Extinction–immigration dynamics lag behind environmental filtering in shaping the composition of tropical dry forests within a changing landscape

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Research

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The impact of rapid habitat loss and fragmentation on biodiversity is a major issue. However, we still lack an integrative understanding of how these changes influence biodiversity dynamics over time. In this study, we investigate the effects of these changes in terms of both niche-based and neutral dynamics. We hypothesize that habitat loss has delayed effects on neutral immigration–extinction dynamics, while edge effects and environmental heterogeneity in habitat patches have rapid effects on niche-based dynamics.

We analyzed taxonomic and functional composition of 100 tree communities in a tropical dry forest landscape of New-Caledonia subject to habitat loss and fragmentation. We designed an original, process-based simulation framework, and performed Approximate Bayesian Computation to infer the influence of niche-based and neutral processes. Then, we performed partial regressions to evaluate the relationships between inferred parameter values of communities and landscape metrics (distance to edge, patch area, and habitat amount around communities), derived from either recent or past (65 yr ago) aerial photographs, while controlling for the effect of soil and topography.

We found that landscape structure influences both environmental filtering and immigration. Immigration rate was positively related to past habitat amount surrounding communities. In contrast, environmental filtering was mostly affected by present landscape structure and mainly influenced by edge vicinity and topography.

Our results highlight that landscape changes have contrasting spatio-temporal influences on niche-based and neutral assembly dynamics. First, landscape-level habitat loss and community isolation reduce immigration and increase demographic stochasticity, resulting in slow decline of local species diversity and extinction debt. Second, recent edge creation affects environmental filtering, incurring rapid changes in community composition by favoring species with edge-adapted strategies. Our study brings new insights about temporal impacts of landscape changes on biodiversity dynamics. We stress that landscape history critically influences these dynamics and should be taken into account in conservation policies.

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Keywords: assembly processes, ecological modelling, edge effects, extinction debt, habitat loss, neutral dynamics

Introduction

Habitat loss and fragmentation are global concerns for biodiversity conservation (Myers et al. 2000, Haddad et al. 2015, Taubert et al. 2018), and how they affect species persistence and coexistence in space and time is a critical question in community ecology (Niebuhr et al. 2015, Fahrig 2018, Figueiredo et al. 2019, Miller-Rushing et al. 2019). Specifically, understanding how dispersal and stochastic demography, on one hand and environmental filtering, on the other hand, jointly influence diversity patterns in a context of habitat loss and fragmentation remains challenging (Matthews and Whittaker 2014, Püttker et al. 2015).

The equilibrium theory of island biogeography (ETIB, MacArthur and Wilson 1967) provides a conceptual foundation to understand how the balance between stochastic immigration and extinction processes influences biodiversity in habitat patches (MacArthur and Wilson 1967, Wilson and Willis 1975). ETIB predicts that immigration decreases with increasing patch isolation, and extinctions increase with decreasing patch area (MacArthur and Wilson 1967, Wilson and Willis 1975, Laurance 2008, Püttker et al. 2015). From another perspective, the habitat amount hypothesis (HAH, Fahrig 2013) states that immigration–extinction equilibrium in a given site primarily depends on the amount of habitat in the surrounding landscape. Both ETIB and HAH emphasize that local biodiversity rely on immigration and local stochastic extinction (i.e. ecological drift, Vellend et al. 2014) and assume that species have equivalent probabilities to establish in local habitat, so that they lean on neutral assembly dynamics (Hubbell 2001, Volkov et al. 2003, Püttker et al. 2015). However, environmental heterogeneity within and among patches can differentially filter species according to their ecological attributes (i.e. functional traits), which determine their ecological strategies and influence their probability to establish and persist in a given environment (Chase 2005, McGill et al. 2006, Violle et al. 2007, Püttker et al. 2015). Hence, if species are functionally different, local community composition in heterogeneous habitat patches should depend on both immigration–extinction dynamics and trait-based environmental filtering (McGill 2010, Matthews and Whittaker 2014).

Although landscape changes may affect both immigration–extinction dynamics and environmental filtering, their respective signature on diversity patterns can emerge with different tempos. First, reaching a new immigration–extinction equilibrium after habitat reduction and/or isolation may involve a substantial delay and incur an extinction debt, especially because this relies on stochastic demography (Kuussaari et al. 2009, Jackson and Sax 2010). Second, edge effects can entail strong changes in environmental conditions within patches, so that habitat fragmentation should affect environmental filtering (Ewers and Didham 2005, Harper et al. 2005, Didham et al. 2012). However, such environmental change can directly affect species persistence and should more quickly influence local community composition (Gilbert et al. 2006, Kuussaari et al. 2009). Nonetheless, how such distinctive temporal influences affect observed diversity patterns at a given time remain little studied.

Extensive process-based simulation of community dynamics has proved helpful to disentangle the respective influences of stochastic and trait-based assembly processes on diversity patterns (Jabot et al. 2008, Zurell et al. 2010, Munoz et al. 2018, Denelle et al. 2019). Indeed, community functional composition should reflect the imprint of environmental filtering (McGill et al. 2006), while taxonomic diversity should better capture the influence of stochastic immigration–extinction dynamics (Munoz et al. 2007). Comparing community composition simulated under various immigration rates and environmental filters to an observed community pattern allows to explicitly infer the contribution of these processes to community assembly (Zurell et al. 2010, Munoz et al. 2018).

Tropical forests have been largely studied through the prism of habitat loss and fragmentation (Laurance et al. 2011, Haddad et al. 2015, Taubert et al. 2018). Likewise, the imprint of neutral and deterministic processes on tropical forest composition have been a major focus of community ecology during the last two decades (Hubbell 2001, Gilbert et al. 2006, Kraft et al. 2008, Swenson 2013). Yet, the pace at which such processes influence tree community patterns in the context of landscape changes remains poorly addressed.

