Effects of land-use change on functional and taxonomic diversity of Neotropical bats

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Abstract

Human land-use changes are particularly extensive in tropical regions, representing one of the greatest threats to terrestrial biodiversity and a key research topic in conservation. However, studies considering the effects of different types of anthropogenic disturbance on the functional dimension of biodiversity in human-modified landscapes are rare. Here, we obtained data through an extensive review of peer-reviewed articles and compared 30 Neotropical bat assemblages in well-preserved primary forest and four different human-disturbed habitats in terms of their functional and taxonomic diversity. We found that disturbed habitats that are structurally less similar to primary forest (pasture, cropland and early-stage secondary forest) were characterized by a lower functional and taxonomic diversity, as well as community level-functional uniqueness. These habitats generally retained fewer species that perform different ecological functions compared to higher-quality landscape matrices, such as agroforestry. According to functional trait composition, different bat ensembles respond differently to landscape change, negatively affecting mainly gleaning insectivorous bats in pasture, narrow-range species in cropland, and heavier animalivorous bats in secondary forest. Although our results highlight the importance of higher-quality matrix habitats to support elevated functional and taxonomic bat diversity, the conservation of bat species that perform different ecological functions in the mosaic of human-modified habitats also depends on the irreplaceable conservation value of well-preserved primary forests. Our study based on a pooled analysis of individual studies provides novel insights into the effects of different human-modified habitats on Neotropical bat assemblages.

Key-words: Chiroptera; conservation biology; countryside ecosystems; functional traits; habitat loss; land-use change; matrix quality; wildlife-friendly farming

1. Introduction

Given the unrelenting pace of land-use change across the tropics, being able to make accurate predictions about the persistence of biodiversity and associated ecosystem services across the complex, increasingly fragmented and human-dominated landscapes of the Anthropocene is crucial for informing conservation strategies and policy (Barlow et al., 2007; Jetz, Wilcove, & Dobson, 2007; Phalan et al., 2013). Tropical deforestation accounted for 32% of global forest loss between 2000 and 2012, nearly half of which occurred in South America (Hansen et al., 2013). Resulting landscapes typically comprise a mosaic of human-modified habitats that include remnants of old-growth forest, cattle pasture, cropland, secondary forest regenerating after clearance or burning, agroforestry systems, wood plantations and logged forest (Barlow et al., 2007; Gardner et al., 2009; Chazdon, 2014; Reid, Fagan, Lucas, Slaughter, & Zahawi, 2018).

In human-modified landscapes, the effects of edge, area and isolation on biota may be more or less pronounced, depending on how similar the matrix is structurally to the original habitat (Driscoll, Banks, Barton, Lindenmayer, & Smith, 2013; Laurance et al., 2017). Furthermore, matrix quality and permeability may regulate the use of corridors and stepping stones by species and strongly influence their occurrence and abundance (Kupfer, Malanson, & Franklin, 2006; Watling, Nowakowski, Donnelly, & Orrock, 2011; Didham, Kapos, & Ewers, 2012). Community-wide functional contributions depend not only on which species and functional traits are present, but also on species abundances (Stuart-Smith et al., 2013; Gagic et al., 2015). As the ecological effects of a species are generally proportional to its abundance or biomass, functional diversity (i.e. the value and variation of traits between species that affect its performance, fitness and ecological functions, Weiss

& Ray 2019) weighted by abundance offers promising insights into how community assembly mechanisms are influenced by environmental changes (de Bello, Lepš, Lavorel, & Moretti, 2007), and more accurately reflects functional community structure compared to metrics based on simple species counts (Mouillot, Graham, Villéger, Mason, & Bellwood, 2013; Stuart-Smith et al., 2013; Gagic et al., 2015).

From a functional perspective, phyllostomid bats are a well-suited indicator group for studying effects of landscape changes in the tropics because they display high species richness, abundance, variation in morphology, foraging behavior and fulfill crucial roles as pollinators, seed dispersers, prey and predators (Kunz, Torrez, Bauer, Lobova, & Fleming, 2011; Meyer, Struebig, & Willig, 2016). Few studies to date have explored the impact of human-induced habitat changes on the diversity and structure of Neotropical bat assemblages focusing on the functional dimension of biodiversity (but see Cisneros, Fagan, & Willig, 2015; Garcia-Morales et al., 2016; Farneda et al., 2018a; Pereira, Fonseca, & Aguiar, 2018). These studies generally point to an inverse relationship between functional diversity and land-use intensity, suggesting that the preservation of a large proportion of the ecological functions in a community requires the conservation of vast areas of primary forests. However, so far no attempt has been made to generalize beyond these single case studies by comparing Neotropical bat assemblages in well-preserved forest and different human-disturbed habitats in terms of functional diversity based on a comprehensive analysis of available datasets.

