

# ECOGRAPHY

## Research

### Anthropogenic disturbance and rainfall variation threaten the stability of plant–ant interactions in the Brazilian Caatinga

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Climate change is projected to exacerbate the effects of anthropogenic disturbance, with negative impacts on ecosystem stability and functioning. We evaluate the additive and combined effects of chronic anthropogenic disturbance (CAD) and rainfall variation on the temporal stability of mutualistic EFN-bearing plant–ant networks in a Caatinga dry forest. We evaluated whether changes in the stability of these interactions are driven by changes in the stability of the communities of partners involved and/or in ant behavior. We sampled EFN-bearing plant–ant networks in sixteen 20 × 20 m plots distributed across CAD and rainfall gradients. The stability of EFN-bearing plant and attendant–ant communities were measured as the inverse of temporal differences in their community structure and composition. We also computed the stability of EFN-bearing plant–ant networks by measuring the inverse of temporal differences in network specialization metrics. We found that, in general, the structure and composition of plant and ant interacting communities were similarly stable along both environmental gradients. Only CAD and its interaction with rainfall affected the temporal stability of EFN-bearing plant diversity, which declined as CAD increased, with a more pronounced relationship in wetter areas. However, variation in levels of CAD and, to a lesser extent, rainfall greatly modulated the stability of EFN-bearing plant–ant network specialization. CAD reduced the stability of network generality (specialization at the ant level), an effect that was much stronger in wetter areas. Meanwhile, the stability in network vulnerability (specialization at the plant level) decreased with the increase of CAD and the decrease of rainfall levels. Finally, there was a trend of decreasing stability in specialization of the overall network with increasing CAD. Our results suggest that changes in the structure of interaction networks are mainly driven by a switch in ant behavior rather than by changes in the structure and composition of plant and ant communities between years.

Keywords: chronic anthropogenic disturbance, climate change, ecosystem stability, environmental fluctuation, mutualisms, plant–animal interactions



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## Introduction

Ecosystem stability, i.e. the invariability in ecosystem function over time, is often beneficial for the reliable provision of ecosystem functioning and services, and is important to the ability of ecosystems to deal with future disturbance events (Holling 1973, Carpenter et al. 2001, Colwell et al. 2008, Magurran et al. 2010, Mori 2016). Thus, insights about potential improvements to conservation efforts can be gleaned from our understanding of temporal dynamics of ecological communities (Butchart et al. 2010). Global climate projections have been becoming increasingly concerning, with not only increases in global mean temperature and changes in global rainfall regimes, but also increasingly variable conditions and a higher frequency of extreme weather events (IPCC 2014, Ozturk et al. 2015). Moreover, climate change can also affect ecosystems by modifying disturbance regimes (Dale et al. 2001). In the face of this pessimistic scenario, assessing the stability of ecological communities and ecosystems under human-driven environmental change is becoming a major goal in conservation ecology (Fisher et al. 2016, Mori et al. 2017).

Globally, human populations have been responsible for acute changes in land-use, fire regimes and increases in intensity and severity of droughts over vast swaths of land, likely affecting many aspects of ecosystem functioning, especially ecosystem productivity, stability and biodiversity (Vitousek et al. 1997, Sala et al. 2000, Hooper et al. 2012, Hautier et al. 2015). However, our current knowledge of ecosystem stability in areas affected by chronic anthropogenic disturbance (CAD) is limited. CAD is especially prevalent in dry areas of the tropics, where very dense human populations are dependent on forest ecosystems and resources (Singh 1998, Specht et al. 2015). In these areas, it is essential to understand how CAD may harm ecosystem stability, and consequently, compromise the future use of these ecosystem resources by humans. Thus, in areas where people are continuously extracting natural resources, ecological communities might be in a constant process of secondary succession, and species colonizations and extinctions might also occur continuously (Lehtilä et al. 2016). Consequently, ecosystem stability would be lower in more disturbed areas than in relatively undisturbed areas. In tropical dry areas, aridity is a relevant factor that might also affect ecosystem stability, where harsh environmental conditions in the driest areas may harbor more dynamic communities than wetter areas, where environmental conditions are more favorable for stability (Diamond et al. 2016). Moreover, aridity may interact with disturbance to intensify ecosystem instability (Pulla et al. 2015, Puig-Gironès et al. 2017).

The study of mutualistic ecological interaction networks has contributed to our understanding of the mechanisms that maintain ecosystem stability (Benadi et al. 2013, Rohr et al. 2014). Plants bearing extrafloral nectaries (EFNs) produce high carbohydrate-rich resources, which attract several ant species (i.e. attendant ants) that potentially defend their hosts from herbivores (Bentley 1977). Such mutualisms form

stable networks of interacting species which are likely resilient to disturbance (Díaz-Castelazo et al. 2010, 2013). However, some studies have reported that the decline in abundance of some EFN-bearing plants in human-disturbed habitats is related to decreases in the number of species of arboreal dominant ants (Câmara et al. 2016) and ant visitation rates (Leal et al. 2015). As most plant and ant species are vulnerable to climate change (Moritz and Agudo 2013, Resasco et al. 2014, Diamond et al. 2016), the combined effects of disturbance and climate change might cause an impoverishment of plant and ant communities in the driest disturbed habitats (Gibbs et al. 2015, Rito et al. 2017). It is unclear, however, whether changes in plant and ant communities across gradients of CAD and rainfall might alter EFN-bearing plant–ant mutualism networks over time.

The mechanisms that shape the stability of free-living mutualistic networks are complex; even when both mutualistic partners co-occur, they may not necessarily interact (Poisot et al. 2015). Thus, environmental change might not only affect the temporal stability of ecological networks by altering community structure and composition of mutualistic partners, but also by climate-induced changes in the behavior of mutualist partners (Kiers et al. 2010). Ant preferences for EFN-bearing plants depend on EFN nectar amount and composition (Blüthgen and Fiedler 2004a, b, Bixenman et al. 2011), and nectar production is highly dependent on abiotic and biotic factors (Bixenman et al. 2011, Alves-Silva and Del-Claro 2014). In addition, the physical conditions of microhabitats determine the spatial and temporal foraging patterns of ants (Fitzpatrick et al. 2014, Arnan and Blüthgen 2015). Thus, in more environmentally unstable areas (probably the most disturbed and arid areas), shifts in ant foraging patterns and plant preferences may be more pronounced from year to year, thus increasing temporal instability in interaction networks.

