

Climate change reshapes the eco-evolutionary dynamics of a Neotropical seed dispersal system

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Abstract

Aim: Global changes will redistribute biodiversity, reshaping ecological interactions and ecosystem processes. The decoupling in the distribution of plants and their mutualistic seed dispersers, for instance, may have overlooked eco-evolutionary effects. How animal-dispersed plants will respond to changes in the distribution of their seed dispersers remains largely an open question. Here, we forecast the consequences of climate change and frugivory interactions for the spatial distribution and seed size evolution of a Neotropical palm species.

Location: Atlantic forests of South America.

Time period: Present day, end of 21st century.

Major taxa studied: Thirty-two species of frugivorous birds, and a palm (*Euterpe edulis*).

Methods: Future patterns of animal–plant co-occurrence were derived from ecological niche models, climate forecasts, projections of future forest loss, and seed dispersal simulations. We further explored the evolutionary effect of the spatial reorganization of interactions by modelling palm seed sizes as a function of changes in the distribution of frugivore traits.

Results: Our models indicate that future climate change and deforestation may reduce the palm’s suitable distribution by 20%–50%. However, our simulations suggest that 66% of all remaining future suitable distribution (76,200 km²) would still be inaccessible to the palm without the active dispersal of seeds by frugivores. In addition, novel frugivore communities are projected to have smaller mean body mass and gape size (–23% and –10%, respectively), due to the loss of large frugivores, which may translate into a 6%–17% reduction of seed sizes across the palm’s remaining distribution.

Main conclusions: Our projections indicate that frugivore seed dispersal may be critical to allow occupancy of future habitat by animal-dispersed plants. However, loss of large frugivores may affect trait selection regimes, creating hotspots of plant evolution towards smaller seeds. We argue that such complex dynamics emerging from species-specific responses to global change may reshape the distribution and evolution of several interacting partners worldwide.

KEYWORDS

defaunation, dispersal simulation, downsizing effect, ecological niche models, forest loss, interaction networks, novel communities, mutualism

1 | INTRODUCTION

The dispersal of plants' seeds by frugivores is a key biotic interaction, especially in the tropics, where up to 90% of the woody plants rely on animals to disperse their seeds (Howe & Smallwood, 1982). Under climate change, animal-mediated seed dispersal may be critical to allow plants to track their future suitable climates (González-Varo et al., 2017), because plants may only track changing climates if seeds are successfully

moved towards newly available habitats (Corlett & Westcott, 2013) (Figure 1a,b). Some researchers have estimated that plants may need to move as fast as 10 km/year to keep pace with climate change in the tropical lowlands (Feeley et al., 2020; Loarie et al., 2009). Such long-distance dispersal events in fleshy-fruited plants are typically performed by large-bodied frugivores (Nathan et al., 2008; Peres et al., 2016), which face local extinctions and population declines across the globe, mostly due to habitat loss and hunting (Dirzo et al., 2014; Redford, 1992).

