Climate niche mismatch and the collapse of primate seed dispersal services in the Amazon

Lilian Sales[a,*], Laurence Culot[b], Mathias M. Pires[a]

[a] *Laboratório de Estrutura e Dinâmica da Diversidade (LEDDiv), Departamento de Biologia Animal, Instituto de Biologia, Universidade Estadual de Campinas - UNICAMP, Campinas, São Paulo, Brazil*
[b] *Laboratório de Primatologia, Departamento de Biodiversidade, Universidade Estadual Paulista - UNESP, Rio Claro, São Paulo, Brazil*

ARTICLE INFO

ABSTRACT

Animal-plant interactions are threatened by ongoing climate change, deforestation, and defaunation. The disruption of biotic interactions leads to loss of ecosystem services but estimates of the magnitude of reductions are rarely available. Using a seed disperser primate community in the Amazon as study case, we forecast the magnitude of seed dispersal services to be lost as function of the future redistribution of species. In the most likely scenario, our projections indicate average contractions of 56% (23 to 100% reduction) on the suitable areas for the studied primates. As result, we found billions of seeds of a model tree (*Manilkara bidentata*) might fail to be dispersed by this primate community on each fruiting season. Primate contribution to seed dispersal was, however, uneven among species, highlighting the endangered large-bodied woolly monkey *Lagothrix cana* as a keystone disperser. That species alone was responsible for about 64% of all *Manilkara* seeds dispersed in the present and up to 71% in the future. Niche mismatch will, however, lead to 37% of the future plant distribution not being able to host its second top disperser (the tufted capuchin *Sapajus apella*), exacerbating losses on potential seed dispersal. Our projections indicate that seed dispersal in tropical forests might be hampered by global changes, even if defaunation by poaching is controlled. The forecasted magnitude of loss in seed dispersal services is alarming and may have been overlooked in conservation assessments. In a similar manner, niche mismatch and disruption of biotic interactions will likely impair ecosystems functions and resilience worldwide.

1. Introduction

Climate is changing at accelerated rates, threatening not only biodiversity but the ecosystem services that species are involved with. The magnitude of observed and forecasted changes is comparable to the most expressive global transformations in the past 65 million years (Diffenbaugh and Field, 2013; Kemp et al., 2015). As novel climates arise, species will either be extinct, adapt, or migrate towards newly suitable environments (Urban, 2015). Species ranges move once populations at leading edges colonize environments as they become suitable, while those at the rear edge fail to persist (Hampe, 2011). However, colonization of suitable environment depends on species dispersal abilities (Schloss et al., 2012) and the existence of permeable dispersal routes across landscapes (Lawler et al., 2013). Yet, many of these passageways have already or are projected to be disrupted by land use change (Sales et al., 2019). The relocation of species ranges can form novel biotic communities, allowing new interactions to arise (Post, 2013), but disrupting key relationships among species (Thomas and Ohlemüller, 2010).

Seed dispersal is an essential animal-plant interaction, especially in the Neotropics, where at least 75% of plants disperse their seeds via frugivore consumption (Howe and Smallwood, 1982). Frugivore-based seed dispersal is a dynamic interaction between plants and animals, usually with benefits for both groups: plants get their offspring dispersed, often increasing seedling establishment and viability, while animals obtain food (Chapman, 1995; Howe and Smallwood, 1982; Jordano, 2000). Climate-induced changes in the distribution and abundance of animal seed-dispersers may reduce the seed dispersal services they provide (Mokany et al., 2014) and are likely to weaken existing mutualisms involving plants (Tylianakis et al., 2008). In addition, plants are sessile organisms, for which seed dispersal may be the only mechanism to track their suitable habitats on changing climates (Hampe, 2011). In this way, niche tracking via animal-mediated dispersal may be necessary for plants to colonize novel suitable environments otherwise inaccessible (González-Varo et al., 2017).

Primates are remarkable seed dispersers, comprising up to 40% of

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* Corresponding author.
  E-mail address: lilianpsales@gmail.com (L. Sales).

frugivore biomass in tropical forests (Chapman, 1995). Primate seed dispersal affects plant population genetics, demography and community assembly in forested ecosystems (Andresen et al., 2018). In the Amazon, for example, defaunation of large-bodied primates reduces tree species richness by 55% (Nuñez-Iturri and Howe, 2007), due to a dispersal vacuum in the seedling recruitment of primate-dispersed trees (Levi and Peres, 2013). Yet, primates are especially vulnerable to climate change for inhabiting environmental conditions close to the upper thermal physiological limits (Dillon et al., 2010; Huey et al., 2012). Adaptive evolution towards warmer climates does not happen often among lineages (Araújo et al., 2013), so that small temperature increases can pose deleterious stress on primate populations (Clee et al., 2015). Furthermore, the Neotropical platyrrhine primates are mostly dependent on closed-canopy forests to feed, reproduce and to move (Mittermeier et al., 2013), so their ability to disperse across open habitat is limited (Schloss et al., 2012), reducing their potential to track suitable habitats in fragmented and human-dominated landscapes (Sales et al., 2019).

In this work, we project the synergistic effects of climate change, deforestation and dispersal limitation on the seed-dispersal services provided by Amazon primates. To do so, we combined ecological niche models with dispersal simulations accounting for natural and anthropogenic geographical barriers that might constrain primate movement. Then, we assessed the magnitude of changes in the potential amount of seeds dispersed by primates. We consider forecasts of shifts on distribution and co-occurrence between a plant and its frugivore primate community, in addition to values of potential per-capita seed dispersal (from Levi and Peres, 2013). This integrative approach rendered conservative but alarming projections showing that the ecosystem function of seed dispersal is threatened by disruption of biotic interactions, due to climate change and deforestation.