The present study used a pooled analysis of individual ecological studies to evaluate how changes in multiple human-modified habitats affect the taxonomic and functional dimensions of Neotropical phyllostomid bats. Additionally, we investigated how key ecological functions provided by bats are being imperiled by land-use intensification. Our general hypothesis was that functional and taxonomic diversity increase with decreasing land-use intensity and disturbance. We predicted that, (1) functional and taxonomic diversity and community-level functional uniqueness (sensu Ricotta et al., 2016) would be strongly affected by structural complexity and patch-matrix contrast of each landscape, being lower in high-contrast matrices (pasture, cropland and early-stage secondary forest) and higher in relatively low-contrast systems (agroforestry) relative to undisturbed forest, and (2) trait-based responses should converge according to fragment-matrix contrast, being stronger in more intensively disturbed matrices (pasture, cropland) due to a greater loss of suitable foraging and roosting sites for bats. In contrast, for lower-contrast landscapes we anticipated the functional composition in the matrix to mirror more closely that of well-preserved primary forest.

2. Material and methods

We followed a systematic review methodology (Lortie, 2014) to synthesize information about bat responses to type of habitat modification. Studies were identified based on Meyer et al. (2016) and through a comprehensive search in SCOPUS and Google Scholar (accessed in July 2018) using the keywords: “bat* AND Neotropic* AND (assemblage* OR community* OR diversity* OR fragment* OR deforestation* OR disturbance* OR pasture* OR cropland* OR secondary forest* OR agroforestry*)”. No restriction on date was used. The publications retrieved were subsequently screened for suitability for inclusion in the analysis based on the article’s title, abstract and text. This resulted in a total of 30 studies conducted in eight countries throughout the Neotropics (Figure 1) which were deemed relevant based on the following criteria: studies (1) were published in an indexed, peer-reviewed scientific journal, (2) compared bat assemblages between well-preserved primary forest plots and at least one type of terrestrial human-disturbed habitat, (3) provided species abundance data for each habitat (see Supporting Information, Table S1), and (4) provided information on sampling effort per habitat. Furthermore, to avoid biases in the results that might be introduced by different sampling methods, we (5) included only studies in which ground-level mist-nets were used, and consequently restricted our analysis to phyllostomid bats as they can be well-sampled with this method (Kalko, Handley, & Handley, 1996). As our purpose here was to review evidence for the effects of *anthropogenic* habitat modification in unpopulated terrestrial systems on Neotropical bat assemblages, we (6) excluded studies that were conducted in naturally fragmented landscapes (e.g. forest patches embedded in grasslands or in a matrix dominated by savannas, such as presented by Montiel, Estrada, & León, 2006 and Bernard & Fenton, 2007), islands (Meyer & Kalko, 2008), and urban landscapes (Jung & Threlfall, 2018). Our review thus focuses on a range of human-modified habitats varying in structural complexity and landscape contrast: (1) pasture, (2) cropland, (3) secondary forest, and (4) agroforestry. We excluded "wood plantation" and "logged forest" because these habitats were only represented by a small number of studies (four studies each).

Throughout all studies included, well-preserved forest represented primary, old-growth forest with minimal or no anthropogenic disturbance. Secondary vegetation included sites where, after forest removal, natural succession had occurred for between one and 30 years. We analyzed early- and late-stage secondary forest jointly due to small sample size for late succession (only one study assessed secondary forest with more than 20 years of regeneration). Approximately 65% of the studies were conducted in secondary forest with less than 10 years of regeneration. In agroforestry systems, only the understory had been removed, and large trees were kept to provide shade for mainly cocoa, coffee and banana. In croplands, the forest had been completely cut and replaced by sun crop monocultures, such as corn, citrus, coffee, palm and allspice. In pastures, the understory had been removed to allow cattle grazing, although in some cases a few trees were maintained.