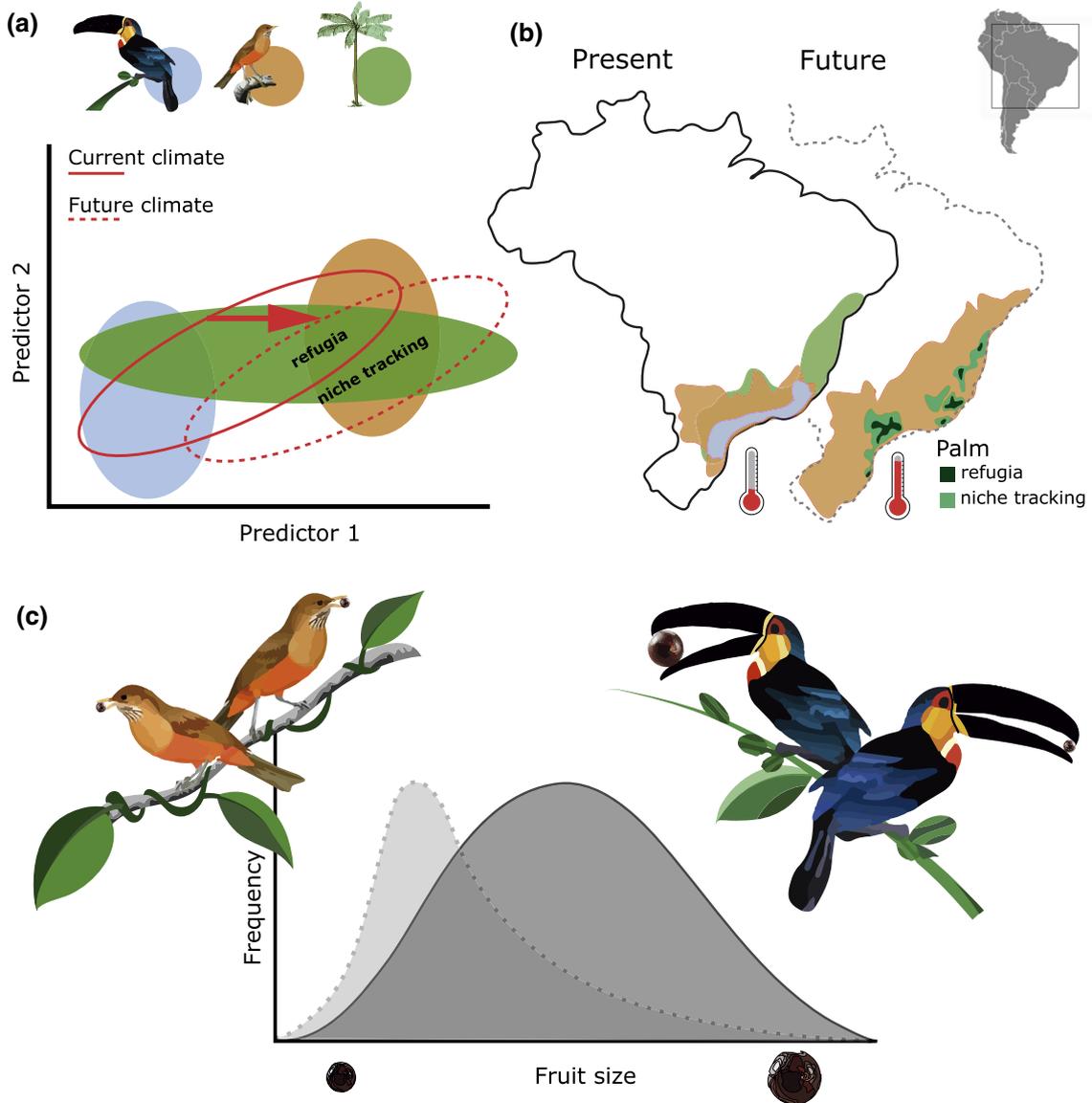


FIGURE 1 Conceptual model on how climate change will affect the distribution and trait evolution of animal-dispersed plants. (a) Climate niche space of two frugivores (blue, orange) and one plant (green) depicted as ellipsoids along two climate axes, with red-lined ellipsoids representing climatic conditions in the study area at the present (solid) versus the future (dashed). (b) The current and future climate defines the potential co-occurrence of the plant and its two seed dispersers in geographic space. Dark green represents climate refugia of the plant (i.e. climatically suitable areas in the present that remain suitable in the future), while pale green indicates climatically suitable regions in the future that are only accessible via frugivore seed dispersal (niche tracking). (c) The composition of novel frugivore assemblages may affect the evolution of plant traits such as fruit and seed sizes because the gape size of avian dispersers imposes limits to the sizes of fruits and seeds that may be consumed and dispersed. The loss of large-bodied frugivores such as toucans, which can feed on both small and large fruits (illustrated by the dark grey frequency distribution of consumed fruit sizes), results in a truncated distribution of dispersed seed sizes because small-bodied frugivores such as thrushes can only ingest seeds below a certain size (illustrated by the light grey frequency distribution of consumed fruit sizes)

The loss of large-bodied frugivores triggers cascading effects, with consequences for ecosystem functions and services (Enquist et al., 2020; Pérez-Méndez et al., 2016). Smaller-bodied frugivores often feed on smaller fruits and seeds, failing to disperse seeds above certain sizes (Galetti et al., 2013). Because of this size-specific constraint, the dispersal of seeds of a given size depends on the remaining frugivore community and the morphological traits (e.g. gape size) that are represented among seed dispersers (Figure 1c). Climate itself will possibly pose new natural selection regimes (Nadeau & Urban, 2019; Siepielski et al., 2017). However, climate-driven changes in the composition of ecological communities may also affect evolutionary processes, once biotic interactions impose selective forces on interacting species (Medeiros et al., 2018). Hence, these novel communities may affect evolutionary pressures and re-shape adaptive landscapes locally (Medeiros et al., 2018).

Although extensive empirical work suggests that the loss of large-bodied frugivores alters local selection regimes in seed dispersal interactions (Emer et al., 2019; Peres et al., 2016; Pérez-Méndez et al., 2015, 2016), we lack a large-scale perspective on how the spatial re-organization of species and their interactions can affect their evolutionary trajectories. Here, we combine empirical data on seed dispersal of a Neotropical palm with ecological niche modelling, cellular automata dispersal simulations, and a model of trait evolution to forecast how novel frugivore communities may affect the fate of animal-dispersed plants under climate change. We focus on the seed dispersal interactions of the palm *Euterpe edulis* in the Brazilian Atlantic forest, one of the few tropical systems for which species' life-history attributes (Rodrigues et al., 2019), geographic distributions (Hasui et al., 2018), plant population genetics (Carvalho et al., 2016; Galetti et al., 2013), and frugivory interactions (Bello

et al., 2017) are well known. Galetti et al. (2013) have shown that defaunation, besides hindering seed dispersal, alters the local evolutionary dynamics of seed size in *E. edulis*, favouring small seeds in those sites that have lost large seed dispersers. To understand the possible implications of such responses geographically we ask (a) to what extent climate-driven movements of seed dispersers may facilitate the response of animal-dispersed plants to climate change and deforestation, and (b) how the redistribution of seed dispersal interactions and the formation of novel frugivore communities may affect seed size evolution of plants.