2. Methods

2.1. Seed dispersal quantification

To calculate the magnitude of the effect of climate change and deforestation on the seed dispersal services provided by Amazon primates, we build upon a previous work, using a unique study system for which daily per-capita seed dispersal data is available (from Levi and Peres, 2013). The seed dispersal system, formed by the fleshy-fruited Sapotaceae tree *Manilkara bidentata* [hereafter referred to solely as *Manilkara*] and a frugivore community of sympatric primates, was extensively studied in a non-defaunated *terra firme* forest landscape in the Amazonas State, Brazil. Levi and Peres (2013) estimated the primate dispersal of the *Manilkara* small-to-medium sized globose fruits (21.6 ± 4.3 mm), each typically containing a single seed (15.5 ± 3.2 mm), which are super-abundant during the wet season. They also showed that the manipulation by frugivore primates and the passage through their digestive tract ("endozoochory") cleans the seeds, prevents rotting and increases seedling recruitment. Seed cleaning was the only tested factor that significantly affected (and increased) seedling recruitment; the other tested factors were dispersal distance and seed predation by vertebrates. Therefore, these results suggest that seed dispersal is the most important factor determining seedling recruitment and survivorship of this plant population.

Potential seed dispersal was calculated for the large-bodied woolly monkey *Lagothrix cana*, a locally abundant primate species. Based on the stomach content of four adults and one sub-adult individuals of L. *cana* killed by hunters, Levi and Peres (2013) calculated the mean number of seeds and seed mass per digesta. The daily total seed dispersal was then estimated assuming that 1) L. *cana* performs three daily feeding bouts during the *Manilkara* fruiting season, and 2) one third of the satiation-point stomach capacity of individuals is allocated to *Manilkara* fruits during each feeding bout. These assumptions are considered a good proxy of the L. *cana* feeding habits (Peres, 1996). From

relationships of allometric body mass scaling and previous knowledge on species-specific feeding ecology, Levi and Peres (2013) obtained estimates for nine other primate species found to consume *Manilkara* and identified and censused in the area (*Ateles chamek*, *Cebus albifrons*, *Cheracebus torquatus*, *Pithecia albicans*, *Plecturocebus cupreus*, *Saguinus fuscicollis*, *Saguinus mystax*, *Saimiri ustus*, *Sapajus apella*). Basically, the seed dispersal estimate for each primate species was considered to be the ratio of body mass to that of *L. cana* multiplied by the number of species-specific daily feeding bouts, divided by the proportion of stomach capacity allocated to *Manilkara* seeds, multiplied by the total amount of seeds available in one L. *cana* digesta (Levi and Peres, 2013). The species *Alouatta seniculus* was reported to disperse *Manilkara* seeds but was not present in the study area so was not considered in this study.

To estimate the number of seeds potentially dispersed by each species per km², Levi and Peres (2013) established the relationship between primate abundance and per-capita seed dispersal rates. Mean abundance of each primate species was estimated using line-transects conducted by a team of trained observers, following standard guidelines for survey of medium to large-bodied mammals in the Amazon (Peres and Cunha, 2011). By doing so, the number of seeds potentially dispersed by each species per km² every day of the 24-day fruiting season of this *Sapotaceae* tree was estimated. Here, we use those estimates as the basis to project changes in seed dispersal services across space and into the future. We focus on the same set of primate species and project their potential to contribute to seed dispersal within their current and projected ranges.

Population densities were not used here to model distribution, yet the potential to disperse seeds depends on the densities of primate populations. Estimating population densities across species ranges is, however, fraught with uncertainties, especially in under-sampled regions with major data gaps such as the Amazon (Vale and Jenkins, 2012). Thus, instead of trying to estimate density variation across space, we assume a homogeneous population density across the species distribution and perform a series of sensitivity analysis varying these abundances. We conducted simulations with low and high densities, establishing a range of possible values of total seed dispersal services those primates potentially provide currently and in the future. To do so, we varied the estimates of population density from zero to twice the values obtained locally by Levi and Peres (2013). These values are within the range of relative changes observed on population abundances of mammal communities in the Amazon under low and high levels of hunting pressure (Peres and Palacios, 2007). In addition, we caution that our estimates should not be taken at face value, as we are more interested in understanding whether seed dispersal is projected to decrease or increase, as well as the magnitude of such variation, while climate change and deforestation advance in the Amazon (Escobar, 2019).

2.2. Seed dispersal scenarios

Co-occurrence precedes biotic interactions. Therefore, to estimate the amount of *Manilkara* seeds that could potentially be dispersed by primates, we limited the area of potential seed dispersal to cells of shared suitability for both the plant and each frugivore (Fig. S1). Therefore, we first restrict our analysis to the potential seed dispersal services these primates provide for the *Manilkara* plant species only. However, our modelling offers a baseline estimate for the loss of seed dispersal services across the whole primates' geographic ranges. We consider two seed dispersal scenarios: i) the total amount of seeds of this plant that may be dispersed by the frugivore primates studied here, with a focus on *co-occurrence* and *niche mismatch*, and ii) the variation on *potential seed dispersal* of individual primate species, assuming per-capita dispersal values equivalent to those of the *Manilkara* across all the potential distribution of each primate. In the first approach, we focus on the specific values from the interaction between the fleshy-

fruited *Manilkara* plant and a subset of its frugivore primates, while the latter is targeted at the animal's perspective of provision of seed dispersal services.

