

## Journal Pre-proof

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PII: S0048-9697(22)02250-1

DOI: <https://doi.org/10.1016/j.scitotenv.2022.155157>

Reference: STOTEN 155157

To appear in: *Science of the Total Environment*

Received date: 12 November 2021

Revised date: 6 April 2022

Accepted date: 6 April 2022

Please cite this article as: P. Lemes, F.G. Barbosa, B. Naimi, et al., Dispersal abilities favor commensalism in animal-plant interactions under climate change, *Science of the Total Environment* (2021), <https://doi.org/10.1016/j.scitotenv.2022.155157>

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Dispersal abilities favor commensalism in animal-plant interactions under climate change

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## Abstract

Scientists still poorly understand how biotic interactions and dispersal limitation jointly interact and affect the ability of species to track suitable habitats under climate change. Here, we examine how animal-plant interactions and dispersal limitations might affect the responses of Brazil nut-dependent frogs facing projected climate change. Using ecological niche modeling and dispersal simulations, we forecast the future distributions of the Brazil nut tree and three commensalist frog species over time (2030, 2050, 2070, and 2090) in the regional rivalry (SSP370) scenario that includes great challenges to mitigation and adaptation. With the exception of one species, projections point to a decrease in suitable habitats of up to 40.6%. For frog species with potential reductions of co-occurrence areas, this is expected to reduce up to 23.8% of suitable areas for binomial animal-plant relationships. Even so, biotic interactions should not be lost over time. Species will depend on their own dispersal abilities to reach analogous climates in the future for maintaining ecological and evolutionary processes associated with commensal taxa. However, ecological and evolutionary processes associated with commensal taxa should be maintained in accordance with their own dispersal ability. When dispersal limitation is included in the models, the suitable range of all three frog species is reduced considerably by the end of the century. This highlights the importance of dispersal limitation inclusion for forecasting future distribution ranges when biotic interactions matter.

**Keywords:** biotic interaction, changing climate, dispersal limitation, ecological niche model, frog-plant interaction, MigClim

## 1. Introduction

Climate change is causing a global redistribution of species (e.g., Pecl et al. 2017; Taheri et al., 2021) as well as of other levels of biological organization (Bellard et al., 2012), from genetics (Pauls et al., 2013; Abreu-Jardim et al., 2021) to ecosystem levels (Grimm et al. 2013; Mishra et al., 2021). Future climate conditions are projected to further alter species geographic distributions (Pereira et al., 2010; Lavergne et al., 2010; Thuiller et al., 2011; Weiskopf et al., 2020), exacerbating extinction risk (Maclean and Wilson, 2011; Urban 2015) and compounding the negative effects of other environmental changes such as disease, invasive species and land-use change (e.g., Peterson et al., 2008; Hof et al., 2011; Ferrel et al., 2013). When biodiversity is incapable of keeping pace with climate change through genetic adaptation (Salamin et al., 2010), phenotypic plasticity (Valladares et al., 2014; Herrando-Perez et al., 2019) or microhabitat use and behavioral adjustments (González-del-Pliego et al., 2020), it does so by expanding, contracting, or shifting their geographic distributions (Van der Putten et al., 2010; Garcia et al., 2014). Future extinction risks are thus often associated with contractions in species geographical ranges (Sinclair et al., 2010; Urban 2015), which in turn affect the viability of the surviving populations (Brook et al., 2009; Fordham et al., 2013). Understanding the multi-dimensional nature of climate change effects on species redistributions across scales is far from simple (Wisz et al., 2013), particularly because of the great uncertainties associated with the compounding or buffering effects of biotic interactions (Meir et al., 2010; Wisz et al., 2013), the difficulty to predict species abilities to disperse across long distances (Travis et al., 2013; Kerr, 2020), and the complexities associated with interactions between dispersal and biotic interactions under climate change (e.g., García-Valdés et al., 2015).

Beyond changes in range size, climate changes can reduce suitable overlapping areas differently for each species in the community (Flores-Tolentino et al., 2020), considering that species could move at different speeds and directions (Singer et al., 2013; HilleRisLambers et al., 2013), leading to biota redistribution (Pecl et al., 2017). Biotic interactions are fundamental

for ecosystem maintenance and function (Hulme-Beaman et al., 2016; Boukal et al., 2019), thus species range shifts imposed by climate change can impose a complex combination of threatening processes (Bascompte et al., 2019; Schleuning et al., 2020). Following climate change, species interactions may be disrupted (Zarnetske et al., 2012; Brambilla et al., 2020) and new interactions developed (Blois et al., 2013; Bascompte et al., 2019; Schleuning et al., 2020). When individuals or populations influence one another, climate changes can also result from spatial mismatches in such species relationships due to the dispersal limitations of each (Araújo et al., 2011; Urban et al., 2013). Areas projected to be climatically suitable in the future can be inaccessible to the species (Sahlean et al., 2014; Miller and Holloway, 2015) due to species dispersal limitations or habitat connectivity (De Kort et al., 2020) are not commonly integrated into ecological niche models (ENMs) (Peterson et al., 2011; Zurell et al., 2020; De Kort et al., 2020). Therefore, changes in landscape configuration and structure can create barriers preventing the dispersal of the organisms (Becker et al., 2007; Boulangeat et al., 2012; Arntzen et al., 2017).

Advances are being made to better encompass biotic interactions (e.g., Boulangeat et al., 2012; Fordham et al., 2013; Anderson 2017, Dorman et al., 2018; Flores-Tolentino et al., 2020) and dispersal limitations (Engler et al., 2012; Miller and Holloway, 2015) in ENMs. For species that strongly depend on biotic interactions, their interactions and dispersion capacities are important to the determination of their geographic distribution in response to future climate changes (Araújo and Luoto, 2007; Boulangeat et al., 2012; Urban et al., 2013). Some pairwise interactions involve damages or benefits for one species and no effects for others. The climate change effects have been evaluated for interactions of parasitism (Araújo and Luoto 2007; Chapman et al., 2013; Feldman et al., 2017), predation (Fordham et al. 2013), mutualism (Gorostiague et al., 2018; Morales-Linares et al., 2021), commensalism and ammensalism (Singer et al., 2013; Flores-Tolentino et al., 2020), with most studies lacking explicit treatments of dispersal (but see Fordham et al. 2013).