2 | MATERIALS AND METHODS

2.1 | Study area and species

To understand how the redistribution of seed dispersal interactions under climate change and deforestation may affect eco-evolutionary patterns, we focused on one of the most extensively studied seed dispersal systems in the Neotropics, formed by the palm *Euterpe edulis* and its frugivorous seed dispersers (Bello et al., 2017; Galetti et al., 2013; Pizo et al., 2006). This species used to be hyper-dominant in the Atlantic Forest yet has been depleted from all but the largest forest remnants, due to the illegal harvesting of the palm's edible meristem (Galetti & Fernandez, 2002). The round fleshy fruits produced by this palm range from 8.3 to 14.1 mm in diameter (Pizo et al., 2006) and are consumed by at least 78 frugivores (Galetti et al., 2013). Here, we consider the 32 bird species (Figure 2, Supporting Information Figures S2, S3) that are known to act as legitimate seed dispersers, that is, regurgitating or defaecating

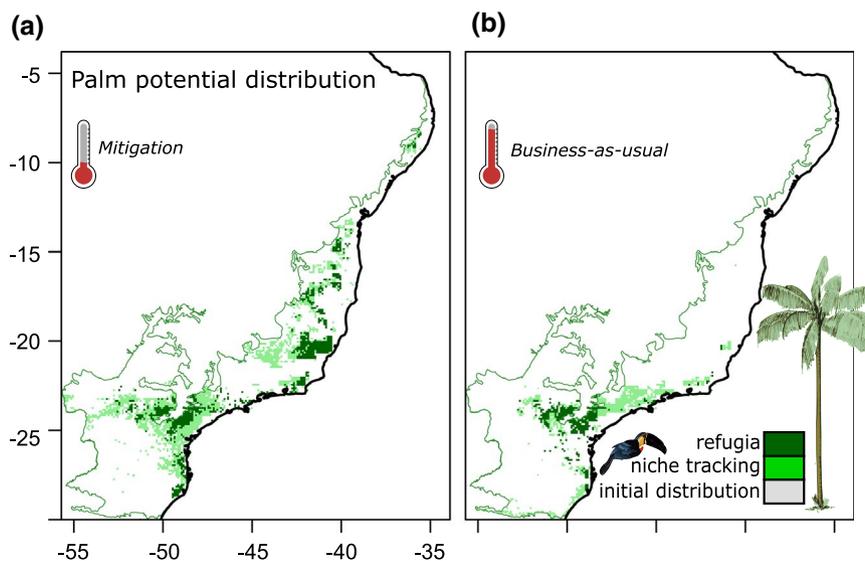


FIGURE 2 Potential distribution of the Neotropical palm *Euterpe edulis* in the present (grey) and under future climate and forest loss given two seed dispersal scenarios (green). Dark green colours ('refugia') indicate the potential future distribution of the palm under climate change, forest loss and passive dispersal, that is, forested areas that are climatically suitable in the future and that may be reached without animal-mediated seed dispersal. Pale green ('niche tracking') refers to forest areas that are climatically suitable for the palm in the future, but only accessible via animal-mediated seed dispersal through at least one of the frugivorous birds. Forecasts of climate change and forest loss are based on a (a) mitigation and a (b) business-as-usual scenario

the seeds of *E. edulis* away from the parent tree, and which have been shown to affect the evolution of seed size in this palm species (Galetti et al., 2013). Interactions with these avian frugivores account for 87% of all seed-dispersal interactions of this palm (Bello et al., 2017). These bird species encompass large-gaped frugivores that feed on a wide array of seed sizes, such as cotingas (Cotingidae), toucans and toucanets (Ramphastidae), and guans (Cracidae), with a mean gape size of 30 mm (Galetti et al., 2013; Rodrigues et al., 2019), but also small- to medium-sized birds such as thrushes (Turdidae), with gape sizes up to 12 mm (Galetti et al., 2013; Rodrigues et al., 2019) (Supporting Information Figure S2).

2.2 | Frugivore community redistribution

We modelled the future redistribution of the palm *E. edulis* and its frugivore community from species-specific distributional data, taken from diverse datasets of Neotropical frugivore distributions (sources provided in Supporting Information, *Methods* section, subsection *Species occurrence*). Occurrences were thoroughly checked and had their completeness and reliability quality-checked. After data cleaning, we ended up with a total of 14,531 records, with an average of 435 ± 267 occurrences per frugivore species (Supporting Information Table S1). The thrush *Turdus rufiventris* was the species with the largest number of records (1,146 records) and the guan *Crax blumenbachii* was the species with the fewest records (42 records). The clean dataset of *E. edulis* comprised 575 occurrence records (all occurrences are given in Supporting Information Data S2).