2.3. Distribution data

Primates climatic preferences were assessed with polygons of extent of occurrence [henceforth *range maps*], from the International Union for the Conservation of Nature (IUCN – www.iucnredlist.org.com). At first, we converted such IUCN range maps into gridded files of 0.1° lat/long, in which locations within species extent of occurrence were considered "presumed presences". Environmental conditions from those locations were, then, sampled to establish species bioclimatic envelopes, using ecological niche models (ENMs, detailed in following Methods subsections). To avoid model overfitting from using an excessively large dataset to calibrate niche models, we selected random locations within each species polygons, proportionally to species current range size, following methods recently described (Sales et al., 2019). Species with large range sizes (> 1000 cells) had only 12.5% of their cells sampled. Species with range sizes varying from 501 to 1000 and from 101 to 500 cells had, respectively, 20% and 50% of their cells sampled. Finally, species with small range sizes (< 100 cells) had all their cells used for calibration of ecological niche models.

We acknowledge, however, that distribution data derived from range maps are not the ideal input to calibrate ecological niche models (Araújo et al., 2019). That is because these models attribute "presences" all over species ranges, which leads to higher levels of commission error (Lobo et al., 2010). Ideally, species' realized niche should be depicted from a comprehensive and non-autocorrelated dataset encompassing a detailed representation of bioclimatic envelopes, taken from confirmed on-ground presences and absences (Araújo et al., 2019). That scenario is far from the reality of Amazon primate data, once constraints on road transport, lack of funding for biodiversity field surveys (Vale and Jenkins, 2012), in addition to local extirpations due to defaunation (Dirzo et al., 2014; Levi and Peres, 2013) impose biases to distribution information. Had we chosen to assess the climatic preferences of Amazon primates from such under-sampled records could result in false relationships between habitat suitability and environmental predictors due to the sub-setting of realized niches (Peterson et al., 2018). These truncated bioclimatic envelopes underestimate biodiversity predictions (Faurby and Araújo, 2018) and overestimate the forecasted impacts of future environmental change (Lima-Ribeiro et al., 2017).

To estimate potential co-occurrence between frugivore primates and the Amazon fleshy-fruited plant *Manilkara*, we obtained occurrence records from the National Center for Flora Conservation (*Centro Nacional de Conservação da Flora* - in Portuguese, CNCFlora; cncflora.jbrj.gov.br), and complemented with occurrence records from the Global Biodiversity Information Facility (GBIF; www.gbif.org). Online databases were downloaded using the function *occ()* and then collapsed into the same string using the function *fixnames()*, both from the R package *spocc* (Scott et al., 2016). To minimize spatial autocorrelation, we further thinned occurrences < 0.5 km from each other, using the function *thin()* from the R package *spThin* (Aiello-Lammens et al., 2015). By doing so, we eliminated a few records to weaken the effect of clustered sampling, while simultaneously retaining sufficient information for modelling species distributions (Aiello-Lammens et al., 2015). No IUCN range map was yet available for this plant, but the remaining 365 records were here considered a sufficient representation of the plant distribution.

2.4. Climate data

Climate information was obtained as gridded raster files from the *WorldClim* online database, containing information referred to the present-day climate conditions, produced by interpolation of averaged data among years 1960–1990 from weather stations (www.worldclim.

org/version1, date of access: November 11th, 2019). Downloaded data was upscaled to the resolution of 0.1° lat/long, once interpolated data for the Amazon is mostly based on scarce satellite information, with uncertainty increasing in higher-resolution products (Hijmans et al., 2005). We solely downloaded the *bioclimatic variables*, which are derived from monthly temperature and rainfall values but converted into more biologically meaningful variables, such as annual trends, seasonality and/or extreme climatic events (Hijmans et al., 2005).

Future climate forecasts rely on projected trajectories of greenhouse gases emission rates from different expectations of human development (IPCC, 2014a). Such climate forecast models, therefore, provide information on surface air maximum temperature (tas_{max}), surface air minimum temperature (tas_{min}), and monthly precipitation (*pr*), according to different emission scenarios. Here, we considered two representative concentration pathways, namely *rcp45* and *rcp85*, to represent an "optimistic" *Mitigation* scenario where emission rates are expected to slow by year 2030, and a "pessimistic" or baseline *Business-as-usual* (*B.A.U*) scenario, according to historical trends of emission rates without additional future efforts to constrain emissions (IPCC, 2014b). We caution, however, that the latter has been experiencing a debate on the degree of "pessimism" it carries on (Hausfather and Peters, 2020).

Climate forecasts from the 5th Assessment Report of the International Panel on Climate Change are based on various types of climate models. These models rely on distinct sets of code with different initial parameters, yet global forecasts of temperature and precipitation are relatively similar (Sanderson et al., 2015). In addition, all models produce some spatially-structured bias on geographical or environmental space (Knutti et al., 2008). Here, we chose to include a single model, the HadGEM2-ES (HE) (Martin et al., 2011), known to produce the least-biased estimates of current temperature and precipitation for the Northern South America (Sierra et al., 2015). By doing so, our projections neglect the uncertainty that arises from multiple climate forecasts (Sales et al., 2017), yet takes into account the most reliable information for the region (Sierra et al., 2015).