2.1 Species traits

To calculate the various aspects of functional diversity, we used four species traits that comprise important functional components of Neotropical bat diversity, and that are related to species responses to human-modified tropical landscapes and ecosystem functioning (Luck, Lavorel, McIntyre, & Lumb, 2012; Farneda et al., 2015): (1) body mass – based on the average of each species, (2) trophic level – two broad trophic categories: “animalivorous” or “phytophagous”, (3) diet – based on the main food item of each species, and (4) habitat breadth – based on the number of habitat types in which a species occurs, varying from 1 (more restricted distribution) to 6 (more widespread) (see Table S3 for trait values of individual species). Trait information was obtained from the Ecological Register database (ecoregister.org, accessed on 15 July 2018), a repository of published ecological survey data from around the world (Alroy, 2019). Logarithmic transformations and standardization to a mean of zero and a standard deviation of one were performed on body mass to normalize values and to facilitate comparison of their relative effects.

2.2 Data analysis

We followed the methodological framework introduced by Ricotta et al., (2016) to quantify functional and taxonomic diversity and community-level functional uniqueness of bat assemblages. This approach takes into account relative species abundances, thus adequately accommodating differences in sampling effort between studies. It does, however, not control for potential variation in species detectability related to differences in habitat complexity (Meyer et al. 2011). Relative species abundance was based on capture rate in each assemblage, which was calculated by multiplying the area of each net by the time they remained exposed in the field by the number of sampling repetitions by the number of nets (m^2.h; sensu Straube & Bianconi, 2002).

To quantify functional diversity, we calculated Rao's quadratic diversity index *Q*, which takes the differences (trait-based variance) between species pairs into account. For taxonomic diversity, we computed the Simpson index *D*, which considers all species maximally dissimilar (Botta-Dukát, 2005). Furthermore, we calculated community-level functional uniqueness *U* (*Q*/*D*) (Ricotta et al., 2016). For all index values (*Q*, *D* and *U*), pairwise comparisons between well-preserved primary forests (control group) and disturbed habitat (treatment group) were performed using paired permutational tests with 9999 randomizations. The calculations of *Q*, *D* and *U* were performed with the 'uniqueness' function provided by Ricotta et al., (2016).

To assess how habitat-level changes affect bat functional trait composition, we calculated community-weighted mean trait values (CWM; Lavorel et al., 2008). This method allows assessing shifts in mean trait values weighted by relative species abundances (Lavorel et al., 2008), thus equalizing differences in capture effort between studies. We calculated CWM traits using the 'functcomp' function of the R package FD (Laliberté & Legendre, 2010). For each trait, pairwise comparisons between primary forests and matrix type were performed using paired permutational tests with 9999 randomizations.

The functional pairwise dissimilarity matrices in all analyses were calculated using Gower's distance since our trait matrix (see Table S3) included a mix of continuous and categorical traits. Paired mean differences for *Q*, *D*, *U* and CWM were calculated using bootstrap medians, i.e. difference between the median of the control group and of the treatment group, as implemented in the R package dabestr (Ho et al. 2018). The result of the bootstrap is 1000 difference values per habitat, which were used to determine the 95% confidence intervals. All analyses were conducted using R software (R Development Core Team, 2017).

3. Results

A total of 50,925 individuals of 103 bat species were used in the analysis. Species richness was highest in primary forests, followed by agroforestry, early-stage secondary forest, cropland, and pasture (Table 1). Primary forests were functionally and taxonomically more diverse than modified habitats (Figure 2). Pasture, cropland and secondary forest had significantly lower functional diversity than primary forest ($p < 0.05$). In contrast, differences for agroforestry were not significant ($p = 0.434$) (Figure 3; Table 2). Secondary forest and cropland had significantly lower taxonomic diversity and community-level functional uniqueness *U* than primary forest ($p < 0.032$) (Figure 3; Table 2), reflecting a substantial loss of species that perform different ecological functions in these habitats.

The most pronounced differences in functional trait composition between primary forest and modified habitats were found for secondary forest, for which paired permutation tests comparing CWM trait values revealed significant changes for body mass, trophic level, diet and habitat breadth ($p < 0.05$) (Figure 4; Table 2). While phytophagous species represented by nectarivores with a more widespread geographic distribution increased significantly in secondary forest relative to undisturbed forest, animalivorous species represented by carnivores, insectivores and sanguinivores, were markedly underrepresented (Figure 4). Furthermore, bats in secondary forest had slightly, but significantly lower body mass than those in primary forest ($p = 0.026$) (Table 2). For pastures, we found significantly lower CWM trait values for bats with an insectivorous diet ($p = 0.049$), while croplands were characterized by a significant increase in habitat breadth associated to wide-ranged species ($p = 0.030$) (Figure 4; Table 2). Statistical support for changes in functional trait composition in agroforestry system was limited (Figure 4; Table 2).