We established the relationship between occurrences and environmental conditions using ensembles of ecological niche models (ENMs; Araújo et al., 2019) and by projecting realized niches into environmental forecasts (Peterson et al., 2018) (Supporting Information Figure S1a–f). The ENMs were calibrated and evaluated using present-day occurrences of species, modelled as a function of gridded cell-based information of climate (Fick & Hijmans, 2017) and edaphic features (palm models only; Hengl et al., 2017) (predictor used for each species are given in Supporting Information Table S3). Following the relevant standards (Araújo et al., 2019), we used four commonly used methods, namely random forests (RF; Breiman, 2001), boosted regression trees (BRT; Friedman, 2001), bioclim (Busby, 1991) and MaxLike (Royle et al., 2012), implemented in the *sdm* R package (Naimi & Araújo, 2016; R Core Team, 2020). Details on model parameterization can be found in Supporting Information, section *Ecological niche models*, in file named Data S1.

Future climate forecasts were based on the fifth Intergovernmental Panel on Climate Change (IPCC) assessment using five climate models (CESM1-BGC, MPI-ESM-MR, MIROC5, IPSL-CM5A-MR, INMCM4) that represent uncertainty in future climate projections. For each climate model, we considered two extreme scenarios of climate change, obtained as representative concentration pathways, or expectations of greenhouse gas emissions from anthropogenic actions. We considered the representative concentration pathway *rcp45* as an 'optimistic' *Mitigation* scenario where

emission rates are expected to slow by the year 2030, and the *rcp85* as a 'pessimistic' or baseline *Business-as-usual* scenario, according to historical trends of emission rates without additional future efforts to constrain emissions (IPCC, 2014).

Although climate is a strong driver of species distribution, other non-climatic landscape features affect species survival in human-dominated sites. Here, we simulated the effect of thresholds of forest loss on the persistence and movement of frugivorous birds, using ecological information from multiple sources (del Hoyo et al., 2015; IUCN, 2019; Stotz et al., 1996; Vale et al., 2018). To simulate species persistence in fragmented landscapes (Supporting Information Figure S1g–k), we superimposed species-specific thresholds of forest cover (Melo et al., 2018) onto climate suitability surfaces. Cells with unfavourable climate conditions and/or cells with less than the minimum forest cover required for species persistence were both attributed as 'unsuitable'. By doing so, our definition of a 'suitable' cell includes not only climate but also landscape attributes known to affect species persistence at human-dominated sites. Accessibility to such suitable areas (suitable climate and minimum forest cover) was then modelled as the probability of colonization given the landscape matrix and dispersal constraints (Boeing et al., 2018) (details in Supporting Information, file Data S1, sections *Forest loss thresholds* and *Dispersal-restricted potential distribution of frugivores*).

2.3 | Seed dispersal and occupancy of future climate analogues

We simulated the effects of frugivore seed dispersal on the distribution of the palm using a cellular automata dispersal model (Engler & Guisan, 2009; Engler et al., 2012). To investigate the effect of seed dispersal on forecasts of the palm distribution, we compared scenarios of palm occupancy in the absence of frugivores – *passive dispersal*, to the dispersal of palm seeds by animals – *frugivore-based dispersal*. We assume that under passive seed dispersal at the local scale there is no dispersal at the geographic scale. For both the palm and the frugivores, occupancy of a target cell in this model at time $t + 1$ depends on its environmental suitability (projected climate suitability and forest cover thresholds), the distance from a source cell at time t (as a function of species-specific dispersal kernels), and the structure of the surrounding landscape (reflected as barriers to dispersal) (Engler & Guisan, 2009; Engler et al., 2012). Colonization of suitable environments by the palm was allowed if (a) environmental conditions became suitable for the palm and the frugivore, and (b) the target cell was within reach of a potential source cell, given the dispersal ability of the frugivore. This process was repeated considering pairwise palm–frugivore interactions of the 32 frugivore species and the palm. Barrier cells (e.g. non-forest habitats) were incorporated to simulate species-specific landscape resistance to animal dispersal, as the frugivore is assumed to be the movement agent for palm seed dispersal events (see section *Palm seed dispersal scenarios* in Supporting Information, file Data S1).

