

Dispersal-related plant traits are associated with range size in the Atlantic Forest

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Abstract

Aim: The efficiency of animal-mediated seed dispersal is threatened by the decline of animal populations, especially in tropical forests. We hypothesise that large-seeded plants with animal-mediated dispersal tend to have limited geographic ranges and face an increased risk of extinction due to the potential decline in seed dispersal by large-bodied fruit-eating and seed-dispersing animals (frugivores).

Location: Atlantic Forest, Brazil, South America.

Taxon: Angiosperms.

Methods: First, we collected dispersal-related traits (dispersal syndrome, fruit size, and seed size), growth form (tree, climber, and other) and preferred vegetation type (open and closed) data for 1052 Atlantic Forest plant species. Next, we integrated these with occurrence records, extinction risk assessments, and phylogenetic trees. Finally, we performed phylogenetic generalised least squares regressions to test the direct and interactive effects of dispersal-related traits and vegetation type on geographical range size.

Results: Large-seeded species had smaller range sizes than small-seeded species, but only for species with animal-mediated dispersal, not for those dispersed by abiotic mechanisms. However, plants with abiotic dispersal had overall smaller range sizes than plants with animal-mediated dispersal. Furthermore, we found that species restricted to forests had smaller ranges than those occurring in open or mixed vegetation. Finally, at least 29% of the Atlantic Forest flora is threatened by extinction, but this was not related to plant dispersal syndromes.

Main Conclusions: Large-seeded plants with animal-mediated dispersal may be suffering from dispersal limitation, potentially due to past and ongoing defaunation of large-bodied frugivores, leading to small range sizes. Other factors, such as deforestation and fragmentation, will probably modulate the effects of dispersal on range size, and ultimately extinction. Our study sheds light on the relationship between plant traits, mutualistic interactions, and distribution that are key to the functioning of tropical forests.

KEYWORDS

defaunation, extinction risk, frugivory, phylogeny, range size, seed dispersal, tropical forest

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1 | INTRODUCTION

Animal-mediated seed dispersal is essential to sustain tropical forests biodiversity, as most tropical flowering plants have evolved fruits and seeds adapted for animal dispersal (Howe & Smallwood, 1982; Tabarelli & Peres, 2002). Yet, tropical forests worldwide are experiencing escalating rates of defaunation, which refers to the decline and extinction of animal populations. Defaunation predominantly impacts the largest animals, particularly large vertebrates, that is, 'megafauna' (Moleón et al., 2020). The Neotropics have experienced two major periods of megafauna extinctions, the first one caused by the Great American Biotic Interchange with the arrival of new predators and competitors ca. 3 million years ago (Ma) (Bacon et al., 2015; Carrillo et al., 2020; Faurby & Svenning, 2016), and the second one caused by human habitat alteration and hunting of megafauna from ca. 10,000 years ago (Lima-Ribeiro & Diniz-Filho, 2013; Prates & Perez, 2021). The latter event included the extinction of charismatic ground sloths (Megatheriidae) and elephant-like gomphotheres (Gomphotheriidae). This human-driven extinction event is still ongoing, with intensification of animal extinctions in recent decades (Dirzo et al., 2014).

Defaunation impacts essential ecosystem functions and services, such as forest regeneration, carbon storage, and animal-mediated seed dispersal (Bello et al., 2015; Gardner et al., 2019). Indeed, defaunation may limit dispersal of vertebrate-dispersed plants with large seeds and fruits, because these species often depend on large-bodied animals to swallow, digest, and disperse their seeds (Campos-Arceiz & Blake, 2011; Méndez et al., 2022; Pires et al., 2018; Wheelwright, 1985). Consequently, defaunation may lead to evolutionary decreases in seed size (Galetti et al., 2013), changes in plant population allele frequencies (Carvalho et al., 2016), reductions in carbon storage (Bello et al., 2015), species turnover across plant communities (Méndez et al., 2022), and contraction of species geographical ranges through local extinctions (Doughty et al., 2016).

The geographical range size of a species is the area where a species is naturally found (Gaston, 2003) and is a critical and widely used criterion to estimate extinction risk in the framework of the IUCN Red List - Criterion B (IUCN, 2018). Several factors determine species geographical range size, such as climate, geographical barriers, niche breadth, species age, and the species' dispersal ability (Alzate et al., 2023; Alzate & Onstein, 2022; Sheth et al., 2020). For almost all plants, the effectiveness of dispersal, the distance of dispersal, the opportunities for long-distance dispersal, and hence the geographical range size, rely on external seed dispersal mechanisms, and successful dispersal may therefore primarily depend on the environment (Nathan, 2006). For example, wind patterns or water flow affect seed dispersal on an ecological time scale by constraining dispersal distance and direction for plants with abiotic dispersal (Merritt & Wohl, 2002; Willson et al., 1990). Similarly, for species that depend on animals for seed dispersal, the availability, behaviour, and movement ability of the seed-dispersing animals influence dispersal success (Zwolak & Sih, 2020). Consequently, plants have evolved traits to facilitate dispersal, such as winged seeds for wind

dispersal, or fleshy fruits for dispersal by animals (van der Pijl, 1982). In tropical forests, plants often depend on animal-mediated dispersal, because animals can move effectively through dense forests (Clark et al., 1999; Tabarelli & Peres, 2002). Furthermore, large-seeded fruits, that are predominantly dispersed by large-bodied frugivores (Lim et al., 2020; Wheelwright, 1985), may experience more frequent long-distance dispersal and less spatial clustering of conspecifics than small-seeded species (Onstein et al., 2019; Seidler & Plotkin, 2006), because large-bodied animals move over longer distances and have longer gut passage times than small-bodied animals (Pires et al., 2018; Whitmee & Orme, 2013). This may increase range sizes of large- compared to small-seeded species when large-bodied frugivores are abundant.

