity. These results suggest that landscape and local scale management to promote functional diversity in pollinator communities may be an effective mechanism for supporting increased pollination services.

Keywords: Brazilian landscapes, pollinators, agricultural fields, ecological intensification, functional richness, functional diversity, functional divergence, functional dispersion

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INTRODUCTION

Animal pollination is considered an essential ecosystem service. About 300,000 (90% of total angiosperm species) plant species depend on animal pollination (Ollerton et al., 2011), and 75% of agricultural food crops benefit in some way from the ecosystem services provided by pollinators (Klein et al., 2007). Among these animals, bees are considered the most expressive pollinators in both temperate and tropical areas, having diverse nesting habits, different degrees of sociality, and feeding habits. Despite their importance, studies point out the decline of species in some regions of the world (e.g., in Europe and North America) (Girão et al., 2007; Cameron et al., 2011; Dupont et al., 2011; Becher et al., 2013). Landscape changes driven by natural vegetation conversion into intensively managed agricultural fields, such as landscape simplification and native environment loss, are among the most critical factors to explain this loss of pollinator diversity (Stein et al., 2014). However, the landscape structure effects on pollinator species diversity is not always straightforward with mixed results being present in the literature (Williams et al., 2010; Coutinho et al., 2018). Additionally, different pollinator species do not respond equally to the same types of landscape changes. Therefore, much consideration is needed to understand how these landscape changes may increase or decrease pollinator diversity in different contexts.

Furthermore, most studies dealing with the decline of species focus on species' taxonomic diversity, but this approach may have limitations in explaining cause and effect relationships because pollinator species are not functionally equivalent. For instance, in a recent meta-analysis, Woodcock et al. (2019) show that the magnitude of functional differences between species plays an important role in predicting the yield of oilseed rape. Similarly, Martins et al. (2015) show that pollination success depends on a core of effect traits that increase the probability of transferring pollen grains in a particular environmental context. Because of the increasingly recognized importance of functional traits in ecological systems, the study of functional diversity (FD) has been explored to establish links between biological diversity and ecosystem functions and services (Loreau, 2000; Díaz et al., 2003, 2007; Cadotte et al., 2011; Lavorel et al., 2011). Environmental filters and the species ability to disperse in space may influence the functional diversity in a community (Aiba et al., 2012; Biswas et al., 2016; Cisneros et al., 2016). However, there are different approaches to study the impact of environmental changes on FD, ranging from single response traits (Eviner and Chapin, 2003) to indexes describing community properties, such as dispersion and functional composition (Botta-Dukát, 2005; Peres-Neto et al., 2012; Cisneros et al., 2016). Traits can also be classified into two dimensions of FD: response and effect traits. The degree of correlation between these traits can indicate how resistant an ecosystem can be to environmental changes (Oliver et al., 2015). Uncorrelated traits indicate greater ecosystem resistance because species' responses to environmental change are decoupled from their effects on ecosystem function (Larsen et al., 2005). Effect traits are related to one or more ecosystem functions, establishing direct mechanistic links between functional diversity and ecosystem function (Wood et al., 2015). Response traits can predict which species are present under a given environmental regime, elucidating the role played by the drivers modified by these regimes (Kremen and M'Gonigle, 2015; Wood et al., 2015).

Generally, the perspective of a single response trait links the most abundant species in a community to its performance in delivering a service (Sonkoly et al., 2019). In contrast, some studies emphasize the importance of trait diversity in a community to optimize ecosystem services because the larger the set of traits, the greater the likelihood of complementarity among species (Martins et al., 2015). Trait diversity is influenced by environmental and spatial filters that operate at different scales (Flinn et al., 2010; Aiba et al., 2012). A set of functional traits can occur in each location depending on the traits considered and their interaction with the environmental filters and spatial structure of patches and landscapes (Chase, 2014; Biswas et al., 2016), generating the expectation of FD to be spatially structured (Siefert et al., 2013). For bees, the most prominent pollinator group (Klein et al., 2007), solitary species are generally more affected by habitat loss than social species considering that solitary bees are more likely to be specialists in habitat use (Krauss et al., 2009). Within the bee group, FD can be highly impacted as there is great variation in other traits, such as diet breadth, foraging range, and body size (Banaszak-Cibicka and Zmihorski, 2012). Bees' functional dispersion, considering response and effect traits is higher in natural habitats than in organic and conventional agricultural systems (Forrest et al., 2015), indicating a greater diversity of traits in unmanaged environments. However, there is still a need to understand the set of appropriate measures associated with ecosystem functions and the elucidation of mechanisms underlying multiple indices and scales' variation.

Functional diversity can be separated into three components: functional richness (expressed as the space occupied by the species present in the community in a multidimensional space of traits); functional dispersion (defined as the average distance of individual species to the centroid of all species); and functional divergence (expressed as the distance of the species to the gravity center of the functional space). Functional richness represents the number of different traits in a community. The dispersion indicates the degree of differentiation between species, according to their functional characteristics. On the other hand, functional divergence represents how each species in the community separates itself from the most abundant species in this community. These functional diversity indexes are complementary, and the degree of correlation between them is one of the primary objectives in linking environmental changes and ecosystem function performance (Hooper et al., 2002; Oliver et al., 2015). However, most studies concentrate on one index, and the relationship among multiple indexes is mostly unknown (Bartomeus et al., 2018).

Some theoretical models have been used to explain the processes that regulate the formation of a community in heterogeneous environments (Warzecha et al., 2016). The species sorting model emphasizes effects of local abiotic features on population vital rates and species interaction (Leibold et al., 2004). On the other hand, the mass effect model focuses on immigration and emigration and its effects on local population dynamics, emphasizing the spatial dynamics role in local population densities (Leibold et al., 2004). Agroecosystems formed by a mosaic of agricultural and natural landscapes can be good scenarios in which to investigate the empirical support of these models because the different spatial arrangements of different types of land cover may indicate complementarity between multiple ecological processes.

From the perspective of landscape ecology, the landscape structure, comprising composition and configuration, can help us understand the mechanisms underlying these models (Holzschuh et al., 2010). Landscape composition has profound effects on the structure of communities as it is related to habitat availability for species. Configuration may have a direct influence on the movement pattern of many species. However, an integrated framework of these predictions considered from FD has been little explored (but see Silva and Hernández, 2015). Understanding the ecological processes that regulate FD can be fundamental for planning agricultural landscapes.

In this sense, to understand how different properties of FD respond to different land-use regimes, we address the questions of whether (1) landscape and/or environment local structures explain the functional structure of bee communities and (2) FD components (richness, divergence, and dispersion) of bee communities respond differently to environmental predictors.

MATERIALS AND METHODS

Study Area

The data used in this study were collected from 27 sampling points in 2011 in the Mucugê-Ibicoara agricultural development region, Chapada Diamantina, Bahia, Brazil (41°28′40″ S, 13°09′10″ W) (**Figure 1**). The region has elevations that vary between 900 and 1400 m of altitude and an annual average temperature of 21°C with a minimum of 16°C and a maximum of 26°C (data provided by the Bagisa S/A Agropecuária e Comércio meteorological station). The vegetation of the region is xerophytic, which is typical of savannah, and dominated by two physiognomies: parkland and wooded savannah. The parkland is characterized by graminoid savannah vegetation with a substantial presence of hemicryptophytes and geophytes. The wooded savannah consists of nano cryptophytes, hemicryptophytes, and continuous graminoid vegetation with many stunted woody plants and dwarf palms (Veloso et al., 1991).

Sampling Unit Selection

A buffer of 3 km was used as the minimum distance between sampling units (minimum nearest neighbor distance = 4.6 km, mean = 25.5 km, maximum = 63.6 km). For that purpose, we used the software ArcGIS 9.3 ESRI 2008. Through the classification of the bee community, according to their response and effect traits, we calculate the richness, dispersion, and functional divergence varied through a gradient of agricultural and natural physiognomies. In addition, we observed how the configuration of landscape elements could influence this response. We chose sampling points according to landscape composition gradient. For this purpose, a land cover map was drawn based on the supervised classification of satellite images, according to Moreira et al. (2015). We used a geographic information system (GIS) containing a SPOT satellite image with 5 m spatial resolution for the selection of our 27 sample units. As selection criteria, we used the vegetation stratification at the sampling point, the proportion of agricultural area, and the diversity of land cover types within a radius of 3 km from the sampling point. A GIS and field checks were used to select the sampling units. Visual inspection was performed by contrast of colors after previous classification of a SPOT satellite image with high spatial resolution (5 m pixels). The preselected units were checked in the field, and if they were different from what was expected by the image inspection, this point was moved to the nearest location with the desired characteristics. For more details, see Moreira et al. (2015). To choose the sampling points, we actively searched for an orthogonal gradient between the two descriptors of the landscape, agricultural proportion, and Shannon landscape diversity index (SDI) to minimize spatial autocorrelation. SDI is a relative measure of patch diversity and is equal to zero when there is only one patch in the landscape, increasing as the number of patch types or the proportional distribution of patch types increases in the landscape (Moreira et al., 2015).

Biological Surveys

Biological data were collected in each sampling unit, which was positioned on a gradient of landscape proportion of agriculture and habitat types diversity at a 3-km scale. Two complementary sampling strategies were used: passive, using pan traps (Cane et al., 2000), and active through entomological nets (Moreira et al., 2015). The active sampling with entomological nets was made by two collectors walking through two isosceles triangles within a reference hexagon with 25-m sides (**Supplementary Figure 1**). All floral visitors seen on the flowers were collected with the nets between 07:30 and 17:30. Each group was sampled every 2 months between January and November 2011, corresponding to two rainy seasons and two dry seasons to avoid possible systematic effects of seasonality. Each sample unit was sampled for 40 h throughout the entire campaign. Collectors alternated the units they sampled to minimize possible systematic effects on collection (Moreira et al., 2015). Pan traps were placed in each of the 27 sample units and removed 24 h later. For the collection with pan traps, we used the three most common colors to attract bees: yellow, white, and blue. Blue and yellow traps also had ultraviolet radiation (Cane et al., 2000). In each pan trap, we put 120 ml of water and approximately five drops of neutral detergent to break the surface tension. The pan traps were installed at the height of 1 m from the ground using 25-mm-diameter PVC pipes and perforated metal ribbons, used as support for 18-mm-diameter colored dishes. Traps were 5 m distant from each other in an equidistant triangular shape in which each one was positioned at a vertex of this triangle. At each sampling point, three groups of three plates of different colors were installed, totaling nine pan traps for each sampling point (**Supplementary Figure 2**). This set of nine pan traps formed a larger triangle

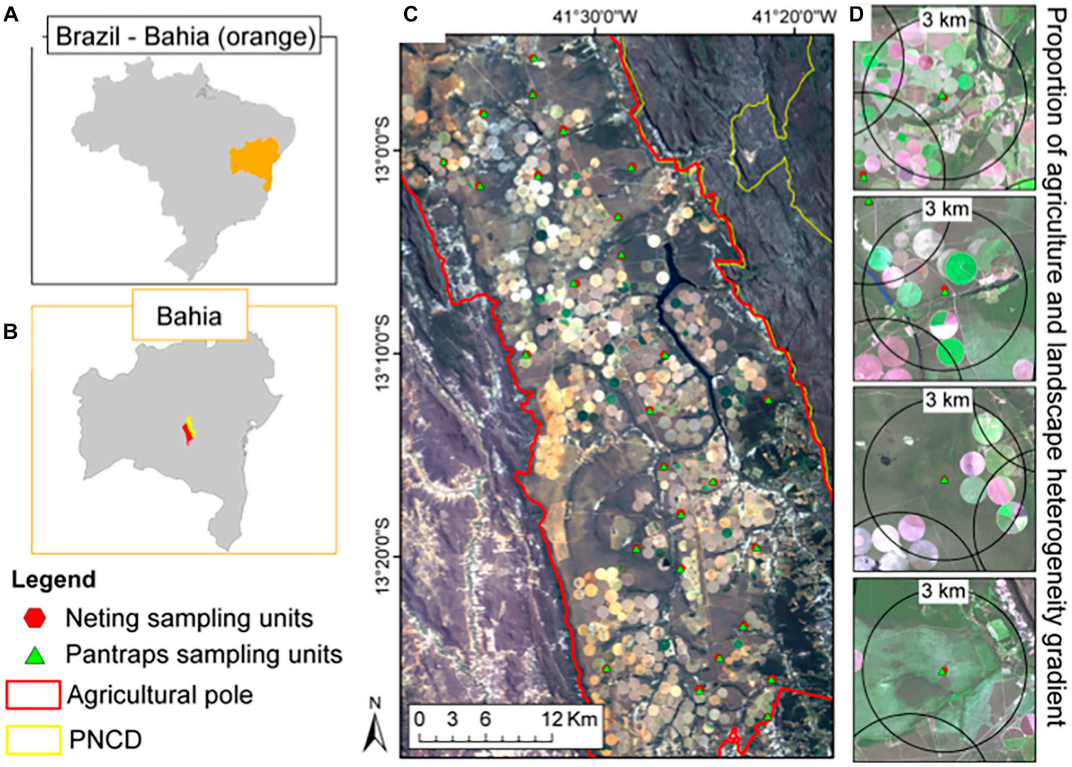

FIGURE 1 | (A) Highlighted in orange and light gray, the state of Bahia and Brazil, respectively. **(B)** At the center of the state of Bahia (red), the studied region, with the lands of the agricultural partnership in red and Chapada Diamantina National Park in yellow. **(C)** Location of the 27 selected sampling units (red dots and green triangles) in the study region and the land cover classification used for the calculation of landscape metrics. **(D)** Example of the 3-km buffer used for the selection of sampling units. Modified from Moreira et al. (2015).

in each sample unit. Each group of three was 15 m from the next nearest group.

Environmental Descriptors

To assess the influence of the landscape structure and the local environment on the bees' FD, we used images from LANDSAT 5 Thematic Mapper (TM) satellite (dated September 14, 2011) with 30 m spatial resolution. Images underwent geometric correction, georeferencing, atmospheric correction (DOS2), and radiometric calibration before the classification procedure was applied (Moreira et al., 2015). Classifications were made considering a total of 13 classes (as Moreira et al., 2015; Hipólito et al., 2018), including nine classes of vegetation and four complementary classes: disturbed vegetation (recently abandoned areas occupied by ruderal vegetation), grassy woody savannah, parkland savannah, wooded savannah, forested savannah, semideciduous forest, rocky park savannah, rocky wooded savannah, rocky steppe savannah, anthropic area (primarily including agricultural lands with minor contributions from roads, buildings, and bare soils of anthropogenic origin), clouds, water, and shadow.

Sampling points within the landscape considered the proportion of agriculture (PA), SDI, and the configuration of landscape elements (mean shape index or MSI) at spatial levels ranging from 200 to 12,500 m from the sampling point (more details on Moreira et al., 2015). The diversity of habitat types was based on the different types of land cover, using the landscape SDI (McGarigal et al., 2012). PA and SDI are part of landscape compositional heterogeneity (Fahrig et al., 2011). For the configuration, we used the landscape MSI, which describes the degree of the interposition of landscape elements weighted by area. Landscape metrics were calculated using the module Patch Analyst (Queens Press, Ontario Ministry of Natural Resources, 2012) in ArcGIS 9.3 (ESRI 2008). The PA and diversity of habitat types (SDI) were used as descriptors that reflect the influence of the environmental gradients (sorting species model) on bees' FD at several spatial scales. The MSI was used as a measure of the degree of the structural complexity of the elements that compose this landscape in order to establish a proxy that can indicate the degree of difficulty that the landscape imposes for the movement of bees in the agroecosystem (mass effect) (Leibold et al., 2004). Although it is an indirect measure, this index reflects an important structural characteristic that, measured in broad spatial scales, can indicate the role that the dispersion can have in the functional structure of bees in a metacommunity. Finally, at the local scale, which varied between 25 and 150 m from the sampling point, we used the mean of the two-band enhanced vegetation index (EVI2) to describe the local vegetation structure. This index, used in previous works in the same area, is a good descriptor of the number of branches and the richness of plants in the savannah, which are two important characteristics in the composition of the niche spaces of bee species (Moreira et al., 2015).

For all descriptors, we considered multiple spatial scales (i.e., local vegetation: 25 to 150 m, proximal landscape scale: 250 to 3000 m, broad landscape scale 6000 to 12,500 m), which we used to select the most appropriate scale of effect. For this, the best explanatory power (R^2) was adopted as the selection criterion. To detect the best explanatory measurement scale for the combinations of factors and FD indexes, we performed linear models of the different radii of MEVI2 and surrounding landscape metrics and searched for the highest value of R^2. This analysis was performed using the lm function in R software, package "vegan."

Functional Diversity

Trait Assignments

To calculate the FD indexes, we used response and effect traits. Through this approach, we can understand the role of environmental descriptors in FD and how it can potentially affect the pollination service. For all species in the data set (**Supplementary Appendix 1**), we compiled information on their life history traits, considering response and effect traits. For response traits, we used body size, dietary specialization, nesting location, nest construction behavior, and sociality. For effect traits, we used hairiness (density of hair because it affects pollen grain deposition on stigmas) (Stavert et al., 2016); glossa length, which is associated with a range of floral types that bees can access; mean of pollen uptake and transportation, both related to the versatility of interaction with pollen grains; and specialty in obtaining some resource (Michener, 2000; Martins et al., 2015) (**Table 1**). Body size was the quantitative functional attribute measured, and for this, we used the mean inter-tegular distance of the specimens collected (Greenleaf et al., 2007).

Measures for each species (or morphotype when identification was not possible) considered at least five individuals. For species of which we had fewer than five individuals, we used the number of individuals available in our data set. Information on the categorical functional attributes was obtained from the extensive survey of the specialized literature. Species were excluded from the analysis if we could not confidently assign a trait category.

To obtain complementary information regarding bee FD, we used three indexes that reflect the important properties of this diversity (Hooper et al., 2002). The functional richness is the volume in a multi-trait functional space that is occupied by a community (Villéger et al., 2008). The functional divergence reflects how much the species of a community diverge in their distances from the center of gravity of the functional space, considering the abundance of these species (Mason et al., 2005). There would be a low divergence if the majority of the most abundant species is close to the center of the values of this multi-trait space; this divergence is high when the most abundant species occupy the extremes of this multi-trait space (Villéger et al., 2008). The functional dispersion quantifies the mean distance of each species from its community centroid in a multivariate space defined by all included traits (Laliberté and Legendre, 2010). To calculate functional dispersion (FDis), functional richness (FRic), and functional divergence (FDiv), we used the function dbFD in package FD, in R version 3.4.4 (2018) with the Cailliez correction for non-Euclidean distances generated by the inclusion of categorical traits (Laliberté et al., 2014).

Statistical Analyses

We verified the role of environmental descriptors at three different levels, following the same logic of Moreira et al. (2015): local vegetation, proximal landscape, and broad landscape, considering the relevance of a multiscale approach to understand the trait distribution pattern in agricultural landscapes (Motzke et al., 2016). This division was performed to try to capture potential processes that operate at these three levels and is important and complementary in explaining the functional diversity of the bees, considering the response traits listed for this study, taking into account assumptions of species sorting and mass effect models. Bees are multi-habitat users and use resources within their radius of flight, which, on average, can be contemplated within this range of spatial scales (Ricketts et al., 2008; Warzecha et al., 2016). Finally, in relation to the broad landscape level, which ranged from 6000 to 12,500 m from the sampling point, we expect that population processes involving dispersal movements across the landscape occur at this spatial scale, being crucial to understanding the species occurrence patterns at smaller scales (Fahrig, 2013).

To standardize the effect sizes and reduce the influence of the range of each variable on the parameter estimation, both response and explanatory variables were rescaled. For this, we scaled and centered to zero each variable by subtracting its mean value and then dividing it by its standard deviation. This transformation preserves the original characteristics of the variables by adjusting the numerical values, making the results comparable (Moreira et al., 2015).

To evaluate the influence of the environmental predictors on the three indexes of FD (richness, divergence, and functional dispersion), we chose the scales that presented the highest R^2 value and constructed an additive model with all the predictive variables for each functional diversity index. From this initial full model, a set of models was derived resulting from all possible combinations of the seven effect variables (MEVI2, SDI at the proximal and broad landscape levels, MSI at the proximal and broad landscape levels, PA at the proximal and broad landscape levels), (MuMIn package, *dredge* function) (Barton, 2014). The best models were compared with a "null" model without any fixed predicting variable to understand whether they provide any relevant fit. We then compared the models using the values of the second order Akaike information criterion (AICc), which is suitable for small samples ($n < 40$). The delta AICc (Δi) value for each model, namely the difference between the AICc value for that model and the lowest AICc value in the set of models, was used to evaluate the plausibility of the candidate models. Models with values of delta AICc (Δi) < 2 were considered equally plausible. We also considered the Akaike weights (Wi) of the models, the evidence ratio

TABLE 1 | Traits used in analyses of functional richness, functional divergence, and functional dispersion.

Trait (units)	Trait type	Categories	Source
Body size	Continuous	N/A	
Dietary specialization (lecty)	Categorical	(1) Oligolectic (pollen specialist) (2) Polylectic (pollen generalist)	Michener (2000); Menezes et al. (2012); Paula (2014)
Nesting location	Categorical	(1) Above-ground (2) Below-ground (3) Mixed*	Stockhammer (1966); Michener (2000); Almeida (2008)
Nest construction behavior	Categorical	(1) Nester or (2) Cleptoparasitic	Michener (2000); Paula (2014); Rozen (2001)
Sociality	Categorical	(1) Social (including multiple forms of sociality) or (2) Solitary	Michener (1969, 2000); Almeida (2008)
Glossa length	Categorical	(1) Very long (>12.0 mm); (2) Long (7.0 to 12.0 mm); (3) Intermediate (3.0 to 6.9 mm); (4) Short (<3.0 mm) and (5) Short bilobate (<3.0 mm)	Roubik (1989); Michener (2000); Viana and Kleinert (2005)
Hairiness (density of hair)	Categorical	(1) Dense or (2) Sparse	Michener (2000); Viana and Kleinert (2005); Paula (2014)
Means of pollen transportation	Categorical	(1) Corbiculae; (2) Ventral scopa; (3) Scopa (hind femurs and tibias); (4) Scopa (femurs, trochanters, hind coxae and middle)	Michener (2000); Viana and Kleinert (2005); Paula (2014)
Specialty in obtaining some resource	Categorical	(1) Oil collector; (2) Essence collector; (3) Resin collector; (4) No specialist	Michener (2000); Paula (2014); Viana and Kleinert (2005)
Means of pollen uptake	Categorical	(1) First leg; (2) Ventral scopa; (3) Mandible or (4) Vibration	Michener (2000); Viana and Kleinert (2005)

*Trait information was taken from the specialized literature (sources listed); when necessary (notably for some effect traits), we relied on educated guesses based on capture patterns in our data set (e.g., means of obtaining floral or nest resources and means of pollen uptake). Species were excluded from analysis if we could not confidently assign a trait category. In "source," we present the three main references used. *Mean inter-tegular distance of five haphazardly selected individuals (or, if fewer than five, as many as possible) from our collection.*

in relation to the minimum AICc model (W1/Wj), and the importance of the variables in each selection process (SW) to evaluate the normalized differences between the equally plausible models as well as the differences relative to the null model. Parameter estimates for models presented in **Table 2** were obtained using the restricted maximum-likelihood method (Zuur et al., 2009). The model parameter estimation and model selection were performed with the "MuMIn" package (R Core Team, 2018).

RESULTS

By using the combination of active and passive sampling methods, we collected a total of 2825 bee individuals from 125 species (families Apidae, Halictidae, Andrenidae, and Megachilidae). The most abundant species were *Apis mellifera* Linnaeus, 1758 (1454 individuals); *Trigona spinipes* (Fabricius, 1793) (306 individuals); *Lasioglossum* sp. (78 individuals); *Geotrigona* sp. (78 individuals); *Bombus brevivillus* Franklin, 1913 (59 individuals); *Augochlora* sp. (51 individuals); *Augochlorella* sp. (44 individuals); and *Melipona quinquefasciata* Lepeletier, 1836 (42 individuals).

Functional Richness

Functional richness indicates how much of a multi-trait space is occupied by a sample of species from a biological community. It is a good predictor of environmental filters, indicating whether there is any threshold imposed by the investigated environmental gradient (Mouchet et al., 2010). The best model combines the positive effects of the proportion of agriculture and negative effects of landscape compositional heterogeneity (SDI) at the proximal level with the positive effect of the landscape compositional heterogeneity at the broad level (**Figure 2** and **Table 2**, $R^2 = 0.42$). The volume occupied in a community of bees considering a multi-trait space is strongly dependent on the diversity of land cover types at broad spatial scales. The other five models in the set can be considered as equally plausible (ΔAICc < 2) and include models with other variables besides those appearing in the best model. The models that presented the proportion of agriculture in both scales pointed to a positive association of this predictor with functional richness. The structural complexity of the landscape had a negative influence on the functional richness regardless of spatial scale (**Table 2**). However, the only variable that was present in the set of the equally plausible models was the landscape compositional heterogeneity at the broad level with a consistent positive effect

TABLE 2 | Overview of minimal adequate models describing landscape and local effects on functional richness, functional divergence, and functional dispersion of bees in agricultural landscape.

Response variable	AICc	Δ AICc	Selected models	Weight	Wi/Wk	R^2
Functional richness	73.6	0.00	*Y* = 0.35*AGRI_3Km – 0.41*SDI_0.25Km + 0.56*SDI_12.5Km	0.27	67.5	0.42
	74.7	1.11	*Y* = −0.26*MSI_0.25Km + 0.37*AGRIC_6Km + 0.45*SDI_12.5Km	0.15	37.5	
	74.7	1.13	*Y* = −0.39*MSI_0.25Km + 0.48*SDI_12.5Km	0.15	37.5	
	74.9	1.35	*Y* = −0.42*MSI_0.25Km + 0.32*AGRIC_3Km + 0.46*SDI_12.5Km	0.14	35.0	
	75.0	1.37	*Y* = −0.33*SDI_0.25Km + 0.30*AGRIC_6Km + 0.54*SDI_12.5Km	0.14	35.0	
	75.0	1.46	*Y* = −0.25*MSI_8Km – 0.36*SDI_0.25Km + 0.37*AGRIC_3000 + 0.45*SDI_12.5Km	0.13	32.5	
Functional divergence	72.0	0.00	*Y* = −0.36*MEV2_0.05Km + 0.37*AGRIC_7Km + 0.67*SDI_0.25Km	0.38	76.0	0.46
	73.34	1.36	*Y* = −0.39*MEV2_0.05Km + 0.61*SDI_0.25Km – 0.29SDI_8Km	0.17	34.0	
	73.62	1.64	*Y* = −0.39*MEV2_0.05Km + 0.79*SDI_0.25Km – 0.23*AGRIC_1Km	0.17	34.0	
Functional dispersion	76.57	0.00	*Y* = 0.41*MSI_11Km – 0.42*1.5Km	0.41	11.7	0.27

Models were selected using the dredge function (MuMin package in R) based on second order Akaike information criterion (AICc). Only the models with $\Delta < 2.0$ are presented in the table. ΔAICc, differences in AICc relative to the lowest value of AICc of all models; MEVI2, mean vegetation index; PA, proportion of agriculture (will be called AGRIC from now on); SDI, Shannon diversity index; MSI, mean shape index; Wi/Wk, evidence ratio between minimum AICc model and null model.

on the functional richness and which was, by far, the most important explanatory variable [SDI (w + j) = 73%] (**Figure 3**).

Functional Divergence

Functional divergence indicates how far the species in a community distance themselves from the more functionally redundant species in that community. The best of the three models combines predictors in different spatial scales: MEVI2 (in the spatial scale of 50 m), the proportion of agriculture (at the broad landscape level), and landscape diversity (at the proximal landscape level; R^2 = 0.46). In all three models, the diversity of the landscape at the proximal landscape level showed a positive relationship with the functional divergence (**Figure 2** and **Table 2**). The opposite trend was seen in the local scale, where MEVI2 (spatial scale of 50 m) was present in all the selected models, showing a negative relation with functional divergence (**Table 2**). The proportion of agriculture at the broad landscape level showed a positive relationship with the functional divergence in one of the three best models. On the other hand, the structural complexity (MSI) at the proximal landscape level and the proportion of agriculture at this same scale were present in only one model and presented a negative relationship with functional divergence. The evaluation of the predictors' relative importance indicated the landscape diversity at the proximal landscape level as the most important predictor of functional divergence (**Figure 3**) (SDI = 90%).

Functional Dispersion

Functional dispersion captures the average distance between species based on their functional attributes and relative abundance in a multidimensional space. In this way, this metric quantifies the breadth of functional roles across species, and on average, systems with species pools representing higher dispersion should display greater functional dissimilarity and a broader range of responses to environmental perturbations (Mouchet et al., 2010; Laliberté et al., 2013). For functional dispersion, the clearest pattern observed was that landscape structural complexity (MSI) showed an opposite trend when distinct spatial scales were considered: a positive relation at the broad landscape level and a negative relation at the proximal landscape level. The best model combined effects of landscape structural complexity in both spatial levels (**Figure 2** and **Table 2**, R^2 = 0.27). The evaluation of the relative importance of the predictors indicated the landscape structural complexity at the proximal landscape level was the most important predictor of functional dispersion (MSI = 45%) (**Figure 3**).

DISCUSSION

In general, our results indicate that landscape compositional and configurational heterogeneity are major predictors of three important and complementary properties of bee FD in agricultural landscapes: functional richness, functional divergence, and functional dispersion. However, the effects of these predictors on the response variables are dependent on the spatial scale. The observed patterns were distinct among the FD descriptors, indicating that different processes must regulate these three properties.

Functional Richness

Functional richness had a positive association with landscape diversity at the broad landscape level (**Figure 2** and **Table 2**). This result may indicate that the variety of elements in the landscape, on a broad scale, can serve as a source of species with the diversity of traits that occupy new regions in the functional trait space. This may indicate that the premise of the mass effect model can be applied on a broad scale. Landscape diversity is an essential predictor of bee species richness (Steffan-Dewenter et al., 2002; Williams et al., 2010; Murray et al., 2012). More heterogeneous landscapes can safeguard species with different requirements in terms of habitat use, providing various floral and nesting resources over space and time (Kennedy et al., 2013). However, when this effect is dependent on the spatial scale, other mechanisms besides landscape complementation come into play, and more detailed mechanistic explanations are necessary.

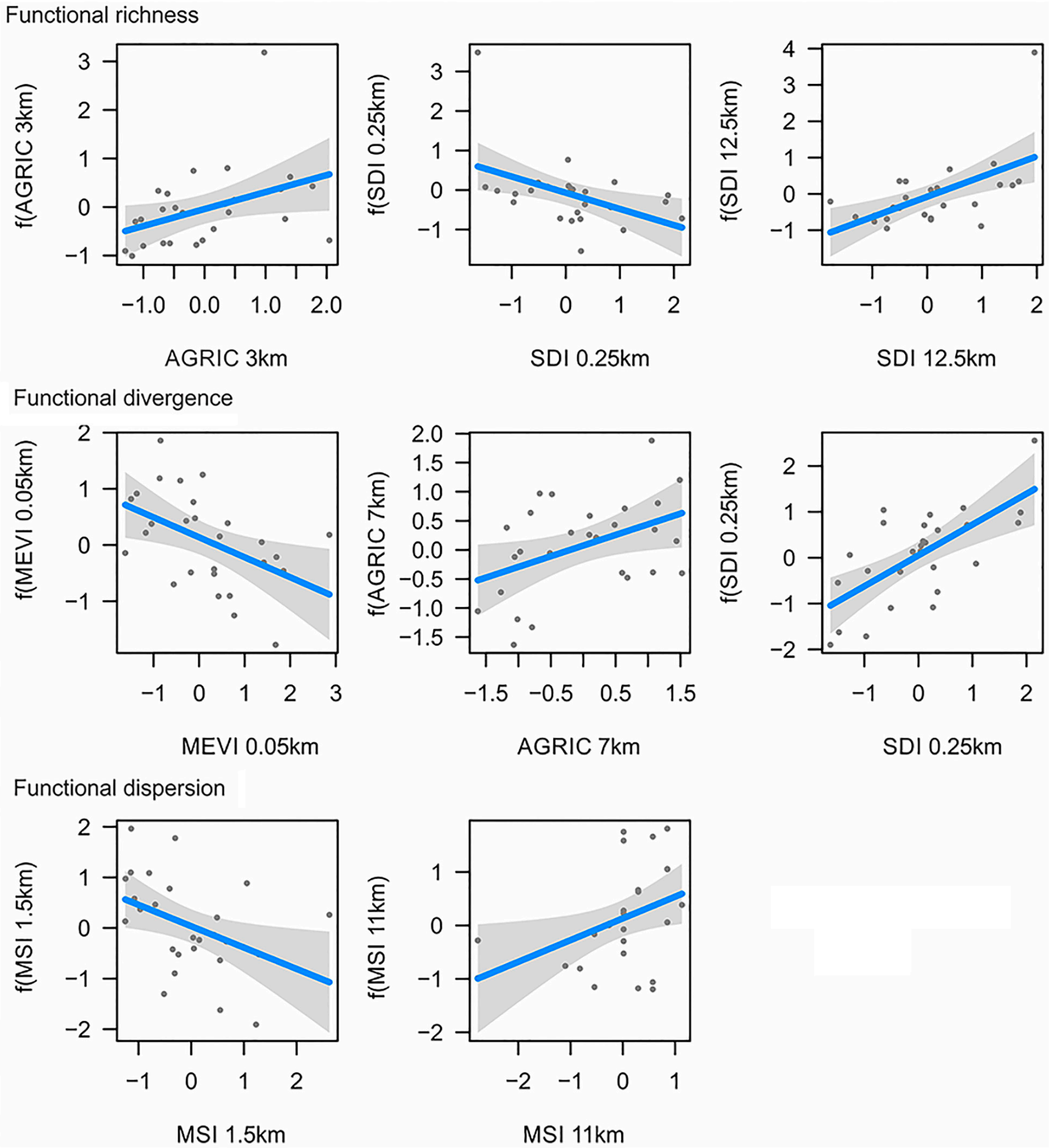

FIGURE 2 | Influence of landscape and local vegetation descriptors on bee functional richness, functional divergence, and functional dispersion in the agricultural region at Mucuge-Ibicoara, Chapada Diamantina, Bahia, Brazil. The numbers in parentheses indicate the best spatial scale for landscape variables. Shaded areas indicate confidence interval at level 95% for the predicted values.

More heterogeneous or diverse landscapes may present an additional discontinuity of specific soil cover types, increasing the range of trophic and non-trophic resources available (Okuyama et al., 2008; Zurbuchen et al., 2010). This scenario may favor species with different combinations of response and effect traits, increasing the functional volume occupied by a community of bees. Suppose this positive relationship is occurring at broader spatial scales. In that case, these more diverse landscapes may contribute to a large volume of response and effect traits that serves as a source for less diverse regions (Leibold et al., 2004). This critical spatial dynamic avoids local extinctions when we consider taxonomic diversity (Kuussaari et al., 2009; Metzger et al., 2009) and may increase the chances of retaining certain combinations of functional traits in local communities by considering a multi-trait approach. The assumptions deriving from species sorting (gradients influencing the species distribution) and mass effect (heterogeneous landscapes as sources for areas with less diversity) can be verified with the observed pattern toward functional richness (Urban et al., 2008; Tscharntke et al., 2012). In this way, the volume of the multi-trait space occupied by bee communities at the local level may be a subset of what is available at broader spatial scales when there is evident heterogeneity at these scales (Loreau et al., 2003). The proportion of agriculture had a positive effect on functional richness when this effect was combined with an increase in landscape diversity (**Figure 2**

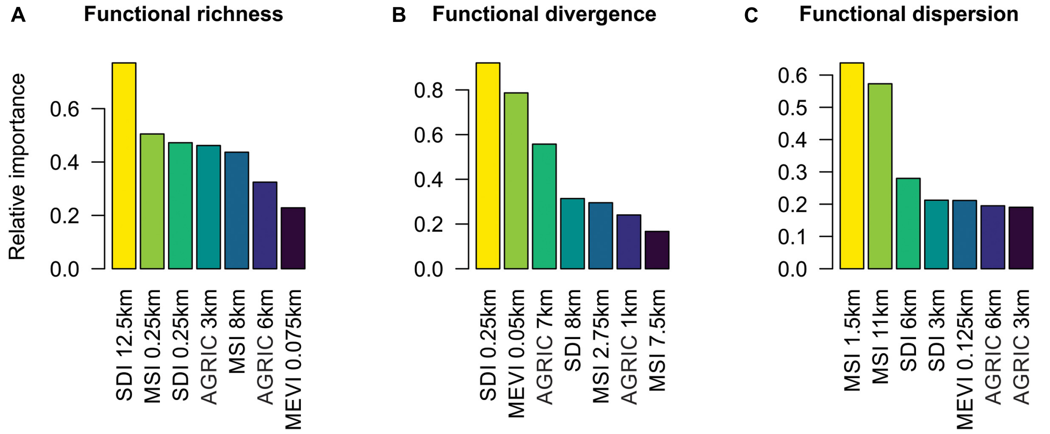

FIGURE 3 | Relative importance of environmental predictors on functional richness **(A)**, divergence **(B)**, and functional dispersion **(C)**. The relative importance is the sum of the Akaike information criterion weights of the models with each predictor. Shannon Diversity Index (SDI) was the best predictor for richness and functional divergence but in different spatial scales. Mean shape index (MSI) was the best predictor of functional dispersion at the proximal landscape level. The numbers associated with predictors represent the spatial scale with the highest R^2 value. MEVI2, mean vegetation index; AGRIC, proportion of agriculture.

and **Table 2**). This result can be explained given the additional supply of resources that agricultural areas may offer in diverse environments (Coutinho et al., 2020), attracting species with different combinations of functional traits.

At the proximal landscape level, the trend associated with landscape diversity was opposite to that found at the broad level. This pattern may be related to a phenomenon named the 'area-heterogeneity trade-off' (Kadmon and Allouche, 2007; Allouche et al., 2012). According to this mechanism, the niche width of the species is not unlimited. An increase in the environmental heterogeneity within a fixed space may reduce the average amount of effective area of use of a given species. Thus, we must explain the observed differences in responses to landscape heterogeneity for different species groups. Wide- and narrow-ranging species represent differences in habitat breadth: generalist species, mainly in trophic resources, tend to be wide-ranging, whereas specialist species tend to be narrow-ranging (Katayama et al., 2014). In a study with birds, Katayama et al. (2014) found a negative impact of landscape heterogeneity on species richness with narrow diet breadth. However, this richness was positively associated with open areas and low forest cover. For example, in our study, open areas, such as Savannah Park, can provide many resources for oligolectic species that nest in the ground. These bees may not benefit from very heterogeneous environments with different land cover types. Thus, although heterogeneity is positively associated with species richness, this relationship must be scale-dependent. Thus, when we refer to the functional richness, mechanisms that operate in fine scales should be approached. At the proximal scale, the increase in heterogeneity may favor the occupation of a volume of functional traits with more generalist species using the available resources.

Functional Divergence

The most plausible models include a negative association of vegetation's structural complexity at the local scale as well as a positive effect of landscape diversity at the proximal scale and PA at the broad scale (**Figure 2** and **Table 2**). The structural complexity of vegetation at the local scale was a good surrogate measure for the number of branches and plant richness of savannah physiognomies in the studied region (Moreira et al., 2015). This negative association can be explained by the fact that a site with high plant richness can be associated with high resource availability, which favors the occurrence of the community's dominant species.

Generalist species tend to be the most abundant, and this condition places great weight on these species when we consider the asymmetry of plant–pollinator interaction networks concerning the less abundant species (Stang et al., 2007; Moreira et al., 2015; Ferreira et al., 2020) for example. Similarly, the most abundant species in our study share a core of response traits, which favors the high weight of these species in decreasing the functional divergence. About 62% of the total abundance of bees was shared between the species *Apis mellifera* and *Trigona spinipes*. Both species are social, polylectic, and above-ground nesting and with a short proboscis (Viana and Kleinert, 2005) and are able to thrive in environments that provide a high supply of resources (high plant richness) and structural complexity of the vegetation for nesting. The PA positively influenced the functional divergence at the broad spatial scale when combined with the diversity of the landscape at the proximal scale. Many species can survive in agricultural areas mainly because of the potential supply of trophic resources. When these areas are associated with more heterogeneous environments, these environments can attract species with contrasting traits. In this sense, more diverse areas inserted in regions with a large proportion of agriculture promote *rescue effects* on functional traits (Brown and Kodric-Brown, 1977).

Positive association between functional divergence and landscape diversity at the proximal landscape level can be explained by the fact that the increase in landscape heterogeneity increases the probability of variation in the spatiotemporal supply of trophic and non-trophic resources (Parrish and Bazzazz, 1979). In a functional perspective, more heterogeneous environments should increase productivity (number of offspring) of species with different response traits (Fahrig et al., 2011) because of the wide offer of trophic and non-trophic resources. Thus, for species that occupy the functional volume of traits in a community, the increase in the diversity of resources should favor the increase of the functional divergence in the multi-trait space.

Functional Dispersion

Functional dispersion was favored with increased structural complexity of the landscape at the broad landscape level, but this trend was opposite at the proximal landscape level. Recent findings in the literature have found differences in functional dispersion when comparing intensively managed agricultural systems with less managed areas, indicating that less managed areas are important to maintain high functional dispersion (Forrest et al., 2015). However, our study provides strong evidence of the role of landscape configuration in the functional dispersion of bees in agroecosystems.

The positive association between the functional dispersion with the mean shape index and the broad landscape scale can provide support to the mass effect model, indicating that dispersion plays an important role in the range of traits present in an agroecosystem. In parallel, as this index reflects the degree of irregularity of landscape elements and how much interspersion between them exists, this result also highlights the importance of functional connectivity between these elements (Boscolo et al., 2017). However, this relation is valid only in wider spatial scales, indicating that there is an important trade-off between scales that must be carefully evaluated.

The increase in structural complexity to the proximal landscape scale has been negatively associated with functional dispersion. This finding can be explained by the functional identities of the species that are favored with increasing structural complexity at this spatial scale. At the proximal scale, a high flux of organisms through the landscape can lead to a homogenization of the community from a taxonomic perspective (Mouquet and Loreau, 2002). We can extrapolate this effect by analyzing functional traits, which may contribute to increase the functional redundancy of the system as an effect exerted mainly by the most dominant species in the system, which form a cluster of traits, as explored above.

Our integrated approach between response and effect traits can be a useful tool to predict the impacts of land use on the pollination services in heterogeneous agricultural environments. We have evidence that divergence and the functional dispersion are indexes that depend on species abundance and were influenced by two dominant species, *T. spinipes* and *A. mellifera*. Both species are generalists with *T. spinipes* having a wide distribution and inhabiting diverse habitats, among which we can cite the "Cerrado" (neotropical savannah) and tropical forests throughout South America (Schwarz, 1948; Roubik, 1989). *T. spinipes* was the second most frequent floral visitor in native flowers in the sampled region, but this does not imply the delivery of efficient pollination. Similarly, *Apis mellifera* was the most abundant visitor in the region (46.4% of total recorded visits) but may also not be efficient in pollinating all plant species. Thus, pollinator identity should be considered carefully before providing information on FD in agricultural landscapes.

In a study with 41 crops worldwide, Garibaldi et al. (2013) show that the fruit set increased significantly with the visitation of *Apis mellifera* in only 14% of cultivated plant varieties. The authors verified that the rates of visitation by *Apis* and wild insects promote the increase in the fruit set independently and that high abundances of *A. mellifera* have a complementary effect but do not substitute for the role played by the native bees in the pollination of these crops. Viana et al. (2014) verified in the same study region of our study that the stingless bee *Melipona quadrifasciata anthidioides* (Lepeletier) could improve honeybee performance as pollinators of apple flowers because the presence of both of these bees results in increases in apple fruit and seed number. These studies point to the complementarity of responses and effect traits as a promising way to increase pollination success for wild and cultivated plants.

Here, the inclusion of effect traits and response traits on the functional classification of bee species can help us identify response and effect groups that maximize divergence and functional dispersion. This strategy presupposes identifying the factors that would contribute to increasing the chances of persistence of these species as well as the increase in the number of individuals of their populations.

Note that, at the proximal landscape level, functional richness has a negative association with landscape heterogeneity, but this relationship is positive with functional divergence, indicating a clear trade-off. However, this aspect should not be a problem if the landscapes are planned in a hybrid perspective (Ekroos et al., 2016) with multiple forms of habitat use, including open areas and dense vegetation, with different degrees of irregularity among the elements that compose this landscape. Thus, if functional richness is not favored in specific regions of this landscape, other areas (lower heterogeneity in some regions of the landscape) may serve to increase this richness. Most importantly, the design of this landscape is expected to increase the flux of organisms with distinct and complementary traits, which may increase the probability of delivering pollen between crops and wild vegetation.

CONCLUSION

Our study points to the influence of landscape descriptors on important properties of the FD of bees in agroecosystems in the tropical zone. Our results indicate that both the sorting species and mass effect models have empirical support in our study. Both the characteristics of the landscape composition (sorting species) and the irregularity of the landscape elements, which influence the displacement of the species (mass effect model), are important factors that influence FD. The indexes used describe different aspects of FD and point to the complementarity of properties that must be considered when planning agricultural landscapes. Maintaining compositional and configurational heterogeneity is a promising way to enhance FD (**Supplementary Figure 3**). However, the effects of these predictors are scale-dependent. This fact highlights the importance of considering hybrid management systems at multiple spatial scales (Kennedy et al., 2013; Moreira et al., 2015) that contemplate multiple states of landscape composition and configuration, favoring different dimensions of bee FD.

Besides our approach, considering the set of response and effect traits can contribute to the delineation of response and effect groups in a less arbitrary manner, arbitrariness that has been criticized in the literature (Mason et al., 2005; Petchey and Gaston, 2006; Bartomeus et al., 2018). The identification of the species that most contribute to the reduction of divergence and functional dispersion provides the possibility to back and evaluate which traits are shared by these most abundant species and which traits are disadvantaged in certain contexts, indicating more or less sensitive species groups to certain landscape composition and configuration.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: https://datadryad.org/stash/dataset/, doi: 10.5061/dryad.n5tb2rbtn.

AUTHOR CONTRIBUTIONS

JC, EM, DB, RS, and BV conceived the ideas and designed methodology, collected the data, analyzed the data, and led the writing of the manuscript. JC, JH, DB, RS, and EM contributed to the writing and manuscript revision. All authors contributed critically to the drafts and gave final approval for publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.624835/full#supplementary-material

Supplementary Figure 1 | Scheme of a sampling unit hexagon and movement of the collectors during sampling; yellow circles represent the flagged polyethylene pipes used for marking the limits of the hexagons; arrows and numbers represent the trajectory and the sequence of motion, respectively, of the two collectors, who are identified by the colors red and blue; A–F: Sequence of movements conducted by the collectors during the sampling, covering all sides of the triangles that formed the hexagons. Extracted from Moreira et al. (2015).

Supplementary Figure 2 | Scheme representing the collection with pan traps in a mosaic of agricultural and natural physiognomies, Chapada Diamantina, Bahia, Brazil. The vertices of the smaller triangles indicate the position of each pan trap. Central point sampling indicates the point of reference for choosing the points that represented the agricultural proportion gradient; landscape diversity and structural complexity (see text for details).

Supplementary Figure 3 | General overview of the main conclusions of this study. Functional diversity is the result of filters operating at different spatial scales. Functional richness is benefited by the diversity of the landscape at the broad landscape level and less diverse landscapes at the proximal landscape level, which increases the volume occupied by the species in a multi-trait space. Functional divergence benefits from more diverse landscapes at the proximal landscape level and a lesser structural complexity of vegetation on the local scale. Finally, functional dispersion benefits from the structural complexity of the landscape at the broad landscape level and from a lower structural complexity to the proximal landscape level, which shifts the centroid from a multi-trait space to more extreme values of that space. Only the descriptors with the highest relative importance are shown.

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Long-Term Tree Regeneration of Fragmented Agroforestry Systems Under Varying Climatic Conditions

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Iberian dehesas and montados are agroforestry systems protected by the European Habitats Directive due to high levels of biological diversity associated to their savannah-like structure. Tree scattering in dehesas, montados and other agroforestry systems is, however, known to compromise tree regeneration, although recent work suggests that it may protect tree populations from climate warming by alleviating plant-plant competition. We analyze how climatic conditions, tree isolation and their interactions influence the outcomes of regeneration stages, from flower production to early seedling establishment, using data gathered during the long-term monitoring (2001–2018) of ca. 300 Holm oak *Quercus ilex* trees located in central Spain. Holm oak reproductive effort, predispersal seed losses, and early seedling recruitment were sensitive to climate change, especially to year-round drought. Effort and early seedling recruitment decreased, while abortion and predispersal seed predation increased, with higher drought intensity. Spring warming increases pollination effectiveness, but had no further effect on acorn crops. Forest clearing seemed to have little scope to ameliorate these negative effects, as shown by weak or no interactive effects between the spatial configuration of trees (cover or isolation) and climate variables (spring temperature or drought intensity). Forest opening aimed at decreasing adult tree mortality under climate change scenarios would then have little or no effects on tree recruitment. Landscape-scale rotations alternating shrub encroachment and thinning along periods adapted to changing climate are proposed as the main management option to preserve both oak forests and dehesas in the long term.

Keywords: climate change, dehesa, drought, landscape-scale management, montado, regeneration cycle, tree scattering

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INTRODUCTION

Increasing tree mortality associated to drought events (Jump et al., 2017) and to introduced pests (Roy et al., 2014) is threatening forests worldwide. Several recent papers conclude that forest thinning can be an efficient management option to deal with the negative effects of global change on tree growth and mortality (Ruiz-Benito et al., 2013; Astigarraga et al., 2020). Tree recruitment during benign inter-event periods may also compensate for increasing tree mortality (Jump et al., 2017). However, open woodland configurations resulting from thinning usually imply chronic regeneration deficits of tree populations (Pulido et al., 2001; 2010; Gibbons et al., 2008; Morán-López et al., 2016c), so that management actions directed to increase tree survival and growth may indirectly compromise forest survival by reducing tree recruitment. Knowledge on the interactions between climatic drivers and the forests structures resulting from management are thus essential to develop management practices aimed at ensuring the maintenance of tree populations under global change scenarios (Valladares et al., 2014).

Natural regeneration is a multistage process that ensures the long-term persistence of a plant population by the replacement of the old mature individuals by the new recruits (Jordano and Herrera, 1995; Pulido and Díaz, 2005). Regeneration is strongly determined by the processes occurring in the early stages of seed production, dispersal, and early seedling survival (Schupp et al., 2010; Johnson et al., 2014).

Agroforestry systems are usually considered as prime examples of sustainable management (Wilson and Lovell, 2016). Among them, the Spanish dehesas and Portuguese montados (dehesas, hereafter) are by far the best-known examples of the so-called working landscapes, that integrate multiple land uses and ecosystem services at landscape scales (Campos et al., 2013). Agricultural and livestock uses are integrated with forestry practices aimed at preserving an open tree layer of evergreen oaks (*Quercus ilex* and/or *Q. suber*; Díaz et al., 1997). Open tree layers imply high conservation and economic values linked to intimate mixtures of open and forested ecosystems (Díaz et al., 1997, 2013; Moreno et al., 2016); in fact, dehesas are one of the few man-made habitats protected under the European Habitats Directive (Díaz et al., 2013).

Whole-cycle analyses have detected bottlenecks of the regeneration cycle in dehesas, associated to tree isolation (Pulido and Díaz, 2005; Pulido et al., 2010). However, the spatial configuration of trees can have contrasting effects depending on the life-stage being evaluated. At the predispersal stage, general positive effects have been found, with increased tree fecundity, and decreased seed abortion rate and predispersal seed predation, in more isolated trees (Díaz, 2014; Morán-López et al., 2016a). These effects are apparently mediated by alleviation of plant-plant competition for scarce water supplies during drought events (Pulido et al., 2014; Morán-López et al., 2016a), as happens with climate-related mortality of adult trees (Ogaya et al., 2019). In contrast, isolation can negatively impact dispersal and post-dispersal survival rates. In particular, key seed dispersal services to safe sites, where seedlings can cope with water stress and recruit, collapse in open woodland due to changes in the foraging behavior by avian and rodent scatter-hoarders (Morán-López et al., 2015, 2016c). Thus, incorporating multiple stages of recruitment is needed to obtain a realistic view about the effects of tree isolation on oak recruitment, as well as to evaluate whether potentially conflicting effects of isolation and climate warming can cancel each other.

Effects of tree isolation on the stages of the regeneration cycle can also be strongly modulated by climatic conditions (references above and in Monks et al., 2016). However, no study has systematically evaluated how isolation modulates climatic effects across pre and post-dispersal regeneration stages. Moreover, to date, little is known about how these interactive effects can be modified by increased drought, probably because studies available are usually short-term. In the Mediterranean basin, climate is characterized by high inter-annual variability (especially in summer), and such trends are expected to increase in the coming decades (IPCC, 2018). Thus, long-term data can provide new insights about the joint effects of tree spatial configuration and climate on oak regeneration.

Here we took advantage of data gathered during a long-term (18 years, from 2001 to 2018) monitoring of ca. 300 holm oak *Q. ilex* trees growing under contrasting pseudoexperimental levels of tree isolation. Our main aim is to evaluate how positive and negative effects of isolation on the stages of the regeneration cycle are modulated by changing climatic conditions. The effects of isolation and climate and their interaction will be also integrated across stages of the regeneration cycle to derive management options aimed at improving the resilience of agroforestry systems to expected climate change.