Commensalistic interactions are particularly interesting because they are arguably among the most commonly found in nature (often referred to wildlife-habitat interactions with habitats encompassing - but not exclusively based on - the plants giving shelter to animals of varying types). An example of commensalism is the interaction between Amazonian frogs and the plants in which they lay their eggs in water-containing fruit capsules for offspring development (Moravec et al., 2009; Camera and Krinski, 2014); the plants are unaffected but their capsules are hugely important for the long term persistence of their populations. This is the case between three tropical frog species - *Adelphobates castaneoticus*, *Osteocephalus castaneicola*, and *Rhinella castaneotica* - and the Brazil nut tree (*Bertholletia excelsa* Bonpl.). Frogs do not cause any damage to the tree, but they need its capsule to develop their water life cycle, highlighting the Brazil nut tree's essential role for their occurrence and distribution. The *B. excelsa* occurs throughout the Amazon region (Thomas et al., 2014), and their fruits are hard and usually opened by scatter-hoarding rodents (Haugaasen et al., 2010). Empty after removal of the seeds, the capsule is not easily decomposed and creates small pools of rainwater inside them. By accumulating rainwater, these become an excellent place for frogs to deposit their eggs for tadpole development (Caldwell and Myers, 1990; Moravec et al., 2009).

Among the most endangered vertebrate groups (Powers and Jetz, 2019), amphibians are especially threatened by habitat modification (Becker et al., 2007; Arntzen et al., 2017; Ribeiro et al., 2017; Murray et al., 2021) and many species are currently on the edge of extinction (Stuart et al., 2004; Ficetola et al., 2015). Amphibians are particularly sensitive to changes in temperature and humidity (Greenberg and Palen, 2021), which makes climate an important factor for shaping their geographic distribution (Enriquez- Urzelai et al., 2019). If the temperature rises, it will most likely alter the distribution of amphibians (Zhang et al., 2020) and their responses to climate change could be species-specific (Miller et al., 2018). Climate change impacts on frog-plant interaction have been investigated (Vasconcelos et al., 2017; González-

del- Pliego et al., 2020) mainly for organisms that spend their entire life cycle inside plants for their development and breeding (Sabagh et al., 2017). In such cases, there is a mutual benefit since plants also increase their nutrient intake (Romero et al., 2010). If a species is highly dependent on beneficial interactions, it is likely to be particularly sensitive to climate change (e.g., Araújo and Rozenfeld 2014; Foden et al., 2018). Furthermore, future changes in the geographic distribution of the Brazil nut tree due to climate change may thus affect the distribution of frogs because of their reproduction requirements (e.g. Moravec et al., 2009) and amphibian limited dispersal abilities (D'Amen et al., 2011).

Knowledge of how climate change will alter interactions among organisms and the role of dispersal limitation can help us deliver conservation strategies in order to face a future of increasing warming. Considering these issues, we evaluated how animal-plant interaction and dispersal might affect the three selected frog species under climate change. To do so, we (i) used ensemble forecasts of ecological niche models (ENMs) to predict the potential redistribution of species under climate change, (ii) calculated the spatial overlapping between the potential geographic distribution of the modeled three frog species and the Brazil nut tree, and (iii) used a cellular automaton-based-dynamic model to predict the potential distribution of each frog species restricted by biotic interaction, climate, dispersal and landscape constraints.

## 2. Materials and Methods

### 2.1. Study system

The Brazil nut tree (*Bertholletia excelsa* Bonpl.) is a flagship species which extends throughout the Amazonian Forest and its distribution range is fragmented in the terra firme (non-flooded) forest between 5°S and 14°N (Mori and Prance, 1990). It's mostly found in groups – the “castanhais” – with densities from 10 to 20 trees per hectare (Mori and Prance, 1990; Scoles and Gribel, 2011), and most likely past human influences have contributed to shape its current

distribution (Thomas et al., 2015). The Brazil nut tree depends on bee pollination and seed dispersal by the agouti (*Dasyprocta spp.*) (Mori and Prance, 1990; Haugaasen et al., 2010), but projections of climate change impacts have shown a decline in pollinator diversity that might threaten ecosystem services provided by the Brazil nut (Sales et al., 2021). In addition, the Brazil nut tree also plays an important social role, providing food resources that support the livelihood of traditional indigenous societies (Kainer et al., 2018). Because Brazil nuts have suffered anthropogenic and natural pressures (Peres et al., 2003; Escobar, 2019), this species is now considered threatened by the Brazilian Ministry of the Environment (law #443/2014 MMA, 2014).

## 2.2 Species data

We obtained presence records for the Brazil nut tree from the Global Biodiversity Information Facility (GBIF, <http://www.gbif.org>), SpeciesLink (<http://splink.cria.org.br>), and complemented these data with data from the National Center for Flora Conservation (Centro Nacional de Conservação da Flora - in Portuguese, CNCFlora; [cncflora.jbrj.gov.br](http://cncflora.jbrj.gov.br)). Virtual databases were searched and matching records were downloaded using the function *occ()*, then collapsed into a single string with the function *join\_names()*, both available in the *spocc* package (Chamberlain et al., 2016). For the three tree species, we obtained presence records from the following sources: (i) literature data for *Adelphobates castaneoticus* (Camera and Krinski, 2014) and *Osteocephalus castaneicola* (Silva et al., 2016; Carvalho et al., 2017), and (ii) two virtual databases - the GBIF and Brazilian biodiversity website (Portal da Biodiversidade - in Portuguese, <https://portaldabiodiversidade.icmbio.gov.br/portal/>) - mainly for *Rhinella castaneotica*. The species occurrence records are available in Table S1.

