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

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, 2011b). 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).
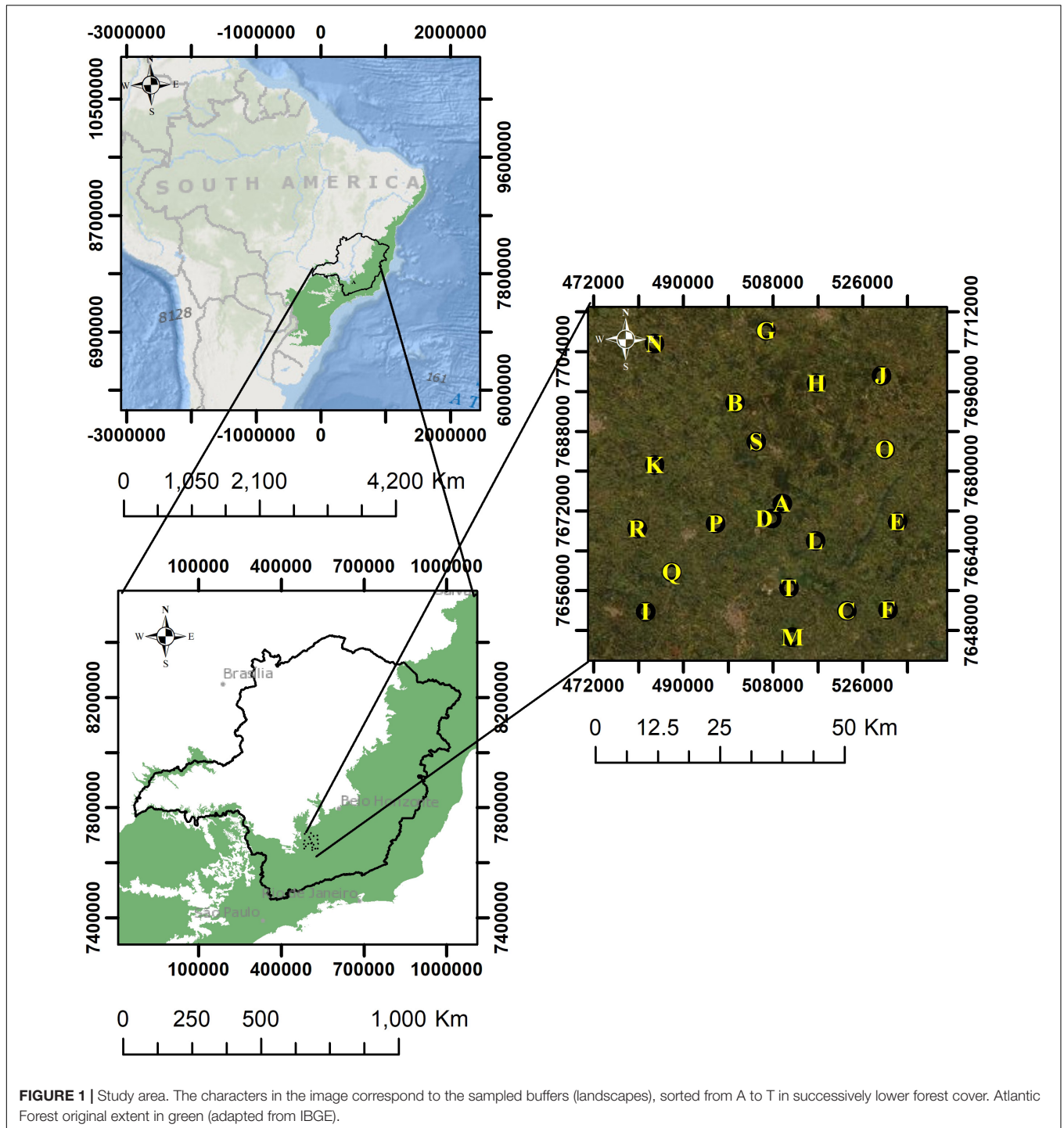
Sampling Design

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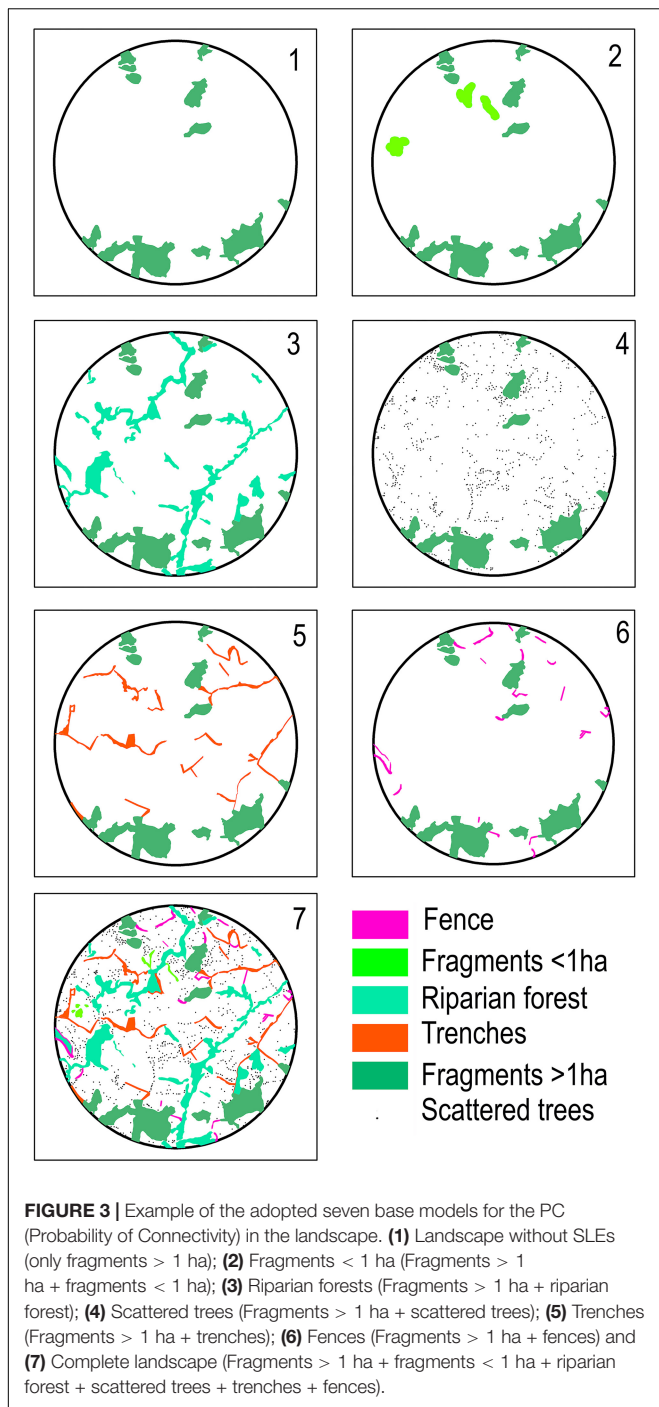
We calculate the graph connections in the landscapes using the software Conefor 2.6 (Saura and Torne, 2009).

