Drivers of Ecological and Evolutionary Disruptions in the Seed Dispersal Process: Research Trends and Biases

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As the sole opportunity for most plants to move, seed dispersal influences the biodiversity and functioning of plant communities. Global change drivers have the potential to disrupt seed dispersal processes, affecting plant communities and ecosystem functions. Even though much information is available on the effects of seed dispersal disruption (SDD), we still lack a comprehensive understanding of its main causes at a global scale, as well as the potential knowledge gaps derived from research biases. Here we present a systematic review of biotic and abiotic SDDs to ascertain the global change drivers addressed, dispersal modes impacted, plant processes affected, and spatial focus of existing research on this topic up-to-date. Although there are many modes of dispersal and global change drivers in temperate and tropical ecosystems worldwide, research efforts have predominantly addressed the effect of alien species for biotic seed dispersal in temperate systems and oceanic islands as well as how defaunation of bird or mammal dispersers has affected seed removal in the Neotropics. SDD studies were also biased toward forest ecosystems, with few in shrublands or grasslands. Finally, the effects of climate change, ecological consequences at the whole community level, and evolutionary changes were largely unrepresented in SDD studies. These trends are likely due to a combination of true geographic and ecological patterns in seed dispersal and global change and bias in research focus. We conclude that increased research investment in the less-studied systems and a better understanding of potential synergies and feedback between multiple global change drivers will be important to forecast the threats to plant biodiversity and those ecosystem functions derived from seed dispersal in the Anthropocene.

Keywords: dispersal failure, global change, anthropogenic disturbance, non-native species, climate change, defaunation, habitat loss, fragmentation

INTRODUCTION

The movement of seeds away from the mother plant allows them to colonize specific microsites and new areas, reduces sibling competition and attack by natural enemies (e.g., herbivores, pathogens), and determines the potential area of recruitment, acting as a template for the subsequent stages of plant growth as well as the plant spatial patterns (Howe and Smallwood, 1982; Howe and Miriti, 2004; Jordano, 2014; Traveset et al., 2014; Rogers et al., 2021a). The dispersal vectors can be both biotic (i.e., transported in the digestive tracts, fur, plumage or feet of animals) or abiotic (i.e., transported by wind, water, or gravity). Besides moving seeds across the landscape, animals that ingest fruits and pass viable seeds through their digestive tracts can further play an important role in plant establishment as they can modify the rate of seed germination and seedling growth (Traveset and Verdú, 2002; Rogers et al., 2021b). Biotic and abiotic movement of seeds supports plant communities, the biodiversity they contain, and the ecosystem services they provide, including fruit, wood and non-timber products, in addition to enhanced carbon sequestration, at no cost to humans (Leverkus and Castro, 2017; Egerer et al., 2018; Chagas et al., 2021).

Animals play an important role as seed dispersers for more than half of the plant species around the globe (Levey et al., 2002; Dennis et al., 2007; Rogers et al., 2021a), thus contributing to numerous ecosystem functions. Birds, mammals, lizards, fish and invertebrates are common dispersers, although their relative importance varies across habitat types (Fleming and John Kress, 2011; Albert et al., 2015; Correa et al., 2015; Gómez et al., 2019; Anjos et al., 2020; Araujo et al., 2021; Rogers et al., 2021a). Within studies involving avian frugivores, most research has focused on those species dispersing fleshy-fruited plants, but many birds can serve as dispersers including waterbirds which move many wetland species (Green et al., 2016, 2021). Among mammals, key dispersers include frugivores like primates and bats which disperse seeds primarily through endozoochory (Fuzessy et al., 2018), herbivores like deer and sheep which disperse non-fleshy fruits both through ectozoochory and endozoochory (Albert et al., 2015), and rodents which typically disperse seeds through scatter-hoarding (Gómez et al., 2019).

Multiple drivers of global change have been documented to cause pervasive disruptions in the seed dispersal process (SDD, hereafter), with poorly understood consequences for the functioning of communities and ecosystems. In the case of animal seed dispersal, plants are susceptible to dispersal failure when the animal populations on which they depend decline or even become extinct (Traveset and Richardson, 2006; Traveset et al., 2012; Pérez-Méndez et al., 2016; Rogers et al., 2017; Tucker et al., 2021). Habitat loss, land use change, overhunting, and invasive species are key threats underlying animal seed disperser population declines, extinctions, and range reductions (McConkey et al., 2012; Dirzo et al., 2014). The disruption of plant-seed disperser interactions have shown to have serious consequences for plants, which can cascade to affect other species, as well as the whole community and ecosystem (reviewed in Rogers et al., 2021a). Widespread rapid changes in seed disperser assemblages—which likely translate into changes in the seed dispersal process—have occurred since prehistoric times, when humans started colonizing new regions, strongly modifying landscapes and defaunating ecosystems by hunting mainly large-body animals, leading to many megafaunal extinctions in the Pleistocene (Janzen and Martin, 1982; Malhi et al., 2016; Galetti et al., 2018). Megafauna frugivores and herbivores are still the most susceptible seed dispersers to defaunation in tropical forests (Young et al., 2016) and globally (Ripple et al., 2015; Atwood et al., 2020). Islands mostly lack megafauna, but the pattern of greater threat to larger-bodied animals holds true on islands as well, where large-bodied birds, bats, and lizards are those suffering the largest declines (Traveset et al., 2012; Pérez-Méndez et al., 2016; Kingston et al., 2021). It is important to recognize that small-bodied bird and mammal dispersers tend to be less threatened although they also have experienced declines (Davidson et al., 2009; Rosenberg et al., 2019), which could cause imperceptible but pervasive impacts on seed dispersal (Rogers et al., 2021a).