4. Discussion

The global terrestrial human footprint continues to expand towards the remaining pristine habitats, threatening biodiversity, ecosystem services and human well-being (Ehrlich & Ehrlich, 2013; Ceballos et al., 2015). Across the Neotropics, conversion of native vegetation to cattle pasture and crop monoculture constitute one of the main causes of biodiversity decline, leading to frequent and pervasive large-scale changes in biological communities (Phalan et al., 2013; Poore & Nemecek, 2018). Our findings indicate that the direction of these effects on Neotropical bat assemblages is fundamentally influenced by the type of matrix surrounding primary forest patches in human-modified ecosystems. Matrix habitats which are less similar to primary forest in terms of vegetation structure and composition (pasture, cropland, early-stage secondary forest) displayed significant decreases in bat functional and taxonomic diversity, community-level functional uniqueness, and stronger shifts in functional trait composition compared to lower-contrast systems (agroforestry).

The importance of matrix quality in sustaining biodiversity and ecosystem functioning in fragmented landscapes has widely been documented in the literature (e.g. Laurance et al., 2017; Kupfer et al., 2006; Watling et al., 2011; Driscoll et al., 2013; Mendenhall, Karp, Meyer, Hadly, & Daily, 2014). Our results confirm previous findings that matrix quality can intensify (in the case of cropland, pasture and early-stage secondary forest) or mitigate (as observed for agroforestry systems) the negative impacts of deforestation on multiple dimensions of bat biodiversity. Conceptually, the matrix is a habitat structurally and compositionally different from primary forest (Driscoll et al., 2013), and this has implications for the occurrence and abundance patterns of its bat assemblages (Avila-Cabadilla, Stoner, Henry, & Añorve, 2009; Farneda et al., 2015; Gonçalves, Fischer, & Dirzo, 2017), which in turn may significantly affect their taxonomic and functional diversity.

Our results indicate that bat responses in pasture, cropland and secondary forest are linked to species-specific differences in terms of foraging requirements. Despite some studies suggesting that these habitats harbor considerable bat taxonomic diversity and provide important foraging habitats for some phytophagous bat species (Medellín, Equihua, & Amin, 2000; Moreno & Halffter, 2001; Avila-Cabadilla et al., 2009), they host assemblages that significantly differ in richness and composition from those in primary forest (Faria, 2006; Barlow et al., 2007; Meyer et al., 2016; Farneda et al., 2018a). The conservation value of pasture, cropland and secondary forest for bats critically depends on landscape context, generally being greater in mosaic landscapes where patches of residual tree cover (e.g. riparian vegetation, live fences) are located close to old-growth forest

(Estrada, Coates-Estrada, & Meritt, 1993; Vleut, Levy-Tacher, Galindo-González, de Boer, & Ramírez-Marcial, 2012). For secondary forest in particular, their long-term protection against human land-use changes is pivotal to achieving significant taxonomic and functional recovery of Neotropical bat assemblages in fragmented landscapes (Farneda et al., 2018a, b; Rocha et al., 2018).

Our findings are also consistent with the assertion that higher-quality matrix habitats, such as agroforestry systems are biodiversity-friendly with the potential to be of considerable conservation value for bats. Traditional agroforestry systems provide refuge and food resources for different bat ensembles under a stratified canopy that resemble primary forest habitats (Bhagwat, Willis, Birks, & Whittaker 2008; Garcia-Morales, Badano, & Moreno, 2013). Similar canopy structure to old-growth forest and an understory that is often comprised of native shrubs can mitigate edge effects and create corridors or stepping stones for bats to forage and shelter (Meyer et al., 2016).

Different bat ensembles respond in different ways to spatiotemporal variation in resource distribution associated with changes in landscape structure and composition (e.g. degree of fragment-matrix structural contrast, size and isolation of primary forest patches) due to their ecological differences (e.g. diet, movement ability, foraging behavior) (Cisneros et al., 2015; Marciente, Bobrowiec, & Magnusson, 2015; Voss, Fleck, Strauss, Velazco, & Simmons, 2016; Farneda et al., 2018a). Our results regarding functional composition (CWM trait values) reveal that certain gleaning insectivorous bats are adversely affected by pasture intensification. This finding probably reflects the scarcity of food and roost resources provided by these habitats as well as elevated predation pressure. A similar pattern was found in a recent meta-analysis (Gonçalves et al., 2017), with livestock ranching affecting mainly carnivorous and gleaning insectivorous Neotropical bat species. Species with a greater habitat breadth (e.g. *Carollia* spp., *Sturnira* spp.) responded positively to habitat conversion, reaching highest abundances in cropland. The simplified vegetation structure of agricultural fields strongly affects and limits the distribution of many forest-dependent bat species (Medellín et al., 2000; Willig et al., 2007). Phytophagous bats (represented here mainly by nectarivores as they showed a significant response, see Figure 4) tend to increase in abundance in secondary forest matrices due to additional food resources (Delaval & Charles-Dominique, 2006; Muscarella & Fleming, 2007; Farneda et al., 2015), whereas the abundance of animalivorous bats with larger body mass, such as many carnivores, insectivores and sanguinivores, tends to decrease in response to insufficient roosting and prey resources (Gorresen & Willig, 2004; Meyer & Kalko, 2008; Farneda et al., 2015).

