

Herpetofaunal responses to anthropogenic forest habitat modification across the neotropics: insights from partitioning β -diversity

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Abstract Habitat change is the primary cause of biodiversity loss worldwide. Large tracks of primary forest can be (1) degraded by human-induced disturbance to the point of total conversion into alternative non-forest land-use types, or (2) reduced into small forest fragments isolated within an anthropogenic matrix. Such disturbed habitats are further prone to be colonized by disturbance-adapted species, which can offset species extinctions therein. Here we investigate amphibian and lizard responses to different degrees of habitat degradation and fragmentation, in terms of both species richness and composition, across the neotropics. We then partitioned the β -diversity into its species replacement and richness-difference components to further examine changes in amphibian and lizard species composition. Based on a comprehensive compilation of 67 studies, we observed increasing rates of amphibian and lizard species loss, particularly along the habitat degradation gradient. There were considerable shifts in species composition for both taxa at human-disturbed sites, which were compounded by species replacements. Novel environmental features of disturbed sites clearly benefited synanthropic generalists at the expense of strict forest habitat specialists. As such, we recommend avoiding the use of species richness as a single metric in evaluating the effects of habitat disturbance on biodiversity. Our findings further highlight the critical importance of retaining large expanses of relatively

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undisturbed forest within anthropogenic landscapes to prevent pervasive species losses and changes in community structure.

Keywords Amphibians · Anthropogenic landscapes · Biodiversity loss · Forest disturbance · Lizards · Species replacement · Tropical forests

Introduction

Habitat loss and degradation are currently the primary drivers of biodiversity loss worldwide (Sala et al. 2000; Arroyo-Rodríguez et al. 2013; Newbold et al. 2014). Only a few contemporary localities on Earth effectively remain free of human influence (Kareiva et al. 2007), even in the hyper-diverse Neotropical region (Dirzo and Raven 2003). To enhance the persistence of forest biodiversity in rapidly changing land-use mosaics, it is essential to focus our attention on anthropogenic landscapes (Vandermeer and Perfecto 2006; Overbeck et al. 2015). Eventually, understanding the consequences of forest changes on biodiversity can ensure effective management, considering the conservation value of remaining habitat relicts (Gardner et al. 2009; Melo et al. 2013). In our definition of forest change, we include all forest sites that were subjected to any degree of anthropogenic disturbance, leading to differences in either the structure or the total remaining amount of the original forest habitat. As such, we considered two ‘types’ of forest habitat change: (1) habitat degradation, in which the impacts of human activities range from partial modification of the original forest cover (e.g. logging, wildfires, and agroforestry) to the total forest conversion into non-forest land-cover (e.g. pastures, croplands, and tree plantations); and (2) habitat fragmentation, through which small to large primary forest remnants are left within the anthropogenic landscape. We further refer to the contrast between either the structure of primary forests and degraded sites, or the area available in continuous forest and forest remnants, as the level of anthropogenic step-change.

Loss in habitat quality scales along increasing levels of anthropogenic step-changes, so low-contrast changes are more amenable to native biodiversity persistence, both in terms of habitat degradation (Sambuichi et al. 2012) and fragmentation (Fahrig 2003). Indeed, while disturbed forests retaining part of its original structure can still provide habitat for many forest species (Vandermeer and Perfecto 2007; Sambuichi et al. 2012), newly converted anthropogenic habitats do not provide similar resources (e.g. food and shelter) and typically host entirely different microclimatic conditions than previous forest cover (e.g. elevated temperatures and severe desiccation; Hardwick et al. 2015). Different forms of disturbed forest therefore tend to retain greater conservation value compared to deforested areas (Barlow et al. 2007; Gibson et al. 2011). Likewise, local biodiversity in forest fragments is constrained by the reduction and isolation of suitable habitat areas (Fahrig 2003; Hanski et al. 2013), further affected by edge effects (Laurance and Yensen 1991), and the quality of the intervening matrix (Gascon et al. 1999).

Step changes in biodiversity typically consist of reduced species richness, which can often be expressed as local extinctions of those species that are unable to persist under novel disturbed habitat conditions (Devictor et al. 2008; Newbold et al. 2016). Those species usually correspond to strict forest specialists, and changes in their site occupancy are consequently cumulative in determining species compositional differences therein (Lehtinen and Ramanamanjato 2006). However, those changes can additionally result from

the proliferation of common or introduced habitat generalist species (Newbold et al. 2014; Filgueiras et al. 2016; Lososová et al. 2016). For example, species typical of open-areas often expand their distribution into closed-habitat areas, resulting in the substitution of native species by those better adapted to more open conditions (Gardner et al. 2007a; Bitar et al. 2015). Although responses of key functional groups linked to land-use change can severely diminish the integrity of key ecosystems processes (e.g. seed fate and invertebrate predation; Ewers et al. 2015), these processes are rarely considered when evaluating the effects of habitat disturbance (Gotelli and Colwell 2001; Su et al. 2004). The species-area relationship, for instance, assumes species extinction rates as proxies of habitat loss in fragmented landscapes (Rosenzweig 1999), but fails to consider that colonization by disturbance-adapted species can offset extinctions in newly created habitats (Suarez et al. 1998), as observed in avian assemblages of the Brazilian Atlantic Forest (Banks-Leite et al. 2012).

