BIODIVERSITY RESEARCH

Spatial patterns of species richness and functional diversity in Costa Rican terrestrial mammals: implications for conservation

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ABSTRACT

Aim Functional diversity is a relatively recent approach to quantify species diversity and may provide a better understanding of the linkages between biological diversity and ecosystem functioning. Understanding the relationships between mammal species richness and functional diversity, the factors that influence these relationships, and the spatial scale at which they operate, can improve our knowledge of ecosystem functioning and may benefit conservation planning.

Location Costa Rica (8°0′–11°14′N and 82°32′–85°56′W).

Methods We evaluated spatial patterns of species richness and functional diversity for terrestrial mammal species in Costa Rica using regression techniques and assessed the influence of environmental, biological and anthropogenic factors on those patterns.

Results Environmental and anthropogenic factors influenced species richness and functional diversity, while a biological factor (i.e. species' geographic origin) only influenced functional diversity. Observed patterns of species richness and functional diversity resulted in identification of three regions which could be differentiated by ecosystem type and the occurrence of bats and rodents. The spatial scale at which variation in these diversity measures also differed, with species richness most affected at fine spatial scales (local) and functional diversity best explained at the meso-scale (regional level).

Main conclusions Both diversity measures varied spatially in relationship of examined factors, and the extent at which influencing factors affect both measures also varied across the country and scales. Our results highlight that investigating the interaction of scales is necessary for also further understanding macroecological patterns. Considering multiple measures of biological diversity and the spatial scales at which they operate may improve our understanding of biodiversity and the efficacy of species and community conservation planning.

Keywords
biodiversity, biogeography, functional traits, geographically weighted regression, ordinary least squares spatially explicit patterns.

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INTRODUCTION

Knowledge of biological diversity is fundamental for understanding ecological processes and anthropogenic influence and thus as a basis for conservation planning (Brooks & Helgen, 2010). The loss of a single species or population can have major irreversible effects on ecosystem functioning and services (Ceballos & Ehrlich, 2002). Given the accelerated rates of species and population losses, and the current biodiversity crisis (Ceballos *et al.*, 2010), characterizing spatial patterns of species diversity at scales relevant to conservation (e.g. ecoregions) is needed to inform decision-making (Safi

et al., 2011; González-Maya *et al.*, 2012). Traditional studies of biological diversity have emphasized species richness (Petchey & Gaston, 2002b; Rondinini *et al.*, 2011b) and have recently been conducted at global scales (Ceballos *et al.*, 2005; Schipper *et al.*, 2008; Brooks *et al.*, 2010; Boitani *et al.*, 2011). However, more recent measures of diversity including genetic, phylogenetic and functional are receiving increased attention as they can improve our understanding of species diversity and associated ecological processes (Tilman, 2001; Petchey & Gaston, 2002b; Magurran & McGill, 2011).

Functional diversity (FD) is considered the degree of complementarity between species' trait values estimated by their dispersion in trait-multidimensional space (Petchey & Gaston, 2002a). This measure incorporates species richness, evenness and divergence (Mason *et al.*, 2005), providing a measure of taxonomic diversity and species' roles in ecosystem functioning (Tilman *et al.*, 1997; Tilman, 2001). Thus, it can influence ecosystem and community productivity, which in turn can affect functionality and resilience (Tilman *et al.*, 1997; Petchey, 2003). Functional diversity has gained increasing attention among ecologists and has been used to characterize the provisioning of ecosystem services (Daily *et al.*, 1997; Dias *et al.*, 2013). Although originally applied to plants (Tilman *et al.*, 1997; Tilman, 2001), FD has been applied to other taxa as well (Blaum *et al.*, 2011; Cardoso *et al.*, 2011). For mammals, FD has been assessed in relation to dispersal and pollination from regional (Stevens *et al.*, 2004) to global scales (Kunz *et al.*, 2011; Safi *et al.*, 2011).

Because FD is directly related to ecosystem resilience and services (Mouchet *et al.*, 2010), it is important to identify factors that influence FD and the scales at which these factors operate (Wright *et al.*, 1998; Kraft & Ackerly, 2010; Messier *et al.*, 2010; Belmaker & Jetz, 2011). However, information at the desired resolution is not always available or is not used or consistent with conservation planning (Boitani *et al.*, 2011). For example, global assessments can provide coarse-scale identification of conservation priority areas (Brooks *et al.*, 2006, 2010), but conservation planning typically occurs at local or regional scales (Groves *et al.*, 2002). Therefore, finer scale analyses may provide better understanding of local processes relevant to planning (Belmaker & Jetz, 2013).

We compared patterns of species richness and FD for terrestrial mammals at multiple scales for Costa Rica. We selected Costa Rica because of its key role in ecological, evolutionary and biogeographical processes in the Western Hemisphere, its important diversity of mammal species and available information (Sánchez-Azofeifa *et al.*, 2001; Rodríguez-H *et al.*, 2002; González-Maya *et al.*, 2015). Our objectives were (1) to assess spatial patterns of terrestrial mammal species richness and FD, (2) to evaluate the influence of environmental, biological and anthropogenic factors on species richness and FD, and (3) to compare patterns at different scales at which various factors influence species richness and FD.

METHODS

Study area

Costa Rica is located in Central America (8°0′–11°14′ N, 82°32′–85°56′ W), with a continental area of 51,100 km². Due to its geographical position and geological history, it has rich biota, containing about 4% of the known global biodiversity in only 0.03% of the global continental area (Obando, 2008). Costa Rica harbours 238 mammal species, including 208 terrestrial species (18 endemic) in 140 genera and 44 families (Rodríguez-H *et al.*, 2002, 2012). This represents about 4.5% of all known mammal species globally (Schipper *et al.*, 2008) and 11.3% and 28.7% of known genera and families, respectively (Wilson & Reeder, 2005).