We then critically reviewed this dataset by deleting ambiguous, duplicate, or unreliable records and removing those whose geographical location or taxonomic information were not

precisely defined using a suite of *coord\_functions()* from *scrubr* package (Chamberlain, 2016). After data cleaning, we spatially thinned the occurrence localities by 10 km to minimize clustering of records due to biased sampling by using *thin()* available in the *spThin* package (Aiello-Lammens et al., 2015). We reached a frog dataset containing 14 presence records for *A. castaneoticus*, 15 records for *O. castaneicola*, and 40 records for *R. castaneotica*, along with 148 records for the Brazil nut tree. All spatial analyses were performed in R (R Core Team, 2020).

### 2.3. Environmental data

For frog species and the Brazil nut tree, we used 19 bioclimatic variables as candidate baseline predictors with a spatial resolution of  $0.08333^\circ$  ( $\sim 9\text{km} \times 9\text{km}$ ) from the global dataset of WorldClim2 (Fick and Hijmans, 2017; Table S2). In addition, for the Brazil nut tree, we also included topsoil predictors acknowledged as physiologically important to plants, namely: cation exchange capacity, clay fraction, gravel fraction, pH in water, organic carbon content (in percent and volume-weighted), silt fraction and soil depth (Mod et al., 2016; Figueiredo et al., 2018). Only topsoil features were included since the Amazon territory is mostly composed of shallow soils. These data were obtained from the RegridDED Harmonized World Soil Database v1.2 (<https://daac.ornl.gov/SOILS/guide/HWSD.html>), containing global soil parameters in the form of NetCDF files at 0.9 degree x 1.25 degree resolution, and further downscaled to the same resolution of climate predictors using the *resample()* function and the nearest-neighbor interpolation method. To avoid problems associated with multicollinearity, the candidate predictors were selected by the variance inflation factor (VIF, Zuur et al., 2010) and we only retained the variables with VIF values  $< 10$  (Dormann et al., 2013) using the function *vifcor()* from the *sdm* package (Naimi et al., 2014; Naimi and Araújo, 2016) in R (R Core Team, 2020). Once collinearity was evaluated using species occurrence records, distinct subsets of

environmental predictors were selected for each species, which were then used to calibrate species-specific ENMs.

Once the species-climate relationships were estimated, we projected the estimated conditions across temporal bins in the future (2030, 2050, 2070, and 2090) using available projections and scenarios in Wordclim2 (Fick and Hijmans, 2017). We used the downscaled data from three general circulation models (GCMs), namely, BCC-CSM2-MR, CanESM5, and MIROC6 (CMIP6, Eyring et al., 2016) for one shared socio-economic pathway (SSP; Eyring et al., 2016): SSP370. These GCMs characterize the wide variety of models based on the latest update on expected future climate change projections (Brunner et al., 2020). The future climate conditions were simulated into shared socio-economic pathways (SSPs), which are driven by changes to both precursor emissions and climate (Eyring et al., 2016). Specifically, the SSP370 represents the medium-to-high end of future emissions and forecasts a 4.1°C warming until 2100 (Riahi et al., 2017).

#### **2.4. Ecological Niche Modelling**

The species spatial distribution records were associated with environmental data to characterize the conditions experienced by species and to predict their potential geographic distribution during the baseline period. We used the sdm package (Naimi and Araújo, 2016) in order to develop a large ensemble of forecasts (Araújo and New, 2007) of ENMs (Peterson and Soberón, 2012), that combines the output of multiple models to generate a single prediction through consensus. For each species, we calibrate models using Bioclim (Booth et al., 2014), DOMAIN (Carpenter et al., 1993), MaxLike (Royle et al., 2012), Support Vector Machine (SVM; Vapnik, 1995), Boosted Regression Tree (BRT; Friedman, 2001), and Multivariate Adaptive Regression Splines (MARS; Friedman, 1991). Because some methods required zeros to be fitted, we generated a random sample of 10,000 sites for modeling each species. For model performance of

*A. castaneoticus* and *O. castaneicola*, we used a bootstrapping replication method due to a small number of species presence records (Hastie et al., 2009), repeated 30 times. For models of *R. castaneotica* and *B. excelsa*, we used 30 runs of subsampling replication methods by splitting the data into training and test datasets (70 and 30 percent, respectively). Models were parameterized using default options of the sdm package (Naimi and Araújo, 2016) and performed in R (R Core Team, 2020).

We used the area under the curve (AUC) of the receiver operating characteristic (ROC) to assess the accuracy of ENMs (Fielding and Bell, 1997). A ROC curve estimates the proportion of instances of presence correctly predicted as presence (omission errors) and the proportion of instances of absence wrongly predicted as presence (commission error) across all possible thresholds between 0 and 1 (Jimenez-Valverde, 2012). AUC values of 0.5-0.7 correspond to low accuracy, 0.7-0.9 indicate good accuracy, and values above 0.9 indicate high accuracy (Swets, 1988). The true skill statistic (TSS) considers both model sensitivity and specificity (Allouche et al., 2006), and ranges from -1 to +1. If TSS is +1, this implies perfect agreement, while a value of 0 indicates agreement expected by random, and a value of less than 0 indicates agreement lower than expected by chance. We generated 90 individually calibrated models for each species, and we used the TSS to create a weighted average of each prediction model. For each species, we generated ensemble forecasting using the output models for each time slice. We classified continuous predictions into presence and absence maps based on maximizing the TSS (Allouche et al., 2006). Further, we assembled the binary maps by simple mean values for each species from single methods under current and future climate conditions. Also, we evaluated the variable importance (Murray and Corner, 2009) and plotted the predicted response curve (Elith et al., 2005) for inferring the relationship between the environmental variables and predicted habitat suitability.