Here, we investigate the additive and combined effects of CAD and rainfall on the temporal stability of mutualistic EFN-bearing plant–ant networks in a Caatinga dry forest. Caatinga is a typical seasonally dry tropical forest that supports a high density of EFN-bearing plants (Melo et al. 2010, Leal et al. 2017). Despite the wide range of ecosystems where EFN-bearing plants interact with ants (Rico-Gray and Oliveira 2007), there is some evidence that this protective service is more effective in arid environments (Leal and Peixoto 2016). However, the Caatinga is continuously degraded by human activities such as wood extraction, overgrazing by livestock (cattle and goats) and collection of non-timber forest products (Albuquerque et al. 2007, Ramos and Albuquerque 2012, Ribeiro et al. 2015, Arnan et al. 2018a). These human activities can threaten important ecosystem services provided by mutualists, such as ant-mediated seed-dispersal (Leal et al. 2014) and plant protection against herbivores (Leal et al. 2015, Câmara et al. 2018). In addition, the Caatinga is also threatened by climate change, with an increase of mean annual temperature between 1.7°C and 6.7°C and a reduction in rainfall of 22–40% predicted for the end of the twenty-first century (IPCC 2014). Because

the Caatinga encompasses different rainfall regimes (Sampaio 1995), even within small geographic ranges (Rito et al. 2017), it offers an excellent opportunity to study the potential effects of CAD and rainfall reduction on the stability of plant–ant mutualistic networks. We tested the following two hypotheses: 1) the additive effect of increasing CAD and decreasing rainfall will reduce the temporal stability of EFN-bearing plant–ant networks, and 2) the combined effects of increasing CAD and decreasing rainfall will negatively affect the temporal stability of EFN-bearing plant–ant networks, whereby the temporal stability will be lowest in the most arid and disturbed sites. We then investigated three non-exclusive mechanisms that might explain changes in temporal stability of EFN-bearing plant–ant networks along the gradients: 1) changes in the interacting EFN-bearing plant community, 2) changes in the attendant–ant community, and/or 3) changes in attendant–ant behavior.

## Material and methods

### Study area

The study was conducted in the Catimbau National Park, Pernambuco state, northeastern Brazil (8°24'00" and 8°36'35"S; 37°09'30" and 37°14'40"W; Fig. 1). The Park

covers an area of 607 km<sup>2</sup> dominated by low stature (6–8 m) Caatinga vegetation. The climate is semi-arid, with an average temperature of 23°C and mean annual rainfall ranging from 480 to 1100 mm, mostly received between March and July (Rito et al. 2017). Predominant soils are quartzite sandy soils (72.3% of the park), but planosols, latosols and vertisols are also present (Rito et al. 2017). The most representative plant families are Fabaceae, Euphorbiaceae and Cactaceae (Rito et al. 2017). Such families are the most dominant EFN-bearing plants in the world (Weber et al. 2015), and together with other EFN-bearing plant families such as Anacardiaceae, Capparaceae, Passifloraceae and Turneraceae, they comprise 15% of woody species and 39% of individuals in the Catimbau flora (Leal et al. 2017).

Catimbau National Park has been protected by law since 2002; however, there are still low-income rural populations living inside the park borders who use the forest resources for their survival (Rito et al. 2017). These populations contribute to CAD through, for example, extraction of non-timber forest products (e.g. exploitation of tree bark for medicinal purposes and hunting), animal husbandry (especially goats and cattle) and wood extraction (e.g. firewood, for the construction of houses, fences and handy crafts) (Rito et al. 2017, Arnan et al. 2018a). These varied sources of disturbance spread out across the Park, show high and independent spatial variability, and point to complex patterns of resource

