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Research

Predicting biodiversity loss in island and countryside ecosystems through the lens of taxonomic and functional biogeography

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We investigate how variation in patch area and forest cover quantified for three different spatial scales (buffer size of 500, 1500 and 3000 m radius) affects species richness and functional diversity of bat assemblages in two ecosystems differing in fragment–matrix contrast: a landbridge island system in Panama and a countryside ecosystem in the Brazilian Amazon. Bats were sampled on 11 islands and the adjacent mainland in Panama, and in eight forest fragments and nearby continuous forest in Brazil. Species–area relationships (SAR) were assessed based on Chao1 species richness estimates, and functional diversity–area relationships (FAR) were quantified using Chao1 functional diversity estimates measured as the total branch length of a trait dendrogram. FARs were calculated using three trait sets: considering five species functional traits (FAR_{ALL}), and trait subsets reflecting 'diet breadth' (FAR_{DIET}) and 'dispersal ability' ($FAR_{DISPERSAL}$). We found that in both study systems, FAR_{ALL} was less sensitive to habitat loss than SAR, in the sense that an equal reduction in habitat loss led to a disproportionately smaller loss of functional diversity compared to species richness. However, the inhospitable and static aquatic matrix in the island ecosystem resulted in more pronounced species loss with increasing loss of habitat compared to the countryside ecosystem. Moreover, while we found a significant $FAR_{DISPERSAL}$ for the island ecosystem in relation to forest cover within 500 m landscape buffers, FAR_{DIET} and $FAR_{DISPERSAL}$ were not significant for the countryside ecosystem. Our findings highlight that species richness and functional diversity in island and countryside ecosystems scale fundamentally differently with habitat loss, and suggest that key bat ecological functions, such as pollination, seed dispersal and arthropod suppression, may be maintained in fragments despite a reduction in species richness. Our study reinforces the importance of increasing habitat availability for decreasing the chances of losing species richness in smaller fragments.

Keywords: conservation biogeography, environmental filters, forest area loss, functional diversity–area relationship, species–area relationship, tropical bats

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Introduction

The ongoing division of continuous forest habitats into smaller and isolated patches surrounded by some sort of human-modified habitat has pervasive and deleterious effects on biodiversity (Fahrig 2013, Rybicki and Hanski 2013, Haddad et al. 2015). One of these effects is the well-known decline in local species richness, to which the application of the theory of island biogeography (MacArthur and Wilson 1967) has added considerable understanding (Rybicki and Hanski 2013, Mendenhall et al. 2014a, Whittaker et al. 2017, Ross et al. 2019). However, although species richness has been the most common metric used to represent all aspects of biological diversity (Cadotte et al. 2011), a focus on the taxonomic dimension of biodiversity and how it decreases as habitat area is lost is unlikely to fully capture the extent to which ecological processes and services may collapse following habitat loss (Laurance 2008, Flynn et al. 2009, Matthews et al. 2014, Jarzyna and Jetz 2017). A purely taxonomic-based approach considers all species as equally distinct, disregarding functional similarities among them. In contrast, analyses based on functional traits (i.e. characteristics of an organism or species that potentially affect its performance, fitness and ecological functions in a community, Violle et al. 2007) are more suitable than species richness for understanding the recovery of ecosystem functioning and stability after biodiversity loss (Cadotte et al. 2011, Mouillot et al. 2013, Gagic et al. 2015). Therefore, the inclusion of functional metrics in ecological studies can bring new insights that complement those gained from island biogeographic theory (Violle et al. 2014, Karadimou et al. 2016, Jacquet et al. 2017, Whittaker et al. 2017).

With the emergence and promise of a predictive focus of ecology in the Anthropocene, advancing functional biogeography should become a priority avenue for future research (Violle et al. 2014). Although an integrative approach that links biogeography and functional ecology will benefit species- and ecosystem function-based conservation (Devictor et al. 2010), attempts at this to date have been scarce. Furthermore, while differences in species–area relationships (SAR) between island and countryside systems have been a matter of considerable research interest, showing that island SARs have lower slopes than terrestrial islands (Mendenhall et al. 2014a), the corresponding situation with functional diversity–area relationships (FAR) remains little explored (but see Ding et al. 2013, Whittaker et al. 2014, Si et al. 2016, Ross et al. 2019). Moreover, the pervasive influence of island biogeographic theory has long led many ecological studies to focus exclusively on processes occurring within forest remnants, without addressing how the effects of changing forest area and isolation are mediated by the surrounding matrix (Kupfer et al. 2006, Laurance 2008, Mendenhall et al. 2013, 2014b). Research over the last decade has abundantly demonstrated the overwhelming importance of matrix quality on within-remnant animal community dynamics (Watling et al. 2011, Rybicki and Hanski 2013, Mendenhall et al. 2014a, Wolfe et al. 2015, Farneda et al. 2018a).