MATERIALS AND METHODS

Study Species

The holm oak (*Quercus ilex*) is a late-successional species that shows a typical masting behavior (Koenig et al., 2013). Wind pollination occurs between April and May, fruit development during summer and early autumn, and acorn fall between October and January (Vázquez, 1998). Variable proportions of the reproductive effort are lost along the regeneration cycle. Caterpillar herbivory, pollination failure, fruit abortion, predispersal insect seed predation, postdispersal vertebrate predation, germination failure and seedling mortality are the main sources of propagule loss (Pulido and Díaz, 2005; Díaz, 2014; **Figure 1**). Predispersal losses depend on the landscape configuration where tree populations are growing. In general, tree isolation favors reproductive effort and decreases, or has no effect on, pollination failure, abortion, and pre- and post-dispersal seed predation under mother trees (reviews in Díaz et al., 2011; Díaz, 2014). Acorns are dispersed by mice *Apodemus sylvaticus* and *Mus spretus* and European jays *Garrulus glandarius*. Proportions of seeds dispersed are quite variable among both seed dispersers and landscape configurations: mice remove 0–100% acorns in both forests and dehesas, with large among-trees variation, whereas jays remove ca. 35% acorns in forests and 5% in dehesas on average. Less than 2% acorns dispersed by mice are cached in dehesas vs. 2–23% in forests (Muñoz and Bonal, 2011; Morán-López et al., 2015, 2016c). Usually, 100% of acorns not dispersed and cached are predated by postdispersal seed predators such as pilfering mice, ungulates or livestock (Pulido and Díaz, 2005; Muñoz and Bonal, 2011). Seedling germination occurs in winter and seedlings emerge between March and June (Pulido and Díaz, 2005). Nurse shrubs increase post-dispersal seed predation because they attract pilfering mice, at least in open woodland (Smit et al., 2008), but greatly improve seedling survival to the first summer drought (Smit et al., 2008; Gavinet et al., 2016). Net effects of shrubs are positive as seedling recruitment

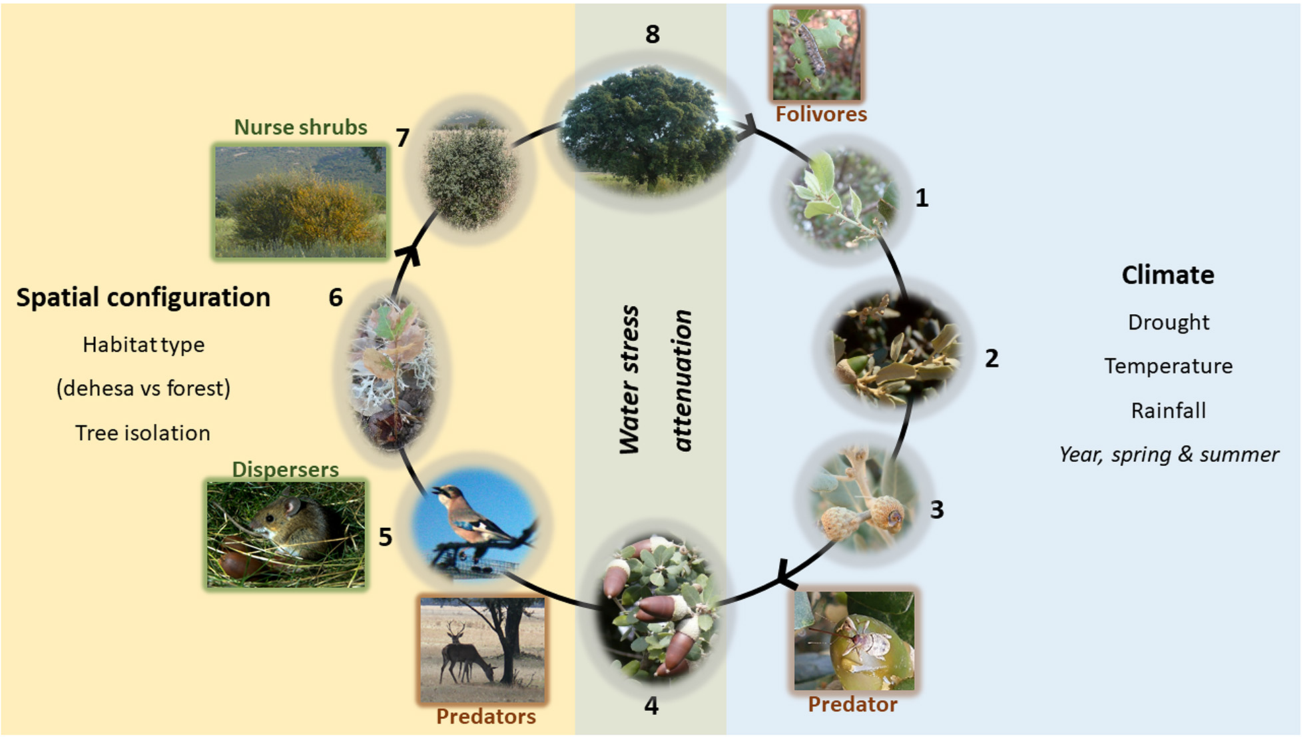

FIGURE 1 | Factors affecting losses of reproductive potential in each stage of the reproductive cycle of Holm oaks (1, flowering; 2, pollination; 3, fruit growth/abortion; 4, fruit ripening; 5, dispersal; 6, seedling emergence: 7, seedling establishment; and 8, adult tree). Mutualist interactions are represented in green (dispersers, represented by a mouse, and nurse shrubs), while antagonistic organisms are shown in brown boxes (leaf-eating insects, insect predators of growing fruits, and seed-eating vertebrates). Holm oak interactions occur within a spatial (yellow) and climatic (blue) context. Spatial configuration of trees (i.e. isolation) and climate can affect interaction outcomes in an additive or interactive manner (i.e., water stress attenuation). After Pulido and Díaz (2005); Díaz et al. (2011), and Díaz (2014). Photographs by I. Torre (wood mouse *Apodemus sylvaticus*), C.L. Alonso (European jay *Garrulus glandarius*) and M. Díaz (*Malacosoma neustria*, *Quercus ilex*, *Curculio elephas*, *Cervus elaphus*, and *Citysus scoparius*).

is closely related to shrubs at both local and landscape scales (Ramírez and Díaz, 2008).

Study Area

We established long-term monitoring programs of holm oak fecundity and early seedling establishment from 2001 onward at the National Park of Cabañeros (39°24’ N, 4°29’ W), central Spain (Díaz et al., 2011; Koenig et al., 2013; **Supplementary Figure 1**). Spatial configuration of oak woodlands follows two contrasting types: forests and dehesas (Morán-López et al., 2015). Forests occupy hills and lower slopes. Tree density is 97 trees ha^{-1}, on average, and understory cover is well developed ($>$ 60% of shrub cover). Dehesas occupy plain lowlands and are savannah-like woodlands (12 trees ha^{-1}, on average). Scattered trees grow in an open grassland matrix with almost no shrub cover ($<$ 1%). Dehesas were opened from forests similar to the current ones at the end of the 1950s (Vaquero, 2000), by removing shrubs, thinning and pruning trees, plowing the ground and introducing a free-ranging cow flock (Díaz et al., 1997; Campos et al., 2013). The area had no human uses before except for occasional firewood and charcoal harvest (Vaquero, 2000). Livestock was replaced by wild ungulates (mainly red deer *Cervus elaphus* and wild boar *Sus scrofa*) for big game hunting in the late 1970s and, finally, it became a Park, first Natural and then National, in 1995. Cabañeros Park can thus be considered a large-scale, long-term thinning experiment of oak tree populations (Díaz et al., 2011).

Long-Term Monitoring of Predispersal Seed Loss

Predispersal seed losses were monitored from 2002 onward (17 years) in up to 145 trees scattered over a 750-ha area covering the forest-dehesa transition (**Supplementary Figure 1**). Trees were selected to represent the full ranges of spatial arrangements found in both forests and dehesas, from clumped to isolated (**Supplementary Figure 1**). We selected 103 trees in dehesa and 42 in nearby forest sites to uncover the larger local variation of these arrangements in dehesas. Each tree was provided with 2–11 seed traps (cylindrical plastic containers 0.12 or 0.132 m^2 wide and 0.5 m deep, hanging from tree branches by means of galvanized wire) covering 1.5–2% of the canopy area. No attempt was made to exclude rodents or birds by means of wire mesh, as mesh could have prevented large acorns to fall into the traps and we demonstrated lack of acorn removal from traps by means of marked acorns placed in them (Bonal et al., 2007). Trap contents were collected at the end of winter, and the numbers of unpollinated flowers, aborted seeds, seeds infested by pre-dispersal seed predators, and sound seeds were counted (**Figure 1**). We estimated the reproductive effort as the total number of propagules (unpollinated flowers, aborted fruits, infested seeds, and sound seeds) per unit area. Rates of pollination failure, abortion and infestation rates were calculated by dividing numbers of propagules lost at each stage by numbers surviving to that stage (e.g., number of unpollinated flowers divided by reproductive effort, number of aborted fruits divided by number of pollinated flowers, and so on). Tree size was estimated as its canopy projection using crown diameter measurements taken when the tree was provided with traps; subsequent measurements revealed no significant increases in canopy projections during the study period. Tree isolation was measured from aerial photographs as the proportion of area within a buffer with a 50 m radius from each focal tree not covered by other tree canopies.

Long-Term Monitoring of Early Seedling Establishment

We monitored the effects of acorn crops on seedling establishment from 2001 onward (18 years) in three nearby oak subpopulations in forest areas with no current, and scarce past, human use, located 30 km northwest of the trees provided with seed traps (**Supplementary Figure 1**). Each subpopulation was sampled by marking 50 oak trees at ca. 20-m intervals along a linear itinerary. To measure seedling establishment, from each focal tree and in direction to the next reference tree, we established transects 10-m long and 2-m wide. Seedlings emerged each year were mapped on transects and marked permanently with colored wire for long-term monitoring. Seedlings differ from resprouts by having cotyledons still attached or cotyledon marks if removed by acorn dispersers (Díaz et al., 2011). Annual surveys were done in October. Densities of current-year seedlings and of seedlings surviving from earlier years (No./m^2) were computed for each transect and year. In addition, we recorded crop production of reference trees. Crop production was estimated visually on a 0–4 scale (0: no acorns or catkins; 1: < 10% of the canopy covered by acorns; 2: 10–50%; 3: 50–90%; and 4: > 90% (Díaz et al., 2011; Koenig et al., 2013). Tree canopy projections over each transect were mapped in October 2019 to estimate covers providing shade to seedlings and protection from early mortality during summer drought (Pulido and Díaz, 2005; Smit et al., 2008).

Climatic Variables

Drought is the main environmental factor limiting seedling recruitment in Mediterranean *Q. ilex* populations (Pulido and Díaz, 2005; Granda et al., 2014). Drought also increases seed losses by increasing the likelihood of acorn abortion during ripening, as well as the proportion of not aborted seeds that are subsequently attacked by predispersal seed predators (Espelta et al., 2008). We used the SPEI drought index (Standardized Precipitation Evapotranspiration Index) to estimate drought conditions (Vicente-Serrano et al., 2010). High SPEI values indicate wet conditions and low values, drought. We computed SPEI indices for both whole calendar years (January to December) and summer (July to September) periods only from the online-available SPEI dataset[1] (Vicente-Serrano et al., 2010). Values for the 1° × 1 ° grid cell corresponding to the site coordinates were downloaded directly. We also estimated monthly rainfall and temperature records for the populations provided with seed traps. For this, we used records of the closest weather station available (Toledo, 61 km northeast from Cabañeros[2], corrected using regression models built with data from an automatic station sited in the study area between December 2005 and December 2007 (Díaz et al., 2011). Target covariates were mean year temperature and overall rainfall, mean spring (April to May) temperature and rainfall, and summer rainfall.

Data Analyses

Temporal trends in climatic variables were analyzed performing linear regressions with year as the independent variable. The effects of climate, habitat type (forest vs. dehesa) and tree isolation on reproductive effort and on the proportion of propagules surviving each predispersive stage of the regeneration cycle (pollination, abortion, and predispersal seed predation) were analyzed by fitting generalized mixed models (GLMMs) with individual trees nested in year as the random factor. This random effects structure controls for year and tree effects other than those derived from effects of the fixed factors. We used a Poisson distribution with log link function in the case of reproductive effort (number of propagules produced) and a binomial distribution with logit link function (Zar, 2013) for pre-dispersal rates (proportion of flowers pollinated, acorns aborted and infested). Fixed effects were habitat type, tree isolation, a climatic variable, and their double and triple interactions. For each climatic variable—SPEI (annual and summer), temperature (annual and spring), and rainfall (annual, spring, and summer) we built a model. Models were compared and selected by using the Akaike Information Criterion (AIC; Burnham and Anderson, 2004). The alternative procedure of fitting a single model with all climate variables then testing their relative effects was precluded by the high multicolineality of climate variables. Continuous factors were standardized (Mean = 0, $SD = 1$) previous to data analyses to allow direct comparison of effect sizes and to make main effects biologically interpretable even when involved in interactions (Schielzeth, 2010). Effect sizes were computed as Pearson's product–moment correlation coefficients from t values (Lipsey and Wilson, 2001) and judged small ($r < 0.10$), intermediate ($r = 0.11$–0.49) or large ($r > 0.50$) following Cohen (1988).

Seedling emergence was modeled at the scale of individual transects performing GLMMs with transect identity as the random factor. Negative binomial distribution of errors was used since Poisson distributions produced overdispersion (Sánchez-Mejía and Díaz, under review). Fixed effects were the acorn production index of the reference tree (semiquantative index, 0–4), density of conspecific seedlings (No./m^2), tree cover (proportion), the SPEIs (annual and summer), and two- and three-way interactions between climate and vegetation variables.

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[1] https://spei.csic.es/map/

[2] https://opendata.aemet.es/centrodedescargas/productosAEMET

Density and climate data were included in the model in t + 1 since the emergence of a given cohort occurs the year after the crop production. Covariates were standardized before analyses and effect sizes were computed as above. Statistical analyses were conducted in R using the package "glmmTMB" (Brooks et al., 2017).

RESULTS

Climatic Trends

Climate became drier in summer from 2001 to 2018 in the study area ($r_{18} = 0.344$ and $r_{18} = 0.516$ for annual and summer drought, $p = 0.162$ and $p = 0.028$, respectively). Increased drought levels were mostly due to warming ($r_{18} = 0.430$, $p = 0.037$), with no additional significant trends in overall rainfall ($r_{18} = 0.049$, $p = 0.847$). On average, temperatures increased 0.88 ± 0.47°C and drought indices increased (i.e., SPEI decreased) 10.0% and 16.9% (annual and summer; **Supplementary Figure 2**).

Climatic and Isolation Effects on Reproductive Effort and Predispersal Propagule Losses

Data on reproductive effort and predispersal propagule losses were gathered for 145 trees, 103 in dehesa, and 42 in nearby forest sites to uncover the larger local variation of tree spatial arrangements in dehesas. Tree isolation (measured as the proportion of area around trees without cover) was 88.7 ± 0.9% (SE; range 63.2–99.5%). Mean isolation was larger in open woodland (**Supplementary Figure 1**), but ranges overlapped widely due to deliberate selection of trees within heterogeneous landscape configurations (**Supplementary Figure 3**). Sample sizes (years with data) for reproductive effort, pollination failure, abortion rates and predispersal losses of marked trees were 12.8 ± 0.3, 12.5 ± 0.3, 12.2 ± 0.3, and 11.8 ± 0.3 years/tree, respectively. Mean reproductive effort varied between less than 10 and over 250 propagules/m^2 along the study period, with wide among-years variation in both effort and predispersal seed losses both among and within trees (**Figure 2**).

The lowest AIC values in models testing for tree isolation x climate interactions were obtained when considering year-round drought (abortion rates and predispersal seed predation), summer drought (reproductive effort) or mean year-round temperature (pollination failure; **Table 1**). Other models had AIC values more than two units larger (ΔAIC > 2) so that they were less parsimonious (Burnham and Anderson, 2004). Decreasing SPEI, which indicates increasing drought intensity, was associated to decreasing reproductive effort and increasing abortion and predispersal seed predation rates. Increasing spring temperature resulted in lower pollination failure rate (**Table 1**). Effect sizes for climatic effects were small to intermediate. Habitat type had an intermediate effect on reproductive effort, which was 1.17 times larger in dehesa than in forest. Tree isolation had no further significant effects, but a small marginal negative

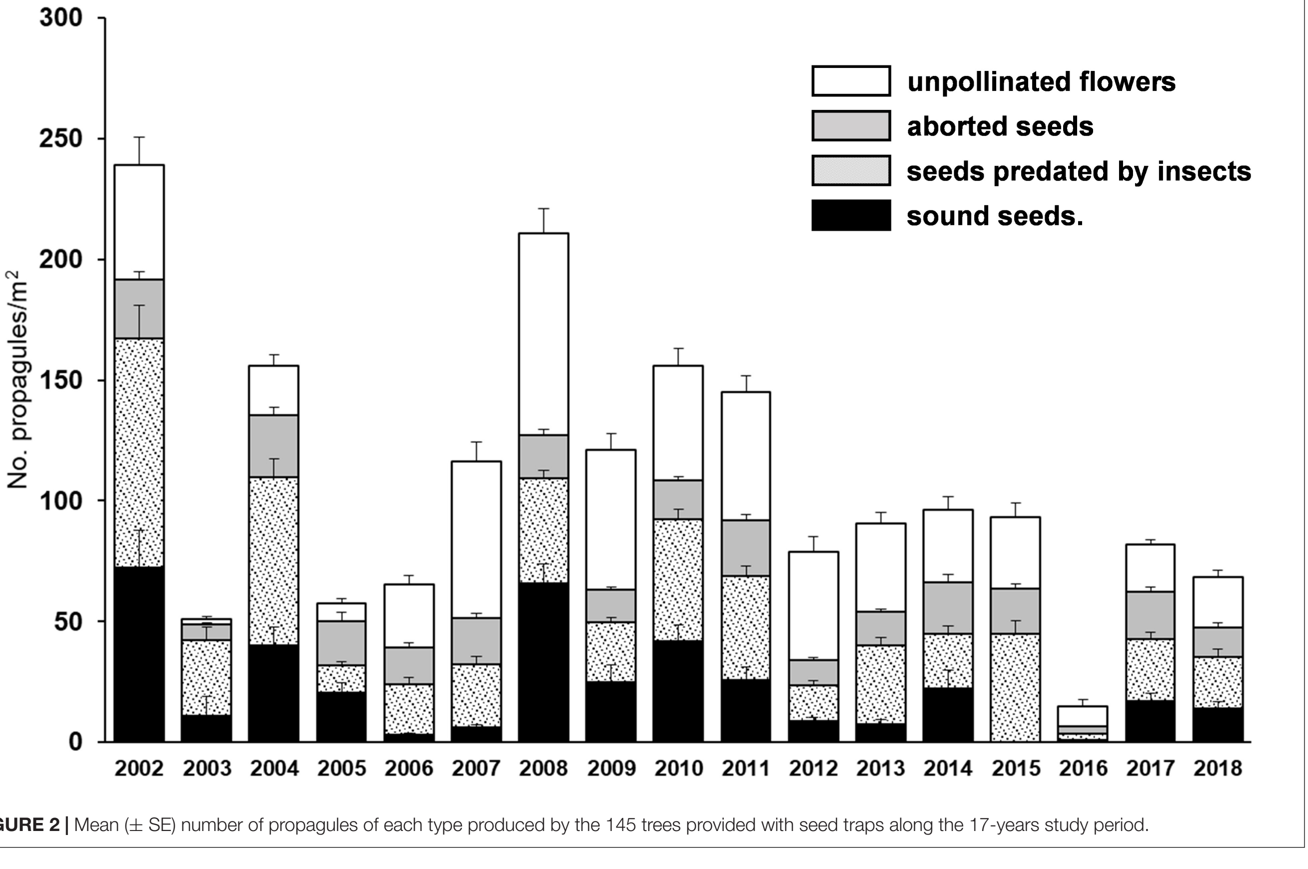

FIGURE 2 | Mean (± SE) number of propagules of each type produced by the 145 trees provided with seed traps along the 17-years study period.

TABLE 1 | Lowest-AIC GLMM models testing for effects of climate variables on the predispersal stages of Holm oak regeneration process.

	Effect	*B*	SE (B)	*t*	*p*	Effect size	(r)
REPRODUCTIVE EFFORT	**Habitat**	**1.17**	**0.13**	**9.182**	**<<0.001**	**0.209**	**(i)**
	Tree isolation	0.01	0.10	0.069	0.945	0.002	
	Summer SPEI	**0.16**	**0.06**	**2.851**	**0.004**	**0.066**	**(s)**
	Isolation × Habitat = dehesa	0.15	0.12	1.21	0.226	0.028	
	Isolation × SPEI	−0.02	0.05	−0.38	0.702	0.009	
	Habitat = dehesa × SPEI	**0.18**	**0.07**	**2.72**	**0.006**	**0.063**	**(s)**
	Isolation × Habitat = dehesa × SPEI	−0.02	0.07	−0.28	0.776	0.007	
	AIC = 20402.3						
POLLINATION FAILURE	Habitat	−0.03	0.12	−0.28	0.780	0.007	
	Tree isolation	0.08	0.10	0.81	0.417	0.019	
	Spring temperature	**−0.22**	**0.05**	**−4.56**	**<<0.001**	**0.107**	**(i)**
	Isolation × Habitat = dehesa	−0.15	0.12	−1.24	0.216	0.029	
	Isolation × temperature	**−0.19**	**0.04**	**−4.26**	**<<0.001**	**0.100**	**(i)**
	Habitat = dehesa × temperature	**0.17**	**0.06**	**2.96**	**0.003**	**0.070**	**(s)**
	Isolation × Habitat = dehesa × temperature	**0.19**	**0.05**	**3.66**	**<0.001**	**0.086**	**(s)**
	AIC = 13116.4						
ABORTION RATE	Habitat	−0.13	0.09	−1.53	0.127	0.036	
	Tree isolation	*−0.13*	*0.07*	*−1.87*	*0.061*	*0.045*	**(s)**
	Year-round SPEI	**−0.14**	**0.04**	**−4.01**	**<<0.001**	**0.095**	**(s)**
	Isolation × Habitat = dehesa	0.07	0.08	0.86	0.390	0.021	
	Isolation × SPEI	−0.02	0.03	−0.46	0.646	0.011	
	Habitat = dehesa× SPEI	*−0.08*	*0.04*	*−1.92*	*0.054*	*0.046*	**(s)**
	Isolation × Habitat = dehesa × SPEI	*0.07*	*0.04*	*1.84*	*0.066*	*0.044*	**(s)**
	AIC = 10443.1						
PREDISP. PREDATION	Habitat	−0.02	0.06	−0.42	0.674	0.010	
	Tree isolation	0.00	0.04	−0.06	0.954	0.001	
	Year-round SPEI	**−0.09**	**0.03**	**−2.91**	**0.004**	**0.066**	**(s)**
	Isolation × Habitat = dehesa	−0.03	0.05	−0.52	0.603	0.012	
	Isolation × SPEI	0.01	0.03	0.53	0.594	0.012	
	Habitat = dehesa × SPEI	0.03	0.03	0.86	0.387	0.020	
	Isolation × Habitat = dehesa × SPEI	0.01	0.03	0.43	0.665	0.010	
	AIC = 10139.7						

Both main effects of climate and its interactions with habitat (dehesa open woodland vs. closed forest) and tree isolation were tested. Effect sizes were computed from t test values following Lipsey and Wilson (2001) (s, small effect; i, intermediate effect, after Cohen, 1988). SPEI, standardized precipitation evapotranspiration index, that decreases as drought intensity increases (Vicente-Serrano et al., 2010). Boldface indicates significant results.

effect on abortion rates that tended to interact, also marginally, with habitat and SPEI effects (**Table 1**). Finally, isolation and/or habitat modulated climate effects on reproductive effort and pollination failure, but had no main or interactive effects on abortion or predispersal predation. Tree isolation decreased temperature effects on pollination failure, especially in open dehesa woodland, with intermediate and small effect sizes, respectively. Positive SPEI effects on reproductive effort (hence negative effects of increasing drought) were stronger in dehesas (positive interaction), with small effect sizes, meaning that negative effects of drought on effort were attenuated in open woodland (**Table 1**).

Climatic and Vegetation Effects on Early Seedling Recruitment

We censused 1222 seedlings from 2001 to 2018 in 2850 transect × year combinations. First-year mean seedling densities varied widely between almost zero to more than 500 seedlings/ha (**Figure 3**). After accounting for the significant small effect of local acorn crops on seedling emergence in the following year, early seedling recruitment was positively associated to sites with higher densities of seedlings surviving from previous years and with years with higher SPEI, i.e., with milder drought conditions year-round (**Table 2**; the model including summer drought had higher AIC values). Tree cover had no significant main effects, although higher tree covers reduced the positive effects of local density of surviving seedlings on early recruitment (**Table 2**). Effect sizes were small except for conspecific seedling densities, that had intermediate effects.

DISCUSSION

Holm oak reproductive effort, predispersal seed losses, and early seedling recruitment were sensitive to climate change. Small

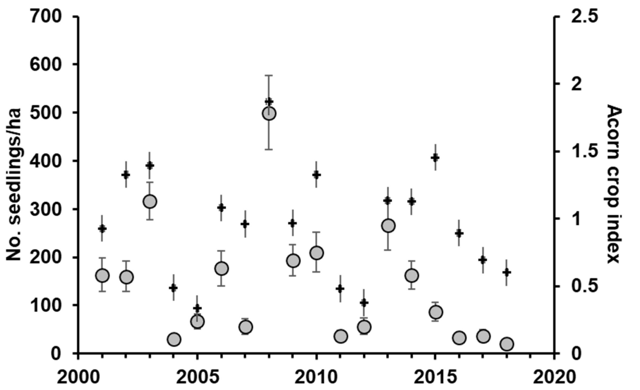

FIGURE 3 | Mean (± SE) seedling densities along the 18-years study period (gray circles). Data on mean (± SE) acorn crops are also shown (crosses).

(c.a. 10%) increases in drought severity during the last 18 years were related to reduced reproductive effort, enhanced abortion rates and predispersal seed predation by specialist insects, and a lower early seedling recruitment (Espelta et al., 2008; Sánchez-Humanes and Espelta, 2011; Fernández-Martínez et al., 2012; Pulido et al., 2014; Pérez-Ramos et al., 2015; Morán-López et al., 2016a; see Monks et al., 2016 for a theoretical review). Higher pollination rates associated to warmer springs (Fernández-Martínez et al., 2012) did not compensate for negative effects of warming as acorn crops were reduced. Overall, climate change expectations for the Mediterranean basin (more intense drought events; IPCC, 2018) will decrease reproductive output, acorn crops and early seedling recruitment, thus exacerbating negative effects of these climatic trends on the survival of adult trees (Ogaya et al., 2019).

Reproductive Effort and Predispersal Propagule Losses

Contrary to our expectations, tree isolation effects were generally weak and less important than those of climate, except for intermediate positive effects of dehesa opening on the reproductive effort of trees. This is not surprising since dehesa formation from oak forests seeks for increased acorn production, as tree thinning and removal of understorey shrubs decrease plant-to- plant competition for water resources (Pulido and Díaz, 2005; Pulido et al., 2010; Díaz, 2014). Such water stress alleviation can prevent oaks from functioning close to their point of stomatal closure at dawn during summer months, which implies photochemical inhibition and low availability of carbohydrates for acorn production, thus reducing abortion rates and enhancing overall acorn production (Forner-Sales et al., 2020). Even though we expected reduced pre-dispersal predation in isolated trees due to the limited dispersal capabilities of the predispersal acorn predators of holm oaks (mostly chestnut weevils *Curculio elephas*; Debouzie et al., 1996; Bonal et al., 2007; Díaz et al., 2011; Tong et al., 2017), predation rates were independent of the spatial configuration of trees. Weevils may arrive at lower rates to isolated trees but stay sedentary after arrival, increasing seed predation and mitigating the effects of reduced migration rates (Bonal et al., 2012). In addition, drought-induced changes in acorn production may have led to different levels of predator satiation in trees (Bonal et al., 2007), outweighing the potential effects of tree isolation (Díaz, 2014) on predation rates by specialist insects. Alternatively, isolation effects may have been found weak because the spatial scale of measurement may have been too small for detecting them (e.g., Bonal et al., 2012 for weevil infestation; see below for scales of pollination effects). The chosen scale was fixed according to typical rages of variation of tree distribution in dehesas (**Supplementary Figure 1**), and was proven useful in previous work (Díaz, 2014).

Proposed interactive effects of isolation and climate were generally weak, except for the modulation of spring temperature effects on pollination success by isolation and habitat. Increased temperatures represent a double-edged sword for pollination, warmer and drier conditions can increase the amount of airborne pollen (Fernández-Martínez et al., 2012), but if drought stress is too intense pollen production by trees can be disrupted (Bykova et al., 2018). Positive effects of warming on pollination were stronger in dehesa woodlands, probably due to enhanced water status of trees in low density stands where shrub cover is also much lower than in forests (Moreno and Cubera, 2008). In addition to habitat-type effects, isolated trees were less responsive to warmer springs. Despite that long-distance pollen dispersal is frequent in holm oak stands (Ortego et al., 2014), most pollen is deposited locally (< 100 m; Morán-López et al., 2016b). Isolated trees may have received decreased pollen loads (Morán-López et al., 2016b) or lower quality pollen coming from related neighboring individual trees (Ortego et al., 2014) resulting in lower fertilization success (García-Mozo et al., 2007), and hence, attenuating the positive effects of spring temperature on fertilization. In the rest of the stages, when significant effects were found, their magnitudes were generally small. Therefore, our results suggest that management options to ameliorate negative effects of climate change on reproductive output and predispersal seed losses would be limited as compared to options to reduce negative effects on adult trees (Ogaya et al., 2019).

Seedling Recruitment

Higher acorn crops resulted in higher local early recruitment of oak seedlings, as expected from the masting strategy of most oaks (Pearse et al., 2016). Effect sizes of acorn crops were, however, small, as compared with the positive effect of the local abundance of older seedlings. Since local acorn crops were estimated form crops of the tree heading each transect only, low effect sizes may have been due to underestimates of the seed rain coming from other neighboring trees. Alternatively, unmeasured traits of transects different from direct local seed rain may have favored recruitment, so that it was concentrated in the same microsites year after year. Holm oak recruitment would thus be site- rather than seed-limited (Eriksson and Ehrlén, 1992). This conclusion would concur with the generally accepted idea that intense summer drought in the Mediterranean region is the main limiting factor for recruitment (Gómez-Aparicio et al., 2005),

TABLE 2 | Lowest-AIC GLMM models testing for effects of local density of seedlings surviving from previous years, tree cover, and drought on fist-year Holm oak seedling recruitment after accounting for effects of previous-year acorn crops.

	Effect	B	SE (B)	*t*	*p*	Effect size (r)	
EARLY SEEDLING RECRUITMENT	**Acorn crop**	**0.22**	**0.05**	**4.68**	**$\ll$0.001**	**0.090**	**(s)**
	Density of surviving seedlings	**1.67**	**0.09**	**18.17**	**$\ll$0.001**	**0.331**	**(i)**
	Tree cover	0.09	0.07	1.40	0.162	0.027	
	Year-round SPEI	**0.19**	**0.06**	**3.41**	**0.001**	**0.066**	**(s)**
	Seedlings × tree cover	**−0.28**	**0.09**	**−3.10**	**0.002**	**0.060**	**(s)**
	Seedlings × SPEI	−0.08	0.08	−1.00	0.315	0.019	
	Tree cover × SPEI	0.01	0.06	0.18	0.859	0.003	
	AIC = 2834.2						

Both main effects of climate and its interactions with seedling density and tree cover were tested. Effect sizes were computed from t test values following Lipsey and Wilson (2001) (s, small effect; i, intermediate effect, after Cohen, 1988). SPEI, standardized precipitation evapotranspiration index, that decreases as drought intensity increases (Vicente-Serrano et al., 2010). Boldface indicates significant results.

which tends to be concentrated in microsites where water stress is mitigated (i.e., under canopy cover, Gómez-Aparicio et al., 2005; Pugnaire et al., 2011; Granda et al., 2014).

Close dependence on facilitation by shrub understoreys for early recruitment has been repeatedly demonstrated in Mediterranean oaks growing in open woodland (Ramírez and Díaz, 2008; Gómez-Aparicio, 2009), as shading and improved soil conditions under shrub canopies enhances seedling survival to the first summer drought (Smit et al., 2008, 2009). Local tree cover in the study area had no significant effect on early recruitment, indicating that neither shading nor seed rain coming from nearby trees were the factors defining safe microsites. In fact, tree cover weakened the positive associations between early recruitment and density of seedlings from earlier cohorts, suggesting higher intraspecific competition under tree canopies, at least in closed forests. In accordance, conspecific tree canopies have been shown to limit holm oak recruitment in Mediterranean forests (Granda et al., 2014). Drought conditions decreased early recruitment, as expected from the sensitivity of holm oak seedlings to drought during its first year of life (Gómez-Aparicio et al., 2008), but local microsite conditions did not ameliorate the increased drought effects, as shown by the lack of interactive effects of older seedlings or tree cover with SPEI. Therefore, microsite effects on recruitment would not be based on protective shading against drought, and forest clearing would not be a promising management option to ameliorate negative effects of climate change on early seedling recruitment of Holm oaks. Alternative microsite effects on recruitment such as protection against herbivory or attraction of seed dispersers would be worth of further study (Smit et al., 2008, 2009; Morán-López et al., 2015, 2016c).

Forest clearing has been shown to collapse the regeneration cycle of Holm oaks because of the strong negative effects of clearing on acorn dispersal effectiveness (Pulido and Díaz, 2005; Pulido et al., 2010). Such negative impacts are mostly due to changes in the foraging behavior of dispersers under opened, risky conditions (Morán-López et al., 2015, 2016c), rather than to low disperser's populations (McConkey and O'Farrill, 2016). Current research effort on the effects of climate change on animals is focused on changes in abundance and distribution, with little effort on effects of climate on behavior and interspecific interactions (Díaz et al., under review and references therein). It is thus unknown whether climate change may decrease (or increase) negative effects of forest clearing on the behavior of seed dispersers (Valladares et al., 2014; Morán-López et al., 2015, 2016c).

Managing Conflicting Effects of Isolation and Climate During the Regeneration Cycle

Most stages of the reproductive cycle of Holm oaks were negatively affected by drought. Positive effects of higher spring temperature on pollination rate did not seem to compensate for the remaining negative effects. In addition, alleviation of plant-plant competition though forest clearing seemed to have little scope to attenuate the negative impacts of drought, as shown by weak or no interactive effects of climate and tree cover or isolation. Management options aimed at decreasing adult tree mortality under climate change scenarios (Ruiz-Benito et al., 2013; Astigarraga et al., 2020) would then have little or no effects on tree recruitment.

Conflicting effects of management options for the maintenance of the economic and ecological sustainability of Mediterranean oak forests and dehesas have been analyzed previously (Díaz et al., 2013). Open configurations increase the economic and conservation values of oak woodlands, but, paradoxically, compromise their ecological sustainability because openness collapses tree regeneration (Campos et al., 2013). Our results agree with the solution proposed to solve the economic/ecological sustainability of dehesas by means of management practices designed at landscape scales, including open and closed areas that will rotate over long (decadal) periods. This will ensure both tree recruitment (in closed areas) and economic and conservation values (in open areas; Díaz et al., 2003, 2013; Morán-López et al., 2016c). Such landscape-scale designs can be covered by several tools of the current and reformed Common Agricultural Policy, namely the former greening and the coming Eco-scheme tools (Pe'er et al., 2020). In this way, climate and land use change effects on the life cycle of the keystone trees of agroforestry systems can be solved and integrated into effective systems of adaptive management (Díaz and Concepción, 2016).

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors upon request.

AUTHOR CONTRIBUTIONS

MD conceived the idea of the study and led the long-term monitoring experiment. TS-M and TM-L have made a substantial, direct and intellectual contribution to the work, and approved it for publication. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.640143/full#supplementary-material

Supplementary Figure 1 | Maps of the study areas for long-term monitoring of predispersal seed losses (lower) and seedling recruitment (upper-right) and its location in the National Park of Cabañeros (mid-left). Dark gray: holm oak forests; white: open holm oak woodland; black: pine plantations. Dots indicate the ca. 300 holm oak trees monitored from 2001 onwards. Aerial photographs (150 × 150 m) show examples of the spatial configuration of oak trees (after Díaz et al., 2011; Díaz, 2014; Sánchez-Mejía and Díaz, under review).

Supplementary Figure 2 | Drought trends along the study period. Closed circles, continuous line: summer drought; open circles, dashed line: annual drought. Lines are regression lines (SPEI = 218.8 - 0.11·YEAR and SPEI = 124.5 - 0.06·YEAR, respectively). SPEI drought indices (Standardized Precipitation Evapotranspiration Index; Vicente-Serrano et al., 2010) estimated drought conditions. High SPEI values indicate wet conditions and low values, drought. See texts for details.

Supplementary Figure 3 | Isolation (percent area in 50-m circles centered in focal trees not covered by the canopies of other trees) of the 145 trees provided with seed traps according to habitat type. Dots: individual trees; small square: median; box: interquartile range.

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Ant Communities Resist Even in Small and Isolated Gypsum Habitat Remnants in a Mediterranean Agroecosystem

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Natural and seminatural habitat remnants play a crucial ecological role in intensified agroecosystems. Assumptions on the conservation value of small and poorly connected fragments in a hostile matrix come from generalization obtained from a limited number of taxa, mostly plants, and vertebrates. To date, few studies have analyzed the effect of fragmentation on ant communities in Mediterranean agroecosystems, despite the importance of this group of animals on several key ecosystem functions and services. Here, we analyze the effects of fragment area and connectivity on ant communities in gypsum outcrops in a large cereal agroecosystem of Central Spain. Ant communities were described by their species composition, abundance (total number of occurrences), and number of species, standardized both by area (species density), and abundance (species richness). Observed number of species was relatively high in comparison with other studies in the Mediterranean, and we found no effects of fragment characteristics on species density, species richness and species composition, which implies that even small and isolated patches do have a value for ant conservation. Moreover, total number of occurrences were higher for smaller and more isolated fragments. This finding contrasts with the results reported for other taxa in similar gypsum habitats and suggests that certain ant traits and strategies make them particularly resistant to fragmentation and capable to take advantage of small habitat patches. Given the important ecological role played by ants, we recommend the preservation of these small habitat fragments in the management plans of agroecosystems in these drylands, especially in those cases in which intensification of agricultural practices greatly diminish natural habitat availability.

Keywords: agroecosystems, ants, biodiversity conservation, drylands, fragmentation, gypsum habitats

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INTRODUCTION

There is consensus on the necessity of maintaining a certain amount of remnants of natural or semi-natural habitats in extensive agroecosystems, which act as reservoirs of biodiversity and provide key ecosystem services (Altieri, 1999; Tscharntke et al., 2008; Kennedy et al., 2013). It is not clear, however, to what extent small, isolated fragments can fulfill these functions. According to the most classical view of fragmentation, there is a threshold in which remnants are too small and isolated from each other, inducing population declines, increasing extinction risk, and exacerbating species loss (Andrén, 1994; Ewers and Didham, 2006). Fragmentation is therefore considered by many authors one of the most pervasive drivers of biodiversity loss (Fletcher et al., 2018). Some of the mechanisms proposed to explain these negative processes are related to the higher vulnerability to environmental and demographic stochasticity for small and poorly connected populations, or the reduction in colonization and rescue events, under a metapopulation perspective, which can become too infrequent to overcome local extinctions (Andrén, 1994; Ewers and Didham, 2006). These negative effects would emerge as a function of the specific characteristics of the landscapes, the habitat configuration and the biological groups involved (Villard and Metzger, 2014). Thus, for example, megafauna requires large patches to maintain viable populations, while in the case of invertebrates very small patches could be enough to host viable populations (Ewers and Didham, 2006).

Recently, however, it has been questioned whether fragmentation necessarily means a real loss of species. Fahrig (2003, 2017) considers that we should only attribute to the so-called fragmentation *per se*, those effects on populations and communities independent of the effects of habitat amount and, definitively, resource availability. The controversy is significant for conservation, since the lower conservation value assigned to small patches have derived in the protection of few large rather than many small fragments ("single large vs. several small," or SLOSS debate; Fahrig et al., 2019). Much of the controversy has to do with the difficulties of distinguishing between the effects expected by simple species—area relationships or sampling effects, and those produced by mechanisms of another nature (Gotelli and Colwell, 2001; Whittaker et al., 2001). To face these confounding effects, Whittaker et al. (2001) propose to fix by design the sampling area, and recommend the use of species density to make comparisons, while (Gotelli and Colwell, 2001, 2011) propose the use of rarefaction curves to standardize datasets to a common number of samples, individuals or occurrences to assess species richness. Both species density and species richness are worth to be explicitly considered in this context, since while species density is of interest for conservation purposes, species richness is appropriated for testing models and theoretical predictions, and along with species abundance, is critical for determining species density (Gotelli and Colwell, 2001).

Agriculture intensification and maintenance of large and homogeneous agricultural fields has induced a critical and massive destruction of habitat and biodiversity loss (Emmerson et al., 2016). In this context, the value in conservation terms, but also as providers of ecosystem services of habitat remnants, is critical (Haddad et al., 2015). Although it exists a wide consensus that agroecosystems should maintain and extend the number and extension of natural and seminatural habitats fragments for maximizing the services provided, there is no information of the role these fragments have for many biological groups.

Despite their enormous biomass and importance in the functioning of terrestrial ecosystems (Folgarait, 1998; Del Toro et al., 2012), ants as a group have been rarely studied in relation to fragmentation. This is significant since ground dwelling ants, as invertebrates living in sessile colonies, probably respond to fine-scale effects better than larger or more mobile organisms. To our knowledge, however, there are no published studies specifically aimed to evaluate the effect of fragmentation on ants in Mediterranean agroecosystems, despite the ecological importance of ants in Mediterranean regions (Baraibar et al., 2009; Silvestre et al., 2019) where they provide important ecosystem services (Comas et al., 2016; Baraibar et al., 2017). Most of the existing studies on fragmentation and ants have been conducted in tropical regions (Armbrecht et al., 2001; Assis et al., 2018; Santos et al., 2018), forests (Melliger et al., 2018), or grasslands (Golden and Crist, 2000; Brascheler and Baur, 2003; Dauber et al., 2006). Few generalizations can be obtained from them, since apart from their variability in the target ecosystem, they also differ greatly in the spatial scale, ranging from < 1 m (Brascheler and Baur, 2003) to several thousand square meters (Melliger et al., 2018).

Here, we aim to evaluate the effects of patch size and connectivity on ant biodiversity in an extensive cereal agroecosystem in the drylands of Central Spain. We assume that larger patches have a higher total number of species because of a simple random sampling effect, therefore this variable will not be measured in this study. Instead, we fix sampling area in each patch, and focus on species density, species richness and total abundance. If small or isolated patches add negative effects for ant populations other than simple random sampling effects, then we expect to find lower values of species density, richness and abundance. Conversely, if low and isolated patches are not affected by negative affects additional to random sampling effects, ant species richness, abundance and density should be similar to larger and better connected patches.

Our approach will provide additional conservation criteria for these valuable ecosystems, contributing to preserve their diversity and therefore their functionality and ecosystem services.

MATERIALS AND METHODS

Study Area

The study area is in central Spain, near the locality of Belinchón (Cuenca, Spain), at an altitude of ∼700 a.s.l (**Figure 1**). The climate is continental Mediterranean, with an average annual temperature of ca 14°C, rainfall of ca 500 mm per year, severe summer drought and cold winters. The lithology of the area is mostly composed of tertiary evaporites, and the relief is gentle, with alternating hills and plains. Soils are gypseous (i.e. soils which main component is gypsum; Herrero and Porta, 2000), which imposes harsh conditions for the development of vegetation (Escudero et al., 2015). In spite of this, and especially from the mid-20th century (Matesanz et al., 2009), the expansion of rain-fed agriculture has progressively fragmented the landscape, which now consists of a mosaic of natural vegetation remnants interspersed in a matrix of dry herbaceous croplands, mostly cereal (**Figure 1**). Natural vegetation in these remnants is composed by dwarf shrublands dominated by creeping and cushion-like specialized gypsophytes

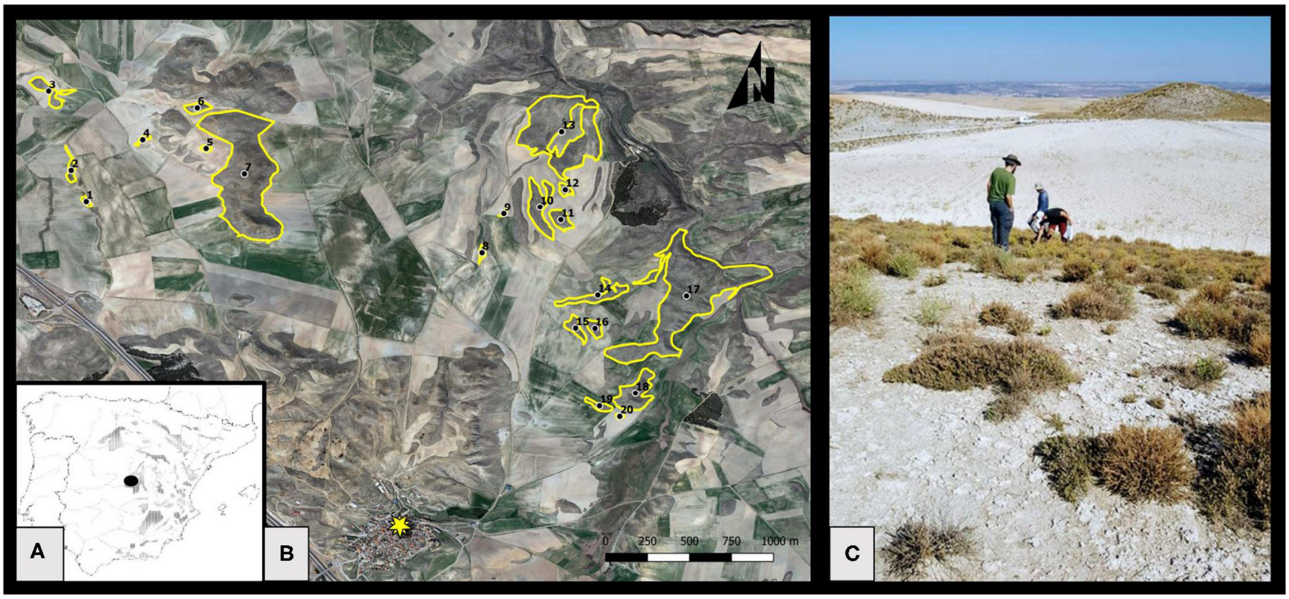

FIGURE 1 | (A) Map showing the distribution of gypsum outcrops of the Iberian Peninsula, re-drawn from Escavy et al. (2012), and the study area location (black dot). **(B)** Studied habitat remnants. The black dots indicate the centroid of each remnant, and the yellow star indicates the village of Belinchón. Note that the area includes other habitat remnants that were not sampled. However, all remnants were considered for the calculation of the connectivity index of the sampled ones. **(C)** General view of the study area showing a habitat remnant on the forefront with typical gypsum shrubby vegetation, another habitat remnant in the background, and a fallow field in the middle.

(e.g., *Helianthemum squamatum* (L.) Dum.-Cours., *Lepidium subulatum* L., *Centaurea hyssopifolia* Vahl., *Gypsophila struthium* L) and the tussock-forming grass *Stipa tenacissima* L. Perennials cover is around 30% and alternates with clearings partially covered by a biological soil crust, dominated by crustose lichens and fairly diverse annual plant communities (Luzuriaga et al., 2018).

Data Collection

Twenty natural habitat remnants were selected, separated from each other by a continuous cropland matrix (**Figure 1**, **Table 1**) and including a representative sample of existent range of size and connectivity in the study area. Fragment characteristics (area, connectivity) were measured on orthophotos from 2018, using the software QGIS 3.2.1. Bonn (QGIS.org, 2018). Fragment area ranged from 1,065 to 290,828 m^2, and was log-transformed for all the analysis, given the strong skewness of its distribution. Log (area) ranged from 3.03 to 5.46 (mean = 4.07, s.d. = 0.72).

Connectivity was estimated using the index C proposed by Tremlová and Münzbergová (2007), which accounts for the number of surrounding fragments, considering their area weighted by their distance to the target fragment. Because of the highly dispersed values obtained, we log$_{10}$ transformed the index, following a modification by Matesanz et al. (2015). The modified index can adopt negative values for lowly connected remnants, and is calculated as follows:

$$C_j=\log_{10}\sum_{k=1}^{n}\left(P_k/d_{jk}^2\right),\ j\neq k$$

where C_j is fragment j connectivity, k the fragments surrounding fragment j (in our case, within a radius of 1 km from the center of fragment j), P_k is fragment k area (in square meters), and d_{jk} is the distance between the centroids of fragments j and k (in meters). Connectivity index ranged from −0.42 to 0.80 (mean = 0.41, s.d. = 0.35).

Ant sampling was carried out in July 2018. In each habitat remnant a 10 × 15 m plot was located in a homogeneous vegetation area at a distance of 10 m from the cultivated area, so fixing the possible edge effect (Golden and Crist, 2000; Brascheler and Baur, 2003). On each plot, we placed 12 pitfall traps of 2.5 cm in diameter and 5 cm deep, forming a grid of 3 × 4 rows, with a separation of 5 m between traps. The traps contained a solution composed of 70% ethanol and 30% ethylene glycol (Azcárate and Peco, 2012; Silvestre et al., 2019). The traps were kept in the field for 7 days, and after their collection, all ant workers were sorted in the laboratory, and identified to the species level.

Data Analysis

We characterized each plot by its species density, species richness and overall abundance, following Gotelli and Colwell (2011). Species density per plot was assimilated to the total number of species captured in the set of 12 pitfall traps. Total number of occurrences was used as an indicator of overall abundance (Longino et al., 2002). Each species present in one trap was counted as one occurrence, regardless the number of workers captured in the trap, and total number of occurrences was calculated as the sum of the occurrences of all the species present in one plot. We preferred the total number of occurrences instead

TABLE 1 | Fragment characteristics and ant community metrics obtained for the 20 sampling units considered in this study.

	Area (m^2)	Connectivity	W	O	S	S_{44}	ICE	S/ICE
F1	2466.70	−0.11	476	92	14	13.24	14	99.9%
F2	6700.50	−0.42	642	96	13	12.01	13.47	96.5%
F3	18403.37	−0.25	221	59	13	11.61	23.99	54.2%
F4	2682.67	0.40	600	60	11	10.65	11.54	95.3%
F5	2395.05	0.77	340	52	9	8.75	12.54	71.8%
F6	9299.88	0.79	329	51	10	9.92	10.33	96.8%
F7	279539.94	−0.02	391	55	10	9.82	10.45	95.7%
F8	3097.74	0.38	316	69	11	10.31	12.12	90.8%
F9	1065.62	0.80	254	70	12	11.46	12.53	95.8%
F10	38232.22	0.70	249	70	13	11.91	14.74	88.2%
F11	14106.15	0.71	208	53	11	10.33	16.25	67.7%
F12	5619.14	0.74	228	75	13	11.67	15.25	85.2%
F13	177775.24	0.47	279	65	11	10.7	11.3	97.3%
F14	24792.99	0.45	261	63	12	11.15	14.53	82.6%
F15	11841.91	0.39	258	63	11	10.45	12.15	90.5%
F16	9318.67	0.58	289	66	14	12.47	17.43	80.3%
F17	290828.16	0.35	198	44	9	9	10.18	88.4%
F18	41693.84	0.38	283	65	17	15.15	25.81	65.9%
F19	6920.26	0.48	243	53	10	9.64	11.40	87.7%
F20	1469.28	0.52	464	81	12	11.3	12.53	95.8%
Total			6,529		23			

Area considers the whole remnant surface. Connectivity was estimated using the C index (Tremlová and Münzbergová, 2007) modified by Matesanz et al. (2015). Ant community metrics were measured from 12 pit-fall traps arranged regularly in a 10 × 15 m plot within the remnant. W, Total number of workers; O, Total number of occurrences; S, Species density; S_{44}, Species richness estimated for 44 occurrences; ICE, Incidence-based coverage estimator.

TABLE 2 | Ant species identified in this study, with information on their subfamily, and general data on the frequency & abundance observed in this study.

	Subfamily	Plots (0–20)	Traps (0–240)	N° workers
Aphaenogaster iberica Emery. 1908	M	7	36	90
Aphaenogaster senilis Mayr. 1853	M	14	123	540
Camponotus foreli Emery. 1881	F	19	114	246
Cataglyphis iberica (Emery. 1906)	F	20	206	955
Crematogaster auberti Emery. 1869	M	18	142	1,117
Goniomma blanci (André. 1881)	M	5	5	6
Goniomma hispanicum (André. 1883)	M	1	3	6
Messor barbarus (Linnaeus. 1767)	M	18	93	429
Messor bouvieri Bondroit. 1918	M	16	69	212
Messor capitatus (Latreille. 1798)	M	4	10	18
Oxyopomyrmex saulcyi Emery. 1889	M	4	6	7
Pheidole pallidula (Nylander. 1849)	M	9	56	1,024
Plagiolepis pygmaea (Latreille. 1798)	F	8	12	24
Plagiolepis schmitzii Forel. 1895	F	15	39	116
Proformica sp1	F	19	123	302
Solenopsis sp1	M	1	1	1
Tapinoma erraticum (Latreille. 1798)	D	1	3	20
Tapinoma gr. *nigerrimum* Nylander. 1856	D	1	11	87
Temnothorax formosus (Santschi. 1909)	M	13	43	96
Temnothorax universitatis (Espadaler. 1997)	M	3	4	10
Tetramorium gr. *caespitum* (Linnaeus. 1758)	M	18	122	697
Tetramorium forte Forel. 1904	M	11	58	399
Tetramorium semilaeve André. 1883	M	11	23	127

Subfamilies: D, Dolichoderinae; F, Formicinae; M, Myrmicinae. Plots, total number of plots in which the species occurred; Traps, total number of traps in which the species occurred, considering the 20 plots; N° of workers, total number of workers collected in the set of 20 plots.

of the total number of individuals, because in ants the number of workers captured by pitfall traps is extremely influenced by slight differences in the distance to foraging trails or nests, which results in a strong spatial clumping of individuals within traps. Anyhow, some analyses were replicated using total number of individuals, obtaining similar results to those reported in this study (**Supplementary Table 1**). Species richness was estimated as the expected number of species for a given number of randomly sampled occurrences. To assess it, we built occurrence-based rarefaction curves (Gotelli and Colwell, 2011), averaging 500 resamples with replacement, and then estimated for each plot the mean species richness expected for the lowest number of occurrences observed in any of the 20 plots. As a complement to these variables, and to check the capacity of our sampling to cover a representative proportion of the assemblage richness, we calculated the incidence-based coverage estimator (ICE), an asymptotic estimator of species richness based on incidence data (Gotelli and Colwell, 2011). Rarefaction analysis and ICE estimation were done using the software EstimateS v. 9.1.0 (Colwell, 2013).

We built generalized linear models for species density, total number of occurrences and species richness, as function of log (area) and connectivity, including their interaction. We used Poisson errors and log link functions for species density and total number of occurrences, and Gaussian errors and identity link function for species richness. This latter variable is non-integer, due to the fact that it is estimated from the rarefaction curves. We identified the best descriptive models using the Akaike information criterion corrected for small samples (AICc). Models were estimated with package MuMIn (Bartoń, 2009) of R 4.0.0.

We performed a PERMANOVA analysis in order to check whether there were differences in species composition related to area, connectivity and/or their interaction. We used frequency data to estimate species composition in each habitat fragment and calculated dissimilarity matrices based on Bray Curtis distance. Significance of the model was tested using a Monte-Carlo test with 9,999 permutations. Finally, we performed non-metric multidimensional scaling (NMDS) to visualize the differences in the species compositions. PERMANOVA and NMDS analyses were performed with the vegan package in R 4.0.0 (Oksanen et al., 2015).

RESULTS

We collected 6,529 ant workers belonging to 23 species, all of them native (**Table 2**). The recorded number of species per plot

TABLE 3 | Parameter estimates and *P*-values for the GLM (Poisson distribution, log link function) built for species density as a function of Log (Area), Connectivity and the interaction Log (Area) x Connectivity.

	Estimate	Std. error	*z*-value	Pr(>|z|)
Intercept	3.025	0.651	4.646	<0.0001
Log (Area)	−0.126	0.158	−0.797	0.425
Connectivity	−1.110	1.387	−0.800	0.424
Log (Area) × Connectivity,	0.252	0.351	0.720	0.472

N = 20 fragments.

TABLE 4 | Akaike Information Criterion corrected for small sample sizes (AICc) assessed for the models estimated for species density, total number of occurrences and species richness (for 44 occurrences) as function of the different combinations of the predictors Log (Area) Connectivity and Log (Area) x Connectivity.

Predictors	Species density	Total number occurrences	Species richness
Log (Area), Connectivity, Log (Area) × Connectivity	101.69	**154.28**	81.88
Log (Area), Connectivity	99.06	**155.44**	80.53
Log (Area)	96.66	164.98	78.95
Connectivity	96.41	166.33	77.91
Null model (no predictors)	**76.30**	172.24	**76.39**

In bold the AICc indicating the most plausible models estimated for the different dependent variables. N = 20 fragments. Models were GLM with Poisson distribution and log link function for Species density and Total number of occurrences, and Gaussian distribution and identity function for Species richness.

TABLE 5 | Parameter estimates and *P*-values for the GLM (Poisson distribution, log link function) built for total number of occurrences as a function of Log (Area), Connectivity and the interaction Log (Area) x Connectivity.

	Estimate	Std. error	*z*-value	Pr(>|z|)
Intercept	5.339	0.278	19.167	<0.0001
Log (Area)	−0.262	0.069	−3.821	0.0001
Connectivity	−1.492	0.595	−2.507	0.0122
Log (Area) × Connectivity	0.312	0.152	2.057	0.0397

(species density) was, on average, 86% of the species richness expected by the ICE estimator (**Table 1**). The ratio between the number of detected and expected species showed no correlation with connectivity (Pearson $r = 0.01$) or with the area of the remnant (Pearson $r = 0.17$), so we can assume no sampling bias associated with the fragmentation condition of the remnants.