Seeds dispersed by abiotic vectors may also be disrupted by human activities (Zhang et al., 2011; Teller et al., 2015). For instance, the construction of dams influences the connectivity of riparian plant communities along rivers by affecting seed dispersal distances of hydrochorous species and strongly altering community composition (Jansson et al., 2000; Merritt and Wohl, 2006). In general, landscape structure can have strong effects on the distance that seeds travel (San-José et al., 2019) and, thus, any kind of disturbance (e.g., habitat loss, fragmentation, defaunation, or modification by a non-native species) is likely to change the patterns of seed movement and recruitment, as well as the genetic structure of plant populations. Wind-dispersed seeds, for instance, can travel much further in open landscapes than in dense forests, owing to differences in the shape of the wind profile (San-José et al., 2019). Seed dispersal disruptions (SDDs), in fact, might either increase or decrease dispersal distance depending both on the dispersal mode of the species, the global change driver, and the specific context in which the disruption occurs.

Despite the large amount of information dealing with the effects of SDD, biases in scientific research can limit our understanding of the actual main patterns of SDD at a global scale. Moreover, most studies focus on just one global change driver, when it is widely accepted that such drivers act synergistically on many processes (Tylianakis et al., 2008; González-Varo et al., 2013; Maciel et al., 2021). A previous study by McConkey et al. (2012) pointed out that such synergistic interactions between different types of disturbances could exacerbate the negative impacts on seed dispersal, although they were rarely examined (but see Portela and Dirzo, 2020). Since then, there has been a number of studies that have simultaneously evaluated the effects of more than one driver on SDD, but they remain scarce (e.g., Pejchar, 2015; Rotllan-Puig and Traveset, 2016; Brocardo et al., 2018; de Assis Bomfim et al., 2018; Qie et al., 2019; Kiel et al., 2020; Bello et al., 2021; Marone and Pol, 2021; Sales et al., 2021). Assessing regional trends in research could thus help in understanding the main patterns in the drivers and synergisms between processes that could operate at different scales.

In this study, we review and synthesize the most up-to-date evidence of different drivers of global change causing SDD. Using a comprehensive dataset of 184 studies encompassing all biogeographical regions, our goal is to: (1) identify the realms and ecosystems in which SDD are more frequently documented. Given that a higher proportion of animal-dispersed species is found in tropical areas than at higher latitudes, and given also the high rates of habitat loss in the tropics, we might expect more studies on SDD in the tropics; (2) assess which are the most commonly studied drivers behind SDD, and (3) in the case of animal-seed dispersed species, evaluate what disperser taxa are the most often studied. In addition, we aim to (4) identify general mechanisms by which the different drivers of global change interfere with the seed dispersal process. For this, we evaluate which are the response variables most often measured in SDD studies. Here we move beyond previous reviews by (i) considering both abiotic and biotic SDD, (ii) quantifying research trends accounting not only for ecological consequences but also for evolutionary disruptions and (iii) capturing the latest studies addressing potential synergistic effects among drivers. We conclude by pointing out research gaps and frontiers in the study of global change that can help mitigate SDD and thus avoid their cascading impacts.

MATERIALS AND METHODS

We performed a thorough literature search using Web of Science (WOS)[1] and included all records from 1980 (oldest record found) until May 2021. We used the following search string "seed dispers*" AND "disrupt*" OR "seed dispers*" AND "failure*" resulting in a total of 884 records published in English-language journals. We first read titles and abstracts to exclude papers which were clearly not relevant, and then inspected 489 full texts searching for evidence of SDD. Out of these scientific publications, we developed a final database which retained a total of 184 original papers reporting at least one driver causing SDD from unique case studies (i.e., we exclude review papers). PRISMA guidelines were followed for this systematic revision (Page et al., 2021, see **Supplementary Figure 1**). Although most of the scientific publications were based on empirical data, we also considered theoretical studies aiming at modeling the effects of human impacts on seed dispersal (see e.g., Jones et al., 2017). We realize that the resulting database is not fully comprehensive since there are some articles not captured by our search terms (e.g., Donoso et al., 2020). However, we believe this compilation represents a largely unbiased sampling of the literature which allows us to identify patterns in seed dispersal research. As noted above, our search was mostly limited to English language publications, except for two studies published in Portuguese and one in Spanish that appeared in our search because their abstract was published in English. Therefore, research from regions where publications are commonly in other languages are likely under-represented in our database. Because we aim to provide a

broad understanding of SDD, we focused on both anthropogenic and non-anthropogenic drivers, which were classified according to the following eight categories: (*i*) *non-native species*; (*ii*) *climate change*; (*iii*) *defaunation*; (*iv*) *habitat loss/degradation*; (*v*) *fragmentation*; (*vi*) other *anthropogenic disturbances*; (*vii*) *non-anthropogenic abiotic factors*; and (*viii*) *non-anthropogenic biotic factors*. The criteria used to classify each driver within each category is shown in **Table 1**.