Bridging the well-established field of research on SAR (Arrhenius 1921, Lomolino 2000, He and Hubbell 2011, Rybicki and Hanski 2013, Mendenhall et al. 2014a) with the emergent field of functional biogeography focusing on FAR (Violle et al. 2014, Karadimou et al. 2016), our overarching aim here was to investigate how variation in patch- and landscape-level habitat loss translates into changes in species richness and functional diversity of bat assemblages in two Neotropical fragmented landscapes differing in fragment–matrix contrast but with similar species pools: a landbridge island system in Panama dominated by a water matrix, and a countryside ecosystem in the Brazilian Amazon characterized by a secondary forest matrix. The focal group of this study, bats, display high species richness in the tropics, wide variation in morphology and foraging behavior, susceptibility to land use change (Meyer et al. 2016), and make an important contribution to ecosystem functioning (Kunz et al. 2011). A more pronounced fragment–matrix contrast may create filters that limit functional diversity of local bat assemblages by markedly modifying habitat characteristics that are important to interior-forest dwellers (García-Morales et al. 2016, Farneda et al. 2018a).

Here, we examined three main hypotheses: 1) in both island and countryside ecosystem, species richness decreases faster than functional diversity with increasing loss of forest cover. This is because while SAR treats each species as different to others, thus resulting in a disproportionately greater loss of species than functional diversity, the same does not hold for FAR as many Neotropical bat species are functionally redundant (Stevens et al. 2003, Oliveira et al. 2016). 2) Differences in slope between SAR and FAR will be most marked in the island ecosystem due to more pronounced species loss with increasing loss of habitat compared to the countryside ecosystem. This is because the water matrix constitutes a more hostile scenario than the forested matrix in the countryside ecosystem. 3) Functional diversity based on trait sets reflecting 'diet breadth' and 'dispersal ability' decreases faster in the island than in the countryside ecosystem with increasing loss of forest cover. This is because the aquatic matrix sets greater limits to use resources in a smaller subset of patches and imposes a greater barrier to species' movement than the 'soft' matrix in the countryside ecosystem.

Material and methods

All animals were handled ethically following the guidelines approved by the animal care and use committee of the American Society of Mammalogists (Sikes 2016). We excluded all non-phyllostomid species, except the mormoopid *Pteronotus parnellii*, for they cannot be reliably sampled with mist nets (Kalko et al. 1996). Same-site recaptures were excluded. Bias in capture rates due to net-shyness

was avoided by spacing visits to the same site three to four weeks apart (Marques et al. 2013). To avoid biases in the results that might be introduced by different canopy height across study sites, canopy net data obtained in the interiors of the continuous forest sites and fragments in both study systems were used for assigning species to the 'vertical stratification' trait (see below), not for obtaining information about abundance or site incidence.

Bat sampling on Panamanian landbridge islands

The investigation was conducted on islands in the human-made Gatún Lake and on adjacent mainland peninsulas of the Barro Colorado Nature Monument (9°11′N–79°53′W, 26 m a.s.l.), Central Panama (Meyer and Kalko 2008). The 1914 damming of the Chagres River during construction of the Panama Canal created the lake and more than 200 islands ranging in size from < 1 ha to Barro Colorado Island (BCI) with 1560 ha (Leigh et al. 1993). Together with five adjacent mainland peninsulas, BCI forms the 5400 ha Barro Colorado Nature Monument and is contiguous with 22 000 ha Soberanía National Park. Islands in the lake are covered with lowland tropical moist forest (Holdridge 1979), which is typically shorter in tree stature compared to adjacent mainland (Leigh et al. 1993). The area experiences a dry season from mid-December to April or May (Windsor 1990), with an average annual rainfall of 2100 mm (Handley et al. 1991).

Bats were sampled using six ground-level mist nets (6 × 2.5 m, 16-mm mesh) placed along trails on 11 islands varying in size from 2.5 to 50 ha and at three control sites in the interior of continuous forest on three mainland peninsulas (Bohio, Gigante and Peña Blanca). Each of the 14 sites was sampled for seven or eight nights over a two-year period (October 2003–October 2005, total capture effort = 6981 mnh, one mist-net hour [mnh] equals one 6-m net open for 1 h). Bat sampling was conducted with constant-effort mist netting (from dusk until dawn). See Meyer and Kalko (2008) for a more detailed account of the sampling methodology.

Bat sampling in the Amazonian countryside

The investigation was conducted at the Biological Dynamics of Forest Fragments Project (BDFFP), located ~80 km north of Manaus (2°25′S, 59°50′W, 30–125 m a.s.l.), Central Amazon. In the early 1980s, 11 fragments were isolated from continuous forest by distances of 80–650 m through clearing and subsequent burning. Since then, each fragment was re-isolated on three to four occasions, prior to this study most recently between 1999 and 2001 (Rocha et al. 2017b). The area is characterized by a mosaic of unflooded ('terra firme') Amazonian rainforest, primary forest fragments (1, 10 and 100 ha) and secondary regrowth dominated mainly by *Cecropia* spp. and *Vismia* spp. (Mesquita et al. 2001). The primary forest canopy is ca 23 m tall, with occasional emergent trees reaching 55 m (Gascon and Bierregaard 2001). The BDFFP experiences a dry season between July and October, and annual rainfall varies from 1900 to 3500 mm (Ferreira et al. 2017).