Species density ranged from 9 to 17 species per plot (average 11.80, s.d. = 1.94), and did not respond to any of the predictors (**Table 3**). None of the combinations of the predictors produced a plausible model, according to the AICc (**Table 4**).

The total number of occurrences per plot ranged from 44 to 96 (mean = 65.10, s.d. = 13.33), and responded significantly to log (Area) and connectivity both in in the complete model (**Table 5**) and in the model without interaction. AICc was very similar for the two models (**Table 4**). The percentage of explained residual deviance (D^2) was 52.7% for the complete model and 44.1% for the model without interaction. Opposite to our expectations, the effects of both connectivity and Log (Area) were negative (**Figure 2**), suggesting that neither the reduction of fragment size nor the increase in isolation imply a loss of habitat quality for ants. Moreover, the significant interaction suggested that the increase in total number of occurrences observed for small remnants was greater if they were more isolated.

Species richness was estimated for a sample size rarefied down to 44 occurrences (the lowest observed value for any of the plots), using individual-based rarefaction curves (**Figure 3**). Estimated values ranged between 8.75 and 15.15 species (mean = 11.08, s.d. = 1.49). Similarly to species density, rarefied species richness did not respond to any of the considered predictors (**Table 6**), and the null model was the one that showed the smallest AICc (**Table 4**)

The NMDS/PERMANOVA approaches also did not reveal any trend in relation to patch size or connectivity (**Table 7**, **Supplementary Figure 1**).

DISCUSSION

According to the expectations of the classical theory of ecological fragmentation, too small and isolated habitat remnants should undergo an accelerated species loss (Andrén, 1994; Ewers and Didham, 2006). In our case study, however, neither ant species density, nor richness or community composition, responded to fragment size or connectivity. A possible first explanation could be related to the fact that processes causing species loss in habitat remnants (Levins, 1969; Andrén, 1994; Ewers and Didham, 2006) are not necessarily linear, and, even more, they could appear below certain thresholds of size or isolation or combination (Villard and Metzger, 2014). Therefore, the hypothetical negative effects of fragmentation on ant communities would only be detectable in remnants smaller and more isolated than those here considered. Furthermore, the total number of occurrences not only did not decrease but tended to increase in small and less connected patches, making clear that these fragments do not undergo any loss of quality as ant habitats.

These results contrast with those obtained for other organisms in the same region and type of agroecosystem. For example, Matesanz et al. (2009) and Matesanz et al. (2015) observed clear population-level effects for plants, and at the community level, other studies have reported reductions in species density for plants (Luzuriaga et al., 2018) and lichens (Concostrina-Zubiri et al., 2018). Fragmentation in gypsum agroecosystems also seems to negatively affect species richness of pollinator communities, as well as the frequency, diversity and topology of pollination interactions and network metrics (Santamaría et al., 2018). Fragmentation in this type of agroecosystem in drylands also influenced the risk of seed predation, although its effect was not straightforward and it appeared as highly dependent on each plant-animal interaction (Rabasa et al., 2005, 2009; Moncalvillo et al., 2021). Although we do not have studies specifically aimed at analyzing the effects of fragmentation on ants in Mediterranean agroecosystems, it has been observed that the presence of certain keystone structures is sufficient to provide a high number of ant

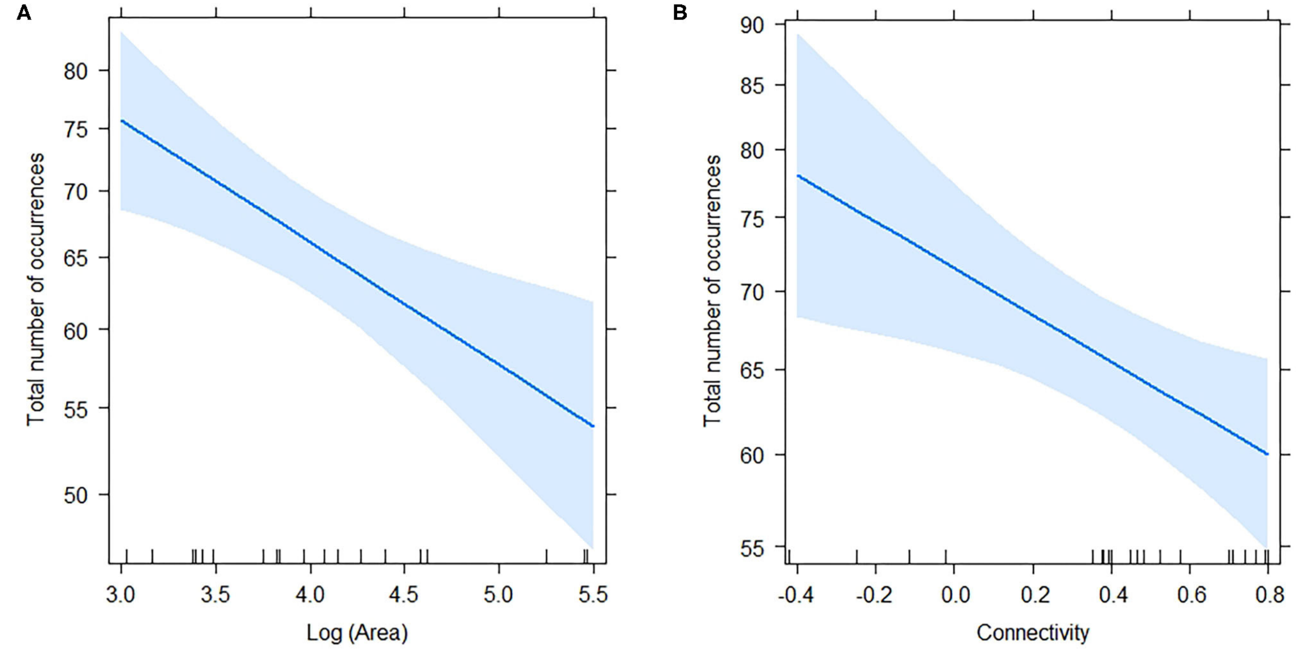

FIGURE 2 | Effects of Log (Area) **(A)** and Connectivity **(B)** on Total number of occurrences estimated by the complete model (including the interaction; see **Table 5**). Shaded regions represent 95% confidence intervals. The model was a GLM with Poisson distribution and log link function.

species (Hevia et al., 2013; e.g., grassland corridors in agricultural landscapes: Azcárate et al., 2013). In other environments, such as forest remains in urban matrices (Melliger et al., 2018) or grassland remnants in forest matrices (Dauber et al., 2006), the capacity of ants to maintain relatively rich communities in small fragments has also been highlighted. Ants, therefore, would show less vulnerability to fragmentation than other groups.

This apparently surprising ability to resist in small, relatively isolated patches may be related to some ant features. Possibly, the eusocial organization provides mechanisms to manage the greater environmental stochasticity of small patches. For example, most ant colonies are long-lived, and can maintain food reserves that buffer fluctuations in resource availability (Davidson, 1977), as well as regulate the size of their colonies, or modify the task allocation of workers depending on conditions (Gordon and Mehdiabadi, 1999). Ants are in general central-place foragers (Harkness and Maroudas, 1985), so their resource-catching strategy is based on the use of a particular territory, not necessarily a large one (Azcárate and Peco, 2003). It is likely, therefore, that the patch size threshold below which negative population effects appear will be lower for ants than for other animal groups such as bees, whose foraging depends on spatial scales that can be very large (Greenleaf et al., 2007). Moreover, most ant species produce winged sexuals, which gives them a dispersal ability that may be enough to minimize isolation between fragments (Dauber et al., 2006). Dispersal ability is often complemented by other effective strategies to deal with habitat patchiness, like poligyny or multiple queening (e.g., *Plagiolepis, Proformica, Solenopsis, Tapinoma*) or flexible modalities of nuptial flights (Bourke and Heinze, 1994). In addition, foraging strategies may be completed in the apparently hostile matrix (especially in the case of granivores) were weeds and crops can provide some valuable resources (Baraibar et al., 2009, 2017). Matrices in fragmented landscapes are not necessarily hostile for all species, and in fact, management of the matrix has often been pointed out as a key factor for the conservation of the biodiversity within fragments (e.g., Armbrecht et al., 2001). Lastly, resistance to habitat loss can be higher for generalist species (Armbrecht et al., 2001; Marvier et al., 2004), and we should not discard that the regional species pool is impoverished since long ago, so that today it is dominated by generalist ants, more tolerant to fragmentation. We think, however, that this explanation is unlikely, given the elevated species densities found in this study (higher than those observed in nearby locations, Flores et al., 2018), and the fact that some of the species recorded in our samplings are not so common in the Iberian context (*Temnothorax formosus, T. universitatis,* and *Goniomma blanci*).

Particularly noteworthy is the unexpected negative effect exerted by fragment area and connectivity on the total number of occurrences per plot, a result that was also observed when repeating the analysis with the total number of workers per plot (**Supplementary Table 1**). Interestingly, this increase in abundance for small and poorly connected patches was not linked to any change in species composition, suggesting a general effect favoring ants as a group. One possible explanation could be that these remnants have a higher edge effect, which may have more positive than negative consequences on ants (e.g., possibility of foraging in matrix habitats, higher productivity of edges especially in agroecosystems where farmlands are fertilized, etc.; Braschler and Baur, 2003; Fahrig, 2017; Fahrig et al., 2019).

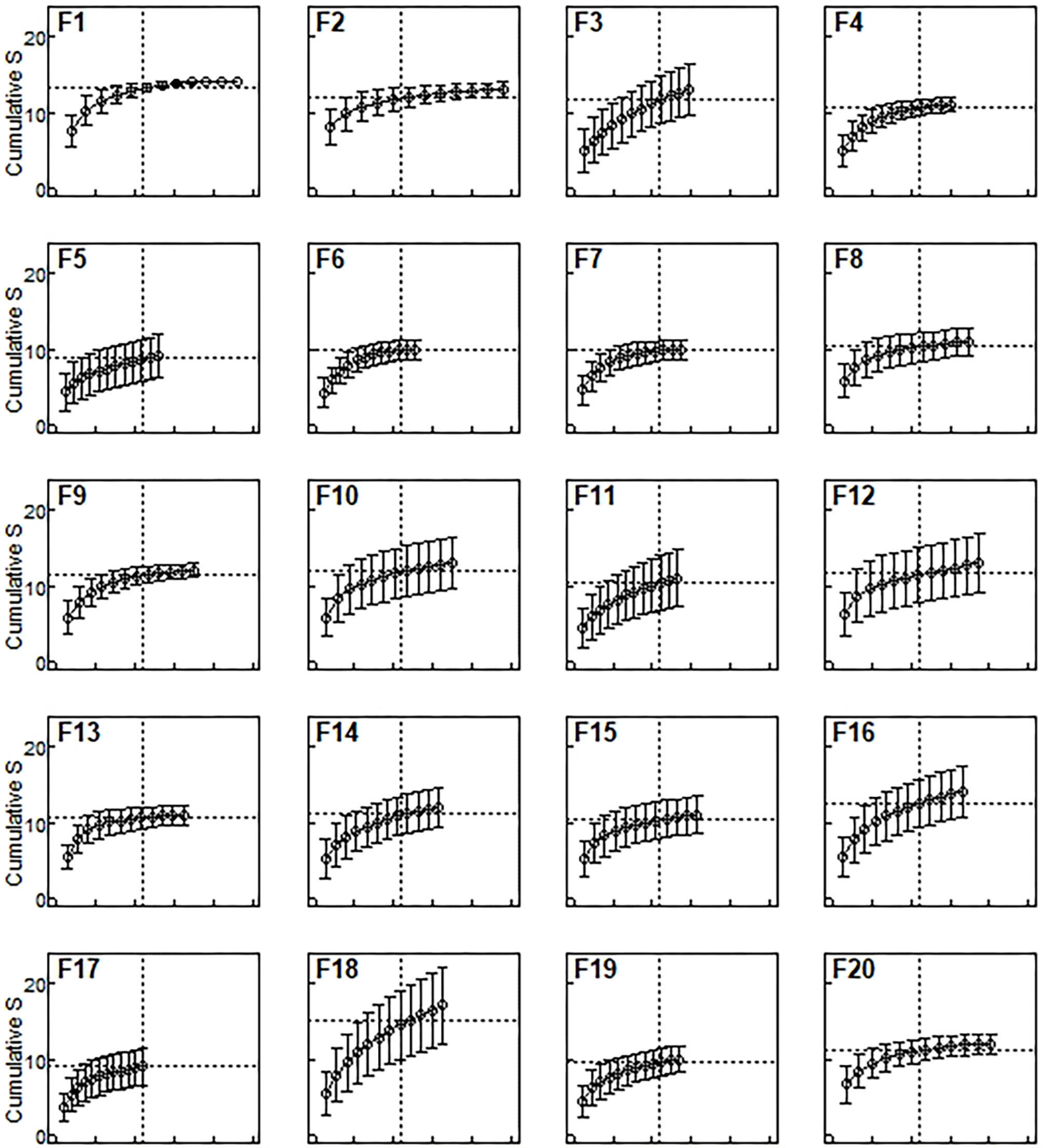

FIGURE 3 | Species richness estimated from rarefaction curves for each remnant. Species richness (horizontal lines) was estimated as the expected number of species for 44 occurrences (vertical lines), which was the minimum number of occurrences observed in any of the 20 plots (F17). Occurrence-based rarefaction curves (Gotelli and Colwell, 2011) were estimated by averaging 500 resamples with replacement. Bars are ±95%confidence intervals.

However, this explanation should be taken with caution since plots were located at the same distance from the field edge (10 m) regardless of fragment size. Other plausible explanation would be related to the existence of refuge effects of small and isolated patches against predators or parasites (Fahrig, 2017). In any case, the observed effect would be limited to the range of sizes

TABLE 6 | Parameter estimates and *P*-values for the GLM (Gaussian distribution, identity link function) built for species richness rarefied to 44 occurrences as a function of Log (Area), Connectivity and the interaction Log (Area) x Connectivity.

	Estimate	Std. error	*t*-value	Pr(>|t|)
Intercept	16.404	3.261	5.030	0.0001
Log (Area)	−1.196	0.782	−1.528	0.1460
Connectivity	−10.589	6.848	−1.546	0.1416
Log (Area) × Connectivity	2.390	1.722	1.388	0.1842

N = 20 fragments.

TABLE 7 | Parameter estimates and *P*-values for the Permanova analysis built to test the effect of area and connectivity on ant species community composition in 20 habitat remnants.

	Df	F. Model	R^2	Pr(>F)
Area	1	0.79	0.04	0.553
Connectivity	1	2.01	0.09	0.129
Area × Connectivity	1	2.51	0.12	0.063
Residuals	16		0.75	

We used frequency data to estimate species composition and calculated dissimilarity matrices based on Bray Curtis distance.

analyzed here, and we cannot exclude a hypothetical unimodal response if smaller and more isolated remnants were included in the study. Finally, it is also interesting that the increase in ant abundance in small and isolated patches did not translate into an increase in species density, suggesting that the rise in abundance is experienced mostly by common species.

In the context of a generalized loss of habitat and fragmentation exacerbation, protection of small and isolated habitat remnants has traditionally been rarely considered in favor of large patches (SLOSS debate), even though the same amount of habitat spread over many small patches can result in more biodiversity than when it is grouped into one or very few large areas (Fahrig, 2017; Fahrig et al., 2019). Recently, however, several studies have highlighted the important role of small reserves and habitats in harboring biodiversity (Wintle et al., 2019; Volenec and Dobson, 2020), which advises revisiting the SLOSS debate. While there is no doubt that larger patches host higher numbers of species in absolute terms, this effect is at least in part a consequence of random sampling effects and species—area relationships, and does not necessarily imply negative effects attributable to fragmentation *per se* (Fahrig, 2017; Fahrig et al., 2019), nor a higher conservation value for the area gathered in large patches. There are also other mechanisms by which habitat distribution in many smaller patches can provide positive effects for biodiversity conservation and ecosystem services. These mechanisms include the provision of spatial subsidies by the matrix (Ewers and Didham, 2006), positive edge effects (Ewers and Didham, 2006; Fletcher et al., 2018), landscape or habitat complementarity (Fahrig, 2017) or a general increase of beta diversity in heterogeneous landscapes (Andrén, 1994), which ultimately means that fragmented landscapes often have more diversity than non-fragmented ones when considered as a whole. A higher fragmentation (therefore, a higher habitat patchiness) can also produce positive effects at the population level, by spreading the risk of extinction over a large number of sites, thus reducing the risk of simultaneous extinction of all local populations, stabilizing predator—prey or host—parasitoid systems, or by reducing intraspecific and interspecific competition (Fahrig, 2017). In addition, the existence of a high number of small fragments in the territory can contribute to overall landscape connectivity by acting as key "stepping stones" for species able to move long distances (Herrera et al., 2017).

Finally, it should be noted that the small, poorly connected patches of the dry agroecosystem studied here were not only effective in maintaining ant communities, but also showed high diversity values when compared to geographically close areas. Thus, for example, Flores et al. (2018) analyzed ant communities in grassland ecosystems of central Spain along a wide environmental gradient using the same protocol as the one followed here, and found that species density ranged from 2 to 15 species per plot, well below the 9–17 species per plot found in our area. The cited study estimated the expected species density as a function of altitude, obtaining values from 7 to 8 species per plot for the altitude corresponding to our study area (700 m), also below the mean value of 11.8 found here. Therefore, as with other groups (Escudero et al., 2015), the high conservation value of gypsum ecosystems must also be highlighted in the case of ants. Furthermore, this group plays a central role in the functioning of terrestrial ecosystems, and participates in the delivery of a number of ecological services (Del Toro et al., 2012), so maintaining an appropriate mix of species rich fragments interspersed with croplands is of particular interest. In Mediterranean agroecosystems, the service of weed control stands out, and is mainly performed by ants of the genus *Messor* (Baraibar et al., 2009), which are very present in the communities studied here. Other important services of direct interest to agriculture are pest control, soil movement, decomposition and nutrient cycling (Del Toro et al., 2012, 2015).

In summary, this study corroborates that the ecological phenomena related to landscape configuration are complex and can give rise to very different outcomes depending on the group and the type of environment. It is therefore necessary to pay attention to the particularities of each case, and to be aware of the possible importance for biodiversity conservation of small ecological fragments or structures, even though at first sight they may not seem important, and especially when we are talking about organisms that are valuable for the provision of ecosystem services. This seems to be the case of ants in Mediterranean gypsum agroecosystems, where we have observed that small and weakly connected patches do not present losses of diversity with respect to larger patches and higher connectivity. As a take home message, we also want to recommend the maintenance of the smallest remnants of natural habitats because they can shelter important levels of biodiversity completing the list of services of any agroecosystem.

DATA AVAILABILITY STATEMENT

The original contributions generated for the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

FA, AE, and AS planned and designed the research. AA-M, FA, and AS conducted field work. AA-M and FA conducted laboratory work. FA and AS conducted data statistical analyses. FA wrote the manuscript with extensive input from the rest of the authors. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.619215/full#supplementary-material

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Landscape-Scale Effects of Irrigation on a Dry Cereal Farmland Bird Community

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Landscape modification and habitat fragmentation are one of the major current threats to biodiversity. The main source of habitat fragmentation is the loss of focal habitat area, but changes in the composition of the surrounding landscape also have a direct effect on biodiversity. These changes may lead to the loss of some species but also may favor species replacement. Farmland birds in Europe are affected by landscape changes due to farmland intensification, such as the spread of irrigation, which may occur at different spatial scales. As irrigation is expected to increase in the coming years, which may affect protected areas, it is necessary to evaluate its potential consequences over focal biodiversity. In this study we assess the relationship between the increase of irrigated land at different spatial scales and changes in a dry cereal farmland bird community, bird abundance and species richness, using generalized linear models. We used a dry cereal farmland affinity index to describe the level of community specificity for dry cereal farmland. The increase in irrigated tree orchards produced an increase in species richness up to 500 m away from the irrigated area, which had a negative effect on the dry cereal farmland bird community, by triggering a replacement of specialist by generalist species. Our results show the importance of landscape-scale effects of irrigation occurring outside protected areas on the farmland bird community inside Natura 2000 sites, as well as how these effects are detected even at long distances from the disturbance source.

Keywords: habitat loss and fragmentation, irrigation, farmland intensification, protected areas, indicator, bird community

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INTRODUCTION

Local species diversity and abundance often depend on spatial scales larger than the focal habitat patch (Fahrig, 2003; Villard and Metzger, 2014; De Camargo et al., 2018). Apart from quality and total surface of focal habitats at the patch (local) scale, surrounding landscape composition and configuration have effects on species diversity (Jules and Shahani, 2003), as it may modify animal movements and dispersal (Moilanen and Hanski, 1998), provide or limit alternative resources (Norton et al., 2000) and alter survival and reproduction rates (Prevedello and Vieira, 2010). In general, the more similar the matrix is to the focal habitat, the higher is its functional connectivity for those species occupying each individual patch (Prevedello and Vieira, 2010; Fahrig et al., 2011). Therefore, ecologists and conservationists need to be aware of the importance of linking landscape scale patterns and ecological processes when estimating basic structural parameters (e.g., abundance and species richness) of natural communities (Fahrig, 2003; Fischer and Lindenmayer, 2007).

Habitat loss is a main threat to biodiversity across the world (Pimm and Raven, 2000; IPBES, 2019). In Europe, farmland intensification is one of the main current drivers of habitat loss as it often results in landscape homogenization (Emmerson et al., 2016), and has been clearly linked to the widespread decline of different taxa, including farmland birds in recent decades (Donald et al., 2001; Benton et al., 2003; Geiger et al., 2010). Intensification through irrigation, for example, has been favored in many dry regions, and particularly in southern Europe, to increase crop yield or to allow new crop types in low productivity areas (Paracchini et al., 2007). In the Iberian Peninsula, extensive areas of dry cereal farmland (pseudo-steppes, sensu Suárez et al., 1997) have been replaced or fragmented by other crop systems such as irrigated fruit-tree orchards and herbaceous crops (e.g., maize and alfalfa). Thus, irrigation represents a drastic, quick, and large-scale change of dry cereal farmland landscapes, with predicted and demonstrated negative effects on biodiversity, and specifically on farmland and steppe birds (Brotons et al., 2004; González-Estébanez et al., 2011; Traba et al., 2013; Cardador et al., 2015; De Frutos et al., 2015). Because irrigated land is expected to continue increasing in the next years and given that landscape changes may affect protected areas or biodiversity hotspots, even if changes occur outside their borders, it becomes necessary to evaluate its potential consequences over high nature value areas (e.g., Natura 2000 sites) that have been designed to preserve dry cereal bird communities.

Birds are widely recognized as indicators of environmental changes acting at different scales (Fraixedas et al., 2020). However, not all the species respond equally to these changes because some of them (e.g., habitat specialists) are more susceptible than others to habitat degradation (Rooney et al., 2004; Julliard et al., 2006), contributing to a decrease of species diversity. On the contrary, certain changes in the landscape matrix could benefit widespread and habitat generalist species, increasing bird richness and diversity in focal habitats (Devictor et al., 2008). Specific indices for particular communities that may respond to particular ecological process and anthropogenic changes, such as measures of species specialization (Julliard et al., 2006; Devictor et al., 2008) may help to understand changes not occurring at specific but at the community level. Whether and how communities change in species composition because of the landscape context is thus crucial for predicting the consequences of habitat loss, planning conservation strategies, and managing protected areas.

In this study we evaluated the response of bird richness and abundance of a dry cereal farmland bird community within protected areas in Catalonia region (NE Spain) to the amount and type of irrigated land (herbaceous and arboreal irrigated crops) surrounding those protected sites. To evaluate in a more holistic way how the dry farmland bird community responded to nearby agrarian intensification, we calculated a dry cereal affinity index for the bird assemblage based on species-specific habitat selection indices that were derived from the Catalan Breeding Bird Atlas (Estrada et al., 2004). We expected that increases in the amount of irrigated land in the nearby landscape would negatively affect the dry cereal bird community decreasing the abundance of most representative species inside protected areas, independently of the effect on total species richness and abundance. Furthermore, a different response to irrigated herbaceous crops and tree orchards was also expected given the adaptation of dry farmland birds to open and treeless environments.

MATERIALS AND METHODS

Study area

The study was carried out in the Lleida plain (1,000 km^2), on the north-eastern edge of the Ebro Valley (Catalonia, Spain) (**Figure 1**). Climate is continental Mediterranean, with annual rainfall between 300 and 450 mm and an average annual temperature of 14.5°C (Cantero and Moncunill, 2012). The landscape is flat and mostly devoted to agriculture with a central area occupied by irrigated lands and an outer belt with remaining dry cereal farmland (i.e., pseudo-steppe habitat) (**Figure 1**). The irrigated area was first established at the beginning of the 20th century and later consolidated with new irrigation projects still currently ongoing. Irrigated land is characterized by herbaceous crops like alfalfa, maize, and winter cereal, or tree orchards like apple, pear, and peach. The remaining 600 km^2 pseudo-stepped area is dominated by dry winter cereal crops, mainly wheat and barley, representing 70% of the area, and to a lesser extent, fallows and permanent woody crops like olive and almond trees, and vineyards. Interspersed in the agricultural matrix, there are still small patches of natural vegetation areas, mainly sparse scrubland. Due to its value for steppe birds (Traba et al., 2007), most of this pseudo-steppe area is included in Special Protection Area (SPA) sites (ES5130038, ES0000021, ES0000479, ES0000478, ES5130035, ES0000477, ES5130021, and ES0000321), and included in the Natura 2000 network. The aim of this network is to ensure the long-term survival of Europe's most valuable and threatened species and habitats, listed under both the 2009/147/EC Birds Directive and the 92/43/EEC Habitats Directive.

Bird and Land-Use Data Collection

Bird data were collected on 178 linear transects (Järvinen and Väisänen, 1975) of ∼500 m of length, spaced more than 1 km apart and repeated yearly in 2010, 2011, and 2013 (mean number of transects/year was 155.7 ± 11.0). All transects were in dry cereal farmland areas and at 0.1 km to about 10 km from the irrigated edge. Three distance bands (<25, 25–50, and 50–100 m) were defined on both sides of the transect and each bird observed or heard was assigned to one of them. For the present work we considered only breeding species in the area with reference to the Breeding Bird Atlas of Catalonia (Estrada et al., 2004). All birds seen actively migrating or flying over the transect were excluded. To prevent potential detectability

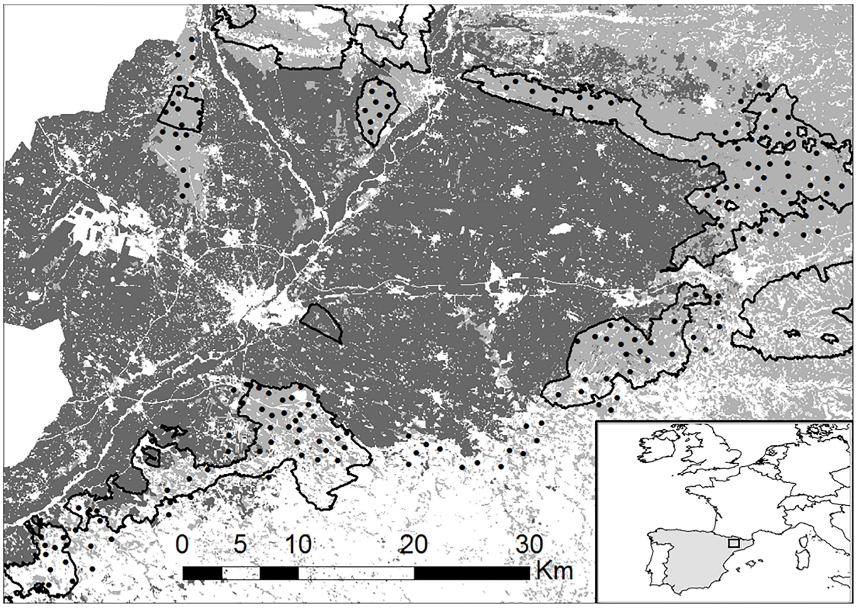

FIGURE 1 | Location of the study area in NE Spain and distribution of the 500 m transects (points) across the studied dry cereal farmland areas (lighter colored areas). Intermediate and dark gray areas represent irrigated herbaceous crops and orchards and white areas represent other land uses (urban, etc.). Polygons represent the Special Protected Areas included in Natura 2000 network.

errors (Sanz-Pérez et al., 2020), we estimated species richness and abundance including only the individuals detected up to the 50 m band from both sides of the transect line, except for Little bustard (*Tetrax tetrax*) males, Eurasian stone-curlew (*Burhinus oedicnemus*), Red-legged partridge (*Alectoris rufa*), Pin-tailed sandgrouse (*Pterocles alchata*) and Cattle egret (*Bubulcus ibis*). These are large sized species that remain highly visible or audible up to 100 m and thus estimation of their abundance is not significantly affected by detection up to that distance (Sanz-Pérez et al., 2020). Bird surveys were conducted by hired observers with previous demonstrated experience in the identification of bird species and with similar skills, so we reasonably assumed no significant differences in detectability due to observer identity. Censuses were carried out by foot and performed once per season, in May from sunrise to 4 h later, and only with good weather conditions (with no rain nor wind). Census period matches the breeding season of the target species, as well as their peak daily activity.

For each transect and year, we calculated species richness and total bird abundance, as well as the abundance of three species highly specialized in dry cereal farmland and of conservation interest: Calandra lark (*Melanocorypha calandra*), Little bustard and Eurasian stone-curlew. Crested (*Galerida cristata*) and Thekla's (*Galerida theklae*) larks, as well as Common (*Sturnus vulgaris*) and Spotless (*Sturnus unicolor*) starlings were considered as unique species (i.e., *Galerida* larks and Starlings), because they could not always be differentiated in the field. Because transect length was not always exactly 500 m (mean ± SD was 524 ± 46.5 m), all abundances and species richness were expressed as the number of individuals or species per hectare, respectively. Within-transect crops (100 m band) were mapped just after bird censuses, in order to calculate the proportion of area occupied by the following land-use categories: dry orchards (almond and olive trees), dry herbaceous crops (mostly cereal but also fallows), natural vegetation (mainly shrubland or open woodland) and other non-cropped areas (urban and watercourses).

Bird Community Dry Land Affinity Index

Although the presence of some bird species in certain ecosystems may be an indicator of each community's degree of habitat specialization (Julliard et al., 2006), not all species in an assemblage usually have the same degree of affinity for that particular habitat. Thus, indices incorporating and combining that species-specific degree of habitat affinity may provide a more integrated way to evaluate the degree of habitat specialization of the community. Steppe birds are good indicators of irrigation-driven impacts (Brotons et al., 2004; De Frutos et al., 2015), since their presence and abundance are affected by irrigation. For this reason, we devised a Dryland Affinity Index (DAI hereafter), which measures bird community affinity for dry cereal habitats, and calculated its value per each transect and year (Equation 1). To do so, we used existing habitat affinity indices (*K* in Equation 1) for dry cereal areas estimated for each bird species in Estrada et al. (2004).

$$\mathrm{DAI} = \sum_{i=0}^{n} \mathrm{Kj} \times \mathrm{Abundance\ j} \qquad (1)$$

Where *n* is the number of species present in the transect; K is the index of dry cereal farmland habitat affinity for species *j* estimated by Estrada et al. (2004); and Abundance *j* is the abundance of species j per hectare in the transect. The *K* index was calculated in Estrada et al. (2004) for each species and habitat as the ratio between habitat occurrence in the 1 × 1 km Universal Transverse Mercator squares where that species was present and habitat occurrence in the whole set of squares in Catalonia (Spain). To make its interpretation easier, Estrada et al. (2004) subtracted one from this ratio. Therefore, *K* represents an index of affinity of any given species for a given habitat, with positive and negative values reflecting positive and negative affinity for that habitat, respectively. To calculate the DAI we only used the *K* index of species for dryland cereal, and ignored *K* values for the rest of habitats. Since the range values of *K* varied between species, we previously standardized this parameter in a range of values between -1 and $+1$ in two steps. We first subtracted the minimum value and divided it by the range, and then multiplied the resulting value by two and subtracted one. The higher the DAI value, the stronger the community's affinity for dry cereal farmland is.

Irrigated Farmland Area in the Landscape

To assess the effect of irrigated land on our six response variables (DAI, total abundance, species richness, Little bustard abundance, Eurasian stone-curlew abundance, and Calandra lark abundance), we calculated and log-transformed the total area of irrigated herbaceous crops and orchards included in sequentially greater buffers around each transect, as two different variables (see **Table 1**). Using the centroid of each transect and based on the regional Geographic Information System of Farming Land (SIGPAC), total irrigated land of each type was calculated at three different buffers (radius of 500, 1,000, and 2,000 m). These buffers cover the home ranges of all species in our bird community, except for Marsh harrier (*Circus aeruginosus*) whose mean ranging distance is 3,070 ± 1,487 m during the nesting period in the study area (Cardador et al., 2009). Because in preliminary analyses we observed very low inter-annual variability across the 3-year study period in the area covered by irrigated orchards and herbaceous crops around transects, we extracted these variables from 1 year only (2011). All calculations were performed with the gvSIG 1.12.0 software.

Statistical Analysis

We first checked collinearity between the six predictor variables (irrigated herbaceous crops and irrigated tree orchards at 500, 1,000, and 2,000 m) and discarded total area of irrigated herbaceous crops and tree orchards between 0–1,000 m from the transect (HC-1000 and TO-1000), due to high correlation (above 0.55) with the other variables (Dormann et al., 2013). To perform the analyses, the six response variables were averaged across years to cancel annual variation. In order to control for the local effect of transect habitat composition and to avoid correlation between proportion values, we performed a Principal Component Analysis (PCA) on the proportion of each habitat type within a 100 m wide buffer around each transect and included PCA factors as model covariates.

After checking normality assumptions prior to the analysis, we used general linear models to study the linear response of DAI index, species richness and total bird abundance to landscape composition in terms of area occupied by both irrigated herbaceous crops and irrigated orchards. To analyze the effects of irrigation on species-specific abundance (Calandra lark, Little bustard, and Eurasian stone-curlew) we used Compound Poisson Generalized Linear Models, which can handle extra zero inflation and be applied to continuous data (Zhang, 2013).

To assess the linear models, we used a multimodel inference approach based on Akaike's Information Criterion (AIC). Model-averaged parameter estimates were calculated using the natural average method when more than one model was selected based on an $\Delta\text{AIC} \leq 2$ (Burnham and Anderson, 2002). Predictor variables were standardized in order to achieve comparability in the averaged models. Significance of explanatory variables was evaluated based on whether the confidence interval (CI) at 95% of its estimator excluded the value 0 (Burnham and Anderson, 2002).

Model fit was checked by exploring residuals normality and homoscedasticity. As Moran's index estimation revealed significant spatial autocorrelation in the residuals, and in order to control for it, we included x and y coordinates of the transect centroids in all models. All analyses were performed using the software R (v. 3.5.3) and packages Stats (v. 3.6.2.), MuMin (v. 1.43.17), and cplm (v.0.7-9).

RESULTS

A total of 6,662 individuals of 85 different bird species were detected across all transects and years. Mean DAI, total bird abundance and species richness across transects ($n = 178$) was -0.53 ± 0.93 (range -3.57–3.21), 2.55 ± 1.18 birds/ha (range 0.39–7.52 and 0.69 ± 0.36 species/ha (range 0.22–2.39), respectively. Both total bird abundance and species richness were lower in the 10 transects with highest DAI value (**Table 2**). Little bustard and Calandra lark were more abundant in transects with a high DAI value, but the opposite occurred for Eurasian stone-curlew (**Table 2**). Indeed, transects with high DAI values were mainly dominated by typical dry cereal farmland species such as Calandra lark and Little bustard, as well as other dry farmland species such as Corn bunting (*Emberiza calandra*) and *Galerida* larks (**Supplementary Table 1**). On the other hand, transects with low DAI values were dominated by more generalist species such as House sparrow (*Passer domesticus*), Common/Spotless starling and Feral pigeon (*Columba livia* var. *domestica*) (**Supplementary Table 2**).

The PCA describing land use variability within transects (local scale) yielded two factors explaining 74.84% of variance in the data (**Table 3**). The first factor (Habitat-F1) explained the 39.50% of variance and can be interpreted as a gradient from only-crop areas to more heterogeneous transects with natural vegetation patches (mainly open scrubland). The second factor (Habitat-F2) explained 35.34% of variance and it segregated dry cereal monocultures from mosaic transects where both

TABLE 1 | Habitat variables measured within and around each linear transect.

Abbreviation	Meaning	Mean ± SD	Range
Habitat-F1	Result of the first axis of the PCA describing the habitat composition within transects (see **Table 3**)	0.05 ± 1.10	−0.99–6.32
Habitat-F2	Result of the second axis of the PCA describing the habitat composition within transects (see **Table 3**)	0.23 ± 1.00	−1.70–3.59
TO-500	Area of irrigated herbaceous crops between 0–500 m of the transect (ha)	2.4 ± 8.4	0.0–82.2
TO-1000	Area of irrigated herbaceous crops between 0–1,000 m of the transect (ha)	12.5 ± 27.8	0.0–186.3
TO-2000	Area of irrigated herbaceous crops between 0–2,000 m of the transect (ha)	72.1 ± 114.3	0.0–631.8
HC-500	Area of irrigated tree orchards between 0–500 m of the transect (ha)	1.9 ± 7.3	0.0–56.4
HC-1000	Area of irrigated tree orchards between 0–1,000 m of the transect (ha)	16.9 ± 41.6	0.0–292.3
HC-2000	Area of irrigated tree orchards between 0–2,000 m of the transect (ha)	101.6 ± 149.3	0.0–584.8

Area of irrigated crops was log transformed before analyses.

TABLE 2 | Mean and standard deviation (SD) of dryland affinity index (DAI), species richness (species/ha) and total and specific species abundance (birds/ha) of the 10 transects with highest and lowest DAI values.

Transects	DAI	Species richness	Abundance	Little bustard	Calandra lark	Eurasian stone- curlew
Highest DAI	1.56 ± 0.76	0.44 ± 0.20	2.97 ± 0.79	0.08 ± 0.07	1.84 ± 0.79	0.06 ± 0.06
Lowest DAI	−2.54 ± 0.41	1.25 ± 0.99	5.60 ± 0.99	0.01 ± 0.02	0.02 ± 0.00	1.25 ± 0.37
F-test	$P < 0.0001$	$P < 0.0001$	$P < 0.0001$	$P < 0.001$	$P < 0.0001$	$P < 0.0001$

P-values of ANOVA F-test for the comparison of transects are showed.

TABLE 3 | Results of the principal component analysis (PCA) carried out to synthesize variation in habitat composition within transects.

Variable	Habitat-F1	Habitat-F2
% Dryland tree orchards	−0.114	−0.358
% Dryland herbaceous crops	−0.122	0.965*
% Natural vegetation	0.993*	0.079
% Other non-cropped areas (urban and watercourse)	−0.055	0.024
Accumulated variance explained (%)	39.50	74.84
Eigenvalues	113.81	101.80

Factor score coefficients based on covariances are given. Asterisks indicate significant variables ($P < 0.05$).

TABLE 4 | Results of the multi-model inference analyses and model averaging for the effects of local habitat within transects (Habitat-F1 and F2) and landscape context (around transects) on dryland affinity index (DAI), species richness and total abundance of birds ($n = 178$ transects).

Dryland affinity index (DAI)	β_{mean}	Lower 95% CI	Upper 95% CI
TO-500	−0.580	−0.861	−0.299
X-Coord	−0.493	−0.784	−0.203
Y-Coord	0.687	0.372	1.001
Species richness			
TO-500	0.133	0.019	0.248
Y-Coord	−0.241	−0.365	−0.117
Total abundance			
Y-Coord	−0.736	−1.146	−0.325

Average coefficient values (β_{mean}) and its 95% confidence interval for the significant factors selected in best models are given.

dry herbaceous and woody crops (almond and olive trees) co-dominated (**Table 3**).

The multi-model inference procedure for DAI selected six models with ΔAIC ≤ 2 (**Supplementary Table 3**). The area occupied by irrigated orchards (TO-500) within 500 m around transects had a negative effect on DAI (**Table 4** and **Figure 2**).

For total bird abundance and species richness, 10 and 6 models were selected and averaged, respectively (**Supplementary Table 3**). Contrary to DAI, species richness presented a positive relationship with TO-500, while bird abundance did not respond to any landscape variable related to the amount of irrigated area. None of the local habitat variables had any effect on DAI, species richness or total bird abundance (**Table 4**).

Calandra lark abundance decreased with the amount of TO-500 and increased with the amount of natural vegetation within transects (Habitat-F1) (**Table 5**). Eurasian stone-curlew abundance positively responded to the area of dry cereal at local scale but no effect of irrigation was detected on this species, nor on Little bustard abundance (**Supplementary Table 4**).

DISCUSSION

An extensive literature argues about the importance of landscape change and habitat fragmentation on biodiversity (Fisher and Lindermayer, 2007; Fahrig, 2013; Villard and Metzger, 2014; De Camargo et al., 2018). At the same time, the irrigation effects on biodiversity are still poorly known, though they are acknowledged as one of the main drivers of agrarian intensification and sources of bird-farmland decrease (e.g., Emmerson et al., 2016). Our results show the effects of changes in landscape composition for dry cereal farmland bird communities, and specifically how the amount of irrigated areas located at up to 500 m can alter species richness and community composition inside protected areas of the Natura 2000 network.

On one hand, irrigated orchards increased species richness present in dry cereal farmland areas up to 500 m away from the irrigated area. This seems to be due both to an increase of

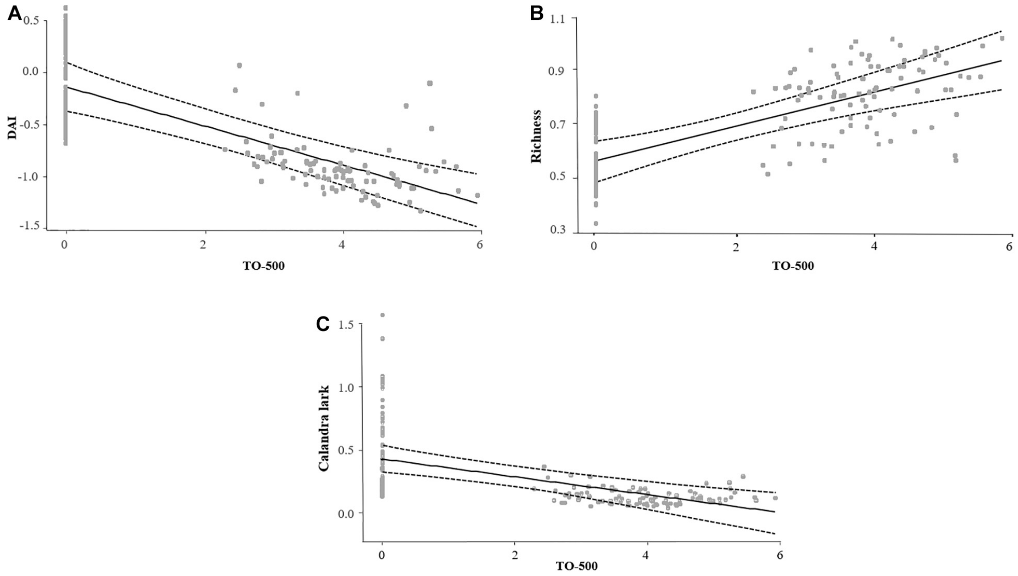

FIGURE 2 | Relationship between model's predicted values of **(A)** the dryland affinity index (DAI), **(B)** species richness, and **(C)** Calandra lark abundance and the log transformed area (ha) of irrigated orchards up to 500 m (TO-500) around transects. Mean (solid line) and CI (dashed line) of predicted values are shown.

TABLE 5 | Results of the Compound Poisson Generalized Linear Model for the effects of local habitat within transects (Habitat-F1 and F2) and landscape context (around transects) on Calandra lark abundance (*n* = 178).

Calandra lark	β_{mean}	St.Error	*P* value
Intercept	−0.879	0.991	0.376
TO-500	−0.305	0.071	0.000
TO-2000	−0.089	0.216	0.678
HC-500	0.102	0.062	0.104
HC-2000	0.066	0.075	0.379
Habitat- F1	0.197	0.092	0.032
Habitat-F2	−0.098	0.121	0.420
X-Coord	−0482	0.151	0.002
Y-Coord	0.212	0.158	0.180

widespread or more generalist species (i.e., Common/Spotless starling and House sparrow) that positively selected both dry cereal farmland and irrigated areas (Estrada et al., 2004), and to the entry of new species such as the Great tit (*Parus major*) and the Mistle thrush (*Turdus viscivorus*), probably because the woody component of orchards increases landscape heterogeneity and thus the number and type of available resources (Benton et al., 2003; Fahrig et al., 2011) (see **Supplementary Tables 1, 2**).

As expected, not only species richness was altered by surrounding irrigation, but the whole dryland bird community composition was negatively affected when the area occupied by irrigated orchards increased at up to 500 m away. A decrease of DAI value means a decline in dryland specialization of the community (De Frutos et al., 2015), even if the total number of species and bird abundance increases. These results are also consistent with those of Devictor et al. (2008) who found that specialists are more vulnerable to habitat degradation, while less specialized species would win competitive interactions. Furthermore, in our case, a decrease of dryland specialists can be translated into a decrease of conservation values since these SPA sites are devoted to these group species. For example, Calandra lark, the most abundant species in dryland protected areas, decreased when irrigated orchard area increased at up to 500 m away, which suggests that this species can be a good indicator of landscape fragmentation (Morgado et al., 2010) and conservation status of dryland communities. On the contrary, we did not find any landscape effect of irrigated crops on Eurasian stone-curlew and Little bustard. While the former species is much more flexible in habitat selection, Little bustard is known to be negatively affected by irrigation (Brotons et al., 2004; Cardador et al., 2015). Variability in Little bustard abundance might be more sensitive to other key resources such as food availability or some habitat feature not captured by our predictor variables (Morales et al., 2008; Traba et al., 2008s).

Although the habitat loss and fragmentation processes themselves are the greatest threats associated with species conservation in landscape ecology (Fischer and Lindenmayer, 2007), several studies showed that the type of change in landscape composition is key to understanding positive or negative effects of habitat loss on biodiversity at focal sites (Vandermeer and Carvajal, 2001; Jules and Shahani, 2003; Fahrig, 2013). For example, less negative effects of habitat loss and fragmentation should be expected if low structural contrast exists between the original and the new habitat (Prevedello and Vieira, 2010). This is because species' habitat associations are largely dictated by the availability of key resources in such habitats, rather than the habitat *per se* (Morales et al., 2008; Fahrig et al., 2011). Our study partially supports this idea since we find no effect of irrigated herbaceous crops on the dryland cereal bird community. Unlike irrigated herbaceous crops, irrigated orchards further involve a sharp change in vegetation structure and landscape visibility, which are key parameters for the survival of the dry cereal bird community (Cardador et al., 2014).

The change from a dry cereal farmland community to a more generalist one has important conservation implications, as changes within protected areas devoted to conservation of dryland specialists (e.g., steppe birds) may be triggered by factors occurring outside their limits, where no conservation measures are implemented. An increase of irrigated areas around the cereal steppes currently included in the Natura 2000 network can be expected in the future, considering the increase of irrigated area observed in recent years in Spain (MAPA, 2019). Our study shows that this negative effect would be relevant if irrigation allows the increase of irrigated orchards in the vicinity of the dryland protected areas, while no effects at the community level would be expected with a less drastic transition dominated by irrigated herbaceous crops. Therefore, from a conservation planning point of view, it would be advisable to consider a buffer zone around protected areas where irrigated orchards should be avoided in favor of irrigated herbaceous crops (i.e., low structural contrast between the original and the new habitat). The purpose of a buffer zone is to insulate protected areas from potentially damaging external influences, such as those caused by unsuitable land uses (Bennett and Mulongoy, 2006).

Our results offer an opportunity to optimize conservation in future irrigation schemes that are implemented close to dryland farmland protected areas while keeping the irrigated area constant, by avoiding some crops in contrast to others. However, more detailed studies (e.g., on vital rates such as breeding success and survival) should be conducted to understand the exact mechanisms (demographic, behavioral, etc.) by which the species of conservation concern respond to those landscape changes.

DATA AVAILABILITY STATEMENT

The datasets generated for this study will be available on request to the corresponding author (DG) and with the permission of "Infraestructures de la Generalitat de Catalunya SAU", who funded most part of data acquisition.

AUTHOR CONTRIBUTIONS

DG, GB, MM, and JT conceived and designed the study. JP and DG implemented the analysis and wrote the manuscript. DG coordinated fieldwork. GB secured funding. All authors contributed to subsequent drafts and gave final approval for publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.611563/full#supplementary-material

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Proportion of Grassland at Landscape Scale Drives Natural Pest Control Services in Agricultural Landscapes

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Managing regulating ecosystem services delivered by biodiversity in farmland is a way to maintain crop yields while reducing the use of agrochemicals. Because semi-natural habitats provide shelter and food for pest enemies, a higher proportion of semi-natural habitats in the landscape or their proximity to crops may enhance pest control in arable fields. However, the ways in which the spatial arrangement of these habitats affects the delivery of this beneficial ecosystem service to crops remains poorly known. Here, we investigated the relative effects of the amount of grassland in the landscape versus the distance to the nearest grassland on the predation rates of weed seeds and aphids into 52 cereal fields. We found that both seed and aphid predation levels increased with the proportion of grassland in a 500 m radius buffer while the distance to the nearest grassland displayed no effect. We show that increasing from 0 to 50% the proportion of grasslands in a 500 m radius, respectively, increased seed and aphid predation by 38 and 20%. In addition to the strong effect of the proportion of grassland, we found that seed predation increased with the proportion of forest fragments while aphid predation increased with the proportion of organic farming in the landscape. Overall, our results reveal that natural pest control in cereal crops is not related to the distance to the nearest grassland, suggesting that natural enemies are not limited by their dispersal ability. Our study indicates that maintaining key semi-natural habitats, such as grasslands, is needed to ensure natural pest control and support food production in agricultural landscapes.

Keywords: ecosystem services, agricultural intensification, predation, agroecology, natural enemy, aphid, weed

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INTRODUCTION

Agricultural intensification, which manifests through a massive use of pesticides, low crop diversity or landscape simplification, has major impacts on biodiversity (Beketov et al., 2013; Maxwell et al., 2016). Since biodiversity is one of the main determinants of ecosystem productivity (Tilman et al., 2014), this decline may threaten the long-term sustainability of food production

(Cardinale et al., 2012). A paradigm shift is therefore needed to meet the double challenge of maintaining – and in some cases, enhancing – food production and minimizing negative environmental impacts (Godfray et al., 2010; Garibaldi et al., 2017). One possible way forward is to increase regulating and supporting ecosystem services in agricultural fields to replace agrochemical inputs (Bommarco et al., 2013).

Among key functions supported by biodiversity, natural pest control, i.e., the suppression of pest species by their predators, is a major one. Natural pest control can benefit farmers by limiting crop yield loss (Maas et al., 2013; Bengtsson, 2015; Schneider et al., 2015; Ali et al., 2018) and pesticide use (Naranjo et al., 2015; Huang et al., 2018). High diversity in natural enemy communities is often associated with high levels of pest suppression (Letourneau et al., 2009). Indeed, a large body of research has focused on understanding the mechanisms operating at multiple spatial scales, from the plant to the landscape, driving the presence of natural enemies and the level of pest suppression in agroecosystems (Bianchi et al., 2006; Rusch et al., 2010, 2016; Chaplin-Kramer et al., 2011). While these studies have demonstrated that landscape heterogeneity is a major predictor of the level of natural pest control, the relative importance of landscape composition (i.e., amount of habitats) and of its configuration (i.e., spatial arrangement of habitats) on this key function remains poorly explored (but see Martin et al., 2019).

Population and community dynamics at the landscape scale can be viewed as a "source-sink" dynamic between habitats, under which both landscape configuration (e.g., fragmentation) and composition (e.g., amount of habitat) are strong drivers of biodiversity dynamics and ecosystem functioning (Haddad et al., 2017). These effects act in concert over multiple spatial scales and are mediated by dispersal abilities of species, rates of colonization and local extinction (Haddad et al., 2015, 2017; Hanski, 2015; Watling et al., 2020). In agricultural landscapes, semi-natural habitats such as woodlands, hedgerows, or grasslands are important sources of natural enemies because they provide alternative sources of food or hosts, refuges from disturbances and overwintering and breeding sites for a large range of species (Landis et al., 2000; Veres et al., 2013; Sarthou et al., 2014). Natural enemies disperse from semi-natural habitats to crops, and their spatial dynamics can be explained by the distribution of source habitats in the landscape through complementation or supplementation processes (Dunning et al., 1992; Rand et al., 2006; Blitzer et al., 2012). The importance of semi-natural habitats for natural pest control mainly comes from studies exploring how the amount of semi-natural habitats in the landscape enhances the activity of natural enemies or the amount of pest control in arable fields (Rusch et al., 2013, 2016; Veres et al., 2013; Haan et al., 2020). However, how the spatial arrangement of semi-natural habitats affects natural pest control remains poorly explored and the few studies investigating the effect of the distance of semi-natural habitats on natural pest control show idiosyncratic effects (Farwig et al., 2009; Thomson and Hoffmann, 2013; González et al., 2017; Lindgren et al., 2018; Aristizabal and Metzger, 2019). In addition, due to their strong correlation in the landscape (Fahrig et al., 2011), the relative importance of composition and configuration of semi-natural habitats on natural enemies and pest control services remains largely unknown (Haan et al., 2020).

Distance of arable crops to semi-natural habitats is expected to be a critical driver of the spillover of natural enemies. The distances are highly species-dependent because dispersal abilities vary from poor dispersal abilities (<1,000 m) for ground-dwelling species such as carabids or spiders, to high dispersal abilities for flying predators, such as ladybirds or syrphids (Schmidt et al., 2005; Saska et al., 2008; Jauker et al., 2009; Maes et al., 2014). Dispersal capacities further interact with the spatial distribution of semi-natural elements: natural enemies with "passive" dispersal (*sensu* Holt, 1985) forage near their semi-natural habitat source, and natural pest control increases with the proximity to the source habitat (Holzschuh et al., 2010; Haenke et al., 2014). Conversely, natural enemies with "active" dispersion depend less on adjacent natural habitats. As such, identifying the scale of effects of habitat sources for natural enemy communities involved in the delivery of pest control services is of major importance to understand the functioning of agricultural landscapes.

Among semi-natural habitats, grasslands are key habitats for many species, including natural enemy species (Bengtsson et al., 2019) and contribute to many ecosystem services in agricultural landscapes (Habel et al., 2013; Bengtsson et al., 2019). Grasslands shelter more natural enemies in early spring than any other type of semi-natural habitats and are therefore a major source of predators in agricultural landscapes (Albrecht et al., 2010; Sarthou et al., 2014; Werling et al., 2014). However, in most studies, grasslands are aggregated with other types of semi-natural habitats, thus their individual effect on pest control services remains poorly understood (Holland et al., 2017). In the few cases where the effect of grasslands was specifically considered, grassland proportion was shown to increase natural enemy abundance or pest predation, and reduce pest abundance in crops (Rusch et al., 2011; Trichard et al., 2013; Alignier et al., 2014; Koh and Holland, 2015; Petit et al., 2017). The distance effect of grasslands on natural pest control services is even less informed, but proximity to grasslands increases pest predation or pest abundance in adjacent crops (French et al., 2001; Badenhausser et al., 2020). However, to our knowledge, the relative importance of grassland proportion in landscape versus distance-decay effects on pest control has never been studied simultaneously in a single study.