Here, we investigated the influence of habitat loss and fragmentation on tree community assembly in New-Caledonia's highly threatened tropical dry forest (Gillespie and Jaffré 2003), with two main purposes: 1) deciphering the respective contributions of neutral and niche-based assembly processes, and 2) identifying different tempos of their influence on diversity patterns. We characterized functional and taxonomic composition of 100 observed tree communities, and inferred plausible contributions of neutral and trait-based processes with intensive coalescent-based simulations and approximate Bayesian computation (Munoz et al. 2018). We examined how estimated parameters were related to past and present landscape structure, in terms of distance to edge, patch area and habitat amount surrounding communities. We also assessed the influence of soil and topography within habitat patches, which should contribute to environmental filtering apart from spatial habitat structure (Jucker et al. 2018, Blanchard et al. 2019). We hypothesized that immigration–extinction dynamics depended on community isolation and has a delayed influence on community composition, while compositional shifts due to environmental filtering should occur more quickly and be related to edge influence on local environmental conditions.

Material and methods

Study area

New Caledonia is an archipelago located in southwest Pacific (20–23°S, 164–167°E). The study area is a 20 × 20 km landscape located in a plain surrounded by

low-elevation mountains (500–1000 m), on the west coast of the main island (Kone–Pouembout plain). It receives ~1000–1400 mm yr^{-1} rainfall and the mean annual temperature is ~23–24°C (WorldClim2 database, Fick and Hijmans 2017). The vegetation is a mosaic of evergreen dry forest patches ('tropical dry forest', Holdridge 1947) surrounded by secondary thickets and farmlands. All patches considered in this study were located on volcano-sedimentary substrate below 300 m a.s.l. The whole area was probably mainly covered by forest before anthropogenic landscape modification (Jaffré et al. 1998). Then, the current forest cover results from clearing and fires dating from both pre-European (i.e. since 3500 yr ago) and post-European time (i.e. since about 200 yr ago), with an intensification over the last century (Jaffré et al. 1998). Overall, tropical dry forest of New-Caledonia has been reduced to 2% of its original extent, which makes it the world's most endangered tropical dry forest (Gillespie and Jaffré 2003).

Sampling design and landscape metrics

We first characterized the present-day landscape structure by digitizing all forest patches at a scale of 1:3000 scale (i.e. 1 cm on the map represents 30 m), using recent georeferenced aerial photographs (2012). We also digitized past georeferenced aerial photographs (1954) to assess past landscape structure. Both recent and past aerial photographs were available online (<www.georep.nc>). We used Qgis software (QGIS Development Team) for digitization.

Then, we designed a random sampling scheme stratified by patch area. Based on a present landscape map, we selected 36 accessible patches spanning a wide range of area (0.5–272.2 ha, median 23.6). We excluded areas recently colonized by the forest (i.e. areas currently covered by forest, but which were open in 1954). Then, we applied a 25 × 25 m square grid and, in each patch, we randomly selected a number of grid nodes proportionally to the logarithm of patch area. The resulting number of points per patch ranged from 1 to 12, with a total of 100 points. Within a circular 400 m^2 plot (i.e. 11.30 m radius) at each selected point, we identified all trees with diameter at breast height (DBH, 1.3 m above ground) above 10 cm. We ensured that the entire plots were actually within forest patches by relocating the center of plots away from the edge if necessary. All the plots were established during years 2017 and 2018.

For both past and present landscapes, we calculated three metrics characterizing landscape structure around sampling points: 1) the minimum distance to patch edge, 2) the area of the embedding fragment and 3) the proportion of surrounding forest area (i.e. the habitat amount). Forest habitat amount was calculated within buffers of 250, 500, 1000 and 2000 m around sampling points. As suggested by Fahrig (2013) we used the Akaike information criterion (AIC) to select the buffer yielding the best univariate relationship between species richness (i.e. the number of species in sampled plots) and habitat amount. Using this method, we retained a 500 m buffer for past landscape and a 250 m buffer for present landscape (Supplementary material Appendix 1). Distance to edge and patch area were log-transformed prior to analyses.

As variation in water and nutrient availability related to soil and topography may influence environmental filtering (Blanchard et al. 2019), we calculated topographic indices, including elevation, curvature, aspect and topographic wetness index, from a 10 m DEM (Direction of Technologies and Information of New Caledonia, DTSI). In addition, we extracted the log-transformed distance to the nearest river (Direction of Infrastructures, Topography and Land Transport of New Caledonia, DITTT) and the lithology of the soil substrate, defined as volcanic or sedimentary (Direction of Industry, Mines and Energy of New Caledonia, DIMENC).

Trait sampling

For all sampled species, we measured five wood and leaf functional traits involved in resource-use strategies and stress resistance, following standardized protocols in Pérez-Harguindeguy et al. (2013). Trait were collected during years 2017 and 2018. For leaf traits, we collected five leaves per individual and sampled five individuals per species. For compound leaves, we considered a leaflet as the laminar unit. Petioles and petiolules were removed from leaves before measurement. We measured leaf area (the area of a leaf in cm^2), specific leaf area (the leaf area per dry mass in $cm^2\,g^{-1}$) and leaf dry-matter content (the leaf dry mass per fresh mass in $mg\,g^{-1}$). Specific leaf area and leaf dry-matter content capture species investment in leaves, and represent a trade-off between acquisitive (high specific leaf area) and conservative (high leaf dry-matter content) strategies along the leaf economic spectrum (Wright et al. 2004). Leaf area represents the light-capturing and transpiration surface and is thus related to water-use efficiency (Moles 2018). We measured the wood density of one wood sample per individual and five individuals per species. Wood density is a key trait of the wood economic spectrum, from water use efficiency and high growth rate to lower growth rate and drought resistance (Chave et al. 2009). Furthermore, we measured bark thickness. Thick bark provides stem protection from heat and fire (Pausas 2015), as well as from other damages (Rosell 2016). For bark thickness, we calculated the mean of two bark measures on individual trees, and sampled at least 15 individuals per species (mean = 17.8). For wood density and bark thickness of 38 species, data were complemented from the New Caledonian plant inventory and permanent plot network (NC-PIPPN) database, in which trait measurements were carried out using identical protocols (Ibanez et al. 2017a). In subsequent analyses, we used the mean trait value per species for leaf traits and wood density. As bark thickness varies with DBH (Pausas 2015), we used the maximum value per species, to better approximate an upper bound reached during tree growth. We used a Box–Cox transformation (Box and Cox 1964) on each trait to get distributions closer to normality. The five functional traits were finally informed for 99 species, representing

90% of the identified species (n = 110), and more than 99% of the identified individuals (n = 3089). We used this subset of 99 species in further analyses.