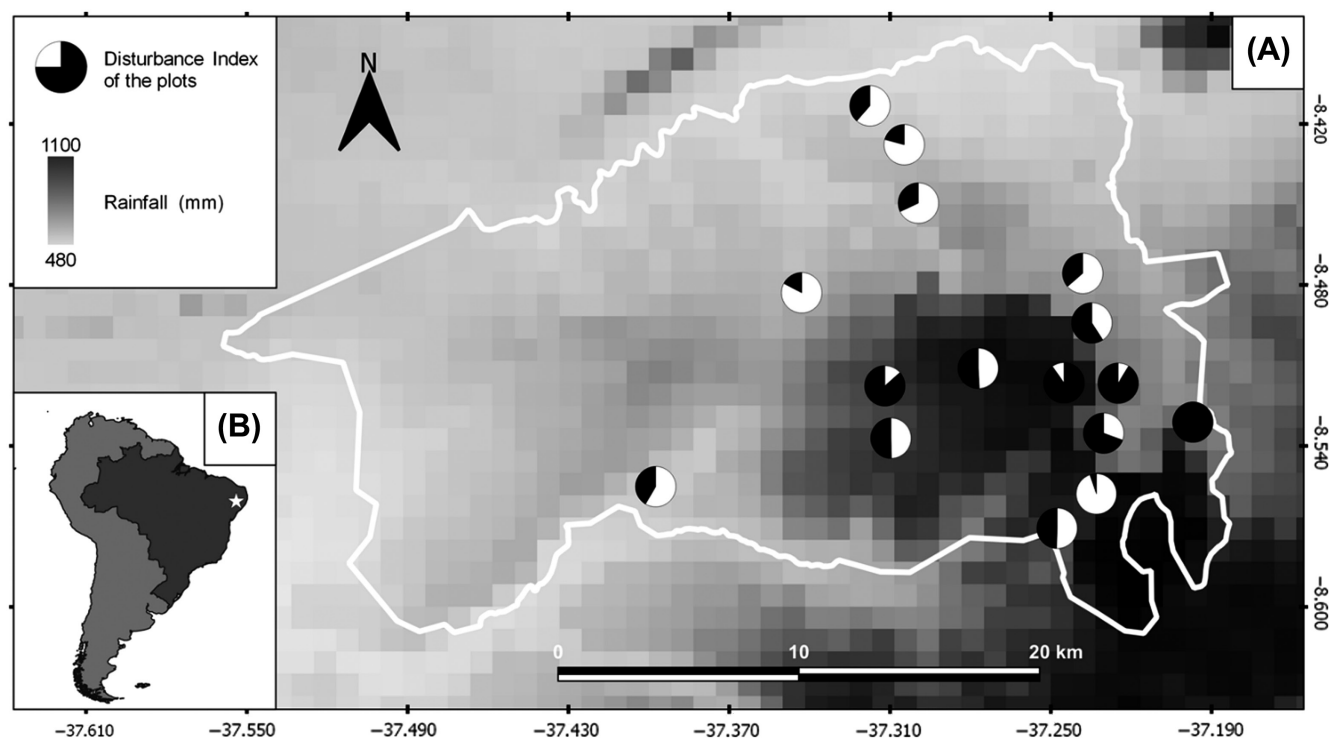


Figure 1. Representation of the study area at different scales: distribution of the sixteen 50×20 m plots (circles) over rainfall and chronic anthropogenic disturbance (CAD) gradients in the Catimbau National Park (map with white outline) (A) and the localization of the Catimbau National Park (white star) in Brazil (dark grey) (B). The proportion of black within each circle represents the level of CAD with the higher proportion of black indicating more disturbance. The background black and white color scale depicts the mean annual rainfall gradient.

use by local communities with different areas targeted for different resources (Arnan et al. 2018a). We established sixteen 20×20 m plots with a minimum 2-km distance within a 214 km<sup>2</sup> landscape (Fig. 1). All plots were on sandy soil, had similar slope, and supported old-growth vegetation that had not experienced slash-and-burn agriculture for at least 50 yr. These plots were exposed to varying levels of CAD and rainfall, thus forming gradients of both CAD and rainfall.

### Characterization of disturbance and rainfall gradients

We characterized the level of CAD in each plot by computing a global multi-metric index that integrates eight disturbance indicators related to the three main sources of CAD in the Catimbau National Park: livestock pressure (herbivory by goats and cattle), wood extraction (live and dead wood) and exploitation of non-timber forest products (poaching/hunting, medicinal plants, collection of food items for human consumption and livestock fodder) (Rito et al. 2017, Arnan et al. 2018a). Livestock pressure and wood extraction were directly measured in the field through assessments of goat trail length, goat dung frequency, cattle dung frequency, live wood extraction (stem cuts) and coarse woody debris extraction (litter) within each plot (Arnan et al. 2018a). Non-timber products were estimated via three variables related to the accessibility and influence of human activities in each plot: proximity to the nearest house, proximity to the nearest road and number of people living in each house that engage in the practices described above (Arnan et al. 2018a). These three indirect disturbance indicators were integrated into a single metric – people pressure – by means of PCA analysis (Arnan et al. 2018a). Data from the single disturbance metrics (livestock pressure, wood extraction and people pressure) were integrated into a compound, additive index in which different kinds of disturbance contribute to an overall level of chronic anthropogenic disturbance. The compound index ranged from 2 to 58 (from the lowest to the highest level of disturbance) among the plots. For more details on the characterization of disturbance and calculation of the global multi-metric index, Arnan et al. (2018a).

Data on mean annual rainfall was obtained from the WorldClim global climate data repository ver. 1 (<www.worldclim.org>, Hijmans et al. 2005), which contains spatial climate data from 1960 to 1990. We downloaded the dataset at 30 arc seconds resolution, and the mean annual rainfall at each plot was extracted using the 'maptools' package (Bivand and Lewin-Koh 2015) in the R software ver. 3.3.1 (R Core Team). This resulted in a spatial resolution of 1 km<sup>2</sup>, which provides climatic data that are directly applicable to the scale of sampling where interactions between EFN-bearing plants and ants were observed and avoids overlapping in climatic conditions among plots (plots were separated by at least 2 km). Mean annual rainfall ranged from 510 to 940 mm, representing almost a 50% variation in rainfall over a small geographic area. Past studies conducted in the same study

area using the same plots and Worldclim data, showed strong effects of climate gradients on plant (Rito et al. 2017) and ant (Arnan et al. 2018b) communities, and in their interactions (Câmara et al. 2018, Oliveira et al. 2019). Thus, the Catimbau National Park provides an excellent opportunity to investigate the effects of rainfall variation on the stability of interaction networks. CAD and rainfall gradients were not significantly correlated ( $r=0.23$ ,  $p>0.05$ ), and therefore were statistically independent.

### EFN-bearing plant–ant networks

We observed attendant–ant species visiting EFN-bearing plants in all plots from March to July in 2014 and March to April in 2016. These months comprise the rainy season in the Caatinga, when extrafloral nectar secretion is high (Câmara unpubl.). First, we performed preliminary censuses using direct observations to determine which plant species bear EFN. Then, we performed censuses twice in all plots (once in 2014 and once in 2016) on all EFN-bearing plants with height  $\geq 1$  m and diameter basal height (DBH)  $\geq 3$  cm in the morning, from 06:00 to 10:00 am. Each EFN-bearing plant was inspected for up to 10 min and ants were considered feeding nectar when mouthparts were in contact with EFNs. These procedures have been widely adopted in studies describing EFN-bearing plant and attendant–ant interactions (Leal et al. 2015, Câmara et al. 2018). EFN-bearing plant and attendant–ant species that were not identified in the field were collected and transported to our laboratory where they were identified to the species level or sorted into morphospecies whenever this was not possible. We only considered interacting plants and ants and not the entire plant and ant communities.

For each of the sixteen plots, we constructed a matrix based on the records of interactions between EFN-bearing plant species and attendant–ant species in 2014 and 2016. Since ants are social insects, to avoid bias due to the proximity between plants and ant trails or nests (Gotelli et al. 2011), interactions between ants and EFN-bearing plant species were considered as the number of individual EFN-bearing plants on which an ant species was recorded, regardless of the total number of ant workers. That is, when two different ant species visited a single EFN-bearing plant, or if one ant species visited two individuals of the same EFN-bearing plant species, we considered both cases as two different interactions.