In addition, we extracted the following information. First, the *bioregion* was assigned according to the 11 broad realms identified by Holt et al. (2013), with the exception of oceanic islands that were treated as a separate region (following Fricke and Svenning, 2020). Second, the *ecosystem* in which the disruption was reported was categorized according to the IUCN Habitats Classification Scheme (Version 3.1) into: forest, savanna, shrubland, grassland, wetland, desert and artificial habitat (i.e., agricultural, gardens, pastures and urban areas). We established two additional categories to consider a few cases in which we were unable to assign one of the above-mentioned-categories. These categories corresponded to agroforests (e.g., agricultural crops such as coffee or cacao under canopy of shade trees) and others, in which we included gypsum soils and dunes. Third, in those studies focused on biotic seed dispersal, we identified the *seed dispersers* under study, which were assigned according to the following eight functional groups: bats, birds, fishes, invertebrates (mainly ants, beetles and gastropods), primates, reptiles, rodents, and other mammals (e.g., carnivores, herbivores, marsupials). Mammals were classified into four functional groups given their heterogeneity in terms of functional traits and handling

TABLE 1 | Categorization of the main drivers causing SDD.

Categories	Definitions
1. Non-native species (*n* = 54)	Studies reporting introduced plant or/and animal species
2. Climate change (*n* = 7)	Studies considering climate change projections, involving human-induced global warming and extreme weather events
3. Defaunation (*n* = 46)	Defined as seed disperser loss, mainly due to hunting/poaching activities
4. Habitat loss/degradation (*n* = 40)	This category encompasses those studies reporting deforestation, logging, reduced patch size or/and land use intensification
5. Fragmentation (*n* = 39)	Studies reporting fragmentation *per se*, involving changes in habitat spatial configuration
6. *Anthropogenic disturbances* (*n* = 25)	Any other disturbance derived from human activities which were not considered in categories 1–5. This category includes road constructions, urbanization and pollution
7. Non-anthropogenic abiotic factors (*n* = 14)	Any abiotic factor not derived from human activity, such as wildfires
8. Non-anthropogenic biotic factors (*n* = 9)	Any biotic factor not related to human activities such as herbivory, natural changes in plant spatial distribution or behavioral changes of seed dispersers

All global change drivers reported in the literature were classified according to eight different categories defined above. The number of studies within each category (n) is shown between brackets. Note that a single study may fall in more than one category if it reported more than one driver.

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[1]www.webofscience.com

behavior (e.g., flying vs. non-fly ability; diurnal vs. nocturnal habits, frugivory vs. scatter-hoarding) compared to other taxa. Lastly, to explore the general mechanisms by which the different drivers interfered with the seed dispersal process, we identified the *response variables* that were assessed in each publication. To homogenize the broad terminology used among studies, we established 10 categories trying to represent the main stages of the seed dispersal cycle (Wang and Smith, 2002; Carlo and Yang, 2011; see classification in **Table 2**). This information was further interpreted based on the seed dispersal effectiveness framework proposed by Schupp (1993), and re-classified into four main categories to identify whether SDD interfered with the seed dispersal process by causing: (*i*) community changes, (*ii*) disruptions in the quantity component of seed dispersal, (*iii*) disruptions in the quality component of seed dispersal, or/and (*iv*) by triggering evolutionary changes (see **Table 2**).

We completed our dataset by including the following information: (*i*) in the case of abiotic dispersal, the main seed dispersal vector (e.g., gravity, wind, water), (*ii*) whether SDD occurred on an island, and if so, the type of island (i.e., continental vs. oceanic); (*iii*) if the study considered SDD at a species- or at community- level; and (*iv*) whether the main results were based on empirical data, simulations, or the combination of these two approaches.

To identify general trends in the study of SDD, we estimated the percentage of scientific publications (out of the 184 studies) reporting each category per variable in our dataset. However, for some of the studies we identified more than one case per variable; i.e., the authors considered more than one bioregion, ecosystem, driver, disperser or response variable within the same study. Thus, percentages can add up to >100% because each paper could contain more than one category per variable.

RESULTS

Overall, we found studies addressing SDD in all biogeographical regions (**Figure 1A**) but they were unevenly distributed worldwide. Disruptions have been more frequently documented in the Neotropics, with almost a quarter of the publications reporting SDD in this realm (**Figure 1B**). Studies in the Palearctic are also highly represented (21%), followed by almost 15% of the studies carried out in the Nearctic. For the rest of bioregions, including the oceanic islands, disruptions in the seed dispersal process are reported in less than 10% of the publications.