Species ecological strategies

We evaluated trait covariation to identify main functional dimensions (trait spectra) across species by performing a principal component analysis (PCA) of species traits values, with varimax orthogonal rotation of the three first components. Trait values were centered and scaled to unit variance before performing PCA. We considered species scores on the first three rotated PCA (RPCA) axes as synthetic trait values representing species ecological strategies along the main functional dimensions. The synthetic trait values where standardized between 0 and 1 prior to further analyses.

Community assembly model

We used the coalescent-based model of community assembly provided by Munoz et al. (R package 'ecolottery') to simulate community composition under a joint effect of deterministic and neutral processes. This model rebuilds the genealogy of individuals in a community by sampling their immigrant ancestors from a reference species pool, while conditioning establishment success and subsequent persistence to both trait-based environmental filtering and stochastic demography (Munoz et al. 2018).

In the model, immigration determines how stochastic species extinctions in the community are counterbalanced by an influx of new immigrants. The balance of migration and stochastic demography is quantified with the migration rate m, which represents the probability that a dead individual in the community is replaced by a migrant from the pool ($1-m$ being the probability that the dead individual is replaced by the offspring of the remaining individuals of the community). When the value of m is 1, there is no effect of local stochastic demography and the community is a random sample of the source pool of immigrants. As m decreases, the influence of demographic stochasticity conversely increases. We also examined the related immigration parameter $I = m(J-1)/(1-m)$, where J is the number of individuals in the community. I represents the number of immigrants competing with local offspring to replace a dead individual in the community, and is insensitive to sample size (Etienne and Olff 2004, Munoz et al. 2008, 2018).

Then, environmental filtering is defined as the probability that the immigrants establish in the community depending on how their trait values differ from a functional optimum related to local abiotic conditions. This probability can classically be defined as a Gaussian function of t (species trait values), centered around some optimal trait value topt, with standard deviation σ quantifying how fast the performance decreases away from the optimum (Loranger et al. 2018, Munoz et al. 2018, Denelle et al. 2019). As we considered three main axes of ecological strategies (synthetic traits) in our study, the probability of establishment and persistence of migrants was defined as the product of three Gaussian filters each representing environmental filtering on one of the synthetic traits. Thus, the function defining environmental filtering depended on six parameters, namely, topt1, σ1, topt2, σ2, topt3, σ3.

Parameter estimation and predictive accuracy of assembly models

We estimated parameter values of neutral and deterministic processes for the sampled tropical tree communities by performing approximate Bayesian computation (ABC, Csilléry et al. 2012). The method relies on intensive simulation of community composition for a range of parameter values defined in prior distributions. Then, statistics summarizing community composition, called summary statistics, were compared between simulated and observed communities, so as to characterize the most plausible parameter values complying with actual composition (Munoz et al. 2018).

We simulated the composition of each community over a broad range of parameter values of migration and environmental filtering (coalesc function in R package ecolottery, Munoz et al. 2018). In each simulation, the values of migration parameter (m) and the mean values of the three Gaussian filters (top1, topt2, topt3) were each randomly assigned from a uniform prior distribution between 0 and 1. The standard deviation values of the three Gaussian filters (σ1, σ2, σ3) were each randomly assigned from a uniform prior distribution between 0.01 and 0.25, which represents a wide range in filter intensity from strong to weak, respectively. The observed number of individuals was kept unchanged in each simulation and set to actual sample sizes. In addition, a larger σ could represent a looser filter, and thus a community closer to neutrality.

We quantified summary statistics representing 1) taxonomic composition, i.e. species richness (S, the number of species) and Shannon diversity (ES), and 2) functional composition, i.e. community weighted mean (CWM) and community weighted variance (CWV) of each synthetic trait. Because ecological drift reduces species diversity (Hubbell 2001, Gilbert and Levine 2017), we expected immigration intensity to be positively linked to SR and ES. For each synthetic trait, we expected CWM to be related to topt and CWV to be related to σ, as the variance of the theoretical Gaussian filter is equal to σ^2. As filtering intensity could reduce species diversity, we also expected σ to be positively related to SR and ES.

We performed 10 000 simulations for each of the 100 observed communities, and characterized the posterior distributions of parameters using ABC. The medians of the posterior distributions of parameters provided reference parameter estimates for each community. We log-transformed the immigration parameter I for further analyses. We performed cross-validation to evaluate the reliability of parameter estimation, and to choose the best tolerance level for ABC (a tolerance of 0.05 was chosen, see R package abc, Csilléry et al. 2012).

In order to evaluate the predictive accuracy of the assembly model, we designed posterior predictive checks (Csilléry et al. 2010). First, we used the same model with 100 sets of parameter values randomly sampled from their posterior distribution to generate 100 simulated communities for each observed community. Then, we obtained the posterior predictive distributions of each summary statistics from the simulated communities. We used graphical checks to compare the obtained posterior predictive distributions with the observed values of summary statistics (Csilléry et al. 2010).

Statistical analyses

In order to analyze the effect of past and present landscape structure on community assembly dynamics, we tested the relationships between estimated parameters of the community assembly model, representing filtering and neutral processes, and landscape metrics of both past and present landscape. We also tested the effect of soil and topographic conditions, since we expected them to influence environmental filtering.