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 × 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 × aj × Pij* when i = k or j = k and i ≠ 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 × aj × Pij* when i ≠ k, j ≠ 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**.

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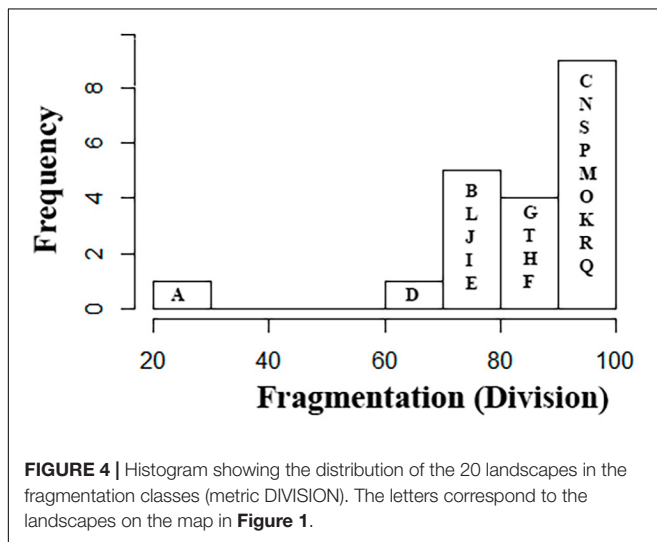
FIGURE 4 | Histogram showing the distribution of the 20 landscapes in the
fragmentation classes (metric DIVISION). The letters correspond to the
landscapes on the map in **Figure 1**.