The aim of this study is to disentangle the relative effects of the amount of grassland from the effect of distance to the nearest grassland on natural pest control in focal cereal fields. We used predation sentinel cards, and focused on predation rates of two different types of prey, i.e., aphids and weed seeds, which are known to incur cereal yield loss (Ali et al., 2018; Adeux et al., 2019). Both aphids and seeds are predated by a large number of predators, with highly variable dispersal abilities and diets. These include carabid beetles, birds and small rodents for seeds (Bohan et al., 2011; Eraud et al., 2015; Tschumi et al., 2018a,b); ladybirds, carnivorous ground beetles, spiders or syrphid larvae for aphids (Schmidt et al., 2005; Saska et al., 2008; Jauker et al., 2009; Maes et al., 2014). However, in most cases, the identity of natural enemies responsible for pest suppression remain unknown (Furlong and Zalucki, 2010). We hypothesized that if natural pest control services are driven by local and passive diffusion, then the level of pest control should be more affected by the distance to the nearest grassland than by its proportion in the landscape. On the contrary, if natural pest control services are mainly driven by complementation processes mediated by active dispersal from sources habitats to crops, then grassland proportion is more important than the distance to the nearest grassland.

MATERIALS AND METHODS

Study Area

The study took place in 2016 in the Long Term Social-Ecological Research site "Zone Atelier Plaine & Val de Sèvre" (ZAPVS), an agricultural landscape located in central western France (Bretagnolle et al., 2018), in the Nouvelle Aquitaine Region (46.23°N, 0.41 W). Land use is surveyed annually in each of the c. 13,000 fields of the study site (435 km^2 managed by c. 450 farms), and is stored in a GIS database (Bretagnolle et al., 2018). The area is mainly used for intensive cereal farming. Grasslands (including meadows and long-term set-a-sides, but excluding alfalfa) represent only 7.1% of the ZAPVS, while cereals, mainly winter wheat varieties, are the dominant crop (37.1% cover). The other main crops consist of oilseed rape (7.1%), sunflower (7.4%) and maize (8.9%). Forests cover about 13.7% of the ZAPVS (including the large Chizé forest, **Figure 1**). The remaining area is comprized of other crops such as alfalfa, pea, linseed or ryegrass, and urbanized surfaces. Crop fields have an average size of 5.7 ha, ranging from 0.4 to 35.2 ha.

Site Selection and Landscape Metrics

Two landscape gradients of interest were particularly studied: the first gradient, related to landscape configuration, was the distance between the barycentre of sentinel card position and the nearest grassland field (represented by its border), while the second gradient was the proportion of grassland in the landscape at a given buffer size (radius). We selected 52 cereal focal fields (45 winter wheat and 7 winter barley fields) along these two landscape gradients which could influence the predation rates of aphids and weed seeds in these fields (Rusch et al., 2010, 2013). The fields were randomly selected with a moving window aiming at lowering the correlation between two landscape gradients of interest and making them independent (see Fahrig et al., 2011; Sirami et al., 2019). Correlation between the distance to the nearest grassland and the proportion grassland never exceeded 0.52 whatever the radius (**Supplementary Figure 1** shows correlations between distance to the nearest grassland and proportion of grassland for the different buffer scales). Distance to closest grassland varied from 25 to 972 m (average: 289.9 m, see **Figure 1**), while the area of the nearest grassland varied from 0.26 to 7.6 ha (average: 2 ha). In addition to these two landscape metrics, we also calculated the proportions of crops organically farmed, forests and hedgerows, since these landscape metrics are known to affect natural pest control as well as natural enemies presence and abundance (Farwig et al., 2009; Rusch et al., 2010; Muneret et al., 2019). All these landscape metrics were calculated at six different radii ranging from 250 to 1,500 m around the barycentre of sentinel prey card position (see below, Martin et al., 2015; Rusch et al., 2016; Tschumi et al., 2018a). **Table 1** shows habitat proportions in the six different buffer sizes. Correlations between organic farming, hedgerow, forest and grassland metric were lower than 0.6 (see **Supplementary Figure 2** for all correlations between landscape metrics).

Experimental Design

We used sentinel preys to estimate natural pest control potential as it is a standard and efficient method related to predator activity (Lövei and Ferrante, 2017; Boetzl et al., 2020a) and pest regulation (Perez-Alvarez et al., 2019). In each cereal field, we measured natural pest control as the realized predation rate on two common pests: the aphid *Acyrthosiphon pisum* (Ximenez-Embun et al., 2014) which is commonly used to estimate aphid predation in cereal fields (Winqvist et al., 2011; Ricci et al., 2019), and the weed *Viola arvensis* (Petit et al., 2017) which is relatively common in cereal fields (Bourgeois et al., 2020). Weed seeds were bought at Herbiseed (Reading, United Kingdom). Aphids colonies were bought at Monster-Souris (Nantes, France) and raised on peas (*Pisum sativum)* in the laboratory from the beginning to the end of the sentinel card experiment under ambient temperature and natural day-night cycle. Predation rates were quantified using sentinel cards, on which either three dead aphids or 10 weed seeds were glued (Aero'Colle, Cléopâtre) on the rough side of 5 cm × 6 cm sandpaper cards (Boetzl et al., 2020a; McHugh et al., 2020, **Figure 1**). Cards were placed 24 h in the freezer at −20°C before the experiment to avoid attractive or deterrent effect of predator due to glue evaporation (Boetzl et al., 2020a).Two parallel transects of 21 m were selected per field, distant by at least 10 m from each other to ensure independence between transects. To limit potentially confounding field margin effects, we set up transects at least two tractor bays (i.e., approximately 25–35 m) away from the field border, (**Figure 1**). On each transect, four cards of each prey type were set on the ground, held a pin (Winqvist et al., 2011; Boetzl et al., 2020a), from the 7th April to 30th June (i.e., from heading to grain ripening of cereals), each being 7 m apart (**Figure 1**; Ricci et al., 2019; Boetzl et al., 2020b). Seed and aphid cards were put on the same position on the transect and spaced 40 cm apart. Cards were folded in half to provide a tent-like with aphids facing to the ground to limit the deterioration of the aphid or seed gluing by climatic conditions (rain, sun, wind…) as advised by Winqvist et al. (2011). The position of cards in the fields was recorded with a GPS. The barycentre of global card positions in a given focal field was used as the center of buffer and to measure the distance to the nearest grassland. Each field was sampled twice over the spring and summer seasons to account for temporal variation of predation rates throughout the season (Ximenez-Embun et al., 2014). A total 832 cards per prey type were set up (i.e., 8 cards per field and per session). On average, 44.1 days (range: 28–56 days) separated the two sampling sessions for a given field. Seed cards were left 4 days in the field whereas aphid ones were collected after 1 day (24 h) because of much higher predation rates (see

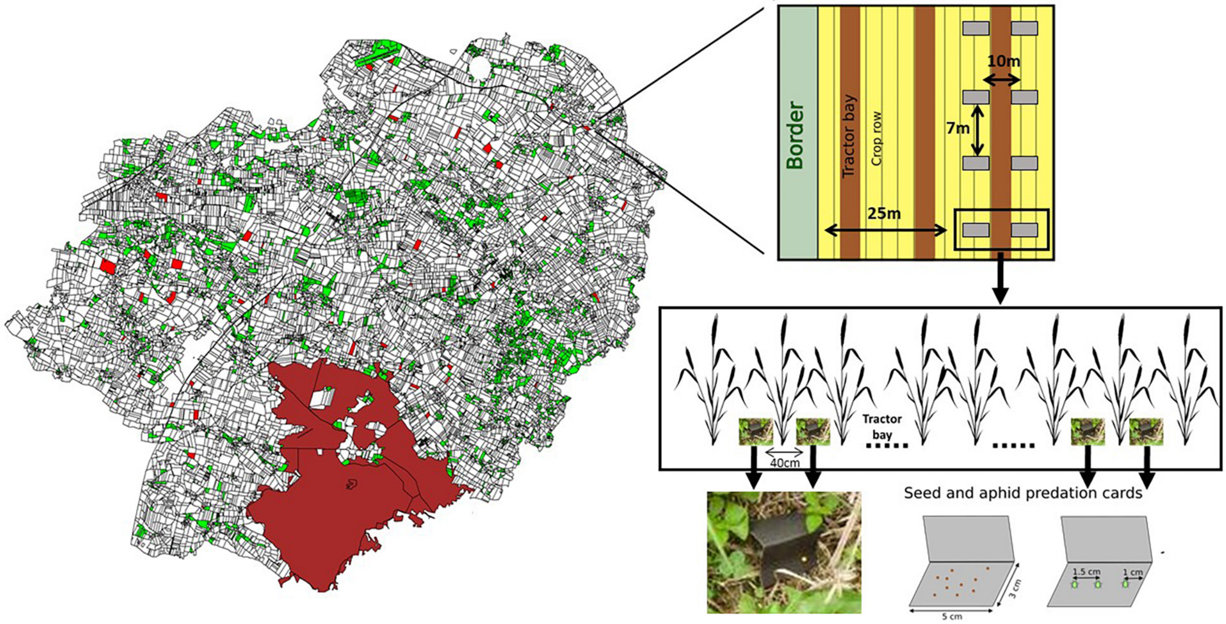

FIGURE 1 | The left panel shows a map of the study area with grassland fields in green and the 52 selected cereal fields in red. The right panel shows the field experimental design. Seed cards were put on the same position as aphid card spaced to 40 centimeters apart. Chizé forest is in brown.

TABLE 1 | Habitat proportions calculated in different buffer radii.

Buffer size	Grassland	Hedgerow	Forest	Organic farming
250 m	5.7 (0 – 48.4)	1.2 (0 – 6.6)	2.9 (0 – 49.9)	5.8 (0 – 47)
500 m	7.3 (0 – 50.7)	1.2 (0 – 5.4)	2.8 (0 – 33)	7.2 (0 – 58.8)
750 m	7.1 (0 – 46.0)	1.2 (0 – 4.6)	3.1 (0 – 27.3)	7.3 (0 – 49.8)
1,000 m	7.4 (0 – 39.3)	1.3 (0.1 – 4.1)	3.5 (0 – 28.5)	7.7 (0 – 39.8)
1,250 m	7.4 (0.5 – 33.6)	1.3 (0.2 – 3.9)	4 (0 – 29.1)	7.7 (0 – 36)
1,500 m	7.6 (1.2 – 30.6)	1.3 (0.2 – 3.7)	4.4 (0 – 26.7)	7.6 (0.1 – 35.2)

Mean (min and max) are given.

results, Ximenez-Embun et al., 2014). This period is standard in studies using predation sentinel cards (Lövei and Ferrante, 2017; Perez-Alvarez et al., 2019; Boetzl et al., 2020a). A total of 817 seeds cards and 818 aphid cards were recovered from the 832 initially installed, 15 and 14 were lost, respectively. In one field, one session was lost for both seed and aphid cards. We counted the number of aphids or seeds remaining on the cards to estimate predation rates, and then removed cards from fields.

Statistical Analyses

To disentangle the importance of proportion of grassland in the landscape from the importance of the distance to the nearest grassland on aphid and seed predation rates in cereal fields, we used Generalised Linear Models (GLM). For weed seed predation, we used the ratio of the number of weed seed predated on the total number of seeds placed in the fields as response variable and used a Gaussian error distribution. For aphid predation, we used 1- the number of aphids predated on the total number of aphids placed in the fields (i.e., the number of non-predated aphids) due to the very high predation rates of aphids (49% fields have more of 90% aphids predated) and used a Poisson-Gamma distribution from the family Tweedie (Dunn and Smyth, 2018). This distribution handles zero values uniformly with positive and continuous values thanks to a power variance function and a log-link function (Lecomte et al., 2013). This distribution performed better than models such as hurdle or negative-binomial models with zero-inflated data (Lecomte et al., 2013; Saha et al., 2020).

First, we investigated how predation rate (seed or aphid and response variable) was explained by the distance to the nearest grassland or the proportion of grasslands. As the correlation of predation rates between the two sessions was very weak (Pearson correlation test between the two sessions, $\rho = 0.09$, $t = 0.62$, $df = 49$, p-value = 0. 54 for seeds, and $\rho = 0.15$, $t = 1.06$, $df = 49$, p-value = 0.29 for aphids), we used the two sessions as independent observations and included the Julian date in the model as a co-variate to account for season. Six models per pest type were fitted using the two landscape variables calculated in six-buffer radius size (**Table 1**). The six models were compared using the Akaike Information Criterion (AIC;

Burnham and Anderson, 2002) and we retained the best model for each response variable, i.e., the model with the lowest AIC. The effect of the interaction between grassland proportion and the distance to the nearest grassland was also tested by adding an interaction term to the best model, and was removed in next models if it was not significant.

Since predator activity may depend on weather, e.g., rainfall potentially modifies predator activity (Zaller et al., 2014), we included weather variables in the models. We added average rainfall per day during the experiment as co-variables to these models, calculated over 4 days for seed predation measures (average 1.76 mm per day, range: 0–8.26 mm) and over 2 days for aphid predation measures (average 1.73 mm per day, range: 0–6 mm), to consider rainfalls from the first day where cards were deposited in the fields to the day when they were retrieved. We did not consider average temperature as an explanatory variable in our models as temperature was strongly correlated to Julian days (Pearson correlation test between Julian days and average temperature on 4 days, $\rho = 0.8$, $t = 13.32$, $df = 102$, p-value < 0.001, Pearson correlation test between Julian days and average temperature over 2 days, $\rho = 0.76$, $t = 11.65$, $df = 102$, p-value < 0.001). All weather metrics were obtained from a weather station located in the city of Niort, within the study zone, and data were downloaded from United States National Oceanic and Atmospheric Administration.

We further tested whether a grassland that is small in surface but close to the focal crop could be equivalent – in terms of source habitat for natural enemies – to a grassland that is large but distant. Thus, in a separate analysis, we incorporated the area of the nearest grassland by replacing the distance to the nearest grassland by the distance to the nearest grassland divided by its area. Finally, because the proportions of hedgerows, forests and organic farming in the landscape are known to affect natural pest control, we explored their potential effects (Farwig et al., 2009; Rusch et al., 2010; Muneret et al., 2019) in additional models. We added these three metrics as co-variates in the best models for aphid and seed predation. Adding these landscape metrics variables allows quantifying their individual effect on predation rates but also their additional effect with grassland effects (both proportion and distance).

All analyses were performed using the software R (R Core Team, 2015), version 3.6.2 with "stats" package for GLMs and AIC estimation, "tweedie" and "statmod" for GLM models with Tweedie distribution (Giner and Smyth, 2016; Dunn, 2017). All explanatory variables were centered and reduced to facilitate the interpretation of coefficients.

RESULTS

Overall, 1998 (of 2454) aphids and 3446 (of 8170) seeds were removed across the two sessions in the 52 focal cereal fields. Seed predation rate was in average of 0.42 ± 0.29 (median: 0.42) while aphid predation rate was 0.81 ± 0.24 (median = 0.88). Seed and aphid predation rates were positively correlated (Pearson correlation, $\rho = 0.2$, $t = 2$, $df = 100$, p-value = 0.048).

The best-fit models were models including explanatory variables calculated in the 500 and 750 m radius (ΔAIC < 2) both for seed and aphid predation rates (**Supplementary Figures 3A,B**). Effect of grassland was similar between models with landscape variables estimated at 500 and 750 m (**Table 2** and **Supplementary Table 1**), but models with landscape variables calculated at 500 m had lowest AIC for both aphid and seed, thus were chosen. Best models, respectively, explained 15.9 and 15.5% of the variance in seed and aphid predation rates. The proportion of grassland had a positive effect on seed and aphid predation rates, contrasting with the distance to the nearest grassland which had no effect on the predation rates of either prey species (**Table 2** and **Figures 2A,B,E,F**). Predation rates of seeds and aphids, respectively, increased by 42 and 21% along the gradient of grassland proportion (proportion of grassland ranged from 0 to 50% in the 500 m radius). No significant interaction was detected between distance to the nearest grassland and grassland proportion (seeds: *Estimate* = −0.082, p-value = 0.49, and aphids: *Estimate* = −0.31, p-value = 0.6; **Supplementary Table 2**). Including the area of the nearest grassland in the models did not affect the influence of its distance on predation rates for either preys (seeds : *Estimate* = −0.012, p-value = 0.7, and aphids: *Estimate* = −0.19, p-value = 0.2; **Supplementary Table 3**).

Adding the proportion of forest, hedgerow and organic farming in the landscape additionally explained 8–10% of the variance in predation rates of seeds and aphids (R^2 = 24% for seeds and R^2 = 22.3% for aphids). The proportion of forests increased seed predation rates (**Table 2** and **Figures 2C,G**), while the proportion of organic farming increased aphid predation rates (**Table 2** and **Figures 2D,H**). The effect of grassland proportion was partially reduced with the inclusion of other landscape metrics compared with the simpler models (**Table 2**). In such models, predation rates of seeds and aphids, respectively, increased by 38 and 20% along the gradient of grassland proportion (from 0 to 50% in a 500 m radius, **Figures 2B,F**). Finally, predation rates of seeds and aphids increased with Julian days and marginally with rainfall (**Table 2**).

DISCUSSION

Our study explores the interactive effects of the amount and spatial configuration of grasslands on the predation rates of two types of cereal prey in agricultural landscapes. Our analyses indicate that the proportion of grassland rather that the distance to the nearest grassland increased both seed and aphid predation rates in cereal fields with, respectively, an increase of 38 and 20% from 0 to 50% of grassland in a 500 m-radius buffer. In addition, seed predation increased with the proportion of forests while aphid predation increased with the proportion of organic farming in the surrounding landscape.

The relative importance of habitat composition and configuration at the landscape scale to maintain biodiversity and ecosystem functions is highly debated although few studies examined their relative effects on ecosystem functions and services (Watling and Donnelly, 2006; Haddad et al., 2017;

TABLE 2 | Summary of generalized linear models for seed and aphid predation rates explained by date (Julian day), average rainfall, and landscape metrics.

	Seed predation rate						**Aphid predation rate**					
	Only grassland			**All landscape metrics**			**Only grassland**			**All landscape metrics**		
	Estimate	**χ^2**	***p*-val**	**Estimate**	**χ^2**	***p*-val**	**Estimate**	**χ^2**	***p*-val**	**Estimate**	**χ^2**	***p*-val**
Julian days	**0.070**	**6.970**	**0.008**	**0.072**	**7.951**	**0.005**	**0.321**	**7.907**	**0.005**	**0.305**	**7.303**	**0.007**
Rainfall (mm)	0.048	3.258	0.071	0.044	2.976	0.085	**0.256**	**4.291**	**0.038**	0.232	3.545	0.060
Distance to grassland (m)	0.052	2.800	0.094	0.028	0.769	0.380	0.242	2.979	0.084	0.227	2.299	0.129
Grassland (% at 500 m)	**0.083**	**7.162**	**0.007**	**0.077**	**6.205**	**0.013**	**0.495**	**7.623**	**0.006**	**0.483**	**6.978**	**0.008**
Forest (% at 500 m)	–	–	–	**0.071**	**7.412**	**0.006**	–	–	–	−0.034	0.096	0.757
Hedgerow (% at 500 m)	–	–	–	−0.028	0.873	0.350	–	–	–	0.076	0.268	0.605
Organic farming (% at 500 m)	–	–	–	0.033	1.579	0.209	**–**	**–**	**–**	**0.275**	**4.002**	**0.04**
R-squared			0.159			0.24			0.155			0.23

In a first set of analyses (first and third columns), landscape metrics only include distance to the nearest grassland and proportion of grassland. In the second and fourth columns, other landscape metrics (hedgerow, forest, and organic farming cover) are added to the model. All landscape metrics are estimated in a buffer of radius 500 m. Significant effects (P < 0.05) are in bold. For the sake of understanding, we inversed coefficients of aphid models in reported results to have the ratio of predated aphids as for seed model rather of coefficient for 1-ratio of predated aphids.

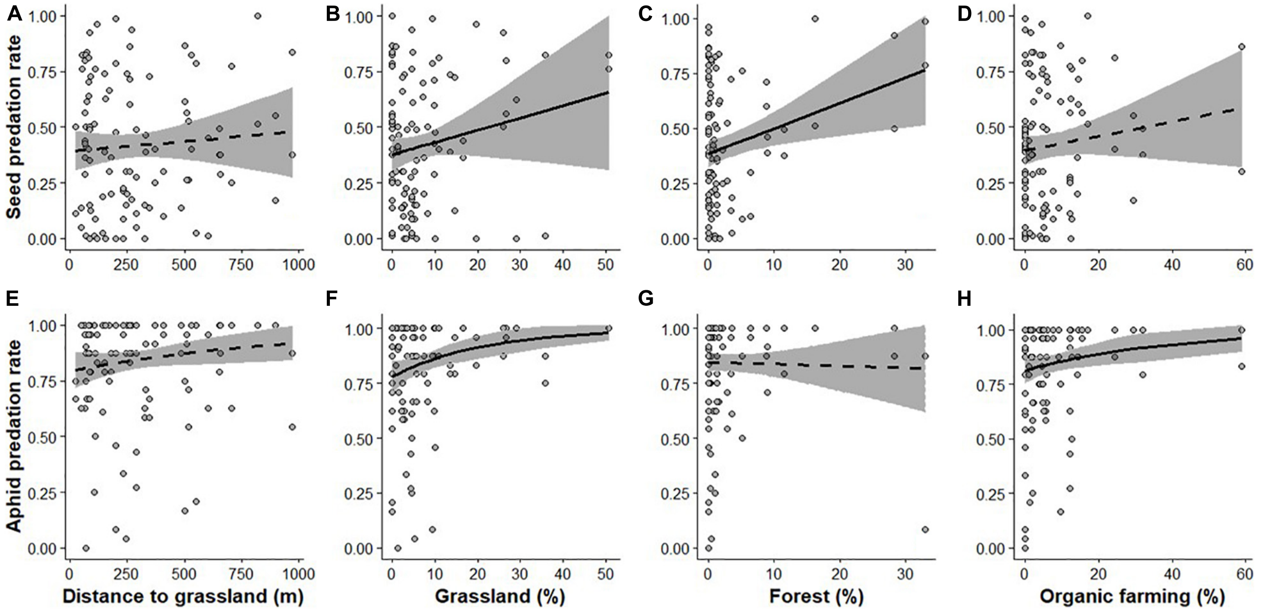

FIGURE 2 | Predation rates for seed **(A–D)** and aphid **(E–H)** in relation to distance to the nearest grassland **(A,E)**, proportion of grassland **(B,F)**, forest **(C,D)** and organic farming **(D,H)** in a buffer size of 500 m. The two sampling sessions are combined in a single analysis (see section "Materials and Methods"). Black lines represent the relationships as predicted by generalized linear models, among which solid lines represent significant effects, whereas non-significant effects are dashed. The gray areas represent the 95% CI.

Bueno and Peres, 2019; Watling et al., 2020). A recent meta-analysis regrouping 35 study sites from different biomes showed that in most cases, composition (in the form of proportion) was more important than configuration to maintain species richness whatever the taxon identity (Watling et al., 2020). Indeed, both the composition and the configuration of agricultural landscapes shape natural enemy communities and pest damage (Martin et al., 2019; Haan et al., 2020), and more specifically the amount of semi-natural habitats enhances the activity of natural enemies or amount of pest control (Rusch et al., 2013, 2016; Veres et al., 2013; Haan et al., 2020). In most cases, the spatial arrangement had no effect on natural enemies or pest control (Farwig et al., 2009; Thomson and Hoffmann, 2013; González et al., 2017; Lindgren et al., 2018). However, only few studies included both composition and configuration in their analyses (González et al., 2017) as they are strongly correlated in most ecosystems (Fahrig, 2013). Our landscape selection method allowed to disentangle the effect of grassland proportion from the effect of distance to the nearest grassland. Our results suggest that grassland proportion is more important than their distance to crops to increase aphid and seed predation in cereal fields, indicating that the effect of landscape composition on communities also holds for ecosystem functions (Lamy et al., 2016; Duarte et al., 2018). Our results are consistent with previous studies which showed that aphid and seed predation in cereal fields increase with surrounding grassland proportion (Trichard et al., 2013; Alignier et al., 2014; Petit et al., 2017). Similarly, seed and aphid predation in midfield islets did not decrease with distance to grassland (Lindgren et al., 2018). However, none of these studies accounted for both the configuration and the amount of grassland in their experiments, and grasslands were usually aggregated with other types of semi-natural habitats in a large majority of studies (Holland et al., 2017). Only González et al. (2017) integrated both aspects and showed comparable results with stinkbug egg-predation on soybean crops which increases with forest proportion rather their distance to crops. The landscape context of our study region may, however, limit the extrapolation of our results to other farmland landscapes. It should be noted that only three cereal fields were more of 750 m away from a grassland (**Supplementary Figure 1**), stressing that additional experiments may be needed with cereal fields more than 1 km from closest grassland to confirm our results. In landscape contexts with few grasslands, and therefore higher distances to the nearest grassland, one may expect a higher effect of distance. Moreover, landscapes with high amount of grassland (>15%) were scarce in our study (7 fields on 52), therefore limiting the scope of our conclusions. Conducting this study with the same experimental design over a large range of landscape gradients and in different pedoclimatic contexts would certainly help to consolidate our conclusions. In addition to the effect of grassland proportion, we found that forest proportion increased seed predation rates while organic farming proportion enhanced aphid predation rates, which suggests a complementation effect of habitat for natural enemies. Diverse semi-natural habitats in agricultural landscape provide alternative prey or additional shelter, hence maintain higher diversity of natural enemies (Tscharntke et al., 2007) and pest predation (Letourneau et al., 2009).

The dispersal and behavioral capacity of natural enemies likely determine the relative importance of composition and configuration of semi-natural habitats for natural pest control (Keinath et al., 2017). We found that the scale of effect of grassland proportion on pest control is at spatial extent ranging from 500 to 750 m radius, rather than small spatial extent. This spatial extent is larger than the one found in a previous meta-analysis which showed that pest predation is best explained by landscapes metrics estimated at small scales (250 m, Karp et al., 2018). High dispersal capacity had been predicted as a key trait of natural enemies effectiveness to remove pests (Bianchi et al., 2010). Natural enemies with high dispersal capacity are less susceptible to landscape heterogeneity (Bianchi et al., 2010). Among seed predators, small mammals, ants and carabids have dispersal capacities ranging from 500 to 750 m (Wegner and Merriam, 1990; Holland et al., 2004; Zumeaga et al., 2021). Moreover, small mammals, ants and carabids can benefit from grasslands (Fischer and Schröder, 2014; Petit et al., 2017; Assis et al., 2018) as well as forest patches (Wegner and Merriam, 1990; Holland and Fahrig, 2000; Assis et al., 2018) to maintain their population and may explain why seed predation rates increase with forest proportion. For aphids, spiders and carabids are natural enemies with dispersal capacities that match the 500 – 750 m spatial extent (Holland et al., 2004; Schmidt and Tscharntke, 2005; Maes et al., 2014) and appear as potential candidates involved in aphid predation rates here. Abundances of these species were previously found to increase with grassland proportion in agricultural landscapes (Koh and Holland, 2015; Petit et al., 2017; Badenhausser et al., 2020). There is also some evidence that carabids and aphids control by their natural enemies in cereal crops benefit from the proportion of organic farming in surrounding landscape (Caro et al., 2016; Diekötter et al., 2016; Djoudi et al., 2018; Muneret et al., 2019) which may explain why aphid predation rates increased with amount of fields under organic farming. A camera-trap experiment may help to identify the natural enemies responsible for aphid and seed predation (Petersen and Woltz, 2015); especially because the ground position of aphid cards in our study may have excluded predation from aerial predators such as birds or ladybirds. Including such predators might change the spatial extent of the landscape effects detected in our study.

Finally, we found that meteorological conditions modified predation rates. Predation rates of both preys increased with Julian days, but only aphid predation rates increased with rainfall, though we could not disentangle the respective effects of Julian days and average temperature which were strongly correlated. There is clear evidence that both variables affect predator activity: predator dynamics increase with Julian days (Caro et al., 2016), and predator activity and pest predation increase with average temperature (Korenko et al., 2010). It is therefore likely that the increase of predation rates observed in our study resulted from seasonal effect such as increase in average temperature. Predator activity or abundance was also found to be higher with rainfall (Irmler, 2003; Lundgren et al., 2006; Zaller et al., 2014; Wróbel and Bogdziewicz, 2015), confirming our results on aphid predation rates. However, the absence of relationship between seed predation rate and rainfall may suggest that different natural enemies may contribute to seed and aphid predation and/or that the effect of rainfall is less pronounced on a 4-day (seed predation) than on a 2-day (aphid predation) period. Further studies are now needed to determine how natural enemies of each prey behave under contrasted weather conditions. Similarly, it would be interesting to consider prey abundance or pesticide applications as covariables in our models because these factors can affect natural pest control potential. A high prey abundance can dilute natural pest control by distracting predators from sentinel cards (Lövei and Ferrante, 2017) while pesticide applications can buffer landscape effects (Ricci et al., 2019). These effects need further investigations to fully understand the mechanisms driving natural pest control in agricultural landscapes.

CONCLUSION

In this study, increasing grassland proportion at landscape scale (500 m buffer radius) by 50% resulted in 38 and 20% increase in seed and aphid predation rates. Conversely, the nearest grassland, whatever its area, displayed no statistical effect on predation rates. These results highlight the importance of maintaining sufficient amount of grassland habitats in agricultural landscapes to enhance natural pest control services, which might help reducing pest pressure and pesticides applications in agricultural landscapes (Naranjo et al., 2015; Huang et al., 2018). However, a more mechanistic understanding of the effect of landscape context on the delivery of natural pest control and its impact on yield and farmers' income is crucially needed (Schneider et al., 2015; Ali et al., 2018). Pest abundance can also vary with landscape structure, and higher predation rates of pests may not lead to lower abundance and damage (Tscharntke et al., 2016). Consequently, the study of the relationships between pest control potential, as measured in our study, and actual pest abundance deserves more attention. In addition, increasing grassland area at the landscape scale will result in reducing arable crop area; and this might affect farmers' income. Except for livestock farmers, grasslands have no direct economic benefits, at least under the current European common agriculture policy. Such key topic should now be explored to determine the optimal landscape configuration reducing pest infestation and damage, while maintaining crop yield and farmer profitability (Zhang and Swinton, 2009).

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: 10.5281/zenodo.4555503.

AUTHOR CONTRIBUTIONS

AR, SG, and VB designed the study. TP and CC prepared the data and conducted the statistical analysis and wrote the first draft of the manuscript. All authors substantially contributed to revisions.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.607023/full#supplementary-material

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The Interplay Between Thematic Resolution, Forest Cover, and Heterogeneity for Explaining Euglossini Bees Community in an Agricultural Landscape

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Human activities have modified the landscape composition. The changes in the landscape structure can be evaluated by metrics, which are influenced, among other factors, by the number of cover classes used for the landscape classification (thematic resolution). In high thematic resolutions, landscape covers that can influence biological responses are identified and detailed. In low thematic resolutions, this detail level is lower because it aggregates different landscape covers in a few classes. However, how the thematic resolution influences our ability to understand landscape structure on biodiversity is poorly explored, particularly for pollinators. Here we asked how thematic resolution affects the explanatory power of landscape composition on explaining Euglossini bees (richness and abundance) within 15 landscapes composed mainly of coffee and pasture. To address this issue, we quantified the association between five attributes of the euglossine bee community and landscape composition: landscape cover classes (%) and landscape heterogeneity. Moreover, we also evaluated how the thematic resolution influences bee responses to landscape structure. We found a strong and positive influence of landscape heterogeneity in low thematic resolutions (i.e., few cover classes on maps) over the richness and rare species abundance. We also observed that- in addition to the forest cover in the landscape- the pasture cover (%) quantified in high thematic resolution positively influenced the total abundance and abundance of common and intermediate species. Our study highlights the importance of maintaining compositional heterogeneity for the orchid bee community in agroecosystems, and forest cover for the biological requirements and conservation of these pollinators. Moreover, the use of different thematic resolutions showed how specific types of landscape covers influence the euglossine community attributes. This can highlight the species preferences for habitats and landscape covers.

Thus, we call the attention of landscape ecologists to the importance of the definition of thematic resolution, as our ability to quantify the association between biological responses and landscape structure may be influenced by the number of classes used when building thematic maps.

Keywords: Atlantic Forest, Brazil, orchid bees, landscape structure, landscape diversity, mapping, pollinators

INTRODUCTION

The changes in land use may lead to habitat loss and fragmentation. These processes are the main threat to biodiversity, ecosystem functions, and several ecosystem services in the world (Fahrig, 2003; Haddad et al., 2015; Duarte et al., 2018). Human activities, as urbanization and agriculture, have modified the landscape structure and habitat quality across space and time (Fischer and Lindenmayer, 2007; Haddad et al., 2015). These changes reduce patch size and proximity, scattering habitats into anthropogenic matrices (Neel et al., 2004; Haddad et al., 2015). Moreover, forest fragmentation as a process (*sensu* Fahrig, 2003) has consequences related to the increase of the edge effect, with changes in microclimate conditions, thus influencing habitat quality and species persistence at the landscape level (Bender and Fahrig, 2005; Prevedello and Vieira, 2010; Martello et al., 2016).

The landscape changes influence the landscape composition (i.e., number and area of the patches). The use of landscape metrics is crucial for quantifying these elements and inferring the functional landscape heterogeneity, i.e., the diversity of landscape cover based on the functionality of each cover type for a given biological group (Fahrig et al., 2011). However, landscape metrics estimates are influenced by grain size and thematic resolution (Castilla et al., 2009; Liang et al., 2013). Grain size refers to the level of spatial resolution used to describe a data set (Allen and Hoekstra, 1991; Turner and Gardner, 2015), while thematic resolution, the central subject of our study, refers to the number of cover classes used in mapping for the landscape classification (Lechner and Rhodes, 2016).

The choice of thematic resolution in a study is based on the species requirements (e.g., available habitats, nesting) and on which patches might contain these requirements (Fahrig et al., 2011). Since the patches number increases with the number of classes (Castilla et al., 2009; Liang et al., 2013), the decision to include, exclude or aggregate patches in cover classes implies several ways of quantifying spatial patterns in the same landscape (Li and Wu, 2004; Bailey et al., 2007; Castilla et al., 2009; Marshall et al., 2020). Lower thematic resolutions with a small number of cover classes have a more straightforward classification and may aggregate different functional covers, suppressing the necessary level of details to explain biological variables from landscape attributes (Lawler et al., 2004; Marshall et al., 2020). Higher thematic resolutions, on the other hand, result in more detailed mapping of landscape composition and functional covers (e.g., habitat specialists) (Kendall et al., 2011; Liang et al., 2013), increasing the probability to detect associations between biological attributes (e.g., species richness) and landscape structure (Qiu et al., 2019; Marshall et al., 2020). For these reasons, increasing or decreasing the number of cover classes can modify landscapes' functional heterogeneity quantification (Li and Wu, 2004; Lechner and Rhodes, 2016). Thus, our ability of understanding spatio-temporal effects of landscape structure on biodiversity depends on the choice of a thematic resolution that represents the landscape elements that have the most significant explanatory power for ecological responses (Buyantuyev and Wu, 2007; Kendall et al., 2011; Qiu et al., 2019).

The landscape heterogeneity is an essential predictor of biodiversity and positively influences biological attributes such as animal richness and abundance, besides ecological interactions as plant-pollinator (Fahrig et al., 2011; Stein et al., 2014; Moreira et al., 2015, 2018). There is a higher diversity of landscape covers in more heterogeneous landscapes, which may be the niche or complementary habitats for different species (Dunning et al., 1992; Fahrig et al., 2011; Boscolo et al., 2017). The positive effect of landscape heterogeneity has been reported for different biological groups, including bees (Moreira et al., 2015; Boscolo et al., 2017; Coutinho et al., 2020). The higher bee diversity in heterogeneous landscapes has been linked to a high resource diversity essential for feeding, nesting, and maintaining populations in the landscape (Moreira et al., 2017; Nery et al., 2018). However, estimating the effects of landscape heterogeneity on bees depends on choosing a thematic resolution that can distinguish necessary habitats and meaningful landscape covers for the different bee species (Kallioniemi et al., 2017; Marshall et al., 2020).

Bees are essential for the maintaining of the ecosystem's functioning and services through pollination. However, they have been critically affected by landscape degradation and simplification processes (Garibaldi et al., 2011; Viana et al., 2012). The neotropical Euglossini bees constitute an important model for understanding the impact of landscape changes (Brosi, 2009; Cândido et al., 2018). Besides the high dependence on forest environments (Powell and Powell, 1987; Nemésio and Silveira, 2010), euglossine males are easily sampled with aromatic baits (Dodson et al., 1969; Roubik and Hanson, 2004). This tribe comprises about 240 species distributed in five genera (Moure et al., 2012), with a higher diversity reported for the tropical rain forests of South America (Roubik and Hanson, 2004; Nemésio, 2009). Previous studies already showed that changes in the structure of the Euglossini bee community are associated with changes in the landscape (e.g., Powell and Powell, 1987; Brosi, 2009; Cândido et al., 2018; Rocha-Filho et al., 2020). The increase in isolation between forest patches influenced the decline in the species richness of these bees (Powell and Powell, 1987), while the total abundance and richness seem to depend on variables such as shape, size (ha) and isolation (m) of the patches (Brosi, 2009; Nemésio and Silveira, 2010). In addition to forest cover, euglossine bees can be positively influenced by the landscape compositional heterogeneity (Opedal et al., 2020), including different anthropogenic surrounding matrix types (i.e., pasture, agriculture, forestry, or urban areas) (Aguiar et al., 2015; Brito et al., 2017; Cândido et al., 2018). Some species with remarkable environmental plasticity may use these environments to obtain floral resources, as nectar and perfumes (Briggs et al., 2013; Aguiar et al., 2015). Therefore, analyzing non-forest covers is essential to evaluate the euglossine community's responses to the landscape composition and the importance of such environments for these pollinators.

The Euglossini bee communities are characterized by a few dominant species and many rare species (Aguiar and Gaglianone, 2008; Cândido et al., 2018; Rocha-Filho et al., 2020). The dominant euglossine species are habitat generalists and have wide occurrence and tolerance to landscape changes (Aguiar and Gaglianone, 2008; Silva and Marco, 2014; Aguiar et al., 2015). In contrast, rare species are generally restricted to more preserved areas (Tonhasca et al., 2002; Ramalho et al., 2009), resulting in a high sensitivity of these species to landscape disturbances. It is important to consider that the responses of species, communities, or species assemblages to landscape structure at different scales of effects (i.e., the extent of analysis in which a landscape attribute has a high influence on the biological response) can be divergent (Boscolo and Metzger, 2009; Fahrig, 2013; Gestich et al., 2018). An alternative to measuring the scale of effect of a community is to focus on which species were sampled because the species have different life histories, which influence their responses to landscape changes (Fischer and Lindenmayer, 2007; Fahrig, 2013; Hanski, 2015). Therefore, defining the proper spatial extents (i.e., scales of effect) when assessing ecological processes is challenging but is an essential step when considering landscape-based effects.

In this study, we aimed to evaluate how thematic resolution influences our ability to assess the influence of landscape composition on the euglossine bee species. Moreover, we also aimed to understand how species sensitivity to landscape disturbance can be influenced by landscape structure quantified in different thematic resolutions. For this, species dominance and occurrence frequency in the community were used as a proxy of species sensitivity. Specifically, we evaluated the association between five attributes of the euglossine bee community (richness, total abundance, abundance of common, intermediate, and rare species) with compositional metrics [cover (%) of landscape classes and landscape heterogeneity]. We hypothesized that the landscape composition in high thematic resolutions result in a higher explanatory power on bee community attributes (**Figure 1**). We also hypothesized that the euglossine community is mainly influenced by forest cover followed by spatial heterogeneity and non-forest covers (**Figure 1**). Given the dependence of Euglossini bees on forest environments (Roubik and Hanson, 2004), we expected: (a) the richness, total abundance, and species group abundance (common, intermediate, and rare) increase with the forest cover (%) (**Figure 1A**). Given the positive influence of heterogeneity on biodiversity, particularly on insects (Fahrig et al., 2011; Boscolo et al., 2017; Coutinho et al., 2020), we expected: (b) the richness and rare species abundance increase with heterogeneity but decreases when heterogeneity is high (**Figure 1B**), and (c) total abundance, abundance of common and intermediate species increases with heterogeneity (**Figure 1B**). Since non-forest environments are less permeable to some Euglossini species and negatively correlated with richness and abundance (Briggs et al., 2013; Aguiar et al., 2015), we also expect (d) a negative effect of non-forest covers on the five attributes of the Euglossini community (**Figure 1C**). We used euglossine males as our ecological model because (a) they have high flight capacity and respond to landscape degradation (Janzen, 1971; Brosi, 2009; Cândido et al., 2018), (b) they have requirements of nectar and floral perfumes that can be found in several habitats types and landscape cover, resulting in plant pollination in fragmented ecosystems (Roubik and Hanson, 2004; Rocha-Filho et al., 2012; Aguiar et al., 2015), and (c) they can indirectly indicate the abundance of Euglossini females (Opedal et al., 2016).

MATERIALS AND METHODS

Study Area

We carried out this study in 15 landscapes (L01-L15) in the Southeast of Brazil, located in Rio de Janeiro, Espírito Santo, and Minas Gerais states (**Figure 2** and **Supplementary Table 1**). The region has a subtropical altitude climate of the Cwa, and Cwb types, with hot and rainy summer and cold and dry winter. This area was originally covered by phytophysiognomies of the semideciduous seasonal forest and dense montane and submontane forest, characteristics of the Atlantic Forest (Lumbreras et al., 2004; Garbin et al., 2017). The fragmentation process in the region occurred mainly during the economic coffee cycle in the nineteenth century. Coffee crops (*Coffea arabica* L., and *Coffea canephora* P.) occur mainly in many small farms, between 1 and 3 ha, which together span large areas (**Figure 2**). We selected the landscapes along a gradient of forest cover (10–66%).

Bee Sampling

We sampled bees on each landscape for 3 days in the rainy season (November 2019 to March 2020) and 2 days in the dry season (August to September 2019, July 2020). We chose a greater sampling effort in the rainy season because the euglossine bee species show a higher activity during this season (Roubik and Hanson, 2004). Some species also have been associated with the rainy season (Roubik and Hanson, 2004).

A sampling point was selected within a forest fragment in each of the 15 landscapes (**Figure 2**). The minimum distance from the fragment edge was 200 m, and the minimum distance between each sampling point was 2,500 m. We chose forest fragments from secondary successional stages for sampling bees. We used five bait traps to attract euglossine males at each sampling point. These traps were built with polyethylene terephthalate- PET bottles (Aguiar and Gaglianone, 2008), containing one of the five baits soaked in cotton (methyl cinnamate, eugenol, eucalyptol, methyl salicylate, and vanillin). These scents are widely used to sample Euglossini bees (Aguiar and Gaglianone, 2008, 2012;

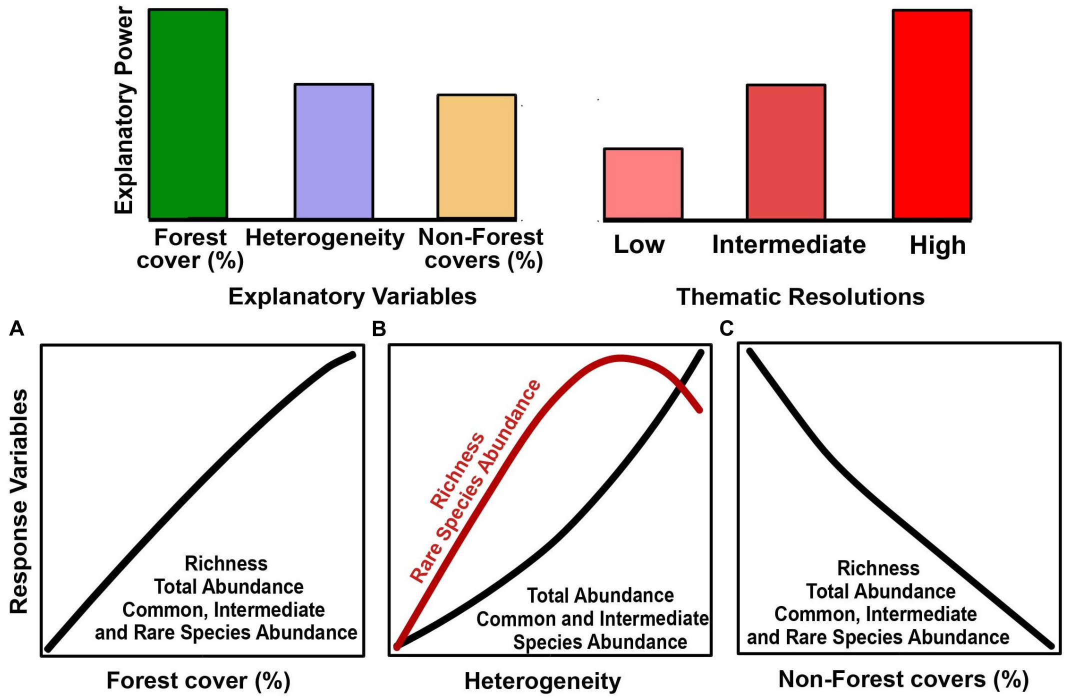

FIGURE 1 | Hypotheses and predictions of the effects of explanatory variables [forest cover **(A)**, heterogeneity **(B)**, and non-forest covers **(C)**], and thematic resolution (low, intermediate, and high) on the parameters of the Euglossini bee community (richness, total abundance, common species abundance, intermediate species abundance, and rare species abundance).

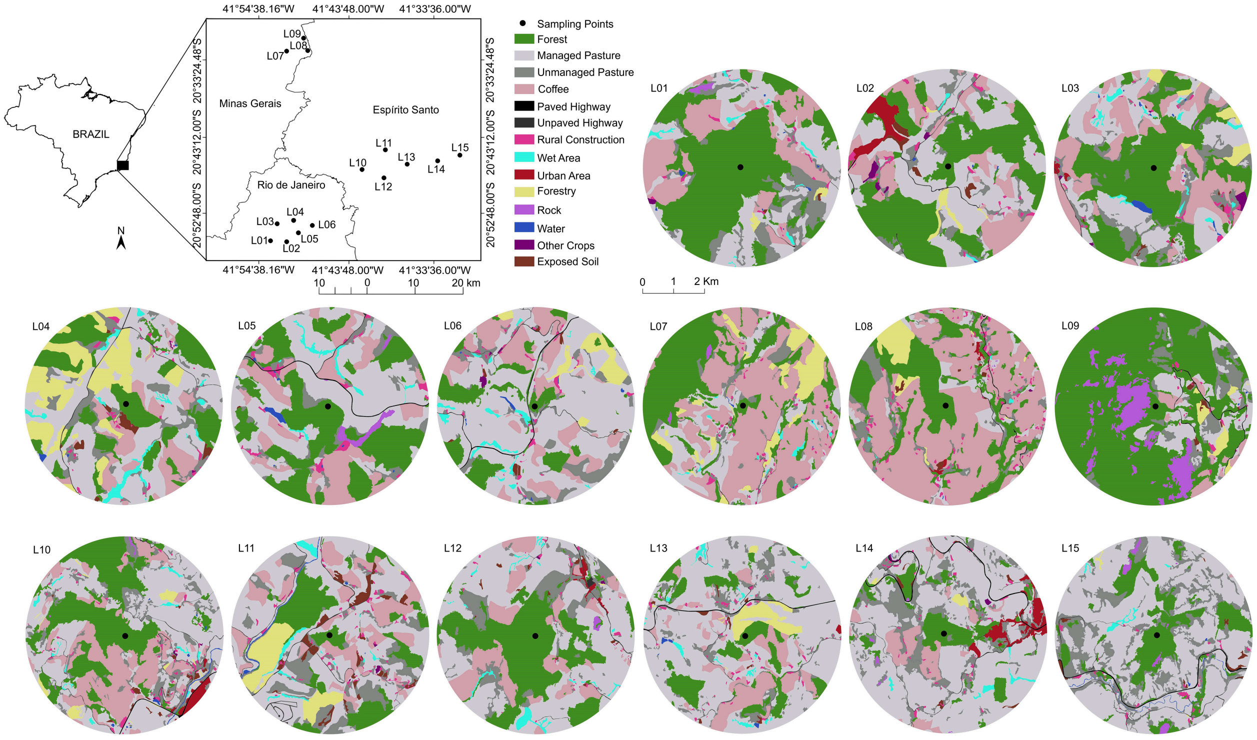

FIGURE 2 | Geographic location and composition of the 15 landscapes in 14-class thematic resolution used for sampling Euglossini bees in the Southeast of Brazil.

Aguiar et al., 2015; Rocha-Filho et al., 2020). The traps were hung in the vegetation, at the height of 1.5 m from the ground, and a minimum distance of 2.0 m between each other (Aguiar and Gaglianone, 2008). We distributed the traps randomly in each landscape on sunny days, early in the morning (06:00–08:00 h), and removed them in the afternoon (03:00–05:00 h). This passive sampling method allows standardization and also sampling in several areas simultaneously. When necessary, the sampled individuals were killed in a chamber with ethyl acetate for taxonomic identification. We deposited the specimens dry in the entomological collection of the Ecologia Experimental sector of the Laboratório de Ciências Ambientais- LCA, Universidade Estadual do Norte Fluminense Darcy Ribeiro- UENF.

Landscape Delimitation and Land Cover Classification

The landscapes were delimited by buffers with a radius of 1,500 m from the centroid of bee sampling locations. We mapped the land cover classes of each landscape using high-resolution satellite images (1-m resolution) available in ArcGis software on a 1:2,500 scale. The mapping was made by generating vector polygons in ArcGIS, followed by visual classification. We used a thematic resolution of 14 land cover classes for mapping (**Figure 2**). The biological importance of each of the 14 classes for euglossine bees is shown in **Table 1**. The vector maps was converted into raster files (5-m resolution). Because we aimed to quantify the effect of thematic resolution on our ability to explain bee responses, we used the R raster package (Hijmans, 2020) and aggregated the 14 land cover classes onto lower thematic resolutions maps: 12, 6, and 3 classes. For the thematic resolution with 3 classes, we generated two different classifications- see 3 and 3.1 in **Table 2**.

We downgrade the thematic resolution based on land use and management similarities, and the class functionality for the bees. Thus, we aggregated classes that could be perceived and used similarly by euglossine species. We first aggregated subtype classes into single classes, as expected to have a similar effect on the explanatory power. Thus, in the 12-class thematic resolution, we only aggregated the pasture and highway subtypes into two unique classes ("Pasture" and "Highway"). In the

TABLE 1 | Description and biological importance of the 14 classes used in landscape mapping.

14-class thematic resolution	Description and biological importance of classes	References
Forest (FO)	Most important habitat for Euglosssini bees. Essential resources for species requirements such as pollen, nectar, resins, nesting sites, and perfumes are found in this environment.	Dressler, 1982; Rocha-Filho et al., 2012
Managed pasture (MP)	Grass species (e.g., *Brachiaria* sp.) are predominant in this environment, with more hard environmental conditions (e.g., temperature, humidity) and few floral resources for bees. Euglossine species can disperse between forest patches through these environments.	Kruess and Tscharntke, 2002; Tonhasca et al., 2003
Unmanaged pasture (UP)	There is heterogeneous vegetation (e.g., pioneer plants, shrubs) in these environments that can support floral resources for euglossine species.	Aguiar et al., 2015
Wet area (WA)	This wet soil environment allows vegetation growth such as unmanaged pasture, which may provide floral resources for euglossine bees.	
Coffee (CF)	Crops of *Coffea arabica* and *Coffea canephora* varieties under different management systems (e.g., organic, traditional). They are permeable to Euglossini species depending on the management intensity and can provide floral resources through pioneer plants in the crop.	Briggs et al., 2013; Carneiro, personal observation
Forestry (FY)	Crops of *Eucalyptus* sp. with high management intensity (e.g., pesticides) and low heterogeneity. In this environment, the euglossine community is composed of few species, with higher environmental plasticity.	Aguiar et al., 2015
Other crops (OC)	Crops of *Saccharum* sp., *Mus*a sp., *Cocos* sp., and *Citrus* sp. in small areas and polyculture systems. Agroforestry and polycultures benefit the euglossine community, because their support a diversity of floral resources.	Briggs et al., 2013; Rosa et al., 2015
Paved highway (PH) and Unpaved highway (UH)	These environments are impermeable (paved) or compacted (unpaved), with hard environmental conditions (e.g., high temperatures, noise, low humidity) and absence of floral resources, negatively affecting bees.	Boscolo et al., 2017
Rural construction (RC)	Human constructions, usually with impermeable or compacted soil. They may have floral resources for euglossine bees through exotic or native plants (e.g., Orchidaceae).	Carneiro, personal observation
Urban areas (UA)	This environment negatively influences the euglossine species richness. Euglossini species with higher environmental plasticity may benefit from floral resources of native and exotic plants from this environment.	López-Uribe et al., 2008; Cândido et al., 2018
Rock (RO)	Rocky outcrops that despite conditions such as higher temperatures and wind intensity may provide resources (e.g., nesting sites) for euglossine bees through plants adapted to this environment (e.g., Bromeliaceae, Orchidaceae).	Dressler, 1982; Boff and Alves-dos-Santos, 2018
Water (WT)	Natural (rivers) and artificial (lakes) environments. Water is a fundamental element for the organisms' requirements.	
Exposed soil (ES)	This environment is generally a consequence of anthropic activities (e.g., plowing, erosion). Some species of euglossine nest in the soil.	Roubik and Hanson, 2004; Augusto and Garófalo, 2007

6-class thematic resolution, we also considered the different levels of human activities over the landscape. Four covers resulted of human activities were aggregated in "Anthropic constructions". We aggregated as "Semi-natural environments" three covers distributed naturally in the landscape but may be subject to anthropic changes (**Table 1**). Likewise, the class "Pasture" aggregated three cover classes, including managed and unmanaged pasture, and "wet areas" that are spatially associated (**Table 1** and **Figure 2**). We aggregated "Forestry and other crops" as a single cover class. However, we kept "Coffee" as a single cover class in this resolution because of its high proportion in the landscape and potential influence on the Euglossini communities (see **Table 1**). In the 3-class thematic resolution, we aggregated all covers with arboreal-shrub vegetation (**Table 2**) that can provide floral resources for euglossine bee species in "Non-forest vegetation" (**Table 1**). Likewise, we aggregated all covers with open but non-arboreal vegetations or occupied by humans in "Anthropic and semi-natural environments" since their abiotic conditions could be less friendly to euglossine bees (**Table 1**). Finally, in the 3.1-class thematic resolution, we aggregated all covers that could be fundamental or complementary habitats for Euglossini bees in "Unmanaged land cover" (**Tables 1**, **2**). We aggregated in "Farming and semi-natural environments" covers with high management intensity or open environments that could present less suitable environmental conditions for euglossine bees (**Tables 1**, **2**). In the last class ("Anthropic environments"), we aggregated covers including anthropic constructions or those spatially associated ("Other crops") (**Tables 1**, **2**).

Landscape Metrics

We used the *lsm* function of the R landscapemetrics package (Hesselbarth et al., 2019) to calculate two landscape metrics for the five thematic resolutions: (a) cover (%) of classes in the landscape (PLAND = percentage that each class occupies regarding the landscape area), and (b) landscape heterogeneity (SHDI = Shannon diversity index calculates the proportion and diversity of classes in the landscape) (McGarigal, 2015). The forest is an essential habitat for the Euglossini species requirements (e.g., nectar, pollen, resin, floral perfumes, nesting sites) (Roubik and Hanson, 2004; Rocha-Filho et al., 2012). The landscape heterogeneity represents the environmental diversity that Euglossini species can use and also influence the community composition of Euglossini (Aguiar et al., 2015; Opedal et al., 2020). The cover of classes also allows measuring non-forest covers in the landscape (e.g., pastures, crops) that may represent complementary habitats for euglossine bees (Briggs et al., 2013; Aguiar et al., 2015). Moreover, it is known that cover (%) of classes and heterogeneity are good predictors of Euglossini bee communities (Cândido et al., 2018; Opedal et al., 2020). We calculated these landscape metrics at different spatial scales: 500, 750, 1,000, and 1,500 m. As we have an interest in quantifying the relative contribution of forest cover (%) and heterogeneity on explaining bee responses, we calculated the Pearson's correlation between these metrics for all the spatial scales and all the thematic resolution to identify which spatial scale presents the lower correlations. Therefore, we evaluated the low ($r < 0.5$) and non-significant ($p > 0.05$) Pearson's correlation between the forest cover and heterogeneity in the five thematic resolutions (14, 12, 6, 3, and 3.1 classes). After critical analysis and based on previous

TABLE 2 | Number and arrangement of classes used to classify the landscape in five thematic resolutions.