Regarding the main drivers of SDD, the introduction of non-native species is the anthropogenic factor most frequently studied, with almost 30% of the publications, followed by defaunation (25%), habitat loss (~22%) and fragmentation (~21%) (**Figure 2**). On the contrary, the effect of non-anthropogenic abiotic and biotic factors, as well as the impact of climate change on SDD have been rarely documented, with < 8% of the publications in all three cases. Only about one fourth (26%) of the publications reported more than one driver of SDD.
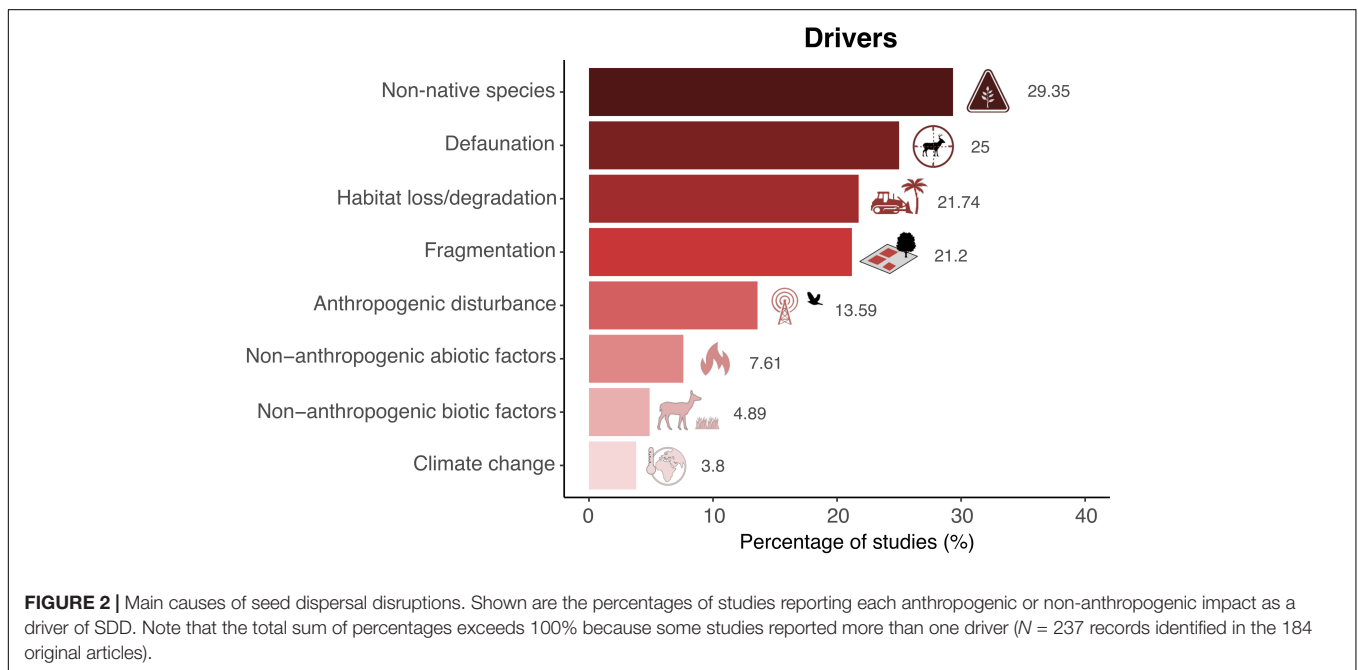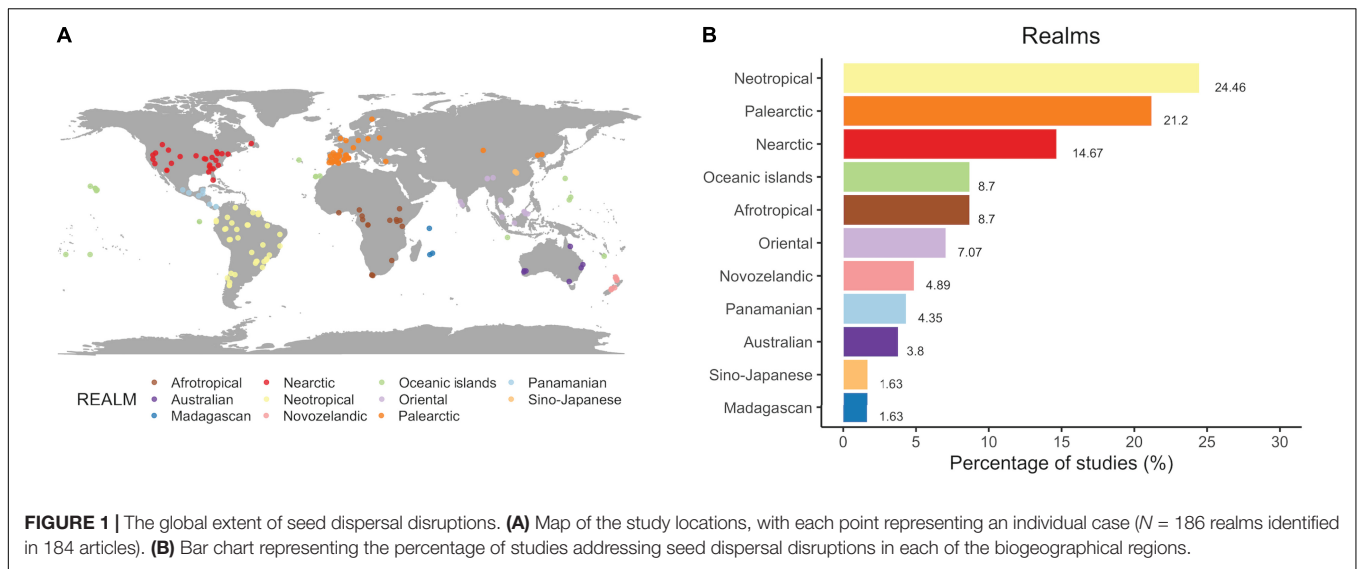
Most SDD studies (75%) have been documented in forest ecosystems. By contrast, only 16 and 4% of the studies have been performed in shrublands and grasslands, respectively (**Figure 3A**). Among the functional groups assessed, disruptions involving birds were addressed in 45.6% of the studies, followed by mammals such as herbivores and carnivores (19%), rodents (16%), and primates (14%) (**Figure 3B**). While we detected that seed dispersal failure in interactions involving invertebrates occurred in almost 12% of the studies, only 4 and 1% of the publications considered bats and fishes, respectively.