First, we selected for each parameter the combination of topographic and soil predictors yielding the lowest corrected AIC when regressed against the parameter (AICc, corrected for sample size and number of predictors). Then we grouped predictors in three matrices: 1) present landscape metrics, 2) past landscape metrics and 3) soil and topography (i.e. the previously selected subset). We performed partial regressions (varpart and rda functions of the vegan R package, Oksanen et al. 2019) to partition the total and independent effects (i.e. adjusted R^2) of the three groups of predictors on each parameter of deterministic and neutral processes. Then, we partitioned the nested total and independent effect of each landscape metric (i.e. distance to edge, patch area and habitat amount) for both past and present metrics. We assessed the significance of the total and independent effects of each predictor and groups of predictors using a permutations test with 9999 permutations (Legendre and Legendre 2012). Finally, in order to evaluate if the effect of landscape structure varied when considering only communities far from the edge, we carried out the analysis on forest interior communities only (i.e. communities being at more than 50 m from past and current edges, n = 32). All analyses were performed using R (R Core Team, R Foundation for Statistical Computing, Vienna, Austria).

Results

Changes in landscape structure

From 1954 to 2012, forest cover declined from 3350 ha to 2050 ha (i.e. a 37% reduction), while the number of forest patches more than doubled (from 137 to 296, Fig. 1). Over this period, distance to edge decreased by more than 10 m for 36 communities, while it increased by more than 10 m for 20 communities (Supplementary material Appendix 2). Surrounding patch area and habitat amount increased for 13 and 27 communities, while they decreased for 87 and 73 communities, respectively (Supplementary material Appendix 2).

Species ecological strategies

The three first axes of the rotated principal component analysis (RPCA) represented more than 82% of species functional variation (Fig. 2). The first axis of the RPCA (31.87%) was positively related to species investment in leaves, and to a lesser extent in wood, running from high specific leaf area to high leaf dry-matter content and wood density. The first axis thus represented species strategies along an acquisitive–conservative spectrum. The second axis of the RPCA (28.1%) represented a trade-off between high hydraulic efficiency (high leaf area, low wood density) on the negative side, and drought resistance provided by low transpiration (low leaf area, high leaf dry-matter content) and low embolism risk (high wood density) on the positive side. The third axis (22.1%) was positively related to bark thickness, and to a lesser extent negatively correlated with species investment in wood and leaves (wood density and leaf dry-matter content). Therefore, we referred to these axes as acquisitive–conservative (axis 1), drought resistance (axis 2), and stem protection (axis 3).

Parameter inference and posterior predictive checks

The estimated immigration parameter (I) was highly variable among communities (min = 2.3, max = 180.5, mean = 40.7). With the selected tolerance of 0.05, mean prediction errors from cross validation were between 0.20 and 0.25 for topt values, and between 0.5 and 0.65 for σ and I (Supplementary material Appendix 3). As expected, estimated optimal trait values (topt1, topt2, topt3) were strongly correlated with observed values of CWM for each of the three synthetic traits (Supplementary material Appendix 4). Likewise, estimated standard deviations of the Gaussian filters (σ1, σ2, σ3) were strongly correlated with CWV values for related synthetic traits, and positively correlated with taxonomic diversity (SR: species richness and ES: Shannon diversity). Estimated values of the immigration parameter were strongly and positively correlated with taxonomic diversity (Supplementary material Appendix 4). Using sampled values of parameters from their posterior distributions obtained with ABC, the model was able to simulate communities whose summary statistics accurately fitted to the observed values for CWM and SR values, and with reasonable accuracy for ES (Supplementary material Appendix 5). However, CWV values were less well predicted as they tended to be lower than the observed ones when they become large (Supplementary material Appendix 5).

Influence of landscape structure on community parameters

Estimated immigration mainly depended on past landscape metrics, with a significant independent effect (Table 1).

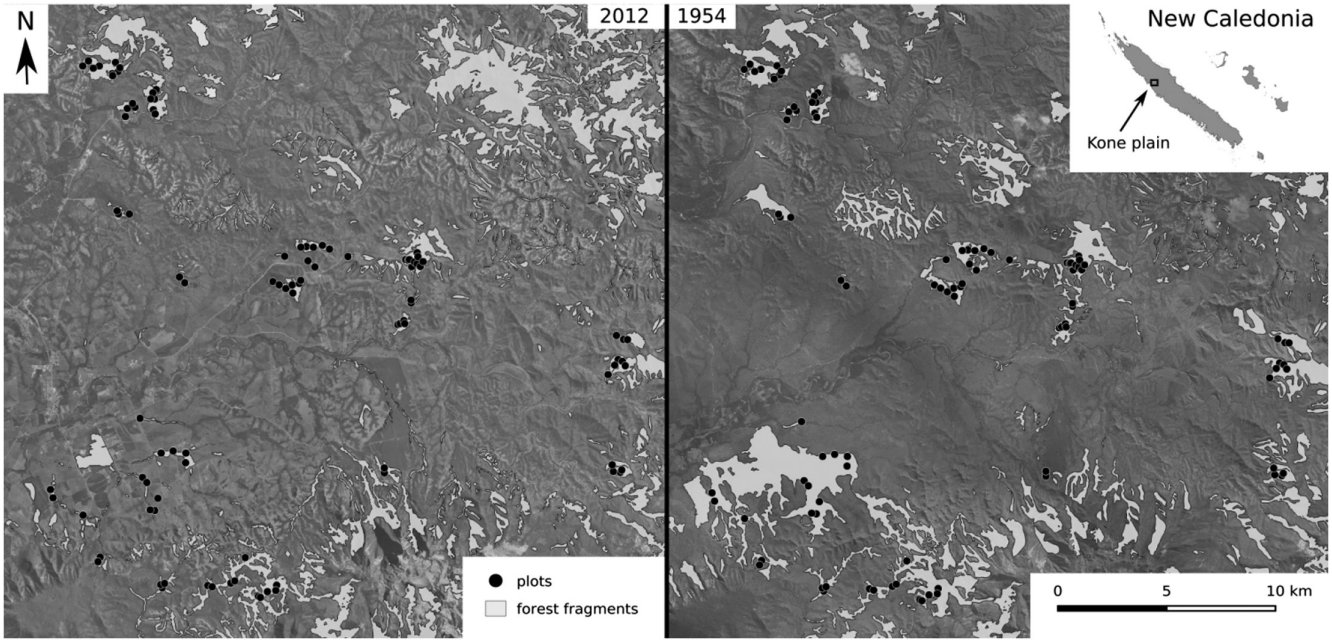

Figure 1. Maps of forest patches in the Kone–Pouembout plain (light grey), derived from recent (2012, left) and past (1954, right) aerial photographs. The positions of the 100 sampled plots are indicated on each map (black points).

