

## Remote sensing improves prediction of tropical montane species diversity but performance differs among taxa



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### ABSTRACT

Texture information from passive remote sensing images provides surrogates for habitat structure, which is relevant for modeling biodiversity across space and time and for developing effective ecological indicators. However, the applicability of this information might differ among taxa and diversity measures. We compared the ability of indicators developed from texture analysis of remotely sensed images to predict species richness and species turnover of six taxa (trees, pyraloid moths, geometrid moths, arctiinae moths, ants, and birds) in a megadiverse Andean mountain rainforest ecosystem. Partial least-squares regression models were fitted using 12 predictors that characterize the habitat and included three topographical metrics derived from a high-resolution digital elevation model and nine texture metrics derived from very high-resolution multi-spectral orthophotos. We calculated image textures derived from mean, correlation, and entropy statistics within a relatively broad moving window (102 m × 102 m) of the near infra-red band and two vegetation indices. The model performances of species richness were taxon dependent, with the lowest predictive power for arctiinae moths (4%) and the highest for ants (78%). Topographical metrics sufficiently modeled species richness of pyraloid moths and ants, while models for species richness of trees, geometrid moths, and birds benefited from texture metrics. When more complexity was added to the model such as additional texture statistics calculated from a smaller moving window (18 m × 18 m), the predictive power for trees and birds increased significantly from 12% to 22% and 13% to 27%, respectively. Gradients of species turnover, assessed by non-metric two-dimensional scaling (NMDS) of Bray-Curtis dissimilarities, allowed the construction of models with far higher predictability than species richness across all taxonomic groups, with predictability for the first response variable of species turnover ranging from 64% (birds) to 98% (trees) of the explained change in species composition, and predictability for the second response variable of species turnover ranging from 33% (trees) to 74% (pyraloid moths). The two NMDS axes effectively separated compositional change along the elevational gradient, explained by a combination of elevation and texture metrics, from more subtle, local changes in habitat structure surrogated by varying combinations of texture metrics. The application of indicators arising from texture analysis of remote sensing images differed among taxa and diversity

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measures. However, these habitat indicators improved predictions of species diversity measures of most taxa, and therefore, we highly recommend their use in biodiversity research.

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## 1. Introduction

Information derived from remote sensing (RS) provides cost-effective proxies for primary productivity and habitat structure (Rocchini et al., 2016, 2015; Wang et al., 2010). Species occurrence of individual species and species diversity are often correlated to these proxies (Cintra and Naka, 2012; Coutron et al., 2005; Estes et al., 2010; Goetz et al., 2007; Mairota et al., 2015; Rocchini et al., 2010; Tews et al., 2004). Therefore, RS provides useful information for models of ecological variables across large extents with a high spatial resolution. Such spatially-explicit models are of considerable importance in conservation planning if recurrent RS information is available as they provide maps and offer effective indicator systems for area-wide monitoring. However, the success of these models varies considerably among taxa and modeled variables of biodiversity. A deeper understanding of this variation in predictability of diversity measures would be helpful for planning and establishing monitoring systems for documenting environmental change, especially in biota where biodiversity inventories are difficult to achieve.

Particularly the use of RS texture metrics has strengthened statistical models of biodiversity (Culbert et al., 2012; Estes et al., 2010; Wallis et al., 2016b; Wood et al., 2013). In textural approaches, a new value is assigned to each pixel and characterizes the distribution of spectral values in a particular neighborhood, which is defined by a moving or fixed window (Haralick, 1979). Depending on the considered textural feature, which ranges from simple metrics (e.g., mean, variance) to complex metrics (e.g., contrast, correlation), such variables characterize different spatial aspects of habitat structure (e.g., habitat heterogeneity). For example, image textures based on very high-resolution optical imagery successfully predict and map the structure of forests (Wood et al., 2012) and distributional patterns of bird diversity (St-Louis et al., 2014). Models of a montane forest in southwestern Colorado that include texture metrics from RS are more strongly correlated with biomass than models using topographical or spectral metrics (Kelsey and Neff, 2014). Similar results have been obtained for mature biomass in a moist tropical forest (Lu and Batistella, 2005). Therefore, textural information from RS images might address the relationship between environment and biodiversity more effectively than raw spectral bands or common vegetation indices.