## 2.5. Potential co-occurrence

From binary consensus maps, we forecasted how climate change may affect the potential co-occurrence between Brazil nut trees and each frog species. For this purpose, we superimposed the binary maps and afterward we calculated the number of suitable cells between the species pair, in the current and in the future (e.g., Araújo et al., 2011; Sales et al., 2021). These cells represent potential co-occurrences that indicate areas that host environmental conditions considered most suitable for each frog-plant binomial. Since the frog species studied here depend on the indehiscent fruit armory to lay eggs and reproduce, we considered that the absence of Brazil nut trees (in the form of unsuitable cells in maps of binary potential distribution) would prevent frog occupancy of climatically suitable cells. By doing so, we assume that frog occupancy of climatically suitable cells is also dependent on plant occurrence and, therefore, on shared environmental suitability.

## **2.6. Incorporating dispersal limitation**

In order to dynamically explore the climate change consequences over time, we implemented species dispersal constraints through a cellular automaton-based model (Engler and Guisan, 2009). Therefore, we used the MigClim model (Engler et al., 2012) that calculates the probability a given cell will become colonized and simulates species dispersal under a changing climate by including (i) current map of habitat suitability, (ii) species dispersal ability, (iii) barriers to dispersal for our focal species, (iv) and future maps in  $p$  climate conditions. The simulations start with source pixels represented by actual occupied pixels and target pixels are considered those that will be climatically suitable for species colonization under future conditions. The resulting map of cellular automata represents the potential distribution restricted by dispersal over time.

Our simulations included the frog binary maps of habitat suitability filtered by Brazil nut tree presence. This assumes frogs' dependency on the fruit capsules of the Brazil nut for

breeding (Caldwell and Myers, 1990; Moravec et al., 2009; Camera and Krinski, 2014). As no information on dispersal distances potentially traveled by unit time for our focal frog species, we used two extreme datasets of kernel dispersal distance for incorporating dispersal limitation previously used in another study (Uribe-Rivera et al., 2017) as follows: *Bombina bombina* (minimum dispersal) and *Rana temporaria* (maximum dispersal) (Kovar et al., 2009). Furthermore, some landscape constraints can interpose the species' ability to colonize new areas (Ribeiro et al., 2017), and ongoing habitat transformation will become increasingly more susceptible to discontinuing their life cycle (Becker et al., 2007). We used a global model that predicts the potential future tree cover persistence for 2029 (Flewton et al., 2019) in generating a dispersal barrier layer from landscapes forecasted to host less than 30% remaining tree cover in the future. The first environmental step started in the current climate (1970-2000) followed by predictions of future climate in the years of 2030, 2050, 2070, and 2090, thus the cellular automaton model produced a total of four dispersal steps. The MigClim output informs species dispersal constraints and suitable areas until the end of the time period (2080-2100). Demographic criteria were parameterized using default options of the MigClim package (Engler et al., 2012) and performed in R (R Core Team, 2020).

### 3. Results

#### 3.1. Potential species distribution

Forecasts of the Brazil nut tree's distribution matched the species' observed distribution (mean AUC =  $0.80 \pm 0.04$ ; TSS =  $0.54 \pm 0.03$ ) (Table S3 in Supplementary Material). Future climatic conditions will alter the habitat suitability of the Brazil nut tree, increasing suitability where mean temperature of the wettest quarter ranges from 20°C - 25°C and where precipitation of the wettest month exceeds 500mm, and decreasing where the pH levels become neutral, which is most likely to occur in its current easternmost distribution (Fig. 1ab). Forecasts showed that

Brazil nut tree species could lose roughly 7% of their suitable areas by the end of the century (Table S4).

The predictive accuracy of the frog species was high for almost all methods with an AUC average of  $0.83 \pm 0.06$  and TSS of  $0.65 \pm 0.12$  (Table S2 in Supplementary Material). The distribution of the frog species is fundamentally determined by precipitation. While the habitat suitability of *A. castaneoticus* increases in the areas where the precipitation of the coldest quarter (bio 19) is greater than 1,750mm, the habitat suitability (Fig. 1ef) of *O. castaneicola* increases in areas with precipitation up to 1,000mm in the warmest quarter (bio 18; Fig. 1ef). *Rhinella castaneostica* distribution is determined by precipitation seasonality (bio 15) with the relative importance of 36.5% (Fig. 1g). The response curve shows a decrease in the habitat suitability when precipitation seasonality is between 750mm and 1500mm (Fig. 1h). Whereas *O. castaneicola* and *R. castaneostica* should decrease up to 40% of climatic suitability areas, *A. castaneoticus* will probably increase their suitable areas in the last half century (Table S4).

### 3.2. Potential co-occurrence

By overlaying maps of the potential geographic distribution of the Brazil nut tree and each frog species, we assessed patterns of potential co-occurrence and their variation in space and time (Fig. 2). The overlap in current modelled distributions was highest for *O. castaneicola* with 94.4% (18.8% of the Brazil nut tree species' range overlapping with the latter), followed by *A. castaneoticus* with 93.8% (15%), and *R. castaneostica* reach 93.6% (50.6%, see Table S5 for absolute values). The potential overlap between the Brazil nut tree and *A. castaneoticus*, however, will change over time (Fig. 2a; Table S5). Almost the entire range of *A. castaneoticus* is predicted to be unsuitable in 2050 (Fig. 2a), but it is likely to substantially increase its suitable range by 2090. The potential co-occurrence between the Brazil nut tree and *O. castaneicola* will decrease in the future due to the latter's distribution contraction (Fig. 2b). The likely overlap

between the Brazil nut tree and *R. castaneotica* will decrease in absolute values (Fig. 2c, Table S5). Considering the predictive species distribution, the average climatically suitable range of the Brazil nut tree and three commensalist frog species are projected to maintain animal-plant interaction (Fig. 2).