Immigration increased with edge distance, patch area and habitat amount, with a stronger and independent effect of habitat amount (Table 1, Fig. 3a).

Estimated parameters of environmental filtering mainly depended on present landscape metrics and topography. Along the acquisitive–conservative axis (RPCA axis 1), the optimal trait value (topt1) of communities was positively linked to present landscape metrics (distance to edge, patch area and habitat amount, Table 1, Fig. 3b), with significant independent effect. We also detected independent effects of past landscape metrics on the intensity of filtering along the acquisition–conservation functional dimension (σ1), with an additional effect of topography. Specifically, we found weak but positive independent effect of habitat amount on σ1 (Table 1, Fig. 3c).

Environmental filtering related to drought resistance (RPCA axis 2) mainly depended on soil and topography (Table 1), as the optimal trait value (topt2) increased with distance from rivers, terrain convexity and on sedimentary soils (Supplementary material Appendix 6). Conversely, we found significant negative effects of current distance to edge on topt2 (Fig. 3d). The intensity of drought-induced filtering decreased (i.e. σ2 increased) with past distance to edge (Fig. 3e).

Environmental filtering related to stem protection (RPCA axis 3) depended on both past and present landscape metrics, with an independent effect of past landscape metrics (Table 1). topt3 decreased with increasing distance to edge (Fig. 3f), patch area and habitat amount, without any independent effects. Filtering intensity on stem protection (σ3) also depended on past and present landscape metrics, as well as on topography (Table 1). σ3 increased with present edge distance (which had an independent effect, Table 1, Fig. 3g), past edge distance, past patch area and past habitat amount.

Forest interior communities

In communities far from the edge (> 50 m), the effects of landscape metrics on environmental filtering were generally weaker or no more significant (Fig. 3, Supplementary material Appendix 7). Yet, environmental filtering depended more on topography and soil in these communities (Supplementary material Appendix 7, 8). Contrastingly, the immigration parameter was still related to past habitat amount for communities of forest interior (Fig. 3, Supplementary material Appendix 4).

Discussion

We estimated parameters of deterministic and neutral assembly processes by performing intensive community simulation and approximate Bayesian computation (ABC) (Munoz et al. 2018). We found that both types of processes drove tree community dynamics in a dry tropical forest landscape that experienced recent habitat loss and fragmentation. Despite a relatively moderate explained variance, all inferred parameters were significantly affected by landscape metrics, emphasizing the pervasive influence of landscape structure on community dynamics. Specifically, landscape structure influenced both deterministic and stochastic assembly processes, but yet with different tempos. Recent changes in landscape structure (< 65 yr) could entail local shifts in tree community composition through rapid environmental filtering of persisting species depending on their functional strategies. Contrastingly,

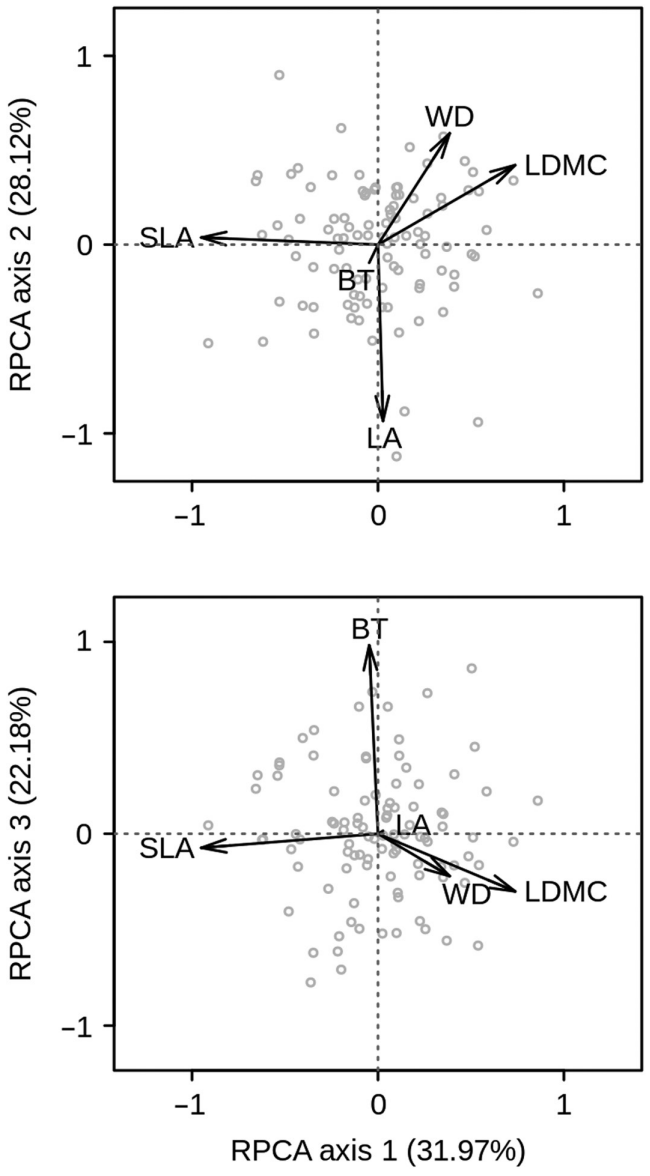

Figure 2. Rotated principal component analysis of mean values of the five measured species traits (SLA: specific leaf area; LA: leaf area; LDMC: leaf dry-matter content; WD: wood density; BT: bark thickness). Traits coordinates are projected on the two first axes on the upper plot, and on the first and the third axes on the lower plot. The three axes represent more than 82% of species functional variation and are considered as synthetic traits.

the immigration parameter representing how dispersal can balance demographic extinction depended on past landscape structure. Landscape influence on immigration–extinction dynamics across habitat patches could thus impact community composition more slowly, leading to possible extinction debt in recently isolated communities.