To avoid collinearity and overfitting of ecological niche models, we reduced the dimensionality of bioclimate predictors with a Principal Component Analysis - PCA. Dominant patterns from the whole dataset are extracted in the PCA, thus summarizing predictors information into eigenvectors (Reimann et al., 2011). We selected the eigenvectors that included 95% of bioclimate information, using the *prcomp()* function of R package *stats* (R Core Team, 2019), thus not the original variables, to calibrate ecological niche models. Then, future climate forecasts were projected onto the basis coordinates (linear combination) of the PCA, the function *predict()* onto the *prcomp* object and the forecasted environmental values from the climate model, to respect the original eigenvectors rotation.

2.5. Ecological niche modelling

Species potential distribution was assessed by projecting realized climatic niches into environmental forecasts derived from climate (IPCC, 2014c) and deforestation scenarios (Soares-Filho et al., 2006), using ecological niche models (Araújo et al., 2019). To predict species potential distribution, we compared the relationship between environmental conditions from species' known distribution to the conditions along the full background using MaxEnt (Elith et al., 2011). This method is robust to the presence of a moderate level of positional error (Graham et al., 2008), with the advantage of balancing goodness-of-fit with model complexity, via "tuning" of model settings (Muscarella et al., 2014). We did so by analyzing different combinations of feature classes - L, LQ, H, LHQ, LQHP, LQHPT (L = linear, Q = quadratic, H = hinge, P = product, T = threshold) (Muscarella et al., 2014) and then comparing the resulting models. Akaike Information Criteria (Akaike, 1974) corrected for small sample sizes (*AICc*) is a presence-dependent continuous metric (Lawson et al., 2014) used here to

Table 1

Frugivore primate community, potential distribution and contribution to seed dispersal. Body mass and the amount of seeds dispersed per km² were obtained from Levi and Peres (2013), under a no-hunting pressure scenario, and are indicated with an asterisk. The dispersal-restricted potential distribution of primates and its co-occurrence with the fleshy-fruited tree *Manilkara bidentata* is also shown for the Present and Future (referred to year 2050, *Business-as-usual* scenario of climate change and deforestation).

| Species	Body mass (kg)*	Seeds dispersed per km²*	Potential distribution (km²)		Co-occurrence (km²)	
			Present	Future	Present	Future
Ateles chamek	7.22	4552.7	7.23E+05	6.96E+05	2.59E+05	2.49E+05
Cebus albifrons	2.16	2623.4	3.47E+05	1.90E+03	1.24E+05	8.00E+02
Cheracebus torquatus	0.96	119.3	2.02E+05	0.00E+00	7.22E+04	0.00E+00
Lagothrix cana	6.97	40662.4	5.54E+05	2.95E+05	1.99E+05	1.07E+05
Pithecia albicans	1.76	1199.2	5.42E+04	0.00E+00	1.96E+04	0.00E+00
Plecturocebus cupreus	0.84	104.6	5.38E+05	6.39E+04	1.93E+05	2.41E+04
Saguinus fuscicollis	0.31	642	1.04E+06	5.52E+05	3.72E+05	1.98E+05
Saguinus mystax	0.41	1187.1	4.64E+05	1.07E+05	1.68E+05	3.94E+04
Saimiri ustus	0.75	1134.7	2.03E+05	1.55E+04	7.29E+04	5.60E+03
Sapajus apella	2.33	4828.2	1.39E+06	9.72E+05	5.00E+05	3.49E+05
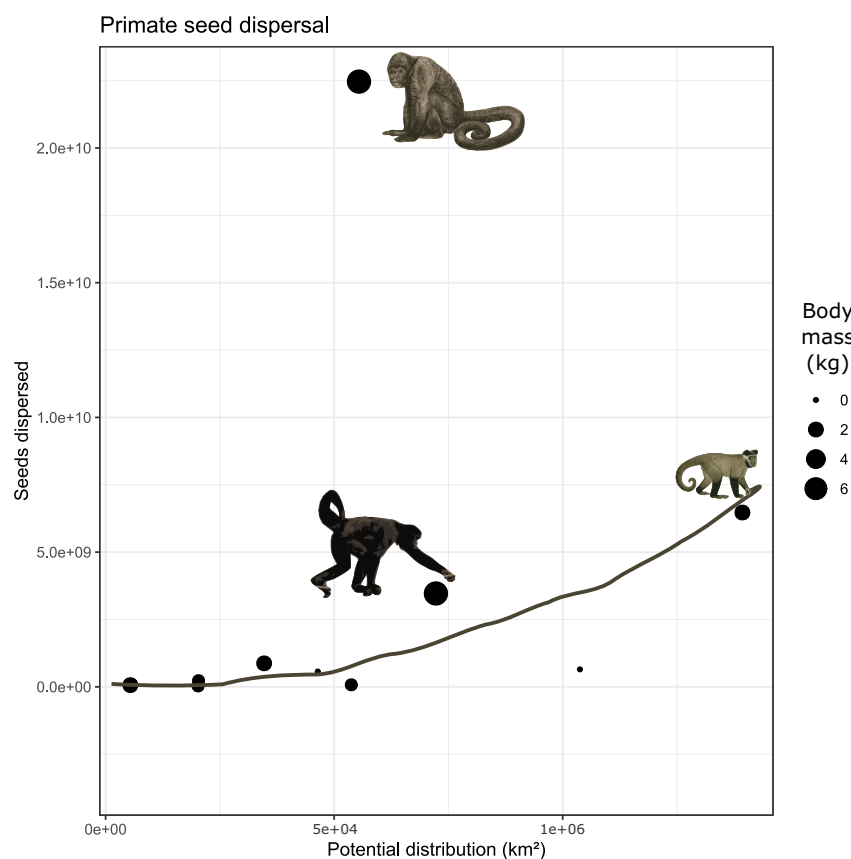
Fig. 1. Total seeds dispersed, current range size and body mass of 10 Amazon primate species. The total amount of seeds dispersed varied with range size and body mass, but the species *Lagothrix cana* (silhouette on top) has a disproportional contribution on seed dispersal services for the *Manilkara bidentata* tree. *Sapajus apella* and *Ateles chamek* (highlighted as mid-height and down silhouettes) are the second and third dispersers. From smallest to largest range sizes are: *Pithecia albicans*, *Cheracebus torquatus*, *Saimiri ustus*, *Cebus albifrons*, *Saguinus mystax*, *Plecturocebus cupreus*, *Lagothrix cana*, *Ateles chamek*, *Saguinus fuscicollis*, *Sapajus apella*.