The elevated number of significant traits supported by the functional trait composition analysis in secondary forests can be associated with the high vegetation heterogeneity of this habitat across the Neotropics. Secondary forests, as analyzed here, show greater variation in vegetation physiognomy and structure (regeneration ranging between one to 30 years) compared to more homogeneous habitats such as cropland, which could explain the larger variation in bat responses. However, although different countryside habitats noticeably accommodate interior-forest dwellers in different ways, the increase and the long-term persistence of bat species that perform different ecological functions in human-dominated landscapes fundamentally depends on the conservation of vast areas of primary forest. This finding may be generalizable to all human-dominated complex landscapes here studied regardless of matrix type. Our results emphasizing the conservation value of primary forests as important functional and taxonomic repositories of bat diversity are in line with findings obtained for large and small terrestrial mammals, birds, amphibians, lizards, butterflies, dung beetles and other tropical animal assemblages (Barlow et al., 2007; Gardner et al., 2009; Watson et al., 2018).

4.1 Conservation implications

The future of biodiversity and associated ecosystem services will critically depend on our ability to increase the quality and permeability of matrix habitats that are strongly impacted by humans (Pereira & Daily, 2006; Melo, Arroyo-Rodríguez, Fahrig, Martínez-Ramos, & Tabarelli, 2013; Mendenhall et al., 2014). Our findings suggest that ecological functions provided by bats in human-modified tropical landscapes depend on a heterogeneous mosaic of different land cover types that provide specific resources for the species. This finding provides an important tool for a more effective land management in countryside ecosystems to conserve the full set of key ecological functions that bats provide. Conservation strategies for maximizing bat functional diversity and composition in human-modified landscapes should, in addition to ensuring the preservation of large (> 100 ha) areas of primary forest (see Farneda et al., 2015), manage the matrix by promoting natural corridors and stepping stones through spontaneous natural regeneration and active regeneration. Residual vegetation, such as strips of riparian forest and scattered trees may enhance functional connectivity between forest patches, favoring bat movements across human-modified landscapes. These measures to increase the number of favorable habitats for foraging and roosting may sustain species-rich bat assemblages and key ecological functions in human-dominated landscapes. Moreover, our findings corroborate earlier studies by Perfecto and Vandermeer (2010) and Watson et al. (2018) in highlighting the fundamental importance of dynamic agroecological matrices (e.g. syntropic farming) as an alternative to the current monoculture intensification model, and the exceptional value of intact forest ecosystems for supporting biodiversity in the Anthropocene.

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Data availability statement

The data used in this study were uploaded as online Supporting Information.

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Table 1. Number of Neotropical bat studies, number of species observed and sampling effort for each habitat category considered in the analysis.

Habitat	Number of studies	Species	Effort (m^2.h)
Cropland	7	44	340,924
Pasture	8	30	285,784
Agroforestry system	14	85	770,781
Secondary forest	17	78	600,845
Primary forest	30	100	2,088,575

Table 2. Statistical significance for (a) functional (Rao's *Q*) and taxonomic (Simpson *D*) diversity, and community-level functional uniqueness *U*, and (b) community-weighted mean (CWM) trait values between primary forest (PF) and pasture (PA), cropland (CL), secondary forest (SF), and agroforestry (AF). Pairwise comparisons of differences between primary forest and the human-modified habitat were performed with a paired permutational test using 9999 permutations. Significant differences are in bold ($p < 0.05$).