The response variables most frequently measured in SDD studies were seed removal and seedling recruitment, reported in ~30% of the publications in each case (**Figure 4**). Overall,

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TABLE 2 | Categorization of the main mechanisms by which the different drivers of global change interfere with the seed dispersal process.

Categories	Response variables	
Community changes	1. Disperser species composition (*n* = 42)	Abundance, density of seed disperser, or functional diversity based on animal species' traits
	2. Plant species composition (*n* = 30)	Abundance (including fruit production), taxonomic diversity and functional diversity based on plant species' traits
	3. Network structure (*n* = 9)	Structural properties of seed dispersal networks (e.g., network specialization, nestedness, etc.)
Quantity component of seed dispersal	4. Seed removal (*n* = 57)	Seed dispersal interactions, including interaction frequency, visitation or fruit removal rates
	5. Dispersed seeds (*n* = 30)	Number of seeds that arrive at a site (e.g., seed rain/deposition)
Quality component of seed dispersal	6. Dispersal distance (*n* = 21)	Seed dispersal kernels
	7. Dispersal site (*n* = 24)	Where seeds end up or the spatial pattern of where plants grow (e.g., spatial organization, plant distribution, etc.)
	8. Seed fate (*n* = 38)	Studies measuring seed germination and/or seed predation
	9. Seedling recruitment (*n* = 55)	Seedling emergence and survival (e.g., seedling/sapling abundance and diversity)
Evolutionary changes	10. Evolutionary changes (*n* = 21)	Genetic diversity and structure, including also changes in species' (plant or disperser) traits

Ten main categories were defined to account for the large heterogeneity used in the literature when describing the response variables under study. The number of studies within each category (n) is shown between brackets. Note that a single study may fall in more than one category if it evaluated more than one response variable.

FIGURE 1 | The global extent of seed dispersal disruptions. **(A)** Map of the study locations, with each point representing an individual case (N = 186 realms identified in 184 articles). **(B)** Bar chart representing the percentage of studies addressing seed dispersal disruptions in each of the biogeographical regions.