Understanding how plant traits relate to geographical range size via dispersal-related mechanisms for range size expansion or contraction, is essential to develop better and more targeted conservation strategies (Alzate & Onstein, 2022; López-Hoffman et al., 2010). Hence, we focus on a biodiversity hotspot – the Atlantic Forest in Brazil – which comprises high biodiversity and endemism, but suffers from high rates of defaunation and is highly fragmented, with only 12% of the original vegetation and on average 30% of the mammal species across assemblages remaining (Bogoni et al., 2018; Marques et al., 2021). The Atlantic Forest comprises a mosaic of vegetation types, including seasonal moist and dry broad-leaf tropical forests, tropical and subtropical grasslands, savannas, and shrublands. We hypothesise that geographical range sizes for large-seeded species with animal-mediated dispersal are smaller than for smaller-seeded species dispersed by smaller-bodied animals or by abiotic mechanisms. This is because past and ongoing defaunation of large-bodied animals may have led to dispersal limitation, local extinctions and ultimately range contractions of large-seeded animal-dispersed plants. Consequently, we also expect that species that rely on animal-mediated dispersal have a higher extinction risk than species that are dispersed by abiotic mechanisms. Finally, we hypothesise that range sizes are additionally influenced by non-dispersal-related factors, such as growth form and vegetation type. Specifically, we expect that ranges for trees, or for species that are restricted to a particular vegetation type, are smaller than for species with other growth forms (e.g., climbers) or for species that occur in a mix of vegetation types. This is because large trees and/or vegetation type specialists are more vulnerable to habitat destruction and deforestation, which may have led to range contractions.

2 | METHODS

2.1 | Species list and traits

We obtained a list of accepted plant species in the Atlantic Forest (Brazil Flora Group, 2021). We limited our selection to angiosperms native to the Atlantic Forest, resulting in a list of 14,771 species. For those species, we assembled data on nine functional traits: fruit length, fruit width, seed length, seed width, fruit type,

fruit colour, growth form, plant height, and dispersal syndrome (Figure 1), as well as information on their preferred vegetation type. We obtained trait information through a literature survey (see Appendix S1 for references) and took measurements from specimens in two Brazilian herbaria: The Botanical Garden of Rio de Janeiro Herbarium (RB) and The Museum of Biology Mello Leitão Herbarium (MBML). We conducted our literature search using Web of Science, with the following keyword search criteria: 'dispersal syndrome OR dispersal traits OR seed dispersal OR floristic composition OR phenology AND Atlantic Forest OR Brazil'. We restricted our search to scientific articles published in English or Portuguese. When more than one trait value per species was reported, we calculated mean values for each species.

We classified dispersal syndrome as "animal-mediated" or "abiotic". We categorised species as having "animal-mediated" dispersal when fruits and/or seeds were described as dispersed by animals through endozoochory (seeds are ingested and pass through the digestive tract), epizoochory (fruits or seeds have structures to attach to animal fur) or zoochory (not specified how animals transport the seeds). Species for which dispersal syndrome was not explicitly described were categorised as 'animal-mediated' if they had fleshy fruits (i.e., fruit type 'drupe' or 'berry') and fruit colours typical for animal dispersal syndromes, that is, orange, red, or purple (Sinnott-Armstrong et al., 2018; Valenta & Nevo, 2020). We categorised species as having "abiotic" dispersal when fruits and seeds were described as dispersed

by wind (anemochory), water (hydrochory), or self-dispersal (autochory) (Figure 1). Abiotic dispersal was not defined based on fruit characteristics only, because dry fruits can be either dispersed via abiotic mechanisms or via animals (e.g., epizoochory), and we lacked information on additional dispersal structures (e.g., wings).

We also collated information on species growth form and preferred vegetation type (Brazil Flora Group, 2021). We classified growth form as: tree, climber, or other (shrub/herb/succulent, i.e., understory growth forms). Species with multiple categories including "liana" were considered climbers. In addition, we used vegetation type to classify species into three categories: closed (i.e., forest ecosystems), open (i.e., field vegetation), or mixed (when a species occurs in both open and closed systems), following Leão et al. (2020).

2.2 | Phylogenetic tree

To correct for phylogenetic non-independence of species and their traits in our models (Rezende et al., 2007), and to perform phylogenetically informed trait imputations, we obtained a phylogenetic tree for the Atlantic Forest species with trait data (1505 species with trait data were available in the phylogeny), based on a backbone megatree, the phylogeny from Smith and Brown (2018), and using the function "phylo.maker" with "scenario 1" from the "V.Phylomaker"



FIGURE 1 Dispersal syndrome diversity in the Atlantic Forest. Examples of Atlantic Forest fruits: (a–c) small (<4 cm) fruits with animal-mediated dispersal (a) *Guatteria* sp., (b) *Eugenia uniflora*, (c) *Schinus terebinthifolia*; (d–f) large (>4 cm) fruits with animal-mediated dispersal, (d) *Duguetia moricandiana* (e) *Carpotroche brasiliensis*, (f) *Anacardium occidentale*; (g–j) fruits with abiotic strategies of dispersal, (g) *Qualea grandiflora*, (h) *Lecythis pisonis*, (i) *Himatanthus bracteatus*, (j) *Paubrasilia echinata*. Photos used with permission from Ricardo da Silva Ribeiro (a, c, d, e, g–j) and Ian Bortolomiol (b, f).

R package (Jin & Qian, 2019) (i.e., with new tips bound to the genus- or family-level basal nodes). This phylogeny was assembled using a hierarchical clustering analysis of DNA sequences collected from GenBank, and was resolved using data from the Open Tree of Life Project, and a backbone provided by Magallón et al. (2015).