The Neotropical region comprises about half of the world's herpetofauna, which simultaneously includes the most threatened and least studied terrestrial vertebrate taxa (IUCN 2015). Amphibians and lizards are ectothermic and thus rely on specific microhabitats and microclimatic conditions, and are particularly sensitive to habitat disturbance (Vitt and Caldwell 2014), which is the main driver of herpetofaunal species losses (Gibbons et al. 2000; Gardner et al. 2007b). Although often considered as an aggregated taxonomic group, amphibians and lizards may diverge widely in their responses to forest changes (Gardner et al. 2007b). Unlike lizards, which have less permeable scaly skin, amphibians require much more moisture to maintain gas exchange, cultivate bacterial symbionts with immune-function, and protect their eggs (Watling and Braga 2015). This makes them generally more sensitive to desiccation in drier environments such as forest habitats with reduced tree cover, forest edges and the wider non-forest matrix.

Within each taxonomic group, species-specific traits may be important for particular responses to habitat disturbance in determining which species are able to persist in modified landscapes (Devictor et al. 2008; Newbold et al. 2014). For example, life histories of some amphibian species require both aquatic and terrestrial habitat components at different seasons or life stages (Vitt and Caldwell 2014). Indeed, human-induced disconnections between habitats used by different life-history stages can lead to a "habitat split", in which forest amphibians with aquatic larvae are forced into risky breeding migrations between suitable aquatic and terrestrial habitats, thereby threatening species with aquatic reproduction (Becker et al. 2007). Likewise, some diurnal lizard species expose themselves to direct sun-flecks to maintain their body temperature, whereas others avoid direct exposure to sun light (Vitt et al. 1998). Thus, small lizards intolerant of direct exposure to solar radiation, that forage underneath the humid forest leaf litter, are expected to be particularly sensitive to forest changes where canopy gaps are larger or denser (Vitt et al. 1998; Palmeirim et al. submitted).

Given current global change scenarios, understanding the full consequences of many forms of habitat change to herpetofauna is imperative to develop strategic conservation policies. Here, we summarize the responses of both amphibians and lizards to different forms of forest change that are widespread throughout the neotropics, distinguishing between different scales of human disturbance within large forest tracts (forest degradation) and those that result in forest fragmentation. As such, we compiled studies across the neotropics (from Mexico to Argentina) reporting information on amphibian and lizard species richness and composition that allowed explicit comparisons between paired disturbed and undisturbed sites. We hypothesize that (1) due to the higher contrasts in terms of forest structure and available area, forest conversion and large reductions in remaining

forest area are the most detrimental forms of forest habitat disturbance; (2) given the higher susceptibility of amphibians to desiccation, the effects of forest change on amphibian species richness and composition are more severe compared to lizards; and (3) changes in species composition between disturbed and undisturbed sites are due to both species losses and colonization of new species absent from undisturbed sites. To test the last hypothesis, we disentangled the contribution of the two components of beta-diversity—differences in species richness and species replacements—that are critical to understanding how communities respond to spatial, environmental and temporal changes (Carvalho et al. 2012).

Methods

Data acquisition

An exhaustive search of published and unpublished studies (i.e. reports and dissertations) reporting the impacts of forest disturbance on local amphibian and lizard assemblages across the neotropics was carried out using both Web of Science and Google Scholar with the search queries (herpetofauna* OR lizard* OR frog* OR reptile* OR amphibian*) AND (degradation* OR conversion* OR fragmentation* OR disturbance* OR logging* OR deforestation*) AND (neotropical* OR America*). These searches were then repeated using the all keyword combinations translated into both Portuguese and Spanish. Any additional studies were further checked by searching the literature cited in the selected studies. Selected studies presented (1) data on the assemblages of amphibians or lizards and contained at least one site corresponding to a large primary continuous forest of at least 10,000 ha, or an equivalent undisturbed forest, and one site matching at least a single type of forest change; (2) data on at least species richness for each of the sampling sites; and (3) the overall sampling effort allocated at each sampling site. Data for snakes were excluded because they were included in fewer than 20% of the herpetofaunal surveys reviewed. We further excluded any studies carried out in deciduous (dry) tropical forests (e.g. Brazilian *cerrado* and the Argentinean dry *chaco*) and natural habitats devoid of forest cover (e.g. grasslands), because they corresponded to only a small part of the selected studies (<5%), and were outliers in further comparisons with studies carried out in wet and seasonally-dry forests (see geographic location of all studies; Fig. 1).