### Data analysis

The temporal stability of EFN-bearing plant and attendant–ant communities was computed for each plot using four different parameters that characterize community structure and composition. First, we computed the absolute difference in abundance of EFN-bearing plant and attendant–ant species between years. Considering again the social nature of ant colonies (Gotelli et al. 2011), the abundances of EFN-bearing plant species were estimated by the number of individuals



interacting with attendant–ant species while the abundances of ant species were estimated by the frequency of each ant species interacting with an individual of a EFN-bearing-plant species. Second, we computed the absolute difference in richness of EFN-bearing plant and attendant–ant species between years. Third, we computed the absolute difference in diversity of EFN-bearing plant and attendant–ant species. Diversity was computed as the exponential of Shannon entropy ( $e^H$ ) which estimates the effective number of species present in a particular community (Jost 2006). Fourth, we computed the Bray–Curtis dissimilarity index, comparing plant and ant (both involved in EFN-bearing plant–ant interactions) community compositions between years. The Bray–Curtis dissimilarity is defined as:

$$d_{BC} = -1 \frac{B + C}{A + B + C}$$

where A is the relative abundance of each species found in both communities (2014 and 2016), while B and C are the relative abundance of unique species found in 2014 and 2016, respectively. This index ranges from 0 to 1, where 0 represents the lowest dissimilarity and 1 the highest dissimilarity in species composition.

In order to evaluate the stability of the interaction networks, we used four specialization network metrics: 1) interaction evenness (IE), which quantifies the equitability of the interaction frequency between EFN-bearing plant and attendant–ant species; 2) weighted quantitative generality (Gw), which is the mean of the effective number of EFN-plants visited per ant species weighted by the interaction frequency of ant species (i.e. specialization at the level of ants); 3) weighted quantitative vulnerability (Vw), that is analogous to generality, but instead of focusing on the highest trophic level, it focuses on the lowest – it is thus the mean of the effective number of ants per EFN-plant species weighted by the interaction frequency of EFN-plant species (i.e. specialization at the level of plants); and 4) network specialization index  $H_2'$ , which provides information about functional complementarity and redundancy among ant and EFN-bearing plant species at the community level (i.e. specialization at the overall network level). This index estimates specialization based on differences between realized and expected associations generated by null frequency distributions of the marginal totals (Blüthgen et al. 2006). For more details on each network metric, Dormann et al. (2009) and Supplementary material Appendix 1. Temporal stability of community interaction networks was then computed (similarly to ant and plant community structure) as the absolute difference of each network between the two years of study (i.e.  $\Delta IE_{obs}$ ,  $\Delta Gw_{obs}$ ,  $\Delta Vw_{obs}$ ,  $\Delta H_2'_{obs}$ ).

Since the stability of network metrics can be affected by richness and sampling effort (Dormann et al. 2009), we also computed the same network specialization metrics controlled for changes in species occurrences and abundances between years to remove network size effects. Given that the effects of different species occurrence and/or species abundance were

removed, this approach allowed us to detect changes in stability due to factors other than changes in ant or plant community structure, i.e. changes in species identity (with different interacting behaviors) and/or changes in species behavior. Thus, we first performed 10 000 randomizations of each interaction network matrix in 2014 and 2016 by using the Patefield algorithm (Blüthgen et al. 2008). This algorithm fixes the marginal totals (i.e. total number of interactions recorded per EFN-bearing plant species and attendant–ant species) and produces random interaction networks. The mean value of each specialization metric was computed from all randomized matrices per plot and year (i.e. we computed 32 random values for each specialization metric). We then computed the absolute difference in the random specialization metrics between the two years of study for each plot (i.e.  $\Delta IE_{rand}$ ,  $\Delta Gw_{rand}$ ,  $\Delta Vw_{rand}$ ,  $\Delta H_2'_{rand}$ ). Finally, the stability in abundance- and richness-controlled specialization network metrics were computed as the difference between the observed and the random network metrics: 1)  $\Delta[IE] = \Delta IE_{obs} - \Delta IE_{rand}$ , 2)  $\Delta[Gw] = \Delta Gw_{obs} - \Delta Gw_{rand}$ , 3)  $\Delta[Vw] = \Delta Vw_{obs} - \Delta Vw_{rand}$  and 4)  $\Delta[H_2'] = \Delta H_2'_{obs} - \Delta H_2'_{rand}$ . Observed and abundance- and richness-controlled specialization metrics were computed using the Bipartite package (Dormann et al. 2009) in R.

For all response variables, low differences between years mean high stability. Therefore, we standardized all response variables according to the following formula:

$$S = - \frac{(y_i - y_{min})}{(y_{max} - y_{min})}$$

where  $S$  is temporal stability,  $y_i$  is the observed value for each response variable found in plot  $i$  (e.g.  $\Delta[IE]$ ),  $y_{min}$  is the minimum observed value found for this variable across all plots and  $y_{max}$  is the maximum observed value across all plots. This standardization puts all variables on the same scale and the stability gradient from low to high values. Thus, temporal stability for each response variable ranged from  $-1$  to  $0$ , where zero is the highest stability (no change between years) and negative values up to  $-1$  represent lower stabilities. Because the difference in EFN-bearing plant richness had few discrete values (ranging between 0 and 2, except one plot with a value of 6) and many zeros, we transformed this variable into a binary variable. Therefore, plant richness with high temporal stability were those that had no differences between years, represented by 0, while plant richness with low temporal stability were those that had some variation in species richness (i.e. values such as 1, 2 or 6) between years, and were represented by  $-1$ .

We analyzed the effects of CAD and rainfall (and their interaction) on the stability of EFN-bearing plant (with the exception of richness) and ant communities, and on network specialization (either observed and abundance- and richness-controlled metrics) using general linear models. In turn, the effects of CAD, rainfall and their interaction on stability of species richness of EFN-bearing plants were analyzed using a generalized linear model with a Binomial distribution and a

logit-link function. All models were rerun only adding CAD and rainfall (and not adding their interaction) as fixed factors when the interaction between CAD and rainfall were initially not statistically significant ( $p < 0.05$ ). We tested the normality of all model residuals using Shapiro–Wilk tests. All analyses were conducted in R.

### Data deposition

Data available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.c5g4qt7>> (Câmara et al. 2019).