2.3 | Trait imputation

Because data on fruit- and seed-sizes (length and width) were only available for ca. 70% of Atlantic Forest species for which we also had dispersal syndrome information (abiotic or animal-mediated), we used phylogenetic trait imputation based on a maximum likelihood method in the “phylopars” R package (Bruggeman et al., 2009) to infer fruit and seed size data for the remaining species. This approach takes a species-by-trait matrix and assumes a Brownian motion trait evolutionary process, where trait values change stochastically along the branches of the phylogenetic tree (i.e., simulating a “random walk”), to impute a maximum likelihood trait value for each species (i.e., each tip in the phylogeny). To ensure the accuracy of the method, the trait matrix used for imputation included all numerical traits with more than 60% trait coverage for all 1505 species in the phylogeny.

2.4 | Geographical range size

To estimate geographical range sizes, we gathered species occurrence records from the Global Biodiversity Information Facility (GBIF, www.gbif.org), resulting in 1,452,901 occurrences for 1448 species (73 species were excluded because occurrences were missing or only available for synonyms). We selected occurrences within South America, dating from 1995 to February 2023, as occurrences before 1995 may be less accurate (Colli-Silva et al., 2020). We removed uncertain coordinates using the flagging steps in the “CoordinateCleaner” R package (Zizka et al., 2019). Specifically, we removed occurrences in the ocean or biodiversity institutions (e.g., museums or universities), in capitals, country or province centroids, and occurrences with equal longitude/latitude or with zeros. The final filtered dataset included 565,667 occurrences.

To determine the geographical range size of each species, we used their occurrence records to calculate the area of occupancy (AOO) and the extent of occurrence (EOO). This was achieved by using the “IUCN.eval” function from the “ConR” R package (Dauby et al., 2017). In our analyses, we considered both AOO and EOO to evaluate the impact of disjunct distributions on the results. AOO is the sum of the area of all the grid cells that contain at least one occurrence point, and will correctly estimate the range of disjunct distributions, but is more sensitive than EOO to sampling bias and gaps. We used a grid cell size of 2 km² around the coordinate point. EOO is the area contained within the shortest continuous boundary

that can be drawn within the sites where a species occurs (a convex hull polygon), and has the advantage that it is robust to sampling bias and gaps in collections, but can potentially become unwarrantedly large for species with disjunct distributions.

To assess whether determinants of range size differed across continental or regional scales, we measured range size based on occurrence records (1) across South America and (2) within the Atlantic Forest boundaries (Figure S1). Range size was estimated for species with more than three coordinate records.

2.5 | Phylogenetic Generalised Least Squares (PGLS) regression models

To investigate the influence of dispersal-related traits on geographical range size, we fitted phylogenetic generalised least squares (PGLS) models using the function “pgls” from the R package “caper” (Orme et al., 2018). This method uses Pagel’s lambda (λ) as a covariance parameter; $\lambda=0$ suggests no phylogenetic signal in model residuals, whereas $\lambda=1$ suggests strong phylogenetic signal in model residuals (Pagel, 1999). All continuous variables were transformed to the logarithmic scale (base 10) to approximate normality in model residuals. In order to avoid problems with trait multicollinearity (Graham, 2003), we checked for correlations among predictor variables (i.e., dispersal-related functional traits that may affect range size) using Pearson correlation coefficients. We considered traits as highly correlated when the correlation coefficient was >0.7 . Following this approach, we detected high correlations between seed width and seed length, and between fruit width and fruit length (Figure S2). Therefore, we only considered fruit length and seed length in our PGLS models.

We assessed which additive and/or interaction effects between predictor variables explained variation in geographical range size across Atlantic Forest species by evaluating the fit of 15 models that differed in combinations of predictor variables. These included five simple models, with a single explanatory variable, four models specifically including a combination of dispersal-related traits (fruit length, seed length, and/or dispersal syndrome), and five more complex models in which we assessed support for an interaction term between dispersal syndrome and seed length, and additional additive effects of growth form and vegetation type (Table S1). Model fit was evaluated using the Akaike Information Criterion (AIC) (Anderson & Burnham, 2004), and we selected the best model given the lowest AIC, with $>2 \Delta AIC$ than the next best model. We checked for non-constant variance and deviation from normality in the model residuals by visual inspection. We repeated this procedure for four datasets (response variables): (1) AOO within South America, (2) EOO within South America, (3) AOO within the Atlantic Forest, and (4) EOO within the Atlantic Forest. We compared outcomes of predictors between these subsets to assess whether results were sensitive to the measure used to approximate range size (AOO or EOO) or to the range size extent (South America or Atlantic Forest).

2.6 | Sensitivity analysis

Since the Atlantic Forest is primarily composed of plants with animal-mediated dispersal (Almeida-Neto et al., 2008; Pozetti et al., 2001), the number of plants with animal-mediated dispersal in the dataset was nearly four times as large as those with abiotic dispersal (835 and 217 species, respectively). To investigate the effect of this unbalanced sample size on model outcomes, we fitted the best PGLS model 100 times, each time randomly subsampling 217 species with animal-mediated dispersal (i.e., matching the species number sampled for abiotic dispersal) as well as including the 217 with abiotic dispersal. We compared estimates of explanatory variables, *p*-values, lambdas, and *r*-squares from the 100 subset simulations to the empirical estimates, and evaluated whether our observed estimate fell within the 95% confidence interval of subsampled dataset estimates.