Bats were sampled along netting transects established in the interiors of eight forest fragments (three of 1 ha, three of 10 ha, two of 100 ha) and nine control sites in three areas of continuous forest (Cabo Frio, Florestal and Km 41). Each of the 17 sites was sampled for eight nights over a two-year period (August 2011–June 2013). Mist-netting was conducted using 14 ground-level mist nets (12 × 2.5 m, 16-mm mesh, ECOTONE, Sopot, Poland) in the fragments and continuous forest interiors (total capture effort = 11.367 mnh; one mist-net hour [mnh] equals one 12-m net open for 1 h). Nets were opened from dusk until six hours later. Detailed site descriptions and methods can be found in Farneda et al. (2015).

Species traits

To calculate FAR, we used five species functional traits (FAR_{ALL}) that reflect diet and foraging behavior, which comprise important functional components of bat diversity (Meyer et al. 2008, Cisneros et al. 2015): 1) body mass, 2) trophic level, 3) dietary specialization, 4) vertical stratification and 5) aspect ratio and relative wing loading as measures of wing morphology. See Farneda et al. (2015) for a description of these traits, and Meyer et al. (2008) for a detailed explanation of the rationale behind selecting these particular trait variables. Trait values of individual species for the island and countryside ecosystem are provided in Supplementary material Appendix 1 Table A1–A2. As different combinations of multiple traits may affect how functional diversity scales with loss of habitat, we also explored FAR in both ecosystems using two different trait sets: 1) 'diet breadth' (body mass, trophic level and dietary specialization – FAR_{DIET}) and 2) 'dispersal ability' (body mass, vertical stratification and wing morphology – $FAR_{DISPERSAL}$). These traits are related to species responses to local habitat loss and to their effect on ecosystem functioning (Luck et al. 2012). Moreover, 'diet breadth' and 'dispersal ability' are two trait sets considered important determinants of the distribution of species abundances and of community organization in fragmented landscapes (Bommarco et al. 2010). Logarithmic transformations were performed on body mass to normalize values. Continuous traits were standardized to a mean of zero and a standard deviation of one prior to analysis to facilitate comparison of their relative effects.

Habitat classification and selection of spatial scales

To characterize the Panamanian island ecosystem, we used the 'BCI Landcover Map 2003' with a 25-m spatial resolution (Panama Canal Authority 2003) to assess the proportional cover of forest, water and other habitats in the landscape. We considered primary and secondary forest as a single habitat because primary forest was only represented by a small area cover (~2% of primary forest remains) and because the

secondary forest is old-growth (> 90 years, Albrecht et al. 2017), which can be regarded to already have reached an equilibrium species richness and composition.

Measurements of habitat characteristics in the Amazonian countryside ecosystem were obtained using a 30-m spatial resolution land cover map of the BDFFP area from 2011. This map was based on the analysis of an extensive (quasi-annual) time series of Landsat Thematic Mapper data acquired since the inception of deforestation in the region (1970s) and up to 2011 (Carreiras et al. 2014). For the purpose of this study, the map was classified into two land cover types, continuous primary forest and secondary forest matrix (Carreiras et al. 2014).

To assess scale-dependency in bat responses to forest cover loss in both ecosystems, we used landscape buffers of three different sizes (500, 1500 and 3000 m radii) centred on each of the 31 sampling sites. This approach combines information about patch size and isolation (habitat amount hypothesis, see Fahrig 2013). Focal scales were selected in order to encompass the home ranges of different-sized bat species (Meyer et al. 2008, Jackson and Fahrig 2015, Rocha et al. 2017a). Percent forest cover ranged between 2.30–96.04 on islands and 4.55–98.52 in the countryside ecosystem (Supplementary material Appendix 1 Table A3).

To analyze how consistent our conclusions are when focusing on patch- rather than landscape-scale forest loss, we calculated SAR and FAR also using actual patch sizes. For this, as control sites in both study systems do not have a defined area, extending well beyond their boundaries, we assigned them an area size of 1000 ha considering the mean distances between interior and edge sampling sites.

Statistical analyses

SAR and FAR were assessed separately for the island and countryside ecosystem using linear regression (type IV curve sensu Scheiner 2003). To account for differences in sampling effort between study systems, we examined SAR based on Chao1 species richness estimates for each site, calculated using the 'estimateR' function of the R package vegan (Oksanen et al. 2019). We used the Chao1 estimator because it performs well with uneven sampling effort (Chao 1987). We estimated the log–log SAR based on the species richness estimates for each site regressed against patch area and percentage forest cover, respectively. The same approach was used to calculate the equivalent FARs (FAR_{ALL}, FAR_{DIET}, $FAR_{DISPERSAL}$).