FIGURE 2 | Main causes of seed dispersal disruptions. Shown are the percentages of studies reporting each anthropogenic or non-anthropogenic impact as a driver of SDD. Note that the total sum of percentages exceeds 100% because some studies reported more than one driver (N = 237 records identified in the 184 original articles).
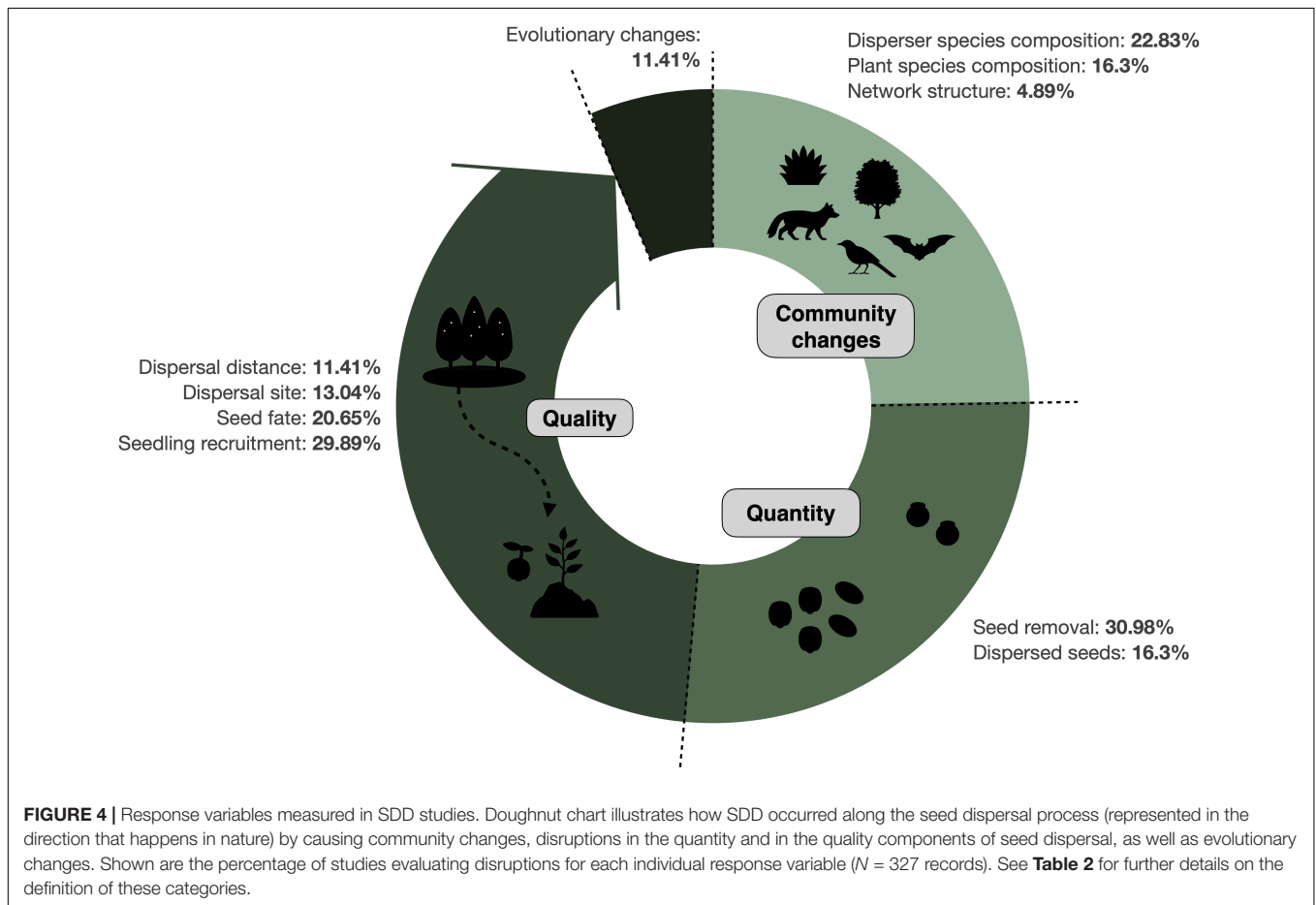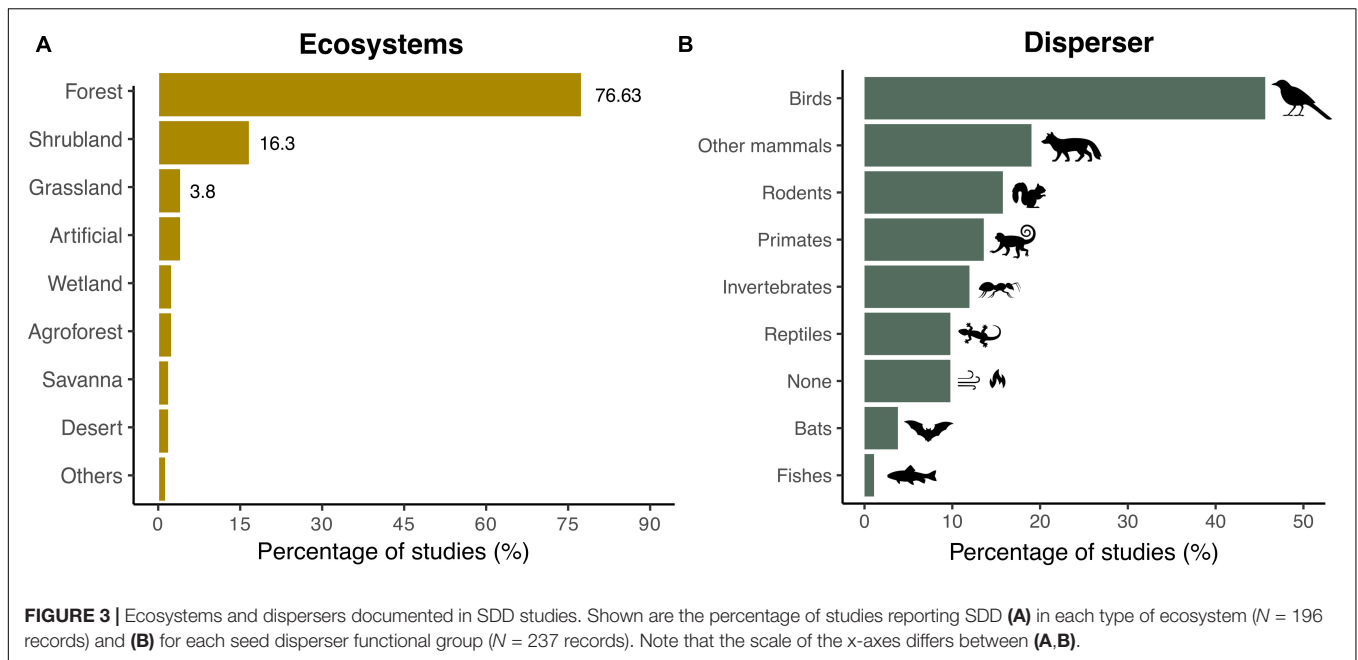
however, the quality component of SDD has received more attention than the quantitative component. Impacts on plant and disperser species composition were also often documented, while only a few studies (<5%) evaluated community changes in terms of network structure. Finally, a small fraction of the studies (11%) has assessed whether there are evolutionary changes involved in SDD, either from the plant or the disperser's perspective.

Although most of the studies reported biotic SDD, abiotically dispersed species have been the focus of ∼ 19% of the publications (see **Supplementary Figure 2**). In addition, regardless of the bioregion, SDD has been especially reported in mainland areas (∼70%), in studies carried out at a species-level (70%), and on empirical studies (87%) (see **Supplementary Figure 2**).

DISCUSSION

Our review identified broad trends and research biases on SDD. The studies documented disruptions in biotically and abiotically dispersed plants, on every continent and many oceanic and continental islands, on every major biome, and involving all major groups of animal dispersers in the case of animal-dispersed plants. About two-thirds of studies have focused on the initial stages of the seed dispersal cycle—seed removal and seedling recruitment—while far fewer have dealt with the longer-term patterns demonstrated through plant community composition and evolutionary changes. Overall, about 70% of the studies focused on individual plant species, and only 30% on plant communities. We foresee that given the widespread nature of

FIGURE 3 | Ecosystems and dispersers documented in SDD studies. Shown are the percentage of studies reporting SDD **(A)** in each type of ecosystem (N = 196 records) and **(B)** for each seed disperser functional group (N = 237 records). Note that the scale of the x-axes differs between **(A,B)**.