2.7 | Extinction risk and dispersal syndrome

We inferred species extinction risk using the “IUCN.eval” function from the “ConR” R package (Dauby et al., 2017). In addition, we used the “iucn_summary” function from the R package “taxize” (Chamberlain & Szöcs, 2013) to directly obtain information on the extinction risk of Atlantic Forest species assessed by the IUCN Red List (IUCN, 2018). IUCN relies on expert assessors, who are trained individuals and/or species experts, that gather information from various

sources, including peer-reviewed papers, books, expert knowledge, indigenous knowledge and citizen science, to classify species into extinction risk categories based on range size and population declines. Species are classified as Least Concern (LC), Near Threatened (NT), Vulnerable (V), Endangered (EN), Critically Endangered (CR), Extinct in the Wild (EW), or Data Deficient (DD).

We used Fisher’s exact tests (Fisher, 1970) to evaluate whether species threat status (not threatened: LC or NT; or threatened: VU, EN, CR) based on range size-based inferences with the “ConR” R package (Dauby et al., 2017) was similar to the status from IUCN Red List assessments (IUCN, 2018). Similarly, we evaluated whether threat status was associated with dispersal syndrome (animal-mediated vs. abiotic). All analyses and data processing were done using R version 4.0.3.

3 | RESULTS

3.1 | Dispersal-related predictors on Atlantic Forest species range sizes

Our dataset included 1510 species with trait information for at least one trait; complete data for traits, vegetation type, range size, and phylogeny were available for 1052 plant species, belonging to 379 genera from 110 families. Fruit lengths ranged from 0.3 to 600 mm, with an average of 31 mm. Seed lengths ranged from <0.1 to 89 mm, with an average of 10 mm.

TABLE 1 Range size predictors of Atlantic Forest plant species.

	AOO/SA	EEO/SA #1	EEO/SA #2	AOO/AF	EEO/AF #1	EEO/AF #2
Intercept	7.27***	15.44***	15.32***	6.45***	13.75***	13.66***
Fruit length (log)	-0.08	-0.06	-0.07	-0.09	-0.11	-0.12
Seed length (log)	0.03	0.29	0.30	-0.06	0.22	0.23
Animal-mediated dispersal syndrome (ref. level: abiotic)	0.54*	1.16**	1.19**	0.23	0.64	0.66
Veg. type: open (ref. level: mixed)	-0.52*	-0.74●	-0.68	-0.82***	-1.16***	-1.11**
Veg. type: forest (ref. level: mixed)	-1.01***	-1.08***	-1.06***	-0.69***	-0.92***	-0.91***
Plant growth form: climber (ref. level: tree)	n.a.	n.a.	0.43	n.a.	n.a.	0.39●
Plant growth form: other (ref. level: tree)	n.a.	n.a.	-0.003	n.a.	n.a.	-0.02
Seed length * Animal-mediated dispersal syndrome	-0.32**	-0.59**	-0.59**	-0.19	-0.46**	-0.46**
Veg. type: open (ref. level: closed)	0.49*	0.34	0.38	-0.13	0.92**	0.91***
Plant growth form: climber (ref. level: other)	n.a.	n.a.	0.44	n.a.	n.a.	0.41
F-value	22.32	9.3	7.438	15.23	10.36	8.313
Degrees of freedom	1045	1045	1043	1045	1045	1043
<i>p</i> -Value	<.001	<.001	.0001	<.001	<.001	.001
Adj. <i>R</i> ²	.108	.045	.0467	.075	.05	.0527
Lambda	0.15	0.132	0.123	0.089	0.093	0.085

Note: Dispersal-related traits and their relationship with range size (area of occupancy, AOO or extent of occurrence, EOO) at the extent of South America (SA) or the Atlantic Forest (AF). Results for the best model (with the lowest AIC) using phylogenetic generalised least squares (PGLS) regressions are shown. If models had <2 ΔAIC compared to the next best model, both models are shown (#1 and #2). ref. level refers to the reference level of the intercept for factors; we repeated the final model with different reference levels to evaluate the difference in response for each level. ‘log’ refers to a log-transformation of the continuous variable; n.a., not applicable (i.e., variable was not included in the best model).

Significant effects are depicted in bold: ****p* < .001, ***p* < .01, **p* < .05, ●*p* = .05.

We found that dispersal-related traits explained substantial variation in range sizes across the Atlantic Forest flora, based on results from the PGLS analyses. The best model for AOO across South America indicated that dispersal syndrome, fruit length, seed length, and vegetation type best explained range size variation (Table 1, Tables S1 and S2). For example, species with animal-mediated dispersal had larger range sizes than species with abiotic dispersal (estimate=0.54, SE [standard error]=0.28, t -value=2.04, p -value<.05). However, we also found support for an interaction term between seed length and dispersal syndrome (estimate=-0.32, SE=0.12, t -value=-2.59, p -value<.01), indicating that the relationship between seed length and range size is dependent on dispersal syndrome. Specifically, seed length and range size were negatively correlated for species with animal-mediated dispersal (Figure 2a), whereas for species with abiotic dispersal, the correlation was positive (Figure 2b). Additionally, we found that species occurring exclusively in open vegetation had larger range sizes than species exclusively occurring in closed forest vegetation (Figure 3a, estimate=0.49, SE=0.23, t -value=2.1, p -value<.05). Moreover, species occurring only in closed or in open vegetation had smaller range sizes than species occurring in mixed vegetation (Figure 3a, estimate=-1.01, SE=0.11, t -value=-9.08, p -value<.001). Finally, there was a tendency for species with larger fruit lengths to have

smaller range sizes, but this was not significant at p <.05 (Figure S3, Tables 1 and S2).

Results for EOO across South America were qualitatively similar to those obtained for AOO (Table 1, Tables S1 and S3, Figures 2e,f, 3b, and 4a), with similar effect sizes and significance levels. There were two exceptions: (1) species in open vegetation had not significantly larger range sizes than species occurring in closed vegetation (Table 1, Figure 3b), and (2) a model in which plant growth form was included fitted equally well as a model excluding growth form (Table 1, Figure 4a). The model including growth form showed a tendency for species with a climbing growth form to have larger range sizes than trees or species with other (understorey) growth forms (Table 1, Table S3b, Figure 4a).