FAR_{ALL}, FAR_{DIET} and $FAR_{DISPERSAL}$ were quantified using the total branch length of a functional dendrogram linking all species in each site (Petchey and Gaston 2002). As with SAR, we examined FARs using Chao1 functional diversity estimates, calculated using the 'alpha.estimate' function in the R package BAT (Cardoso et al. 2015), thus allowing to adequately deal with differences in sampling effort between study areas. A dendrogram-based measure of functional diversity has been widely used in ecological and conservation research for summarizing different aspects of community trait composition (Flynn et al. 2009, Ahmed et al. 2019). Functional pairwise dissimilarity matrices were calculated using Gower's distance, which allows considering different types of traits (Laliberté and Legendre 2010). ANCOVA of log-transformed data was used to examine equality of intercepts and slopes between SAR and FAR_{ALL}, as well as between FAR_{DIET} and $FAR_{DISPERSAL}$, with forest patch area and forest cover as a covariate. All analyses were performed using R software (R Core Team).

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.f735q5p> (Farneda et al. 2019).

Results

A total of 3747 bats captured on the landbridge islands and 1892 bats recorded in the countryside ecosystem were used for analysis. Twenty-four and 41 species, respectively, were captured in the island and countryside ecosystem, of which 17 species were shared. The correlation between Chao1 species richness and functional diversity estimates was significant for the countryside (Pearson correlation, $r = 0.54$, $p = 0.025$) but not for the island ecosystem ($r = 0.20$, $p = 0.487$). However, the correlation between species richness and sampling effort was not significant for both study systems (islands, $r = 0.36$, $p = 0.206$; countryside, $r = 0.42$, $p = 0.090$), as effort was roughly similar among sampling sites of each landscape (Supplementary material Appendix 1 Table A3).

Species and functional biogeography

Across the models considering patch area and the different buffer sizes, SAR slope values (z) varied from 0.13 to 0.34 in the island and from 0.06 to 0.24 in the countryside system, while the corresponding values for FAR were 0.05–0.19 (islands) and –0.04–0.02 (countryside). In both the island and countryside ecosystem, SAR was characterized by larger explanatory power (islands: $R^2 = 0.42$–0.80; countryside: $R^2 = 0.01$–0.29) than FAR_{ALL} (islands: $R^2 = 0.05$–0.17; countryside: $R^2 = 0.00$–0.01) (Table 1).

We found a significant SAR for the island ecosystem in relation to patch area and landscape-level forest cover for all three different spatial scales ($p < 0.02$), whereas FAR_{ALL} was not significant ($p > 0.1$) (Table 1, Fig. 1). In the countryside ecosystem, while SAR scaled significantly with patch area and forest cover loss within 500 m buffers ($p < 0.05$), FAR_{ALL} was not significant ($p > 0.6$) (Table 1, Fig. 1). However, while intercepts between SAR and FAR differed significantly in both island and countryside ecosystem, slopes were indistinguishable (ANCOVA, Table 2).

Table 1. Results of linear regression models for species– (SAR) and functional diversity–area relationships using all traits (FARALL) and two different trait sets: 'diet breadth' (FARDIET: body mass, trophic level and dietary specialization) and 'dispersal ability' (FARDISPERSAL: body mass, vertical stratification and wing morphology). For both study systems, results are shown for forest patch area (PA) and forest cover quantified at three different spatial scales (buffers with 500, 1500 and 3000 m radius) as explanatory variable. C = intercept (standard error, SE); z = slope (SE); df = degrees of freedom; F = F-statistic; R^2 = variation explained by the fitted linear regression line; p = p-value. Significant values are in boldface ($p < 0.05$).

	Panamanian islands						Amazonian countryside					
Model	C (SE)	z (SE)	df	F	R^2	p	C (SE)	z (SE)	df	F	R^2	p
SAR (PA)	2.10 (0.14)	0.133 (0.04)	1,12	13.38	0.53	**0.003**	2.86 (0.18)	0.085 (0.03)	1,15	6.27	0.29	**0.024**
SAR (500 m)	1.50 (0.16)	0.335 (0.05)	1,12	47.10	0.80	**0.000**	2.59 (0.32)	0.182 (0.08)	1,15	4.60	0.23	**0.049**
SAR (1500 m)	1.88 (0.17)	0.246 (0.06)	1,12	17.84	0.60	**0.001**	3.03 (0.65)	0.057 (0.17)	1,15	0.12	0.01	0.739
SAR (3000 m)	1.65 (0.30)	0.283 (0.10)	1,12	8.77	0.42	**0.012**	2.26 (1.45)	0.241 (0.35)	1,15	0.47	0.03	0.505
FAR_{ALL} (PA)	1.33 (0.24)	0.049 (0.06)	1,12	0.58	0.05	0.459	1.74 (0.18)	0.009 (0.03)	1,15	0.08	0.01	0.781
FAR_{ALL} (500 m)	0.89 (0.39)	0.194 (0.12)	1,12	2.50	0.17	0.140	1.71 (0.31)	0.022 (0.08)	1,15	0.08	0.00	0.788
FAR_{ALL} (1500 m)	1.13 (0.31)	0.134 (0.11)	1,12	1.54	0.11	0.238	2.00 (0.55)	−0.056 (0.14)	1,15	0.16	0.01	0.696
FAR_{ALL} (3000 m)	1.05 (0.48)	0.140 (0.15)	1,12	0.86	0.07	0.372	1.94 (1.24)	−0.038 (0.30)	1,15	0.02	0.00	0.901
FAR_{DIET} (PA)	1.81 (0.57)	−0.037 (0.15)	1,12	0.06	0.00	0.814	1.29 (0.15)	0.033 (0.03)	1,15	1.30	0.08	0.272
FAR_{DIET} (500 m)	1.44 (0.10)	0.085 (0.31)	1,12	0.07	0.01	0.790	1.14 (0.26)	0.085 (0.07)	1,15	1.51	0.09	0.238
FAR_{DIET} (1500 m)	1.83 (0.76)	−0.050 (0.26)	1,12	0.04	0.00	0.853	1.54 (0.49)	−0.023 (0.13)	1,15	0.03	0.00	0.855
FAR_{DIET} (3000 m)	1.71 (1.14)	−0.002 (0.36)	1,12	0.00	0.00	0.995	1.81 (1.09)	−0.088 (0.27)	1,15	0.11	0.01	0.745
$FAR_{DISPERSAL}$ (PA)	0.88 (0.15)	0.075 (0.04)	1,12	3.52	0.23	0.085	1.15 (0.13)	0.047 (0.03)	1,15	3.58	0.19	0.078
$FAR_{DISPERSAL}$ (500 m)	0.51 (0.24)	0.201 (0.07)	1,12	7.52	0.39	**0.018**	0.99 (0.23)	0.106 (0.06)	1,15	2.99	0.17	0.104
$FAR_{DISPERSAL}$ (1500 m)	0.78 (0.20)	0.131 (0.07)	1,12	3.55	0.23	0.084	1.52 (0.45)	−0.039 (0.12)	1,15	0.11	0.01	0.741
$FAR_{DISPERSAL}$ (3000 m)	0.70 (0.32)	0.137 (0.10)	1,12	1.85	0.13	0.199	1.51 (1.02)	−0.036 (0.25)	1,15	0.02	0.00	0.887