compare among models and to select the model most supported by data. Resulting "tuned" models selected by *AICc* often exhibit less overfitting and lower omission rates than MaxEnt models under default parameters (Muscarella et al., 2014).

We limited species-specific study areas to accessible regions, a crucial step in distribution modelling (Barve et al., 2011). We did so by defining a bounding box of extreme latitude and longitude cells, plus additional 10° to each bound. This value is close to the maximum dispersal capacity for several Amazonian primates (Schloss et al., 2012). Then, we cropped environmental layers to match the study extent and sampled 10,000 background points from background extent gridded files (one per cell, without replacement) (Barbet-Massin et al., 2012). We used the "block" method to partition the environmental dataset due to its higher transferability across space or time (Muscarella et al.,

2014), to forecast the likely effects of climate change. Data was partitioned by the latitude and longitude grids, dividing environmental cells as equally as possible. These grids define bins, to which occurrences and background cells are attributed. Then, we ran *k* iterative models, with *k-1* bins for the train and the remaining for the test, and model evaluation metrics were summarized across the *k* iterations (Muscarella et al., 2014). To calculate potential distribution areas, continuous predictions of climate suitability were converted into binary maps of "suitable" and "unsuitable". To do so, we used the 10% omission rate threshold, which allows the models to mistake up to 10% of the suitable cells. Characterization of environment was, thus, restricted to the most common conditions across 90% of species' ranges. This simple and relatively less used threshold has the potential to reveal informative suitable areas for species with small numbers of occurrence records
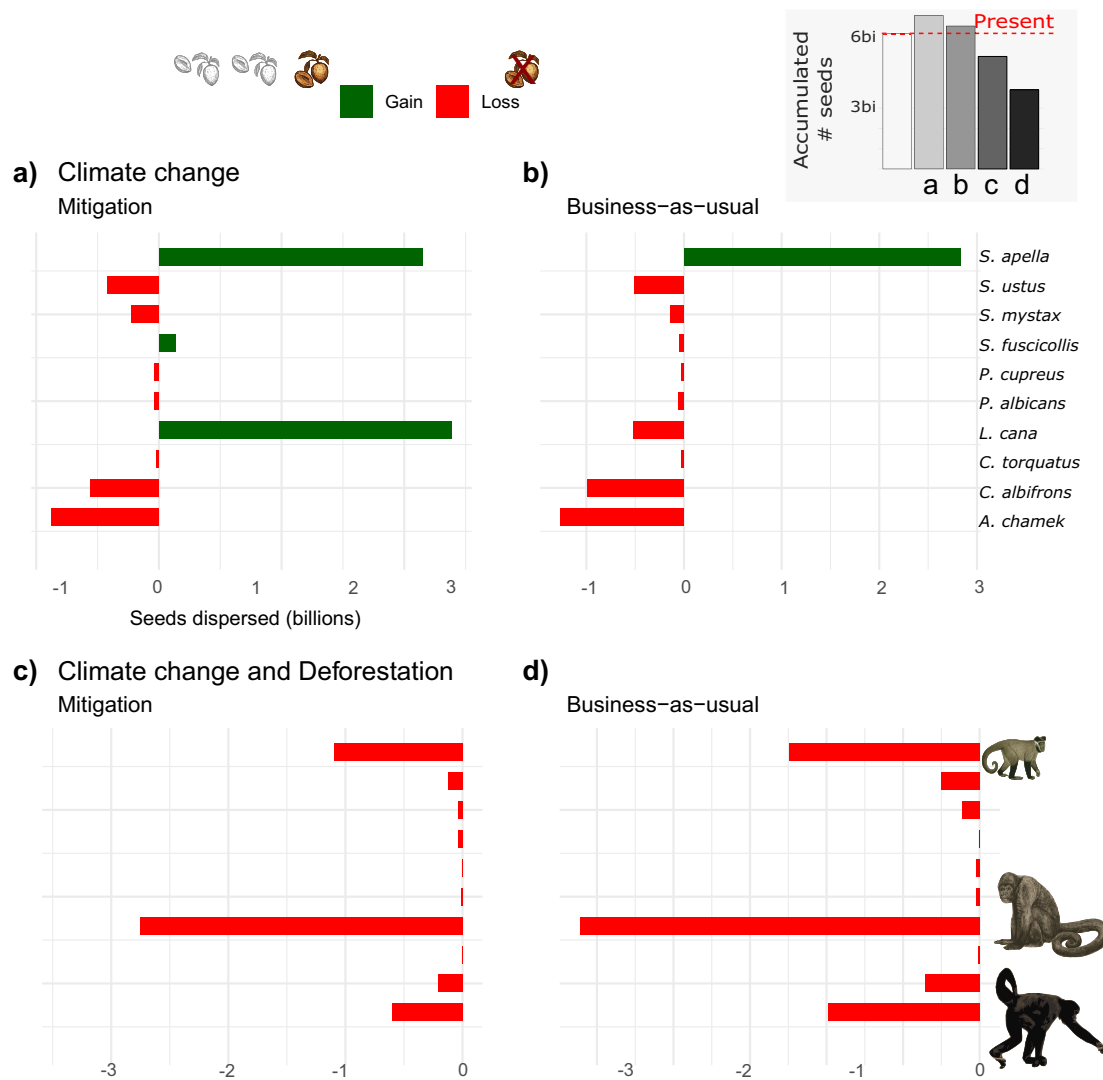
Fig. 2. Change in amount of seeds dispersed by 10 Amazonian primates, in the context of climate change and deforestation. Green bars indicate net increase while red bars represent losses on the potential number of seeds dispersed by each primate species, as function of forecasted changes on primate distribution. Upper panels (a, b) refer to Mitigation (*rcp4.5*) and Business-as-usual (*rcp8.5*) scenarios of climate change, while lower panels (c, d) include both climate change and deforestation. Silhouettes highlight the top-dispersers, namely *Ateles chamek, Lagothrix cana* and *Sapajus apella,* from bottom-up. The upper inset indicates the accumulated amount of seeds that could dispersed by this frugivore community, as function of the size of their potential distribution, where letters (a, b, c, d) refer to respective future scenarios. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Muscarella et al., 2014; Pearson et al., 2007).