Within the Atlantic Forest, analyses of AOO (Table 1, Table S4, Figures 2c,d and 3c) or EOO (Table 1, Table S5, Figures 2g,h, 3d, and 4b) range size generally yielded similar results to the models measuring range size across South America. There were two exceptions: dispersal syndrome by itself did not have a significant effect on range size within the Atlantic Forest, only in interaction with seed length, and only for EOO (Table 1, Figure 2g,h); and (2) we detected a stronger and significant effect of the climbing growth form on EOO compared to the analysis at the South American extent (estimate=0.39, SE=0.2, t -value=1.93, p =.05, Table 1, Figure 4b).

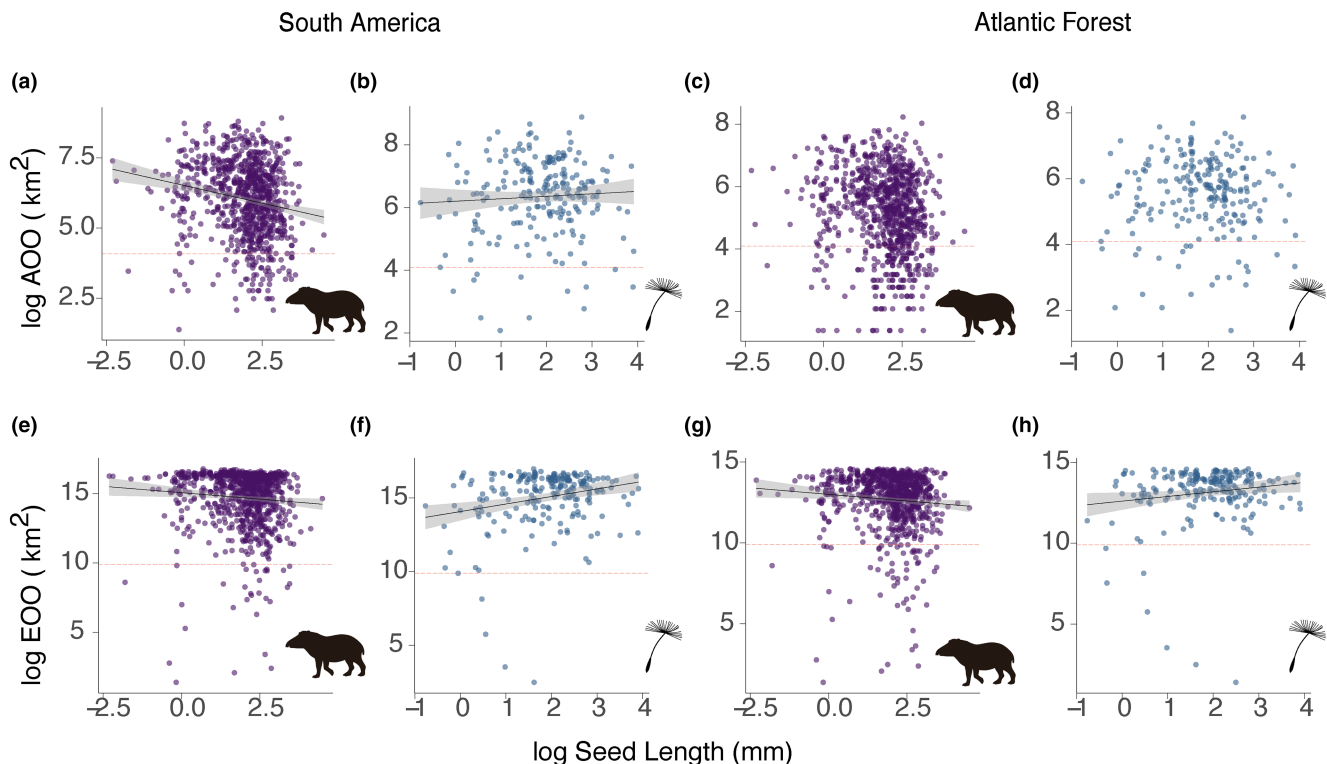


FIGURE 2 The effect of seed length and dispersal syndrome on geographical range size variation in the Atlantic Forest flora. Each dot is a species, including a total of 1052 Atlantic Forest plant species. Regression lines (black) were inferred using phylogenetic generalised least squares (PGLS) regression models, and only shown when a significant relationship was detected. The shaded areas show the standard error around the estimate. Purple dots represent species dispersed by animals, and blue dots represent species dispersed by abiotic mechanisms. Red dashed lines are the values estimated by IUCN as a threshold for extinction vulnerability (together with fragmentation or range size fluctuation, below dashed line: EOO < 20,000 km², AOO < 2000 km²) under Criterion B. Range size was calculated at the South America extent (a, b, e, f) or at the Atlantic Forest extent (c, d, g, h). AOO, area of occupancy; EOO, extent of occurrence.