Functional biogeography based on different trait sets

FAR_{DIET} and $FAR_{DISPERSAL}$ varied depending on fragment–matrix contrast and spatial scale. For the island ecosystem, $FAR_{DISPERSAL}$ was significant for forest cover within 500 m landscape buffers ($z = 0.20$, $p = 0.018$) (Table 1, Fig. 2). In contrast, neither FAR_{DIET} nor $FAR_{DISPERSAL}$ was significant for the countryside ecosystem in relation to patch area or any of the three landscape scales ($p > 0.05$) (Table 1). For patch area and forest cover at all three spatial scales, regression intercepts and slopes between $FAR_{DISPERSAL}$ and FAR_{DIET} were indistinguishable in the island and countryside ecosystem (Table 2).

Discussion

Island biogeographic theory describes species richness on islands as a result of a dynamic equilibrium between area-dependent extinction and isolation-dependent colonization (MacArthur and Wilson 1967). However, the idea that forest fragments are terrestrial analogues to islands has clearly been refuted (Laurance 2008, Mendenhall et al. 2014a, Wolfe et al. 2015). Such criticism led to the increased application of 'countryside biogeography' as an alternative theoretical framework to the study of biodiversity over space and time in areas whose ecosystem qualities are strongly influenced by human activities (Mendenhall et al. 2013, Frishkoff et al. 2019). Our results offer new insights into the nature of the SAR and FAR in island and countryside systems, allowing predictions about the potential gains and losses of species and ecological functions with habitat loss across different spatial scales. We show that while terrestrial fragmented landscapes suffer a considerably lower loss of species than island ecosystems, functional diversity scales in similar ways with habitat loss in both study systems.

Species and functional biogeography

The future of biodiversity in the Anthropocene will be dictated mainly by countryside ecosystems, whose characteristics are strongly influenced by anthropogenic activities (Mendenhall et al. 2013, Frishkoff et al. 2019). In fragmented, human-modified landscapes, bat species persistence may be strongly dependent on the quality and type of the matrix (Mendenhall et al. 2014a, Cisneros et al. 2015, Farneda et al. 2018a). As predicted, the Panamanian island system was characterized by a more typical SAR, with steeper slope (z) values than for the countryside ecosystem. Islands surrounded by an inhospitable water matrix suffer considerably greater loss of species than forest fragments embedded within a matrix of secondary forest, where different successional stages offer a greater diversity of foraging habitats and resources, and more favorable conditions for the dispersal of many species across the degraded landscape (Watling et al. 2011, Rybicki and Hanski 2013, Mendenhall et al. 2014a, Wolfe et al. 2015).