Part of the studies provided separate data from individual sampling sites, while other studies aggregated data from individual sites. Therefore, for each study, species richness and composition were recorded per site or per group of sites (whenever the preferred first option was unavailable). To streamline terminology, however, the term ‘sites’ is used hereafter for both individual sites and clusters of sites. Information on the country, biome, geographic coordinates, study taxa, sampling method and effort, and number of individuals observed by each study was also recorded. Given that we restricted comparisons to only *within* each study, we did not expect any species composition biases within pairwise comparisons, side-stepping variation in sampling methods across studies.

Pairwise classification of anthropogenic step-changes

We considered two ‘types’ of forest change: habitat degradation, defined as large forest tracts that have been variably degraded by human activities; and habitat fragmentation, defined as large forest tracts have been reduced into forest fragments, ranging in size from

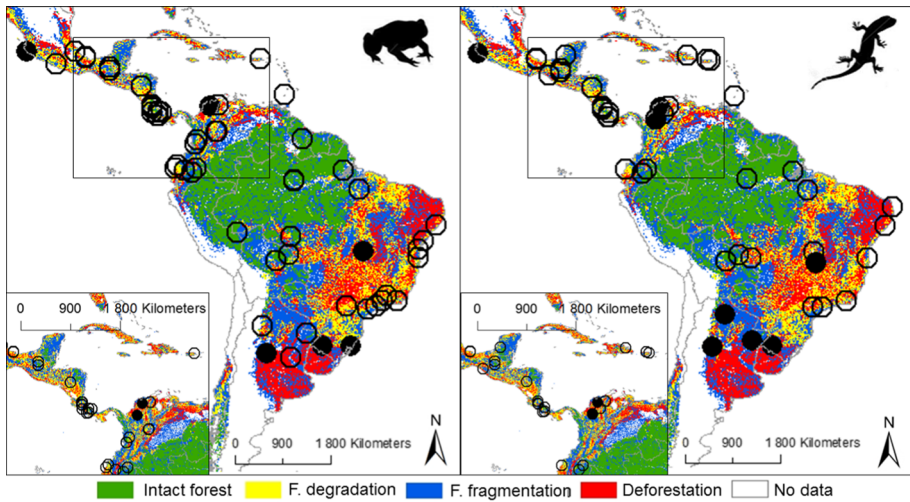


Fig. 1 Geographic locations of herpetofaunal studies reporting responses of amphibians ($n = 60$) and lizards ($n = 48$) to different patterns of forest change across Neotropical wet and seasonally-dry forests (*open circles*) and deciduous (or dry) forests (*solid black circles*). Green background indicates potential forest cover, and different types of forest change considered in this study: forest degradation (yellow), deforestation (red) and forest fragmentation (blue; see text for definition of each type of forest change) Data are sourced from the Global Forest Watch database (http://data.globalforestwatch.org/datasets?q=*%&page=2&sort_by=created_at). (Color figure online)

0.25 to 91.93 ha. Such size restriction of forest fragments resulted from the vast majority of forest fragments sampled by herpetological studies in neotropical fragmented landscapes being <100 ha (Fig. S1), thereby precluding comparisons between fragments across a wider size range. Most studies also reported some degree of forest disturbance in addition to fragmentation-related effects, mainly due to facilitated access in exploiting forest remnants.

We further evaluated amphibian and lizard responses to a gradient of anthropogenic disturbance, resulting from either habitat degradation or fragmentation. Based on the site description provided in each study, values of habitat status were attributed according to the structural contrast between the degraded site and a hypothetically undisturbed primary forest, in terms of complexity of vertical strata and canopy openness (along the gradient of forest degradation), or according to the contrast in terms of forest area lost between a comparable area of continuous forest and the forest fragment (along the gradient of forest fragmentation, Table 1; for a description of each study landscape and corresponding classification, see Table S1 in Supplementary Material). Disturbed and pseudocontrol pairwise comparisons were then assigned a value of anthropogenic step-change defined as the difference between the values assigned to the pseudocontrol and its paired disturbed sites. Pseudocontrol sites corresponded to continuous primary forests, but in 57.3% of cases continuous primary forest had already been lightly to moderately disturbed (e.g. disturbed old-growth forest or large forest fragments). Those disturbed sites were still considered as a pseudocontrol because they represented the best available scenario to measure the impact of forest change but were also assigned a habitat status value ranging from 1 to 10 (Table 1). For studies assessing edge effects along a gradient of edge distances, we included data from only those sampling sites farthest from the edge. We further