Tropical mountain rainforests, particularly Andean rainforests, are among the most diverse and threatened biodiversity hotspots of the world (e.g., Brehm et al., 2016; Tapia-Armijos et al., 2015). Studies of similarly diverse systems have investigated elevation and topography as predictors of biodiversity, and have successfully modeled the occurrence of certain tree species and species richness of moths and ants (e.g., Kübler et al., 2016; Malsch et al., 2008; Nakamura et al., 2015). However, the results are highly taxon dependent, and some taxa are difficult to predict from simple environmental variables (Fiedler et al., 2008; Tiede et al., 2016a). Thus, models of tropical diversity would benefit from the inclusion of structural habitat information.

A great challenge in tropical diverse systems is the assembly of meaningful biodiversity data. The extraordinary high species richness and the low availability of taxonomic and ecological information for most of the species forces ecological studies in tropical rainforest ecosystems to target well-known taxa, e.g., woody plants

(Homeier et al., 2010), or taxa such as ants or birds that occupy different trophic levels within the food webs (Gerlach et al., 2013; Kati et al., 2004; Schuldt et al., 2014; Sekercioglu et al., 2016; Tiede et al., 2017; Donoso and Ramón, 2009).

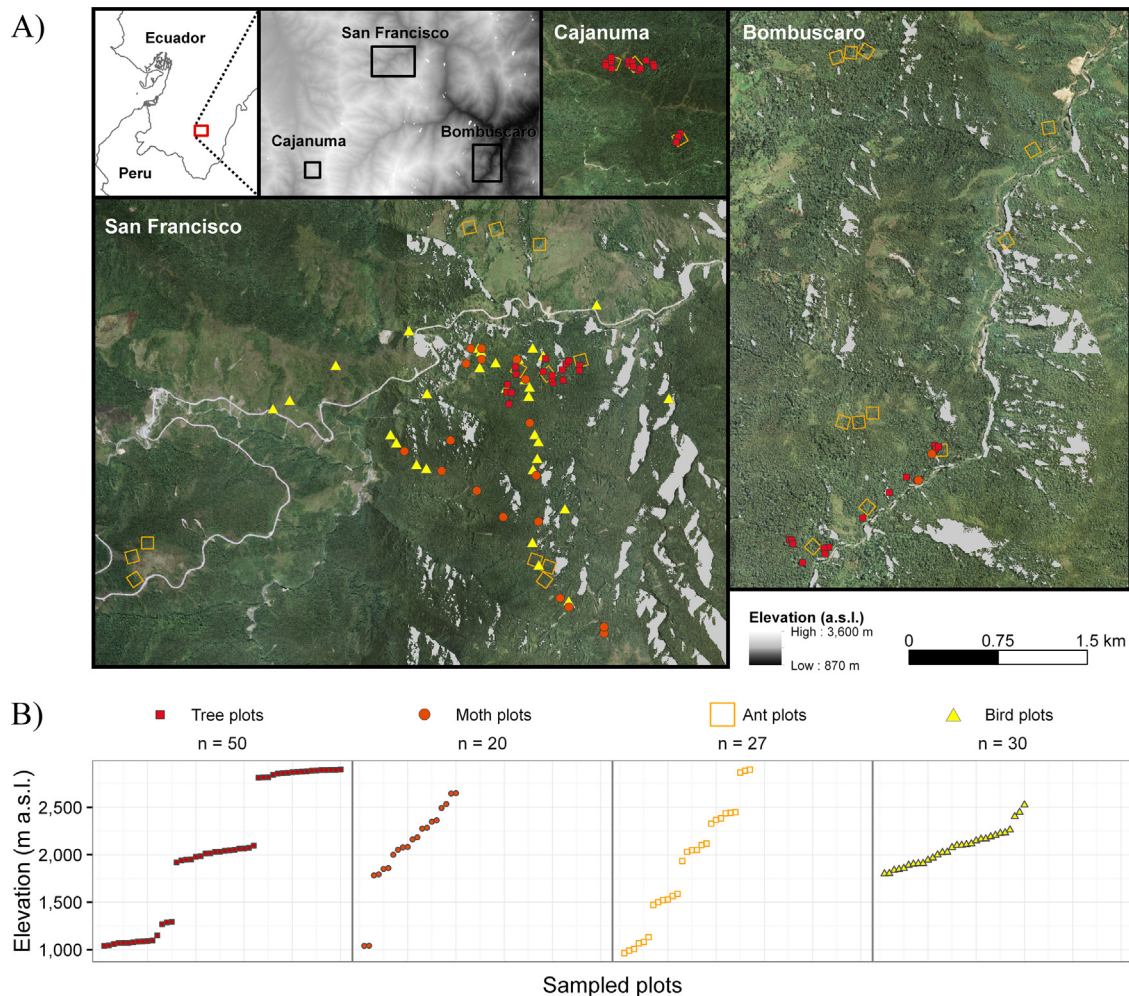
Most RS-based diversity research has focused on measures of alpha-diversity and has ignored community structure. Changes in species composition along environmental gradients are measured by a variety of metrics of species turnover, ranging from dissimilarity measures to scores along ordination axes (Socolar et al., 2016; Whittaker, 1972; Brehm and Fiedler, 2004). Various studies have shown that the composition of species usually provides detailed information on habitat characteristics (Banks-Leite and Cintra, 2008; Cintra and Naka, 2012; Farwig et al., 2014; Müller et al., 2009; Thiollay, 1994). RS-based habitat indicators might improve predictions of species turnover as spectral distances are, for example, strongly correlated to patterns of floristic species composition