A steeper slope (z) of the relationship between species richness and habitat patch area in the landbridge island system compared to the countryside ecosystem is expected because the forest on the islands is shorter in stature and less diverse in tree species than adjacent mainland due to strong dry-season trade winds, which heavily impact forest structure and dynamics. This effect is most pronounced on the more isolated and smaller islands, which are greatly affected by edge effects (Leigh et al. 1993). At the BDFFP, these effects diminished over the course of ~30 years of secondary forest regeneration, as reflected in an increase of

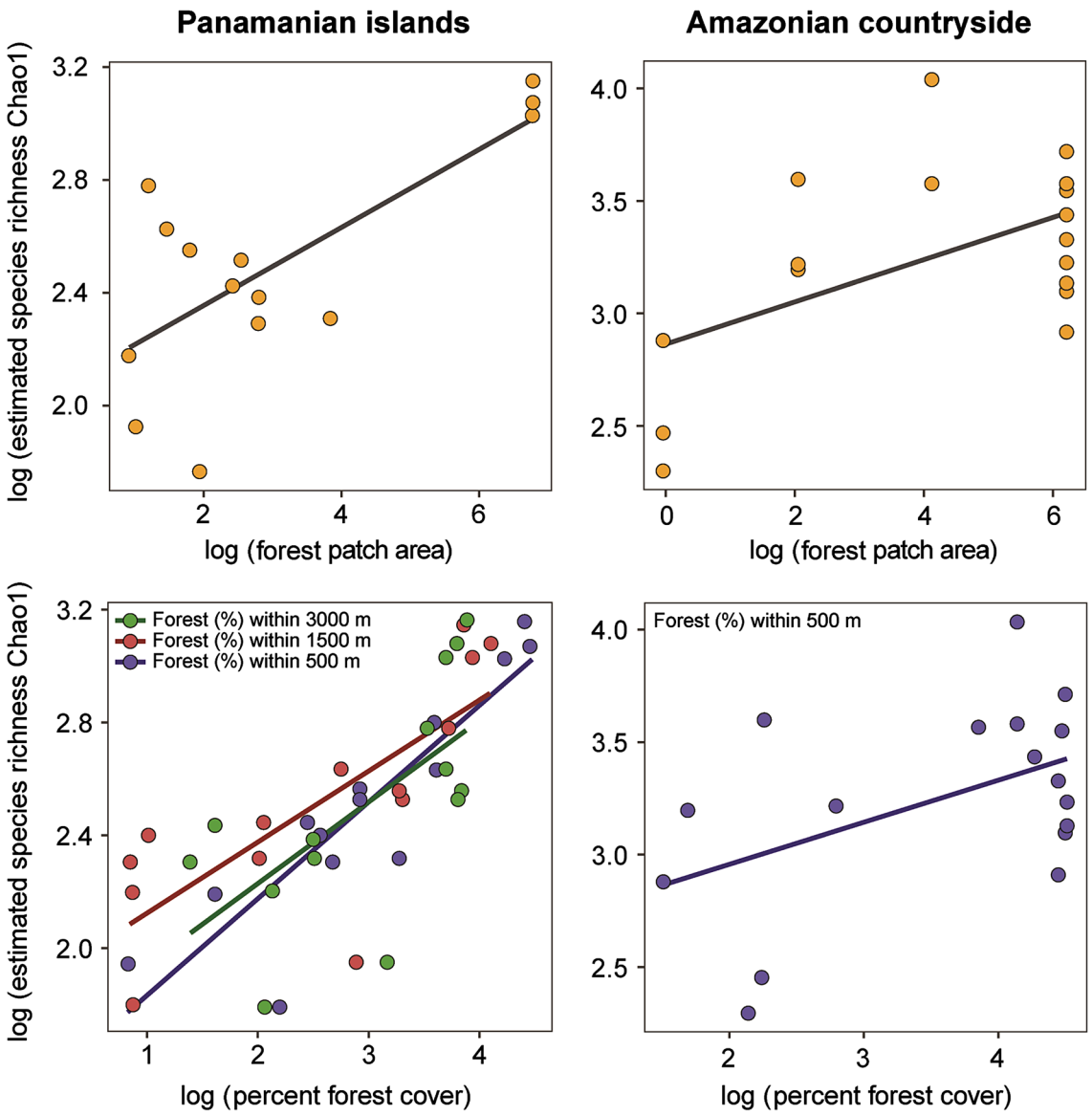

Figure 1. Significant regressions ($p < 0.05$) for species–area relationships (SAR) in a high fragment–matrix contrast ecosystem of Panamanian landbridge islands and a low fragment–matrix contrast Amazonian countryside ecosystem, evaluated for patch area and landscape-level forest cover at three different spatial scales (500, 1500 and 3000 m radii around sampling sites).

primary forest-interior bat species in the matrix over time (Farneda et al. 2018a, b, Rocha et al. 2018). Furthermore, smaller range of forest patch sizes and inferior habitat quality in the island compared to the countryside ecosystem may have equally affected our results. However, terrestrial systems are more likely to show species turnover as a consequence of habitat changes, while islands are more likely to show nested species loss (Mendenhall et al. 2014a, Wolfe et al. 2015).

In stark contrast to SAR, the observed FAR_{ALL} suggests that bat assemblages in both the island and countryside ecosystem provide qualitatively similar ecosystem functions independently of the amount of forest cover, corroborating the findings of De Coster et al. (2015) for bird assemblages across a gradient of habitat loss in the Brazilian Atlantic Forest, and of Ross et al. (2019) for avifauna in the Japanese Ryūkyū archipelago. Similar functions may be performed by different species that provide essentially the same ecosystem services (Cumming and Child 2009, Mayfield et al. 2010). The loss of some bat species implies not only an increase in the sensitivity of SAR to forest reduction, but also suggests the loss of functionally redundant species for FAR_{ALL}. In this context, our results indicate that bat ecological functions, such as seed dispersal, pollination and arthropod suppression might be maintained in smaller fragments even with the reduction in species richness, and that species richness alone may not adequately reflect the full extent of biodiversity change following anthropogenic disturbance.