### 3.3. Dispersal limitation

The MigClim resulting maps allowed us to forecast areas that will be climatically suitable for each frog species even under dispersal constraints (Fig. 3). Climate refugia range was predicted to decrease for all frog species until end-of-century (95.8% for *A. castaneoticus*, 95.7% for *O. castaneicola*, and 85.7% for *R. castaneotica*). By combining areas of climate refugia (*i.e.* always suitable) and potentially migration, *A. castaneoticus*' range may increase up to 207% (Fig. 3a), while both *O. castaneicola* and for *R. castaneotica* should decrease 20.4% (Fig. 3b) and 34.2% (Fig. 3c), respectively at maximum dispersal scenario (see Table S6 for absolute values). Many areas will become unavailable for *A. castaneoticus* due to dispersal constraints (Fig. 3d) and some Colombian and Venezuelan regions appear inaccessible due to dispersal limitation for *O. castaneicola* facing climate change (Fig. 3e). Our simulations suggest dispersal limitation will prevent *O. castaneicola* from occupying climate refugia areas in Peru, western Brazil and the eastern Madeira River (Fig. 3b,e). The Guyanas (French Guiana, Guyana and Suriname) and southeastern edge of the forest also appear to be unsuitable for *R. castaneotica* (Fig. 3f).

## 4. Discussion

We developed models that simulated changes in suitable areas for three Amazonian frogs and the Brazil nut tree, along with the inclusion of the frog species dispersal capacity. Possible disruptions in animal-plant commensalism in response to end-of-century climate change are projected. To track climate-driven shifts and allow species migrations, the species-specific dispersal needed to be surveyed. This is because future frog distribution will be highly reliant on

the existence of permeable migratory routes across the habitat patch. Our findings are consistent with other studies showing that responses to climate changes will likely depend on species dispersal ability (e.g., Anderson et al. 2009; Travis et al., 2013; Sales et al., 2019). A minimum dispersal-case scenario is expected to lead to ecological bottlenecks in the future because species will be incapable of tracking the pace of climate change and only remain within climate refugia areas with high climate stability (e.g., Terrible et al. 2012). Our models forecast a severe reduction in climate refugia for all Brazilian nut tree frogs.

Positive species interactions can influence range limits or affect range expansion (Stephan et al., 2021). The climate-related changes of co-occurrence and biotic interactions should affect ecosystem functions and services mediated by animal–plant interactions (Sales et al., 2021). Even if a mismatch between Brazil nut trees and frogs has gone undetected in our study, biotic interactions are essential to the biological community structure (Brambilla et al., 2020; Flores-Tolentino et al., 2020). Commensalism or mutualism could affect the rate and ultimate extent of range expansion in response to changing environmental conditions, such as those caused by climate change (HilleRisLambers et al., 2013). The complex effects across species ranges arising from species interacting can lead to asymmetric range shift dynamics (Ettinger and HilleRisLambers, 2017; Sales et al., 2021). There are some studies on the response of co-occurrence and indirect interactions to climate change (Araújo et al., 2011; Losapio and Schöb, 2017), these are based on inferred rather than actual direct interactions.

Frogs have low dispersal and our more realistic projections indicate that all three commensalist species may become threatened by climate change in the future. Frog species with aquatic larvae depend on connectivity between aquatic and terrestrial habitats to complete their life cycle and suffer the negative effects of habitat split in discontinuous landscapes (Becker et al., 2007; Fonseca et al., 2013; Lion et al., 2014), even for frog species with specialized aquatic reproductive modes. The movement to and from breeding sites mainly with an aquatic larval

phase is vitally important for not only reproduction (Becker et al., 2007), but also the survival of local populations (Becker et al., 2010). The species' abilities to shift their range limit or to expand their geographic distribution under changing climate, however, will assuredly depend on their dispersal capabilities (D'Amen et al., 2011; Schloss et al., 2012; Bateman et al., 2013; Zanatta et al., 2020), otherwise the species could be confined to unsuitable climate areas (Gouveia et al., 2016). Our models included the ability of species to disperse into a spatially explicit framework, although based on a number of simplifications due to limitations in the availability of empirical data for each frog species.

One of the clearest signs of biotic response to climate change are range shifts where species will need to move into newer climate suitable areas (Kerr, 2020) just as quickly as temperatures increase, in order to maintain spatial insurance and their own persistence (Chen et al., 2011). However, species will depend on intrinsic dispersal ability (Scholls et al., 2012; Estrada et al., 2016) which is becoming especially challenging for frogs with low dispersion abilities (Kovar et al., 2009) and may prohibit them from reaching new areas (Uribe-Rivera et al., 2017). Rather few studies explicitly included species-specific dispersal abilities when modeling species distribution and even running models with unlimited dispersal tend to overestimate the potential future range (Thuiller et al., 2012), especially for species with moderate to low dispersal ability (Urban et al., 2016). By including dispersal ability information, we demonstrated that all three frog species should experience decreases in their geographic distribution over time. Although many studies have assumed no dispersal, unlimited dispersal or a previously defined limited dispersal distance ("buffers") in post-processing ENM analyses, we advocated the inclusion of intrinsic dispersal capability proxies (Travis et al., 2013; Uribe-Rivera et al., 2017; Boyer et al., 2020) or even niche information (Penner and Rödel, 2019).

Inclusion of species dispersal abilities improves distribution models into more realistic scenarios (Thuiller et al., 2019). While there is still some debate on how to integrate dispersal

metrics into ENMs (Monsimet et al., 2020; Zanatta et al., 2020) a variety of methods are already available through some R packages (e.g., 'ENMTML'; Andrade et al., 2020; 'megaSDM'; Shipley et al., 2022). In our study, inclusion of dispersal abilities in our ENMs revealed areas where colonization is highly unlikely and when and where suitable habitat will become accessible. A proposal would be areas where species will be to maintain interconnected suitable areas which should help conserve current habitats and promote species persistence over time, even in a changing world.