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
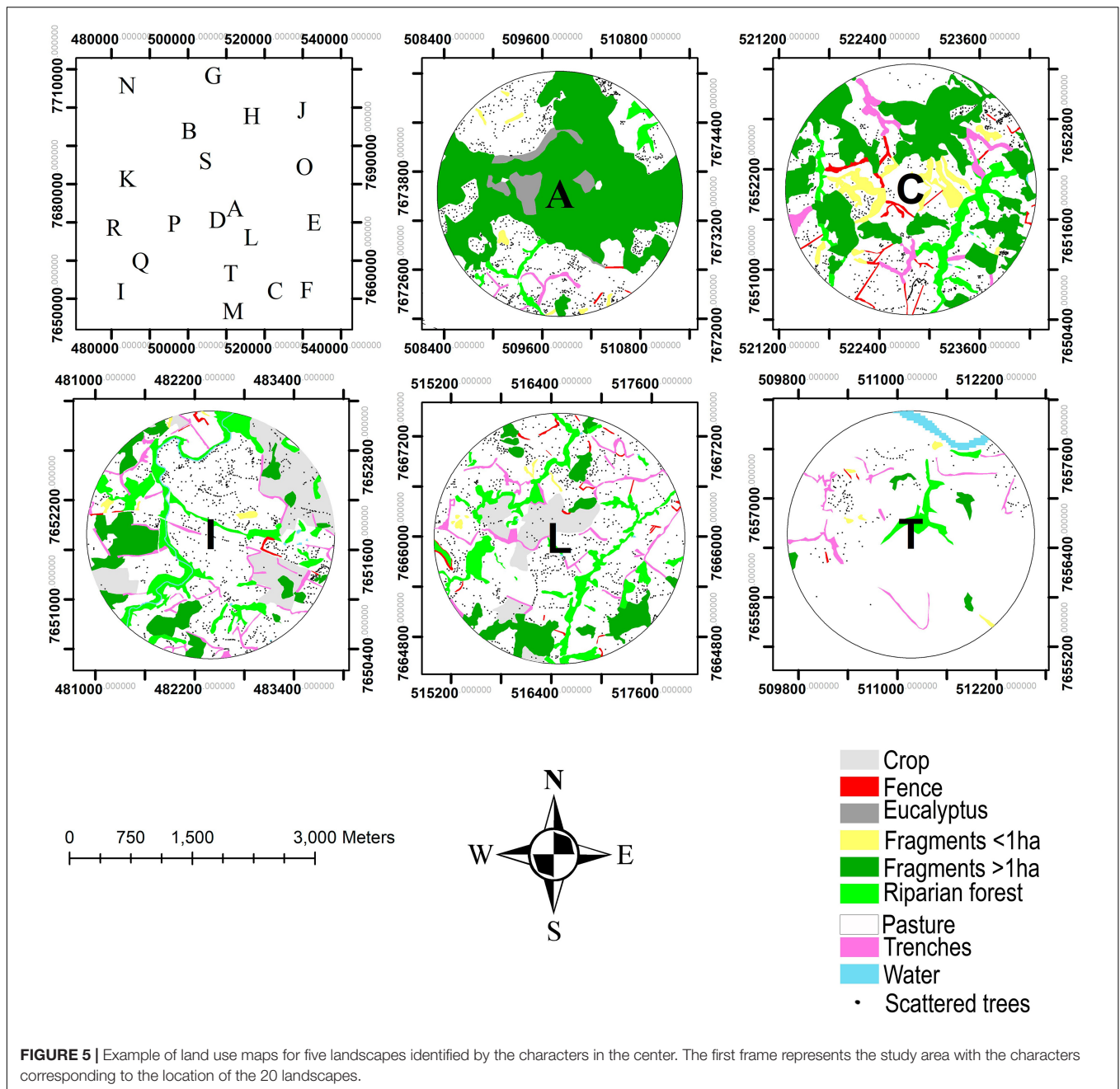and pollinators (**Figure 7**).