Indices/Traits	Habitat category			
	PF-PA	PF-CL	PF-SF	PF-AF
(a)				
Rao's *Q*	**0.045**	**0.031**	**0.001**	0.434
Simpson *D*	0.141	**0.031**	**0.003**	0.399
Functional uniqueness *U*	0.066	**0.031**	**0.001**	0.426
(b)				
Body mass	0.399	0.831	**0.026**	0.062
Trophic level: animalivorous	0.599	0.597	**0.001**	0.690
Trophic level: phytophagous	0.579	0.592	**0.001**	0.692
Diet: carnivore	0.254	0.255	**0.001**	0.230
Diet: frugivore	0.854	0.781	0.748	0.827
Diet: insectivore	**0.049**	0.078	**0.004**	0.113
Diet: nectarivore	0.414	0.761	**0.036**	0.999
Diet: omnivore	0.365	0.842	0.137	0.207
Diet: sanguinivore	0.557	0.841	**0.019**	0.215
Habitat breadth	0.444	**0.030**	**0.045**	0.106

Figure 1. Geographic distribution of the 30 Neotropical bat studies in human-modified landscapes used in the analysis. Different green colours represent the number of studies per country and sizes of orange circles represent the number of studies per site, where a site is defined as a particular study location.

Figure 2. Functional diversity (Rao's index Q), taxonomic diversity (Simpson index D), and community-level functional uniqueness U for the control group (primary forest) and the respective treatment group (pasture, cropland, secondary forest and agroforestry). Individual studies are represented by circles, and the mean difference of each habitat is indicated by the vertical bar.

Figure 3. The paired mean differences between primary forest and the human-modified habitats (pasture, cropland, secondary forest and agroforestry) are shown for functional (Rao's index Q) and taxonomic (Simpson index D) diversity, and community-level functional uniqueness U. Paired mean difference (delta value) is plotted as a bootstrap sampling distribution based on 1000 randomizations. Mean differences are depicted as dots, and 95% confidence intervals are indicated by horizontal lines. Habitats for which significant differences ($p < 0.05$) were found are highlighted in red. Positive and negative values indicate delta values that are greater and smaller, respectively, than for primary forest (zero line).

Figure 4. Comparison of community-weighted mean (CWM) trait values between primary forests and human-modified habitats: pasture, cropland, secondary forest and agroforestry. Paired mean difference (delta value) between the respective human-modified habitat and

primary forest is plotted as a bootstrap sampling distribution based on 1000 randomizations. Mean differences are depicted as dots, and 95% confidence intervals are indicated by horizontal lines. Statistically significant traits ($p < 0.05$) are highlighted in red. Positive and negative values indicate delta values that are greater and smaller, respectively, than for primary forest (zero line).