2.4 | Seed size evolution

Defaunation has been shown to affect the evolution of seed size of *E. edulis* by selecting against large seeds where large-gaped frugivores are absent (Galetti et al., 2013). We investigate the potential change in the evolutionary pressures across the distribution of the palm as a result of the emerging patterns of co-occurrence in the novel (future) assemblages. Because selection acts by constraining the maximum size of dispersed seeds, we use a model of trait evolution in response to selection (Galetti et al., 2013), in which selection acts upon the maximum seed size:

$$Z_{t+1} = Z_t + h^2 (P_f - Z_t) \quad (1)$$

In this model, the trait value resulting from selection, Z_{t+1} , is a function of the maximum seed size ingested by a frugivore (P_f), the current maximum seed size (Z_t), and seed size heritability (h^2). Empirical data on ingested seed size were only available for a subset of frugivores ($n = 7$), so we used a phylogenetic imputation method (Molina-Venegas et al., 2018) to infer maximum ingested seed sizes (P_f) for the remaining species (Supporting Information, section *Evolution of seed size*, file Data S1). To model the spatial variation in the palm's evolutionary response to trait changes in future frugivore assemblages, we compute P_f as the average considering all frugivores projected to occur in each cell. Because small-bodied thrushes (e.g. *Turdus albicollis*) cannot ingest large seeds (> 12 mm), their presence favours selection towards small seeds (Galetti et al., 2013). That effect could, however, be counterbalanced by the presence of large frugivores, such as toucans and toucanets (e.g. *Ramphastos dicolorus* and *Pteroglossus bailloni*), which are able feed on a wider array of seed sizes. Besides seed-dispersal interactions, the evolution of seed size may be affected by environmental factors and other types of interactions such as seed predation. Instead of modelling actual changes in seed size we use this simple model to examine the potential changes in the selection pressure specifically related to seed dispersal. Therefore, we project the difference between Z_{t+1} and Z_t for each grid cell across the geographic distribution of *E. edulis* to obtain a spatial projection of the potential of change in seed size over the simulated time.

3 | RESULTS

3.1 | Novel frugivore assemblages

Our projections indicate that most frugivores (ranging from small-bodied thrushes over medium-sized toucans to large-bodied guans; see Supporting Information Figure S2 and Table S1) may experience reductions of their potential distribution in the future (Supporting Information Table S1). Considering climate change only, nearly 70% of the studied frugivore species (22 out of 32) are expected to lose $> 25\%$ of climatically suitable area by the year 2090, compared to their current range size (Supporting Information Table S2). On average, frugivores were expected to lose $16 \pm 9\%$ climatically suitable area

by the year 2090 using climate-only projections. Adding the effects of deforestation (i.e. future tree cover loss) and dispersal limitation (i.e. movements constrained by landscape barriers) reduced frugivore distributions by more than half (i.e. on average $55 \pm 4\%$), with two high-altitude species (the red-billed curassow and the black-and-gold cotinga) becoming regionally extinct by having no climate analogues in the future given a business-as-usual scenario (Supporting Information Table S3). Only four frugivore species (9%) would show range expansions. Some narrowly distributed species, such as *Lipaugus ater*, are forecasted to lose all suitable distribution in the future.

The future response to climate change and deforestation will further depend on species traits related to dispersal ability and habitat specialization. Frugivores that are large-bodied (> 400 g) forest specialists – such as some toucans (Ramphastidae) and guans (Cracidae) – are known to be vulnerable to habitat loss and fragmentation. For these species, our projections indicate that their potential distribution could contract greatly by losing on average $80 \pm 14\%$ of their distribution in the future (Δ Potential distribution_{climate change only} = $-61 \pm 17\%$; Δ Potential distribution_{climate change and forest loss} = $-86 \pm 12\%$). In contrast, small-to-medium sized (< 400 g) habitat generalists such as certain thrushes (Turdidae) and flycatchers (Tyrannidae) usually thrive well in human-modified landscapes. Four species within the latter group were projected to expand their distributions on average by $10 \pm 7\%$ under business-as-usual and mitigation scenarios of climate change and forest loss.

Our projections allow spatially explicit forecasts of the redistribution and novel composition of frugivore assemblages. Including climate change and forest loss under a business-as-usual scenario, lowland regions (< 500 m above sea level) of the Atlantic Forest are projected to host a smaller richness of frugivore species in the future (Supporting Information Figure S4), losing up to 20 species by the year 2090 (Δ Richness_{lowlands} = -6 ± 6 species). In contrast, some high-altitude coastal areas (> 1000 m above sea level) may gain up to 10 new species, although species richness is projected to decline on average (Δ Richness_{highlands} = -4 ± 4 species). Future projected frugivore assemblages represent a subset of the original trait composition across the Atlantic Forest. In continental lowland areas, the projections indicate a decrease of up to 150 g in the average body mass of future frugivore assemblages (Δ Body_{lowlands} = $-23 \pm 56\%$) and a decrease in mean gape size of up to 10 mm (Δ Gape_{lowlands} = $-10 \pm 15\%$). Some high-altitude assemblages may gain up to 200 g body mass and 10 mm gape size, but the average body size of frugivore assemblages is projected to generally decline in the highlands (Δ Gape_{highlands} = $-7 \pm 9\%$; Δ Body_{highlands} = $-7 \pm 61\%$). These changes in the trait composition of frugivore assemblages would lead to an overall reduction in the functional roles of seed dispersers, especially in the lowlands.