FIGURE 4 | Response variables measured in SDD studies. Doughnut chart illustrates how SDD occurred along the seed dispersal process (represented in the direction that happens in nature) by causing community changes, disruptions in the quantity and in the quality components of seed dispersal, as well as evolutionary changes. Shown are the percentage of studies evaluating disruptions for each individual response variable (N = 327 records). See **Table 2** for further details on the definition of these categories.

SDD and its impacts on the early life history stages in plant populations, there will be increasingly more evidence for changes in plant community composition and evolution.

The trends we identified in SDD research result from a combination of geographic and ecological patterns in seed dispersal and in global change, as well as bias in research focus. For example, islands have experienced more alien species invasions and native species extinctions than mainlands (Sax and Gaines, 2008; Turvey and Fritz, 2011; Blackburn et al., 2019). As such, this global change driver dominates island studies, with mainly birds and reptiles involved in such disruptions (see e.g., Traveset and Riera, 2005; Rumeu et al., 2011; Calviño-Cancela et al., 2012; Rogers et al., 2017; Fricke et al., 2018). Similarly, we found that SDD in the Neotropics is more frequently documented than in other regions. This could be due to Neotropical systems being more disrupted or to more research effort in this realm where biotic seed dispersal is prevalent (Jordano, 2014; Rogers et al., 2021a). The latter seemed to be the most likely reason given the following research evidence up-to-date. First, literature about global biodiversity sampling biases and biodiversity-ecosystem studies have found disproportionally poor tropical sampling overall (Clarke et al., 2017; Hughes et al., 2021). Second, results derived from the IPBES Global Report regarding the temporal trend of each main driver showed that neotropical systems were not under more threat than other high biodiversity regions (Balvanera et al., 2019). In contrast to the Neotropic, the Afrotropic and Oriental regions are understudied, especially given the commonness of biotic dispersal and the frequency of threatened species in these regions (Dirzo et al., 2014; Sridhara et al., 2016; Rogers et al., 2021a). This biogeographic bias mirrors the bias found in research on forest fragmentation and biological invasions, which has been attributed primarily to limited financial resources and political instability (Deikumah et al., 2014; Bellard and Jeschke, 2016; Chong et al., 2021). On the other hand, many studies on abiotic SDD have been carried out in the Palearctic and Nearctic (e.g., De hert et al., 2013; Labatore et al., 2017), probably because abiotic dispersal is more prevalent at higher latitudes (Kling and Ackerly, 2020; Rogers et al., 2021a) and because a good fraction of researchers investigating seed dispersal have home institutions in the temperate realm.

Although forests cover ∼30% of the world's terrestrial landmass (FAO and UNEP, 2020), they are by far the most common ecosystem studied with respect to SDD. This likely reflects the increased prevalence of animal-mediated dispersal in forest systems, as well as a bias toward studying biodiversity, and seed dispersal in particular, in forest systems compared to, for example, grassland systems (Hughes et al., 2021). Indeed, these results might also reflect the large body of scientific research into endozoochory by frugivores addressing how fragmentation could affect seed dispersal in multiple types of forests (e.g., Herrera and Garcia, 2010; Deikumah et al., 2014; Emer et al., 2018; Lander et al., 2019). However, grasslands cover around 40% of the Earth's surface (Bardgett et al., 2021). In grasslands, as well as in arid and wetland systems, many plants also benefit from dispersal by grazing herbivores and ants (Janzen, 1984; Wills and Landis, 2018; Anjos et al., 2020; Green et al., 2021; Hyvarinen et al., 2021). The dearth of research in non-forest ecosystems could be related to a higher proportion of abiotically (e.g., wind) dispersed species, assuming this kind of dispersal might be less limited than biotically dispersed species. Alternatively, it could also be related to the availability of suitable sites to conduct studies. In this sense, research activities could be facilitated in forest ecosystems, which usually fall within or nearby protected areas. Non-forested ecosystems, however, could be more complicated to sample, which can thus limit our global understanding of SDD.

Non-native species and defaunation were the most frequently studied global change drivers of SDD. Research efforts addressing the impact of alien species focused either on the introduction of non-native dispersers to a novel system or the loss of native dispersers caused by the introduction of non-native predators (e.g., Pejchar, 2015; Rogers et al., 2017). Biotic and abiotic seed dispersal have also been acknowledged as ecological processes that are vulnerable to climate change (Mokany et al., 2014; Kling and Ackerly, 2020). However, to date climate change has received much less attention. Given that seed dispersal is critical for species to shift ranges with climate changes (Dawson et al., 2011; Corlett and Westcott, 2013; González-Varo et al., 2021; Fricke et al., 2022), the relative lack of theoretical or empirical studies on this topic suggests SDD disruption due to climate change is an area requiring additional focus. We posit that advancing knowledge in this regard is particularly urgent given the omnipresent impact of climate change, which operates at a higher (i.e., global) scale and could thus worsen the consequences of any other driver of SDD (McConkey et al., 2012; Zhou et al., 2013; Maciel et al., 2021). For instance, one of the latest studies showed that the loss of seed dispersal interactions may impair the potential of a palm species to track climate change, especially in combination with fragmentation and forest loss (Sales et al., 2021). The handful of SDD studies found in our literature review mainly derived from empirical data concerning extreme climatic events (e.g., Zhou et al., 2013; Standish et al., 2018) or the combination of empirical data with simulations based on future climate projections and species distribution models (see e.g., Bello et al., 2021; Sales et al., 2021). More research following such an approach would thus be a promising way to provide insights into SDD under climate change, synergistic effects among drivers, and to guide management interventions for conservation and restoration.