among sites in Ecuadorian Amazonia (Tuomisto et al., 2003). Unfortunately, the computation of spectral distances and species similarities among sites and the mapping of distance-based species turnover is time consuming because the number of spectral distances increases with the square of the number of sampled sites (Rocchini et al., 2016). A number of studies, therefore, have assessed species turnover using ordination techniques (Farwig et al., 2014; Feilhauer and Schmidtlein, 2009; Gu et al., 2015; Muenchow et al., 2013; Wallis et al., 2016b). For instance, Feilhauer and Schmidtlein (2009) performed a detrended correspondence analysis to identify different gradients in the composition of vegetation. Scores of sites along the ordination axes that represent these environmental gradients were regressed against topographical and spectral metrics calculated for the sites. Ordination techniques, therefore, might be the superior choice to assess species turnover when RS information are used to produce continuous maps of environmental gradients, e.g., the compositional change of bird species along habitat structure (Wallis et al., 2016b).

Here, we investigated models that consider species richness and ordinations of compositional change using non-metric multidimensional scaling (NMDS) as a measure of species turnover of trees, moths (Pyraloidea, Geometridae, Arctiinae), ants, and birds in a tropical mountain rainforest ecosystem. We fitted partial least-squares regressions for all taxa and diversity measures separately by assessing topographical metrics derived from a digital elevation model and image texture metrics derived from an airborne multi-spectral sensor. Our aim was to compare the predictability of species richness and species turnover across the six taxa. We identified differences among the selected taxonomic groups and examined which combination of habitat indicators served well for each taxonomic group as well as for the selected diversity measure. Our findings provide guidelines for the development of a RS-based indicator system for monitoring biodiversity in response to environmental changes in complex tropical forests.