Mammal and environmental data sources

We assessed the spatial patterns and factors potentially influencing Costa Rican mammal diversity using species distribution data, life-history traits and environmental and anthropogenic factors. Using global mammal distributions provided by the IUCN Red List of Threatened Species (International Union for the Conservation of Nature, 2011), we extracted all species recorded as present in Costa Rica as determined by the 2008 Global Mammal Assessment (Schipper *et al.*, 2008) and validated these standardized distribution maps using the last updated list of species for the country (Rodríguez-H *et al.*, 2002). These ranges represent the best information available, and each range was delineated, assessed and revised by practicing mammalogists from Costa Rica (Schipper *et al.*, 2008). Our database included 206 terrestrial mammal species from Costa Rica, differing from the 208 reported by Rodríguez-H *et al.* (2002). This difference was a consequence of taxonomic and distribution changes or synonyms (Wilson & Reeder, 2005): four species recorded by Rodríguez-H *et al.* (2002) did not have updated distribution information, two species were synonymized recently (Helgen *et al.*, 2013), and we included four species with marginal distributions in Costa Rica to maintain consistency with the species distribution polygons used for analyses. For each of the 206 species, we compiled information regarding functional traits including body mass, trophic niche (i.e. herbivore, carnivore, omnivore) and habitat mode (i.e. terrestrial, aquatic, arboreal, fossorial, volant) from a published database (Jones *et al.*, 2009), previously published works (Davidson *et al.*, 2009) and other published information sources for species not included in these databases. When no information existed for a species (~4%), we used data from the most closely related species within the same genus (Davidson *et al.*, 2009). For each trait, we plotted the percentage occurrence by category for each mammalian order.

We obtained information on environmental (i.e. bioclimatic, ecosystem and topographic) and anthropogenic

variables from global databases and our own estimates of natural land cover (Table 1), represented as the proportion of undisturbed land cover in each cell (see below; Table 2). Biological variables included species richness (i.e. for FD analyses) and the geographic origin (North or South America) of each species. To estimate geographic origin, we compiled information at the lowest taxon possible (Eisenberg, 1981; Lim, 2009; Wilson & Mittermeier, 2009, 2011; Morgan & Czaplewski, 2012; Mittermeier *et al.*, 2013) and estimated the proportion of species from each continent of origin for each grid cell.

Spatial data

We generated a grid of 617 ~83 km^2 cells adjusted to geography by clipping cells to the land edge, which comprised the entire mainland. We selected this cell size as our mapping unit based on the mean range of the five species with the smallest ranges in the country. Although species polygons were in vector format and could be used at finer resolutions, we used this coarser resolution because finer resolutions would likely increase spatial autocorrelation but not improve analytical performance (Safi *et al.*, 2011). In addition, this resolution better matched interpolated environmental variables (i.e. climatic) and species' distribution data (Belmaker & Jetz, 2011).

We overlaid this grid on the mammal distribution layers and extracted data for the species present within each cell, including taxonomic classification and traits. We estimated environmental variables (Table 1) for each cell; variables at finer resolution were scaled by averaging values to the coarser resolution of our study grid. We quantified natural habitat by calculating the proportion of natural land covers from each cell using national data in vector format (Instituto Tecnológico de Costa Rica, 2008). All spatial analyses were performed using ArcGIS 10.2 (Environmental Systems Research Institute, 2013).

Table 1 Description of biological, environmental and anthropogenic variables potentially related with terrestrial mammals species richness and functional diversity in Costa Rica. All variables were scaled to the same resolution by averaging in case of coarser resolution of our study grid; higher resolution from richness estimated from distribution polygons will likely increase spatial autocorrelation but will not increase analytical performance.

Type of variable	Variable	Description	Resolution	Source
Biological	S	Species Richness: number of mammal species per cell	Grid resolution (83 km^2)	This study
	N.A.Orig.	Proportion of species (from total) of North American origin	Grid resolution (83 km^2)	This study
	S.A.Orig.	Proportion of species (from total) of South American origin	Grid resolution (83 km^2)	This study
Environmental	Elevation	The mean elevation value per cell derived from a Digital Elevation Model	1 km^2	U. S. Geological Survey (2012)
	Aspect	Terrain orientation degree regarding North derived from a Digital Elevation Model	1 km^2	U. S. Geological Survey (2012)
	AMT	Annual Mean Temperature value averaged per cell	~1 km	Hijmans *et al.* (2005)
	AP	Annual Precipitation mean value averaged per cell	~1 km	Hijmans *et al.* (2005)
	PS	The coefficient of variation for precipitation per cell (Precipitation seasonality)	~1 km	Hijmans *et al.* (2005)
	TS	The standard deviation of temperature *100 per cell (Temperature seasonality)	~1 km	Hijmans *et al.* (2005)
	NPP	The net amount of solar energy converted to plant organic matter through photosynthesis averaged per cell (Net Primary Productivity)	0.25 decimal degrees	Imhoff *et al.* (2004a)
	PET	The Potential Evapo-transpiration mean per cell	~1 km	Trabucco & Zomer (2009)
Anthropogenic	NLC	The proportion of natural land cover (NLC) respecting the intervened cover (including crops, cities, roads and highways)	Grid resolution (83 km^2)	This study based on Instituto Tecnológico de Costa Rica (2008)
	HANPP	Human appropriation of net primary productivity (HANPP) through the consumption of food, paper, wood and fibre, alters the composition of the atmosphere, levels of biodiversity, energy flows within food webs and the provision of important ecosystem services averaged per cell	0.25 decimal degrees	Imhoff *et al.* (2004b)
	HD	Estimates of human population for the years 1990, 1995 and 2000 averaged per cell.	2.5 arc-minute	CIESIN – Columbia University (2005)

Table 2 Results for best competing and selected ordinary least squares models for species richness and functional diversity (FD) of mammals using an 83 km² grid, Costa Rica. No. Par indicates the number of estimated parameters for each model, log(L) is the natural logarithm of the maximum likelihood value; AICc is the value of Akaike's information criterion corrected for small sample sizes, ΔAICc is the difference between the model and best supported model, and w is the Akaike weight.