Animal seed dispersal has been the focus of most SDD studies, although abiotic dispersal has also faced major disruptions due to habitat fragmentation, transformation, and destruction, as well as climate change. Among animal dispersers, birds and non-flying mammals are the most frequently studied groups, probably due to research bias on endozoochorous vertebrate dispersers, whereas fishes and bats are rarely studied. Only very recently, a few studies have demonstrated how overfishing may negatively affect seed dispersal, suggesting potential functional homogenization in floodplain ecosystems (Costa-Pereira et al., 2018; Araujo et al., 2021). Similarly, only a few studies showed dispersal limitation for bat-dispersed plants due to habitat loss and defaunation (Henry and Jouard, 2007; Valiente-Banuet and Verdú, 2013). This lack of SDD studies likely reflects the scant research attention of seed dispersers with nocturnal habits (Mello et al., 2011; Seltzer et al., 2013), as well as the limited knowledge on the impact of disturbances on bat's role as seed dispersers,

especially in the Old World (see Aziz et al., 2021 and references therein). These results might be particularly worrisome given the non-redundant resource use and unique ecological role of bats compared to other seed dispersers (Fleming, 1987). For abiotic dispersal, on the other hand, most available information deals with wind-dispersed species that are affected by habitat loss and fragmentation (e.g., Alados et al., 2010; Bagchi et al., 2011), non-anthropogenic abiotic factors such as wildfires (e.g., Ziegenhagen and Miller, 2009; Legras et al., 2010) or how the dispersal of hydrochorous plant species is interfered with dam constructions (e.g., Merritt and Wohl, 2006).

We found that existing research addresses processes at the earliest life stages of plants to quantify outcomes of dispersal disruption on plant populations, by studying processes such as seed removal and seedling recruitment. Few studies track the effects of dispersal long enough to determine the true cost to fitness, and relatively few explore the community-level consequences of SDD. The seed dispersal mutualism can be challenging to study either observationally or experimentally, because seeds can move long distances, few seeds successfully establish and survive to reproduce, and the influence of dispersal on seed fate can take years to discern (Beckman et al., 2020). As a result, few studies comprehensively measure the impacts of SDD. Some of the best examples of population and community-level effects come from places that have experienced widespread defaunation, such as the Canary Islands (Pérez-Méndez et al., 2016), New Zealand (Bombaci et al., 2021), the Mascarenes (Albert et al., 2020, 2021), and Guam (Wandrag et al., 2017). Furthermore, few studies are able to capture evolutionary changes as a result of SDD (Galetti et al., 2013; Carvalho et al., 2016; Traveset et al., 2019). To capture the cumulative ecological and evolutionary effects of SDD on plant species and communities, research designs that match the spatial or temporal scales at which these processes operate are necessary. These may include long-term monitoring at study sites impacted by disruption to monitor change from historical baselines (Harrison et al., 2013), experimental disruption of seed dispersal and comparisons to appropriate controls (Wandrag et al., 2017; Albert et al., 2020), and observations across gradients of SDD through remote sensing or biodiversity monitoring networks (Terborgh et al., 2008).

FUTURE PERSPECTIVES

Seed dispersal is a critical mechanism by which plants respond to environmental change (Nathan et al., 2008). This systematic review captures the latest studies addressing SDD and quantified research gaps in terms of, not only global change drivers, but also different realms, habitats, seed dispersers and response variables less often recorded. It also highlights the potential synergistic effects among drives in both biotic and abiotic seed dispersal process, which could be impacted by one or various global change drivers. Yet, feedbacks between different processes are still rarely investigated and represent an important frontier for forecasting the threats to plant biodiversity and ecosystem services in the Anthropocene. We caution that, as we enter a period of increasing environmental change due to

climate change, the accrued impacts of SDD may only now manifest. Ecosystem tipping points may occur as the pace of environmental change exceeds plants' capacity to respond to these changes (Lenton, 2011). This prioritizes research to understand how seed dispersal function changes in human-modified environments that are impacted by multiple global change drivers. Quantifying the interactions among these drivers would be critical to avoid overestimating or underestimating threats to seed dispersal. A potential way forward to improve the predictability of multiple anthropogenic stressors could be the application of recently developed modeling frameworks based on the distribution of driver effects across targets and ecological scales (Simmons et al., 2021).

We further see the potential for significant advances in understanding the ecosystem services that seed dispersers provide as agents of biotic connectivity (e.g., enabling plant species to track climate change, González-Varo et al., 2021) and for their role in enhancing carbon storage in regenerating or intact forests (Bello et al., 2015). Although benefits of seed dispersal are well-studied and evidence for SDD is widespread, less research effort has focused on building an evidence base for the effective use of habitat corridors (Levey, 2005) or protected areas (Bombaci et al., 2021) to facilitate plant connectivity via seed dispersal. In addition, studying how dispersal mode influences which plant species experience SDD will help forecast biodiversity and ecosystem services. We anticipate that species that are abiotically dispersed or where humans commonly intentionally or unintentionally facilitate dispersal will be winners, to the detriment of many other plant species.

DATA AVAILABILITY STATEMENT

The dataset generated for this study is based on the published literature and is available in Zenodo with the identifier https://doi.org/10.5281/zenodo.5794532.

AUTHOR CONTRIBUTIONS

FUNDING

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.794481/full#supplementary-material

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