Table 1 Rank of habitat status used to classify each site included in the 67 studies compiled and organized into three categories: pseudocontrol sites, disturbed sites under either forest habitat degradation, or fragmentation. Along the gradient of forest degradation, values of habitat status are attributed according to the structural contrast between the degraded site and a hypothetical adjacent primary forest; along the gradient of forest loss, values are attributed according to the contrast in terms of forest area lost between the forest fragment and a comparable continuous forest. Values of habitat status range from 0 (completely undisturbed) to 20 (highly disturbed)

Categories	Habitat status
Sub-categories	
Pseudocontrol sites	
Primary/continuous forest (>3000 ha)	0
Forest remnants	
2001–3000 ha	1
1001–2000 ha	2
751–1000 ha	6
651–750 ha	8
201–650 ha	9
100–200 ha	10
Habitat degradation	
Selective logging	6
Early secondary forest (<15 years old)	7
Abandoned agroforestry	7
Late secondary forest (>15 years old)	10
Agroforestry	13
Burned forest	14
Burned and grazed	15
Abandoned pasture	15
Pasture	16
Abandoned plantation	19
Plantation	20
Habitat fragmentation	
51–100 ha	11
21–50 ha	12
11–20 ha	13
0.3–10 ha	14

excluded from the analysis any study site that could not be matched to one of the forest change patterns considered here.

Data analysis

Responses in the number of amphibian and lizard species were evaluated using the ratio between the species richness of paired disturbed and undisturbed sites (S_{ratio}). Ratios <1 indicate the magnitude of effects, with larger disturbance effects associated with lower ratios. Pairwise comparisons resulting in $S_{ratio} > 1.5$ might reflect sampling artefacts due to

the increased detectability of herptiles in open habitats (e.g. pastures and croplands; Newbold et al. 2014). Overall, it is extremely unlikely that species richness in disturbed becomes 1.5 times or more that of undisturbed sites, hence $S_{ratio} > 1.5$ were treated as outliers and excluded. Effects on species composition were evaluated using the Jaccard dissimilarity index (D_{Jac}) between disturbed and undisturbed sites using species incidence data whenever available.

To evaluate the effects of forest change on amphibian and lizard species richness and composition, we compiled data of both taxa and used generalized linear mixed models (GLMMs) to model S_{ratio} and D_{Jac} according to the interaction between the three explanatory variables: taxonomic group (*Group*), disturbance type (i.e. habitat degradation or fragmentation; *Type*) and level of anthropogenic step-change (*Step-change*). GLMMs considered the case study as the random term to account for natural variability in ecological metrics between study landscapes. To investigate whether the response to overall forest change was similar between the amphibians and lizards, we initially performed model selection considering all additive combinations of fixed factors to construct the candidate model set. We then ranked the formulated models based on their maximum likelihood using the Akaike information criteria (AIC; Burnham and Anderson 2002), and considered that the two groups responded differently to forest change whenever the variable *Group* had been selected in the set of more plausible models (i.e. ΔAIC values between 0 and 2, considering $\Delta AIC = AIC_i - AIC_{min}$ in which $i = i$ th model). If so, amphibians and lizards were then analysed separately, using the modelling procedures described above. These analyses were performed using the *hglm* R package (Rönnegård et al. 2010). We additionally obtained the conditional R^2 of each GLMM (i.e., associated to both fixed and random effects) using the *lme4* package (Bates et al. 2015).

To account for changes in species composition due to either species turnover or direct species losses or gains, β -diversity was partitioned into its species replacement and richness-difference components (Carvalho et al. 2012, 2013), by computing the species incidence data using the *adespatial* R package (Dray et al. 2016). To analyse forest change effects on each of the two resulting components of β -diversity, we modelled species replacement and richness-differences using the same modelling procedures described above for S_{ratio} and D_{Jac} . All data analyses were performed using the R environment (version 2.1.11, R Development Core Team 2015).

Results

Sixty-seven studies fitting our pre-condition criteria, and evaluating the effects of human-induced forest disturbance on amphibian ($N = 54$) and lizard assemblages ($N = 38$) were identified across 15 South and Mesoamerican countries. A total of 1285 pairwise comparisons in terms of species richness ($N = 840$) and composition ($N = 445$) were performed to examine the responses of those major taxa to forest degradation ($N = 365$) and forest fragmentation ($N = 475$). Those studies were not evenly spread across the neotropics, and most of them were located in Costa Rican and Colombian tropical forests affected by habitat degradation, deforestation, and fragmentation. In addition, only a small number of studies were available for relatively recent deforestation frontiers in the southern and eastern Amazon, which represents the largest expanse of tropical forest anywhere (Fig. 1).