Thematic resolutions				
14 classes	**12 classes**	**6 classes**	**3 classes**	**3.1 classes**
FO	FO	FO	FO	Unmanaged land cover (FO + UP + WA + RO)
MP	Pasture (MP + UP)	Pasture (MP + UP + WA)	Non-forest vegetation (UP + WA + CF + FY + OC)	Farming and semi-natural environments (MP + CF + FY + WT + ES)
UP				
WA	WA			
CF	CF	CF		
FY	FY	FY + OC		
OC	OC			
PH	Highway (PH + UH)	Anthropic constructions (PH + UH + RC + UA)	Anthropic and semi-natural environments (MP + PH + UH + RC + UA + RO + WT + ES)	Anthropic environments (OC + PH + UA + RC + UA)
UH				
RC	RC			
UA	UA			
RO	RO	Semi-natural environments (RO + WT + ES)		
WT	WT			
ES	ES			

CF, Coffee; ES, Exposed soil; FO, Forest; FY, Forestry; MP, Managed pasture; OC, Other crops; PH, Paved highway; RC, Rural construction; RO, Rock; UA, Urban area; UH, Unpaved highway; UP, Unmanaged pasture; WA, Wet area; WT, Water.

studies (Moreira et al., 2017; Cândido et al., 2018), we decided to use only the metrics calculated at the 1000 m spatial scale for all the thematic resolutions (see **Supplementary Table 2**).

Euglossini Bee Response Variables

Five aspects of euglossine bee community structure were used as response variables: richness, total abundance, common species abundance, intermediate species abundance, and rare species abundance. We quantified abundances using occurrence frequency (OF) and dominance (D) of each species in the community, in which OF = number of samples with species *i*/number of total samples * 100, and D = abundance of species *i*/total abundance * 100. When OF $\geq$ 50%, the species were classified as very frequent (vf), if OF $<$ 50% and $\geq$ 5%, the species were frequent (f), and OF $<$ 25%, the species were low frequent (lf) (Bodenheimer, 1955). If D $\geq$ 5%, the species were categorized as dominant (d), D $<$ 5% and $\geq$ 2.5% the species were accessory (a), and D $<$ 2.5% the species were occasional (o) (Bodenheimer, 1955). The OF and D values were combined, allowing the categorization of the three groups of species: Ct = vf + d = common species, Ct = lf + o = rare species; Ct = other combinations = intermediate species (Palma, 1975; Aguiar and Gaglianone, 2012).

Data Analysis

Our data analysis comprised two steps. First, we performed exploratory analyses using Generalized Linear Models (GLMs) to find the models in which the landscape attributes best explained the euglossine community in each thematic resolution. In the second step, we made a new GLM selection using only the best models previously selected. In this step, the best models that had the cover (%) of classes or landscape heterogeneity as explanatory variables in each thematic resolution were ranked with each other. Thus, we accessed the landscape attributes with the higher explanatory power on the euglossine community and the thematic resolution (i.e., high or low) in which these attributes were measured. We presented the details of the two steps below.

Step 1

As altitude is a very influential factor in the Euglossini communities (Aguiar and Gaglianone, 2012; Pinto et al., 2019), we first quantified the influence of altitude on species richness and total abundance using linear regressions. Before that, abundance was log-transformed using base 10. The diagnosis of these models was made by the *boxcox* function of the R MASS package (Venables and Ripley, 2002). Given the observed altitude influence on the euglossine community (**Supplementary Figure 1**), we removed the altitude's effect on the response variables by analyzing residuals from linear models, in which the altitude was the explanatory variable (Response Variable $\sim$ Altitude).

We sought to explore through Generalized Linear Models (GLMs) an association of the residues of the euglossine community attributes with the cover (%) of forest and non-forest classes, and landscape heterogeneity in each thematic resolution. We build models that combined the landscape heterogeneity, cover (%) of forest, pastures, and coffee as explanatory variables in resolutions of 14, 12, and 6 classes (**Supplementary Table 3**). These three covers represented the largest proportion of the landscape composition (76–98%) in these resolutions. In resolutions of 3 and 3.1 classes, the models combined landscape heterogeneity and the three types of covers as explanatory variables (**Supplementary Table 3**). We used the residuals of the response variables to associate with the landscape metrics, so the Gaussian distribution was used in the GLMs. We used Akaike's Information Criterion corrected for small sample size (AICc) (Burnham and Anderson, 2002) to rank the models. The model with the lowest ΔAICc was considered the most explanatory model. Also, models in which ΔAICc $<$ 2.0 and the model weight (*wi*) $>$ 0.1 were considered equally plausible to explain the patterns. A null model- that assumes no association between the response and explanatory variable- was also considered in the model comparison. We used the *Ictab* function from the R bbmle package to select the models (Bolker and R Development Core Team, 2020). In this step, we analyzed 255 models in the five thematic resolutions (**Supplementary Table 3**), of which 59 models were selected for Step 2 (**Supplementary Table 4**).

Step 2

From the selected models in step 1, we performed another round of model comparison to identify the thematic resolution that better explain the response variables to the landscape attributes (heterogeneity and cover (%) of classes) (**Supplementary Table 4**). The null model was also included as a competing model in the model selection procedure. The best models were chosen using the same criteria presented above (i.e., ΔAICc $<$ 2.0 and *wi* $>$ 0.1). We accessed the coefficient of determination (R^2) of the "variance-function-based" type of the best GLMs to quantify the variation of the response variable explained by the landscape attributes. For this, we used the *rsq* function from the R rsq package (Zhang, 2020).

RESULTS

Overview

We sampled 1890 male Euglossini bees, distributed in four genera and 14 species (**Supplementary Table 5**). *Eulaema nigrita* Lepeletier (55.1%) and *Euglossa cordata* (Linnaeus) (25.5%) were the most abundant species in the community. The total abundance in the landscapes ranged from 7 to 391 individuals (126 ± 111), while the richness varied between 4 and 9 species (6.4 ± 1.5).

Common species (S = 4) were sampled in all 15 landscapes (N = 1783 individuals; variation in landscapes 118 ± 110), intermediate species (S = 4) were recorded in 14 landscapes (N = 96 individuals, variation in landscapes 6.4 ± 4.2), while rare species (S = 6) occurred in eight landscapes (N = 11, 0.73 ± 0.79) (**Supplementary Table 5**).

Best Thematic Resolutions to Explain the Euglossini Community From Landscape Composition

The Euglossini community showed different responses to the landscape attributes in the thematic resolutions. The low thematic resolution detected significant effects of landscape composition on the residual richness (ΔAICc < 2.0 and *wi* > 0.1). The 3-class resolution showed a positive effect of landscape heterogeneity on the residual richness (R^2 = 0.28) (**Figure 3A** and **Table 3**). The second plausible model in this resolution combined the positive effect of heterogeneity and negative effect of forest cover on the residual richness (R^2 = 0.37) (**Figure 3B** and **Table 3**).

In a high thematic resolution (14-class), the residual total abundance and residual common species abundance presented significant responses to landscape composition. The best models combined positive effects of managed pasture and negative effects of forest cover on both residual total abundance (R^2 = 0.57) (**Figure 3C**) and residual common species abundance (R^2 = 0.56) (**Figure 3D** and **Table 3**).

The landscape composition in both high and low thematic resolutions explained the residual abundance of intermediate and rare species. The 14-class resolution presented a positive effect of forest + managed pasture covers on the residual intermediate species abundance (R^2 = 0.26) (**Figure 4A** and **Table 3**). These species abundance was also negatively related to the non-forest vegetation cover in the 3-class resolution (R^2 = 0.19) (**Figure 4B** and **Table 3**). However, the null model was in the set of plausible models (ΔAICc < 2.0) (**Table 3**). Finally, the residual rare species abundance was best explained by a positive correlation with the landscape heterogeneity of the 3.1-class (R^2 = 0.34) and 14-class resolution (R^2 = 0.27) (**Figures 4C,D** and **Table 3**).

DISCUSSION

This study showed that our ability to explain attributes of the Euglossini community (richness, total abundance, abundance of common, intermediate, and rare species) from the landscape composition depends on the thematic resolution level. We refuted our hypothesis that the euglossine community are mainly influenced by forest cover since the landscape heterogeneity, and non-forest covers had a higher explanatory power on euglossine bees. We supported the hypothesis that high thematic resolution has a higher explanatory power through the relationship of the

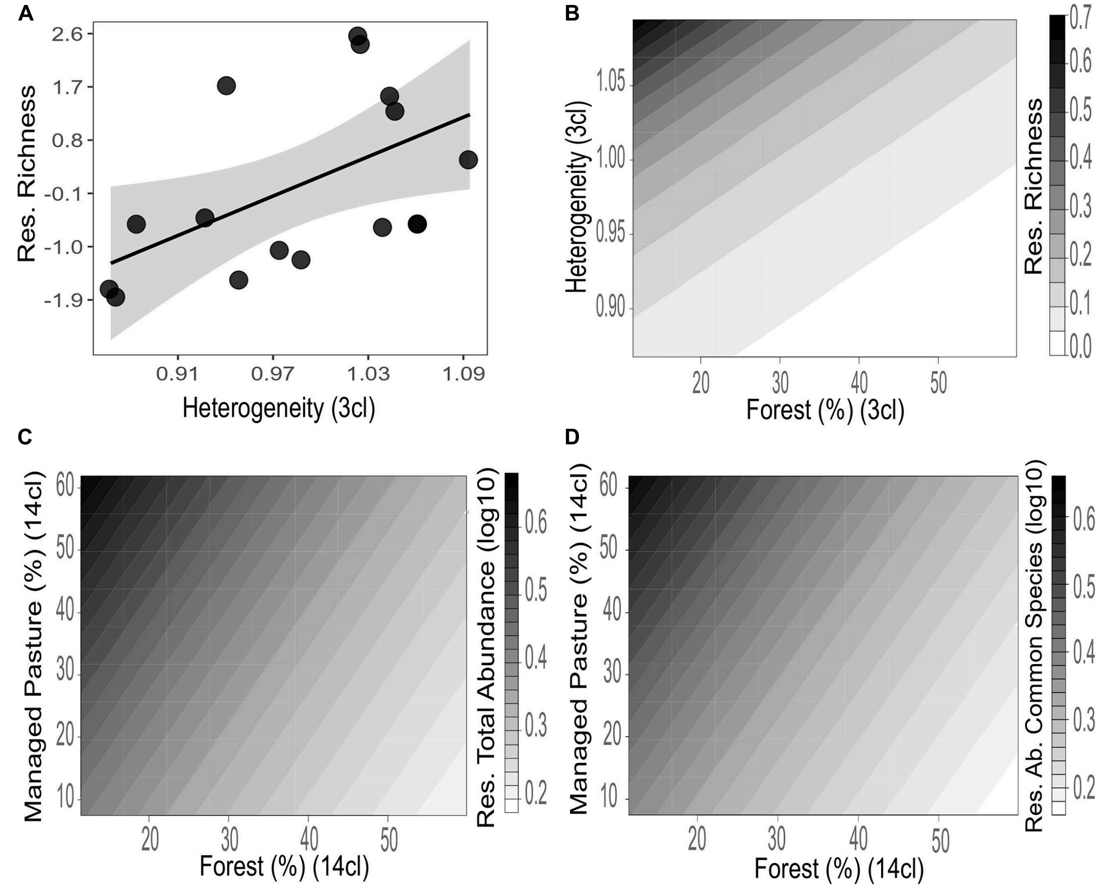

FIGURE 3 | Influence of the landscape composition on the residues of richness **(A,B)**, total abundance **(C)**, and common species abundance **(D)** of Euglossini bees in different thematic resolutions. The black line represents the GLM model fitting and the gray shadow the 95% confidence interval.

TABLE 3 | Best models (ΔAICc < 2.0 and *wi* > 0.1) to explain the attributes of the Euglossini community from the landscape composition in different thematic resolutions.

Response variable	Models	ΔAICc	*wi*
Residual species richness	Heterogeneity (3 classes)	0.0	0.15
	Forest cover + Heterogeneity (3 classes)	0.73	0.10
Residual total abundance (log10)	Forest cover + Managed Pasture cover (14 classes)	0.0	0.20
Residual common species abundance (log10)	Forest cover + Managed Pasture cover (14 classes)	0.0	0.18
Residual intermediate species abundance (log10)	Forest cover + Managed Pasture cover (14 classes)	0.0	0.21
	Non-forest vegetation cover (3 classes)	1.27	0.11
	Null	1.43	0.10
Residual rare species abundance	Heterogeneity (3.1 classes)	0.0	0.43
	Heterogeneity (14 classes)	1.52	0.20

The wi represents the model weight.

total abundance, abundance of common and intermediate species with the landscape composition in high thematic resolution (i.e., 14 classes). However, this hypothesis was refuted for the richness and rare species abundance explained by the landscape compositional heterogeneity in low thematic resolutions (3 and 3.1 classes).

Influence of Compositional Heterogeneity and Thematic Resolution

In fragmented landscapes, biodiversity is influenced by spatial heterogeneity (Fahrig et al., 2011). The positive relationship between the richness of different bee groups and landscape heterogeneity has been reported (Boscolo et al., 2017; Moreira et al., 2017; Coutinho et al., 2020; Opedal et al., 2020), indicating the importance of landscape diversity for the biological requirements of these pollinators. It is expected that the landscape structure in fine thematic resolutions better explains species richness (Lawler et al., 2004; Qiu et al., 2019). The association found between richness and heterogeneity at low resolution may indicate that several Euglossini bee species can perceive the landscape on a coarser scale, where different types of landscape cover have been aggregated into the same class. This may have occurred because, in addition to the forest, these bees use different types of cover for foraging (Aguiar et al., 2015; Brito et al., 2017), which may present a supply of resources, such as nectar and floral scents (Aguiar et al., 2015; Opedal et al., 2020). Despite the landscape heterogeneity in low thematic resolution reflects the aggregation of many landscape covers, the forest cover

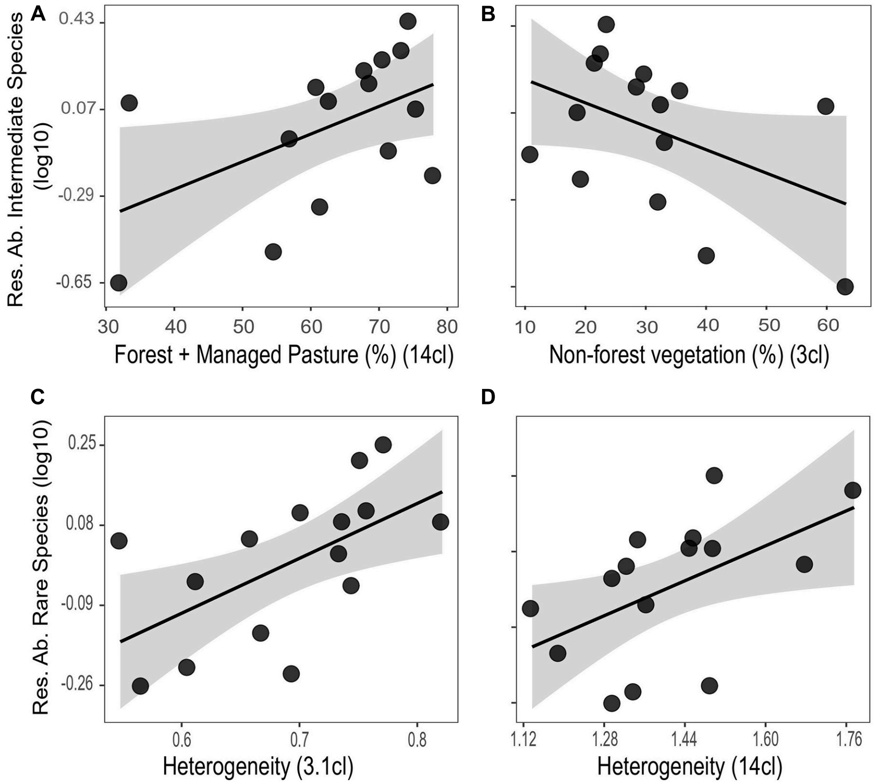

FIGURE 4 | Influence of the landscape composition on the residues of intermediate species abundance **(A,B)**, and rare species abundance **(C,D)** of Euglossini bees in different thematic resolutions. The black line represents the GLM model fitting and the gray shadow the 95% confidence interval.

combined with heterogeneity in the model increased the explanatory power on species richness. This indicates the importance of this landscape composition attribute to explain the euglossine community (Brosi, 2009; Cândido et al., 2018). Although we expected a unimodal response of species richness to heterogeneity, we observed a linear relationship between these two attributes. These landscapes seem to support a level of compositional heterogeneity that results in a high euglossine richness. Unimodal relationships occur at high levels of spatial and environmental heterogeneity because it is when the negative effects of heterogeneity act on population dynamics (e.g., extinction, colonization) (Fahrig et al., 2011; Ben-Hur and Kadmon, 2020).

The highest total abundance and common species abundance were observed in landscapes with low forest cover and a high pasture cover. The association between total abundance and landscape cover was very similar to the association observed for common species abundance (*Eulaema nigrita*, *Euglossa cordata, Euglossa fimbriata* Rebêlo & Moure, and *Euglossa securigera* Dressler). If we consider the relative abundance of these four common species, they represented 94.3% of the sampled individuals. This calls attention to studies that consider only total abundance as a response variable to assess the effects of landscape changes on communities. These dominant species have higher phenotypic plasticity and tolerance to changes in the landscape (Silva and Marco, 2014; Aguiar et al., 2015; Carneiro et al., 2019). Therefore, this may underestimate the effects of these processes on groups of less abundant species in the community.

In addition to the forest, pasture cover (%) had a high influence on the abundance of most euglossine species. These bees have high flight capacity (Janzen, 1971), and several species have already been sampled on the forest edges or within the pasture matrix (Aguiar et al., 2015). Despite presenting different characteristics of forest environments (e.g., high temperatures, low humidity, high wind speed), this matrix may offer floral resources through pioneer plants for euglossine species with higher environmental plasticity (Aguiar et al., 2015). These relationships between total abundance, abundance of common and intermediate species with forest environments, and pasture matrices were best explained by mapping in high thematic resolution (i.e., 14 classes). In higher thematic resolutions, many areas that may be used as habitats are identified (Liang et al., 2013; Marshall et al., 2020). Thus, for these evaluated abundance variables, the 14-class thematic resolution can better indicate the "landscape complementation" (Dunning et al., 1992), as it would represent more realistically the environment mosaic that euglossine males use to obtain resources. Despite a lower explanatory power, the intermediate species abundance was negatively affected by the non-forest vegetation in the lowest thematic resolution. This landscape cover was mainly composed by crops (e.g., coffee, forestry). Some intermediate species (e.g., *Euglossa clausii* Nemésio & Engel, *Euglossa truncata* Rebêlo & Moure) have been known as restricted to forest (Ramalho et al., 2009; Aguiar et al., 2015). This may indicate that crop areas can negatively affect these species and the euglossine communities (Briggs et al., 2013; Aguiar et al., 2015).

The landscape heterogeneity was the most important variable to explain the rare species abundance. Among the response variables that we analyzed, the abundance of this group of species was the only one that showed a strong association with the thematic resolution of 3.1 classes. The responses to compositional heterogeneity for each group of species are distinct and driven by the relationship that organisms have with each landscape cover class (Lawler et al., 2004; Kendall et al., 2011; García-Álvarez et al., 2019). In the resolution of 3.1 classes, we considered 'Unmanaged land cover' as a heterogeneous environment, composed of classes with natural (i.e., forest) and semi-natural vegetation, which can provide resources and conditions for the euglossine species. However, the study area comprises an old forest cover loss, with most of the forest patches composed of secondary vegetation. Thus, many of the bee species categorized as rare may show adaptations to open environments. Some of these species (e.g., *Eulaema atleticana* Nemésio, *Euglossa pleosticta* Dressler) are medium and large size bees, which can forage in matrices neighboring the forest fragments (Aguiar et al., 2015; Rosa et al., 2015). Therefore, the conservation of these environments in the landscape is essential to keep the diversity of these species. The loss of compositional heterogeneity can negatively affect rare and specialist species, resulting in biological homogenization (Gámez-Virués et al., 2015; Martello et al., 2018).

CONCLUSION

This study showed that compositional heterogeneity influences the Euglossini bee community, both positively and negatively, and these responses depend on the thematic resolution used to characterize the landscape. The decision to aggregate class covers in low thematic resolutions showed that different types of patches in the landscape could be functionally similar for euglossine species. On the other hand, high thematic resolutions revealed that non-forest cover (i.e., managed pasture) has a high explanatory power on the most common species in the community. However, it is important to be cautious about the thematic resolution's influence on explaining some euglossine community attributes. This because the abundance of rare and intermediate species were correlated with the landscape composition in both high and low thematic resolutions. Furthermore, we showed that species dominance could be an important proxy for understanding species sensitivity to landscape disturbances. Because in these areas of the Southeast of Brazil, forest cover is threatened by agricultural activities such as coffee crops, we call attention to conserving forest remnants. At the same time, these landscapes still have a high diversity of environments linked to the many types of land use that small farmers maintain on their properties (e.g., agroforestry, unmanaged pastures). These friendly landscapes favored, for example, the species richness and rare species abundance. Agricultural intensification is a growing phenomenon, especially in tropical regions. If these practices are associated with landscape homogenization, pollinators such as bees can be critically affected.

We also call attention to consider the influence of the thematic resolution on the association of biological parameters with landscape metrics in future studies. With the advent of new technologies and spatial data sets, including landscape mapping in large regions (e.g., MapBiomas in Brazil), the use of different thematic resolutions becomes more accessible. As we showed, the choice of thematic resolution is a critical step that influences our ability to explain biological parameters from the landscape structure.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

LC and MG conceived the study design and wrote the manuscript. WA, MG, LC, and MR designed methodological approach. LC and WF-S collected the data. LC and MR calculated the landscape metrics. MR, WF-S, and LC analyzed the data. CP and LC mapped the landscapes. All authors revised the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.628319/full#supplementary-material

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Small Landscape Elements Double Connectivity in Highly Fragmented Areas of the Brazilian Atlantic Forest

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The Atlantic Forest in Brazil is a biodiversity hotspot, yet its diverse ecosystems and species are becoming increasingly threatened by habitat loss and extreme habitat fragmentation. Most habitat patches of Atlantic Forest are dispersed across agricultural landscapes (e.g., grazing and cropping) in relatively small and isolated fragments (80% < 50 ha). Forest fragments < 1 ha, scattered trees in pastures, tree lines on trenches and fences, and remnant riparian forest, collectively called here Small Landscape Elements (SLEs), are very common in this context. While these SLEs make up much of the Atlantic Forests footprint, very little is known about their role or impact on the persistence and conservation of species. In this study, we investigate the role of SLEs on landscape configuration, particularly their contribution toward landscape connectivity of individual species and the genetic flow of species between larger forest fragments. We randomly selected 20 buffers of 707 hectares within a 411,670 hectare area of the Atlantic Forest that was completely covered by forest in the past located in the south of Minas Gerais State, Brazil. The forest cover randomly varied between these buffers. We used graph theory to measure landscape connectivity as the probability of connectivity for different disperser movement types between landscape knots (habitat patches). We used three estimated dispersal distances in the models: pollen disperser insect (50 m), low-mobility seed disperser bird (100 m) and high-mobility seed disperser bird (760 m). The SLEs together increased the probability of connection by roughly 50%, for all model dispersers, if compared to a theoretical baseline landscape containing no SLEs. Of all SLEs, riparian forests contribute the most toward enhancing landscape connectivity. In these highly fragmented landscapes, such as the Atlantic Forest (>70%), the position of SLEs within the landscapes was more important than their respective areas for connectivity. Although the landscapes were deeply fragmented, we showed that the presence of SLEs can increase connectivity and reduce further biodiversity loss in the Atlantic Forest.

Keywords: tropical forest, landscape connectivity, private land conservation, biodiversity conservation, remote sensing-GIS, fragmentation, habitat loss

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INTRODUCTION

Environmental degradation is strongly linked to natural habitat loss. Deforestation transforms landscape configuration, increases forest fragmentation, increases the number of small forest patches, increases isolation among forest patches, ultimately resulting in a reduction of biological diversity (henceforth, biodiversity) (Pardini et al., 2010; Banks-Leite et al., 2014; Ribeiro et al., 2019). Tropical deforestation is most commonly related to the conversion of tropical forests to agricultural land use types such as cropland or pastures (Ribeiro et al., 2019; Levis et al., 2020). Although most of this land use conversion is arguably driven by increasing the land availability for food production (FAO, 2020), losing natural habitat can also lead to perverse outcomes for food production. For example, a decline in insect pollinator abundance can reduce crop yields and changing land use can decrease the availability of water for crops (Garibaldi et al., 2011; Saturni et al., 2016; Fitton et al., 2019). This lack of connectivity caused by high instances of poorly planned land-use change is one of the greatest challenges in modern conservation (Dobson et al., 1997) and thus, maintaining and improving landscape connectivity is one of the challenges for biodiversity conservation in highly fragmented landscapes (Taylor et al., 2006). Understanding how an increasing agricultural footprint impacts the extent and landscape connectivity of tropical forests is essential to minimize further biodiversity loss and maximize agricultural yield in a sustainable way (Melo et al., 2013).

Gene flow is affected both by landscape connectivity and by the dispersal capabilities of different organisms. Landscape connectivity refers to the ease in which organisms can move in a landscape (Taylor et al., 1993), through small patches within (e.g., scattered trees and forest fragments < 1 h) and between existing protected areas (e.g., remnant riparian forest) (Ward et al., 2020). Functional connectivity considers the behavioral responses of an organism to the various landscape elements, while structural connectivity is equated with habitat contiguity and can also be inferred by landscape metrics (Tischendorf and Fahrig, 2000). For example, the area and shape of habitat patches, as well as their distribution in the landscape, using maps produced from satellite images. Landscape connectivity can be measured directly by measuring the movement of organisms within a landscape, including how organisms are affected by landscape elements (Tischendorf and Fahrig, 2000). This can be done using direct observation of an organism's movements (e.g., radio telemetry), or experimentally using computer simulations of species with specific functional traits (Keller et al., 2013). Organisms highly specialized in forest habitats and/or with lower dispersal distances tend to be most affected by the size reduction of habitat patches and by the isolation of those patches caused by non-habitat matrices (Banks-Leite et al., 2014; Barlow et al., 2016).

Maintaining continuous and wide forest corridors is one of the most accepted means to provide functional and structural connectivity between protected areas. Global protected area targets like the Sustainable Development Goal 15 and the Aichi Target 11 both emphasize the importance of maintaining a well connected reserve network. There are also efforts by countries to nationally promote habitat connectivity, for example the Brazilian Pact for Restoration of the Atlantic Forest and the Mantiqueira Corridor is an example of a commitment to protect and maintain continuous and wide forest corridors (Pact for the Restoration of the Atlantic Forest, 20116). Research finds that large protected areas and wide corridors are best to maintain the movement of individuals across populations, avoiding population isolation, and consequently, decreasing the risk of inbreeding depression and the occurrence of genetic bottlenecks (Charlesworth and Willis, 2009; Hedrick and Garcia-Dorado, 2016; Trewick et al., 2017). However, large protected areas that are connected by wide corridors can conflict with more economic use of the land like agriculture, competing for space with crops and cattle grazing. On the other hand, small landscape elements (SLEs) like scattered trees, hedges and hedgerows, and small forest fragments can also provide landscape connectivity in areas under economic use adding significantly to biodiversity conservation (Kremen and Merenlender, 2018), without competing intensely with land economic use.

Small landscape elements (SLEs) in agricultural lands are extremely important for biodiversity. Scattered trees are considered key structures for vertebrates, arthropods, and plants, as they provide shelter, food, and landing places for volante fauna (Prevedello et al., 2018). Scattered trees have also been shown to alter the microclimate under their crowns which can facilitate tree species establishment (Siqueira et al., 2017). Additionally, scattered paddock trees provide environmental services as shade for the cattle, which has been found to increase milk and beef yield in tropical areas (Paciullo et al., 2011; Mello et al., 2017). Hedges, hedgerows and tree lines are common in agricultural lands. These types of SLEs can be very old and are normally used for landscaping or as divisions between land patches under different ownership or management (Baudry et al., 2000). Trees lines can be found along property perimeter fences or in the case of Brazil, can be a consequence of the natural colonization of trenches. These hedgerow-like structures in Brazil have a high historical value, as a heritage from the slavery period, as well as a high ecological relevance working as habitat and corridors for plants and fauna (Castro and van den Berg, 2013; Rocha et al., 2014). Although there is now strong evidence showing the ecological importance of the hedges and hedgerows associated with trenches (Castro and van den Berg, 2013; Rocha et al., 2014), less is known about the ecological importance of tree lines associated with the fences.

In this study, we investigate the role of SLEs for landscape connectivity for insect pollinators, small avian seed dispersers (e.g., genus *Turdus*, locally called "sabiá") and large avian seed dispersers (e.g., genus *Ramphastos*, locally called "Tucano"), in Minas Gerais State, Brazil which is a region containing areas of Atlantic Forest and agricultural land (Kremen and Merenlender, 2018). We aim to identify how fragmented, and in which configuration, is the Atlantic Forest landscape. How landscape metrics change the landscape connectivity in a gradient of fragmentation. The importance of the SLEs for landscape connectivity, and which metrics of the SLEs are important for the landscape connectivity. Answering these questions is fundamental to establish strategies for conservation in agricultural lands, specifically in how we should deal with the SLEs in an agricultural landscape. Although this study was conducted in the Brazilian Atlantic Forest, the results are also relevant for other tropical forest biomes where similar processes of habitat loss and fragmentation have occurred, are still occuring, or are predicted to occur in the future. According to (Joly et al., 2014), the Brazilian Atlantic Forest can be considered as a large natural laboratory where we can test the effects of past human impact and project them to other tropical biomes where those changes will happen in the future.

MATERIALS AND METHODS

Study Area

Areas in Brazil that historically were covered by vast tropical forests, like the Atlantic Forest, have since been converted to agricultural uses, slicing once intact areas of tropical forests into many small forest patches (Laurance et al., 2011; Lewis et al., 2015; Taubert et al., 2018). The area of focus for this study is an area of the Brazilian Atlantic Forest, in Minas Gerais State, south-eastern Brazil (**Figure 1**). The climate Köppen type is CWA and CWB, with warm and wet summer and dry winter (Dantas et al., 2007). The soils are latosols and argisols (dos Santos et al., 2011). Most of the Atlantic Forest in the south of Minas Gerais State was converted to agricultural pasture composed of exotic grasses and, in a minor proportion, to cropland (mainly annual crops and coffee). In this region, milk production is more important than beef. This land-use change occurred in the last 150 years and provoked intense forest fragmentation. Forest conversion to other land uses has been rare in the last 30 years. Other elements are present in the landscape as a large artificial reservoir for hydroelectricity, small urban areas, and eucalyptus plantations.

In Brazil, the SNUC (Sistema Nacional de Unidades de Conservação—National System of Conservation Units, Law No. 9.985/2000) states that integral protected areas must be large and be isolated from farming or other economic activities (Brasil, 2000). Within the Brazilian Atlantic Forest, small forest fragments have a variable shape, often presenting themselves as long and narrow forests (Crouzeilles et al., 2013). These small forest fragments, in general, remain standing on the property due to legal restrictions (e.g., "The General Law for Native Vegetation Protection," Brasil, 2012). This is the case of riparian forests along watercourses partially protected in Brazil by the Law No. 12.651 of 2012 (Brasil, 2012). Small forest fragments are also left standing in gullies, rocky areas, or steep slopes where other economic activities are not viable. Some landowners believe that small forest fragments are important for water conservation and biodiversity conservation (Siqueira et al., 2017). Frequently, landowners preserve small forest fragments because of the environmental services they provide. Tisovec et al. (2019) showed that the most important services realized by landowners in an area of Atlantic Forest, and that lead them to keep the forest in their properties, are rather indirect like legacy gratification, existential gratification, feeling joy and peaceful, air purification, among others. Direct services like food, firewood, timber were less important. By a conservationist perspective, these small fragments are important to maintain the movements of organisms between habitat remnants, which can affect metapopulation structure, community assembly dynamics, gene flow and conservation strategy (Moore et al., 2008). However, the minimum necessary forest patch size will vary with taxonomic group (e.g., invertebrates, amphibians, reptiles, mammals), body size (which is related to home range size in many animals), demography and habitat characteristics (e.g., perch height, predator intensity and resource availability).

Sampling Design

We delineated a rectangular polygon of 411,670 ha comprising an area historically covered by forest (IBGE, 2004). Within this rectangular polygon, we randomly allocated 20 points to be the centers of circular buffers with 1,500 m radius and 707 ha each. To do that, we first manually found within the rectangular polygon the largest area with continuous forest cover and we set a buffer around these points. Based on this first buffer, we then randomly chose the other 19 buffers using the "Random" tool of ArcMap (**Figure 1**). No restriction was used for the randomization process except that the buffers must be at least 700 m from each other. Moving forward will refer to these buffers as "landscapes."

Land Use Mapping

We used "RapidEye" satellite images to map the land use classes for the 20 landscapes. Those images have 5 m resolution which allowed us to identify the following land use categories: pastures, cropland, eucalyptus plantations, water bodies, and native tree cover. The native tree cover was separated into six categories, where five of them we called SLEs (**Figure 2**): scattered trees, trenches (hedgerow-like tree lines colonizing trenches), fences (hedgerow-like tree lines colonizing barbed wire fences), riparian forests, and forest fragments < 1 ha. The last category was forest fragments > 1 ha. The images were provided by the Federal University of Lavras in a partnership with the Brazilian Environmental Ministry.

We identified every scattered tree in the landscapes using the images and checking them for true in the Google Earth images. Considering the RapidEye pixel size, we worked with scattered trees with crowns equal to or larger than 25 m^2. To calculate the size of the crowns we randomly chose 800 scattered trees and measured their crown projections in the field. We found a mean area of 50 m^2 (the smallest crown = 25 m^2, the largest crown = 779.11 m^2, SD = ± 63 m^2) for scattered trees. Based on this information, the cover provided by each scatter tree was arbitrarily set to a fixed value of 50 m^2 in all landscapes.

The trenches where hedgerow-like tree lines thrive in the region are on average 4 m wide and 1.5 m deep. Those trenches were naturally colonized by tree species, resulting in these hedgerow-like structures (Castro and van den Berg, 2013). Those linear structures are easily recognized in the images (10–20 m wide). We also mapped the tree lines along fences, separating them from the ones with trenches based on their smaller width

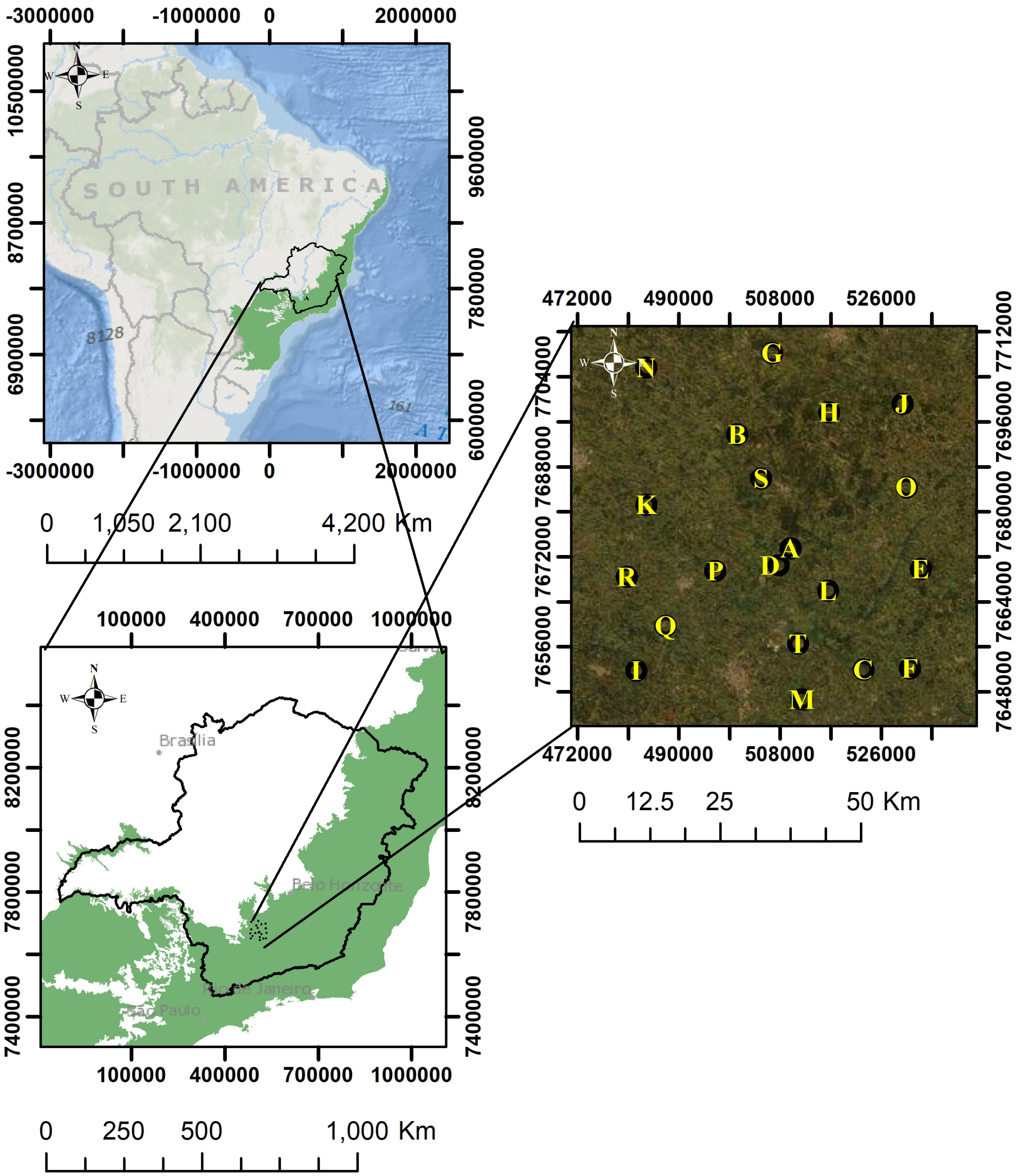

FIGURE 1 | Study area. The characters in the image correspond to the sampled buffers (landscapes), sorted from A to T in successively lower forest cover. Atlantic Forest original extent in green (adapted from IBGE).

(5–10 wide) and also using the RGB-532 band composition where older and denser forest cover (trenches) show darker color shade than tree lines following the fences.

We classified forest fragments as riparian forest when they followed the hydric net produced by the hydric flow model (ArcMap) added to the images.

In the case of clouds in the RapidEye images or doubts about the true classification during the mapping process, we first checked them in Google Earth images, Imagery—ArcGis and if the doubts persisted, we visited the areas.

Landscape Metrics

We calculated 14 metrics (**Supplementary Table 1**) for the landscapes in the ArcGis 10.5, extension "V-LATE 2.0" (Vector-based Landscape Analysis Tools Extension). Using those metrics (variables) we ran a Principal Component Analysis (PCA)

FIGURE 2 | Small landscape elements (SLEs): **(A)** Landscape Google Earth with alls SLEs in Minas Gerais—Brazil, **(B)** local Atlantic Forest Domain, **(C)** Forest fragments < 1 ha, **(D)** Forest fragments < 1 ha, **(E)** Riparian forests, **(F)** Hedgerow-like tree lines colonizing barbed wire fences, **(G)** Hedgerow-like tree lines staring colonization for plants, **(H)** Trenches, **(I)** Scattered trees (*Handroanthus* sp.).

and Spearman's correlation using the 20 landscapes as replicas (**Supplementary Figures 1**, **2**). Based on this, we excluded the high correlated variables resulting in a final set of seven variables for which we ran another PCA. The seven variables were (Lang and Blaschke, 2009):

1) NP (Number of SLEs): number of SLEs in the landscape.
2) TE (Total Edge): the sum of the patches' perimeters.
3) MPE (Mean Patch Edge): the average of patches' perimeters.
4) MSI (Mean Shape Index): it compares the patch's shape with a circle of the same area. Closer is the value to 1, more circular is the shape.
5) MPAR (Mean Perimeter Area Ratio): the average for the landscape of the ratio of each patch perimeter and its area.
6) DIVISION (Division Index): it measures landscape fragmentation intensity, in other words, the probability that two randomly setpoints do not belong to the same undissected area. Further details in Jaeger (2000).
7) PLAND: measure the habitat amount.

A powerful tool for the indirect estimation of landscape connectivity is the use of graph theory together with the species population attributes (Pascual-Hortal and Saura, 2006; Ribeiro et al., 2019). Therefore, also calculated the Probability of Connectivity (Saura and Pascual-Hortal, 2007) to evaluate if the SLEs provide connectivity for fragments larger than 1 ha in the 20 landscapes. The PC is calculated based on the graph theory (further details in Saura and Pascual-Hortal, 2007) and reflects the probability of a successful dispersal event between knots in the landscape as a function of the Euclidean distance between one knot and the other. The PC varies from 0 to 1, where 0 is the absence of connectivity in the landscape, and 1 refers to a landscape where the knots are completely connected among themselves.

Where, n is the number of knots (SLEs and forest patches > 1 ha) in the landscape, ai and aj are the area of the knots i and j, Pij is the maximum probability of connection between the knots i and j (that depends to the functional distance a disperser can cross between knots), and Al is the landscape total area.

To evaluate the importance of the metrics of SLEs and patches > 1 ha for the connectivity, we broke the PC in 3 components: *dPCintra*, *dPCmovement* and *dPCconnector* (mathematical details in Saura and Rubio, 2010). The *dPCintra* (called here simply "area") is the intrapatch connectivity, in other words, it is the contribution of the knot internal area to the connectivity. The *dPCmovement* ("flux") is related to the knot area and its position in the landscape, representing how well is the knot connected to the other knots in the landscape. The *dPCconnector* ("position") shows the importance of the knot position for the connectivity within the landscape (Saura and Rubio, 2010; **Table 1**).

Dispersal Distance for Probability of Connectivity Value

To calculate the Probability of Connectivity (Saura and Pascual-Hortal, 2007) we chose three arbitrary distances (50, 100, and 760 m) to represent dispersers with contrasting mobility and capacity of crossing open non-forested areas. At 50 m range are de pollen dispersers (e.g., insects), which can successfully transport pollen of *Copaifera landsdorffii*, a very abundant species in the whole region, at a distance of 50 m (Tarazi et al., 2010; Manoel, 2011); at 100 m range are the birds with a limited range of dispersal ability, such as *Turdus* (*T. flavipes,T. albicollis, T. rufiventris,T. amaurochalinus, T. leucomela*) and others forest understory species (Cadavid-Florez et al., 2020), called here as low-mobility seed disperser and at 760 m range are the more mobile species such as *Ramphastos (R. tucanus, R. vitellinus)* and others large forest canopy birds (Holbrook, 2011; Cadavid-Florez et al., 2020), called here high-mobility seed disperser.

Probability of Connectivity Models

To understand the role of the SLEs for connectivity among fragments > 1 ha, we ran models for the PC including and excluding the different SLEs. After including and excluding each SLEs, all landscape metrics have been recalculated. In the first model, all SLEs were removed from the landscapes. After that, for each model, we included only one of the SLEs. In the last model, we included all SLEs. We did all this process for the three different dispersal distances, resulting in 420 variations of the seven base models (7 models × 20 landscapes × 3 dispersal distances) (see **Figure 3** for an example of the seven base models applied to the landscape L).

We calculate the graph connections in the landscapes using the software Conefor 2.6 (Saura and Torne, 2009).

For each one of the 420 variations of the models, we produced a map with knots, the distance between the knots, and created a shapefile with the links between the knots. The

TABLE 1 | Decomposition of PC index partitioned into three distinct fractions (intra, movement, and connector) considering the different ways in which a certain landscape (k) can contribute to habitat connectivity and availability in the landscape (Saura and Rubio, 2010).

Index	Description	Formulation	Details
dPCintra	Is the contribution of patch k in terms of intrapatch connectivity	$ai \times aj$ when $i = j = k(ak2)$	Depends only on the habitat patches attributes and not on the distances
dPCmovement	Corresponds to the area−weighted dispersal flux through the connections of patch k to or from all of the other patches in the landscape when k is either the starting or ending patch of that connection or flux	$ai \times aj \times Pij^*$ when $i = k$ or $j = k$ and $i \neq j$	Depends on the number of incoming/outgoing connections and the attributes of the nodes
dPCconnector	Is the contribution of patch or link k to the connectivity between other habitat patches, as a connecting element or stepping stone between them	$ai \times aj \times Pij^*$ when $i \neq k$, $j \neq k$	Depends on the topology of a node and his irreplaceability as a link between nodes

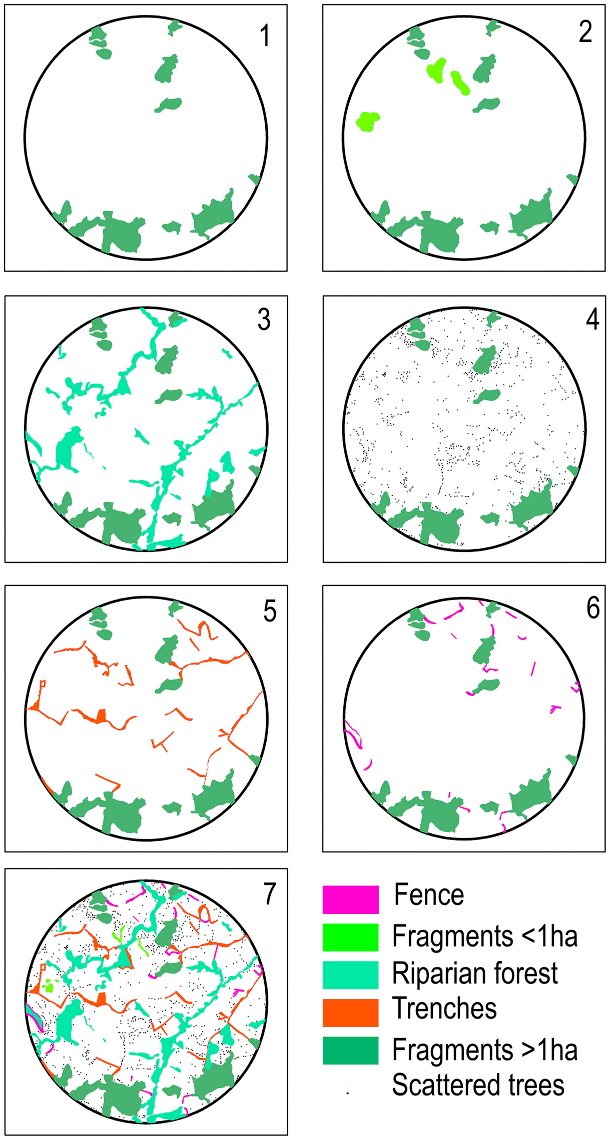

FIGURE 3 | Example of the adopted seven base models for the PC (Probability of Connectivity) in the landscape. **(1)** Landscape without SLEs (only fragments > 1 ha); **(2)** Fragments < 1 ha (Fragments > 1 ha + fragments < 1 ha); **(3)** Riparian forests (Fragments > 1 ha + riparian forest); **(4)** Scattered trees (Fragments > 1 ha + scattered trees); **(5)** Trenches (Fragments > 1 ha + trenches); **(6)** Fences (Fragments > 1 ha + fences) and **(7)** Complete landscape (Fragments > 1 ha + fragments < 1 ha + riparian forest + scattered trees + trenches + fences).

results produced by the ArcGis using extension Conefor were: (1) the knot identities, (2) a matrix with Euclidean distances between knots, (3) a shapefile with the graphs. With these data, we calculated PC, *dPCintra*, *dPCmovement,* and *dPCconector*, in the software Conefor.

Statistical Analyses

We used Generalized Linear Models (GLM) to investigate how the landscape metrics affect the Probability of Connectivity. We ran models first relating PC to (i) the landscape metrics and SLEs metrics together and, after, relating PC to (ii) exclusively the SLEs metrics. For both models, the seed and pollen dispersers were included.

(i) PC - TE (total edge) + NP (number of patches) + MSI (Mean Shape Index) of SLEs + MPE (Mean Patch Edge) + MPAR (Mean Perimeter Area Ratio) + DIVISION (Division Index) + PLAND (amount habitat) + dispersers.
(ii) PC - SLEs area + flux between SLEs + position of SLEs + dispersers.

All models had normally distributed residuals (Shapiro–Wilk normality test, $P < 0.05$). We calculated for each candidate model the Akaike Information Criterion corrected for small samples (AICc), the Δi (= AICci - minimum AICc) and the Akaike weight (wi), which indicates the probability that the model i is the best model within the set.

We carried out all the statistical analysis in the software R (R Core Team, 2013). For the PCA, we used the package Vegan (Oksanen et al., 2010); for the GLM, and we used the package lme4 (Bates et al., 2014).

RESULTS

Landscape Description

The landscapes were dominated by pastures (62.68%) followed by native tree cover (33.38%) and crops (3.02%). The other two classes water and eucalyptus plantations combined contributed to 0.92% of the land cover (**Table 2** and **Supplementary Figure 3**). Considering exclusively native tree cover, fragments > 1 ha responded by 25.93% of the land cover and riparian forest for 4.46%. The other land cover of native tree species together added to 2.99%. Trenches (1.35%) had a greater contribution to land cover compared to fragments < 1 ha (0.87%). Hedgerow-like structures (trenches and fences) (1.67% together) responded for

TABLE 2 | Land use classes for the 20 circular landscapes of 707 ha in the study area.

Land use classes	Mean	SD	Landscape with the smallest amount	Landscape with the largest amount
Pasture	317.05 ha (62.68%)	148 ha	K = 73.53 ha	J = 605.00 ha
Native tree cover	136.4 ha (33.38%)	102.48 ha	T = 42.99 ha	A = 389.02 ha
Crops	15.09 ha (3.02%)	30.93 ha	B, C, E, F, G, H, J, M, O, T = 0.00 ha	S = 103.95 ha
Water	4.41 ha (0.58%)	6.68 ha	B, E, H, O, N = 0.00 ha	R = 30.21 ha
Eucalyptus	1.76 ha (0.34%)	6.66 ha	B, C, E, H, O, N = 0.00 ha	A = 30.45 ha

*The letters for the landscapes' identification correspond to those on the map in **Figure 1**.*

TABLE 3 | Distribution of forest cover for the 20 circular landscapes of 707 ha in the study area.

Land use classes	Mean	SD	Landscape with the smallest amount	Landscape with the largest amount
Fragments > 1 ha	131.31 ha (18%)	92.82 ha	T = 8.70 ha	A = 356.09 ha
Riparian forest	43.45 ha (6.14%)	29.95 ha	B = 4.95 ha	M = 117.84 ha
Trenches	11.72 ha (6%)	9.62 ha	B = 0.00 ha	L = 27.87 ha
Fragments < 1 ha	8.23 ha (1.16%)	7.74 ha	D = 0.98 ha	C = 39.58 ha
Fences	3.48 ha (0.46%)	3.81 ha	G = 0.00 ha	C = 13.92 ha
Scattered trees (ha)	4.06 ha (0.57%)	1.80 ha	T = 0.73 ha	J = 7.63 ha
Scattered trees (#)	813 trees	361 trees	146 trees	1526 trees

*The% cover corresponds to the total landscape area (707 ha). The letters for the landscapes' identification correspond to those on the map in **Figure 1**.*

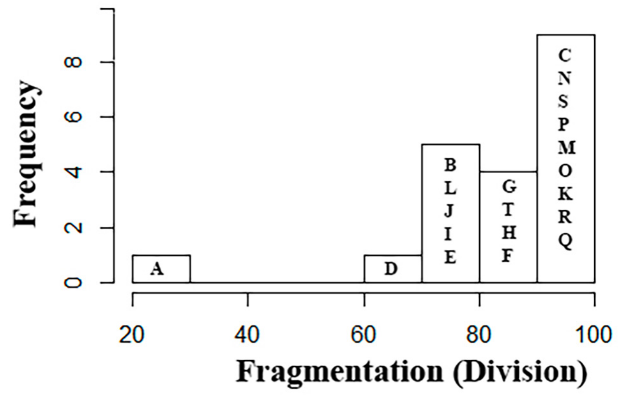

FIGURE 4 | Histogram showing the distribution of the 20 landscapes in the fragmentation classes (metric DIVISION). The letters correspond to the landscapes on the map in **Figure 1**.

55% of native tree cover, excluding fragments > 1 ha and riparian forest (**Table 3** and **Supplementary Figure 3**).

We found that the forest cover in the landscapes is highly fragmented. The metric DIVISION (that measures the habitat splitting) gave values higher than 70% (**Figure 4**). Two landscapes had values under 70%: the landscape A (20%), that was chosen specifically because its amount of forest cover, and the landscape D (62.77%) (**Figures 4**, **5**; with five landscape for example and **Supplementary Figures 4A,B**, all 20 landscapes in **Supplementary Material**).

Probability of Connectivity

Connectivity responded positively to habitat amount (PLAND) and shape closer to a circle (MSI) and negatively to DIVISION, total edge length (TE), and mean patch edge length (MPE) (AICc = -294.14 e ΔAICc = 3.92; **Figure 6A**).

The geographical arrangement of the natural elements in the landscape (position) was more important for the connectivity than the elements' area and flux ($R = 0.12$, $p = 0.005$, AICc = -142.7 and ΔAICc = 0.35; **Figure 6B**).

Probability of Connectivity and the SLEs

The presence of SLEs affected positively the connectivity in the studied landscapes ($p = 0.00002$). Riparian Forests were the most important ones for connectivity, followed by Trenches, Fences, Scattered trees, and Fragments < 1 ha (**Figure 7**).

The greater was the fragmentation, the larger was the SLEs contribution to the connectivity ($p < 0.05$ and $R^2 > 0.54$; **Supplementary Figures 5A–C**). The connectivity was less affected by fragmentation for the models with high-mobility seed disperser than for the models with low-mobility seed disperser and pollinators (**Figure 7**).

The presence of SLEs improved the number of links between knots ($R = 0.955$ and $p < 0.0001$; **Figure 8** and **Supplementary Figure 6** with a zoom of the links in **Supplementary material**). The number of links decreased with the decrease of disperser distance capability.

DISCUSSION

Small landscape elements (SLEs) are a common feature of the Atlantic Forest and agricultural landscape of South of Minas Gerais State, south-eastern Brazil. These SLEs also greatly increased connectivity in the landscape. Land sparing strategies are the cornerstone for conservation, however, most of the original area of distribution of the Brazilian Atlantic Forest is distributed across private lands and extremely fragmented (Rezende et al., 2018) and few opportunities exist for creating new full protected areas. Without denying the importance of this strategy, conservation in agricultural lands (land sharing) is a necessity for Atlantic Forest and other highly fragmented tropical forests around the world. Turning the economic activities in private lands more social, economic and environmentally sustainable, is a powerful complement to land sparing strategies. In this context, protection and restoration of SLEs is essential considering their value for biodiversity conservation, for example by considering how they contribute toward enhancing landscape connectivity (Castro and van den Berg, 2013; Siqueira et al., 2017). The SLEs, as we showed here, occupy a relatively small space in the agricultural lands (~7.5% including trenches, fences, scattered trees, and riparian forests), however, they can strongly promote connectivity, doubling it when including all them together.