2.6. Deforestation and dispersal limitation

Neotropical primates are mostly arboreal, depending on canopy trees to feed, reproduce and to move (Arroyo-Rodríguez and Fahrig, 2014; Pyritz et al., 2010; Sales et al., 2019). Deforestation and the consequent dispersal of closed-canopy tree cover, in addition to reducing and splitting primates habitat (Arroyo-Rodríguez et al., 2013), disrupts potential migratory routes across human-dominated landscapes (Gouveia et al., 2016; Sales et al., 2019). We included the effect of deforestation on primate habitat and dispersal, considering two scenarios from an empirically based, policy-sensitive land-use change model (Soares-Filho et al., 2006). The first deforestation scenario, *Business-as-usual*, considers that historical trajectories of Amazon forest conversion in the last decades will remain constant and that road paving agenda will be followed, while assuming a low compliance to Brazilian Forest Code at the time, without the creation of new protected areas (Soares-Filho et al., 2006). The second deforestation scenario,

Mitigation, establishes an upper limit for deforestation, assuming compliance to environmental law on agro-ecological zones of shared land-use, plus the expansion of the Brazilian Amazon network of protected areas.

We simulate primate dispersal across space using a cellular automata model where dispersal onto areas predicted to be deforested is restricted, thus preventing primate movement (Engler et al., 2012). In this simulation, an unsuitable cell in time t (target) could be colonized if environmental conditions became suitable in time $t + 1$ and if it was within reach of a suitable (source) cell. From the animal's perspective, the absence of trees may be a barrier to dispersal, especially in the case of forest-specialist species such as Neotropical primates. Cells predicted to be deforested were, therefore, considered permanently unsuitable. Contrary to regular unsuitable cells, barrier cells also prevent dispersal across them (Engler et al., 2012). In addition to deforestation, the main tributaries of the Amazon river (namely the rivers Javari, Jutaí, Juruá, Madeira, Purus, Coari, Napo, Putumayo, Negro, Jari, Paru and several medium-sized affluents) were also included as barrier cells. These dispersal constraints were applied to the maps of potential distribution
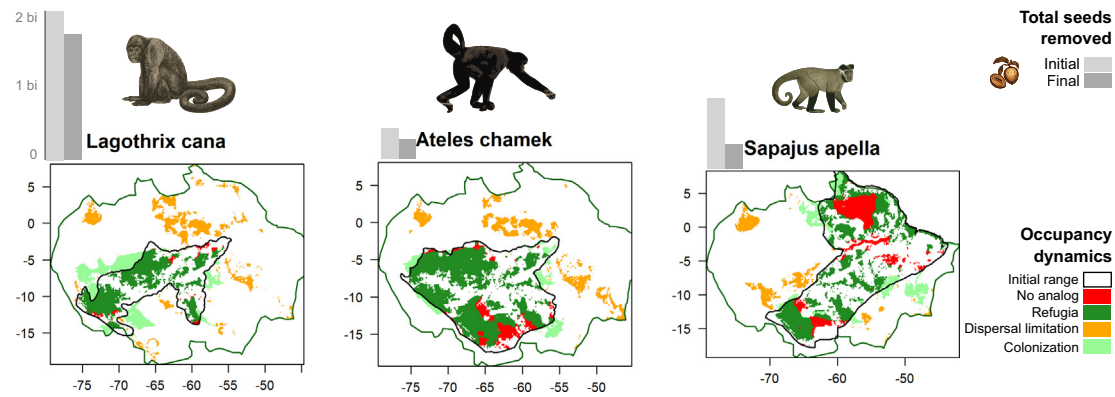
Fig. 3. Dispersal-restricted potential distribution and loss of seed dispersal services by the top-dispersers of the tree *Manilkara bidentata* in the Amazon. Grey bars reflect the proportional amount of seeds dispersed by each species at current (Initial) and future – year 2050 (Final) time periods, considering a B.A.U. scenario of climate change. Dark green cells indicate climate refugia (suitable cells in present and future), pale green shows potential migration (newly suitable cells accessible via dispersal), orange cells are for dispersal limitation (newly suitable cells inaccessible via dispersal) and red cells are non-analogs (cells that are suitable in the present but will become unsuitable in the future, thus exposing populations to non-analog climates). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