Effects of landscape structure on immigration

Most empirical studies addressing the effects of landscape structure on biodiversity are based on measuring diversity (e.g. species richness), and interpreting non-random patterns in terms of underlying mechanisms. Here we used a process-based framework to explicitly assess the imprint of immigration–extinction dynamics in empiric data. Immigration is a key parameter of community dynamics and is expected to reflect community isolation (Munoz et al. 2008). Our results show that immigration was highly variable among communities and mostly linked to past habitat amount (i.e. forest cover within a 500 m-radius buffer in 1954). Furthermore, immigration still depended on habitat amount in forest interior communities, indicating that this relationship did not only concern edge vicinity. Therefore, in line with recent works on plant communities (Martín-Queller et al. 2017, MacDonald et al. 2018), our study supports more the HAH (i.e. habitat amount determines immigration, Fahrig 2013) than the ETIB. Indeed, the amount of habitat in the 'local landscape' surrounding communities represent primary sources of immigration, and should therefore appropriately describe community isolation from immigrants (i.e. the less surrounding habitat there is, the more isolated the community is, see Fahrig 2013). Yet, if this amount of habitat correspond to the area of the surrounding patch, community immigration–extinction dynamics should essentially rely on patch-level metrics, in agreement with the ETIB. In addition, the extent to which immigration–extinction dynamics rely on patch area also depends on species capacity to disperse between patches (Fahrig 2013, Bueno and Peres 2019). In this respect, HAH and ETIB are not opposing theories, but represent the extremes paradigms of a continuum of scenarios depending on habitat spatial structure and matrix permeability to species dispersal (Bueno and Peres 2019). Our studied landscape includes patches with highly variable size, shape and isolation, within a fast-changing heterogeneous matrix, which could explain why community immigration–extinction dynamics appears more related to the HAH paradigm. However, if further habitat loss results in smaller and more isolated patches, community dynamics could switch to a patch-centric context as promoted by ETIB. Species-specific dispersal ability – which could depend on particular traits not considered here – may also influence their response to landscape structure (Ewers and Didham 2005, Bueno and Peres 2019). Although our approach did not account for such differences among species, our study clearly emphases the negative influence of habitat loss on dispersal dynamics.

Time-lag in ecological drift

Although there is compelling evidence that landscape changes can have delayed effects on biodiversity patterns (Ewers and Didham 2005, Metzger et al. 2009), few studies have tested the influence of past landscape properties on present species diversity (Cousins 2009, Collins et al. 2017). Specifically, stochastic species extinctions following habitat reduction and isolation are hypothesized to happen slowly, entailing some delay (i.e. extinction debt) before reaching some immigration–extinction equilibrium (Jackson and Sax 2010, Halley et al. 2014, Huth et al. 2015, Figueiredo et al. 2019).

Table 1. Partition of the effects of present landscape metrics, past landscape metrics and topographic and soil variables on parameter estimates of environmental filtering (top1, σ1, topt2, σ2, topt3 and σ3) and immigration (log-transformed immigration parameter) for all communities (n = 100). The effects of landscape metrics were first tested for groups of predictors (present landscape metrics, past landscape metrics, topography and soil), and then for each metric (edge distance, E.D.; patch area, P.A.; habitat amount, H.A.). For each predictor and group of predictors, the adjusted R^2 (Adj. R^2, i.e. the total effect) and the conditional R^2 (Adj. R^2c, i.e. the independent effect) are reported when significant (ns: p-value ≥ 0.05; *: p-value < 0.05; **: p-value < 0.01; ***: p-value < 0.001). For landscape metrics, the sign of the significant effects (coefficients) are indicated. For each parameter, the unexplained variance are also reported.

Parameter	Groups	Pred.	Coef.	Adj. R^2	Adj. R^2c	Adj. R^2	Adj. R^2c
log(I)	Present landscape	E.D.	(+)	**0.04***	ns	ns	ns
		P.A.	.	ns	ns		
		H.A.	.	ns	ns		
	Past landscape	E.D.	(+)	**0.08****	ns	**0.15*****	**0.13****
		P.A.	(+)	**0.07****	ns		
		H.A.	(+)	**0.16*****	**0.07****		
	Topography and soil	.	.	.	.	ns	ns
	Unexplained	.	.	.	.	0.84	
topt1	Present landscape	E.D.	(+)	**0.14*****	ns	**0.19*****	**0.13****
		P.A.	(+)	**0.16*****	ns		
		H.A.	(+)	**0.09****	ns		
	Past landscape	E.D.	.	ns	ns	ns	ns
		P.A.	.	ns	ns		
		H.A.	.	ns	ns		
	Topography and soil	.	.	.	.	**0.04***	ns
	Unexplained	.	.	.	.	0.82	
σ1	Present landscape	E.D.	.	ns	ns	ns	ns
		P.A.	.	ns	ns		
		H.A.	.	ns	ns		
	Past landscape	E.D.	.	ns	ns	ns	**0.05***
		P.A.	.	ns	ns		
		H.A.	(+)	ns	**0.06****		
	Topography and soil	.	.	.	.	**0.03***	**0.06****
	Unexplained	.	.	.	.	0.91	
topt2	Present landscape	E.D.	(−)	**0.04***	ns	ns	ns
		P.A.	.	ns	ns		
		H.A.	.	ns	ns		
	Past landscape	E.D.	.	ns	ns	ns	ns
		P.A.	.	ns	ns		
		H.A.	.	ns	ns		
	Topography and soil	.	.	.	.	**0.28*****	**0.24*****
	Unexplained	.	.	.	.	0.73	
σ2	Present landscape	E.D.	.	ns	ns	ns	ns
		P.A.	.	ns	ns		
		H.A.	.	ns	ns		
	Past landscape	E.D.	(+)	**0.04***	ns	ns	ns
		P.A.	.	ns	ns		
		H.A.	.	ns	ns		
	Topography and soil	.	.	.	.	ns	ns
	Unexplained	.	.	.	.	0.98	
topt3	Present landscape	E.D.	(−)	**0.12*****	ns	**0.12****	ns
		P.A.	(−)	**0.09****	ns		
		H.A.	(−)	**0.11*****	ns		
	Past landscape	E.D.	(−)	**0.14*****	ns	**0.15*****	**0.05***
		P.A.	(−)	**0.07****	ns		
		H.A.	(−)	**0.09****	ns		
	Topography and soil	.	.	.	.	ns	ns
	Unexplained	.	.	.	.	0.83	
σ3	Present landscape	E.D.	(+)	**0.08****	**0.03***	**0.08***	ns
		P.A.	.	ns	ns		
		H.A.	.	ns	ns		
	Past landscape	E.D.	(+)	**0.09****	ns	**0.1****	ns
		P.A.	(+)	**0.04***	ns		
		H.A.	(+)	**0.09****	ns		
	Topography and soil	.	.	.	.	**0.09****	ns
	Unexplained	.	.	.	.	0.84	