We found that the Atlantic Forest is highly fragmented within the studied region. The metric DIVISION showed that on average, the fragmentation was 82% (maximum possible value would be 100%), with landscape R with 96% and the one with the lowest fragmentation (and largest forest cover), the landscape A, with 20%. The forest cover was mostly replaced by pasture, but also by water (a reservoir), agriculture, and eucalyptus forest plantation. In the last 30 years, very little forest clearing occurred, however, prior to the end of the 1980s, legal protection for

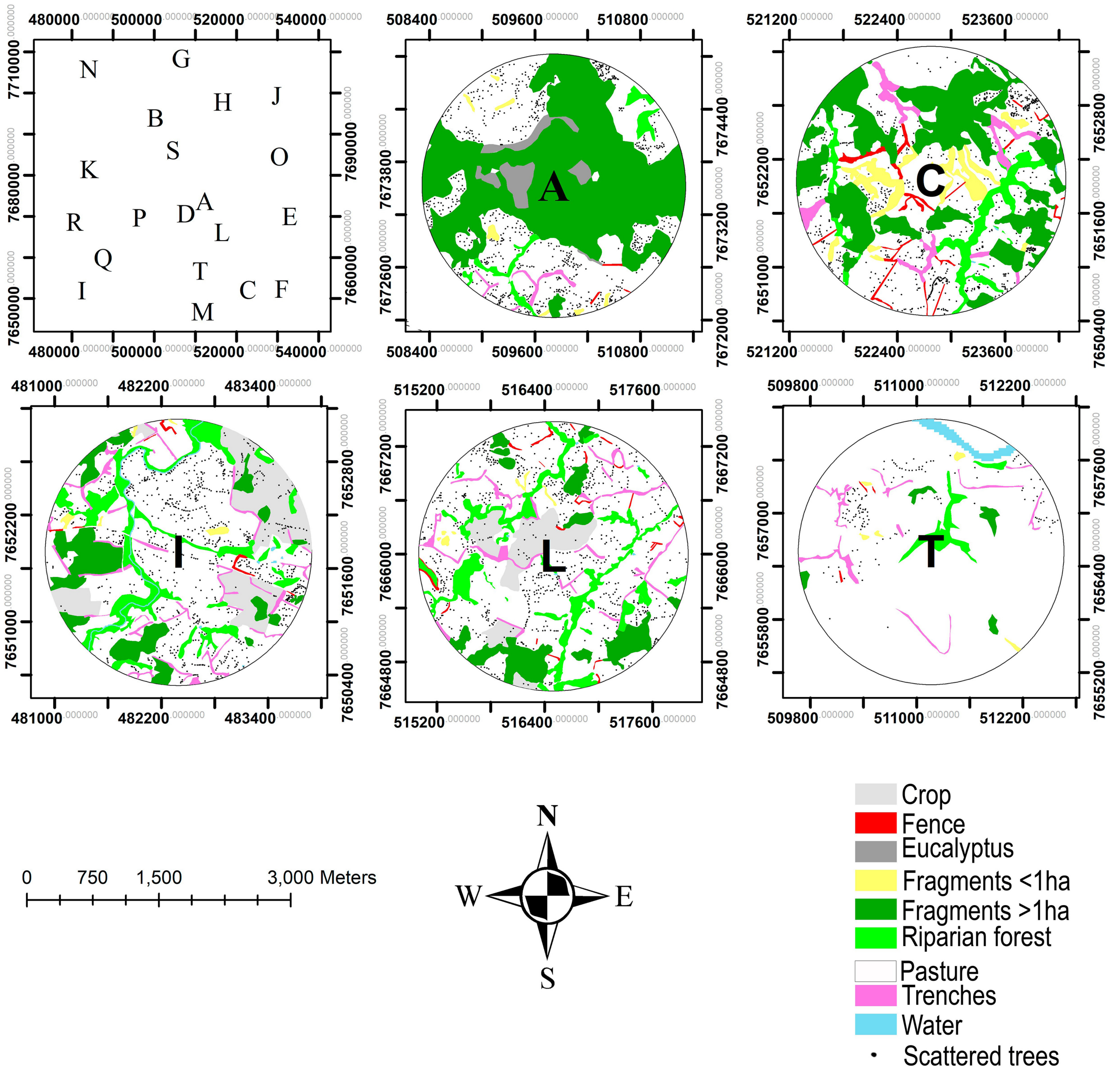

FIGURE 5 | Example of land use maps for five landscapes identified by the characters in the center. The first frame represents the study area with the characters corresponding to the location of the 20 landscapes.

the forests was much weaker. During this period, the Brazilian environmental legislation was still being formulated [Article 225, Constitution of 1988 (Brasil, 1988)] and the existing legislation was poorly enforced. Also, during this period, many properties had more forest cover than the legislation demanded (Legal Reserve: 20% of the property, and Permanently Protected Area: a variable amount related to areas following watercourses and hills tops), resulting in legal forest clearing for economic activities. Nowadays, besides the fact most forest in the properties is legally protected (Law No. 12.651 of 2012, Brasil, 2012), also the forest in the region is considered officially part of the Atlantic Forest, a protected biome (Law No. 11.428 of 2006, Brasil, 2006), therefore, the forest in the region is doubled protected. Environmental law enforcement is also much more efficient now, using remote images and, often, being supported by the population, that observe and denounce illegal forest clearing.

However, although the previous Brazilian environmental legislation (Law No. 4.771 of 1965, Brasil, 1965) did not cover all environmental issues and was rather poorly imposed, it did have a positive effect on preserving riparian forests. This law conditioned the width of the forest protected to the width of the watercourse. This impact is clear on the amount of riparian forest compared to the other SLEs. Not only that, although the law protected those areas exclusively

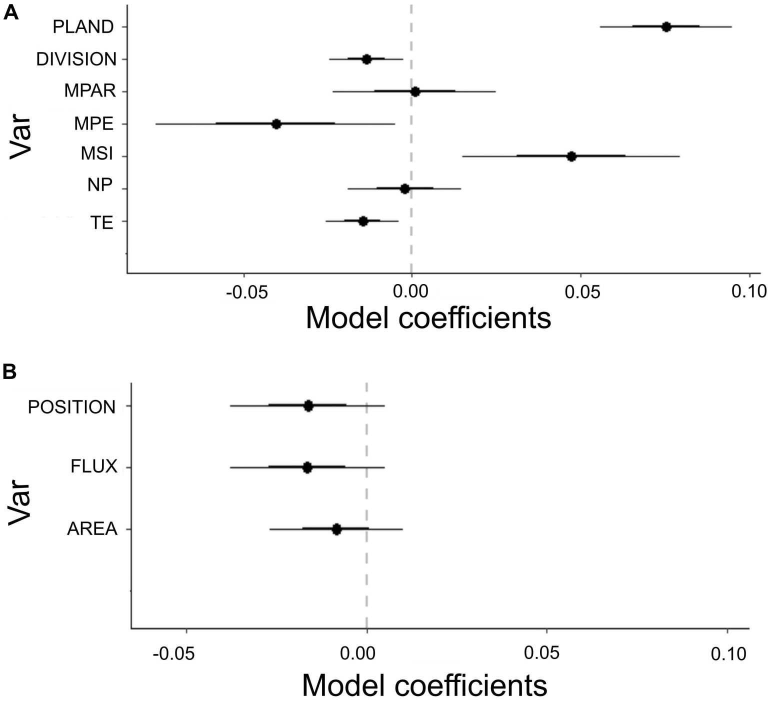

FIGURE 6 | Estimated coefficients of the GLM models fitted to probability of connectivity (PC) when considering the mobility of different animals, **(A)** GLM as a function of landscape metrics: TE, total edge perimeter; NP, number of patches; MSI, patch shape; MPE, mean edge length for the patches; MPAR, patch shape complexity; DIVISION, fragmentation; PLAND, habitat amount. **(B)** GLM as a function of patch level metrics: FLUX, area and its position of the SLEs; POSITION, position of the SLEs for the connectivity within the landscape; AREA, SLEs area.

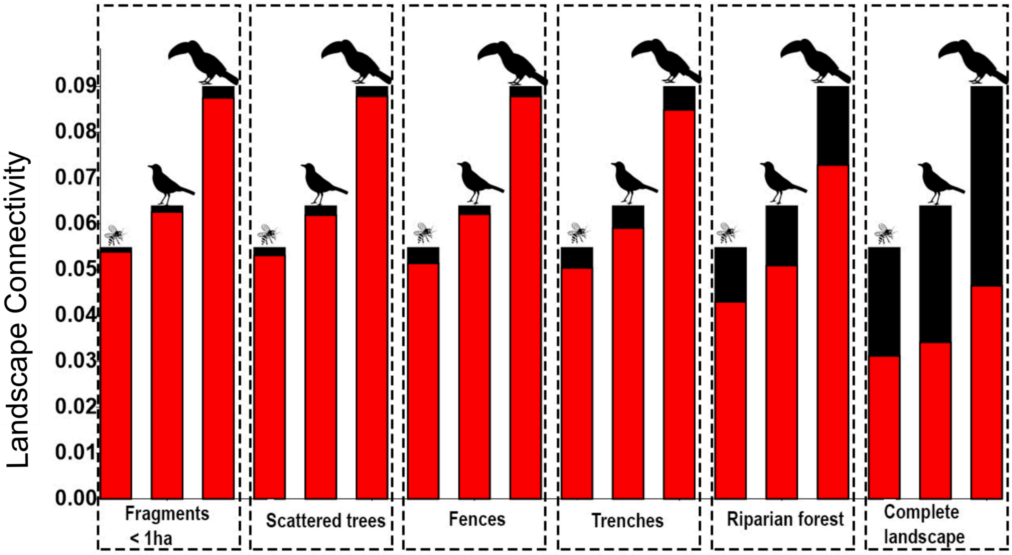

FIGURE 7 | Connectivity (PC: the probability of connectivity) as a function of each SLE and as a function of all SLEs together (last frame). The red bars correspond to the PC without each particular SLE; the black bars indicate the effect of adding the focal SLE to the model. On top of the bars are the dispersers: insects (pollinators), low-mobility seed dispersers (smaller birds), and high-mobility seed dispersers (large body birds). Connectivity was measured in meters.

because of the hydric resources, as an indirect consequence, the connectivity between larger fragments was also favored, being the Riparian Forest the most important SLE for connectivity in the studied landscapes. This legislation was substituted by Law No. 12.651 of 2012 (Brasil, 2012) which establishes that the width of forest along the watercourse depends on the size

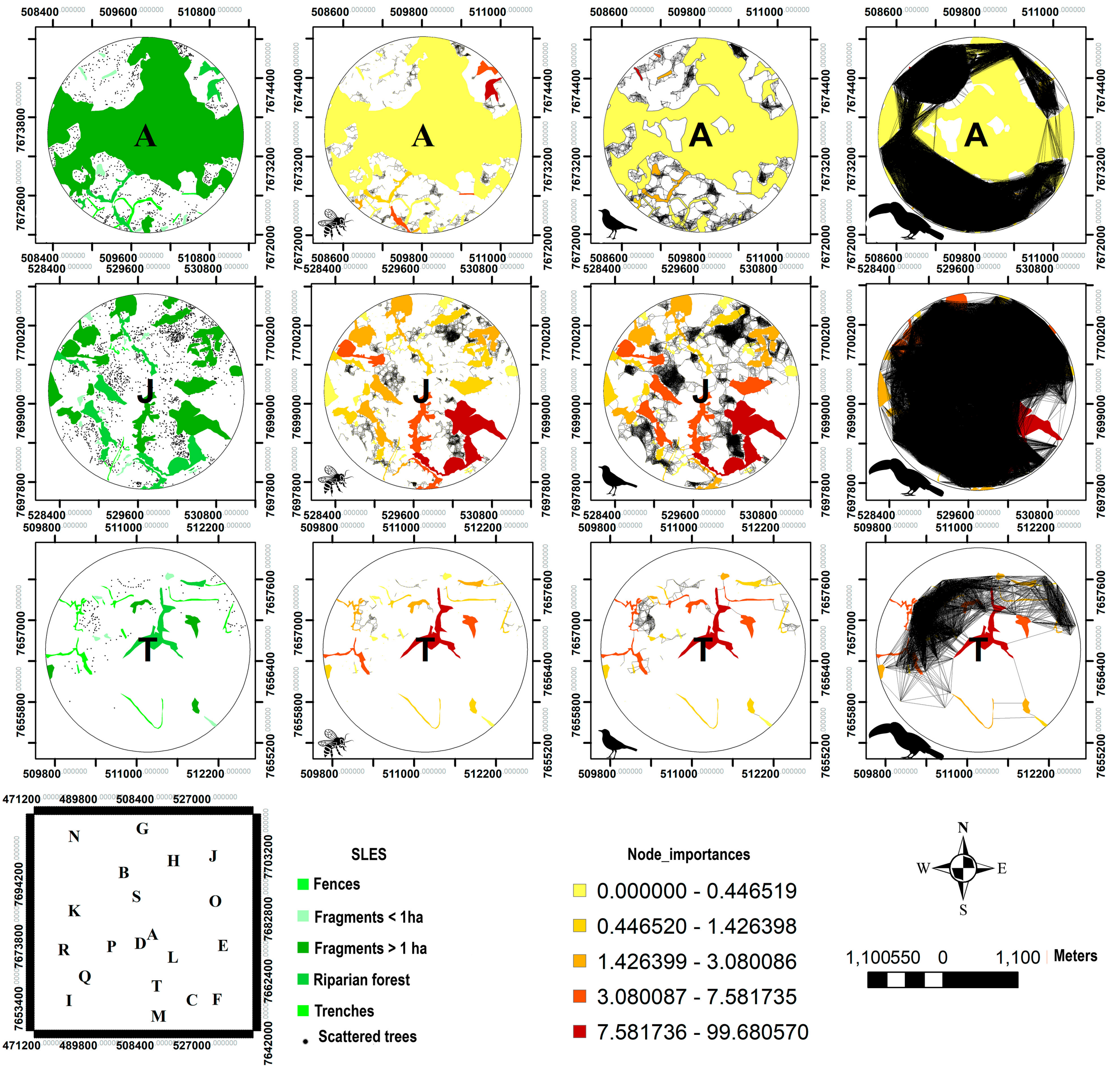

FIGURE 8 | Graph models for connectivity. Graph representation of connectivity for three dispersers in three landscapes (A, J, and T), where A has the largest, J has an intermediary and T has the lowest amount of forest cover among the 20 analyzed landscapes. The first column shows the real tree cover of the landscapes; the second one shows the I connectivity for pollinators; the third one for the seed disperser *Turdus*; and the last one for the seed disperser *Ramphastos*. The black lines represent the graph links between knots and the orange color palette shows the importance of each knot (SLE). The polygon with the letters A-T shows the geographic position of each landscape.

of the property (Soares-Filho et al., 2014), allowing smaller properties to have narrower protected riparian areas. Because of that, the riparian forests are threatened to be reduced in the next years.

Like other studies (Fahrig, 2003; Banks−Leite et al., 2011; Costanza et al., 2019), we showed that connectivity was positively related to less fragmented landscapes, with more habitat and proportionally less edge, and patches with a circular shape. However, we pointed out that not only the presence of SLEs can promote connectivity but also their arrangement in the landscape, as example we found that the position of SLEs within the landscapes is more important than their respective areas for connectivity.

Considering all the SLEs together, the linear elements in the landscape—the riparian forest and the hedgerow-like elements (Trenches and Fences)—were the most important ones for promoting connectivity. However, although the SLEs vary in their effectiveness, they seem to have complementary roles, since although none of them alone contribute to much more than 20% of the connectivity, they all together increased the connectivity in 50% for all analyzed model dispersers.

One of the most important negative consequences of fragmentation is the isolation of populations. Fragmentation decreases pollen and seed dispersal affecting genetic flow (Hamilton, 1999). This dispersal loss is clearly related to the negative effect of fragmentation on the bird community and populations (Bovo et al., 2018). Birds are responsible for long-distance seed dispersal (Clark et al., 2004) promoting plants' genetic exchange and diversity (Tarazi et al., 2010, 2013; Carvalho et al., 2015). The SLEs contribute to connect the fragments and increase genetic flow. Also, the connectivity provided by the SLEs can be very important to the landscape resilience, since birds can change they movement according to the level of landscape isolation (Giubbina et al., 2018), by using stepping-stones, using more pasture or moving farther (Ramos et al., 2020). Consider the example of the scattered trees in pastures, where Siqueira et al. (2017) observed a much larger deposition of animal dispersed seeds under scattered trees than in corresponding areas without the trees. In the present study the landscape J (26.88% of habitat), with 1,526 scattered trees, had 6,927 links for insects: 18,801 links for birds with a limited range of dispersal ability and 302,389 links for large forest canopy birds. However, the landscape K (26.25% of habitat), with 723 scattered trees, had only 1,341 links for insects, 3,413 links for birds with a limited range of dispersal ability and 54,546 links for large forest canopy birds.

In most landscapes, the open non-forested areas did not present itself as a barrier for the high-mobility seed dispersers movement, which are large body birds, however, it was a limitation for low-mobility seed dispersers (smaller birds) and particularly for pollen dispersers insects). This result was expected since large-bodied species, may exhibit higher movement capacity (Spiegel and Nathan, 2007; Neuschulz et al., 2013; Ramos et al., 2020) and, to ensure sufficient resources, should be more likely to change their behavior in response to variation in resource distribution than small-bodied species (Buchmann et al., 2012; Ramos et al., 2020).

For pollen dispersers with relatively short dispersal distance (in our model was 50 m), the open non-forested areas can be a strong barrier. In this case, the SLEs can work as corridors or stepping stones, connecting larger forest fragments. For pollinators of *Copaifera langsdorffii*, the species for which we shaped pollen dispersal distance for the model, areas without forest can be an insurmountable barrier (Tarazi et al., 2013). On the other hand, the large forest canopy birds can cross wide-open areas holding seeds, even large ones (30 mm of diameter) (Galetti et al., 2013; Emer et al., 2019). Therefore, specifically for pollinators and for birds with a limited range of dispersal ability, the SLEs can allow some seed and pollen exchanges between areas otherwise isolated. Nevertheless, for any disperser evaluated, the SLEs increased the connectivity more or less in the same proportion. In addition, we recommend that future research that considers species-specific dispersion distances be carried out.

In the case of pollinators, besides riparian forest, fences and trenches were especially relevant. For animals with little mobility in the non-forest habitats, linear tree structures connecting larger fragments are essential. Those linear structures, besides providing a friendly habitat for locomotion, also provide resources, particularly for insects since they have high sunlight exposition, and consequently larger flowering (Emer et al., 2019).

Although large and protected areas are fundamental for conservation (Crouzeilles et al., 2013), many times those areas are far apart and unconnected to each other. In Brazil, principally in the areas with higher and older European occupation, like the Atlantic Forest, this isolation is even more severe (Ward et al., 2020). We showed here that the SLEs present in private agricultural lands can double the connectivity among larger forest fragments, and, in the same way, between protected areas. In the region of the original Atlantic Forest, most of the large forest patches disappeared or are already in protected areas. This region concentrates 70% of the human population (IBGE, 2020) and has high land prices. In such conditions, conservation in private agricultural lands is essential as a complement to other strategies like forest restoration and protection of the last large remnants. However, very little attention has been given to the SLEs and, most times, they are even not included in the landscape maps (Haddad et al., 2015). Also, there is no specific legislation to protect them. We showed here how we urgently need to change or approach concerning the SLEs, even if we are only thinking about ecological connectivity.

Besides connectivity, the SLEs provide other important ecological services. For example, riparian forests protect watercourses increasing water quality and reducing sediment input (Dosskey et al., 2010). The trenches associated with the hedgerows provide conditions of temperature and moisture that allow the establishment of trees typical of forest interior (Castro and van den Berg, 2013). The barbed-wire fences, the scattered trees, and fragments < 1 ha provide habitat and food for the fauna and also work as nucleation spots for forest re-establishment (Sandor and Chazdon, 2014).

Considering all the above, we advocate for the SLEs are important components for conservation, providing large and irreplaceable connectivity in private agricultural lands and even between protected areas. Most SLEs do not conflict or conflict little with other economic activities in the properties, even providing some services perceived by the owners (like shade provided by the scattered trees to the cattle (Siqueira et al., 2017), or water quality linked to the riparian forests). In Brazil, there is no legislation directly protecting SLEs besides riparian forests, which are only partially protected. Legal protection for SLEs is urgent as well as including them in the studies evaluating connectivity and human-disturbed landscapes.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

FS, DC, and EB: study conception and design. FS: data collection and computer simulations. FS and CA: data analysis and interpretation. FS, DC, JR, CA, VR, and EB: manuscript writing. DC, JR, CA, VR, and EB: review and editing. DC and EB: funding acquisition. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.614362/full#supplementary-material

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Effects of Flower-Enriched Ecological Focus Areas on Functional Diversity Across Scales

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Ecological Focus Areas (EFAs) to benefit biodiversity became mandatory in intensively farmed landscapes after the reform of the European Common Agricultural Policy (CAP) in 2013. The implementation of EFAs as uncropped field margins has been criticized as ineffective but created a window of opportunity to test if augmenting them with annual flower strips can benefit biodiversity. In this study, we investigated if annual flower strips on EFAs benefited functional biodiversity in intensively farmed landscapes. To this end we established eleven annual flower strips with a seed mixture targeted for both natural enemies and pollinators, on areas were farmers had planned for EFAs. We determined effects on aphids and their natural enemies in cereal fields close to six of the flower strips, and for solitary bees and wasp close to and in the surroundings of all eleven flower strips. We found that annual flower strips benefited the abundance of hoverfly larvae and possibly also that of solitary bees. However, there were neither any significant effects on natural enemies (other than hoverfly larvae), nor any difference in natural pest control as shown by lack of differences in aphid numbers and parazitation rates. Abundances of solitary bees and wasps in the surrounding landscapes were unaffected, although there was a tendency for more solitary bee cells closer to the strips. We suggest that the critical issue leading to the mostly negative results is the lack of permanent structures to sustain populations of arthropods that in turn can benefit from annual flower strips. Hence, future agri-environmental policies need to carefully consider if and how annual agri-environmental measures should be implemented in intensively managed agricultural landscapes, e.g., by combining them with more permanent structures.

Keywords: annual flower strips, EFA, CAP, agri-environmental measures, functional biodiversity

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INTRODUCTION

Flower strips are often proposed as a tool to mitigate biodiversity loss in agricultural landscapes (Haaland et al., 2011), especially loss of functional biodiversity such as pollinators (Scheper et al., 2013) and natural enemies of pests (Holland et al., 2016). Supporting biodiversity-related ecosystem services has the potential to increase agricultural production while minimizing negative environmental impacts (Bommarco et al., 2013). Flower strips can be targeted for pollinators (Wood et al., 2015), natural enemies (Tschumi et al., 2015), both pollinators and natural enemies (Campbell et al., 2017; Grab et al., 2018) or serve different purposes (Vickery et al., 2002). Local factors, including plant community composition, size and shape of strips, configuration (e.g., field edge or field interior), can have important positive or negative effects on flower strips' capacity to support functional biodiversity and ecosystem services in croplands (Haenke et al., 2009; Jönsson et al., 2015; Uyttenbroeck et al., 2015; Wood et al., 2016). However, the consequences of agri-environmental measures such as flower strips, on functional diversity may be context dependent, and related to the agricultural intensity in the surrounding landscape (see e.g., Tscharntke et al., 2005, 2016; Bianchi et al., 2006; Scheper et al., 2013; Grab et al., 2018). Thus, the re-occurring critique toward the European Union's (EU), Common Agricultural Policy (CAP), that measures need to be targeted (e.g., Smith et al., 2010; Batáry et al., 2015; Pe'er et al., 2019) and based on a landscape perspective (see e.g., Tscharntke et al., 2005; Batary et al., 2011; Kleijn et al., 2011), applies also to flower strips.

In an attempt in the reform 2013 to make the CAP "greener," and with the objective to safeguard and improve farmland biodiversity in Europe, for many farmers so called Ecological Focus Areas (EFA) became mandatory (through Pillar 1) in 2015 (while the budget for the agri-environmental schemes in Pillar II decreased) (EU, 2013). As one out of three "greening measures" (the others being crop diversification and maintaining permanent grassland at a national level), EFAs were supposed to be simple, generalized, non-contractual, and annual, and can consist of areas such as nitrogen fixing crops and uncropped field margins (EU, 2013). EFAs in the form of uncropped field margins has been criticized as inefficient (Nilsson et al., 2019), but also created a window of opportunity for annual flower strips and are encouraged to be used for such (e.g., by the Swedish Board of Agriculture). The question is what kind of effects that can be expected on farmland biodiversity from these annual strips.

Even though evidence do exist for the potential of flower strips and other non-crop habitat to have positive effects on farmland biodiversity and ecosystem services (Dicks et al., 2014, but see Zamorano et al., 2020), there are many factors that influence the magnitude and direction of these effects (Tscharntke et al., 2016; Karp et al., 2018). Most of the existing knowledge comes from perennial or multi-annual flower strips (see e.g., Jönsson et al., 2015; Wood et al., 2016), whereas little is known about the effects of annual flower strips. Exceptions to this are two studies in Switzerland showing local positive effects of targeted annual flower strips on natural enemies (Tschumi et al., 2015, 2016) and one study in Sweden showing local positive effects on species richness of pollinators (Rundlöf et al., 2018). In the two studies from Switzerland, the landscapes were traditional Swizz agricultural landscapes characterized by a small-scaled mosaic of crop fields. The positive effects in the Swedish study were strongest in the more heterogenous landscapes (Rundlöf et al., 2018).

Given the lack of scientific foundation on the use of annual flower strips on EFAs to benefit functional biodiversity, we in this study aimed to evaluate if they benefited natural enemies and pollinators in the surrounding landscape. Given that EFAs are mandatory mostly in intensively farmed landscapes, and that benefit of functional biodiversity for cash crops is most relevant in these landscapes (Nilsson et al., 2019), we evaluated the effect using experimental implementation of annual flower strips in existing EFAs in replicated simple landscapes. However, to determine if the amount of permanent structures in these landscapes modify responses to annual flower strips, we also analyzed effects of limited variation in the proportion of arable fields in these landscapes. In this way we addressed the following research questions: (I) Do EFAs in the form of annual flower strips have a positive effect on the abundance of natural enemies in adjacent fields? (II) Is there any resulting effect on pest abundance? (III) Do annual flower strips have a positive effect on the reproductive output of adjacently nesting solitary bees and wasps?

MATERIALS AND METHODS

Experimental Design

The study was conducted as an experimental study in the southernmost part of the county Skåne, in southern Sweden, within the most intensive "production area" (Production area GSS). This is one of the most intensively farmed areas in Sweden, characterized by homogeneous landscapes with large crop fields and specialized high intensity production of cash crops. To select EFAs for experimental implementation of flower strips, we focused on large farms. From a complete list, we randomly contacted farms that were >400 ha in size until we had enough participating farms to create 13 flower strips. The average field size in a radius of 1,000 m around the flower strips were 4.6 ha. The conditions for inclusion were that farms should have EFAs in the form of uncropped field margins as part of their management plan and be prepared to establish flower strips on these (**Figure 1**). We also made sure that a flower strip could be established without any other flower strips or late mass-flowering crops (e.g., red clover seed production, *Trifolium pratense*) within 1,000 m. Two farms were sufficiently large to allow the establishment of two and three flower strips, respectively, with sufficient distances between them to assume that they were independent (>10 km). At the rest of the farms, only one flower strip was established on each. To maintain realism, the flower strips were sown where the farmers had already planned for EFAs and the study design was adapted accordingly. All EFAs, and thus the flower strips, were placed on fields with sugar beet, onion and oil seed rape. Because of differences in the assumed scale of effect of flower strips, we studied pollinators and natural enemies in this system using slightly different designs. For natural enemies, we established control sites within the same fields, but at a distance from the flower strips. For pollinators we used transects that extended away from the flower strips, assuming the influence of the flower strips to decline along the transects.

Because the aim of the study was to explore the potential of annual flower strips to enhance natural pest control and conditions for both natural enemies and pollinators, we produced a seed mixture of plant species with the aim to attract both these groups (**Table 1**). By using a functionally diverse plant species composition the aim was to attract a diversity of nectar and pollen eating organisms (Balzan et al., 2014). The plant species were selected based on existing evidence for plants

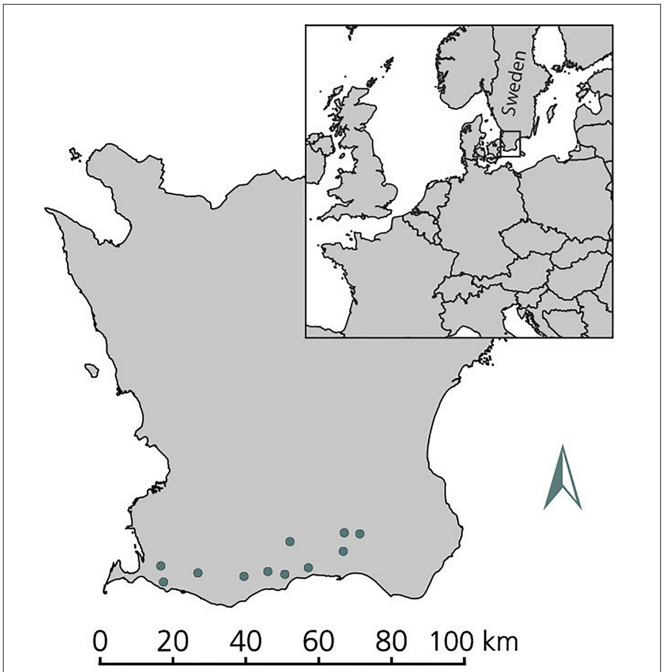

FIGURE 1 | Map showing the locations of the eleven flower strips, in southern Sweden.

supporting pollinating insects [bees (*Apoidea*) and hoverflies (*Diptera: Syrphidae*)] and key natural enemies of aphids and other pests in cereals [hoverfly larvae, lacewings (*Neuroptera: Chrysopidae*), ladybirds (*Coleoptera: Coccinellidae*), as well as parasitic wasps (*Hymenoptera*)] (Vattala et al., 2006; Lixa et al., 2010; Wäckers and van Rijn, 2012; Tschumi et al., 2015). Since the abundance of ground dwelling predators was expected to benefit from the vegetation cover and refuge area provided by the strips rather than the exact flower composition (Lee et al., 2001; Balzan et al., 2016), we did not tailor the composition of flower strips to them. There is not much information available about specific legumes, but in general they (*Fabaceae or Trifolium spp.*) are attractive to bees (Carvell et al., 2006; Gardiner et al., 2008) and the three legume species used were suitable also because they flower later than and have different heights compared to *Phacelia*. The three *Trifolium* species used in the mixture were suggested by Lindström (2010) and *T. resupinatum* was together with *Phacelia tanacetifolia* the most attractive plant species for bees in Eriksson and Rundlöf (2013). For exact quantities of seeds in the seed mixture see **Supplementary Table 1**.

Flower strips were sown at the end of April until the beginning of May 2016. The width and length of strips were adapted to the management plans at the different farms, respectively (**Supplementary Table 2**). In total thirteen flower strips were sown. Two of the strips were later excluded from the study; in one case the flower strip never established probably because of too dry conditions and in the second case the farmer sowed mass flowering crops (field bean and flax seed) next to strips after crop failure in the adjacent cereal fields.

The landscapes within a 1,000 m radius around the flower strips were characterized using digital land-use data from the Integrated Administration and Control System (IACS) provided by the Swedish Board of Agriculture. A radius of 1,000 m was considered appropriate for the type of organisms that were to be investigated (cf. Thies et al., 2003; Greenleaf et al., 2007). To describe the landscape surrounding the flower strips we used the proportions of arable fields, a simple but widely used proxy for land use intensity studies of biodiversity in agricultural landscapes (e.g., Tscharntke et al., 2005; Persson et al., 2010). For the selected flower strip sites, the proportion of agricultural land varied between 75 and 95%. We did not include ley (i.e., grassland on arable land with or without legumes, which usually has a life-length of 2–4 years) when calculating the proportion of arable land, as we considered ley to have the potential to provide resources for all of the studied groups (Weibull et al., 2003; Persson and Smith, 2013; Rusch et al., 2014).

Sampling of Arthropods

Natural Enemies and Pests

We sampled natural enemies and aphids using three different methods: tiller counts, suction sampling and pitfall traps. Parasitoids and predatory larvae were sampled through standardized suction sampling at 5 and 40 m from the field edges, the 5–8 of July. We placed a metal cylinder with a diameter of 30 cm at the ground and sampled within it to make sure that the area sampled always had the same dimensions and were running the suction sampler for 20 × 3 s to cover the whole area. Suction sampling took place in fair weather, i.e., not in strong winds or in temperatures below 15°C, and never directly after rain, to assure dry conditions in the fields. Ground beetles, rove beetles and spiders were sampled using pitfall traps. One pitfall trap was placed in the flower strip/field margin and then at 5, 15, and 40 m from the field edge. The traps were left for 1 week and emptied at three occasions from end of June to mid-July. The traps were moved slightly each time they had been emptied. Aphids, mummies of aphids (parasitized aphids), and hoverfly larvae were sampled from wheat tillers. Along the transects, we randomly picked 25 tillers at each of the distances 5, 15, and 40 m from the field edge, the 23–24 of June. Hoverfly larvae were on top of being included in the group with predatory larvae also assessed separately as they were considered particularly interesting because of the adults flies explicit relationship to flower strips (Haenke et al., 2009).

Six of the EFAs (**Supplementary Table 2**) were on fields adjacent to cereal fields, allowing us to assess the abundance of natural enemies and aphids. At each site, we established two pairs of transects perpendicular to the flower strip (in one case the transects started at the end of the flower strip and went into two different fields instead) and a semi-natural field border, respectively. By having transects adjacent to flower strips and uncultivated field borders within the same field, we attempted to control for between-field differences in crop (wheat/rye) and management. The control transects were mostly on the opposite side of the field compared to the flower strip transects. Transects started close to the flower strip/uncultivated field border and

TABLE 1 | Plants in the flower strips and evidence that they attract pollinators and natural enemies (marked with "x").

Plant species	Organism groups					References
	Bees	Hoverflies	Lady beetles	Lacewings	Parasitic wasps	
Anethum graveolens			x			Lixa et al. (2010)
Centaurea cyanus		x		x	x	Wäckers and van Rijn (2012); van Rijn and Wäckers (2016)
Coriandrum sativum		x			x	Colley and Luna (2000); Ambrosino et al. (2006), Vattala et al. (2006); Wäckers and van Rijn (2012), van Rijn and Wäckers (2016)
Fagopyrum esculentum	x	x		x	x	Carreck and Williams (1997); Colley and Luna (2000), Winkler et al. (2006); Hogg et al. (2011), Wäckers and van Rijn (2012); van Rijn and Wäckers (2016)
Phacelia tanacetifolia	x	x		x		Carreck and Williams (1997, 2002), Wäckers and van Rijn (2012)
Trifolium alexandrinum						–
Trifolium incarnatum						–
Trifolium resupinatum	x					Eriksson and Rundlöf (2013)

extended 40 m into the field, such that any part of them where never closer to another transect than 200 m and control transects never closer to flower strips than 200 m. One site only had one transect of each treatment. All sites had all the transects in one or two winter wheat fields, except for one site were one pair of transects (one treatment and one control) were in a winter rye field. The placement of flower strips on existing EFAs determined by farmers' choice, as part of our strive for policy relevance, led to the presence of an access road, and for three transects a small low-traffic asphalt road, between the flower strips and the focal winter cereal fields. For the study of natural enemies and aphids, the proportion of crop land within 1,000 m from transects, varied between 75 and 95%. By agreement with farmers, pesticide free zones (50 × 20 m) surrounded our transects.

Solitary Bees and Wasps

To assess effects of flower strips on nesting solitary bees and wasps, we used trap nests placed in or in the immediate proximity to all the eleven flower strips and at four distances from them; 200–400 m which could be expected to be in the range of some trap nesting bees and wasps, 600–800 m which could be expected to be out of range for most and, >1,000 m (in one case 966 m) which is outside known foraging range for most trap nesting individuals (Gathmann and Tscharntke, 2002; Holzschuh et al., 2009; Zurbuchen et al., 2010; Hofmann et al., 2020). We placed trap nests in or adjacent to all 11 flower strips, and then in field edges at four different distances (approximately 200–400, 600–800, and >1,000 m from the strip), during three consecutive weeks from June 22nd in 2016 (when at least one of the plant species in a strip was at peak flowering). At one farm, the trap nests at the distance 600–800 m went missing. At each distance, we placed three trap nests. To attract a variety of species, they were of two types: two trap-nests at each distance from the flower strip were filled with reed with a diameter of 2–5 mm to provide nesting sites for small solitary bees and wasps and one trap-nest at each distance was filled with paper tubes with a diameter of 7 and 9 mm to provide nesting sites for intermediate and large solitary bees and wasps. The trap nests were collected in fall, nests and cells counted and the cells identified to taxa or genus. For the trap nests, 51–98% of the surrounding landscape (radius 1,000 m) consisted of arable fields. Since the flower strips differed in size, we also calculated the area flower strip within 1,000 m from each trap nest location. For the trap nests placed within the flower strip or in the immediate proximity this area varied between 509 and 38,310 m^2 (mean: 7,865 m^2). The trap nests were placed next to commercial bumble bee colonies that were used in another study (Klatt et al., 2020) (see section "Discussion").

Statistical Analysis

To test the effects of flower strips on natural enemies and aphids in fields adjacent to flower strips, we used generalized linear mixed-effect models (GLMMs) [glmer-function in Package lme4; (Bates et al., 2015)]. Individual models were created for different organism groups, with the response variables: number of aphids, proportion of aphids parasitized (aphids in the form of mummies), number of hoverfly larva, number of parasitic wasps, number of predatory larva (*Neuroptera* larva, *Coccinellidae* larva, predatory beetle larva, and hoverfly larva) and number of adult predators (*Carabidae*, *Staphylinidae,* and *Araneae* pooled over three sampling rounds). Poisson error distribution was used for all models except for the proportion of mummies, which was analyzed assuming binomial distribution. All full models included the fixed effects treatment (flower strip or control), distance from field edge and the interaction between these, as well as the covariate proportion arable fields within 1,000 m. Likelihood-ratio tests were used to assess the impact of the fixed effects, following recommendations by Zuur et al. (2009). If the interaction between distance and treatment was not significant, it was dropped from the model and distance and treatment effects were evaluated without the interaction. For models based on data where more than two distances from the field edge had been sampled (pitfall traps and

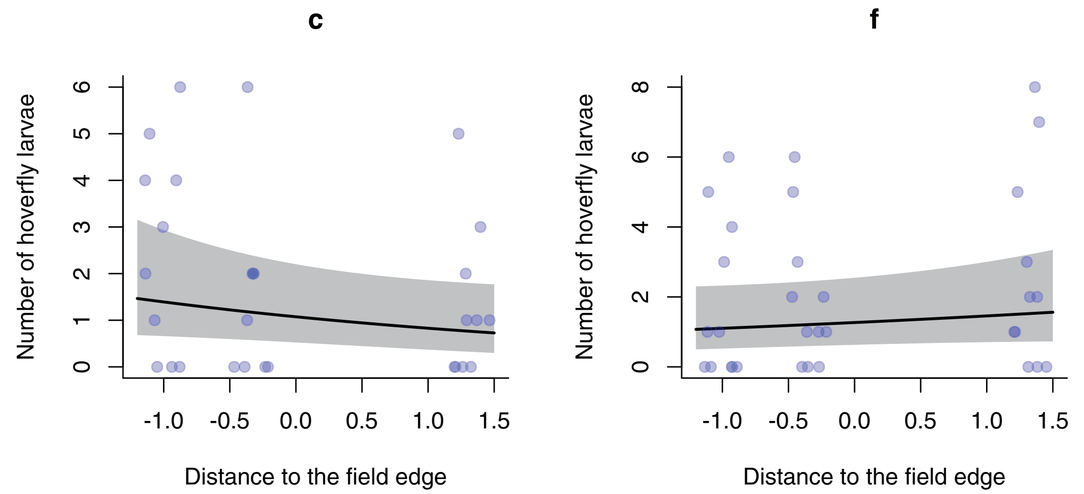

FIGURE 2 | Effects of distance to field edge and treatment for hoverfly larvae. The distances are standardized in the figure, in reality they were 5, 15, and 40 m. There was a weak interactive effect where the number of hoverfly larvae tended to decrease with larger distance from the field edge in control sites (c) and increase in flower strip sites (f).

tillers), distance was handled as a continuous variable. In the models based on data from suction sampling, where only data from two distances were available, distance was handled as a categorical variable.

In the models based on data from the tillers and pitfall traps, offsets (logged) were included to account for different number of tillers sampled (due to loss of samples) and different number of days pitfall traps had been open (due to destroyed traps and weather conditions). An offset was also included in the model for parasitic wasps to account for different number of transects, since transects in same field were pooled due to low number of parasitic wasps in the samples. An observation level random effect was used if the model showed overdispersion. The random structure followed the study design such that transects were nested within treatment and treatment within site. We used likelihood ratio tests to compare models with a random slope and intercept and with only random intercept, respectively (Zuur et al., 2009). If they did not differ significantly, we assumed no random variation in slopes across position in transects and for simplicity used models with only random intercepts. For the natural enemies, variance components for fields or transects were estimated as zero.

To test the effects of the flower strips on solitary bees and wasps, we used generalized mixed effect models (GLMMs) [glmmTMB-function in Package glmmTMB; (Brooks et al., 2017)]. We were interested in if and how the possibility for reproduction for the solitary bees and wasps, respectively, were affected by the presence of a flower strip. In the analysis, we therefore chose to consider only number of cells and did not analyze the number of nests occupied, because bees and wasps of different species may use different number of tubes to lay their eggs in such that this measure is not necessarily a good estimator of reproductive output. Due to low numbers of cells from individual species or families, we pooled the different taxa into two groups: solitary bees and solitary wasps. Models with number of cells per distance as the response variable were fitted assuming a negative binomial distribution to account for over-dispersion. We used two different models with different fixed effects, the full models included either the fixed effect distance from flower strip or area of flower strip within 1,000 m from the trap nest, as well as the covariate proportion arable fields. The models for bees and wasps included the random intercept site. Adding random slopes to these models, resulted in failure to converge.

We checked that residuals of all models (full models and individual fixed effects) showed homogenous variance and followed the assumed distribution ("simulateResiduals"-function; package DHARMa; Hartig, 2018). GLMM models were also checked for over/under dispersion ("testDispersion"-function; package: DHARMa) (Hartig, 2018) and zero-inflation ("testZeroinflation"-function; package: DHARMa) (Hartig, 2018).

We assed collinearity among explanatory variables using pairwise scatterplots, correlation coefficients and variance inflation factors (VIF), with a threshold of 2 for the VIF (Zuur et al., 2009, 2010). To avoid numerical precision problems, all fixed numerical explanatory variables were standardized (mean of zero and standard deviation of one). All data were analyzed in R 3.6.0 (R Core Team, 2019).

RESULTS

Natural Enemies and Pests in Winter Wheat Fields

Flower strips significantly affected hoverfly larvae abundance (**Table 2**), which tended to increase with distance to the field edge in the presence of flower strips but decline if a flower strips was lacking. However, this effect was weak (**Figure 2**). There was also a non-significant tendency that flower strips affected parasitic wasps, with wasp abundance

TABLE 2 | Summary of main fixed effects, treatment (flower strip or control, i.e., normal field margin), distance to field edge and their interaction, on abundances of aphids, proportion of mummies, and abundances of the different groups of natural enemies.

	$c^2_{\text{d.f.}}$	*p*-value
Aphids		
Treatment	0.22531	0.635
Distance	0.49911	0.480
Treatment × Distance	0.22841	0.633
Proportion agricultural land	1.86911	0.172
Proportion mummies		
Treatment	1.06611	0.302
Distance	0.67981	0.410
Treatment × Distance	0.68971	0.406
Proportion agricultural land	2.46211	0.117
Hoverfly larvae		
Treatment	–	–
Distance	–	–
Treatment × Distance	4.3161	**0.038**
Proportion agricultural land	0.86431	0.353
Parasitic wasps[1]		
Treatment	0.12921	0.719
Distance	0.73271	0.392
Treatment × Distance	3.12251	0.077
Proportion agricultural land	0.46181	0.497
Predatory larvae		
Treatment	0.56591	0.452
Distance	7.79981	**0.005**
Treatment × Distance	0.0021	0.964
Proportion agricultural land	0.39711	0.529
Carabidae + Staphylinidae + Araneae		
Treatment	0.09131	0.763
Distance	3.061	0.080
Treatment × Distance	1.13541	0.287
Proportion agricultural land	0.93661	0.333

If $p > 0.05$ for the interaction, distance, and treatment effects were evaluated without the interaction. Degrees of freedom, χ^2-values and p-values from likelihood-ratio test are shown.

[1] Transects in same field pooled due to low number of parasitic wasps.

Values in bold indicate statistically significant results.

decreasing with distance to the field edge in control sites (**Table 2** and **Figure 3**). Aphids and the proportion mummified aphids were not affected by neither the treatment nor the distance, nor their interaction (**Table 2**). For the predatory larvae overall, neither the treatment nor the interaction between treatment and distance explained their abundances. However, there were more predatory larvae 40 m from the field edge compared to five m from the field edge independent on the presence of a flower strip (**Table 2** and **Figure 3**). For ground dwelling predators, abundance was not explained by treatment, distance or their interaction (**Table 2**), they, however, tended to be more abundant further into the fields than to the field edges (**Figure 3**). The proportion agricultural land did not relate to the abundance of any of the groups (**Table 2**).

Solitary Bees and Wasps in the Surrounding Landscape

The bee cells in the trap nests mainly came from the families *Hylaeus* and *Megachile,* there were only a few *Osmia*, *Chelostoma,* and *Heriades*. There was a non-significant tendency that the number of provisioned cells containing solitary bees was higher closer to the flower strips (**Table 3** and **Figure 4**), but for both solitary bees and wasps the proportion arable fields around the trap nests was the most important explanatory variable (**Table 3** and **Figure 4**), with number of solitary bees and wasp cells decreasing with an increasing proportion of arable fields in the landscape. Exchanging the flower strip categorical variable with the area flower strips within 1,000 m from the strip did not change the results qualitatively; also, here there was only a tendency toward a positive effect (**Table 3**).

DISCUSSION

In this study, we demonstrate that annual flower strips can benefit the abundance of hoverfly larvae. However, we could not detect any other significant positive effects on natural enemies and there was no evidence of a difference in natural pest control as shown by lack of flower strip effects on aphid numbers and parazitation rates.

We detected a weak positive effect of flower strips on the abundance of hoverfly larvae, such that they were more abundant further into the field compared to at control sites. This result is consistent with previous studies on the effect of flower strips on hoverflies (Haenke et al., 2009) and may be caused by adult female hoverflies flying further into the fields to lay their eggs when there is a flower strip present to avoid competition from other hoverflies benefiting from local flower availability or that they were less constrained by energy demands due to higher nectar availability and thus able to fly further into the fields. For parasitic wasps, there was a similar but non-significant tendency. Both adult predators (*Carabidae*, *Araneae,* and *Staphylinidae*) and predatory larvae tended to be more abundant further into the fields, but there was no difference between flower strip and control sites. For trap-nesting solitary bees but not for solitary wasps, there was a non-significant tendency that the number of cells was higher closer to flower strips, but not for wasps (in contrast to previous findings; Hoffmann et al., 2018). However, landscape structure best explained the number of cells for both solitary bees and wasps.

We chose to study annual flower strips (Tschumi et al., 2015) rather than multi-annual or perennial flower strips (Jönsson et al., 2015), because our aim was to evaluate the value of using flower strips as EFAs on uncropped field margins in the current CAP policy design. We therefore selected a seed mixture with more or less alien annual plants (flowering in their first year) and adapted the placement and size of the strips in the study to the farmers' management plans for EFAs, which we did not modify. In addition, we selected to study flower strips in the most intensively farmed landscapes in our region, because it is mostly in these landscapes that EFAs are mandatory for farmers.

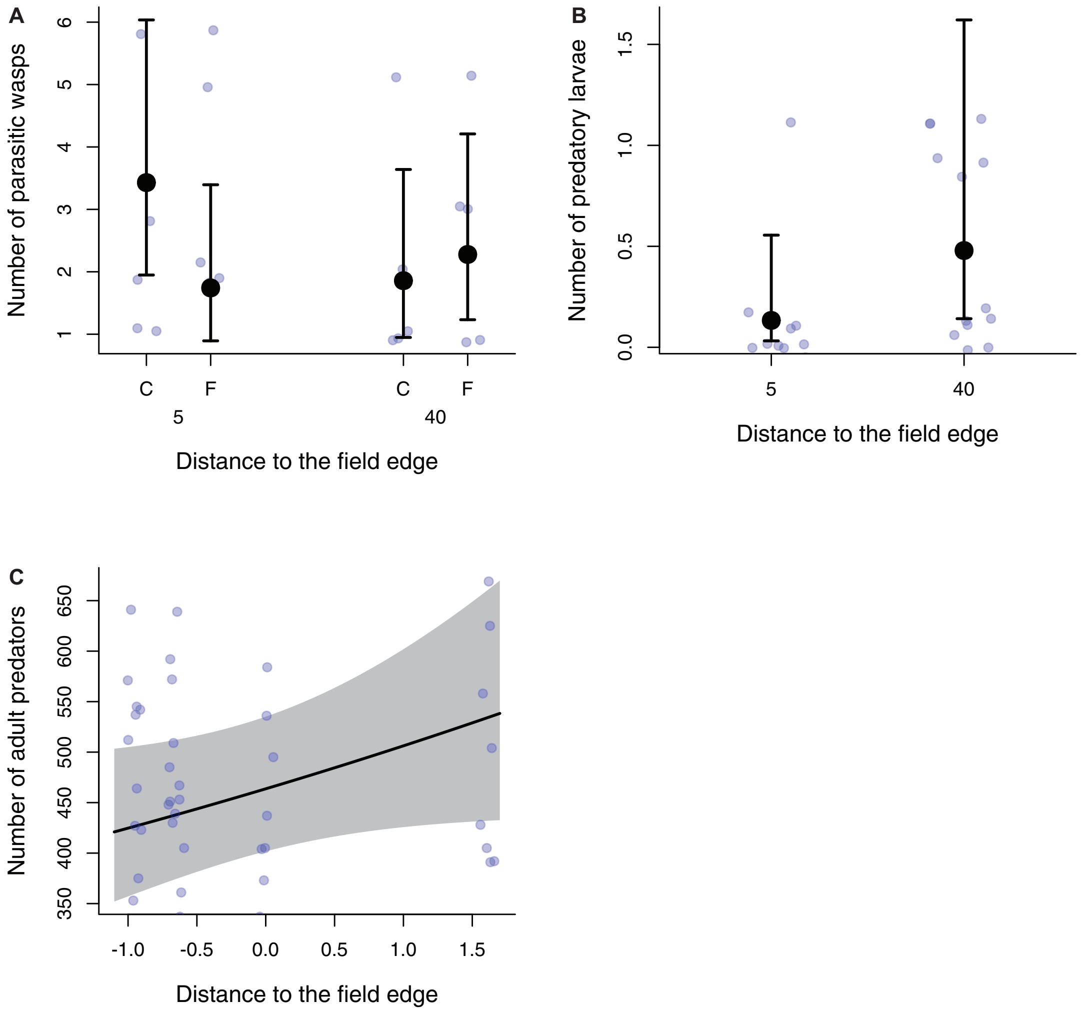

FIGURE 3 | Effects of distance to field edge (m) and treatment. **(A)** The number of parasitic wasps tended to decrease further from the field edge in control sites (C) but not in flower strip sites (F). **(B)** The increasing distance from the field edge positively affected the predatory larvae, independently from presence of a flower strip. **(C)** Adult predators tended to be more abundant further from the field edge, independently from presence of a flower strip. The distances are standardized in the figure, in reality they were 5, 15, and 40 m.

The weak or lack of effects in our study, can be a result of these specifics of our study design.

Compared to most other similar measures, such as perennial or multi-annual flower strips or buffer strips along water bodies, annual flower strips are agri-environmental schemes with a very short duration (Albrecht et al., 2020). They are generally sown in the springs and then plowed up in the fall the same year. The EFA "uncropped field margins," evaluated here, only needs to be present until July 31st in the year they are present (in Sweden). The timing of establishment and flowering as well as termination of annual flower strips may thus be important factors determining their potential to impact organisms in the agricultural landscape. In particular, the flower strips may not be available when many species build up their populations early in the spring or during the previous year, when the annual spring sown EFA flower strips are not yet established and even less flowering. For the solitary bees and wasps, it is likely that our spring sown annual flower strip, flowered too late to provide resources during the period when many of the species are active and lay their eggs, which could explain the rather low numbers of cells in the traps. In the trap nests the bee cells mainly came from the families *Hylaeus* and *Megachile,* there were only a few *Osmia*, *Chelostoma,* and *Heriades.* For bees like *Osmia bicornis*, that are active early in the season (Hofmann et al., 2019) and is one of the most common solitary bee species in southern Sweden, the spring sown annual flower strips most likely flowered too late to be able to provide resources for their offspring. Most species from the families *Hylaeus* and *Megachile* are active later in the summer (Hofmann et al., 2019) which explains why these were the two most common groups in the trap nests we put out in the end of June- beginning of July. It should be noted that there can have been positive effects of the flower strips that we failed to detect due to timing and/or number of sampling efforts; since the flower strips were annual, we chose to only sample during the year they

TABLE 3 | Summary of the fixed effects "distance" and "proportion of agricultural land," as well as "flower strip area within 1,000 m" and "proportion of agricultural land," on the number of bee and wasp cells in the trap nests.

	$c^2_{d.f.}$	*p*-value
Solitary bees – number of cells		
Distance	3.481_{91}	0.062
Proportion agricultural land	5.234_{31}	**0.022**
Solitary wasps – number of cells		
Distance	0.931_{21}	0.334
Proportion agricultural land	5.383_{21}	**0.020**
Solitary bees – number of cells		
Flower strip area within 1,000 m	3.315_{21}	0.069
Proportion agricultural land	5.891_{91}	**0.015**
Solitary wasps – number of cells		
Flower strip area within 1,000 m	1.344_{31}	0.246
Proportion agricultural land	5.845_{41}	**0.016**

Degrees of freedom, χ^2-values and p-values from likelihood-ratio test are shown. Values in bold indicate statistically significant results.

were present. Future studies should further investigate the effects on functional biodiversity also in the years after an annual flower strip has been in an area (see Blaauw and Isaacs, 2014).