corresponding to every timestep, from present time (initial distribution) to future time (year 2050). The resulting raster files, thus, represent a *dispersal-restricted potential distribution*.

3. Results

3.1. Co-occurrence and niche mismatch

Using data on the daily amount of seeds dispersed per km^2 by each primate from a frugivore community, plus their projected co-occurrence with the fleshy-fruited plant *Manilkara bidentata*, we estimated the potential amount of seeds that could be dispersed by each primate across the plant range (Table 1, Supporting Tables S1 and S2). The tufted capuchin, *Sapajus apella*, exhibited the largest potential range overlap with *Manilkara*, sharing a suitable area close to 5×10^5 km^2, closely followed by the brown-mantled tamarin, *Saguinus fuscicollis*. However, in terms of potential seed dispersal, the woolly monkey *Lagothrix cana*, with an overlapping range 2.5 times smaller, was responsible for 64% of all the total estimate of seeds dispersed. The relative contribution of the woolly monkey L. *cana* on dispersal of *Manilkara* seeds was expected to expand in the future, either due to the increase in the number of co-occurrence cells (under no deforestation), or to the disruption of interaction with other dispersers (Supplementary Table S2). Conversely, *Sapajus apella* was expected to experience at least 30% reduction in the number of co-occurrence cells and in the amount of seeds it could disperse. The amount of co-occurrence cells lost by the pair *S. apella* – *Manilkara* was largely resulting from the plant distributional shift towards regions inaccessible by this primate (Supplementary Fig. S1).

Considering the total area of co-occurrence between the plant and its dispersers we estimate a total potential of 12.5 ± 1.75 billion seeds of *Manilkara* currently dispersed by the primates studied here. In the future, climate change could increase seed dispersal to 27.8 – 30.3 billion seeds, as result of newly suitable territory enabling co-occurrence between *Manilkara* and its frugivore community in 1.2 – 1.4 × 10^6 km^2, under *B.A.U.* and *Mitigation* expectations, respectively. However, synergism with deforestation, especially under a *B.A.U.* development scenario, may lead to average accumulated reductions of -8.3×10^5 km^2 on co-occurrence potential, resulting in 28 ± 14% total seed dispersal of *Manilkara* seeds. In absolute terms, we estimate that niche mismatch caused by climate change and deforestation could result in billions of *Manilkara* seeds (*Seed* $_{variation}$ $-3.49 \pm 1.7 \times 10^9$) not being dispersed by these frugivore primates in the future.

Although variation in population densities affected the total amount

of seeds dispersed (Fig. S2), the magnitude of losses was in the scale of billions of *Manilkara* seeds even for the smallest simulated densities. If population densities are half of those used in the baseline analyses, total seeds dispersed would be at the scale of 10^9, while if they are twice the values we used, total seeds dispersed reach 10^{11}. Relative changes were not affected by differences in the assumed population density, once variation is a function of suitable area (in terms of number of cells), while the amount is defined by area and cell-based population density.

3.2. Primate potential distribution and seed dispersal

We also examined how changes across the whole distribution of the frugivore primates could impact the individual contribution of primate species to their seed dispersal potential, assuming, for each primate, per-capita consumption rates equivalent to those calculated for the *Manilkara*. As expected, initial range size was positively related to the potential amount of seeds dispersed across the whole distribution of frugivore primates. Medium and large-bodied primates (*Lagothrix cana*, *Sapajus apella* and *Ateles chamek*) exhibited the largest potential distribution and, consequently, had greatest potential for seed dispersal. However, the woolly monkey *Lagothrix cana* still had a disproportional contribution (Fig. 1). Even though the potential distribution of this species was relatively large, occupying > 10^5 km^2, the amount of seeds it could potentially disperse was more than three times larger than the second-ranked species *Sapajus apella*, whose potential distribution was range twice as large as the former. Small-bodied species such as *Saguinus fuscicollis*, despite the large potential distribution (> 10^6 km^2), contributed to < 2% of the total seed amount, relative to other species. Among the studied species, *Lagothrix cana*, *Sapajus apella* and *Ateles chamek* alone could contribute up to 94% of the summed seed dispersal services, with potential to disperse at least 32 billion seeds (out of a total of 35 billion) across the Amazon (Fig. 2).