Variable	Model	No. Par	log(L)	AICc	ΔAICc	w_i	R^2
Richness							
Species richness	S1	8	0.113	4237.06	4.36	0.08	0.712
	S2	8	0.139	4236.65	3.95	0.09	0.713
	S3	7	0.235	4235.60	2.90	0.16	0.710
	S4	8*	1.000	4232.70	0.00	0.67	0.714
Functional Diversity							
Region 1	FD1	6*	1.000	−434.52	0.00	1.00	0.786
	FD2	9	1.1E-43	−236.77	197.75	< 0.01	0.460
	FD3	9	1.1E-43	−236.77	197.75	< 0.01	0.395
	FD4	7	0.00	1800.75	2235.27	N/E	N/E
Region 2	FD1	4*	1.000	−98.17	0.00	0.65	0.499
	FD2	5	0.156	−94.45	3.72	0.10	0.500
	FD3	5	0.243	−95.34	2.83	0.16	0.506
	FD4	7	0.133	−94.13	4.04	0.09	0.510
Region 3	FD1	7*	1.000	−360.11	0.00	0.93	0.960
	FD2	10	< 0.01	−334.22	25.89	< 0.01	0.960
	FD3	6	0.073	−354.87	5.24	0.07	0.960
	FD4	10	< 0.01	−334.22	25.89	< 0.01	0.960

*Indicates the selected models.

Data analysis

For each cell, we estimated species richness as the total number of species and then estimated a FD score using the Functional Traits Diversity index (Petchey & Gaston, 2002b). We selected this FD index as it can be used with multiple traits, does not require abundance data and performs well for species-rich communities (Petchey & Gaston, 2002b; Flynn *et al.*, 2009; Laliberté & Legendre, 2010; Safi *et al.*, 2011; Mason *et al.*, 2012). We selected traits considered to better represent niche dimensions and resource requirements of species (Flynn *et al.*, 2009; Safi *et al.*, 2011) and consequently better reflect the relationship between biodiversity and ecosystem functioning (Flynn *et al.*, 2009). Furthermore, these traits are available for most species (Davidson *et al.*, 2009; Jones *et al.*, 2009; Dalerum, 2013) and have been informative for exploring functional diversity and threats in mammals (Marquet & Cofre, 1999; Davidson *et al.*, 2009; Safi *et al.*, 2011). The FD index is defined as the sum of the dendrogram branch distances necessary to connect all species in functional space but does not account for abundance (Casanoves *et al.*, 2011; Safi *et al.*, 2011). We constructed a functional dendrogram for each cell using the Gower distance and unweighted pair groups with arithmetic averages, then summed the branches necessary to connect all species. Higher FD scores indicate high complementarity (i.e. species are distant in trait space), and lower values indicate low complementarity (i.e. species are more similar).

Our approach has been demonstrated as reliable across a wide range of trait diversity (Laliberté & Legendre, 2010;

Weiher, 2011) and identified as the only solution for estimating the volume occupied in trait space when trait dimensionality is more than two or three (Weiher, 2011). This index is also appropriate for mixed data, including quantitative (i.e. body mass) and nominal (i.e. habitat mode, feeding niche) data (Gower, 1971; Kaufman & Rousseeuw, 2005; Laliberté & Legendre, 2010; Casanoves *et al.*, 2011). Consequently, similarities among species based on nominal data do not depend on the levels of the variable; each level is treated independently, and similarities between paired species are constructed according to occurrence of each attribute (Gower, 1971; Kaufman & Rousseeuw, 2005; Casanoves *et al.*, 2011). Moreover, similarity analyses use matrices with positive semi-definite properties analogous to a correlation matrix that allows multidimensional representation to estimate the degree of similarity among multiple variables of interest (Gower, 1971; Kaufman & Rousseeuw, 2005). We do acknowledge limitations of this approach. For example, multiple binary variables (e.g. carnivorous, herbivorous, omnivorous) derived from a single categorical variable (feeding niche) are actually not independent. Gower distance assigns these binary variables a weight equivalent to the original categorical variable (Gower, 1971); therefore, multiple levels derived from single categorical variables could artificially inflate the influence of these variables. Nevertheless, we consider this approach the most appropriate when using presence–absence data and believe it provides a reasonable approach to FD despite these limitations.

We initially plotted species richness and FD values by cells and visually identified three groups by their spatial

clustering. We selected the cells in each of these groups, assigned these cells to different regions and assessed the relationship between species richness and FD using simple linear regression. For each region, we explored which variables could explain the groupings, by evaluating both dominant biomes/major habitat types (Olson *et al.*, 2001) and by plotting species richness of dominant groups such as rodents and bats.

We used ordinary least squares (OLS) regression models (Comont *et al.*, 2012; Barnagaud *et al.*, 2014) for species richness at the country and regional scales. All variables except natural land cover proportion were log(10)-transformed before analyses. At each scale, we generated models with all possible variable combinations without interaction terms. We selected the best model using Akaike's information criterion corrected for small samples (AICc; Burnham *et al.* (2011)) and Akaike weights (Wagenmakers & Farrell, 2004). We used model averaging when competing models were equally parsimonious (< 2 ΔAIC; (Symonds & Moussalli, 2010). For selected models, we tested for spatial autocorrelation and difference from the null model using Moran's I test of the residuals (Brunsdon *et al.*, 2010). We evaluated overall model performance and explanatory power using R^2 and coefficients of each variable. We then used Koenker's statistic to assess heteroscedasticity and non-stationarity of the model and the Jarque-Bera test for normality (Brunsdon *et al.*, 2010). To assess multicollinearity, we used the variance inflationary factor (VIF) and considered models with values > 7.5 having potential redundancy (O'Brien, 2007).