Table 2. Analyses of covariance (ANCOVA) comparing intercepts and slopes of species– (SAR) and functional diversity–area relationships (FAR_{ALL}), as well as FAR based on two different sets of traits ('diet breadth' – FAR_{DIET}: body mass, trophic level and dietary specialization; 'dispersal ability' – $FAR_{DISPERSAL}$: body mass, vertical stratification and wing morphology). The results are shown for the Panamanian islands and the Amazonian countryside ecosystem, considering patch area (PA) and landscape buffers of 500, 1500 and 3000 m radius. df = degrees of freedom; F = F-statistic; p = p-value. Significant values are in boldface ($p < 0.05$).

Ecosystem	Relationships compared (spatial scale radii)	Intercept			Slopes		
		df	F	p	df	F	p
Panamanian islands	SAR – FAR_{ALL} (PA)	1,25	42.74	**0.000**	1,24	1.29	0.268
	SAR – FAR_{ALL} (500 m)	1,25	56.46	**0.000**	1,24	1.14	0.297
	SAR – FAR_{ALL} (1500 m)	1,25	47.85	**0.000**	1,24	0.84	0.369
	SAR – FAR_{ALL} (3000 m)	1,25	42.74	**0.000**	1,24	1.29	0.268
	FAR_{DIET} – $FAR_{DISPERSAL}$ (PA)	1,25	3.09	0.091	1,24	0.51	0.484
	FAR_{DIET} – $FAR_{DISPERSAL}$ (500 m)	1,25	3.18	0.087	1,24	0.13	0.720
	FAR_{DIET} – $FAR_{DISPERSAL}$ (1500 m)	1,25	3.09	0.091	1,24	0.44	0.516
	FAR_{DIET} – $FAR_{DISPERSAL}$ (3000 m)	1,25	3.09	0.091	1,24	0.51	0.484
Amazonian countryside	SAR – FAR_{ALL} (PA)	1,31	118.44	**0.000**	1,30	2.46	0.127
	SAR – FAR_{ALL} (500 m)	1,31	115.87	**0.000**	1,30	1.84	0.185
	SAR – FAR_{ALL} (1500 m)	1,31	105.86	**0.000**	1,30	0.26	0.612
	SAR – FAR_{ALL} (3000 m)	1,31	106.52	**0.000**	1,30	0.36	0.553
	FAR_{DIET} – $FAR_{DISPERSAL}$ (PA)	1,31	0.50	0.485	1,30	0.14	0.713
	FAR_{DIET} – $FAR_{DISPERSAL}$ (500 m)	1,31	0.50	0.486	1,30	0.05	0.818
	FAR_{DIET} – $FAR_{DISPERSAL}$ (1500 m)	1,31	0.44	0.514	1,30	0.01	0.922
	FAR_{DIET} – $FAR_{DISPERSAL}$ (3000 m)	1,31	0.44	0.514	1,30	0.02	0.899

Functional biogeography based on different trait sets

Exploring different sets of functional traits to estimate FAR via robustness tests can be a promising approach to gain ecologically more meaningful information about how functional diversity is influenced by environmental changes (Calba et al. 2014). Studies on the consequences of environmental changes for functional diversity do not point to a simple and ubiquitous pattern (Devictor et al. 2010, Mayfield et al. 2010), and different sets of traits can differentially affect functional diversity and its relationship with area. Our results suggest that studying FAR through different trait sets can increase our capacity to detect functional redundancy within communities. For example, in the island ecosystem, the high dissimilarity between FAR_{DIET} and $FAR_{DISPERSAL}$ indicates that habitat loss differentially affects trait selection, and thus differences in FAR based on certain traits can be larger than based on others.

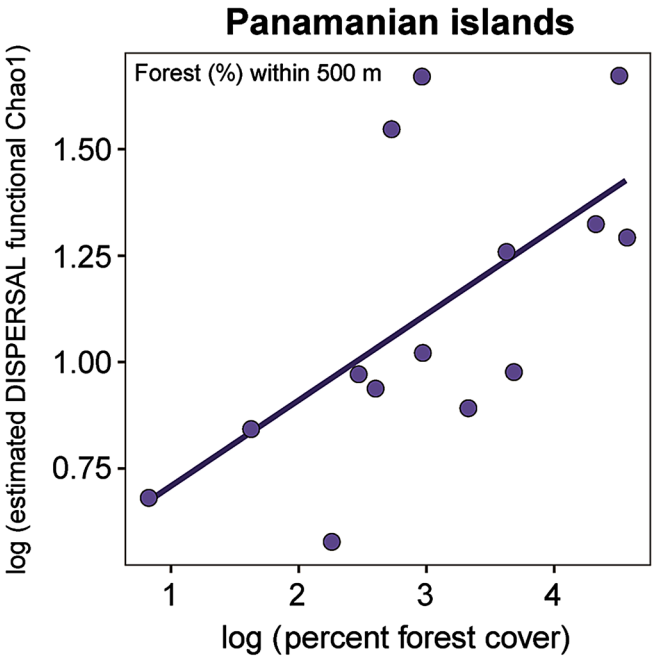

Figure 2. Significant ($p < 0.05$) functional diversity–area relationship based on trait set 'dispersal ability' ($FAR_{DISPERSAL}$: body mass, vertical stratification and wing morphology) in the high fragment–matrix contrast Panamanian island ecosystem.