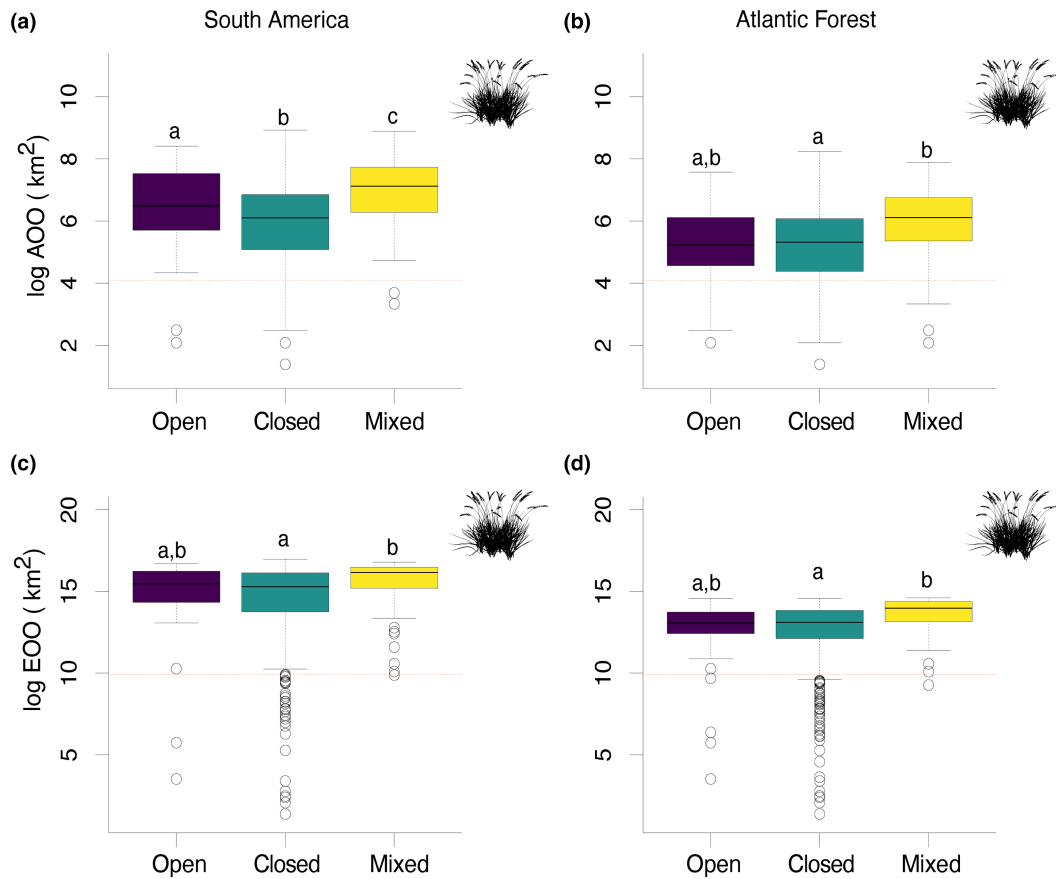


FIGURE 3 The effect of vegetation type on geographical range size variation in the Atlantic Forest flora. Data included 1052 Atlantic Forest species. Plots display range size variation for species occupying different vegetation types, with significance inferred using phylogenetic generalised least squares (PGLS) regression models. Bars with the same letter at the top are not significantly different. Box-and-whiskers indicate median and quartiles (first and third), with 95% limits of range size, and outliers are represented by dots. Red dashed lines are the values estimated by IUCN as a threshold for extinction vulnerability under Criterion B (below dashed line: EOO < 20,000 km², AOO < 2000 km²). Range size was calculated at the South America extent (a, c) or the Atlantic Forest extent (b, d). AOO, area of occupancy; EOO, extent of occurrence.

3.2 | Sensitivity analysis

Our sensitivity analysis showed that when the number of species with animal-mediated dispersal was equal to the number of species with abiotic dispersal (217 species), all explanatory variables that were significant in the full model (that included all species with animal-mediated dispersal), remained statistically significant with similar estimates and *p*-values of predictors on range sizes as in the full model, in at least 95% of the subsets (Figure S4). This analysis shows that the unbalanced occurrence of dispersal syndromes in the Atlantic Forest did not affect model inferences.

3.3 | Extinction risk and dispersal syndrome

From the Atlantic Forest species list (14,771 species), only 2603 species (15%) were assessed for extinction risk by the IUCN Red List, and 29% were categorised as threatened (CR, EN, NT, or VU). In contrast, only 6.4% species (68 out of 1052 species) were considered threatened based on range size-based inferences with the

“ConR” R package (Dauby et al., 2017), suggesting that we under-sampled threatened species in our dataset. However, for the subset of species with extinction risk reported by IUCN (65%, i.e., 679 out of 1052 species), the “ConR” package matched the same extinction threat status for 90.2% of species, thus based on range size inferences only (Fisher’s exact test, *p* < .05). For 7.4% species, the function underestimated the threat category, whereas for 2.4% species, it overestimated the threat category (Figure S5). These results demonstrate that range size estimates based on AOO and EOO can effectively predict extinction threat for a substantial proportion of Atlantic Forest species, by using range size estimates from occurrence records.

We did not find a difference in extinction risk (threatened or non-threatened) for species dispersed by animals versus abiotic mechanisms (Fisher’s exact test, *p* > .05). Indeed, similar proportions of threatened (57 animal-mediated vs. 11 abiotic) and non-threatened (778 animal-mediated vs. 206 abiotic) species are dispersed by animals. This suggests that dispersal syndrome by itself probably does not explain variation in extinction risk of the Atlantic Forest flora.