## 2. Methods

### 2.1. Study area

The study area is located in southeastern Ecuador, an area known for its high climatic and environmental heterogeneity and high levels of species richness with numerous endemic taxa (Bendix



**Fig. 1.** A) Study sites and B) plots of all taxa sampled, covering different elevation levels and environmental gradients. A) Color images represent the true color composite of SIGTIERRAS orthophotos; gray areas are non-vegetation areas or mask out pixels where the sensor signal was low owing to casted shadows. B) The number of samples (n) stratified along the elevational gradient for each taxon.

and Beck, 2016; Brehm et al., 2016, 2008; Tapia-Armijos et al., 2015; Werner and Homeier, 2015; Fig. 1). The climate is humid throughout the year, with mean annual precipitation between 2200 mm at elevations of ~1000 m a.s.l. and 4500 mm at ~3000 m a.s.l. Mean annual air temperature decreases from 20 °C at ~1000 m a.s.l., to 15.5 °C at ~2000 m a.s.l., to 9.5 °C at ~3000 m a.s.l. (Beck et al., 2008; Bendix et al., 2008). Precipitation peaks from June to August, and the period from December to February is relatively dry (Beck and Kottke, 2008; Bendix et al., 2006).

Topographical complexity, heterogeneity of climate regimes along the elevational gradient, and anthropogenic disturbances have formed various forest types: evergreen premontane forest ( $\leq 1300$  m a.s.l., Bombuscaro site), evergreen lower montane forest (between 1300 and 2100 m a.s.l., San Francisco site), and evergreen upper montane forest ( $>2100$  m a.s.l., San Francisco and Cajanuma sites), with characteristic subtypes along valleys, ravines, ridges, and anthropogenic replacement systems (Homeier et al., 2008). These forest types differ in species richness, floristic composition, and structural characteristics, e.g., canopy height decreases with elevation. We focused on taxonomic groups sampled on different forest plots and elevations in the Reserva Biológica San Francisco, or additionally at Bombuscaro and Cajanuma which are parts of the Podocarpus National Park (Fig. 1; Table 1). Outside the protected lands in the study area, the forest has been mostly converted during the last few decades to pastures or further degraded to bracken-

infested areas (Curatola Fernández et al., 2015; Tapia-Armijos et al., 2015).

## 2.2. Sampling of taxa

All woody plants (including palms and arborescent ferns) with a diameter at breast height (dbh)  $\geq 5$  cm and a height  $\geq 1.3$  m were sampled on 50 permanent plots each covering 20 m  $\times$  20 m between 2007 and 2008 (Wallis and Homeier, 2017). GPS points were taken in the middle of each plot. All plots were located in mature forest without visible human disturbance. Tree individuals were identified to the species or morphospecies level when possible.

Nocturnal moths were sampled on 20 plots during three periods between 1999 and 2000 using light traps equipped with two backlight 15 W tubes operated between 18:30 and 21:30 local time (UTC-5:00; Brehm, 2002; Brehm and Fiedler, 2010; Suessenbach, 2003; Suessenbach and Fiedler, 2010a, 2010b). Catches were restricted to periods from three days after full moon until five days before full moon. Specimens were sorted to morphospecies within three diverse taxa: geometrid moths (Geometridae), pyraloid moths (Pyraloidea), and arctiinae moths (Erebidae: Arctiinae). Previous analyses of the same samples have shown that these taxa differ in diversity patterns, body size, host plant affiliations, and other traits (Fiedler et al., 2008). To account for such differences, we



**Table 1**  
Summary of basic information on sampling of the investigated taxonomic groups. See also Fig. 1.

Taxonomic group	Year	Method	Total no. of species	Min. no. of species per site	Max. no. of species per site
Trees	2007, 2008	Counts on 20 m × 20 m plots	443	12	41
Geometridae	1999, 2000	Light traps	1223	135	296
Pyraloidea	1999, 2000	Light traps	753	62	315
Arctiinae	1999, 2000	Light traps	443	34	149
Ants	2014	Nutrient baits	88	1	25
Birds	2000, 2001, 2002	Point counts (30 min)	147	14	46

treated these taxa separately to compare the predictability of biodiversity patterns among putatively rather homogeneous groups of insects.