3.2 | Future redistribution of the palm

We then evaluated how future changes in climate and forest cover could influence the distribution of the palm *E. edulis* (Figure 2).

Currently, nearly 42% of the original Atlantic Forest territory hosts suitable climatic and edaphic conditions for *E. edulis* (Potential distribution $_{Present} = 584,900 \text{ km}^2$). However, future climate change and deforestation are projected to reduce this area by an average of $20 \pm 4\%$ in a mitigation climate change scenario (Potential distribution $_{Mitigation\ mean} = 284,200 \pm 11,368 \text{ km}^2$) and by nearly $50 \pm 3\%$ in a business-as-usual scenario (Potential distribution $_{B.A.U.} = 116,700 \pm 3,501 \text{ km}^2$). Without frugivores, the potential future distribution of the palm would shrink to only 3%–6% of the whole area of the Atlantic Forest (passive dispersal: Potential distribution $_{Mitigation} = 89,700 \pm 1,794 \text{ km}^2$; Potential distribution $_{B.A.U.} = 39,800 \pm 796 \text{ km}^2$). However, modelling the future distribution of the palm while considering seed dispersal via frugivores suggests that most suitable environment would become accessible (frugivore-based dispersal: Potential distribution $_{Mitigation} = 282,000 \pm 9,870 \text{ km}^2$; Potential distribution $_{B.A.U.} = 116,000 \pm 2,668 \text{ km}^2$). Hence, animal-mediated seed dispersal would allow occupancy of an additional area of at least $76,200 \text{ km}^2$ that would be otherwise inaccessible to the palm.

3.3 | Seed size evolution

The model of trait evolution, which we used here to simulate seed size variation over time and space in response to selective pressures posed by novel frugivore assemblages, indicates increased selection towards a reduction of maximum seed size ($\Delta Z_{mean} = -0.89 \pm 0.33 \text{ mm}$; Supporting Information Table S4) across the geographic range of *E. edulis* (Figure 2). The potential for selection towards smaller seed sizes would be stronger in the lowlands, which are more likely to lose several large-gaped frugivore species. Our estimates suggest that the expected reduction in seed size in the lowlands could be up to four times greater than that expected in high-altitude populations, thus creating new geographic mosaics of selective regimes for future palm populations (Figure 3).