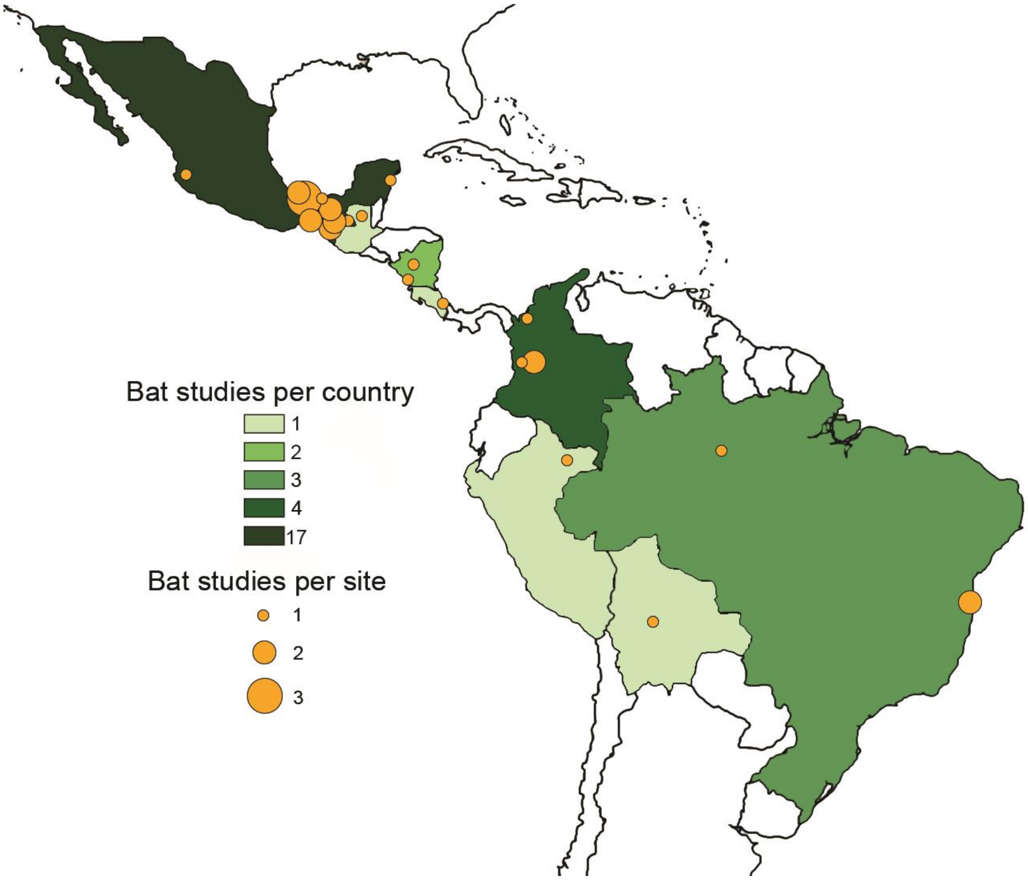
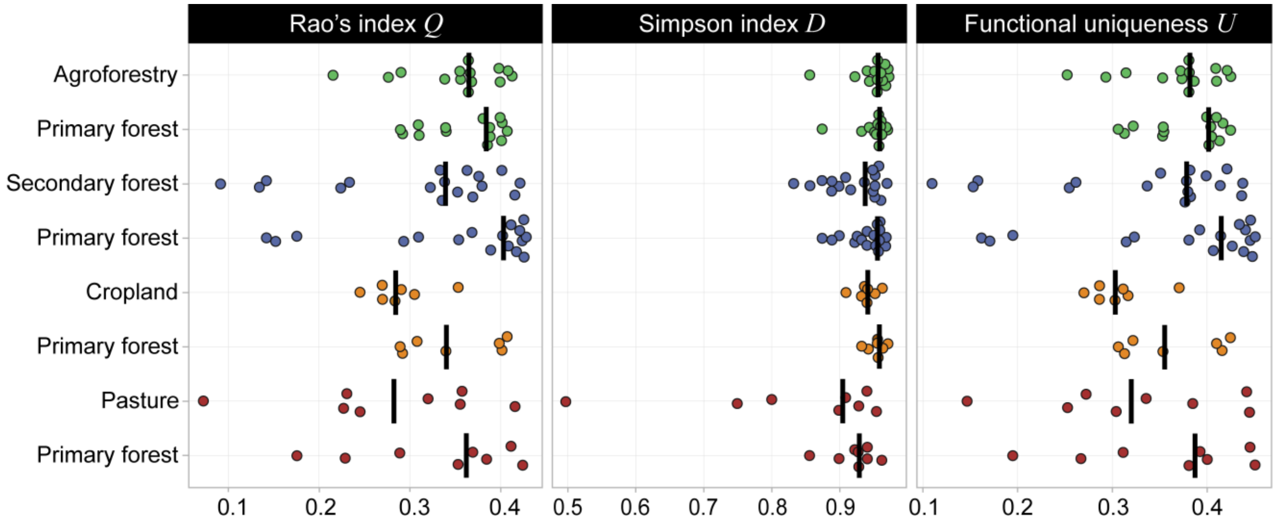


Figure 1.



Rao's index Q
Simpson index D
Functional uniqueness U
Agroforestry
Primary forest
Secondary forest
Primary forest
Cropland
Primary forest
Pasture
Primary forest
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
0.1
0.2
0.3
0.4

Figure 2.