The synergism between climate change and deforestation will likely reduce the distribution potential of nearly all species, and the average seed dispersal services they might provide in nearly 50% (*Mitigation*$_{mean}$ = $-15 \pm 31\%$; *B.A.U.*$_{mean}$ = $-76 \pm 27\%$), especially under an extreme scenario of climate change. Under worst-case expectations, range contractions of the top ranked seed-disperser primates might have extreme consequences for the seed dispersal services they provide (*Lagothrix cana*: -47%, *Sapajus apella*: -30%; *Ateles chamek*: -5%) (Fig. 3).

4. Discussion

By forecasting species distributional shifts of a uniquely well-studied seed dispersal system, we estimate the magnitude of the change in a key ecosystem function mediated by an animal-plant interaction. Seed dispersal via frugivore consumption is essential for ecosystem resilience, especially in the Tropics, where most trees rely on plant-animal interactions for dispersing their seeds (Howe and Smallwood, 1982). We found that the redistribution of Amazon primates, due to the synergism among climate change, deforestation and dispersal constraints, will drastically impair the seed-dispersal services these species provide. Our projections indicate that billions of seeds of a single tree species in the Amazon might fail to be dispersed in the future, due to niche mismatch between a plant and its primate frugivore community.

We also found an uneven contribution to seed dispersal among these primates, where the large-bodied woolly monkey *Lagothrix cana* appeared as a keystone disperser. This species alone was responsible for 64–70% of the amount of seeds of a fleshy-fruited tree that are dispersed at both local and regional spatial scale. That effect was disproportional to the size of its geographic distribution, where at least three other primate species had twice to threefold larger ranges, but the total amount of seeds dispersed was at least three times smaller than that of the woolly monkey. This raises alarming red lights, once the species is listed as "endangered" (EN) by the International Union for the Conservation of Nature, with populations decreasing every year due to continuing decline in area, extent and/or quality of habitat (Palacios et al., 2008), in addition to hunting and poaching (Stafford et al., 2017). We caution, however, that we use estimates from a study at limited spatial scale and then extrapolate into a wider geographical area. Finer scale variation in population density may alter local patterns in the relative contribution of different primate species for seed dispersal. The argument for the *L. cana* as a keystone disperser may indeed become weaker if future studies suggest a lower relative contribution at local scale.

Large frugivores are often key seed dispersers, whose loss deeply affects seed dispersal networks (Vidal et al., 2013). Yet, global changes might preferentially affect large-bodied animals, whose difficulty in dissipating heat (Mitchell et al., 2018) can select for smaller individuals within populations (Gardner et al., 2011). Large-bodied animals are also targeted for pet trade (Tingley et al., 2017), bushmeat (Nuñez-Iturri and Howe, 2007; Stafford et al., 2017) and/or trophy hunting (Stafford et al., 2017). Defaunation and the extirpation of larger animals (Dirzo et al., 2014) may thus interact with climate change to produce a downsizing effect in remaining communities (Pérez-Méndez et al., 2015). Our results suggest that seed dispersal losses associated to range contractions forecasted for such large-bodied seed dispersers may not be quantitatively compensated by species of smaller body mass. This absence of compensatory effects has also been observed in networks of seed dispersal interactions in other degraded tropical rainforests (Emer et al., 2019). Thus, cascading effects against the recruitment of large-seeded trees, which happen at the local scale in the Amazon (Nuñez-Iturri and Howe, 2007), may escalate towards vast geographical areas.

Contraction on species geographical distribution per se is a conservation issue (Urban, 2015). This is particularly challenging for primates (Bodmer et al., 2018; Estrada et al., 2017), whose limited dispersal abilities (Schloss et al., 2012) might prevent species from moving towards novel suitable environments (Sales et al., 2019). However, the loss of animal-plant interactions (Redford, 1992) following local extinction of populations exposed to harsh climates (Bellard et al., 2012) may have profound and often neglected effects on ecosystem services. Here, we found that future mismatch on the niches of a plant and one of its top-seed dispersers, *Sapajus apella*, will reduce potential co-occurrence to < 40% of the present-day area. Although this species contributes to only 8% of seed dispersal at the local scale (Levi and Peres, 2013), the large range of conditions it can occupy increases by more than twofold its relative contribution to the total seed dispersal services it can provide. Our predictions indicate that erosion of the plant potential distribution may also prevent co-occurrence with this essential primate disperser at the regional scale. In this case, climate change and deforestation will likely disrupt local plant-animal interaction due to the exposure of plant populations to non-analog climates across this primate future range.

In conclusion, we found that the synergism among climate change, deforestation and dispersal limitation forecasts imminent range contractions for an ensemble of Amazon primates, in addition to niche mismatch with a fleshy-fruited plant they feed upon. The magnitude of projected deficit on seed dispersal services is at the scale of billions of seeds, over a timespan of decades, for a single tree species. The loss of ecosystem services from disruption of biotic interactions due to global changes will undoubtedly be a major conservation challenge soon. Often neglected by most biodiversity assessments, the extinction of biotic interactions will have unprecedent impacts on worldwide ecosystems in the Anthropocene. Quantifying projected losses is, therefore, the first step towards more informed conservation planning focused on preserving functional ecosystems.

Data and code accessibility

The climate data used in this work can be downloaded at http://worldclim.org. IUCN range maps were downloaded at https://www.iucnredlist.org. Deforestation models are part of the supplementary material of Soares-Filho et al. (2006). High-resolution raster files should be obtained upon email request to the corresponding author.

Author contributions

LS and MP conceived and designed this study; LS performed ecological niche modelling and seed dispersal analysis; LS, LC 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.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2020.108628.

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