The number of amphibian and lizard species decreased considerably along the gradient of increasing habitat degradation ($\beta_{\text{step-change}} = -0.016$, $P < 0.000$), but this was less apparent across a reduction in remaining forest area ($\beta_{\text{type(frag)}} = -0.262$, $P = 0.0641$, Table 2; Fig. 2). Such decline in the number of species in disturbed sites were similar between both taxa (Table S2), corresponding to approximately one-fourth fewer species of amphibians (mean \pm SD: $S_{\text{ratio}} = 0.72 \pm 0.38$) and lizards ($S_{\text{ratio}} = 0.75 \pm 0.36$). Yet much variation in species responses to habitat disturbance was observed between different pairwise comparisons ($R^2 = 0.439$), resulting from studies reporting no impact or a positive impact of forest change in either amphibian or lizard species richness (Fig. 2). Additionally, herpetofaunal responses in terms of species richness to forest habitat change were not significantly correlated with local species diversity (i.e. species richness of the undisturbed sites; amphibians: $r = -0.439$, $P < 0.00$; lizards: $r = -0.256$, $P < 0.00$). Likewise, species composition of both amphibians and lizards was considerably different in the disturbed sites ($\beta_{\text{intercept}} = 0.556$, $P < 0.000$), but not along gradients of anthropogenic step-change in terms of habitat degradation and fragmentation (Table 2; Fig. 2). Once again, compositional differences between pseudocontrol and disturbed sites were similarly observed for both taxonomic groups (Table S3) and averaged (\pm SD) 0.63 ± 0.19 for amphibians and 0.63 ± 0.25 for lizards.

β -Diversity values for both major taxa along the habitat degradation and fragmentation gradients were similarly decomposed into their richness-difference (loss or gain of species; both groups: $\beta_{\text{intercept}} = 0.303$, $P < 0.000$) and species replacement components (amphibians: $\beta_{\text{intercept}} = 0.315$, $P < 0.000$; lizards: $\beta_{\text{intercept}} = 0.210$, $P = 0.017$; Tables 3 and S4; Fig. 3). The amount of dissimilarity driven by each of the two β -diversity components remained constant along increasingly greater anthropogenic step-changes in both habitat degradation and fragmentation, except for amphibians, for which the amount of β -diversity driven by species replacements differed between disturbance type along the step-change gradient ($\beta_{\text{step-change*type(frag)}} = 0.019$, $P = 0.055$). Indeed, as forest area decreased, changes in amphibian species composition were increasingly due to species replacements ($\beta_{\text{type(frag)}} = -0.346$, $P = 0.003$; Table 3).

Table 2 General Linear Mixed Models of differences in species richness and composition for neotropical amphibians and lizards between disturbed and undisturbed sites according to type of forest change (type)—habitat degradation (deg) and fragmentation (frag)—and value of anthropogenic step-change (step-change)

Response variable	Explanatory variables	Estimate	SE	<i>t</i> value	<i>P</i> (> <i>t</i>)	<i>R</i> ²
<i>S_{ratio}</i>	Intercept	0.014	0.062	0.230	0.818	0.060
	Step-change	−0.016	0.004	−4.180	0.0003	
	Type (frag)	−0.262	0.141	−1.854	0.0641	
	Step-change × type (frag)	0.008	0.011	0.740	0.4594	
<i>D_{Jac}</i>	Intercept	0.556	0.041	12.309	<0.000	0.388
	Step-change	0.002	0.003	0.474	0.636	
	Type (frag)	−0.059	0.097	−0.612	0.541	
	Step-change × type (frag)	0.009	0.007	1.189	0.235	

Differences in species richness were given by the observed ratio in the number of species between disturbed and undisturbed sites (S_{ratio} ; $N = 840$) and the compositional dissimilarity as measured by the Jaccard coefficient based on species incidence (D_{Jac} ; $N = 445$). Random effects correspond to the case studies