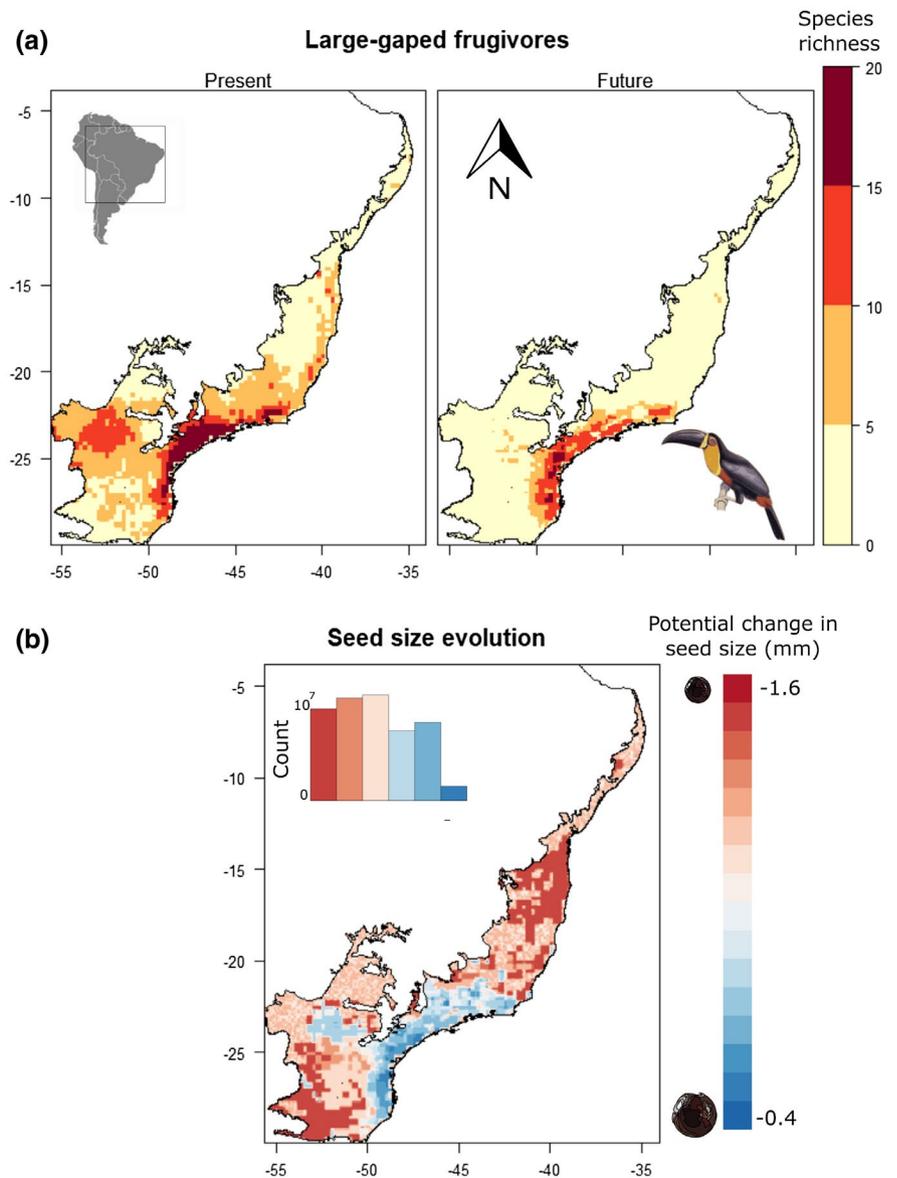
4 | DISCUSSION

Our study projects the potential consequences of climate change and forest loss for the future distribution and seed size evolution of a Neotropical palm. These projections show that while the geographic range size of the palm is expected to shrink under future global change scenarios, climate-driven migrations of frugivores may allow the palm to occupy remaining suitable areas that would be otherwise inaccessible. However, the redistribution of bird seed dispersers would result in novel frugivore assemblages that differ in their trait composition, especially due to reductions in body size and gape width as a consequence of the loss of large-bodied frugivores that depend on forests. We show these changes could result in a new geographic mosaic of size-selective pressures for the seed size evolution of this palm, leading to an overall reduction of palm seed size. Such effects will, however, be stronger in the lowlands, where large-gaped frugivores are forecasted to be lost.

According to our projections, the distribution of large-bodied forest-specialist frugivores such as certain toucans (Ramphastidae) and guans (Cracidae) will likely be constrained to large high-altitude forest remnants. With global warming, many species are expected to move towards cooler zones, such as higher elevations (Colwell et al., 2008; Lawler et al., 2013), especially in the tropics (Sales et al., 2017, 2019, Sales, Ribeiro, et al., 2020). Our projected rates of change in frugivore assemblages are also the greatest in the highlands, suggesting range contractions of frugivores that are adapted to high altitudes and cooler climates and upslope movement of warm-adapted frugivores from the lowlands. The loss of large-bodied forest specialists in the lowlands of the Atlantic Forest is paralleled by the spread of small-bodied generalists with wide climatic and habitat niches. Remaining lowland frugivore assemblages are, therefore, projected to become homogenized and dominated by small-bodied, ecological generalists that may tolerate landscape fragmentation. Climate-driven biotic homogenization via range contractions of specialists and range expansions of generalists has also been shown for plants in the Atlantic Forest (Zwiener et al., 2018) and elsewhere (Savage & Vellend, 2015), and for fish communities (Magurran et al., 2015). Such novel communities exhibit a dominance of generalist interactions, with low trait diversity (Blois et al., 2013; Savage & Vellend, 2015), in a pattern similar to our projections of future frugivore assemblages in the Atlantic Forest.

The loss of large-bodied frugivores reduces the frequency of long-distance dispersal events (Donoso et al., 2017) and impairs seedling recruitment (Pérez-Méndez et al., 2016), affecting plant persistence at the local and regional scale. Here, we show that the loss of seed dispersal interactions may also significantly impair the potential of the palm to track climate change at a geographic scale, especially in combination with forest loss and fragmentation. Our simulations suggest that the colonization of remaining habitats may be conditional on the presence of frugivores and seed dispersal interactions. In the absence of frugivore-based seed dispersal, the future distribution of the palm could be restricted to less than 10% of its current range size. Because plants are sessile, gene flow is highly dependent on both seed dispersal and pollination. Seed dispersal interactions would alleviate the impact of anthropogenic stressors on plant populations, allowing plants to track the geographic projection of their niches through the colonization of newly suitable environments (Johnson et al., 2019; La Sorte & Jetz, 2012; Thomas, 2010; Tingley et al., 2009). The extent to which seed dispersal will be necessary for plant populations to track changing climates in other regions is still poorly known and a missing piece in most forecasts of future plant distributions. Our projections suggest that most of the future seed dispersal services will probably be performed by widely distributed small-bodied frugivores that are resilient to changes in climate and landscape structure. This loss of large-bodied frugivores may reduce long-distance seed dispersal effectiveness (Mokany et al., 2015; Nathan et al., 2008) and hamper the ecosystem functions provided by current frugivore communities (Sales, Culot, et al., 2020; Sales, Rodrigues, et al., 2020).