Because our simulations are based on some simplifications, it is important to highlight some caveats in our findings. Firstly, and most importantly, empirical data of intrinsic dispersal are currently unavailable for the study species. Unfortunately, minimal dispersal data are feasible and remain much less understood in organisms with complex life cycles, as is the case with amphibians (Cayuela et al., 2020). Secondly we assumed an isotropic dispersal, which means, if there is a balance between climate and dispersal constraints, these are colonized; thereby, we ignored other ecological aspects important to maintain viable populations such as demography and other biotic interaction beyond that of our interest (frog species and the Brazil nut tree). Our assumptions imply in an over estimation of colonization rates as that used on Uribe-Rivera et al. (2017) study. Even so, our results show that few areas will be climatically suitable at the 21<sup>st</sup> century's end for three Amazonian frog species (pink areas, Fig 3). Finally, beyond remarks underlying spatial predictions of ENMs (Zurell et al., 2020), we inferred biotic interactions from large-scale data through the spatial analysis of (co)distributions of species (e.g. Sales et al., 2021) to make the models more realistic. Although there are recent advances (Dorman et al., 2018), studies dealing with biotic interaction and dispersal constraints present the greatest challenges in the future.

## 5. Conclusion

In conclusion, we forecast the patterns of climate change response for commensalistic interaction between three Amazonian frog species and the Brazil nut tree, explicitly including the effects of frog dispersal limitation on estimates of potential distribution. Amazonian frog species depends on the Brazil nut tree capsule for completing their lifecycle (Caldwell and Myers, 1990; Moravec et al., 2009; Camera and Krinski, 2014) and our projections indicate their climate niche will maintain the overlap between each pairwise of animal-plant species. By including dispersal limitation, the areas with suitable climate for frog species will drastically reduce until the end of the 21<sup>st</sup> century. To maintain climate change pace, Amazonian frog species should remain in small and disconnected areas of climate suitability as *Adelphobates castaneoticus* does because of low intrinsic dispersal abilities. Our results highlight the important role of integrating dispersal constraints on projections of future distributions for low dispersive species, as Amazonian frogs.

## 6. Acknowledgements

We acknowledge the World Climate Research Programme, which, through its Working Group on Coupled Modeling, coordinated and promoted CMIP6. We thank the climate modeling groups for producing and making their model output, the Earth System Grid Federation (ESGF), available for archiving the data and providing access, and the multiple funding agencies who support CMIP6 and ESGF. We thank Diego Santana for providing Brazil nut tree frog photos of *Adelphobates castaneoticus* and *Rhinella castaneotica*, and Diego Meneghelli for photos of *Osteocephalus castaneicola* in the Graphical Abstract. MBA acknowledges funding from the Spanish Ministry of Science, Innovation, and Universities, through project PGC2018–099363-B-I00. FGB thanks the Universidade Federal do Rio Grande and the Programa de Pós-graduação em Biologia de Ambientes Aquáticos Continentais.