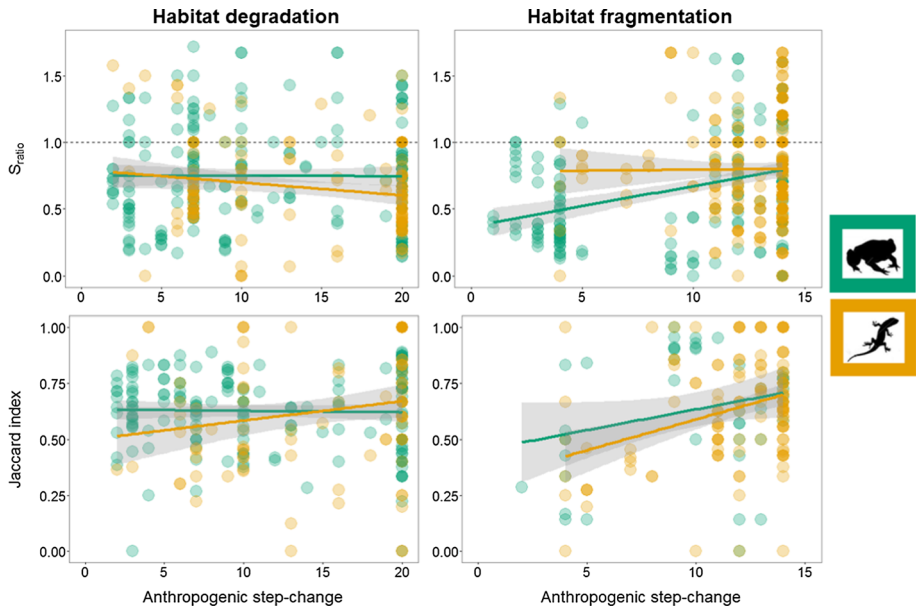


Fig. 2 Responses of amphibians and lizards to different types of forest change (forest habitat degradation and fragmentation) along the gradient of anthropogenic step-change. Responses were evaluated using a species richness ratio (number of species in a disturbed site divided by the number of species in a neighbouring undisturbed site), and Jaccard dissimilarity using species incidence (presence/absence) data. Assemblage change metrics for amphibians and lizards are indicated by *green* and *orange* circles, respectively. In the *top panels*, vertical dashed lines indicate the threshold at which the species richness of disturbed forest sites is equal to that of undisturbed forest. Shaded area represents the 95% confidence region. (Color figure online)

Discussion

Large-scale patterns of land-use change in forest landscapes have significantly reduced native forest biodiversity throughout the tropics (Sala et al. 2000; Fahrig 2003; Gibson et al. 2011; Newbold et al. 2014), and are widely regarded as primary drivers of population declines and community erosion in amphibians and reptiles (Gibbons et al. 2000; Gardner et al. 2007b). Despite the relative paucity of herpetofaunal studies carried out to date in this tropical realm (Gardner et al. 2007b), here we provide a comprehensive quantitative assessment that unravels how forest disturbance affects neotropical amphibian and lizard assemblages in terms of both species richness and species composition. Herpetofaunal species loss was intensified along increasing contrasts in habitat structure resulting from human-induced disturbance, and assemblage composition was consistently different along the step-change gradient. Moreover, such compositional differences were driven by both β -diversity components—richness-differences and species replacement—except for amphibian assemblages in forest fragments smaller than 50 ha, in which species replacements were significantly lower. Notwithstanding this exception, local extinctions of amphibians and lizards induced by habitat disturbance were offset by the colonization of disturbance-adapted species.

Human-induced disturbance led to an average decline in about one-third of the amphibian and lizard species present in large areas of primary forest. In particular, lower

Table 3 General Linear Mixed Models for each of the β -diversity components—richness-differences and species replacements—according to type of forest change (type)—habitat degradation (deg) and fragmentation (frag)—and value of anthropogenic step-change (step-change), for each pairwise comparison performed between disturbed and undisturbed sites across the Neotropical region (N = 445)

Response variable		Explanatory variables	Estimate	SE	<i>t</i> value	<i>P</i> (> <i>t</i>)	R ²
Richness-differences		Intercept	0.303	0.051	6.006	<0.000	0.287
		Step-change	−0.001	0.004	−0.245	0.806	
		Type (frag)	0.036	0.112	0.325	0.745	
		Step-change × type (frag)	0.006	0.009	0.680	0.497	
Species replacement	Amphibians	Intercept	0.315	0.046	6.888	<0.000	0.379
		Step-change	<−0.000	0.003	−0.073	0.942	
		Type (frag)	−0.346	0.115	−3.013	0.003	
		Step-change × type (frag)	0.019	0.010	1.930	0.055	
	Lizards	Intercept	0.210	0.087	2.418	0.017	0.398
		Step-change	0.003	0.006	0.540	0.590	
		Type (frag)	0.125	0.162	0.771	0.442	
		Step-change × type (frag)	−0.010	0.012	−0.825	0.410	