Once models were selected and non-stationarity identified, we used geographically weighted regression (GWR) to identify spatial variation and clusters of high and low predictability or mismatch (Brunsdon *et al.*, 1998, 2010; Fotheringham *et al.*, 1998; Foody, 2003). Coarse-scale (i.e. countrywide) regressions can fail to detect important relationships if variables are spatially non-stationary (Foody, 2003), whereas GWR can identify the spatial variation of these relationships (Fotheringham *et al.*, 2002). Consequently, multiple regression methods are necessary when exploring relationships at multiple spatial scales (Fotheringham *et al.*, 1998; Foody, 2003; Brunsdon *et al.*, 2010). Geographically weighted regression estimates separate equations for each variable and incorporate dependent and independent variables within a defined bandwidth (Fotheringham *et al.*, 1998). We defined our bandwidth using kernel-based adaptive selections with a sample-adjusted AIC which selects the best smoothing factor based on the number of neighbourhood features as an adaptive function (i.e. Gaussian function; Brunsdon *et al.*, 2010). Geographically weighted regression also allows exploring the spatial influence of linear model such as OLS at different resolutions (Brunsdon *et al.*, 1998, 2010; Fotheringham *et al.*, 1998; Foody, 2003). We performed GWRs when non-stationarity was identified for fitted models of species richness at national scale and functional diversity at the identified regions. We used pseudo R^2 values to compare variation

explained by OLS compared to GWR models (McFadden, 1973). Statistical analyses were performed using the R platform for windows (R Team Development Core, 2008) and ArcGIS 10.2, including the spatial analyst extension (Environmental Systems Research Institute, 2013).

RESULTS

Spatial patterns of mammal species and functional diversity

Percentage of species in trait categories varied among mammalian orders with trophic niche containing more carnivore and herbivore species and habitat mode including more terrestrial and volant species (Fig. 1a,b). Body masses for mammals were predominantly small and small–medium, largely represented by bats and rodents (Fig. 1c). Species richness was spatially heterogeneous (Fig. 2a) and dominated by bats and rodents which represented about 75% of all species. Overall mean (± SD) species richness was 128 ± 18, with greatest species richness in and near the Talamanca cordillera piedmont and the Central Volcanic range.

Functional diversity varied with an overall mean (± SD) value of 3.26 ± 0.56. Greatest values were in north-eastern Costa Rica (Guanacaste Province) near the Nicaraguan border, and lowest values were in the central Caribbean plains (Fig. 2b). We categorized the three regional groupings (Fig. 3a) identified during our preliminary analyses as Caribbean and Central and Southern Pacific lowlands (Region 1), high-elevation areas (Talamanca, Central Volcanic and Monteverde ranges) and northern lowlands (Region 2), and the Nicoya Peninsula in the north-eastern portion of the country (Region 3; Fig. 3c). Regression analyses for the three groups indicated a positive relationship between species richness and functional diversity with strongest association in Region 3 ($R^2 = 0.95$, $P < 0.001$), followed by Region 1 ($R^2 = 0.73$, $P < 0.001$) and Region 2 ($R^2 = 0.39$, $P < 0.001$). Intercepts also varied among regions: 1.03, 0.40 and 0.20 for regions 1, 2 and 3, respectively. Regions 1 and 2 are dominated by tropical moist forests (98% each), whereas Region 3 is composed of tropical moist forests and dry forests (46% and 50%, respectively). Region 3 was also influenced by the effect of rodents and bats on functional diversity (Fig. 3b). Spatially, cells with high species richness typically also had high FD.

Variable influence and its spatial variation over mammal species richness

The best model for countrywide species richness included eight environmental and anthropogenic variables (Table 2). Precipitation and temperature seasonality, natural land use and human density were negatively associated with species richness, while remaining variables were positively associated (Table 3). The best model explained 71% of the variation in species richness. We identified heteroscedasticity
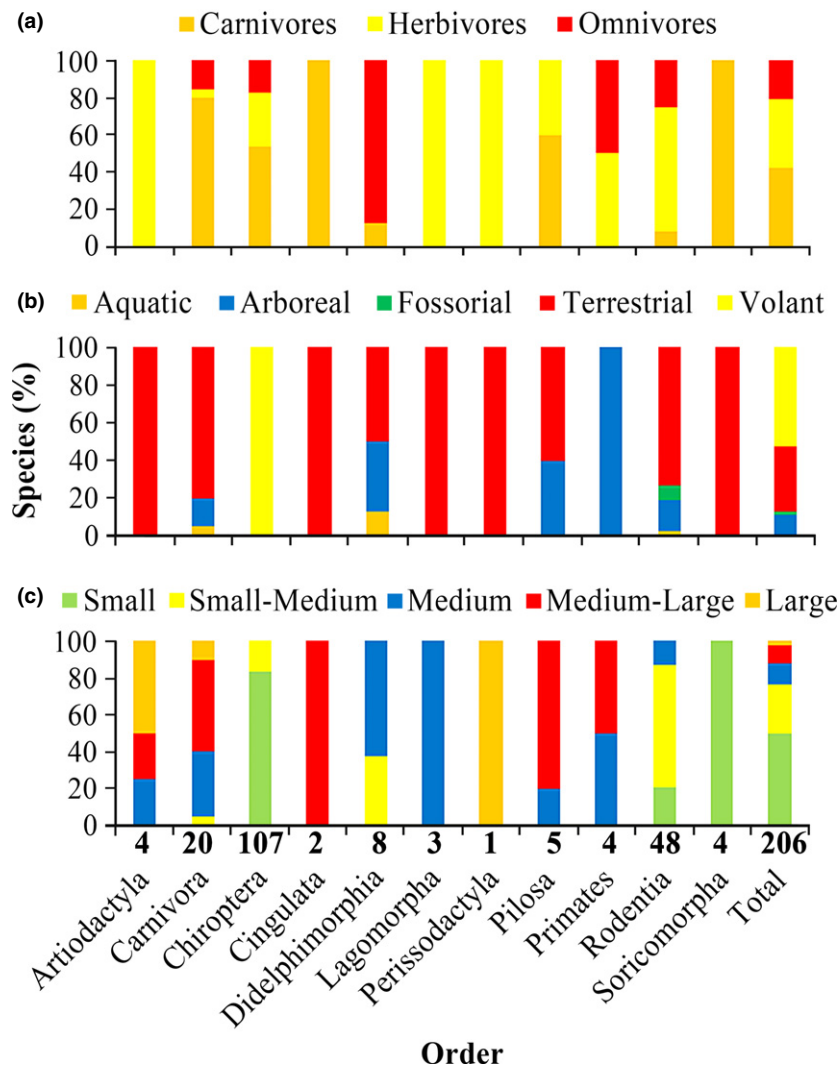
Figure 1 Distribution of species percentage on trait categories grouped by taxonomic order. (a) trophic niche, (b) habitat mode and (c) body size. Bold numbers under x-axis on panel c indicate the total number of species per order. Legends are indicated at the top of each panel.