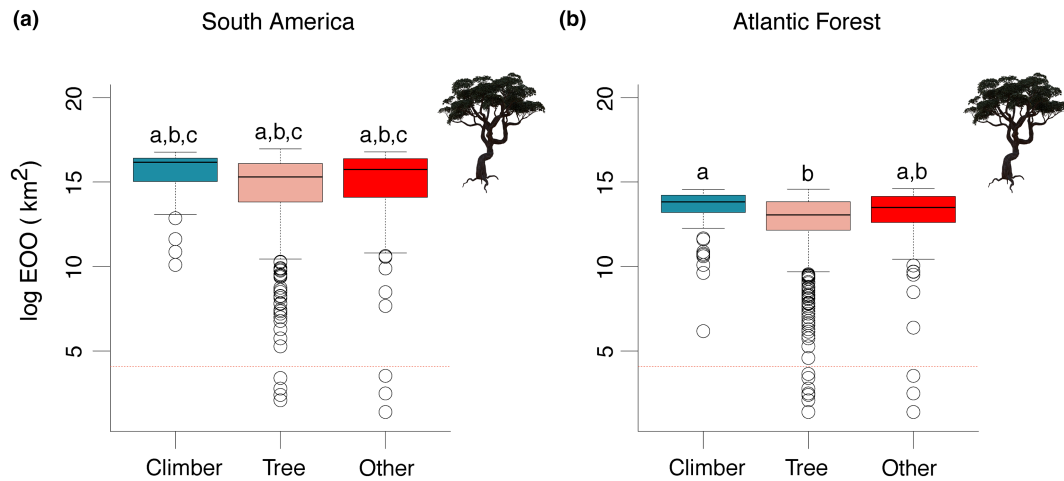


FIGURE 4 The effect of growth form on geographical range size variation in the Atlantic Forest flora. Data included 1052 Atlantic Forest species. Plots display range size variation for species with different growth forms, with significance inferred using phylogenetic generalised least squares (PGLS) regression models. Bars with the same letter at the top are not significantly different. Box-and-whiskers indicate median and quartiles (first and third), with 95% limits of range size, and outliers are represented by dots. Red dashed lines are the values estimated by IUCN as a threshold for extinction vulnerability under Criterion B (below dashed line: $EOO < 20,000 \text{ km}^2$). Range size was calculated at the South America extent (a) or the Atlantic Forest extent (b). EOO, extent of occurrence.

4 | DISCUSSION

We analysed the relationship between dispersal-related traits and geographical range size for 1052 Atlantic Forest angiosperm species. We show that up to 11% of the variation in species range size is explained by dispersal-related traits of the species (Table 1). Specifically, we found smaller range sizes for species with abiotic dispersal, large-seeded species with animal-mediated dispersal (Figure 2), or species with a distribution restricted to closed (forest) vegetation types (Figure 3), compared to species with, respectively, animal-mediated dispersal, smaller seed lengths, and a distribution in open or mixed vegetation. Furthermore, species with climbing growth forms (i.e., lianas) had larger range sizes than trees, but this was only supported when considering extent of occurrence (EOO) within the Atlantic Forest (Figure 4b). These results suggest that large-seeded plant species with animal-mediated dispersal, that often rely on large-bodied frugivores for seed dispersal, may suffer from dispersal limitation, leading to smaller ranges than species dispersed by smaller bodied animals. Possibly, this is the result of past and ongoing defaunation of large-bodied frugivorous vertebrates. Finally, we found that species with animal-mediated and abiotic dispersal syndromes were similarly threatened with extinction.

4.1 | Frugivory-related traits determine species range sizes in the Atlantic Forest

We show that seed size and dispersal syndrome explain variation in geographical range size of native Atlantic Forest plant species – both in South America and within the Atlantic Forest. Dispersal is a complex process that involves departure, transfer, and establishment of

individuals across space (Alzate & Onstein, 2022). Evidently, traits that facilitate dispersal across these stages are often associated with range size, as shown for body size in animals (but not for all taxonomic groups), larvae type in fishes, and height and diaspore size in plants (Alzate et al., 2019; Alzate & Onstein, 2022; Sheth et al., 2020; Thomson et al., 2011).

We found that animal-mediated dispersal may lead to larger range sizes than dispersal by abiotic mechanisms, but this relationship was modulated by seed size. It is well recognised that animal-mediated dispersal is a successful and effective dispersal strategy in the Atlantic Forest (Almeida-Neto et al., 2008; Pozetti et al., 2001), explaining the overall large ranges of plants with animal-mediated dispersal. However, successful dispersal and range expansions rely on the availability and abundance of suitable frugivores. Given the anthropogenic decimation of many Atlantic Forest vertebrate populations, especially large-bodied frugivores (Bogoni et al., 2018; Marques et al., 2021), dispersal limitation may have led to range contractions in large-seeded compared to small-seeded plants with animal-mediated dispersal (Figure 2). This contrasts with historical scenarios in which large-seeded fruits were probably predominantly dispersed by wide-ranging large-bodied frugivores that frequently moved across long distances (Pires et al., 2018; Whitmee & Orme, 2013), thereby increasing connectivity, gene flow, and range sizes of large-seeded plants (Doughty et al., 2016; Onstein et al., 2017). Our findings are consistent with previous studies that illustrate how the extinction of frugivorous animals in the Atlantic Forest has led to mutualism disruptions (Lamperty & Brosi, 2022) and dispersal limitation (Markl et al., 2012). Furthermore, we add to the growing evidence that the extinction of large-bodied frugivores has had far-reaching cascading effects on seed dispersal, plant survival, and range size (Donoso et al., 2020; Doughty et al., 2016; Galetti et al., 2018; Onstein et al., 2018). Importantly,

large-bodied frugivores in the Atlantic Forest may not find suitable habitat under future climate change scenarios, thus posing further threats to plant–frugivore ecological networks (Sales et al., 2021). Alternatively, dispersal rates and range sizes of large-seeded plants that rely on animal-mediated dispersal may be lower than for small-seeded plants, regardless of defaunation. For example, small seeds may benefit from frequent interactions with small-bodied frugivorous birds that increase seed dispersal effectiveness (Godínez-Alvarez et al., 2020).