### Results

We observed 312 interactions between 17 EFN-bearing plant and 25 ant species in 2014, and 243 interactions between 19 EFN-bearing plant and 26 ant species in 2016 (a total of 555 interactions during the two years of study, involving 23 EFN-bearing plant and 33 ant species, Supplementary material Appendix 2, 3). Almost half of the EFN-bearing plant (43% of 23 species) and attendant–ant species (45% of 33 species) interacted exclusively in only one year of the survey (Fig. 2). *Pityrocarpa moniliformis* and *Tacinga palmadora*

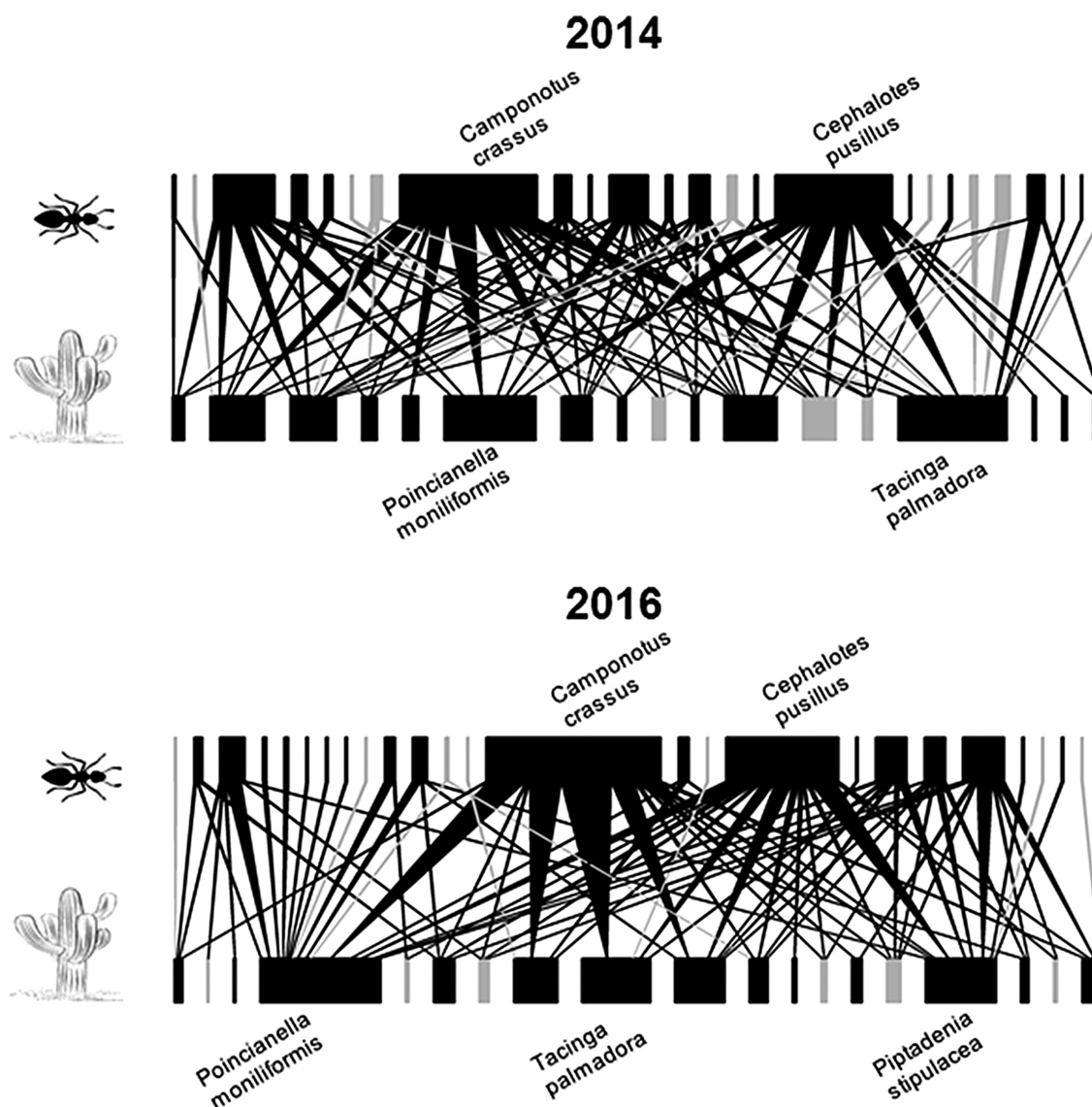


Figure 2. Quantitative EFN-bearing plant–ant networks surveyed during the years 2014 and 2016 across sixteen plots in the Caatinga forest, Brazil. Box width is proportional to the total number of interactions recorded per species, indicating the contribution of each species within the network. Width of links denotes interaction frequency. Upper boxes are represented by attendant–ant species, where black boxes are attendant–ant species that interacted in both years of survey while gray boxes represent attendant–ant species that interacted in only one year of the survey. Lower boxes represent EFN-bearing plant species, while black boxes represent plant species that interacted in both years of survey and white boxes represent plant species that interacted in only one year. The name of the species with the highest contribution to the total number of interactions per year is shown.

were the most common EFN-bearing plant species interacting with attendant–ant species, encompassing near 50% of the interactions in 2014, while *P. moniliformis*, *T. palmadora* and *Piptadenia stipulaceae* were the most abundant plant species encompassing ~52% of the interactions in 2016. In turn, *Camponotus crassus* and *Cephalotes pusillus* were the ant species that visited the most EFN-bearing plants: both were responsible for 62% and 58% of the interactions in 2014 and 2016, respectively (Fig. 2).

Overall, both EFN-bearing plant and attendant–ant communities were similarly stable along CAD and rainfall gradients. From the four parameters used to measure temporal stability (abundance, richness, diversity and composition) of EFN-bearing plant communities, only diversity was affected by CAD and its interaction with rainfall (Table 1). Thus, stability in plant diversity decreased as CAD increased along the entire gradient, with greater reductions in the wetter rather than in the driest areas (Fig. 3A). Moreover, all four parameters used to measure the temporal stability of attendant–ant