and non-stationarity in the model (Koenker = 17.5, $P = 0.025$), but no bias or clustering of the residuals of regressor variables (Moran's I = 0.41). The VIF values for all variables suggested no autocollinearity or variable redundancy (Table 3). Because non-stationarity was identified, we conducted a GWR and found substantial improvement in model performance over OLS results (OLS and GWR pseudo $R^2 = 0.60$ and 0.99, respectively), suggesting differences among regions. Greater association of influencing variables occurred in southern (i.e. Osa Peninsula) and north-western (i.e. Tortuguero) Costa Rica, with an additional area in the Tilarán mountains (Fig. 4a). Higher coefficients were also distributed in the Central Valley and areas with higher human density, while low coefficients were in general concentrated in the areas with higher R^2 values (Fig. 4b).

Variable influence and its spatial variation over mammal functional diversity

Biological, environmental and anthropogenic factors had variable influence on FD across regions. In Region 1,

species richness and South American origin, annual mean temperature and annual precipitation, and precipitation and temperature seasonality were selected with no influence of anthropogenic variables ($R^2 = 0.73$). The Region 2 model identified species richness, annual mean temperature, precipitation seasonality and human density as the most influential variables ($R^2 = 0.49$). Finally, the model for Region 3 contained species richness, North American origin, annual mean