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.
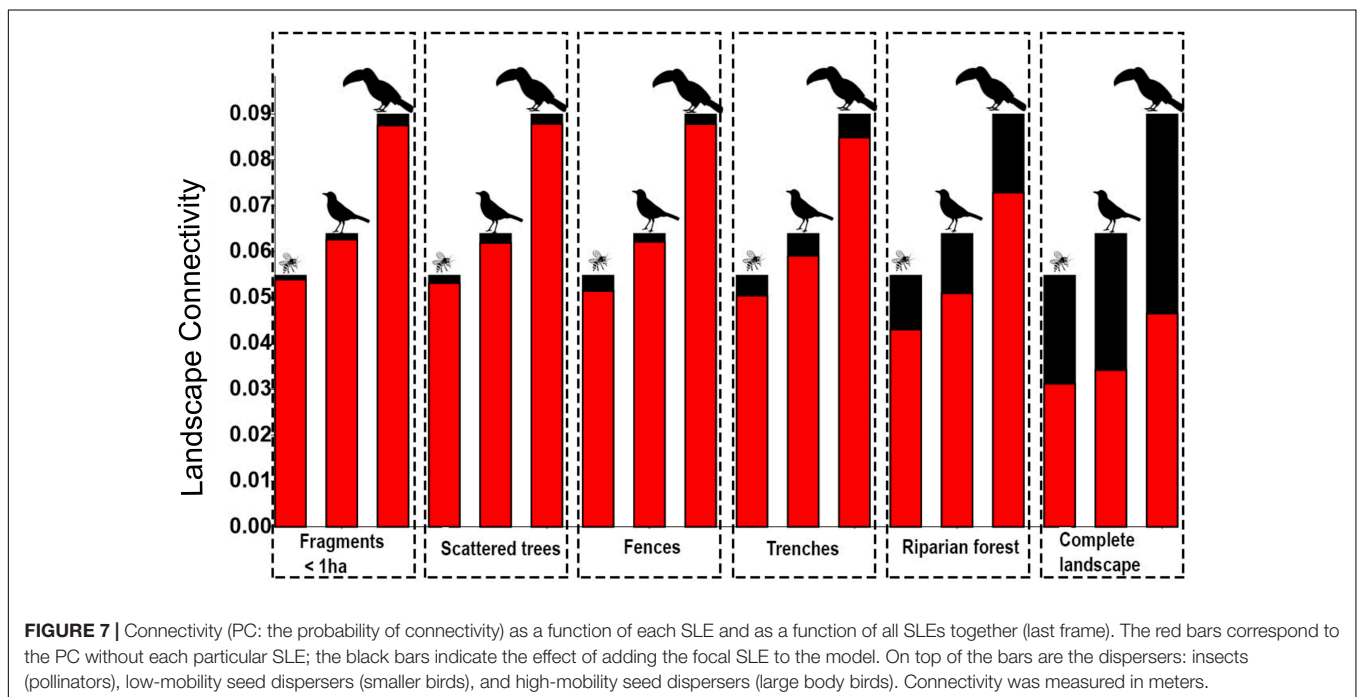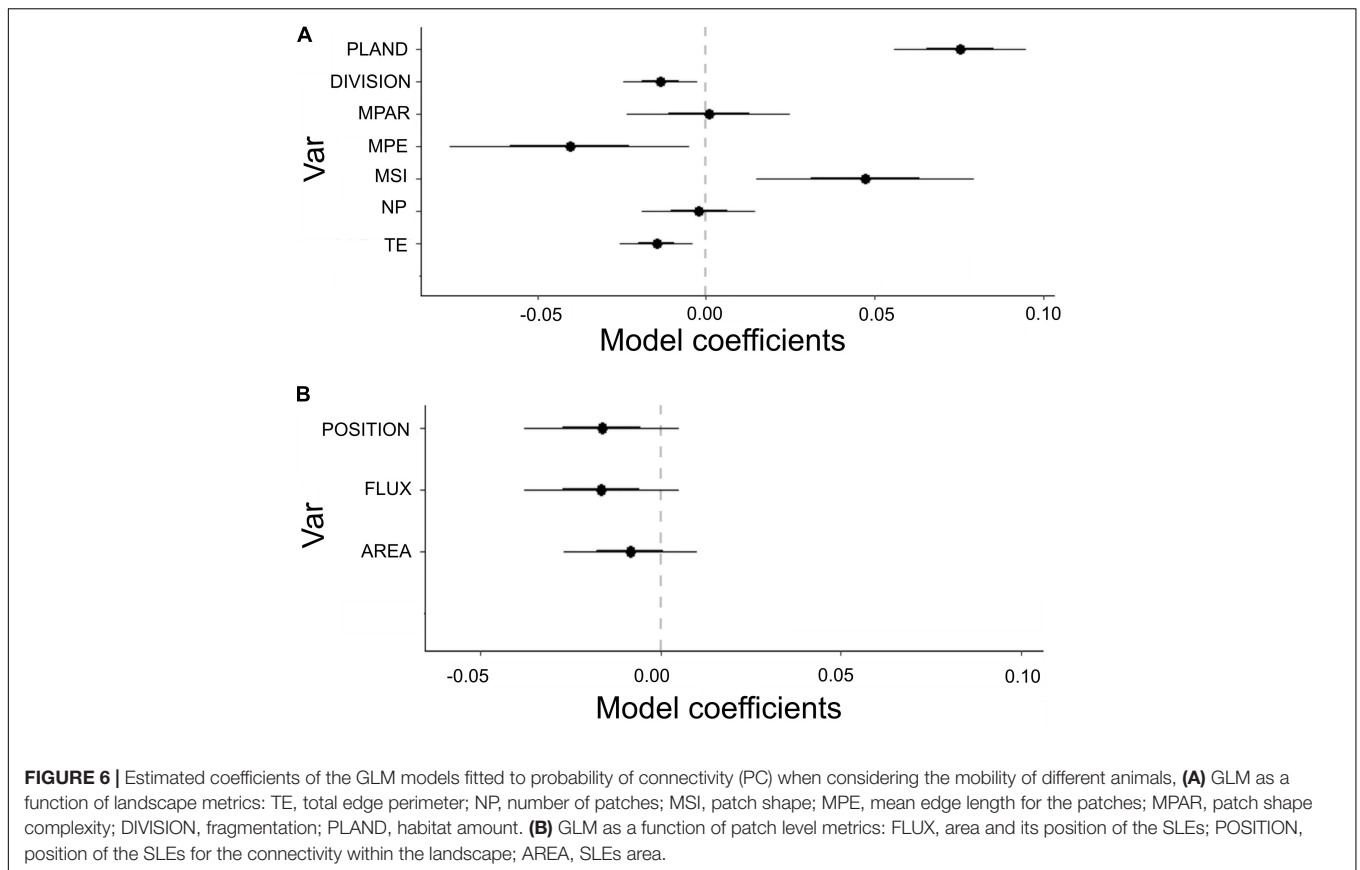
the forests was much weaker. During this period, the Brazilian environmental legislation was still being formulated [Article 225, Constitution of 1988 (Brasil, 1988)] and the existing legislation was poorly enforced. Also, during