Ants (Formicidae) were sampled on 27 plots in two seasons in 2014 using a rapid assessment method with nutrient baits following Peters et al. (2014) and described in detail in Tiede et al. (2017; Wallis et al., 2016a). In short, we exposed six different nutrient baits [H<sub>2</sub>O, NaCl, CHO (sucrose), protein (glutamine), CHO-protein mix, and lipids (olive oil)] in the wet and the dry seasons. The ant fauna of Ecuador consists of species that are taxonomically poorly defined (Salazar et al., 2015). Therefore, we built a COI (mitochondrial cytochrome c oxidase I) barcode reference library that aided us to refine our morphology-based identification framework (Tiede et al., 2016b; see also Domínguez et al., 2016; Tiede et al., 2017). For analysis, ant species collected in the two seasons were pooled.

Bird species occurrence was assessed on 30 plots in the study area under favorable weather conditions at 6:00–10:00 and 16:00–18:00 (UTC–5:00) between 2000 and 2002 (Paulsch and Müller-Hohenstein, 2008; Paulsch and Wallis, 2016). Standardized point counts (30 min) were repeated 12 times on each plot and combined with mist-netting data to comprehensively assess bird assemblages.

### 2.3. Diversity measures

For each taxon, we calculated species richness and aspects of species turnover with the following considerations. In species-rich communities, the number of species recorded in a sample depends on the number of sampled individuals (Colwell et al., 2012). The number of moth individuals attracted to light traps, for example, depends on light conditions and temperature (Beck et al., 2011). In the study area, the number of tree individuals varied considerably across plots, which led to a bias in observed species numbers. Thus, we estimated species richness for trees and all moth taxa at a coverage of 70% of the expected total species richness using rarefaction and extrapolation as recommended by Colwell et al. (2012) using the function estimateD in the R package *iNext* (Hsieh et al., 2016; R Core Team, 2016; for statistics, see Table 1 in Appendix A).

We characterized the change in species composition (beta-diversity) across plots for each taxon using ordination. For each taxon, we calculated pair-wise Bray-Curtis dissimilarities using presence/absence data between all plots for which a species list of the respective taxon was available. Subsequently, we performed NMDS using the R function metaMDS in *vegan*. The stress value for two-dimensional ordinations of all taxa was <0.2 (Table 2 in Appendix A), which indicates an appropriate NMDS solution. We extracted the site scores for the two dimensions. Both dimensions (NMDS I and NMDS II) are a numerical measure of the compositional change in the community across all plots.

### 2.4. Preprocessing of multi-spectral orthophotos

Within the framework of the Ecuadorian program “National System of Information on Rural Lands and Technological Infrastructure”, a digital elevation model (DEM) with a spatial resolution of 3 m and ortho-rectified images with a resolution of 0.3 m and

**Table 2**

Topographical metrics used in addition to texture metrics to fit models which predict diversity of sampled taxa.

Topographical metrics	Abbr.	Metric description
Elevation	DEM	Digital elevation model
Slope	SLOPE	Gradient of DEM in degree
Topographical Position Index	TPI	After Wilson et al. (2007) with a surrounding of 17 pixels

four spectral bands (red, green, blue, near-infrared) were recorded during three flight campaigns in 2010 and 2011 under favorable weather conditions in our study area (Ministerio de Agricultura, Ganadería, Acuacultura y Pesca; Proyecto Sistema Nacional de Información y Gestión de Tierras Rurales e Infraestructura Tecnológica – SIGTIERRAS). We resampled the DEM and orthophotos to 6 m spatial resolution to match the size of canopy tree crowns. However, mountains and the airborne multi-spectral sensor, which flew at a low height, both casted shadows that appeared in orthophotos. We thus had to mask out those regions where shadows could not be corrected owing to a low contrast of the sensor. These areas were detected using the *hillshade* tool in the ‘spatial analyst’ of ArcGIS (version 10.3). Furthermore, we corrected the orthophotos topographically in a Java environment following Curatola Fernández et al. (2015). A problem of our procedure is the time lag between taxon sampling and image recording. The change of tree communities is, however, generally slow, and the protected forest habitats investigated (Podocarpus National Park and Reserva Biológica San Francisco) did not substantially change between the sampling of birds in 2000–2002 and the recording of orthophotos in 2010–2011 (Curatola Fernández et al., 2015; Thies et al., 2014). In addition, all investigated plots of the older sampling campaigns plotted on the digital orthophotos were situated in what appeared to be intact forest, and a visual interpretation of the digital orthophotos of the study area did not reveal disturbances (e.g., caused by landslides) or human-induced habitat changes, such as deforestation.