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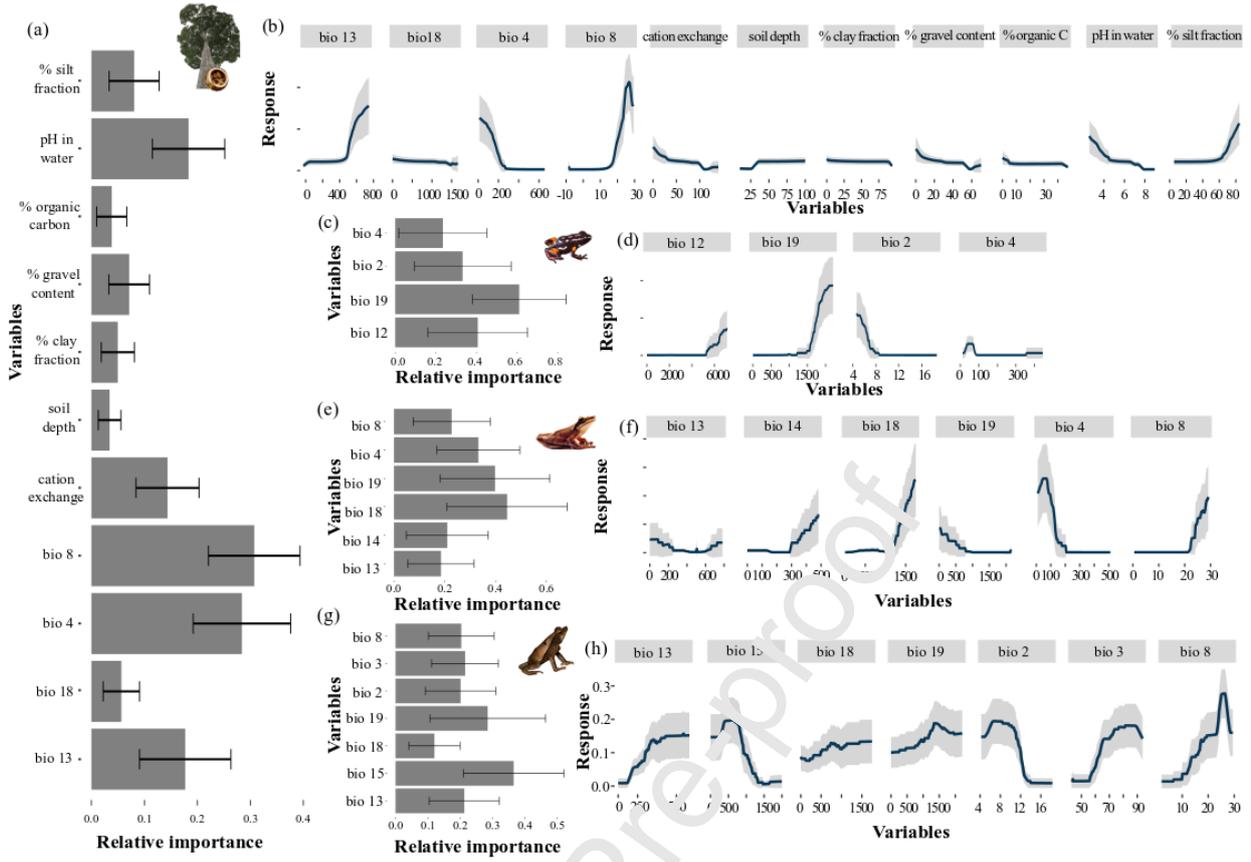
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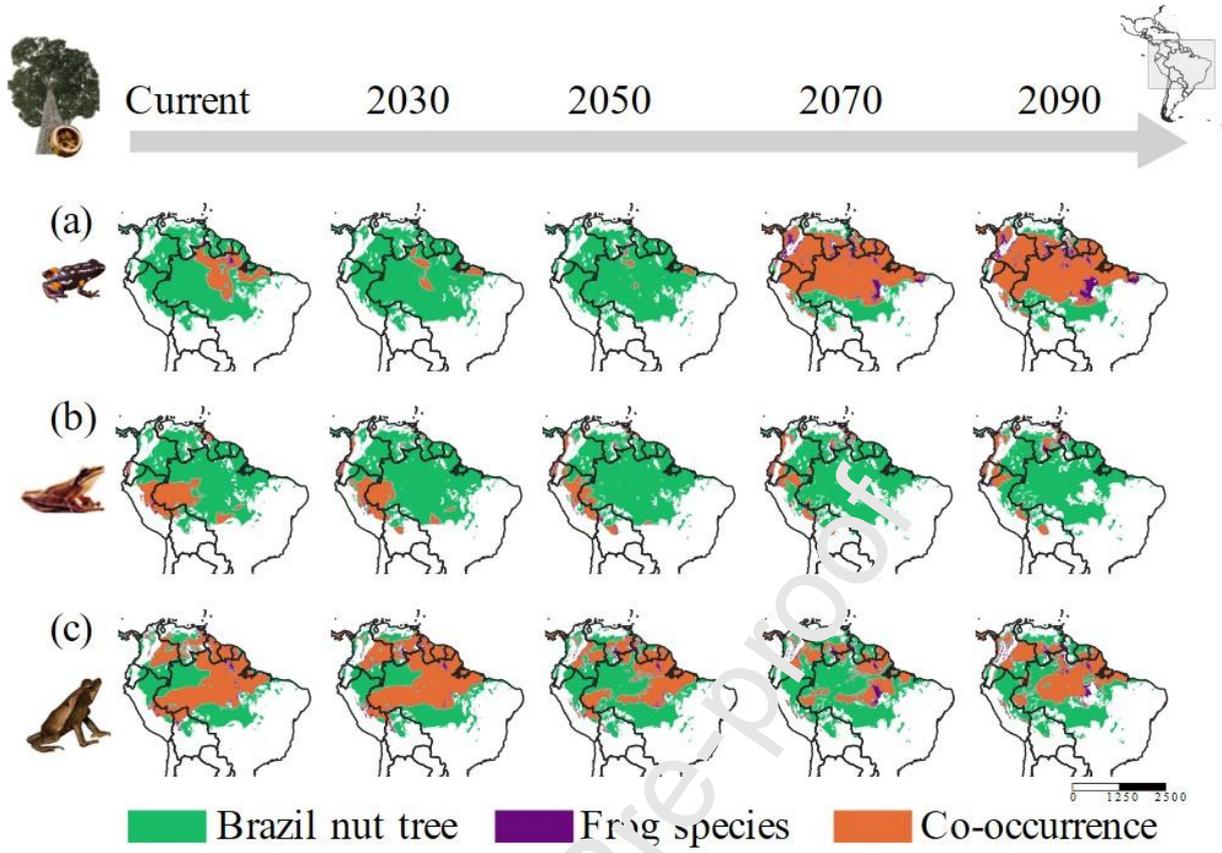
## List of figures

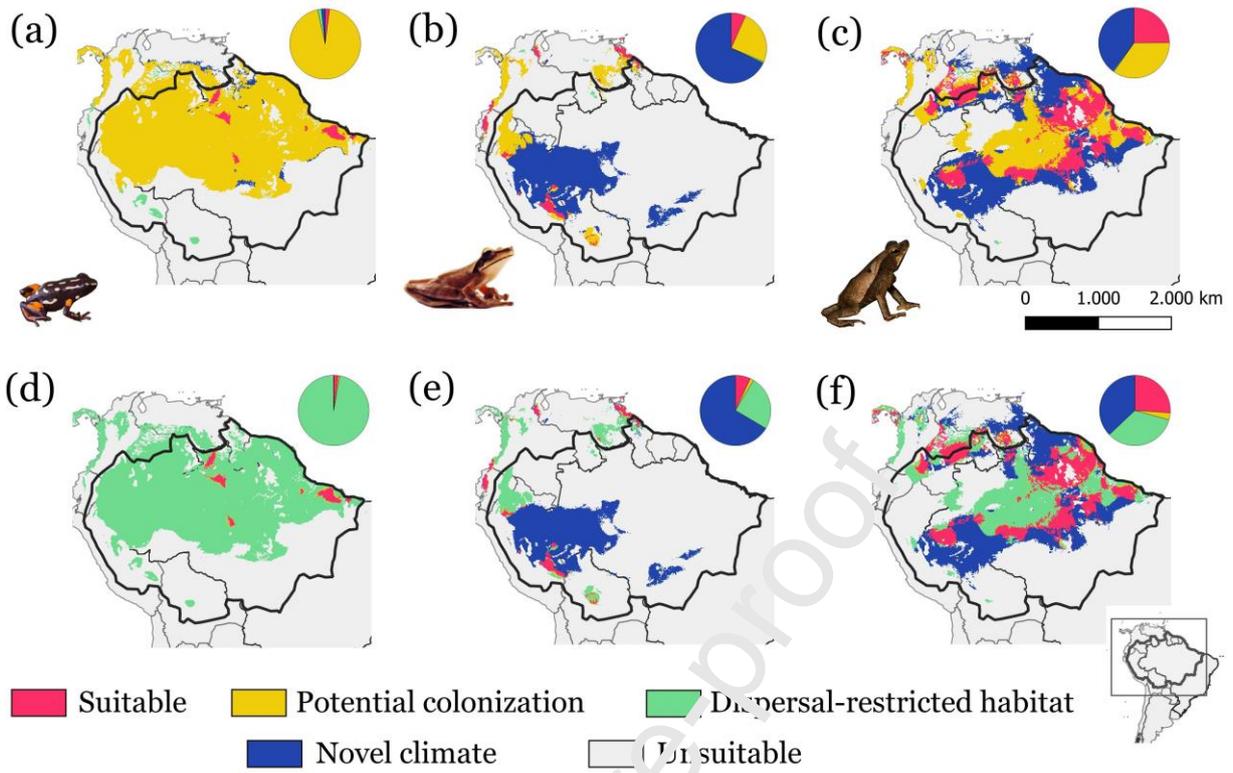
**Fig. 1** Relative variable importance and predictive response curve, respectively, for (a-b) *Bertholletia excelsa*, (c-d) *Adelphobates castaneoticus*, (e-f) *Osteocephalus castaneicola*, and (g-h) *Rhinella castaneotica*. The response curve was fitted by the “glm” method. Error bars show the standard deviation.