Due to differences in the responses between taxonomic groups, species replacement components were modelled separately for amphibians and lizards. Random effects correspond to the case studies

values of anthropogenic step-changes matched moderately degraded habitats retaining much of their original structure (e.g. secondary forests and agroforests), while higher values along this gradient largely matched clear-cut habitats (e.g. cattle pastures and cropland, Fig. S2). As expected, however, degraded habitats harboured comparatively more species than deforested habitats. Forest structure tends to become simplified and more homogeneous as the degree of disturbance increases in severely degraded habitats, (e.g. low understorey tree density, absence of woody lianas, large trees and heavy epiphytic loads; Fayle et al. 2010; Melo et al. 2013). Consequently, clear-cut sites converted into other land uses usually provide a much reduced spectrum of trophic and structural resources (e.g. food and shelter; Benton et al. 2003), higher temperatures, and lower humidity (Hardwick et al. 2015). Declining species are therefore typically represented by forest specialists (Tocher et al. 2001; Gardner et al. 2007a; Jenkins et al. 2014), whose traits preclude them from persisting in markedly different habitat conditions (Lehtinen and Ramanamanjato 2006; Newbold et al. 2014). Similarly, the number of lizard and amphibian species in forest fragments was on average lower than that in large forest tracts. Forest fragmentation leads to inexorable changes in core habitat conditions (i.e. temperature, understorey density, canopy cover, leaf litter cover and depth; Didham and Lawton 1999), even in central portions of small patches. This poses additional constraints well beyond reduced area and increased isolation, which often reduce population sizes and disrupt species movements and interactions (Hanski et al. 2013; Isbell et al. 2015). However, when we excluded large habitat tracts and compared only fragments of different sizes, we failed to detect an association between species extinction rates and forest area. It is likely that the range of forest fragments considered here, <100 ha, may obscure clear

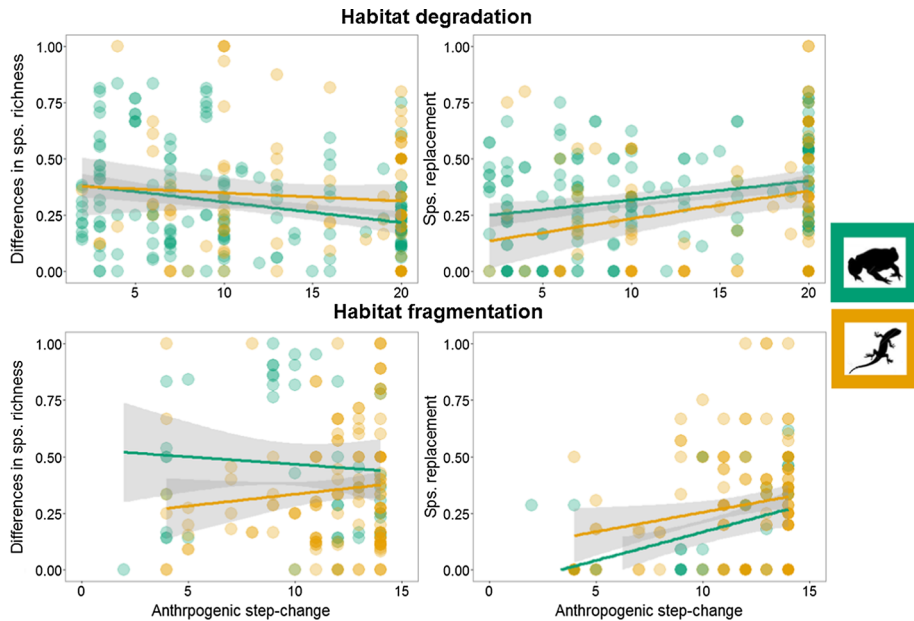


Fig. 3 Partitioning of the compositional dissimilarity between disturbed and undisturbed forest sites into species replacement and richness-difference components for each type of forest change (habitat degradation and fragmentation) along the gradient of anthropogenic step-change. Dissimilarity was measured using the Jaccard coefficient based on species incidence data. *Green and orange circles* indicate assemblage changes for amphibians and lizards, respectively. *Shaded area* represents the 95% confidence region. (Color figure online)

species-area relationships due to the ‘small island effect’ (Lion et al. 2016). Also, variables other than remnant forest area can play important roles in structuring communities in habitat fragments (e.g. isolation, matrix quality and time since isolation; Ewers and Didham 2006), but it was not possible to control those variables for most studies compiled in this review. Moreover, despite idiosyncrasies inherent to each of the two taxonomic groups, both responded similarly to forest change in terms of species richness and composition. Therefore, the higher hypothesized susceptibility of amphibians to desiccation compared to lizards is not supported by this analysis.