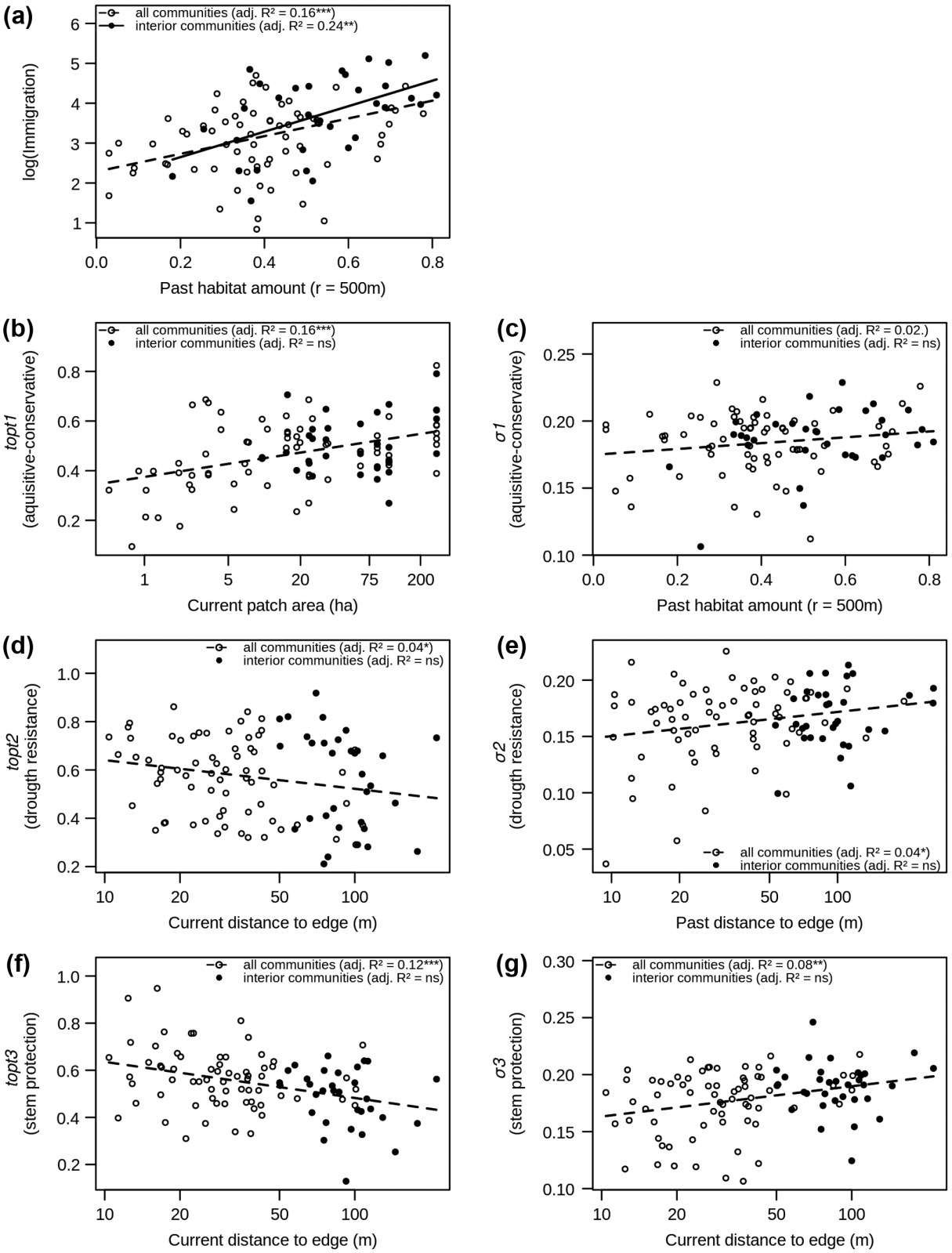

Figure 3. Effects (linear regressions) of landscape metrics on estimated parameters of immigration (log-transformed immigration parameter) and environmental filtering (top1, σ1, topt2, σ2, topt3 and σ3) for all communities (n = 100 plots) and forest interior communities (n = 32 plots). Adjusted R^2 are reported when significant (ns: p-value ≥ 0.05; *: p-value < 0.05; **: p-value < 0.01; ***: p-value < 0.001).

Our results indicate that immigration is better explained by past forest cover (i.e. 65 yr ago). While the time to reach a new immigration–extinction equilibrium after landscape change can be relatively short (i.e. some years) for short-lived species (Ferraz et al. 2003, Grelle 2005), it should be far longer for trees (Cousins 2009, Hylander and Ehrlén 2013). Although quantifying this delay is beyond the aim of this study (Kuussaari et al. 2009, Figueiredo et al. 2019), our results suggest that local extinctions could still be delayed after 65 yr of landscape changes. Conversely, immigration should increase in the few communities for which the amount of surrounding habitat has recently increased. As immigration and establishment of species could also be delayed, these communities may be subject to an immigration credit (i.e. a future gain of diversity, see Jackson and Sax 2010). However, since most parts of the landscape underwent habitat loss since 1954, immigration is likely to decrease in most habitat patches. Nonetheless, we focused on adult tree community (DBH > 10 cm), which could partly explain the observed delay in community response to immigration–extinction dynamics. Finally, further habitat reduction and isolation may reduce this delay by accelerating local extinctions (Haddad et al. 2015).