Another key factor determining the effects of an agri-environmental measure such as flower strips, is the characteristics of the landscape in which it is placed (Tscharntke et al., 2016). The availability of semi-natural habitat is in general important for both pollinators and natural enemies (Shackelford et al., 2013; Rusch et al., 2016; Duarte et al., 2018; but see Karp et al., 2018) and a potential reason for why we did not find any effects of our flower strips on abundance of natural enemies and aphids is that potential source populations of natural enemies in our landscapes were too small (Bianchi et al., 2006; Chaplin-Kramer et al., 2011; Rusch et al., 2016). When a flower strip is annual and the duration of the measure is short, it is likely that the surrounding landscape plays an ever bigger role than for perennial or multi-annual strips where a temporal effect may allow populations to build up over time (Korpela et al., 2013; Jönsson et al., 2015; Ganser et al., 2019). If the flower strips in our study had been present for several years it is possible that they could have had a positive

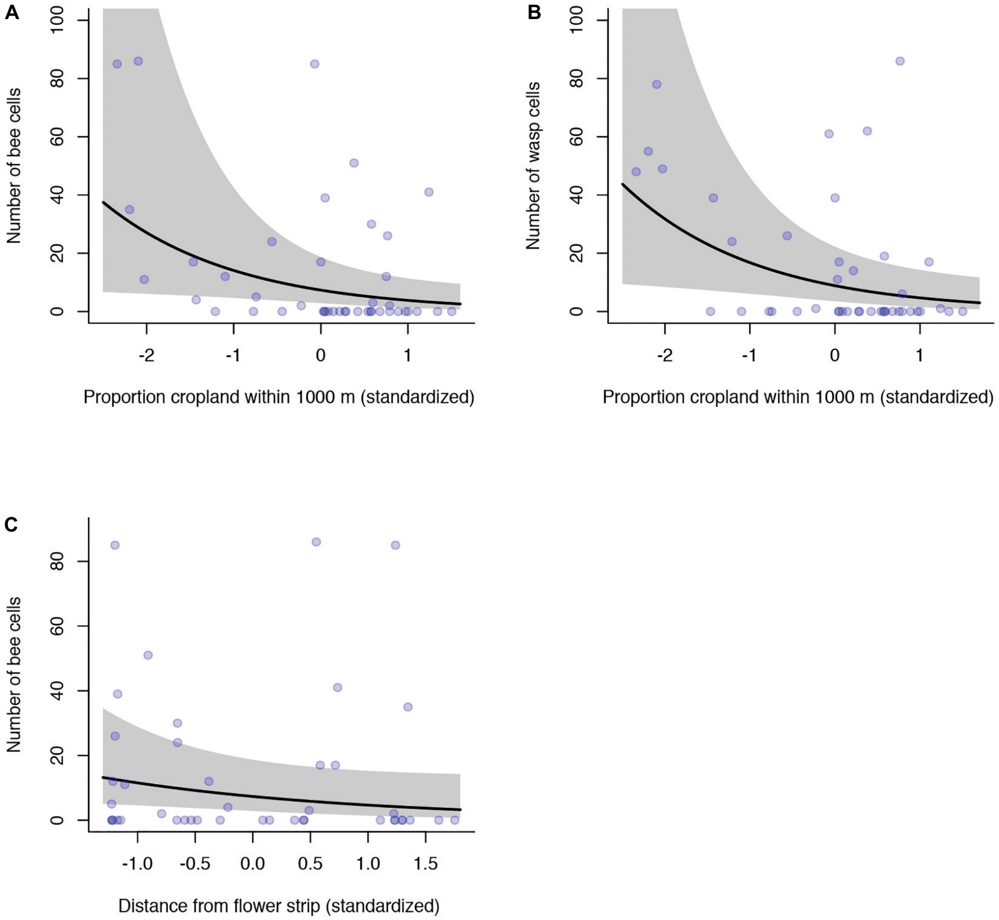

FIGURE 4 | Effect of proportion cropland and distance to flower strip. Increasing proportion cropland negatively influence **(A)** number of bee cells and **(B)** number of wasp cells. The increasing distance to flower strips tends to negatively influence **(C)** number of bee cells.

effect on, e.g., abundance of pollinators (Jonason et al., 2011; Jönsson et al., 2015). A sufficient amount of perennial habitat will be required in the surrounding landscape to provide founding populations that can take benefit of the resources provided by the annual flower strip (Tschumi et al., 2015; Tscharntke et al., 2016). In a recent study by Pollier et al. (2019), there were positive effects of wildflower strips on natural enemies in and close to the strips in the year of establishment. However, the average field sized reported in that study (0.5–3 ha) suggests that the landscapes were more heterogenous (Martin et al., 2019) than the landscapes of the present study (with an average field size of 4.6 ha). The positive effects we detected here, were among mobile organisms. Hoverflies, although also affected by availability of semi-natural habitats (Schirmel et al., 2018), have a life history (e.g., not being central placed foragers (Covich, 1976) allowing them to take advantage of newly established habitats even when the landscape is fragmented and rather simple, whereas the less mobile organisms showed no response (as they are not able to move from the few and fragmented habitats that can sustain a founder population).

We did not find an effect of the surrounding landscape on the abundance of natural enemies or the abundance and parasitation rate of aphids. We suggest that the variation in landscape complexity (75–95% arable land) was such that founding populations were consistently too low for annual flower strips to affect their populations (Tscharntke et al., 2007), whereas Tschumi et al. (2015) also did not find any effect of landscape complexity and suggested this was because landscapes were always very complex. The trap nests in our study were placed in landscapes with a broader range of landscape complexity (51–98% agricultural arable fields within 1,000 m) than the sampling of natural enemies was and for both solitary bees and wasps, there was a negative relationship between the number of cells and the proportion of arable fields around the trap nests. Since bumble bees utilize landscapes at larger spatial scales than solitary bees, landscape effects could theoretically have been mediated by interspecific competition, but we did not find any such competition in another study explicitly focusing on this (Johanna Yourstone, personal communication). We are also aware that the proxy we use to describe the landscape is coarse and acknowledge that there may be important aspects of landscape structure with consequences for natural enemies and pollinators that we did not capture.

An important characteristic of our study was that we used EFAs as planned by farmers independent of our study, but then made farmers experimentally implement flower strips on them. However, by strictly adapting our design to the farmers choices of placement of EFAs, resulted in only six of the EFAs (i.e., flower strips) being located on a field adjacent to a cereal field, reducing the statistical power of the study on natural enemies and pests. In addition, because farmers chose to create the flower strips on sugar beet, oil seed rape and onion fields, the flower strips and the focal fields were separated by a small road, which might have been enough to hamper spill-over from the flower strips, since such effects often are restricted to only a few meters from the flower strips (Pollier et al., 2019). Furthermore, while studying potential effects of the flower strips on natural enemies and aphids we used existing field edges as controls, which differed in appearance and structure, from broad with ample vegetation to narrow with less vegetation, potentially creating a noise hiding any effect of flower strips in the paired design. In addition, except for a small area around transects, pesticides were freely applied on fields, which may have reduced populations able to take advantage from flower strips. In fact, pesticides may even drift from the field into the transects (Ricci et al., 2019). However, regardless of these limitations, we found little evidence that EFAs with annual flower strips as planned by farmers enhance populations or ecosystem services provided by pollinators or natural enemies in intensive agricultural landscapes.

Annual flower strips have become increasingly common in agricultural landscapes. They are agri-environmental measures with potential to increase farmland biodiversity and ecosystem services (Tschumi et al., 2015), as well as being flexible and relatively easy to implement for farmers (Nilsson et al., 2019). Nevertheless, the results from our study highlights that their potential for promoting functional biodiversity such as pollinators and natural enemies, especially in simple landscapes, is limited but also needs to be studied more carefully. For overwintering arthropods annual flower strips, plowed up in the fall, may even act as ecological traps (Ganser et al., 2019). As other studies before, we stress, the importance of basing conservation and agri-environmental measures on scientific evidence (see e.g., Dicks et al., 2014). In intensively managed and ecologically simple agricultural landscapes, where perennial habitat is scarce, the annual flower strips would most likely have a better effect if combined with more permanent agri-environmental measures (Krimmer et al., 2019). This type of management arrangement is something that future research needs to study more specifically. We chose to study annual flower strips because of the annual character of the EFAs and their potential to be more appealing to farmers than permanent measures, though, for long-term positive effects on biodiversity in farmland, networks of perennial or at least multi-annual flower strips (Korpela et al., 2013; Jönsson et al., 2015; Ganser et al., 2019; Albrecht et al., 2020) and semi natural habitats such as semi-natural grasslands (Ekroos et al., 2013) have considerably greater potential.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

HS received the funding. LN, BK, and HS designed the study. LN and BK did fieldwork and data collection. LN wrote the manuscript with input from HS and BK. All authors conducted the statistical analysis.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.629124/full#supplementary-material

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Effect of Land Use History on Biodiversity of Pine Plantations

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The growing replacement of native vegetation by forest plantations is considered a global threat to biodiversity. Significant variation in biotic communities among stands with similar management suggests that previous land use might have an effect on the capacity of forest plantations to harbor native species. The goal of our study was to determine the effect of land-use history on the biodiversity currently present in pine plantations in the coastal range of Central Chile. In particular, we hypothesized that plantations that directly replaced native forests should have higher diversity of plants and birds than plantations that were established in agricultural areas. We also expected that plantations of higher number of rotations should have fewer habitat-specialists and more generalists/exotics, reflecting a process of biotic homogenization. Using aerial photographs and satellite images encompassing a period of six decades, we classified 108 4-ha sampling units into native forests, and mature (17–20 year) pine plantations of first, second, and third rotation, of either forest or agricultural origin. At each site, we collected data on the abundance and richness of diurnal birds and understory plants, and analyzed their behavior in relation to the land-use history using Generalized Linear Models (GLMs). Also, we evaluated dissimilarity of communities of each pine plantation "treatment" to assess the occurrence of biotic homogenization. As predicted, pine plantations that directly replaced native forests had a higher abundance of forest specialists and less abundance of exotics and generalists than plantations of agricultural origin. In contrast, the number of rotations of pine plantations not only did not affect negatively the diversity and abundance of forest specialist species, but the models showed some signs of naturalization in the studied systems over time, such as the increase in the abundance of native herbs and a reduction in the abundance of their exotic counterparts. These results agree with the lack of evidence for a decrease in the dissimilarity of biotic communities in plantations with time, suggesting that the management of pine plantations in Central Chile is not promoting biotic homogenization, beyond the impact of the initial stages of land use change.

Keywords: land-use change, forest plantations, biotic homogenization, understory, birds, *Pinus radiata*

INTRODUCTION

The transformation of natural ecosystems into artificial environments is one of the most ubiquitous expressions of the Anthropocene (Harden et al., 2014). An unfortunate consequence of the latter is that the changes produced by human land use since the 18th century, mostly for agricultural production, are considered one of the most important drivers of global biodiversity loss (Gibbs et al., 2010; Lambin and Meyfroidt, 2011; Ellis et al., 2013).

Among the different mechanisms of land use change, the replacement of natural forests by other land covers is likely one of the most significant in terms of its impact on biotic communities (Brook et al., 2003; Barlow et al., 2016; Sharp et al., 2019). In most cases, this replacement implies the direct removal of most plants from a site, and many other organisms are displaced or killed during cutting or burning operations (Shahabuddin and Kumar, 2007; Escobar et al., 2015; Owen et al., 2019). Moreover, the changes in environmental variables (i.e., luminosity, temperature, water and food availability; Li et al., 2009; Brauman et al., 2015; Andrews et al., 2017; Zhu et al., 2018), also force the evacuation of many animals, and reduce the fitness of the least mobile organisms (Brook et al., 2003; Ranius and Roberge, 2011; Stefani et al., 2017). On the other hand, the new environmental conditions offer suitable habitat for many disturbance-tolerant species that may colonize the area (Cavallero and Raffaele, 2010; Boscutti et al., 2018).

The extinction of habitat-specialist species and the colonization of disturbance tolerant and generalist species are the main mechanisms of biotic homogenization (Devictor et al., 2008; Harrison et al., 2014; Auffret et al., 2018), a process that occurs when different ecosystems subject to similar disturbances converge in terms of species composition and/or function (McKinney and Lockwood, 1999; Robertson et al., 2013; Kusuma et al., 2018). Usually, biotic homogenization takes place gradually, as neither mechanism is instantaneous. The colonization of disturbance-tolerant and generalist species increases over time, modulated by the intensity and frequency of the disturbances associated to the new land use (Acevedo and Restrepo, 2008; Belote et al., 2012; Smith et al., 2019). And even though most habitat-specialists may disappear from the site at the early stages of the land-use change, the populations of some species, especially long-lived ones, may take years or decades to become extinct (i.e., the "extinction debt," sensu Tilman et al., 1994; Kuussaari et al., 2009).

Biotic communities are not only dependent on the physical and biological conditions of the site in which they inhabit, but also on its land-use history (Bremer and Farley, 2010; Cuddington, 2011; Meli et al., 2017). Usually the legacies of past land use can be observed in current communities through lasting alterations in the physical and biotic components that define them (Foster et al., 1998; Hermy and Veyheren, 2007; Fraterrigo, 2013), and the expression of such past effects will depend on the intensity, duration and nature of the disturbance (Foster et al., 1998; Renne and Tracy, 2013).

Forest plantations, comprised of exotic tree species, represent one of the most important land uses that have replaced native vegetation throughout the world, particularly in the Southern hemisphere (Overbeek et al., 2012). Plantations based on fast-growing species of the genera *Pinus* and *Eucalyptus* are usually managed as even-aged stands and harvested through clearcutting (INDUFOR, 2012). These plantations have been shown to generate significant changes in the physical environment in which they are established, including degradation and erosion of soils (Oyarzún and Peña, 1995; Turner and Lambert, 2000; Imaizumi et al., 2008; Soto et al., 2019) and an increase in water consumption (Licata et al., 2008; Scott and Prinsloo, 2008; Little et al., 2009), depending on the local environmental characteristics. In addition, management activities such as logging, weed control, fire or road construction, can have strong effects on biodiversity, for instance, facilitating the arrival of exotics or displacing organisms that are disturbances sensitive (Pauchard and Alaback, 2006; Tardif-Paradis et al., 2015; Cole et al., 2018; Speziale et al., 2018).

Although it is a long-known fact that the biota present in forest plantations may differ significantly from that of the original native forests (Estades and Temple, 1999; Proença et al., 2010; Braun and Koch, 2016; Castaño-Villa et al., 2019), the effect of these artificial forests as promoters of biotic homogenization has only recently received some attention (e.g., see Sweaney et al., 2015; Šibíková et al., 2019; Cifuentes-Croquevielle et al., 2020). One aspect that has been mostly absent from these analyses is the effect of time. Not only biotic homogenization is a process that might require time to develop, but the high variability observed in the biodiversity present in, otherwise similar (e.g., soil type, management) plantations (Simonetti et al., 2013; Trentini et al., 2017; Wang et al., 2019), suggests that the land-use history of the site (e.g., origin, time since the conversion, and number of rotations) may have a significant effect on current community composition.

The goal of this study is to evaluate the effect of land-use history on the biodiversity living in pine plantations, as a way to improve the scientific basis for the design of sustainable forestry management. We tested the hypothesis that land-use history significantly explains part of the variation in the composition of current plant and bird communities present in exotic pine plantations in Central Chile, modulating the expression of biotic homogenization. This history has two components: the time (number of rotations) during which the plantation has been in place, and the land use that preceded the plantation. In particular we tested three main predictions: (1) First, we predicted that the abundance and richness of forest specialists should be higher in plantations that directly replaced native forests, compared to those plantations established in sites that underwent a period of agricultural cultivation after deforestation, and that the richness and abundance of forest specialists should decline in plantations with a higher number of rotations. (2) We also expected that the abundance and richness of generalists and exotics should be higher in plantations that replaced agricultural lands and in plantations with a higher number of rotations. (3) Finally, as a consequence of the latter two, we also predicted that the dissimilarity in the community composition should decline among plantations with higher number of rotations, reflecting the process of biotic homogenization.

MATERIALS AND METHODS

Study Region

The study was carried out in the Coastal Range of the Maule, Ñuble, and Biobío regions (from Putú, 35.2°S, 72.2°W, to Trongol 37.6°S, 73.2°W, **Figure 1**), encompassing approximately 950,000 ha. These regions are considered part of a global biodiversity hotspot (Myers et al., 2000), but hold some of the oldest and most extensive commercial *Pinus radiata* plantations in Chile (Rogers et al., 1955). The climate is Mediterranean with oceanic influence, with warm and dry summers, and cold and rainy winters. Precipitation ranges 650–1000 mm/year (Pizarro et al., 2012; Sarricolea et al., 2016).

This part of the country has a long history of human use that predates the arrival of European settlers (Bengoa, 2000), but the strongest transformations occurred during the 19th and 20th centuries, first as the result of economic incentives for clearing land for crop production and, later, for the establishment of forest plantations (Bauer, 1970; Camus, 2006; Chateauneuf et al., 2011).

The conversion of the landscape into forest plantations began in the mid 20th century, as part of a government program to control soil erosion caused by unsustainable wheat production (Rogers et al., 1955; IREN-CORFO, 1965; Bauer, 1970). Subsidies and environmentally weak regulations further promoted the proliferation of *P. radiata* plantations that, not only were established in eroded lands, but also replaced an important amount of native forests (Echeverría et al., 2006; Nahuelhual et al., 2012; Miranda et al., 2017). Currently, a 37% of the study region is covered by pine plantations while native forests represent only a 13% (Uribe et al., 2020). Most of these remnant native forests correspond to secondary forests, mainly dominated by deciduous species, such as *Nothofagus glauca* and *Nothofagus obliqua*, and also by evergreen species such as *Cryptocarya alba* and *Aextoxicon punctatum*, belonging to the Coastal Mediterranean Sclerophyllous and coastal Mediterranean Deciduous Forests (Luebert and Pliscoff, 2017).

Historical Land Use Classification

We determined the land-use history of pine plantations using aerial photographs (Hycon flight, 1955, OAS project, 1960), Landsat images (1975, 1985, and 1998) and Google Earth Pro images for more recent land covers. For a detailed account of the methods used in this analysis, refer to Uribe et al. (2020).

We classified current pine plantations in relation to their origin (agricultural land or native forest) and the number of rotations that had taken place since their establishment. On average, in Central Chile, pine plantations are harvested at 20 years of age (Lima, 2016), so we used that figure as a reference during the historical reconstruction. Plantations that directly replaced native forests, and were in their first and second rotation, were named NP1 and NP2, respectively. For plantations that were established in agricultural areas we used the codes AP1 for the first, and AP2, for the second rotation. We also found a proportion of plantations in their third rotation, but because the aerial photographs did not allow us to determine the land cover that preceded the plantations, we coded them UP3 (unknown origin and third rotation). However, for interpretation and analysis purposes we consider these sites most likely as pine plantations that replaced agricultural lands since during the early stages of the afforestation program all incentives were for establishing plantations in degraded lands due to intensive and unsuitable agricultural production (Camus, 2006). Finally, in this work we use N as the code to represent native forests. Native forests that were replaced by pine plantations included secondary and degraded forests (Elizalde, 1970; Luebert and Pliscoff, 2017). Agricultural lands replaced by pine plantations were mostly used for wheat production from the middle of the 19th to the middle of 20th century, but also include some vineyards, legumes and small-scale cattle production (Bauer, 1970; Saldivia and De la Jara, 2001). A summary of the evaluated conditions (treatments) stands is presented in **Figure 2**.

Field Data

We established a total of 108 sample units throughout the study region, trying to cover the entire range of conditions detected in the previous classification. The sample size per class was the following: NP1 (12), NP2 (21), AP1 (17), AP2 (13) and UP3 (30). In addition, we included 15 units in native forests (N) to serve as references of community composition. Forty nine units were sampled during 2008–2013, whereas the remaining 59 were assessed in 2016–2018. In all units we sampled woody plants and diurnal birds. Additionally, during the Austral spring and summer of 2017–2018 we collected data on herbaceous plants in 53 of the sample plots (8 NP1, 5 NP2, 12 AP1, 6 AP2, 12 UP3, and 10 N).

Sample units corresponded to 4-ha plots of adult (17–20 year) pine plantations or native forest (**Figure 3**). We selected plantations that had been subjected to a similar management scheme (i.e., pruning and thinning for knot-free wood). This allowed us to control for the effect of canopy closure on understory development (Harrington and Edwards, 1999; Trentini et al., 2017). Also, by working only with mature stands, we reduced the impact of successional changes within each plantation on community composition (Berndt et al., 2008; Uribe and Estades, 2014; Heinrichs et al., 2018). Each sample unit included four 25-m radius circular plots for the evaluation of woody plants, and four 50-m radius point count plots for birds (**Figure 3**). For the assessment of herbs, we used four 10 × 10-m square sub-plots (**Figure 3**).

To estimate the abundance of woody plants in a site, we conducted a visual assessment of the foliage volume in each sub-plot, following the general method used by Estades and Temple (1999) originally designed for the description bird habitat. For this purpose, each sub-plot was divided into four quarters (each evaluated by at least two people from different positions) and vertically sub-divided in three "layers" (0–0.3 m, >0.3–2 m, and >2–6 m), within which we estimated the foliage volume (m^3) of each species. With the data for each layer and quarter for all subplots, we averaged and projected the numbers to estimate the total foliage volume (m^3/ha) for each species. For herbaceous plants we conducted a simple visual estimation of the bi-dimensional cover in the 10 × 10 m plots (Gómez-García, 2008). Any unknown species was collected and/or photographed

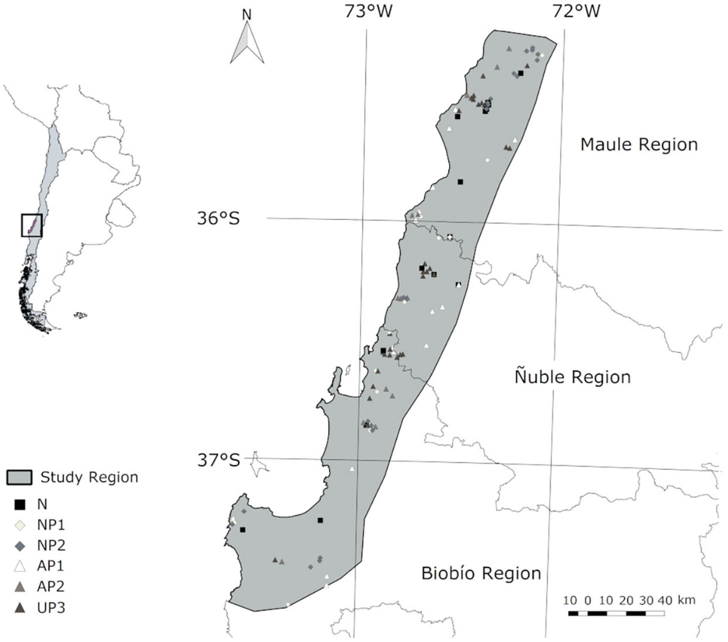

FIGURE 1 | Study region and location of sample units classified as: native forest (N), first rotation pine plantation that replaced native forest (NP1), second rotation pine plantation that replaced native forest (NP2), first rotation pine plantation that replaced agricultural lands (AP1), second rotation pine plantation that replaced agricultural lands and third rotation pine plantation of unknown previous land use (UP3).

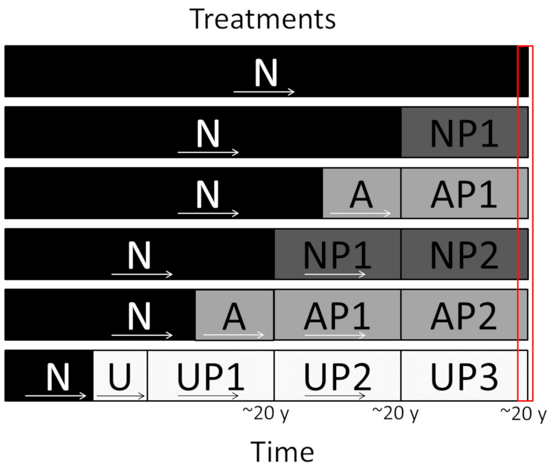

FIGURE 2 | Representation of the conditions (treatments) evaluated. Native forest (N) and pine plantations following the sequence of changes experienced by stands. First rotation pine plantation that replaced native forest (NP1), second rotation pine plantation that replaced native forest (NP2), first rotation pine plantation that replaced agricultural lands (AP1), second rotation pine plantation that replaced agricultural lands and third rotation pine plantation of unknown previous land use (UP3). Agricultural lands (A), unknown previous cover (U). Pine plantation rotations of approximately 20 years. Red rectangle represents the time when samples were collected in each stand class.

for later identification. We averaged the percentage cover for all species in the four subplots to produce a single estimate for each sample unit. Although this approach can have some limitations due to subjectivity of the observer, there is evidence that, compared to other more objective techniques, visual evaluation can detect more plant species, including rare ones (Dethier et al., 1993; Chmura and Salachna, 2016). Besides, in this work, potential individual observer effects were likely minimal, as the field team was roughly the same during the entire evaluation period, thus making data comparable among plots.

We estimated the absolute abundance (ind/ha) of diurnal birds using variable-distance point counts, to allow correction for detectability (Buckland et al., 2001). At each of the four subplots we conducted two 5-min counts (separated by a 5 min waiting period) of all birds seen or heard within the maximum observation radius (50 m). All counts were conducted during the breeding season (October–January), between sunrise and noon, during non-rainy and non-windy days (Bibby et al., 2000). We averaged the results of the eight point counts to produce an estimate of the abundance of each bird species at each sample unit.

Data Analysis

In order to produce the variables required to test the proposed predictions, we conducted the following data classifications and calculations:

To represent forest specialists, we selected all woody plants classified as hygrophiles (following Donoso, 2006), because these species are particularly sensitive to environmental changes such as those imposed by fast growing plantations with high water consumption (e.g., Little et al., 2009; Huber et al., 2010). Due to limited ecological information to assess forest specialization or habitat requirement for many herbaceous plants, we decided to include all native species in this category (in contrast to exotic species), following Rodríguez et al. (2018). Finally, for birds we selected all species classified as forest specialists in the literature (Díaz et al., 2005; Cofré et al., 2007; Ibarra and Martin, 2015).

Generalist and disturbance-tolerant plants were represented by exotic species (both for woody and herbaceous plants) following Rodríguez et al. (2018). Because there is only one exotic bird in the area (*Callipepla californica*), in order to represent disturbance-tolerant birds, we used all species classified as habitat-generalists (Díaz et al., 2005; Cofré et al., 2007; Ibarra and Martin, 2015).

The abundance estimates for woody plant species were produced by adding the foliage volume of all corresponding species, expressed as percentage of total foliage volume (%). In the case of herbaceous plants, their abundance was estimated by adding the percent cover (%) of all corresponding species. Finally, the abundance of birds of each category was generated by adding the density of all corresponding bird species (ind/ha). The richness estimates were produced for each group by counting the number of corresponding species recorded within each sample unit (n). In the case of herbaceous plants, because some species could only be classified to the genus level, we did not use species richness as a response variable.

Finally, we calculated the dissimilarity in the composition of the communities within each forest class (N, NP1, NP2, AP1, AP2, and UP3) by averaging the Euclidean distance (Johnston, 1976) between the abundance of all species (all woody plants, all herbs and all bird species), for all pairs of sample units within the class. For this purpose, we worked with the relative abundance of each species of plants (woody and herbs) and the density of each bird species.

We used two approaches to study the response of species abundance and richness and community dissimilarity to plantation origin and rotation number. First, we conducted multiple comparisons using the method of Benjamini and Hochberg (1995) to test for differences between the studied forest classes (Native forests and plantations of different origin and rotation number). Second, in order to directly account for the effect of time (rotation number: 1, 2, or 3) on the relative abundance and richness of the studied species categories, we used generalized linear models with Poisson or Negative Binomial distribution (Navarro et al., 2001; Zipkin et al., 2014). In these models we excluded the data from native forest sites, in order to focus on the changes occurred during the existence of the pine plantations. For origin we assigned a value of 0 for native forest and 1 for agricultural lands.

We included the following physical covariates in the models: altitude, latitude (UTM) and terrain ruggedness. Because slope was highly correlated ($r > 0.9$) with terrain ruggedness, we only used this latter variable because it is usually considered more informative than slope (Riley et al., 1999). For this purpose we used an Aster Digital Elevation Model (METI and NASA products) available from the Earth Explorer server[1]. For birds, we also included information of the understory, using the foliage volume of woody hygrophiles, exotics, and an additional category: sclerophyllous species, a group of native plants more associated to scrub-type mediterranean ecosystems (Axelrod, 1975; Prentice et al., 1992; Luebert and Pliscoff, 2017). To account for a potential effect of the landscape attributes (Deconchat et al., 2009; Muñoz-Sáez et al., 2020), we also included the percentage of native vegetation and open areas (including forest clearcuts and agriculture-livestock land) in a 500-m radius around each sample unit. This information was obtained using Google Earth Pro 7.3.2., and selecting the images that better represented the condition of the landscape at the time of the field assessment of each unit. All geospatial processes were carried out using the free software QGIS 2.14 Essen.

All explanatory variables were standardized before the analyses. For each case we selected the best model using backward-forward stepwise, based on the Akaike Information Criterion (AIC) (Cavanaugh, 1997) and Model Selection and Multimodel Inference (Calcagno and De Mazancourt, 2010). All statistical procedures were carried out in RStudio 1.2.5033 (RStudio Team, 2019).

RESULTS

Plant Richness and Abundance

We recorded a total of 96 woody plant species in the sample plots (see **Supplementary Table 1**). Fifteen (16%) were exotic species and 81 were native from Chile, 36 (38%) of which were endemic to the Country. Out of 73 identified herbaceous species (see **Supplementary Table 2**), 30 (41%) were exotic, 43 were native species and of these, 19 were endemic to Chile (Rodríguez et al., 2018).

The abundance and richness of hygrophilous woody plants were significantly lower in all pine plantations compared with native forests, although we found no significant differences among plantations of different origin and number of rotations (**Figures 4A,B**). The best models for the abundance and richness of hygrophilous woody plants showed a negative effect of the agricultural origin (**Table 1**). The model for hygrophile richness also included a positive effect of rotation number (**Table 1**).

The abundance of woody exotics increased significantly only in AP1 plantations (**Figure 4C**). The richness of exotics was significantly higher in plantations of agricultural origin, but did not differ among rotations; while in plantations that replaced native forest, the richness of exotics was only higher in NP1 sites (**Figure 4D**). In the case of herbs, only AP1 plantations had a significantly lower cover of native species and a higher cover of exotics (**Figures 4E,F**). Both the abundance and richness of exotic woody plants were positively associated to an agricultural origin (**Table 1**). The abundance of native herbs increased with the number of rotations, while the opposite was true for exotic herbs, which were also positively affected by the agricultural origin. Among the most consistent effects of the covariates were an increased abundance and richness of hygrophilous and exotic woody plants in more southern locations, and a positive effect of open areas in the surrounding landscape on the abundance and richness of exotic woody plants (**Table 1**).

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[1] https://earthexplorer.usgs.gov/

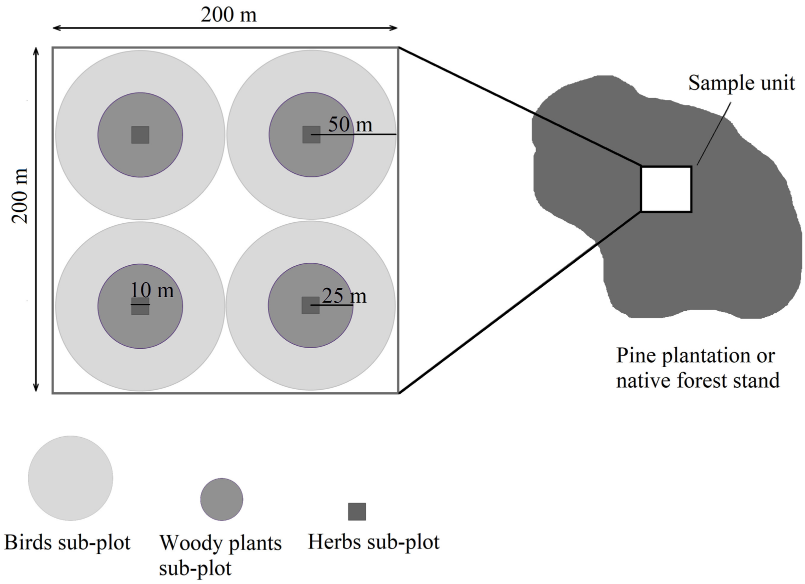

FIGURE 3 | Diagram of one sample unit, showing the sub-plots for the different studied organisms.

Bird Richness and Abundance

We recorded a total of 32 bird species during our field sampling. Thirty one species were native, including two Chilean endemics. Eight species could be classified as forest-specialists, whereas 10 were considered as habitat-generalists (**Supplementary Table 3**).

The abundance and richness of forest-specialist birds declined significantly in pine plantations in relation to the reference native forests (**Figures 5A,B**). However, no significant differences were observed between plantations with different origin and rotation number (**Figures 5A,B**). Some of the significant effects of the studied covariates included a positive impact of the native forest in the surrounding landscape on the abundance and richness of forests specialists in pine plantations (**Table 2**).

In the case of generalist species, no statistical differences were found for any of the studied cases (**Figures 5C,D**). When including the effect of various covariates, the best models for all dependent variables showed only a positive effect of the agricultural origin on the richness of habitat-generalists, and no effect of the rotation number (**Table 2**). Habitat generalists showed a positive association with understory vegetation containing more xerophytic (i.e., +sclerophyllous, −hygrophilous) species (**Table 2**).

Community Dissimilarity

The dissimilarity index of woody plants showed a significant increase in AP1 plantations in relation to that of native forests (**Figure 6A**). Although the index declined in the subsequent rotations, UP3 plantations still had a higher dissimilarity index than N (**Figure 6A**). The woody plant communities in NP2 plantations were significantly more dissimilar than that of native forest sites (**Figure 6A**).

In the case of herbaceous plants there was a clear increase in the dissimilarity index in first-rotation plantations, with both AP1 and NP1 being significantly more heterogeneous than any of the other analyzed forest classes (**Figure 6B**). The dissimilarity of bird communities declined from native forests to AP1 and NP1, and to AP2 and NP2 (**Figure 6C**). However, UP3 sites had bird communities as heterogeneous as native forests (**Figure 6C**).

DISCUSSION

This study is one of the first to directly assess the effect of previous land-use history on current biodiversity in an intensive forestry system. Our data showed that the composition of the understory of pine plantations in Central Chile was strongly influenced by the type of land use that preceded the plantation, and that these legacies may last for several decades. Similarly persistent effects of agriculture have been observed in many other systems (Fraterrigo, 2013; Munteanu et al., 2015; Neumann et al., 2017).

Our work is also among the few that have analyzed the occurrence of biotic homogenization in intensively managed forest systems (Sweaney et al., 2015; Šibíková et al., 2019; Cifuentes-Croquevielle et al., 2020). Studying a six-decade period of pine plantation forestry in Central Chile we assessed the effect of time (i.e., rotations) on the loss of heterogeneity (i.e., community dissimilarity) and the main mechanisms behind biotic homogenization: loss of habitat specialists and colonization by habitat generalists. To the best of our knowledge, this is the first study to take such a comprehensive approach.

Forest-Specialist Species

Although data on forest-specialist woody plants and birds showed the expected decline in richness and abundance from the reference native forests to plantations (Estades and Temple, 1999; Vergara and Simonetti, 2006; Gómez et al., 2009;

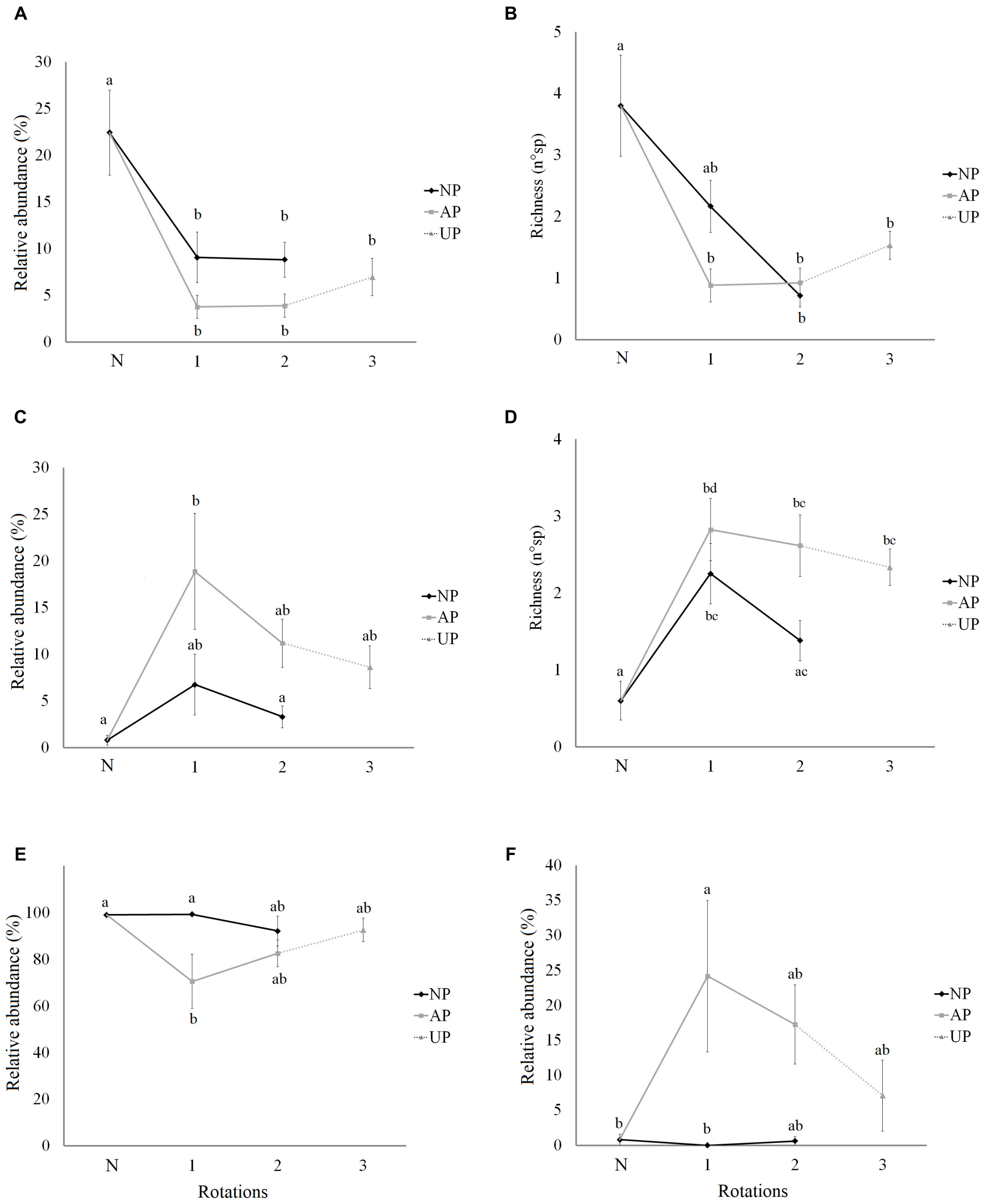

FIGURE 4 | Relative abundance and richness of plants in the understory of native forests and pine plantations with different origin and number of rotations. **(A)** Abundance of hygrophilous woody plants. **(B)** Richness of hygrophilous woody plants. **(C)** Abundance of exotic woody plants. **(D)** Richness of exotic woody plants. **(E)** Abundance of native herbs. **(F)** Abundance of exotic herbs. N in *x*-axis is Native forest. NP, native forest transformed into pine plantation, AP, agricultural land transformed into pine plantation, UP, unknown previous land use (assumed as agricultural land) transformed into pine plantation. Lower case letters indicate the significance of differences among categories obtained by BH multiple comparisons.

Braun and Koch, 2016), the trend was not observed among plantations of different rotation number (**Figures 4A,B**, **5A,B**).

The relative abundance and species richness of hygrophiles were higher in pine plantations that directly replaced native forests than in those that were established in agricultural areas (**Table 1**). There are management-related explanations for the latter result. For example, the persistence of many shrub species after the conversion into pine plantations may be possible due to the resprouting abilities of many species (Ross et al., 1986; O'Hara et al., 2007). However, preparation of the land for crop cultivation

TABLE 1 | Coefficients of the best generalized linear models for the abundance and richness of plants in pine plantations with different origin and number of rotations.

Dependent variables	+Origin	Rotation	Latitude	Roughness	Landscape context	
					Open areas	Native forest
[a]Abundance of hygrophiles	−0.32*		−0.39**		−0.39*	–
[b]Richness of hygrophiles	−0.29***	0.17*	−0.30***			
[a]Abundance of exotics	0.51**		−0.68***		0.75***	
[b]Richness of exotics	0.19*		−0.37***		0.13*	
[a]Abundance of native herbs		0.40*			0.32*	
[a]Abundance of exotic herbs	1.43***	−0.59*		−0.69*		

[a]Negative binomial, [b]Poisson.

****$p < 0.001$, **$p < 0.01$, *$p < 0.05$.*

–Present in the model, without significance.

+Native = 0, Agriculture = 1.

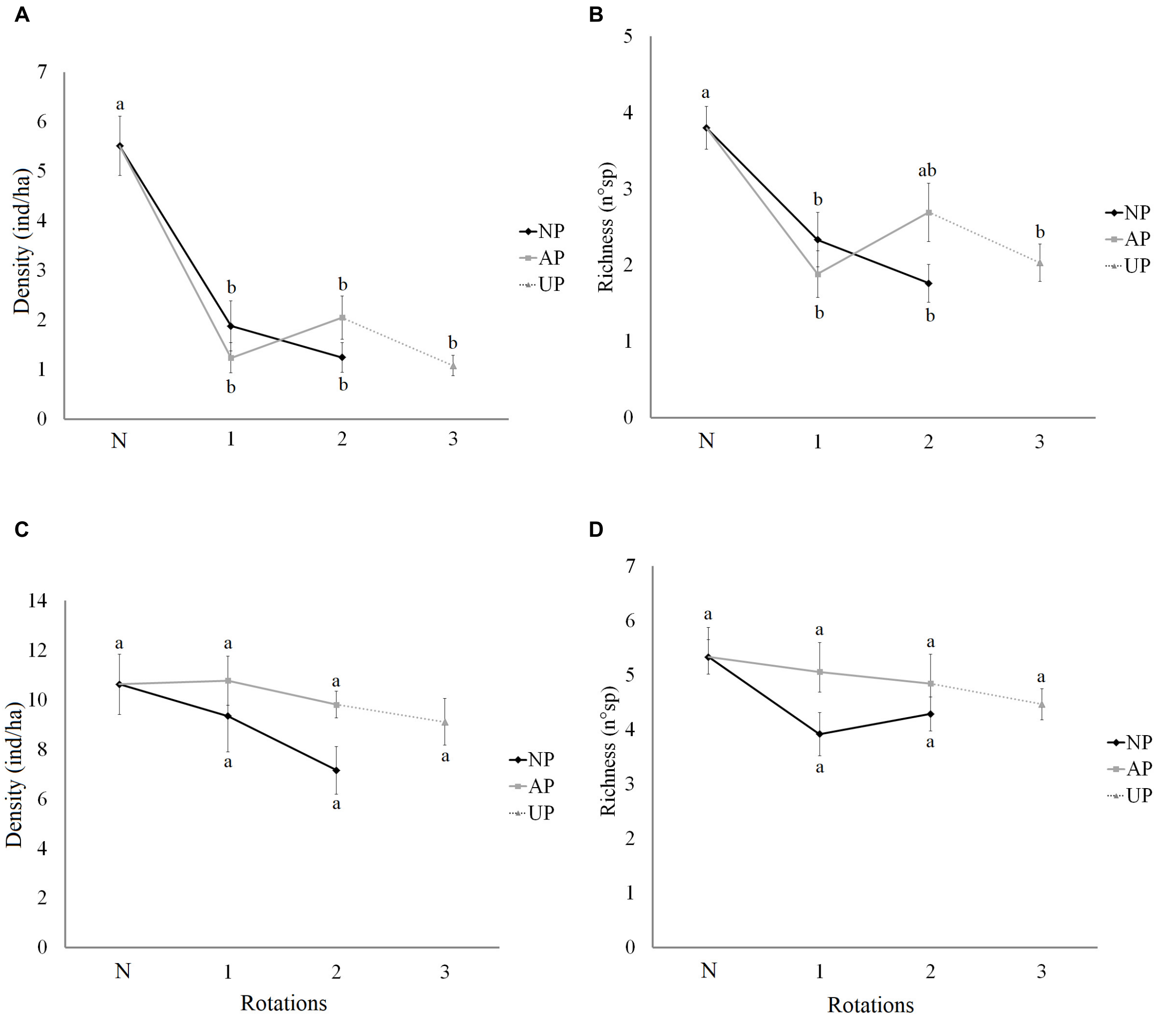

FIGURE 5 | Abundance and species richness of diurnal birds in native forests and pine plantations with different origin and number of rotations. **(A)** Abundance of forest-specialist birds. **(B)** Richness of Richness of forest-specialist birds. **(C)** Abundance of habitat-generalist birds. **(D)** Richness of habitat-generalist birds. N in *x*-axis is Native forest. NP, native forest transformed into pine plantation, AP, agricultural land transformed into pine plantation, UP, unknown previous land use (assumed as agricultural land) transformed into pine plantation. Lower case letters indicate the significance of differences among categories obtained by BH multiple comparisons.

TABLE 2 | Coefficients of the best generalized linear models for the relative abundance and richness of birds in pine plantations with different origin and number of rotations.

					Foliage volume (m^3/ha)			Landscape context	
Dependent variables	**+Origin**	**Rotation**	**Latitude**	**Roughness**	**Sclerophyllous**	**Exotics**	**Hygrophiles**	**Open areas**	**Native forest**
[a]Abundance of forest specialists				0.24*					0.24*
[b]Richness of forest specialists			−0.20**						0.16*
[a]Abundance of habitat generalists	0.11*		−0.3***		0.10*		−0.16**		
[b]Richness of habitat generalists									

[a]Negative binomial, [b]Poisson.
***$p < 0.001$, **$p < 0.01$, *$p < 0.05$.
+Native = 0, Agriculture = 1.

usually requires the removal of stumps and main roots of woody species, which impedes vegetative reproduction of many native plants (FAO, 1977; Jorquera, 2001).

Although we predicted that the abundance and richness of habitat specialists should decline over time, due to the gradual extinction of species not adapted to the environmental conditions imposed by the new land use (Ranius and Roberge, 2011; Auffret et al., 2018), the trend was not observed among plantations of different rotation number (**Figures 4A,B**, **5A,B**). And not only forest specialists did not decline over time, but the richness of hygrophilous woody plants and native herbs increased in plantations with more rotations (**Table 1**). The effect on hygrophiles is particularly interesting since the reduction of water availability is considered one of the main environmental changes produced by pine plantations (Huber et al., 2008; Álvarez-Garretón et al., 2019). Nevertheless, our results suggest that plantations may provide a relatively suitable habitat for some sensitive species, which might be able to recolonize the area after being extirpated during the initial stages of deforestation (Onaindia and Mitxelena, 2009; Jeffries et al., 2010; Becerra and Montenegro, 2013).

Generalist Species

As expected, exotic herbaceous and woody plants were more diverse and abundant in plantations that replaced agricultural areas (**Table 1**). The ubiquitous presence of humans in agricultural areas and the frequent and intense disturbances to which crop fields are subjected, promote, respectively, the arrival and establishment of exotic plants, including undesirable weeds (e.g., *Genista monspessulana*), and naturalized useful plants (e.g., *Rubus ulmifolius*, *Rosa moschata*). The positive effect of the amount of open areas in the surrounding landscape on woody exotics (**Table 1**), indirectly highlights the importance of the distance to propagule source as a factor of invasibility (González-Moreno et al., 2013; Altamirano et al., 2016). The abundance of habitat generalist birds was also higher in plantations established in agricultural areas (**Table 2**), which agrees with our prediction.

Our second prediction stated that exotics and habitat generalists should increase their abundance and richness in plantations with more rotations, reflecting the gradual invasion of species more adapted to the disturbances associated to the management of plantations (Pawson et al., 2009; Moreira et al., 2013; Stokely et al., 2020). As occurred with specialists, the data did not support our expectations. While the richness and abundance of generalist birds did not differ between native forest and any of the studied plantation classes (**Figures 5C,D**), both woody and herbaceous exotics increased their richness and abundance in relation to native forests. However, the latter did not continue increasing in plantations with more rotations (**Figures 4C,D,F**). Moreover, the best model for the abundance of exotic herbs showed a significant decrease with rotation number (**Table 1**).

These results show that pine plantations in Central Chile do not seem to be promoting the invasion of exotic species beyond the effects of the initial stages of land use change. Moreover, the studied plantations might be excluding some exotic plants species over time. We can think of, at least, two potential mechanisms for the latter. First, because the transformation of agricultural land into pine plantations involves a significant reduction in the human population (Tropp, 2003; Rudel, 2009), the persistence of weeds with human-mediated dispersal (Hansen et al., 2005; Pickering and Mount, 2010; Ansong and Pickering, 2014) could have been compromised. Second, the change from a horse and oxen-based logging in the early plantations, to mostly mechanized harvesting operations (Carey and Soto, 2005), has likely reduced the abundance of many alien plants whose seeds are dispersed in ungulate dung (Chuong et al., 2016).

Biotic Homogenization

One of the expected outcomes of the widespread use of production systems such as forest plantations is the process of biotic homogenization (Manor et al., 2008; Sweaney et al., 2015; Kirkpatrick et al., 2018). We predicted that the community dissimilarity between sites in our study region should decline in plantations with higher number of rotations, reflecting the occurrence of biotic homogenization (Kirkpatrick et al., 2018). Having failed to obtain support for the occurrence of any of its mechanisms (i.e., a reduction of habitat specialists and an increase in habitat generalists), it is not surprising that this prediction also proved incorrect.

Interestingly, the plant communities in first-rotation plantations had a higher dissimilarity among themselves than in the reference native forests (**Figures 6A,B**). There are two potential explanations for this pattern. First, the high intersite

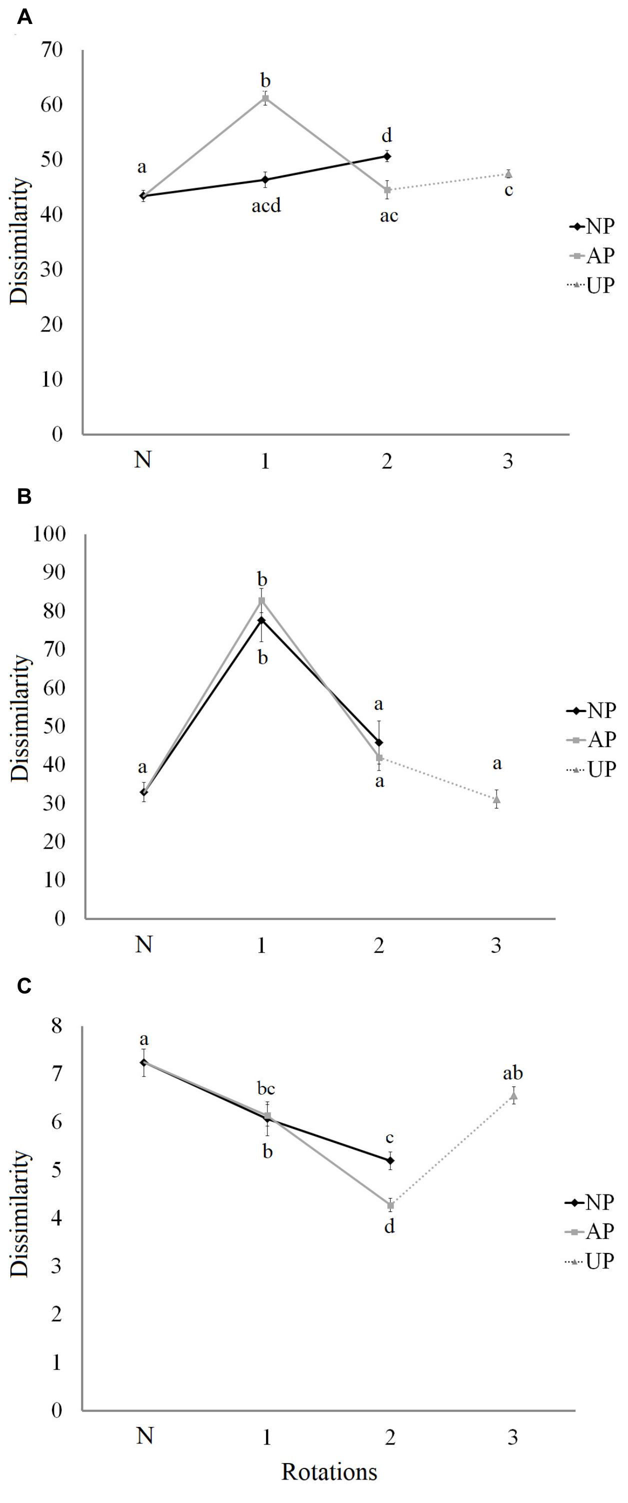

FIGURE 6 | Dissimilarity index for the community of woody plants **(A)**, herbs **(B)**, and birds **(C)** between sites of the same forest class. N in *x*-axis is Native forest. NP, native forest transformed into pine plantation, AP, agricultural land transformed into pine plantation, UP, unknown previous land use (assumed as agricultural land) transformed into pine plantation. Lower case letters indicate the significance of differences among categories obtained by BH multiple comparisons.

heterogeneity may arise from the legacies of the different agricultural uses in different areas. Although wheat was the dominant crop before the advent of pine plantations, other uses included legumes, vineyards, and small-scale cattle ranching (Bauer, 1970; Saldivia and De la Jara, 2001), all of which may promote different sets of accompanying plant communities. Second, although we made an effort to locate native forests in good conditions to act as appropriate references, the studied stands might have already been affected by disturbances, fragmentation and decades of being surrounded by pine plantations (Estades and Temple, 1999; Sweaney et al., 2015; Miranda et al., 2017), likely reducing intersite heterogeneity. A potential sign of the latter is the high proportion of generalist vs. specialist birds recorded in our samples in native forests (**Figures 5A,C**). However, we are confident that the lack of pristine forest sites in the study region (Donoso and Lara, 1995; Bustamante and Simonetti, 2005; Gómez et al., 2011), and in our sample, in no way affects the main results of this study.

Although in most situations the dissimilarity of plant communities declined in the second and third rotation, in no case it reached values lower than in the native forests (**Figures 6A,B**). Moreover, the dissimilarity of woody plants in plantations that replaced native forests actually increased in the second rotation (**Figure 6A**). Although these results do not support the hypothesis of biotic homogenization among plants in the studied pine plantations, it is important to keep in mind that there might still exist an extinction debt that has not yet been paid. The ability of many woody plant species to resprout from stumps may extend their presence even in the absence of sexual reproduction (Ross et al., 1986; O'Hara et al., 2007). Interestingly, there were different trends in herbs and woody plants that might relate to the latter phenomenon (**Figures 6A,B**). Studies on the seed bank and vegetative reproduction abilities in the understory of plantations with different rotations would shed some light on this topic.

Up to the second rotation, the dissimilarity indexes of birds showed the predicted decline in the case of biotic homogenization (**Figure 6C**). However, the trend reversed in the third rotation with an increase in intersite heterogeneity. This result cannot be explained by changes in bird abundance or richness, because none of these variables changed with rotation number (**Table 2**). Instead, this increase in heterogeneity might be due to different relative changes in the abundance of individual bird species in different sites, likely associated to a higher diversity of forest-specialist plants in plantations with more rotations (**Table 1**).

Exploratory Non-metric Multidimensional Scaling (NMDS) analyses for woody plants, herbs and birds (based on Bray-Curtis dissimilarity), support the general patterns described in the previous paragraphs (**Supplementary Figure 1**).

We can summarize our findings with a conceptual model that may serve as a hypothesis for future studies on this topic (**Figure 7**). If we consider that the native forest (N) has the highest level of naturalness (e.g., the difference or ratio between specialists vs. generalist-exotic species), any land-use change (e.g., conversion into forest plantation) will reduce this level to a point that reflects the long-term level of naturalness allowed by the new land use (in this case, the plantation naturalness level, PNL, **Figure 7**). Depending on the severity of the disturbance involved

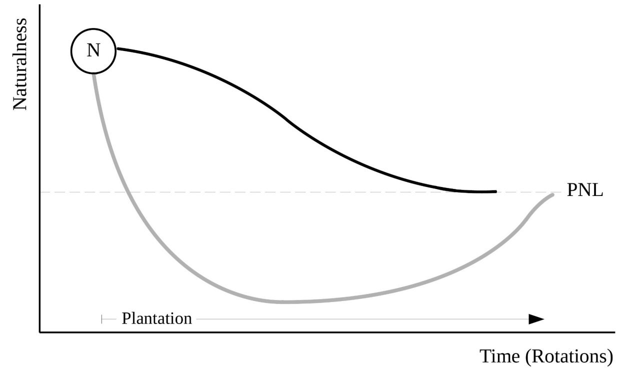

FIGURE 7 | Model for the effect of the conversion of native forests (N) into pine plantations in Central Chile on the level of naturalness of the systems. The black and gray lines represent "soft" and "hard" conversions, respectively. See text for further explanation. PNL and the dashed line represent the plantation naturalness level.

in the transformation, the community may follow different trajectories toward the new equilibrium. For example, the direct replacement of a native forest by a plantation may be considered a "soft" conversion, in which most sensitive species will disappear gradually from the system (black line, **Figure 7**). Alternatively, the native forest may undergo a "hard" conversion by, as in the present study, being first transformed into agricultural use, before the establishment of the plantation (gray line, **Figure 7**). In the latter case, the level of naturalness will drop abruptly, driven by the rapid extinction of many habitat specialists and the invasion of many exotic and disturbance-adapted species. This decline may cause the system to reach naturalness levels lower than PNL, which will later increase as some native species recolonize the area and some of the alien species disappear, converging to the equilibrium point.