temperature, precipitation and temperature seasonality and natural land covers ($R^2 = 0.95$; Table 3). Models for all regions exhibited heteroscedasticity and non-stationarity (Koenker's; Region 1 = 76.12, $P < 0.001$, Region 2 = 53.47, $P < 0.001$ and Region 3 = 14.24, $P = 0.02$), with no clustering of regressor residuals (Moran's I = 0.27, 0.31 and 0.25, respectively) and no significant VIF values (Table 3). Geographically weighted regression models performed better than OLS for Region 1 (OLS and GWR Pseudo $R^2 = 0.04$ and 0.48, respectively), but not for regions 2 (Pseudo $R^2 = 0.30$ and 0.07, respectively) and 3 (Pseudo $R^2 = 0.43$ and 0.26, respectively; Fig. 5a,b).
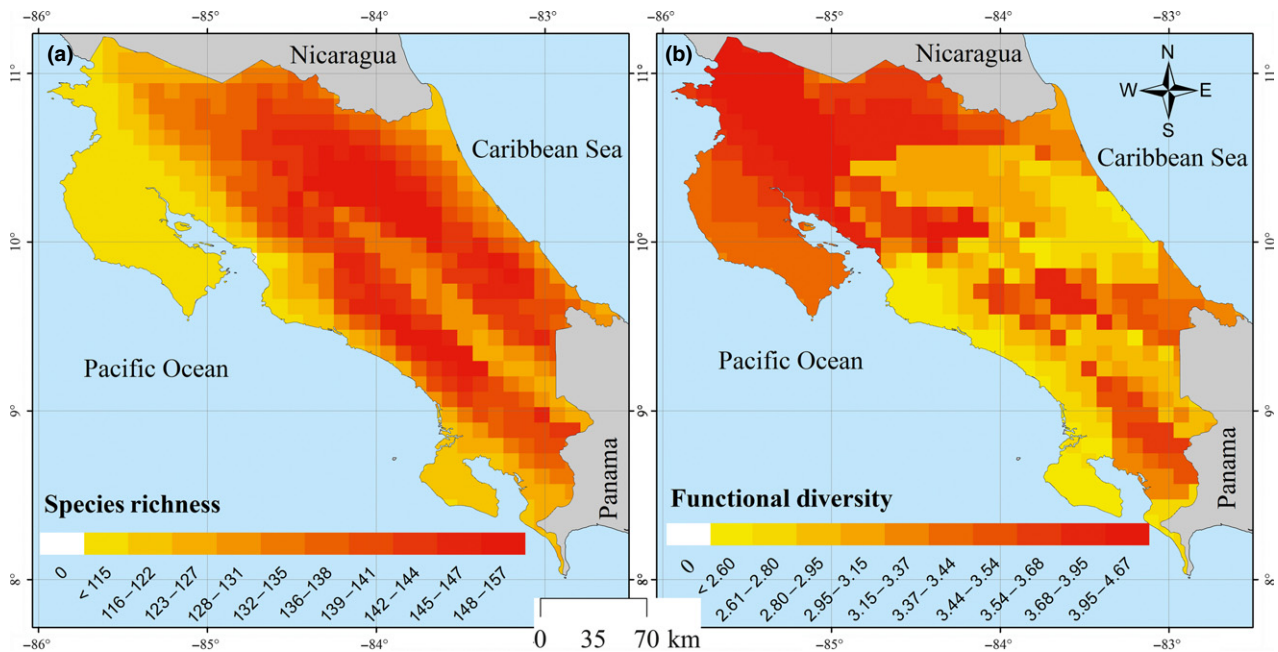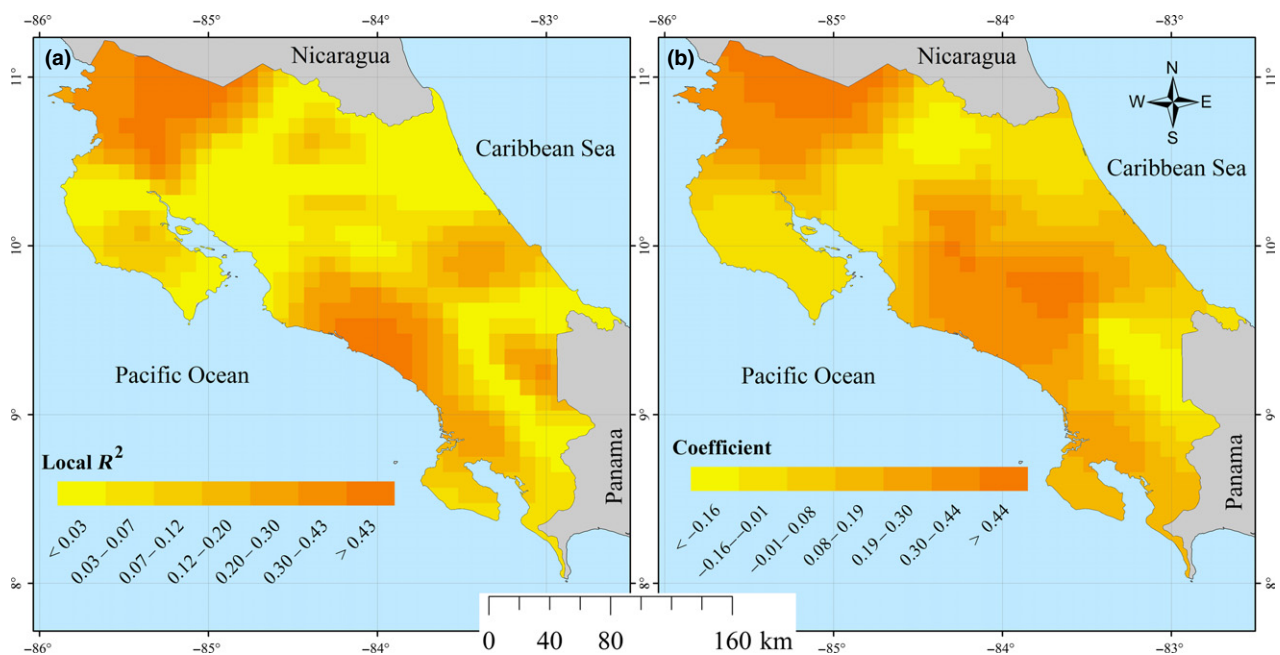
Figure 2 Terrestrial mammal species richness (a) and functional diversity (b) using an 83 km^2 grid, Costa Rica. Note the pattern for high species richness towards the mountain range piedmonts.
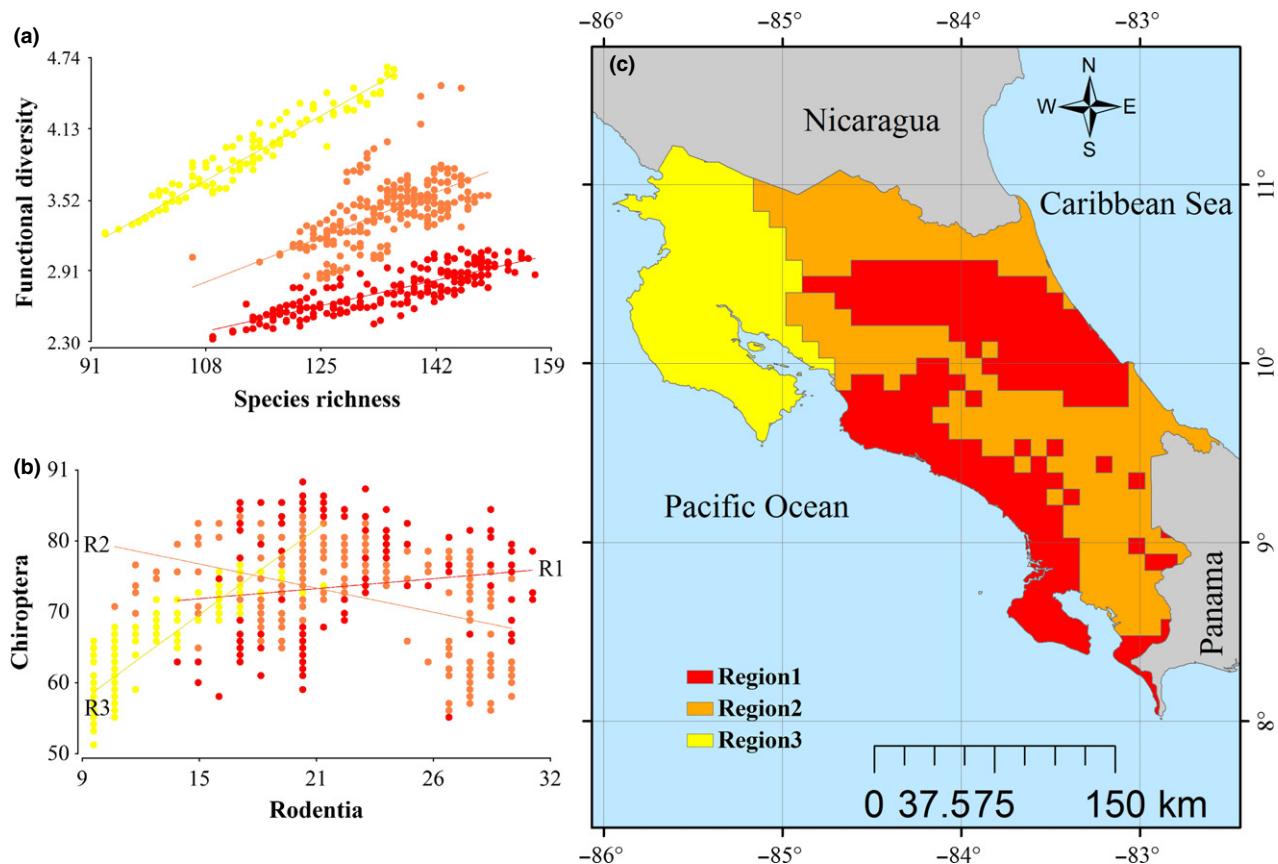

Figure 3 Data dispersion comparing species richness and functional diversity of mammals in Costa Rica. (a) Functional diversity versus species richness, (b) species richness of Chiroptera versus Rodentia orders (R1, 2 and 3 indicate lines for each region) and (c) spatial distribution of the three regions.

Table 3 Ordinary least squares regression results between terrestrial mammal species richness and functional diversity with environmental and human intervention determinants using an 83 km^2 grid, Costa Rica. See Table 1 for variable definitions.