Increased extinction of animals in South America has happened since the Late Miocene, with increased extinction rates since the Late Pleistocene. Theoretical models predict that the Late Pleistocene extinction of most megafauna in the Neotropics has led to a range contraction of 31% for plant species with fruits and seeds that were formerly dispersed by such animals (Doughty et al., 2016). The fact that 78% of the species in our dataset depend on animals for dispersal, and 10% of those have seeds >2cm, suggests that the ongoing loss of frugivores may have detrimental effects on seed dispersal and survival of large-seeded Atlantic Forest plants (Onstein et al., 2018). Loss of large-seeded tropical plants may further influence ecosystem structure, such as community composition and forest structure, and ecosystem functions, such as carbon storage (Bello et al., 2015; Brancalion et al., 2018; Culot et al., 2017; Doughty et al., 2016). Nevertheless, large-seeded plants with animal-mediated dispersal may be able to adapt to the extinction of their large-bodied interaction partners by evolving smaller seeds (Galetti et al., 2013), or by establishing interactions with secondary dispersers (e.g., agoutis, livestock, or humans (Guimarães et al., 2008; Méndez et al., 2023). Whether plant populations will be able to keep up with the pace of frugivore extinctions, in the Atlantic Forest and elsewhere, remains to be seen (Lim et al., 2020).

4.2 | Vegetation type and growth form effects on geographical range size

Besides dispersal-related traits, there are other variables that explain variation in geographical range size across Atlantic Forest plants. For example, we found that plants occurring in mixed open and closed vegetation had larger ranges than species restricted in their distribution to forest or open vegetation types (Figure 3). This suggests that habitat ‘generality’ may be an important feature that allows for large range sizes, and thus reduced extinction risk (Devictor et al., 2008). Several vegetation type specialist species, mostly endemic to the Atlantic Forest, experience loss of habitat, while generalist species are better equipped to cope with the effects of changing environments by shifting their distribution, and thus persist in ecosystems (Arroyo-Rodríguez et al., 2013; Büchi & Vuilleumier, 2014). Losing specialist species – either those specialised on dispersal by large-bodied frugivores, or endemics specialised to certain vegetation types – leads to homogenisation of plant communities and their functions, and thus loss of biodiversity (Clavel et al., 2011; Fricke & Svenning, 2020; Ibarra & Martin, 2015). Furthermore, large range

sizes of open or mixed vegetation type species may have been facilitated by abiotic dispersal syndromes (Table S6), because forests could reduce dispersal distances in species with abiotic dispersal, while such species probably efficiently disperse and spread in open vegetation types.

We also found that climbers had larger ranges than trees in the Atlantic Forest (Figure 4b). This is consistent with previous studies that illustrated that lianas are increasing their abundance and range size in tropical and subtropical forests (Leão et al., 2014; Schnitzer & Bongers, 2011), possibly because of high colonisation rates in disturbed and hunted areas (Schnitzer & Bongers, 2011). This feature becomes particularly advantageous in highly degraded, fragmented landscapes, such as the Atlantic Forest. Large trees may also be particularly threatened by selective logging and deforestation, leading to local extinctions and range contraction, and a general loss of Atlantic Forest biodiversity and biomass (de Lima et al., 2020).

Variables not directly sampled in our study, such as historical factors related to phylogeny and diversification rates, may further affect range size variation in the Atlantic Forest (Alzate et al., 2023; Alzate & Onstein, 2022). For example, lineages with high diversification rates tend to have smaller range sizes in the Atlantic Forest because (allopatric) speciation is expected to lead to descending species with smaller ranges (Leão et al., 2020). Many traits may affect diversification rates (Onstein, 2020) and hence range size, such as breeding system, floral traits, polyploidy, fruit size, and growth form, thus providing future avenues to study the direct and indirect drivers of range size variation.

4.3 | Threat in the Atlantic Forest flora

Animal-mediated dispersal was not associated with higher extinction threat across the Atlantic Forest flora, but IUCN suggests that a minimum of 29% of plants are currently vulnerable to, endangered or critically endangered with extinction. However, this figure is likely much higher (de Lima et al., 2024), especially when accounting for threats such as deforestation and selective logging. The Atlantic Forest is a biodiversity hotspot, requiring conservation prioritisation (Myers et al., 2000) to avoid losing biodiversity and associated ecosystem functions. Deforestation, intense land-use, and climate change are among the major threats. Species adapted to resource-limited environments (e.g., rocky outcrops or scrub vegetation on sandy coastal plains) or those with an epiphytic growth form may have high extinction risk (Leão et al., 2014), and our results suggest that large-seeded species with animal-mediated dispersal may be increasingly entering the threat status as well, given ongoing defaunation rates (Bogoni et al., 2018).

5 | CONCLUSION

We demonstrate that dispersal-related traits are important drivers of plant range size. Our results are consistent with the hypothesis that

the extinction of large-bodied frugivores leads to dispersal limitation and hence range contractions of their large-seeded food plants, which may ultimately lead to co-extinction (Onstein et al., 2018). Furthermore, our results shed new light on how biotic interactions (here animal-mediated seed dispersal) influence plant distribution in tropical ecosystems. We argue that automated extinction risk assessments across tropical floras or keystone lineages (Bellot et al., 2022), combined with the assembly of comprehensive dispersal-related trait data, will improve our understanding of trait-dependent extinctions and the ecological and evolutionary consequences of those (Bello et al., 2015; Galetti et al., 2013; Méndez et al., 2022).

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All data, including phylogeny, species-level dispersal-related trait data, range sizes, and extinction risk assessments, are available from Dryad: <https://doi.org/10.5061/dryad.2fqz612wm>. Supporting information including supplementary tables and figures can be found in the online version of this article.

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BIOSKETCH

Isis Petrocelli is interested in the evolution and biogeography of plant functional traits, particularly those related to frugivory and seed dispersal. She worked on this study during her MSC thesis at the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig under the supervision of Renske Onstein and Adriana Alzate. She currently carries out her PhD thesis on functional island biogeography at the University of Göttingen.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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