communities were not affected by CAD, rainfall or their interaction (Table 1). However, the temporal stability of interaction networks was shaped by environmental change. The stability of observed generality (i.e. stability of specialization at the ant level) was strongly affected by CAD, rainfall and their interaction (Table 2). Overall, stability decreased with increasing CAD, and the reduction was greater in the wettest areas (Fig. 3B). The observed stability in vulnerability (i.e. stability of specialization at the plant level) was significantly affected by CAD and rainfall when the interaction effect from the model was excluded (Table 2, Supplementary material Appendix 4): an increase in CAD led to a decrease in temporal stability of observed vulnerability (Fig. 4A) while a reduction in annual rainfall resulted in a decline in temporal stability of vulnerability (Fig. 4B). The observed stability in interaction evenness and  $H_2'$  (i.e. stability of specialization at the overall network level) were not affected by CAD, rainfall or their interaction (Table 2, Supplementary material Appendix 4). The stability in the abundance- and richness-controlled vulnerability was only affected by CAD (Table 2); that is, an increase in CAD resulted in a reduction in temporal stability of vulnerability (Fig. 4C). The abundance- and richness-controlled  $H_2'$  were only marginally affected by CAD when the interaction effect was excluded from the model (Table 2, Supplementary material Appendix 4), thus the stability of  $H_2'$  decreased as CAD increased (Fig. 4D). However, the stability in the abundance- and richness-controlled interaction evenness and generality were not affected by CAD, rainfall or their interaction (Table 2, Supplementary material Appendix 4). Since we were only able to compute the observed and abundance- and richness-controlled stability of  $H_2'$  for 11 interaction networks due to small network sizes, we repeated the analyses for the other specialization metrics using the same 11 networks. We found similar results to those found when using all sixteen plots (Supplementary material Appendix 4).

## Discussion

We have shown that the increase in human disturbance and a decrease in rainfall do not affect the stability in the structure of interacting plant and ant communities in a consistent manner, but that they (especially CAD) reduce the temporal stability of the structure of EFN-bearing plant–ant mutualistic interaction networks in Caatinga vegetation. Emer and collaborators (2013) showed that changes in the structure of interacting plant and animal communities are important for interaction network structure. Previous studies reported relevant negative effects of land-use changes, on temporal stability of plant and animal communities (Yang et al. 2012, Blüthgen et al. 2016). Meanwhile, climate variation has been highlighted as an important factor shaping plant and animal communities across spatial and temporal scales (Zelicova et al. 2014, Diamond et al. 2016). In general, it is widely accepted that environmental conditions in wetter areas are more favorable for community stability than in drier areas

Table 1. Effects of chronic anthropogenic disturbance (CAD), mean annual rainfall and their interaction on the stability of EFN-bearing plant and ant communities, measured using abundance, richness, diversity and species composition dissimilarity between the years 2014 and 2016 in the Caatinga dry forest, Brazil (n = 16 networks). Significant values are in bold.

Source of variation	t	p
Stability of EFN-bearing plant species abundance		
CAD	1.588	0.141
Rainfall	0.870	0.403
CAD × Rainfall	−1.751	0.108
Stability of EFN-bearing plant species richness		
CAD	1.648	0.099
Rainfall	1.176	1.205
CAD × Rainfall	−1.596	−1.535
Stability of EFN-bearing plant species diversity		
CAD	2.999	<b>0.012</b>
Rainfall	1.660	0.125
CAD × Rainfall	−3.360	<b>0.006</b>
Stability of EFN-bearing plant community composition		
CAD	0.751	0.467
Rainfall	−0.388	0.705
CAD × Rainfall	−0.594	0.563
Stability of attendant–ant abundance		
CAD	0.927	0.374
Rainfall	0.834	0.422
CAD × Rainfall	−1.199	0.256
Stability of attendant–ant species richness		
CAD	0.066	0.948
Rainfall	0.749	0.469
CAD × Rainfall	0.177	0.862
Stability of attendant–ant species diversity		
CAD	−0.884	0.396
Rainfall	−0.274	0.789
CAD × Rainfall	0.852	0.412
Stability of attendant–ant community composition		
CAD	−1.771	0.1020
Rainfall	−1.000	0.3369
CAD × Rainfall	1.870	0.0847

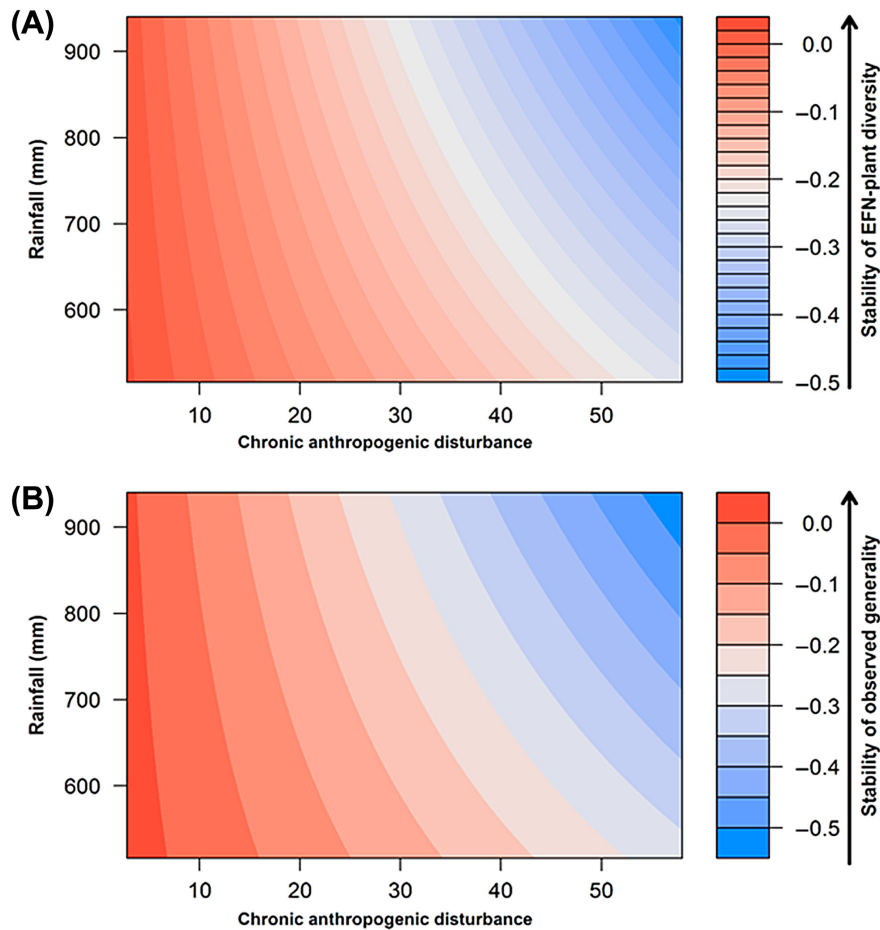


Figure 3. Contour plots showing the interaction effect between chronic anthropogenic disturbance (CAD) and rainfall variation on the stability of EFN-bearing plant diversity (A) and observed generality in EFN-bearing plant–ant networks (B) in the Caatinga dry forest, Brazil.