Diversity measure	Variable type	Variable	Coefficient	Std Error	T	P	Variance inflation factor
Species Richness	Environmental	Intercept	321.71	39.81	8.08	< 0.001	
		Elev.	4.99	0.68	7.31	< 0.001	2.14
		AP	22.88	3.59	6.37	< 0.001	1.88
		PS	−44.29	2.83	−15.66	< 0.001	1.83
		TS	−96.18	9.75	−9.86	< 0.001	2.12
		NPP	2.59	1.18	2.2	0.028	1.35
	Anthropogenic	Interv.	−15.42	1.29	−11.92	< 0.001	1.41
		HANPP	4.73	1.38	3.43	< 0.001	2.92
		HD	−4.19	1.41	−2.98	0.0033	2.39
Functional Diversity	Region 1	Biological	Intercept	−2.77	0.64	−4.31	< 0.001	
		SR	0.02	0.00	20.48	< 0.001	2.40
		S.A. Orig	−1.15	0.27	−4.28	< 0.001	2.35
	Environmental	AMT	0.28	0.11	2.52	0.013	1.50
		AP	0.29	0.08	3.60	0.0004	2.23
		PS	0.24	0.06	4.37	< 0.001	2.41
		TS	0.71	0.19	3.83	0.0001	2.77
	Region 2	Biological	Intercept	−2.41	0.44	−5.43	< 0.001	
		SR	0.02	0.00	13.29	< 0.001	1.01
	Environmental	AMT	0.85	0.12	6.94	< 0.001	1.13
		PS	0.40	0.10	3.98	0.0001	1.14
	Anthropogenic	HD	0.09	0.03	2.78	0.006	1.10
	Region 3	Biological	Intercept	−2.16	1.25	−1.72	0.09	
		SR	0.04	0.00	33.02	< 0.001	3.93
		N.A. Orig	3.13	0.70	4.46	< 0.001	1.52
	Environmental	AMT	−1.29	0.40	−3.19	0.002	2.96
		PS	0.94	0.16	5.79	< 0.001	3.37
		TS	0.71	0.33	2.15	0.03	2.18
	Anthropogenic	NLC	−0.10	0.03	−2.94	0.004	1.53

Figure 4 Geographically weighted regression for terrestrial mammal species richness as influenced by environmental, biological and anthropogenic factors using an 83 km^2 grid, Costa Rica. (a) Local R^2 values and (b) local coefficient values.
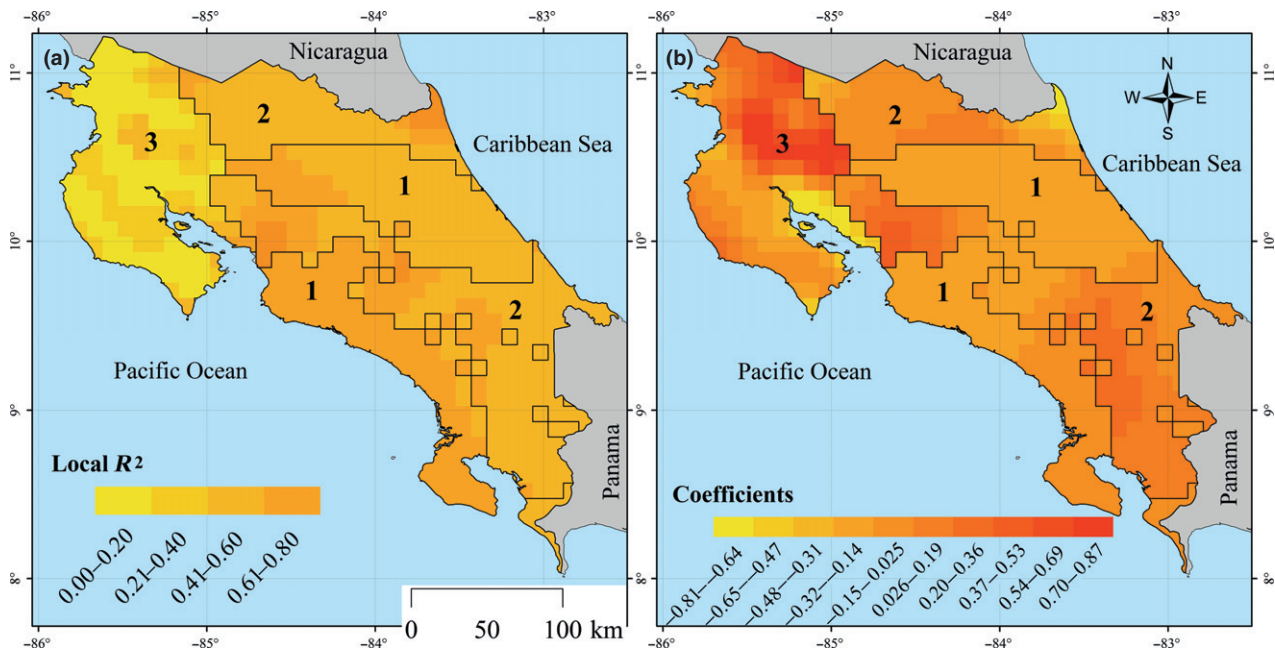
Figure 5 Geographically weighted regression for terrestrial mammal functional diversity as influenced by environmental, biological and anthropogenic factors in the three functional diversity regions using an 83 km^2 grid, Costa Rica. (a) Local R^2 values and (b) local coefficient values.

DISCUSSION

Both species richness and FD were heterogeneous across Costa Rica with spatial clustering of each varying regionally. Species richness showed a more continuous gradient with overall greater richness at intermediate elevations, a pattern expected in mountain ecosystems (Brown, 2001) and identified previously for small mammals in Costa Rica (McCain, 2004). In contrast, FD was patchily distributed with greatest scores in north-western Costa Rica. High FD occurred mostly in tropical dry forests with intermediate scores concentrated in the northernmost portion of the Talamanca range and in central Costa Rica. Lowlands of the Pacific and Caribbean slopes and northern Costa Rica were typically of low FD. That high species richness overlapped spatially with high FD areas was unsurprising as our FD metric was derived in part using species richness (Mouchet *et al.*, 2010; Safi *et al.*, 2011; Mason *et al.*, 2012; Pavoine *et al.*, 2013).