FIGURE 3 Potential change in selection pressure on seed size of the Neotropical palm *Euterpe edulis* as a function of the redistribution of frugivores. (a) Projections of current and future species richness of large-gaped frugivores (i.e. species with gape sizes > 12 mm) for the years 2010 and 2090 (under a business-as-usual scenario), respectively. Dark red colours indicate high species richness. (b) Projected potential for evolutionary change towards smaller seeds due to the loss of large-gaped seed dispersers. The colour gradient represents the potential for a reduction in palm seed sizes in response to selection. The inset histogram shows the frequency distribution of grid cells according to bins of seed size change



The extirpation of large-gaped frugivores capable of dispersing large seeds, largely because of poaching and fragmentation, has been shown to favour evolution towards smaller seed sizes locally (Galetti et al., 2013). Our projected changes in the composition of frugivore assemblages suggest this phenomenon may spread across the palm's distribution range in response to climate change and deforestation. These novel spatial patterns in the evolution of the seed size of this palm would lead to hotspots of selection that favour small seeds in areas that are dominated by small-bodied frugivores. The prevailing scenario would be similar to those currently found in degraded landscapes: a meta-network of forest remnants embedded in a human-dominated matrix, connected by generalist small-bodied frugivores that disperse small seeds via short-distance movements (Emer et al., 2018). Highland zones may, therefore, emerge as evolutionary 'coldspots' in which suitable climate, habitat availability, and persistence of large-bodied frugivores are combined, providing refugia for large-seeded palm populations.

The forecasted directional selection towards smaller seeds could be partially counteracted by other large seed dispersers

not considered here, such as mammals. However, previous work has shown that birds act more frequently than mammals as seed dispersers of *E. edulis* (Galetti et al., 2013). Moreover, field studies have shown that secondary dispersal by mammals such as rodents (da Silva & dos Reis, 2019) or ungulates (Keuroghlian & Eaton, 2009) often results in damaged seeds. Trophic rewiring, or the establishment of novel interactions among species with no prior history of co-occurrence, could compensate the loss of original partners. However, *E. edulis* already interacts with most Atlantic Forest frugivores, so that a compensation of such a magnitude would probably depend on interactions with species from different pools. The recently documented 'faunal savannization' of tropical rain forests (Sales, Galetti, et al., 2020), in which savanna-dwelling species are expected to move inwards degraded forests, may diversify species pools. According to this hypothesis, large-gaped frugivores typical of more open habitat, such as *Ramphastos toco* and *Penelope superciliosus*, could replace their rain forest counterparts.

Smaller seeds are more likely to be dispersed by a wide range of frugivores than larger seeds, but size-related selection might also impact plant population viability (Pérez-Méndez et al., 2016). The recalcitrant seeds of *E. edulis* are prone to desiccation, with smaller seeds being less resistant to drought than larger seeds (Galetti & Fernandez, 2002; Galetti et al., 2013). This relationship between seed size and desiccation may, thus, create a feedback of vulnerability to climate change since climate change forecasts for South America indicate warmer and drier conditions (IPCC, 2019), likely to expose plant populations to enhanced evapotranspiration. Moreover, smaller seeds further result in diminished seedlings in terms of shoot and root biomass, which are less vigorous and less likely to reach adulthood (Pizo et al., 2006). Seed size reduction is, therefore, expected to reduce mean population fitness in this palm (Galetti et al., 2013). The forecasted vulnerability of the seeds of *E. edulis* to future climate is, however, yet to be tested empirically. Finally, we caution that our results are contingent on model assumptions and limited by the availability of ecological information about species and their environment, in addition to the data that we used to calibrate models and to generate the simulations. Although the evolutionary reduction in seed size is documented, the empirical validation of the projected gradients of seed sizes across the entire Atlantic Forest is yet to be performed.

4.1 | Conclusion

Over the past decade, a large body of work has accumulated on how future climate and land use change may affect biodiversity, but species interactions and evolutionary consequences of these novel communities have rarely been included in forecasts of biodiversity change. Here, we use one of the most thoroughly studied tropical seed dispersal systems to show that dispersal and movements of frugivores may be essential to allow climate niche tracking of animal-dispersed plants. Moreover, trait changes in the composition of frugivore assemblages may result in new geographic mosaics of selective pressures, with consequences for plant trait evolution, population fitness, and ecological resilience. Incorporating these ecological and evolutionary consequences of climate change and novel interaction partners into forecasts across space and time will provide fundamental insights into ecological functions and ecosystem processes that are relevant for the conservation and restoration of biodiversity in human-modified landscapes.

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CONFLICT OF INTEREST

Authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

LS, WDK, MG and MP conceived and designed this study; LS and BN performed ecological niche modelling; LS, WDK and MP drafted the manuscript. All authors provided input, approved the final version of this manuscript, and agree to be accountable for all aspects of the work.

DATA AVAILABILITY STATEMENT

The climate data used in this work can be downloaded at Data Distribution Centre of the Intergovernmental Panel on Climate Change and in WorldClim. Tree cover loss forecasts are available at <http://futureclimates.conservations.org>. High-resolution raster files with species-specific maps used in this work, are available at Dryad (<https://doi.org/10.5061/dryad.612jm642s>). An example R code is available as Supporting Information (Data S1), as well as all occurrence records (Data S2).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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