$FAR_{DISPERSAL}$ (500 m landscape buffers) in the Panamanian island ecosystem showed similar declines in functional diversity to species richness for the same loss of habitat area. Functional diversity might decrease at similar rates or even faster than species richness depending on the order of species loss and the importance of lost species in the community functional space (Flynn et al. 2009, Supplementary material Appendix 1 Fig. A1). In this context, extinction of the rarest and functionally unique species in an assemblage may have a disproportionately large effect on its functional structure, disrupting the integrity of key ecological processes and resulting in significant impacts on the long-term provisioning of ecosystem services (Coetzee and Chown 2016, Leitão et al. 2016). The significant positive effect of forest cover on dispersal-related functional diversity in the island ecosystem may be associated with the lower dispersal capacity of certain patch area-sensitive species such as *Lophostoma silvicolum* and *Tonatia saurophila* (Meyer and Kalko 2008).

Corroborating our hypothesis, although the relatively high vagility of bats may buffer some of the negative effects of diminishing food availability in landscapes with high fragment–matrix contrast, the aquatic matrix in the island system seems to impose a greater dispersal limitation

compared to the 'soft' secondary forest matrix at the BDFFP that provides resources for many species. Furthermore, the distances between islands and mainland in Panama are larger than those between fragments and continuous forest in Brazil, which may have constrained the occurrence of certain dispersal-linked traits on smaller and more isolated islands, as observed by Farneda et al. (2015).

Our findings based on FAR_{DIET} in both the island and countryside ecosystem are not in accordance with trophic biogeography theory, which posits that species at higher trophic levels have a lower occupancy than basal species as forest cover decreases (Gravel et al. 2011, Jacquet et al. 2017). A similar pattern has recently been documented for the avifauna of oceanic islands by Ross et al. (2019), who reported different slopes among guilds of birds of the same trophic rank, but did not find support for a relationship consistent with trophic biogeography. Reanalysis of the data from Meyer et al. (2008) by Farneda et al. (2015) indicated trophic level as one of the best predictors of species vulnerability to forest fragmentation in the Panamanian island system and at the BDFFP, suggesting that many of the patch area-sensitive animalivorous species went extinct even from the larger forest fragments in both study systems. These contrasting patterns between Farneda et al.'s (2015) results and FAR_{DIET} may be explained by the effect of relative species abundances calculated on individual traits in the previous study and the different functional metrics employed.

Conservation implications and future perspectives

While species-based biogeography has been widely employed to forecast species extinctions due to habitat loss, functional biogeography and its application to conservation issues is in its infancy (Violle et al. 2014). Elucidating the patterns of biodiversity loss in island and countryside ecosystems jointly through taxonomic and functional biogeography can help policymakers to make better-informed decisions regarding the delineation of priority areas for conservation than if based solely on traditional species-based biogeography.

Our results for FAR_{ALL} suggest that smaller and larger habitat patches in both the island and countryside ecosystem maintain qualitatively similar bat ecological functions, but that different functional trait sets may shift in importance in determining the responses to forest loss and fragmentation in the island system. Marked differences in habitat structure and composition likely translate into more selective environmental filters (Farneda et al. 2015), thus limiting the taxonomic diversity of bats and probably that of other less mobile groups of wildlife inhabiting landscapes with higher fragment–matrix contrast. These findings can provide guidance with regard to the establishment of future protected areas to maximize the preservation of species and functional traits. Conservation strategies aiming to minimize local extinction risk for area-sensitive species should focus on promoting habitat availability in fragmented landscapes.

The sensitivity of certain bat functional traits linked to important ecological processes, such as dispersal capacity and resource utilization, is strongly associated with habitat availability (Cisneros et al. 2015, Farneda et al. 2015). We therefore argue that functional biogeographical studies should consider evaluating FAR based on different ecologically meaningful trait sets and for different spatial scales to gain a more in-depth understanding of which traits mainly drive FAR and of how functional diversity scales with habitat loss in fragmented landscapes.

The classic SAR only predicts how species richness changes with loss of native habitat area, while ignoring the diversity of species responses in landscape mosaics composed of multiple habitat types. Pereira and Daily (2006) proposed the countryside species–area relationship (CSAR) to account for the differential use of native and nonnative habitats by species. It has been shown that CSAR fits observed patterns in countryside systems better than the classic SAR (Martins and Pereira 2017), and we therefore recommend extending this line of research to comparing CSAR and CFAR.

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Supplementary material (available online as Appendix ecog-04507 at <www.ecography.org/appendix/ecog-04507>). Appendix 1.