Regardless of the contrast with large areas of primary forest, herpetofaunal assemblages in human-disturbed habitats presented high levels of dissimilarity, suggesting that environmental heterogeneity may be a key driver of β -diversity, operating as an environmental filter (Arroyo-Rodríguez et al. 2013). Furthermore, the β -diversity partition into its two components revealed that both forms of species turnover drive compositional differences in amphibian and lizard assemblages in anthropogenic habitats, except for amphibians in very small forest fragments. Indeed, disturbed sites are colonized by ‘new’ species that had been previously absent from continuous primary forest, which typically coincide with more disturbance-tolerant generalist species (Devictor et al. 2008) that are better adapted to hydrological stress and higher temperatures (Bitar et al. 2015). This is consistent with previous community-wide studies on several taxa (e.g. dung beetles: Filgueiras et al. 2016; plants: Lososová et al. 2016), including reptiles and amphibians. For example, Gardner et al. (2007a) reported the hyper-dominance of lizard species typical of open-habitats in *Eucalyptus* plantations of northeastern Brazilian Amazonia, but their absence from large

areas of old-growth forest; and Bitar et al. (2015) showed the geographic expansion of anuran species typical of scrub savannah environments of the Brazilian *cerrado* into many areas of eastern and southern Amazonia that have succumbed to widespread anthropogenic impacts.

Changes across degraded sites occur towards drier conditions which may affect amphibian species that are too sensitive to desiccation to the point of being extirpated from degraded sites (Carmona 2007; Furlani et al. 2009). This further supports the observed increase in species losses along the habitat degradation gradient. Such habitat changes can also be further translated into fluctuations in pond hydroperiod, limiting breeding success in certain amphibian species (Neckel-Oliveira 2004), but eventually enabling reproductive success in others. Therefore, while some species go extinct in degraded sites, others seize the opportunity to colonize those sites (Lima and Gascon 1999; Bitar et al. 2015), explaining the pattern of β -diversity partitioning in both richness-differences and species replacements. Edge-dominated forest fragments, in addition to desiccation-related constraints (Watling and Braga 2015), may also lack suitable aquatic environments. Amphibian species with aquatic reproductive modes may be locally extirpated due to their requirement to move elsewhere to complete their life cycle (Becker et al. 2007). Interestingly, variation in amphibian assemblages in forest fragments <50 ha was mainly driven by differences in species richness. These small forest fragments may lack specific reproductive habitats (Hillers et al. 2008; Watling and Donnelly 2008; Lion et al. 2014), and may be too small to allow viable populations of colonist species to persist (MacArthur and Wilson 1967).

Higher rates of lizard species loss in more degraded habitats and lower species richness in forest fragments can be explained by their microhabitat use, which is inextricably linked to their metabolism (Vitt et al. 1999). Some lizard species are restricted to the humid leaf litter of tropical wet forests and avoid direct sun-light to maintain their body temperature (on average 27.7 °C for Amazonian lizards; Vitt et al. 1998). The altered habitat conditions in matrix habitats, degraded forest sites with reduced canopy cover and edge-dominated forest fragments is therefore often incompatible with the energetic ecology and behaviour of shade-tolerant species, thereby aggravating stressors that lead to their local extinction. Conversely, heliothermic lizard species that forage in highly illuminated environments and bask in direct sun-flecks to maintain their high body temperature (on average 36.1 °C for Amazonian lizards) usually benefit from novel microclimatic conditions of human-disturbed sites (Vitt et al. 1998), where temperature is higher and canopy gaps are larger and more numerous. This further explains the proportion of species replacements observed across the entire gradient of anthropogenic step-change in both degraded and fragmented habitats.

Human-induced disturbance induces considerable decreases in the number of amphibian and lizard species, particularly under major changes in forest structure. Yet many degraded habitats cannot be easily detected or mapped (Peres et al. 2006). Species extinctions in highly disturbed habitats may be offset by the colonization of disturbance-adapted species. Using species richness as the only ecological response metric can therefore severely mask forest change effects (Si et al. 2016). This is particularly relevant when setting priorities to allocate species-specific conservation efforts, as there are many cases of disturbed and undisturbed habitats that retain a similar number of species. For example, in a global review of the effects of anthropogenic disturbance across tropical and sub-tropical forests, herptiles were more likely to occur at higher human population density, suggesting that open habitats associated with densely settled areas benefit a greater number of species than do more closed habitats (Newbold et al. 2014). For this reason, we further recommend considering the functional role of each species in order to fully understand the impacts of

forest change on ecosystem functioning. We further highlight the importance of setting aside large blocks of continuous primary forest, which are essential to maintain the full integrity of ecosystem functions and prevent species losses and changes in community structure. In that sense, creating protected area networks that interconnect forested landscapes may be the best strategy. Tropical forest conservation efforts should therefore go beyond reducing deforestation by managing disturbance and edge proliferation in fragmented landscapes.

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