(Diamond et al. 2016), which is also believed to be the case for seasonally dry tropical forests (Allen et al. 2017). However, recent studies have proposed that plant and ant communities appear to be stable temporally even under climate change scenarios (Zelicova et al. 2014, Donoso 2017). In support of this, we found disturbance effects on the temporal stability in the diversity of interacting plant communities only, and no effects on the stability in the structure of interacting ant communities or the composition of interacting plant and ant communities. In addition, both interacting EFN-bearing plant and attendant–ant communities were similarly stable along rainfall gradients. We thus demonstrate that despite the stability of community structure of interacting organisms is similar, there are large changes in the stability of the structure of their interactions along the environmental gradients. This is manifested by the consistent negative effects that increasing CAD impose on the stability of network specialization at the ant (generality), plant (vulnerability) and overall network ( $H_2'$ ) levels. Furthermore, variation in rainfall levels affect differently the components of the stability of network specialization: a decrease in rainfall related to a reduction in the stability of the specialization at the plant level (stability of

vulnerability) but an increase in the stability of specialization at the ant level (stability of generality).

Interestingly, these changes in the temporal stability of interacting EFN-bearing plant communities and their interactions appear to be mostly driven by changes in ant behavior rather than by changes in the structure of interacting communities across the environmental gradients. First, changes in the stability of interaction networks almost parallels changes in the stability in diversity of interacting plants. However, our EFN-bearing plant communities are mostly composed of long-lived shrubs and trees. Although previous studies have reported changes in the structure of woody plant communities at different levels (taxonomic, functional and phylogenetic) along gradients of CAD in the Caatinga (Ribeiro et al. 2015, 2016, 2019, Ribeiro-Neto et al. 2016, Rito et al. 2017), these changes were measured along spatial gradients where disturbed areas were subjected to long periods of disturbance (> 50 yr) rather than short periods. It is thus difficult to envision strong effects of CAD on plant communities in two years. And second, we found effects of CAD on the stability of abundance- and richness-controlled interaction network metrics, particularly on the stability of



Table 2. Effect of chronic anthropogenic disturbance (CAD), mean annual rainfall and their interaction on stability of the observed interaction evenness, generality, vulnerability,  $H_2'$  and their abundance- and richness-controlled equivalents between the years 2014 and 2016 in the Caatinga dry forest, Brazil (n=16 networks). Statistical outputs for independent factors and not their interaction were shown when the initial model failed to find significant interaction effects (for the statistical outputs for complete models, see Supplementary material Appendix 4). Significant values ( $p < 0.05$ ) are in bold.

Source of variation	t	p
Observed interaction evenness		
CAD	0.887	0.394
Rainfall	1.561	0.147
CAD × Rainfall	−0.987	0.345
Observed generality		
CAD	3.305	<b>0.006</b>
Rainfall	2.205	<b>0.048</b>
CAD × Rainfall	−3.717	<b>0.003</b>
Observed vulnerability		
CAD	−2.582	<b>0.023</b>
Rainfall	2.251	<b>0.042</b>
Observed index $H_2'^+$		
CAD	1.299	0.235
Rainfall	0.735	0.486
CAD × Rainfall	−1.707	0.132
Controlled interaction evenness		
CAD	0.458	0.656
Rainfall	0.349	0.733
CAD × Rainfall	−0.656	0.526
Controlled generality		
CAD	1.241	0.238
Rainfall	0.847	0.414
CAD × Rainfall	−1.421	0.181
Controlled vulnerability		
CAD	−2.548	<b>0.024</b>
Rainfall	0.709	0.491
Controlled index $H_2'^+$		
CAD	−2.252	0.054
Rainfall	−0.892	0.398

<sup>+</sup>We analyzed the temporal stability of observed and controlled index  $H_2'$  only with 11 networks due to the impossibility of generating values from null modelling in five networks in 2016.

abundance- and richness-controlled vulnerability (i.e. specialization at the plant level) and  $H_2'$  (i.e. specialization at the overall network level), although only marginally significant effects for the latter. All these results taken together makes it plausible to think that changes in the stability of both the diversity of interacting EFN-bearing plants and interaction network structure along the CAD gradient are driven by temporal changes in ant behavior in response to different abiotic conditions between years. If ant species from the most disturbed areas behave more differently from year to year than species from the least disturbed areas (i.e. they interact more or less intensively with more or less plant species in different years), this implies that temporal changes in ant behavior determine temporal changes in network structure (e.g. generality, vulnerability). Alternatively, although temporal changes in ant composition are constant along the CAD gradient, they

might also be relevant and might involve different changes in species identity (and consequently, behavior) at different ends of the gradient, respectively.

Temporal changes in ant behavior might be explained either by temporal changes in abiotic conditions that regulate the availability of nectar, i.e. the basal resource that mediates these interactions, or by direct effects on ant activity. Vegetation in areas that are frequently disturbed might be in constant early-successional stages, and consequently, their habitat conditions will quickly change. As the secretory activity of EFNs are also induced by abiotic conditions (Bixenman et al. 2011, Lange et al. 2017), nectar production and quality in more disturbed areas might be more variable among years, thus greatly changing plant individual attractiveness to ants from year to year. In fact, these changes might be responsible for changes in the stability of the diversity of interacting plants, because ants might choose to interact more or less intensively with a plant depending on nectar quality and quantity. Similarly, nectar production and quality are largely affected by water availability (Lange et al. 2013, Dáttilo et al. 2015). If the driest areas are unstable environments that experience a great variation in water availability for plants from year to year, this probably will affect the temporal secretory activity of EFNs, and might explain larger inter-annual variations in the ants interacting with a particular plant species (i.e. vulnerability) in most arid areas. Also, Fitzpatrick et al. (2014) showed that physical conditions such as temperature on plants' surfaces might also determine temporal ant foraging patterns. If abiotic conditions on plants' surfaces change between years, which is more likely to occur in more unstable disturbed areas, this might lead to changes in ant foraging activity. Unfortunately, we do not have temperature and/or precipitation measurements for our plots during the collection of interaction data, but it is apparent that microclimatic instability is higher in most disturbed open areas (Chen et al. 1995, Laurance 2002).