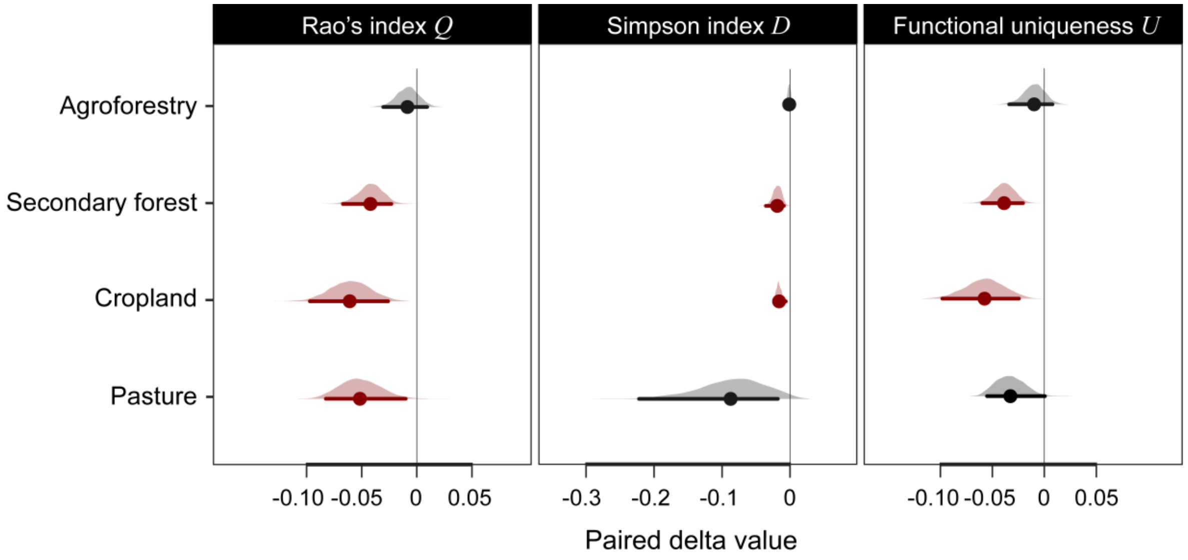

Rao's index Q
Simpson index D
Functional uniqueness U
Agroforestry
Secondary forest
Cropland
Pasture
-0.10
-0.05
0
0.05
-0.3
-0.2
-0.1
0
-0.10
-0.05
0
0.05
Paired delta value

Figure 3.

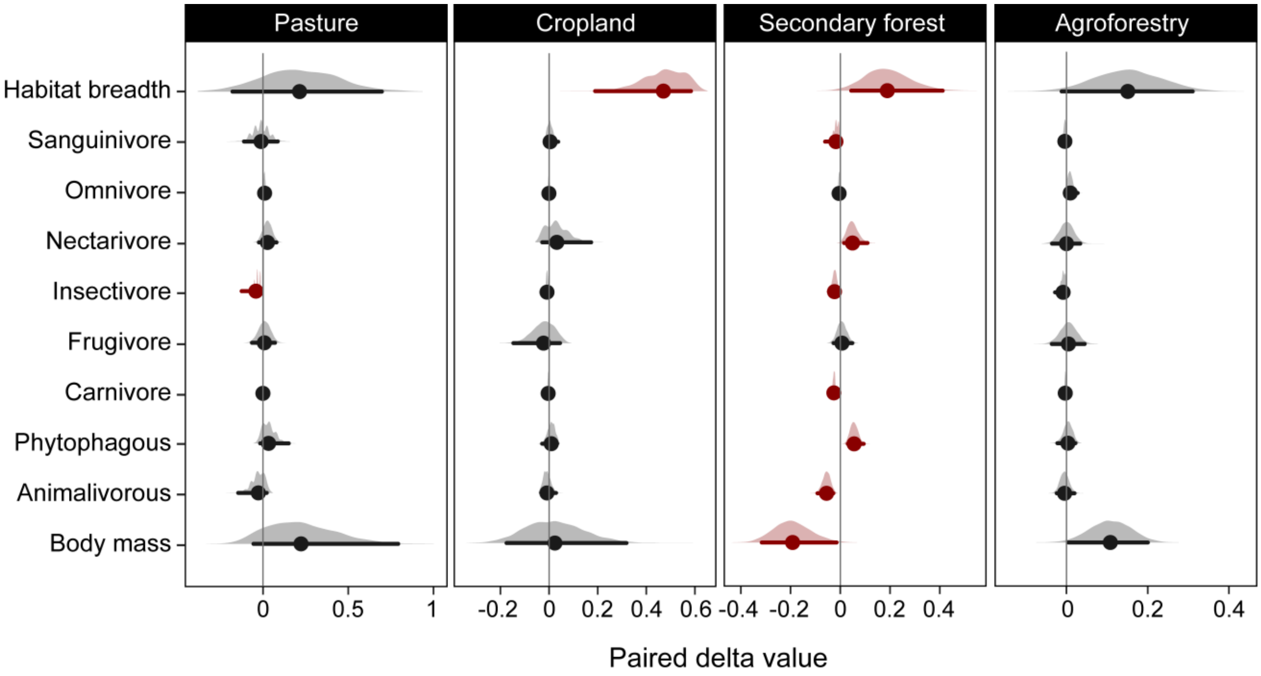

Pasture
Cropland
Secondary forest
Agroforestry
Habitat breadth
Sanguinivore
Omnivore
Nectarivore
Insectivore
Frugivore
Carnivore
Phytophagous
Animalivorous
Body mass
0
0.5
1
-0.2
0
0.2
0.4
0.6
-0.4
-0.2
0
0.2
0.4
0
0.2
0.4
Paired delta value

Figure 4.