this period, many properties had more forest cover than the legislation 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
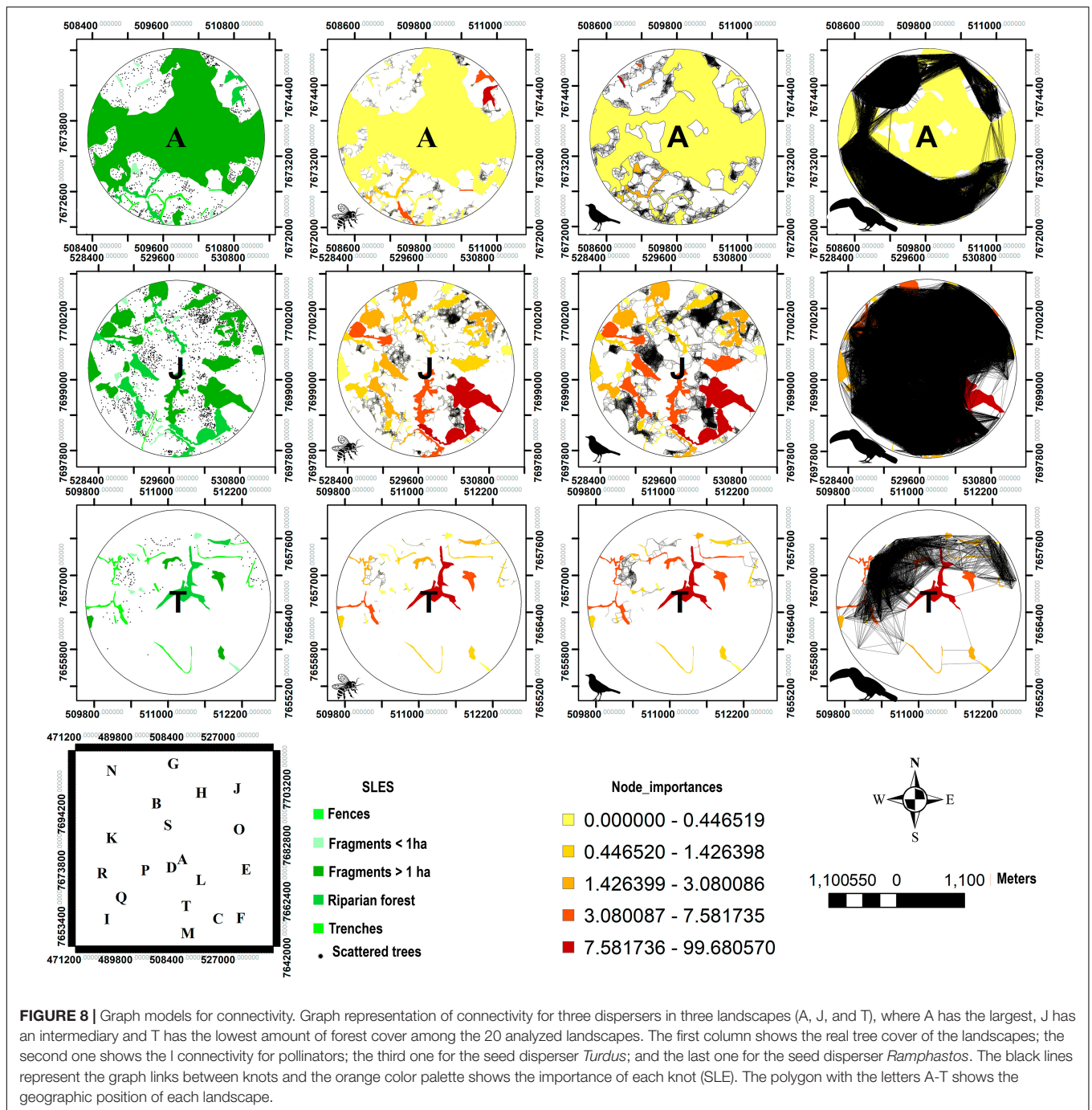
FIGURE 8 | Graph models for connectivity. Graph representation of connectivity for three dispersers in three landscapes (A, J, and T), where A has the largest, J has an intermediary and T has the lowest amount of forest cover among the 20 analyzed landscapes. The first column shows the real tree cover of the landscapes; the second one shows the l 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

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SUPPLEMENTARY MATERIAL

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