Environmental gradients influence species diversity (Buckley & Jetz, 2008) which is most evident at local scales (Andrews & O'Brien, 2001; Belmaker & Jetz, 2011), as found in our study. Most of the observed variation in species richness in our study was explained by environmental variables such as elevation, climatic and productivity variables resulting in spatial clustering at the cells' scale; in contrast, variation in FD was more evident and spatially stable (i.e. stationary) at the regional scale. Anthropogenic factors (i.e. human density, natural land cover and human appropriation of net primary productivity) were also influential, as expected from previous studies (Fox & Fox, 2000; Michalski & Peres, 2007; Flynn *et al.*, 2009; Biswas & Mallik, 2010).

Greater species richness typically occurred in areas with lower anthropogenic intervention (Cuarón, 2008), in contrast with FD which showed a heterogeneous pattern, but with high scores in two regions of high human intervention (i.e. regions composed of dry and montane forests), and influenced only by human density and decrease in natural land covers. Additionally, biological factors, together with ecosystem productivity, are purportedly more influential on FD than are anthropogenic activities (Andrews & O'Brien, 2001). In general, our results suggest that environmental and biological factors are more important for explaining patterns in FD and species richness than anthropogenic intervention at Costa Rica scale, but with overall high variation across regions and scales. The varying contribution of drivers of both measures across scales highlights the importance of conducting multiscale assessments to determine the scale at which potential drivers operate (Belmaker & Jetz, 2011) and how different influences cluster spatially, as the interaction of ecological processes at different scales can explain macroecological patterns (Meynard *et al.*, 2011).

The three regions identified for FD-species richness relationship largely correspond to ecoregions for the country (Olson *et al.*, 2001). Variables that influenced regional FD patterns were species richness followed by annual mean temperature and precipitation seasonality. Previous studies at global scales also identified these factors as important predictors of FD for mammals (Safi *et al.*, 2011). That species of South American origin were strongly associated with FD for Region 1 is not surprising, as this region shares Amazon forest structure and species affinities (Sanchez-Azofeifa *et al.*, 2002). Similarly, species of North American origin explained

more variation in FD in Region 3, which is the southernmost limit of the Mesoamerican Dry Forests (Gillespie *et al.*, 2000) and coincident to the southernmost limits of many Nearctic mammal distributions. Costa Rica, with a mixed mammal fauna composition (i.e. Nearctic 47% and Neotropical 53%; Rodríguez-H *et al.* (2002); González-Maya *et al.* (2015)), shows a strong influence of species' geographic origin over FD having also a substantial contribution to the functional regionalization of the country. Variation in association between species richness and FD among regions was mainly influenced by the composition of species assemblages (especially bats and rodents), ecosystem type, and dominant geographic origins and probably, as previously suggested, by spatial constraints (Mason *et al.*, 2012; Pavoine *et al.*, 2013). Furthermore, phylogenetic analyses of community assembly have suggested that habitat use is a conserved trait among species in a community ('phylogenetic attraction') that potentially explains species composition (Webb *et al.*, 2002). We suggest this assumption could be extended to FD patterns, as demonstrated by the influence of species' geographic origin on observed patterns in Costa Rica.

The spatial relationships we identified between FD and species richness for Costa Rica are similar to global patterns (Safi *et al.*, 2011), with our study detecting greater spatial clustering and stronger relationships with environmental variables. Spatial clustering likely reflects similar species compositions and therefore similar environmental effects across large areas (Swenson *et al.*, 2012). Similar effects of environmental variables across similar ecoregions also could indicate similar species assemblages and ecoregional variation across scales (Belmaker & Jetz, 2013). Geographic origin and evolutionary history of species assemblages could also influence functional diversity (Messier *et al.*, 2010), as previously found at global scales (Safi *et al.*, 2011). Both species richness and FD were strongly influenced by rodents and bats (~75% of species richness); therefore, ecosystem and habitat structure would likely affect both measures as determined by factors influencing these groups' composition and functional complementarity (Rodríguez & Ojeda, 2014). Although many factors can influence species richness gradients (Buckley *et al.*, 2010; Belmaker & Jetz, 2013), little information exists regarding the effects of these factors on FD. Our results indicate FD was influenced at regional scales and varied among habitat types, biological traits and extent of anthropogenic intervention. Thus, FD was influenced by species' geographic origin and assembly rules across scales (Belmaker & Jetz, 2011, 2013; Safi *et al.*, 2011).

Overall, species richness and functional diversity showed markedly different patterns and relationships with environmental, biological and anthropogenic variables. Mammal species richness patterns have been explained by the interaction of ecological factors such as climate, productivity, habitat and historical dispersal (Brown, 2001; McCain, 2004, 2005). Our results provide insights into the effects of these variables and their interactions on FD that differ in magnitude and scale to their effects on species richness. Additionally, FD has

higher spatial congruence, higher stationary patterns, and is driven at regional scale. The greater regional variation observed in FD is likely a consequence of large variation in geographic origin of species and species assembly rules in response to ecosystem heterogeneity (Tilman *et al.*, 1997; Bengtsson *et al.*, 2002).

Understanding spatial patterns of diversity and its congruence with environmental and anthropic factors at multiple scales is at the forefront of ecological, biogeographical and conservation research (Ricklefs, 1987; Ricklefs & Schluter, 1993; Bengtsson *et al.*, 2002; McCain, 2005; Buckley *et al.*, 2010). Understanding such patterns and underlying mechanisms can provide the scientific basis for conservation planning and decision-making (Kraft & Ackerly, 2010; Boitani *et al.*, 2011; Rondinini *et al.*, 2011a; Amori *et al.*, 2013). Although our study is focused in Costa Rica, and therefore could be used at national level for conservation, we believe our approach is useful at other latitudes, and the processes influencing both measures for Costa Rica likely operate at larger extents and could serve as the basis for further explorations in the tropics. We provide an assessment of species richness and FD of terrestrial mammals in Costa Rica at a scale suitable for scientific inquiry and conservation planning (Boitani *et al.*, 2011; Rondinini *et al.*, 2011b; González-Maya *et al.*, 2015) and believe our results could be used to aid national conservation planning and assess the representativeness of current conservation schemes in Costa Rica.

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BIOSKETCH

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