**Fig. 2.** Forecasts of habitat suitability over time: (a) *Adelphobates castaneoticus*, (b) *Osteocephalus castaneicola*, and (c) *Rhinella castaneotica*. Note that green areas indicate only occurrence of the Brazil nut tree; purple areas, only frog species; and orange areas of potential co-occurrence of frog-plant binomial.

**Fig. 3** Range dynamics of frog species considering the dispersal constraints to forecast the potential distribution of Brazil nut frog species over time. Dispersal scenarios are two extreme data of kernel dispersal distance. a-c, maximum dispersal ( $D_{\max}$ ) for *A. castaneoticus*, *O. castaneicola*, and *R. castaneotica*, respectively; and d-f, minimum dispersal ( $D_{\min}$ ), in the same species sequence. The resulting map of dispersal-restricted potential distribution is partitioned into climate refugia (cells in present and future), potential migration (newly suitable cells accessible via dispersal), dispersal limitation (newly suitable cells inaccessible via dispersal) and non-analogs (cells that are suitable in the present but will become unsuitable in the future, thus exposing populations to non-analog climates).







**Credit authorship contribution statement**

Conceptualization, P.L., F.G.B.; Data curation, P.L.; Formal analysis, P.L., F.G.B.; Methodology, P.L., F.G.B., B.N.; Writing-original draft, P.L.; Writing-review and editing, P.L. in coordination with P.L.,F.G.B., B.N., M.B.A. All authors have read and agreed to the published version of the manuscript.

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**Declaration of interests**

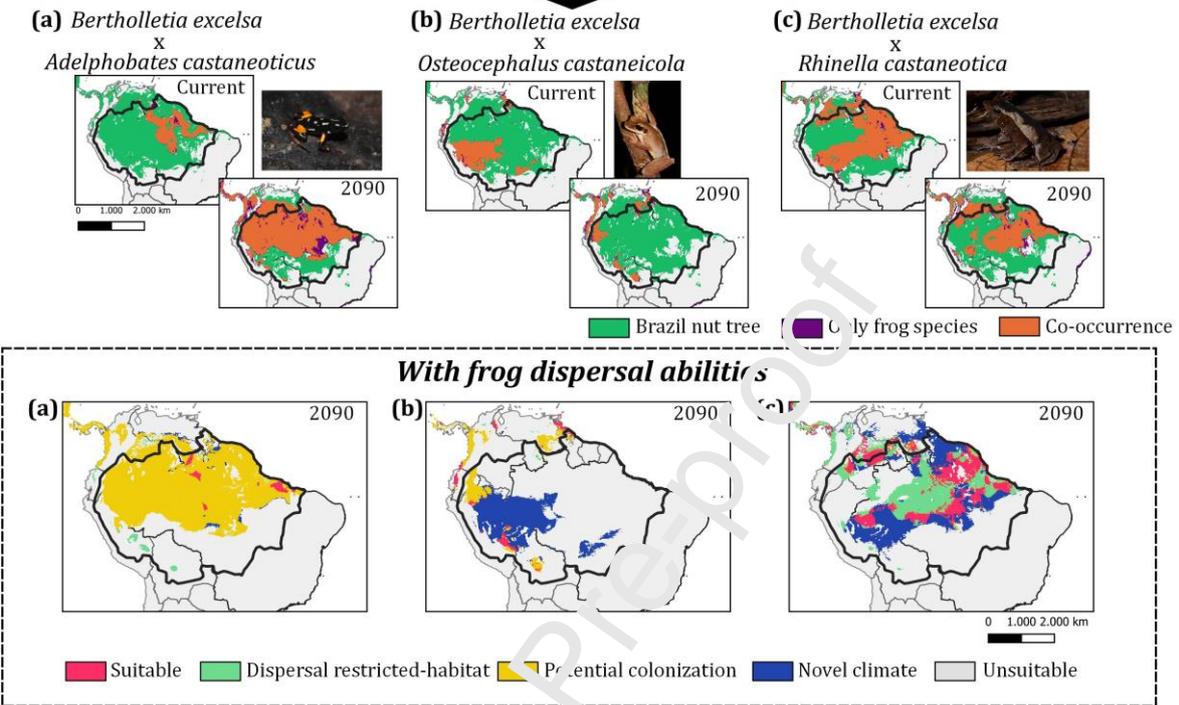
The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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Graphical abstract

**Climate change**  
Ecological Niche Models



## Highlights

- We mapped the distribution of the Brazil nut and three commensalist frog species.
- Climate change will lead to changes in overlapping territory for studied species.
- Including dispersal limitation in simulations reduced the frogs' suitable habitat.
- Integrating dispersal constraints on future projections to make the models more realistic.

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