Management Implications

Over the past two decades an important number of studies have explored ways of improving the compatibility of pine plantation forestry with biodiversity conservation in Central Chile. Authors have highlighted the key importance of promoting a well-developed understory (Tomasevic and Estades, 2008; Taki et al., 2010; Simonetti et al., 2013), the maintenance of woody debris (Rudolphi and Gustafsson, 2011; Uribe and Estades, 2014; Fierro and Vergara, 2019), or the design of landscapes that promote biological connectivity (Acuña and Estades, 2011; Mortelliti et al., 2015; Castillo et al., 2018). The current study provides an additional perspective over which to design the management of these industrial forests, in order to reduce their long-term negative impacts, and to enhance their potential benefits on biodiversity. From the perspective of reducing biotic homogenization, the latter implies reducing the loss of habitat specialists and preventing the invasion of exotic species.

There is strong evidence that the presence of nearby native forest patches increases the abundance of forest-specialist birds in pine plantations in Chile (Estades and Temple, 1999; this study). Although we did not find such an effect for habitat-specialist plants, we can speculate that the movement of birds between native forest fragments and the pine plantations may play a role in the recolonization of plantations by ornithocorous plants (Whittaker and Jones, 1994; Ponce et al., 2012; Spennemann, 2020). The ruggedness of the terrain in most of the study region implies that most plantations are located close to a creek with some native vegetation. Protecting creeks and native forest fragments may play a significant role in the conservation of biodiversity in pine plantation landscape (Estades and Temple, 1999; Lindenmayer et al., 2003).

One factor that might have contributed to the persistence of some forest specialist species in pine plantations in Central Chile, is the relatively low frequency of disturbances involved in their management. Any management decision leading to changes in rotation length could certainly affect the long term composition of the community, by influencing the likelihood of forest specialists to find suitable habitat (Sullivan et al., 2009; Gallé et al., 2016; Castaño-Villa et al., 2019) and by affecting the invasion rate of disturbance-adapted exotics (Zhou et al., 2019).

The main assumptions of the model that we proposed (**Figure 7**) are that there exists an equilibrium point in the composition of the biota that can be found in pine plantations in Central Chile, and that the trajectories of plantations with different histories will tend to converge to this equilibrium over time. It is important to consider that the level of naturalness that can be achieved in pine plantations may depend strongly on the management of these industrial forests, many aspects of which are still not clear, particularly in relation to their long-term effects (Castaño-Villa et al., 2019). One example of the latter is the impact of biomass extraction and soil amendments on the long-term fertility of tree plantations (Woods, 1990; Smaill and Garrett, 2016; Addison et al., 2019). Thus, although our study considered a period of more than six decades, more time and research are certainly needed to confirm or reject our hypotheses.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

SU and CE contributed with study design and the manuscript writing. SU carried out field work and data collection. All authors performed the laboratory work and data analyses.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.609627/full#supplementary-material

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The Effect of Forest Management on the Avifauna of a Brazilian Dry Forest

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The conversion of tropical habitats has dramatic implications on biodiversity and represents one of the greatest conservation challenges of our time. Seasonally Dry Tropical Forests (SDTF), which are disjointly distributed throughout the Neotropics, are especially susceptible to human activities. The Caatinga Dry Forest, located in the semi-arid interior of northeastern Brazil, represents not only the largest and most biologically diverse nucleus of SDTF, but also the world's most densely populated semi-arid region, with ever-growing pressure on its natural resources. To prevent illegal logging, conservation agencies looked at forest management, where an area is divided in smaller stands which are gradually logged and allowed to regrow for a period of time, when a new cutting cycle should reinitiate. The impacts of these management schemes on biodiversity, however, remain largely untested. We conducted standardized avian surveys to evaluate the effects of forest management on the avian community at a 1,670 ha privately owned property located on the Chapada do Araripe, northeastern Brazil. This area was divided in 22 forest stands, half of which had already been logged at the time of our sampling, creating a gradient of logged and natural forests and an 11-yr chrono-sequence of forest regeneration. Our results show that logged areas present fewer individuals, fewer species, and different avian assemblages than unlogged forests. Such differences are mostly driven by forest-dependent species, which were overwhelmingly affected by forest management. Our results show that although logged forests tend to recover its height after a decade, they do not recover the originally forest cover, measured by the Normalized Difference Vegetation Index. Likewise, decade-long recovering stands continue to show lower species richness, lower bird abundance, and different avian composition than unlogged forests. We identified a set of bird species that are more affected by forest management (ecological losers) and a group of birds that apparently benefit from the referred changes in land use (ecological winners). We conclude that completely managing an entire area may cause the extirpation of several forest-dependent species. We therefore suggest keeping logged and unlogged plots intermingled, to avoid local extinctions and the complete modification of the original avifauna.

Keywords: anthropogenic disturbance, ecological loser, landscape fragmentation, avian communities, Caatinga

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INTRODUCTION

Halting the conversion of natural habitats into anthropogenic landscapes represents one of the greatest challenges of the twenty-first century. This is particularly true for tropical regions, which concentrate most of the planet's biodiversity (Laurance, 2007; Blackman et al., 2014). Seasonally Dry Tropical Forests (hereafter SDTF) are patchily distributed throughout the world's tropics and are especially susceptible to human activities (Pennington et al., 2004). Dry tropical forests are subject to multiple threats, often simultaneously, including habitat fragmentation, fire, wood harvesting, conversion to croplands, and climate change (Miles et al., 2006; Antongiovanni et al., 2020). Despite those pressures, SDTF are often considered resilient habitats, because they tend to recover their original stature faster than wet forests (Vieira and Scariot, 2006). Tree species composition recovery should be straight-forward under minor disturbance regimes (Lebrija-Trejos et al., 2008). However, under heavy use, dry forests tend to recover very slowly (Vieira et al., 2006). Not only seedlings need to establish themselves during a short rainy season, but seedling survival rates are very low (Colón and Lugo, 2006; Lebrija-Trejos et al., 2011). Differently from wet forests, where soft-wooded tree species dominate the early succession period, dry forest early succession conditions can be harsh, and only tolerated by slow-growing hard-wooded species (Poorter et al., 2019).

The Caatinga Dry Forest (hereafter Caatinga), located in the semi-arid interior of northeastern Brazil, represents the largest and most biologically diverse nucleus of SDTF in the Neotropics (Miles et al., 2006). However, despite alarming rates of deforestation—nearly 60% of the Caatinga's original vegetation cover has already been modified by human activities (Beuchle et al., 2015)—it remains the least protected ecosystem in Brazil, with ∼1% of its area fully preserved by protected areas (Leal et al., 2005; da Silva et al., 2018). Despite presenting very harsh living conditions, with nearly 30 million inhabitants, the Caatinga represents the most densely populated semi-arid region in the world (da Silva et al., 2018). Human Caatinga populations are mostly rural and present some of the lowest human development indices in Brazil (da Silva et al., 2018). This reality presents the Caatinga with multiple pressures, mainly due to livestock production, itinerant agriculture, and particularly wood harvesting to produce firewood and charcoal (Ribeiro et al., 2015; Antongiovanni et al., 2018). Some of these activities, such as subsistence firewood and overgrazing by goats, represent chronic low-intensity activities, which will affect biodiversity in the long term (Singh, 1998; Ribeiro-Neto et al., 2016; Antongiovanni et al., 2020). Other human activities, such as deforestation for charcoal production, mining, or the total conversion of woodlands for croplands and pasturelands, represent acute disturbances, which are rapid and intense, often removing all forest resources from an area, and are known to affect the biota in more dramatic and pervasive ways than chronic activities (Singh, 1998).

As a way to prevent illegal over-exploration of wood resources, governmental and environmental agencies recommend the rational management of these forests (Soares-Filho et al., 2014). Among the managing schemes, there is a practice that consists of subdividing a large area into smaller forest stands and gradually logging-off the timber of each fragment, allowing regrowth and creating a gradient of forest stands in constant regeneration. In general, they propose 25 year-cycles, after which regenerated forest stands undergo a new cutting cycle. Although modern forest management was introduced between the eighteenth and nineteenth centuries, only recently the activity stopped be seen just by an economic view (Samojlik et al., 2016). Despite its widespread use, the impacts of such forest management scheme on biodiversity remain unclear (MacDicken et al., 2015; Darrigo et al., 2016).

Monitoring biodiversity under the impact of human activities is one of the most traditional strategies for wildlife conservation (Magnusson et al., 2018). However, due to the impossibility of monitoring all species, certain groups are considered indicators of environmental quality (Lindbladh et al., 2020). Birds are often used as indicators because they have a well-defined taxonomy, have consistent information about the habitats they occupy, and are relatively easy to survey (Drever et al., 2008; Lindbladh et al., 2020). Changes in habitat structure are often reported to affect bird assemblages, however, not all species are affected equally (Shahabuddin and Kumar, 2006). Direct and indirect effects can influence different groups of birds, especially demanding species that need specific resources or habitats (Shahabuddin and Kumar, 2006; Drever et al., 2008). In fact, the impact of logging and subsequent forest recovery is predicted to vary depending on specific life history traits of the logged tree species (Vinson et al., 2015). Also, it remains to be seen if forest structure recovery results in complete or even partial recovery of animal species, which may also follow species-specific recovery patterns (Shahabuddin and Kumar, 2006).

There are few studies evaluating the effect of forest management in the Neotropics, but most of these studies were conducted in humid forests (Thiollay, 1997; Berry et al., 2008; Hamer et al., 2015; Poudyal et al., 2018; Bousfield et al., 2020). In fact, few have evaluated the effects of either selective or clear-cut logging follow by forest regeneration in SDTFs (Shahabuddin and Kumar, 2006; Maia et al., 2019). In this study, we evaluate the effect of a forest management scheme at a privately owned property located in the semi-arid interior of northeastern Brazil, where a network of trails subdivided the area in 22 different forest stands. One forest stand has been logged every year and let to regrow since 2004. At the time of our surveys, half of the stands had already been logged, creating a recovering gradient of recovering logged forests and forest in natural condition, offering a unique opportunity to evaluate the effect of forest management on avian biodiversity.

We conducted standardized avian surveys (point counts) to understand the effects of forest management on the avifauna. Specifically, we aim to (i) compare avian diversity (species richness and bird abundance) and avian composition between logged and unlogged forests; (ii) evaluate whether this effect depends on the degree of species disturbance sensitivity between forest-dependent and non-dependent species; (iii) evaluate how species composition recovered along a 11-yr regeneration chrono-sequence; and (iv) understand whether avian changes can be predicted by the structure of the vegetation. Prior to our study, we had a series of expectations, which included: (i) a reduction in avian diversity (species richness and bird abundance) and changes in species composition in logged areas; (ii) that most of this changes will be led by forest-dependent bird species; (iii) a slow recovery of avian diversity in regenerating forests; and (iv) a positive relationship between avian diversity and forest structure (forest height and tree cover). This represents one of the first studies to evaluate the sustainability of forest management in the Caatinga and aims to shed light into the effects of a common management practice.

MATERIALS AND METHODS

Study Area

We conducted this study at the Fazenda Pau D'Arco (7° 20′ S, 39° 34′ W), a privately owned property located ∼26 km southwest of the city of Crato, in the Brazilian state of Ceará (**Figure 1**). The area, located at ∼860 meters above sea level on top of the Chapada do Araripe (Araripe Plateau), is within an Area of Environmental Protection (a category of the Brazilian protected areas system that allows human occupation and sustainable economic activities). The vegetation cover in this area is represented by a thorny dry forest, locally known as *Carrasco* (Prado, 2003), a type of deciduous vegetation characteristic of sedimentary plateaus (Giulietti et al., 2004). *Carrascos* are present on sedimentary soils and show a predominance of sub-arboreal and small tree forms (3–4 m), high density of woody plants and unstratified thin trunks (de Araújo et al., 1999). Precipitation averages ∼1,150 mm/yr, being concentrated between January and April, with a peak in March and the average annual temperature is around 25°C, ranging from 23.8 to 27.4°C (de Araújo et al., 1999; Brito and Silva, 2012).

The area under forest management covers a total of 1,670 ha, which includes 22 forest stands between 69 and 92 ha. Management at the Fazenda is conducted since 2003/2004 (**Table 1**), and until the end of 2014 (time of our sampling) half of the forest stands had already been logged. Until 2014, forest management had created a 11-yr chrono-sequence of forest recovery, including forest in different stages of regeneration. According to the management plan, forest stands will be clear cut every 25 years (**Table 1**) without machine assistance, covering the soil with branches and leaves to avoid further soil impoverishment. All forest stands will be logged by 2028, when a new forest logging cycle should be reinitiated (**Table 1**). According to the Brazilian Forest Code an additional area, known as Legal Reserve, needs to be set aside and preserved (Soares-Filho et al., 2014). Two such areas have been established at our study site, resulting in 24 management plots (**Figure 1**). One of these legal reserves (forest stand X), however, was established in what seems to be a severely modified second-growth area, and probably does not represent a proper control area, as originally envisioned by the law.

Sampling Design and Data Classification

We accessed the entire area using the 12 roads opened for logging, which divided the area in 22 forest stands (besides the legal reserves). These roads vary from 1.3 to 4.0 km (**Figure 1**). We established a network of point counts along these roads, systematically distributed every 250 m, a distance that we considered safe to maintain surveys independent from one another (**Figure 1**). We conducted avian surveys in 160 points, all of which were sampled during the dry season of 2014. Most of the point counts (138) were sampled between 15 and 25 October and the remaining points (22) (trails 2 and 6, see **Figure 1**) between 17 and 19 December. All point counts were conducted by the same experienced observers (JRR and FMCG) throughout the study. Given the temporal proximity of the two sample periods, we pooled all samples for analyses.

Five-minute point counts were conducted between 5:00 and 8:30 a.m., the known peak activity for birds at the site. During this period, all birds heard and observed were noted and identified. We opted for using unlimited distance for the records, but the overwhelming majority of records were likely within a 100 m radius, and given the large size of the forest stands, within the area of a given unit. The location of each observation or sound heard was mapped into a Cartesian coordinate system, which included the side of the road. Recorded individuals were visually and acoustically monitored during the censuses, to avoid double counting individuals. The species recorded at these points were classified according to their degree of forest dependence adapted from Silva and co-authors (da Silva et al., 2003). This classification includes: (1) species that rely on, and are tightly associated to, forested areas (forest-dependent species); (2) species that are often found in forests, but also occupy open areas or species that do not rely on forested areas (forest non-dependent species). We also classified species by endemism, conservation and migratory status. Species classification and nomenclature follow the Brazilian Committee of Ornithological Records (de Piacentini et al., 2015), and recent taxonomic and nomenclature changes (Bravo et al., 2021).

We obtained two types of vegetation data, including (1) a remote measurement, namely the Normalized Difference Vegetation Index (hereafter NDVI) and (2) vegetation height data. The NDVI represents a remote sensing measurement used as an indicator of the biophysical properties of the vegetation (Tucker and Sellers, 1986). We obtained these data through the Land Processes Distributed Active Archive Center (LP DAAC) provided by NASA's Earth Science Data and Information System (ESDIS). These data were collected from a grid with 217 points equidistant for 350 m throughout our study area. Each forest stand included between 5 and 9 NDVI points and the much larger legal reserve A, included 29 points. We extracted these data matching the exact sampling period and obtained the average NDVI for each forest stand. The NDVI data was downloaded and processed using the R package MODISTools (Tuck and Phillips, 2017). We obtained tree height measurements in the field for 160 point counts. Each height estimate was calculated as the mean of three independent measurements obtained at the exact point of our avian surveys, and two measurements obtained 50 meters apart along the road. Forest height was measured using a distance meter, from the base to the highest branch in the perpendicular vegetation to the measurement site. To calculate the average height of each forest stand, we used all

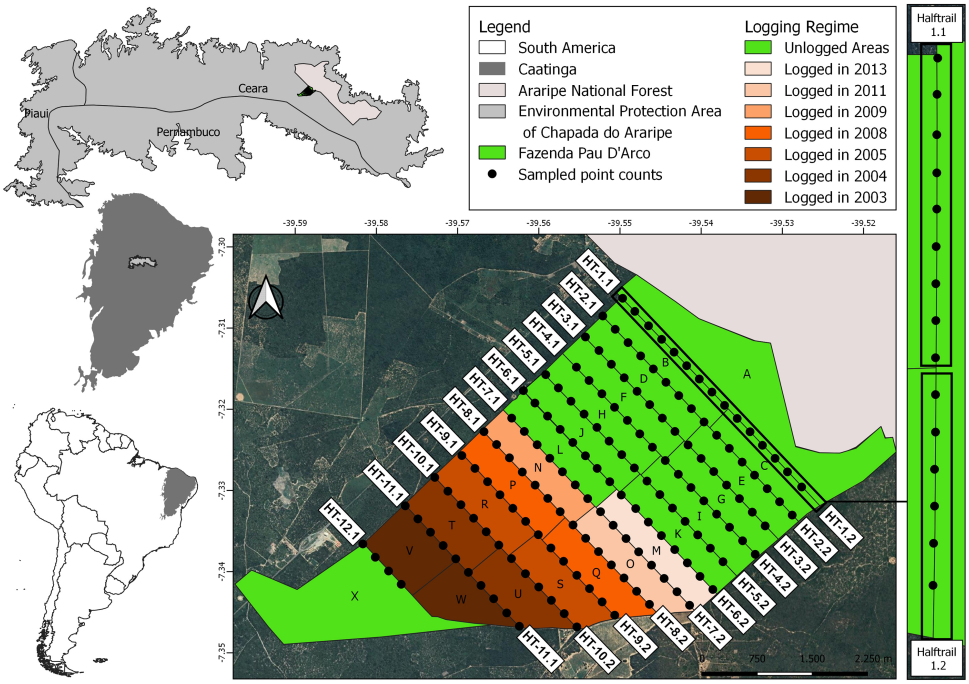

FIGURE 1 | Location of the study area and arrangement of the 160 count points in the forest management area of Fazenda Pau D'Arco, Crato, Ceará, Brazil in 2014. Polygons represent forest stands, green areas indicate unmanaged areas and brown scale indicates different logging times (in years). Trails that divide the forest stands were split into 23 half-trails (with a forest stand on each side) and used as a sample unit.

TABLE 1 | Forest management scheme until 2014 at the Fazenda Pau D'Arco, Crato, Ceará, Brazil.

Logged areas				**Unlogged areas**		
Logged year	**FS**	**Area (ha)**	**Volume wood removed by 2014 (m/st)**	**Logging year**	**FS**	**Area (ha)**
2003/2004	01	71.43	8,553.28	2015/2016	09	69.4
2003/2004	19	72.55	8,685.75	2017/2018	10	69.32
2004/2005	02	72.53	8,659.01	2018/2019	11	74.21
2004/2005	20	72.16	8,648.07	2019/2020	12	73.59
2005/2006	03	72.24	8,639.57	2021/2022	13	92.1
2005/2006	21	72.8	8,727.07	2022/2023	14	92.14
2008/2009	04	71.13	8,484.01	2023/2024	15	81.06
2008/2009	22	72.48	8,689.39	2024/2025	16	81.19
2009/2010	05	72.45	8,640.78	2025/2026	17	86.95
2011/2012	06	71.98	8,606.75	2026/2027	07	69.9
2013/2014	08	70.24	8,369.77	2027/2028	18	85.42

Data divided into logged and unlogged stands. Logging period, volume of wood removed (only for logged areas), and area, are shown for each forest management stand (FS). Logging between 2015 and 2020 was conducted after the conclusion of our avian surveys.

measurements along its perimeter, which ranged from 6 to 16 independent measurements.

Data Analysis

Except for species accumulation curves with Hill numbers, we considered the half-trails as our sample units throughout the analyses (**Figure 1**). These samples were classified as unlogged, transition, and logged half-trails according to the logging status of forest stands on both sides. To calculate bird abundance per sample, we merged individuals detected during point counts conducted along the half-trails. In all, 23 half-trails were analyzed (half-trail X-W was not sampled), except for the analyses involving logging time, as only 9 half-trails had already been logged on both sides at the time of our sampling. Counting species to evaluate species richness may be a biased metric due to differences in (i) the numbers of samples and (ii) the numbers of individuals detected. Even under similar standardize sampling procedures, variation in the number of individuals detected may influence the number of species observed (Gotelli and Chao, 2013). Thus, we extracted the effective number of species interpolating the species richness by the number of individuals from the Hill numbers parameterized by an order $q = 0$ (Chao et al., 2020). By doing this, we controlled for the bias caused by the differential sample effort, and include the estimation of unobserved species in the species richness comparisons (Gotelli and Chao, 2013; Chao et al., 2020).

Sampling effort was evaluated using a species accumulation curve, including the rarefaction and extrapolation with Hill numbers through all the samples (Gotelli et al., 2014). Additionally, we compare the observed general curve between unlogged, transition and logged curves. We compared average effective number of species (hereafter effective richness) and the number of individuals between unlogged, transition and logged areas using two-way ANOVA when data were homoscedastic, and three individual Kruskal-Wallis rank tests when data were heteroscedastic. These tests were conducted for the entire avian community, and according to species dependence on forests (dependent or non-dependent). We ordinated the avian community at each half-trail using two dimensions ($k = 2$) in a Non-Metric Multidimensional Scaling (NMDS), using the Bray-Curtis's dissimilarity index to access avian species composition. To determine the degree of similarity of composition among samples and clustering of unlogged, transition and logged groups in the NMDS, we used an Analysis of Similarity (ANOSIM). Additionally, we used the NMDS scores ($k = 1$) to ordinate the community along the management chrono-sequence to evaluate possible composition recovery patterns.

We evaluated potential ecological winners and losers through a meta-analytic assessment for all community and for species grouped by forest dependence. We calculated the standardized mean difference (SMD) for each species and estimated the fixed effect models and confidence intervals for both all pooled species and species pooled by category of forest dependence, graphically depicted as a forest plot. We removed species with less than 5 records in the whole area and the transition records from this analysis. To evaluate the degree of habitat changes after management in the forest stands, we performed linear regressions relating vegetation height, the NDVI and the time since logging. To access the logging age for each sample, which had different "time since logging" on each side, we used the average age of these sides. Finally, we applied linear regressions to test the effects of forest management on the avifauna relating (i) vegetation height, (ii) NDVI, and (iii) time since logging with the number of individuals, the effective richness, and species composition. Prior to analyses, we tested collinearity between variables through Pearson's correlation tests and tested all model assumptions. No data transformation was required. All analyses were conducted using R (R Core Team, 2019) implemented in RStudio.

RESULTS

Avian Community Structure

During our point counts, we detected 3,789 individuals of 90 bird species, of 34 different avian families, which represents more than 60% of all bird species ever recorded at the Fazenda Pau D'Arco, and virtually all non-occasional residents (de Lima et al., 2021). Nearly a third of the species detected (24 species) were considered forest-dependent, whereas 2/3 (66 species) were forest non-dependent species (**Supplementary Table 1**). Avian assemblages recorded on our point counts were overwhelmingly composed of passerines, which accounted for 73% of the species and 93% of the individuals. Some avian families dominated these assemblages, including flycatchers (Tyrannidae, 18 spp.), antbirds (Thamnophilidae, 8 spp.), tanagers (Thraupidae, 8 spp.), and furnariids (Furnariidae, 6 spp.).

Effects of Forest Management on the Avifauna

Overall, we detected more species and more individuals in areas that had not been logged (79 spp. and 2,093 ind.) than both in transition (50 spp. and 512 ind.) and logged ones (56 spp. and 1184 ind.), an observation that held even when accounting for sampling effort, as observed by comparing species accumulation curves between areas (**Supplementary Figure 1**). Species accumulation curves also provide evidence that the expected species effective richness in unlogged areas contributes with most of the area's species diversity, which is not the case of both transition and logged areas (**Supplementary Figure 1**).

We detected, on average, 26.9 ± 2.8 effective species and 190.3 ± 45.4 individuals per half-trail in unlogged areas, 24.7 ± 3.0 effective species and 170.7 ± 65.8 individuals in transition areas, and 24.2 ± 2.8 effective species and 131.6 ± 37.9 individuals per half-trail in logged areas. Fewer individuals were observed in logged area [Two-way ANOVA for individuals; $F_{(1,\ 40)} = 3.95$, $p < 0.05$; **Figure 2**]. The difference between unlogged and logged areas was driven by forest dependent species, which as expected, presented more individuals [Tukey's (HSD) *post hoc* test for forest dependent individuals $p < 0.05$] and also higher effective richness [Kruskal-Wallis for effective richness—dependent species; $KW_{(1,\ 2)} = 16.1$, $p < 0.01$] in unlogged areas (**Figure 2**). This was not the case for forest non-dependent species, as we found no significant difference in the number of species detected in logged and unlogged areas [Kruskal-Wallis for effective richness—non-dependent species; $KW_{(1,\ 2)} = 0.4$, $p = 0.8$]. Nor for the number of individuals [Tukey's (HSD) *post hoc* test for forest dependent species $p = 0.95$; **Figure 2**].

Avian assemblages were distinct in unlogged and logged areas (ANOSIM; $R = 0.54$, $p = 0.001$). Species composition of unlogged and logged sites were in general more similar to areas under similar managing schemes (**Figure 3**). Transition areas, as expected, appeared between the two distinct groups (**Figure 3**), indicating a bird composition gradient. We also found that species composition (measured by NMDS scores ordinated in a single dimension) in logged regenerated areas remained distinct from unlogged areas, even after over a decade of forest recovery (**Supplementary Figure 2**).

Our analyses identified species-specific responses to forest management in nearly half of the species analyzed (those with adequate sampling). We identified 21 species with lower than average records in logged areas, including 11 species that presented no records in logged forest stands at all (**Figure 4**).

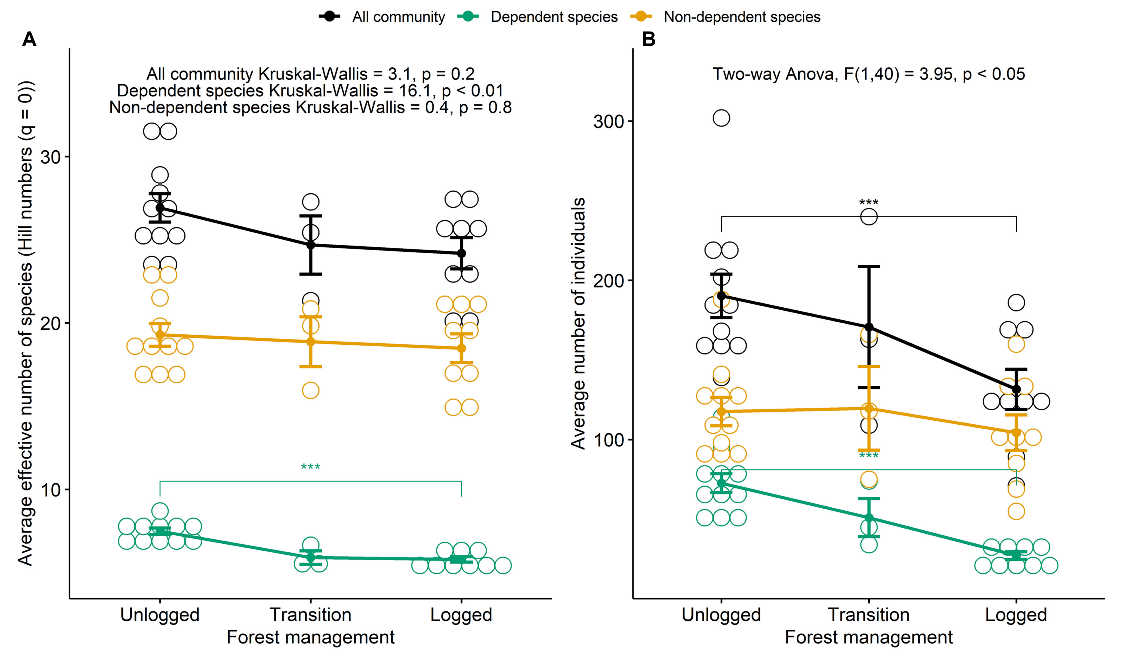

FIGURE 2 | Scatter interval plot with average avian effective number of species **(A)** and average number of bird individuals **(B)** recorded in unlogged, transition and logged forest stands at the Fazenda Pau D'Arco, Crato, Ceará, Brazil, for all species (black), forest non-dependent species (yellow), and forest dependent species (dark green). At the top, the used statistical tests. Three Kruskal–Wallis tests for the effective number of species and a two-way ANOVA for the number of individuals. Asterisks show statistical significance according to Dunn's *post hoc* test for KW and Tukey's (HSD) *post hoc* test for two-way ANOVA.

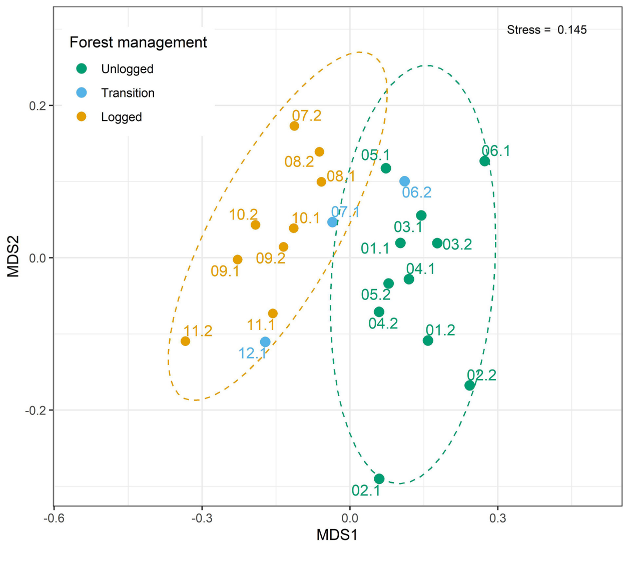

FIGURE 3 | Non-metric multidimensional scaling (NMDS) for bird species (quantitative data) in three groups of unlogged, transition and logged areas collected in 160 point counts of 23 half-trails of the management area at Fazenda Pau D'Arco, Crato, Ceará, Brazil. Color dots indicate unlogged (dark green), transition (blue), and logged (yellow) half-trails.

We found that whereas many forest-dependent species occur exclusively in unlogged forests, only one non-dependent species was found exclusively in logged forests. However, five species were recorded more often in logged areas, suggesting that these species may indeed benefit and even thrive in managed forests (**Figure 4** and **Supplementary Figure 3**).

Evaluating the list of the 20 most commonly detected species in our point counts, we found that most species appeared as most abundant in areas under all managing schemes (unlogged, transition and logged forests), suggesting that abundant species may be less susceptible to changes in land use. On the other hand, whereas four species (*H. ochroleucus*, *T. pelzelni*, *M. parnaguae,* and *H. margaritaceiventer*) presented proportionally fewer individuals in transition and logged areas, three species (*F. melanogaster*, *S. hellmayri*, and *P. plumbea*) increased their abundance in logged areas (**Table 2**).

We found a positive correlation between NDVI and vegetation height. In general, taller forest stands also presented higher index values (**Supplementary Figure 4A**). Interestingly, these two vegetation variables behaved differently along the regeneration chrono-sequence. Forest height was significantly correlated to forest age (time since logging), as older forests stands were taller than recently logged forests (**Supplementary Figure 4B**). On the other hand, NDVI was not correlated to forest age and held a very low explanatory power (**Supplementary Figure 4C**). We interpret this as a mismatch between forest height and forest cover (NDVI) in recovering forests, suggesting that whereas forest may grow quickly, their forest cover may not recover at the same pace.

Avian species composition was predicted by both forest height and NDVI, with relatively high explanatory power (**Figures 5C,F**). The same occurred to the average number

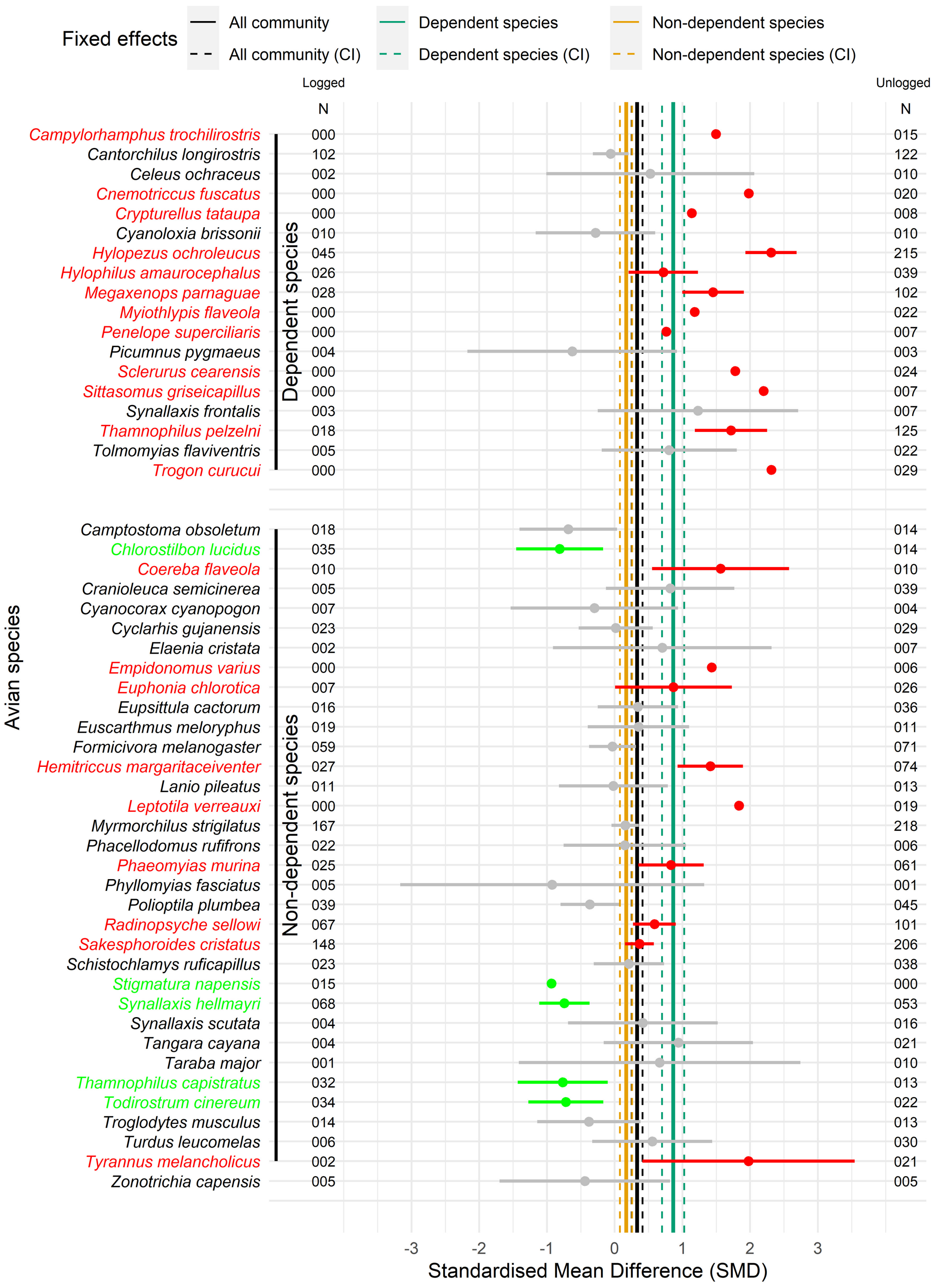

FIGURE 4 | Forest plot of bird species for standardized mean difference (SMD) in number of individuals (N) between logged and unlogged forest stands (excluding transition stands), and respective standard deviations. Were analyzed only bird species with more than five individuals recorded in 23 half-trails of the management area at the Fazenda Pau D'Arco, Crato, Ceará, Brazil. Vertical solid lines represent the fixed effects models from all community, from dependent species and non-dependent species, and vertical dashed lines indicated respective confidence intervals (CI). Red names and point ranges indicated species statistically more abundant in unlogged forest stands and green names and point ranges represents species more abundant at logged stands. Species points without ranges are recorded only in one group of forest stands and the standard deviations are zero.

TABLE 2 | The 20 most detected bird species in 160 point counts conducted in 23 half-trails of the management area at Fazenda Pau D'Arco, Crato, Ceará, Brazil.

Ranking	Bird species at unlogged areas	Ind (%)	FD	Bird species at transition areas	Ind (%)	FD	Bird species at logged areas	Ind (%)	FD
1	*Myrmorchilus strigilatus*	218 (10.42%)	N-Dep	*Myrmorchilus strigilatus*	66 (12.89%)	N-Dep	*Myrmorchilus strigilatus*	167 (14.10%)	N-Dep
2	*Hylopezus ochroleucus*	215 (10.27%)	Dep	*Sakesphoroides cristatus*	48 (9.38%)	N-Dep	*Sakesphoroides cristatus*	148 (12.50%)	N-Dep
3	*Sakesphoroides cristatus*	206 (9.84%)	N-Dep	*Cantorchilus longirostris*	42 (8.20%)	Dep	*Cantorchilus longirostris*	102 (8.61%)	Dep
4	*Thamnophilus pelzelni*	125 (5.97%)	Dep	*Hylopezus ochroleucus*	35 (6.84%)	Dep	*Synallaxis hellmayri*	68 (5.74%)	N-Dep
5	*Cantorchilus longirostris*	122 (5.83%)	Dep	*Megaxenops parnaguae*	28 (5.47%)	Dep	*Radinopsyche sellowi*	67 (5.66%)	N-Dep
6	*Megaxenops parnaguae*	102 (4.87%)	Dep	*Radinopsyche sellowi*	25 (4.88%)	N-Dep	*Formicivora melanogaster*	59 (4.98%)	N-Dep
7	*Radinopsyche sellowi*	101 (4.83%)	N-Dep	*Synallaxis hellmayri*	24 (4.69%)	N-Dep	*Hylopezus ochroleucus*	45 (3.80%)	Dep
8	*Hemitriccus margaritaceiventer*	74 (3.54%)	N-Dep	*Thamnophilus pelzelni*	20 (3.91%)	Dep	*Polioptila plumbea*	39 (3.29%)	N-Dep
9	*Formicivora melanogaster*	71 (3.39%)	N-Dep	*Hemitriccus margaritaceiventer*	19 (3.71%)	N-Dep	*Chlorostilbon lucidus*	35 (2.96%)	N-Dep
10	*Phaeomyias murina*	61 (2.91%)	N-Dep	*Formicivora melanogaster*	18 (3.52%)	N-Dep	*Todirostrum cinereum*	34 (2.87%)	N-Dep
11	*Synallaxis hellmayri*	53 (2.53%)	N-Dep	*Eupsittula cactorum*	16 (3.13%)	N-Dep	*Thamnophilus capistratus*	32 (2.70%)	N-Dep
12	*Polioptila plumbea*	45 (2.15%)	N-Dep	*Schistochlamys ruficapillus*	15 (2.93%)	N-Dep	*Megaxenops parnaguae*	28 (2.36%)	Dep
13	*Cranioleuca semicinerea*	39 (1.86%)	N-Dep	*Chlorostilbon lucidus*	12 (2.34%)	N-Dep	*Hemitriccus margaritaceiventer*	27 (2.28%)	N-Dep
14	*Hylophilus amaurocephalus*	39 (1.86%)	Dep	*Phacellodomus rufifrons*	11 (2.15%)	N-Dep	*Hylophilus amaurocephalus*	26 (2.20%)	Dep
15	*Schistochlamys ruficapillus*	38 (1.82%)	N-Dep	*Phaeomyias murina*	10 (1.95%)	N-Dep	*Phaeomyias murina*	25 (2.11%)	N-Dep
16	*Eupsittula cactorum*	36 (1.72%)	N-Dep	*Hylophilus amaurocephalus*	9 (1.76%)	Dep	*Schistochlamys ruficapillus*	23 (1.94%)	N-Dep
17	*Turdus leucomelas*	30 (1.43%)	N-Dep	*Polioptila plumbea*	8 (1.56%)	N-Dep	*Cyclarhis gujanensis*	23 (1.94%)	N-Dep
18	*Cyclarhis gujanensis*	29 (1.39%)	N-Dep	*Cyclarhis gujanensis*	8 (1.56%)	N-Dep	*Phacellodomus rufifrons*	22 (1.86%)	N-Dep
19	*Trogon curucui*	29 (1.39%)	Dep	*Coereba flaveola*	8 (1.56%)	N-Dep	*Euscarthmus meloryphus*	19 (1.60%)	N-Dep
20	*Euphonia chlorotica*	26 (1.24%)	N-Dep	*Camptostoma obsoletum*	7 (1.37%)	N-Dep	*Thamnophilus pelzelni*	18 (1.52%)	Dep

Numbers refers to the individuals detected (and % of records in each management areas) in unlogged, transition and logged areas. "FD" is Forest Dependence, Dep as Forest dependent species, N-Dep as Forest non-dependent species.

of individuals detected, although with a lower explanatory power (**Figures 5A,D**). On the other hand, the average species richness was only correlated with forest height, albeit with a low explanatory power (**Figure 5E**), but not to NDVI (**Figure 5B**). This means that taller and greener forests sustain more individuals and a different avian assemblage than less green and shorter forests, whereas species richness only responds to the height of the forest and not to the forest cover. Quite surprisingly, we did not detect positive correlations between any of the avian variables measured and forest regeneration time (time since logging) (**Figures 5G–I**). In fact, the only significant correlation found was between the average number of individuals and regeneration time, but this was a negative correlation. In other words, we found less individuals in older regenerating forest stands (**Figure 5G**).

DISCUSSION

As far as we are aware, this study represents the first attempt to evaluate the effect of forest management on the Caatinga avifauna, and one of the first ones in any Neotropical dry forest (Coria et al., 2015; Hilje et al., 2020; Owen et al., 2020). This kind of studies are particularly relevant today, given the widespread decline in natural habitats and the urgent need of more sustainable economic activities (Sanchez-Azofeifa et al., 2005; da Silva et al., 2018). Understanding the effects of current management schemes on biodiversity should be a primary goal of conservation biology and a top priority among governments, land managers, and policy makers. Furthermore, understanding the limitations of different managing strategies is essential to achieve a more sustainable use of ever-shrinking natural landscapes.

Although we do not have data after a complete 25-yr regeneration cycle, our study provides evidence of the potential effect of forest management on the avifauna, including the following four take-home messages. First, forest management as currently conducted at our study site (clear-cut logging followed by passive regeneration) affects the abundance, species richness and composition of the avifauna. In general, we found less individuals, less species, and a different avian composition in forest stands that have been logged. Second, we show that this effect depends on the degree of disturbance sensitivity of each species. Forest-dependent species where overwhelmingly affected by forest management, whereas forest non-dependent species were less affected, or not affected at all. Third, even after 11 years of forest recovery, bird species composition in logged areas had not yet reached the diversity level observed in unlogged areas. In fact, local species assemblages seem to have taken a different regeneration path and remained distinct from the original avifauna found in unlogged areas. We believe that this result can be explain by the fact that regenerating forests do not recover its total height or original vegetation cover after a decade, suggesting that tree species composition may be quite distinct from that found in unlogged forests.

Detecting changes in the number of species and individuals in natural environments due to human interference often represents the first findings in management studies (Chaudhary et al., 2016). Although providing evidence of changes in species composition is often more challenging, it offers important insights about species losses and replacements (Demarais et al., 2017). We detected changes in three important aspects of the avian communities, finding fewer species, fewer individuals, and different species assemblages in logged forest stands. The differences we found at the Fazenda Pau D'Arco were driven mostly by forest dependent species, which represented a third of all species detected. Forest-dependent species are often the most impacted by human activities because they require stable and complex habitats (Barrantes et al., 2016). Although most forest non-dependent species were unaffected by forest management, some of these species were negatively affected or even replaced by less demanding species after management.

This response pattern creates a scenario with ecological losers and winners (Tabarelli et al., 2012). In fact, we revealed that about one fourth of the species recorded in our point counts had fewer individuals in logged forests, whereas half of these species had zero records in forests that had been logged. According to our data, only five species presented more individuals in logged forests, suggesting that the list of "winners" is rather small. Among the ecological "losers" there are two species of global conservation concern (IUCN, 2020) the Vulnerable Ceará Leaftosser (*Sclerurus cearensis*) and the Near Threatened White-browed Antpitta (*Hylopezus ochroleucus*). Whereas the Antpitta was almost five times less abundant in logged forests, the Leaftosser was absent altogether. Similarly, we found ten species with no records whatsoever in logged forests, suggesting that they may be extirpated from the study area after all forest stands are logged by 2028. In general, disturbed environments are known to become less heterogeneous, and more specialized species tend to lose their habitats, being sometimes replaced by more generalist species (Devictor et al., 2008; Dong et al., 2020). Consequently, the identification, protection, and management of key habitats are crucial to afford the requirements of specialized species (Brambilla et al., 2020).

By applying the principle of space-for-time-substitution, where it is possible to infer a temporal trend from a study of different aged sites (Pickett, 1989), we were able to infer changes without involving a research that would take two decades to be concluded. One of the main limitations of the space-for-time approach is that areas under study may be heterogeneous or may have suffered from different histories of land use (Foster and Tilman, 2000). The Fazenda Pau D'Arco represents a rather homogeneous patch of dry forest vegetation, with virtually no differences in altitude or climatic regimes throughout its area (de Lima et al., 2021). Our results from the chrono-sequence studied, including an 11-yr regeneration period, are somewhat concerning. Avian composition, species richness, and abundance along the chrono-sequence differed from unlogged areas, even after more than a decade of forest recovery. Surprisingly, bird abundance decreased in older regenerating forest stands, compared to more recently logged forests.

These results are likely related to known patterns of tree regeneration in Neotropical dry forests. Differently from humid forests, ecological succession in dry forests is slower and pushed by high wood-density species, which are those than can cope

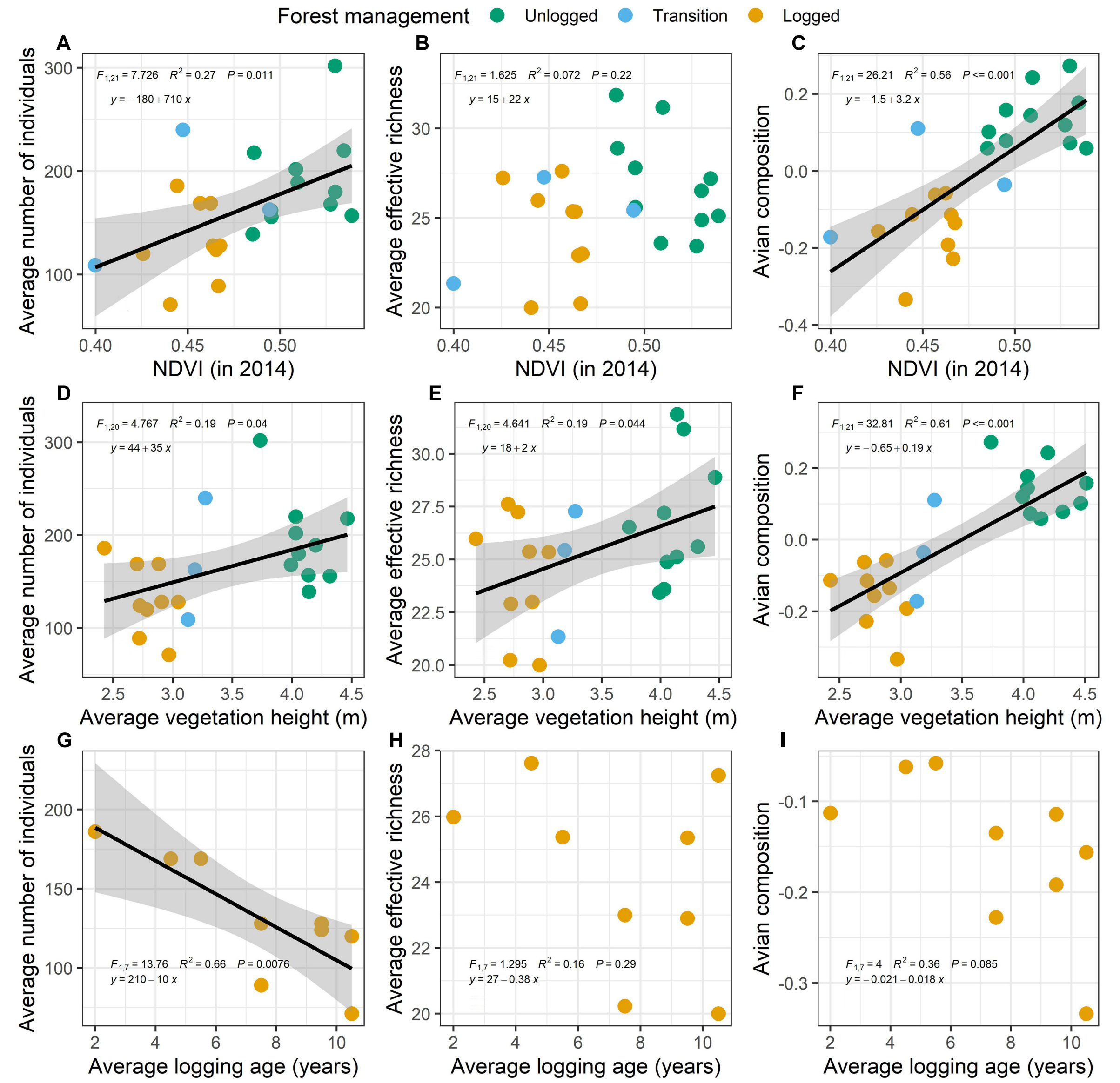

FIGURE 5 | Linear regressions models between avian abundance **(A,D,G)**, species richness **(B,E,H)**, and avian composition **(C,F,I)** obtained from 160 point counts and averaged by 23 (or 9 as logging age) half-trails sampled and the normalized difference vegetation index (NDVI in 2014) **(A–C)**, vegetation height **(D–F)**, and the logging age (in years prior to 2014, the time of our sampling) **(G–I)**, averaged from the two forest stands aside of each 23 (or 9 as logging age) half-trails of the management area at Fazenda Pau D'Arco, Crato, Ceará, Brazil. Dots indicate unlogged (dark green), transition (blue), and logged (yellow) half-trails. The regression line was derived from the data points and smooth areas are the standard deviation for significant regression models.

better with low water availability and higher solar radiation (Poorter et al., 2019). It is only then that the understory becomes less hot and dry, allowing the establishment of other plant species of more rapid growth (Poorter et al., 2019). Therefore, the dynamics of recovery may vary depending on land use (Arroyo-Rodríguez et al., 2017), creating a difficulty for landscapes that need to fully recover from a clear-cut activity, as is the case at our study site. In addition to land use, the recovery of dry forests also depends on the availability of water, being more effective during the rainy season (Lebrija-Trejos et al., 2011). Besides the natural climatic conditions of the region, the limited availability of water may hamper the recovery capacity of these forests (Álvarez-Yépiz et al., 2018). In fragmented and disturbed landscapes, active methods of restoration can be more effective (Morrison and Lindell, 2011). However, passive forest restoration is more often used because is less expensive, especially when adjacent vegetation cover is present (Morrison and Lindell, 2011).

Vegetation height and forest cover are factors that can influence the richness, abundance, and composition of bird species in dry forests (Martensen et al., 2012). We did find a positive association between these three aspects of avian assemblages and both forest height and a measure of vegetation canopy greenness (NDVI), indicating the importance of assessing forest structure to understand avian responses. Human disturbance frequently reduces the complexity of the forest and affects habitat availability, followed by changes in biodiversity (Barlow et al., 2016). A third vital piece of information is related to forest composition, which we lack for our study area. Which tree species are being recovered? How tree species composition affects the structure of the vegetation? How interrelated are bird and plant species? These are questions that require immediate answers and would be key to understand habitat regeneration after clear-cut logging. Our data indicates that recovering forest tend to reach around 2.8 m within 7.5 years, but do not reach the average height of ∼4 m of unlogged forests even after a decade after logging. They also indicate that a decade may not be enough to recover the original vegetation cover.

We failed to find a positive trend between time since logging and avian regeneration. This mismatch between older regenerating stands and the avifauna may indicate that the original plant and animal composition may not be coming back in the short term, a topic that requires immediate attention. Despite the potential negative effects of habitat management on the avifauna, secondary forests still represent valuable habitats for many tropical species (Chazdon et al., 2009; Edwards et al., 2017; Sayer et al., 2017). Data on Neotropical dry forests are still incipient, and there is an ongoing debate on how birds respond to forest regeneration (Latta et al., 2018; Owen et al., 2020). Recent studies, however, suggest that secondary forests can be useful to many species, and even conserve relatively high values of avian phylogenetic diversity (Edwards et al., 2017). Furthermore, secondary forests may also be key to support the provision of ecosystem services, although these services may be less stable than in primary forests (Sayer et al., 2017). Unlike humid forests, which have been studied over the past 70 years, Neotropical dry forests have only become a focus of research in the past three decades (Stoner and Sánchez-Azofeifa, 2009).

This information is particularly important for the development of management protocols (Espírito-Santo et al., 2009). Multiple factors can influence the effectiveness and sustainability of forest management practices, including (i) local climatic conditions; (ii) the proximity and conservation of preserved areas; and (iii) natural regeneration time, which need to be compatible with ecological succession. There is evidence that forest management, like other land-sparing approaches (such as high intense timber extraction with the protection of natural reserves), is capable of sustaining higher bird abundance and species richness and maintaining higher functional diversity, than land-sharing approaches (such as moderate land use integrated with wildlife-friendly habitats across a concession) (Edwards et al., 2014; Cannon et al., 2019). Nevertheless, the environmental context and scale also seems to be an important function for biodiversity maintenance (Ekroos et al., 2016). The persistence of biodiversity is strongly linked to the proximity of surrounding contiguous natural habitats (Gilroy et al., 2014), highlighting the value of intermingling unlogged lands for sustainable forest management and to enhance forest restoration (Watson et al., 2018).

We conclude that the complete clear-cut logging and subsequent conversion of the study area into secondary forest will likely drive to the extirpation of several bird species, particularly those that depend on healthy forests to thrive. On the other hand, our results suggest that many of these forest-dependent species may manage to live in relatively smaller forest plots and could potentially recover their populations. Therefore, we strongly encourage the use of protected forest patches intermingled with logged areas, as a way to ensure the survival of all species in these logged forests. In fact, the kind of forest management applied at our study site may be sustainable for some species, but not for others. Despite the undeniable value of secondary forests for the maintenance of generalist species, we found a large number of ecological losers that seem to be less abundant in logged forests or even incapable of occupying regenerating stands, at least in the time frame studied. Having completed nearly half of the logging cycle (11 years), regenerating forests do not seem adequate to provide habitat requirements for more demanding bird species. We strongly argue for the continuous monitoring of regenerating forests, both for birds and plants, which appears to be essential in determining whether older forest stands will be able to meet the fauna needs.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

ETHICS STATEMENT

The animal study was reviewed and approved by the Instituto Chico Mendes de Conservação da Biodiversidade—ICMBio.

AUTHOR CONTRIBUTIONS

JR, LN, and WS contributed to the research design. JR, HL, LN, and FL-C collected the data in the field. JR analyzed the data. JR and LN wrote the manuscript. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.631247/full#supplementary-material

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