In line with our second hypothesis, our results showed synergistic effects between CAD and rainfall on the temporal stability of observed network generality (i.e. the effective number of plant species visited by ant species or specialization at the ant level). Thus, CAD effects on stability were higher in wetter than in drier areas of the park, and rainfall variation only affected network stability in most disturbed areas. Puig-Gironès et al. (2017) reported rainfall effects on the post-fire recovery patterns of plant and bird populations in a Mediterranean region. They found plant and bird populations recovered more slowly in arid areas compared to wet environments. Similarly, Salvatierra and collaborators (2017) showed that drier deforested areas had slower plant recover than wetter deforested areas in the Caatinga. These studies thus suggest that communities that are constantly in early-successional stages will be more similar from year to year in the driest areas. Moreover, these studies were focused on acute disturbances (i.e. complete loss of forest biomass), whereas our study targeted chronic anthropogenic disturbance (constant removal of small fractions of

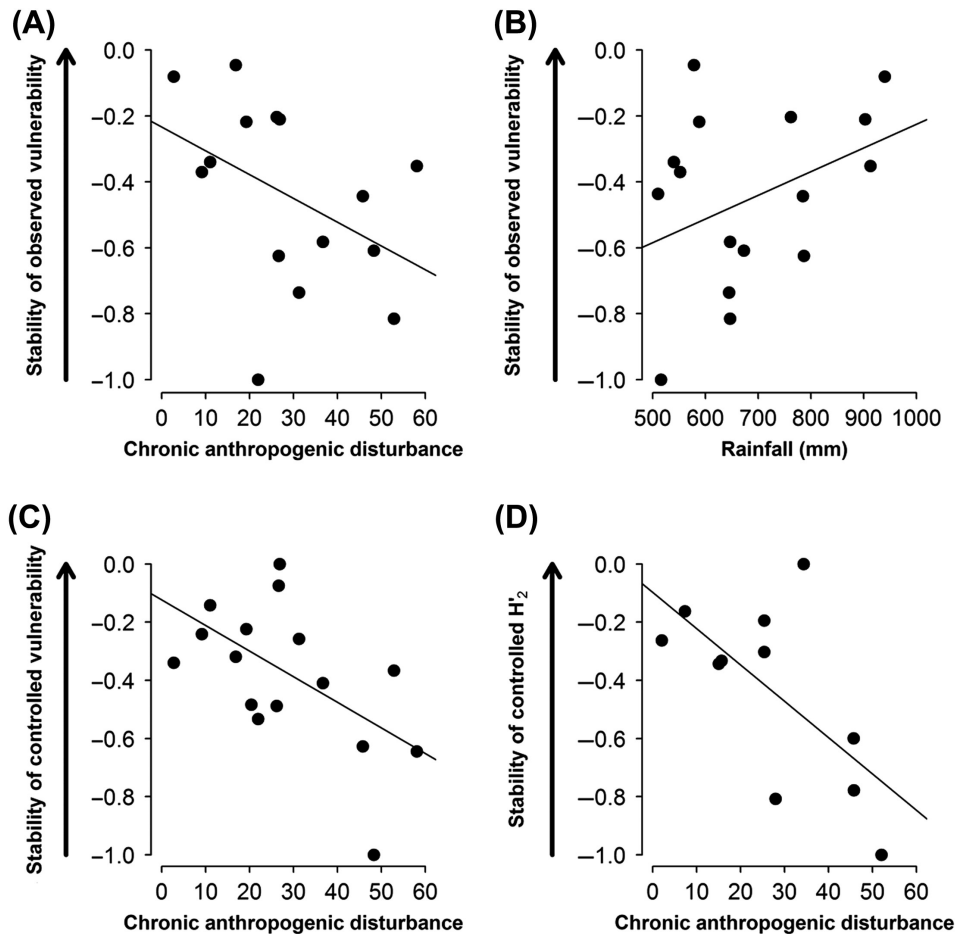


Figure 4. Effect of chronic anthropogenic disturbance (CAD) (A) and rainfall variation (B) on the temporal stability of observed network vulnerability, and the effect of chronic anthropogenic disturbance on the temporal stability of abundance- and richness-controlled network vulnerability (C) and index  $H_2'$  (D) in EFN-bearing plant–ant networks in the Caatinga dry forest, Brazil.

forest biomass). If the post-disturbance recovery of vegetation is faster in wetter areas than in drier ones, wet areas are probably important sources of forest products and become increasingly used by local populations. Thus, wet areas might be subjected to a more continuous exploitation of forest resources over time than dry areas, which may make them more unstable.

Although two years might not seem long for a study of ecosystem stability, we provide several pieces of clear evidence that inter-annual changes in the structure of the interaction networks follow spatial patterns driven by variations in disturbance and rainfall levels. Our study highlights the fact that CAD keeps the system continually in the early stages of secondary succession, that is, the more unstable stages that are less resilient to future disturbances. Several studies have found that plant–animal interactions are altered by anthropogenic disturbance and climate change, compromising the quality of the provided services in disturbed areas (Kiers et al. 2010 and references therein). However, most studies focus on spatial patterns between disturbed and undisturbed habitats.

Since biotic interactions are not static but highly dynamic over time, it is essential to consider how plant–animal interactions vary through time (Poisot et al. 2015) along environmental gradients. Our results showing inter-annual variation in EFN-bearing plant–ant networks along chronic anthropogenic disturbance and rainfall gradients complement our understanding about potential impacts of human activities and climate change on biodiversity, and especially on ecosystem functioning. Anthropogenic disturbance and decreasing rainfall are important drivers that might cause destabilization of EFN-bearing plant–ant interactions, compromising the quality of the anti-herbivore defense service. High inter-annual variation in the number and abundance of ant species visiting a particular plant species in disturbed habitats and in more arid areas might compromise the protection service, since ant species vary markedly in the quality of the defensive service they provide to their host plants (Del-Claro and Marquis 2015, Fagundes et al. 2017). It is thus essential to expand protected areas in the Caatinga for the maintenance of ecosystem functioning and stability. Since our results show

that rainfall variations mediate anthropogenic disturbance effects by reducing the temporal stability of mutualistic interactions in wetter disturbed areas, conservation policies should give special priorities to wet areas.

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Supplementary material (available online as Appendix ecog-04531 at <[www.ecography.org/appendix/ecog-04531](http://www.ecography.org/appendix/ecog-04531)>). Appendix 1–4.