Intertwined effects of landscape structure on environmental filtering

Niche-based mechanisms encompass environmental filtering, that can be of various type including stabilizing or disruptive (Loranger et al. 2018), and competitive interactions, that can drive limiting similarity (Abrams 1983). While we only considered stabilizing filters in our study (i.e. gaussian filters), our approach allowed us to identify non-random variations of functional optimums and filtering intensity related to landscape metrics. As suggested by the posterior predictive checks, our model could overestimate filtering intensity in communities with high trait variance, which could result from the multiplicative nature of the gaussian filtering function. Although we were able to distinguish the effects of past and present landscape structure on assembly processes, independent effects of distance to edge, patch area and habitat amount on environmental filtering were generally weak or not discernable, highlighting some interdependence. In addition, these joint effects of landscape metrics on environmental filtering were weaker or absent in forest interior. Confounding effects of edge vicinity and habitat area has already been reported in highly fragmented landscapes (Ewers et al. 2007, Didham et al. 2012, Ibanez et al. 2017b). Indeed, distance to edges geometrically decreases along with patch size, leading to cumulative edge effects (Laurance et al. 2011). Thus, we hypothesize that the interdependence between the effects of patch area and distance to edge reflects a pervasive influence of edge effects in small patches.

Edge-related environmental filtering at the forefront of community changes

In tropical forests, edge vicinity is known to influence abiotic conditions (Laurance et al. 2002, Broadbent et al. 2008), and then to entail shifts in community composition (Harper et al. 2005, Laurance et al. 2006). However, the underlying niche-based processes have rarely been explicitly linked to trait-based ecological strategies (Magnago et al. 2014, Benchimol and Peres 2015). Our study demonstrates that edge effects directly impact the nature and the strength of trait-based environmental filtering in communities, by driving shifts in species selection with respect to distinct ecological dimensions. In addition, we showed that landscape changes slowly influence immigration–extinction dynamics, while edge-effect immediately determine establishment success and persistence of species.

Edge vicinity entails modifications in forest abiotic conditions, including increasing drought intensity, temperature, light availability and wind disturbance. These modifications entail increasing tree damages and mortality (Laurance et al. 2011, Magnago et al. 2015), and more open canopy closer to the edge (Harper et al. 2005). Rapid increase in abundance of pioneer species can results from edge-mediated environmental changes in South America (Laurance et al. 2006, Magnago et al. 2014, Benchimol and Peres 2015). Our results highlight that edge-mediated shifts in community composition reflect trait-based filtering of species with respect to their position along a basic acquisitive–conservative ecological axis. Indeed, species with light-demanding, acquisitive strategies (high specific leaf area, low leaf dry-matter content) were favored in communities located near recent edges, suggesting that such compositional shift occurs quickly after edge creation, as suggested by Laurance et al. (2006).

Furthermore, we found that decreasing distance to edge favored species with thicker bark and increased filtering intensity on bark thickness. Our results thus provide strong support for an important role of stem protection in species establishment and survival in communities near the edge. One consequence of forest fragmentation and edge vicinity is increasing exposure to fire (Cochrane 2003, Laurance et al. 2011). Edge-related fire disturbance has been reported to increase tree mortality (Brando et al. 2014), and to impact tree community composition (Michalski et al. 2007). As bark thickness has a key role in species resistance to fire (Hoffmann et al. 2009, Pausas 2015, Pellegrini et al. 2017), fire regime can have substantial influence on species filtering in the studied landscape. Nevertheless, greater herbivory and mechanic injuries at the edge could also favor species with thick bark (Rosell 2016). In addition, filtering related to bark thickness depended on both present and past landscape, suggesting both rapid and persistent influences of edge vicinity after landscape changes.

Conversely, we found weak influence of distance to edge on environmental filtering along the drought resistance axis, with more drought-resistance species (i.e. species with denser wood and smaller leaves) favored near the edge. While edge proximity favored acquisitive species, drought resistance was also involved in species survival near the edge. Indeed, edge proximity is known to increase temperature and drought intensity (Harper et al. 2005, Ibanez et al. 2013). However, these effects are expected to be weaker in dry forests than

in rainforests (Arroyo-Rodríguez et al. 2017). In our study, topographical heterogeneity mainly influenced species filtering depending on hydraulic strategies, as suggested by Jucker et al. (2018) and Blanchard et al. (2019). Thus, local community composition not only depends on landscape structure and edge effects but also on habitat heterogeneity within patches.

Conclusion

Our study suggests that temporal and spatial variations in landscape structure influence both niche-based and neutral mechanisms of community assembly in tropical tree communities. However, the resulting impacts on community composition differ in space and time. On one hand, our results suggest that landscape-level changes slowly impact immigration–extinction dynamics, entailing a slow decrease in diversity along with an extinction debt following habitat loss and isolation. On the other hand, edge creation locally modifies environmental filtering and entails rapid and directional shifts in community composition through the selection of species with edge-adapted ecological strategies. Our study highlights the need to develop approaches that encompass trait-based ecology, ecological modelling, as well as spatial and historical data to better understand and predict how habitat loss and fragmentation can impact biodiversity dynamics in space and time. This is particularly relevant in landscapes with highly reduced habitat density, which are a priority in conservation strategies (Vellend et al. 2013).

Data availability statement

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.jwstqjq5r> (Blanchard et al. 2020).

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Author contributions – GB, FM and PB conceived the study. GB planned the field campaign and collected the data. GB and FM did the analyses. GB, FM and PB wrote the paper.
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Supplementary material (available online as Appendix ecog-04870 at <www.ecography.org/appendix/ecog-04870>). Appendix 1–8.

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