### 2.5. Habitat indicators

We used indicators derived from topography and textural information of RS images for characterizing topographical complexity, vegetation structure and habitat heterogeneity. For the indicators derived from topography, we used three topographical metrics, namely the DEM, the slope calculated in degrees (SLOPE), and a Topographical Position Index (TPI) using the *raster* package in R (Hijmans et al., 2015; Table 2). The TPI was calculated according to Wilson et al. (2007) with a surrounding of 17 pixels; this TPI compares the elevation of a pixel with the mean elevation of its environment.

For the indicators derived from textural information, we used the near-infrared (NIR) band and two vegetation indices, namely the normalized difference vegetation index (NDVI), which is based on the red and NIR bands, and an approximation of the anthocyanin reflectance index (ARI), which is based on the red and blue bands

**Table 3**  
Optical band and vegetation indices used as base layers for the calculation of texture metrics (see Table 3 Appendix A).

Optical metrics	Abbr.	Metric description
Near infra-red band	NIR	Pre-processed near infra-red band
Normalized difference vegetation index	NDVI	$(\text{NIR} - \text{red}) / (\text{NIR} + \text{red})$ sensitive to chlorophyll pigments
Anthocyanin reflectance adjusted index	ARI	$(\text{red} - \text{blue}) / (\text{red} + \text{blue})$ , sensitive to anthocyanin

of the multi-spectral orthophotos (Table 3). We chose these indices to account for different vegetation properties that might shape the habitats of our study sites. Both the NIR band and the NDVI are often used as a proxy for biomass or to account for primary productivity (Huete et al., 1997). ARI accounts for the accumulation of anthocyanin pigments in leaves (Gitelson et al., 2001; Sims and Gamon, 2002). Based on the NIR band, NDVI, and ARI, we calculated texture metrics derived from the gray-level co-occurrence matrix using the *gcm* package in R (Zvoleff, 2015). Among various texture statistics, we applied the statistics ‘mean’, ‘correlation’, and ‘entropy’ because we identified them as the most uncorrelated ones (Haralick, 1979; Table 3 in Appendix A). We used a moving window size of 17 pixels  $\times$  17 pixels matching a surrounding of 102 m  $\times$  102 m to account for textural information within a relatively broad spatial scale. The image textural approach resulted in nine texture metrics. We also calculated texture metrics derived from a second moving window (3 pixels  $\times$  3 pixels, 18 m  $\times$  18 m) to account for differences among taxa with regard to the spatial scale of their habitat demands, subsequently used as additional metrics in a second model approach (Table 5 in Appendix A).

All topographical and texture metrics were extracted for the corresponding plots and polygons, respectively, of each taxon. To avoid random noise (pixel values with no relation to the image scene) in predictor images, we extracted the mean of all spatial predictor variables within polygons for ant samples, and we extracted the mean of all spatial predictor variables within a buffer of 10 m around each sample point for the remaining taxa.

## 2.6. Statistical approach

For the core analysis, we performed partial least-squares (PLS) regressions to model diversity measures for each taxon using textural and topographical metrics. PLS regressions were developed for situations where a low number of samples has to be modeled against a large number of inter-correlated predictor variables (Carrascal et al., 2009). To reduce the number of predictors and to deal with multi-collinearity, PLS regression models derive latent vectors from the predictors that explain the maximum variance of the response variable. Even though this regression is a reliable method, the generation of latent vectors by the PLS algorithm is unfortunately a black-box procedure. Since the structure of latent vectors would change if predictors are added or removed, no precise information on the explained variance of single predictors can be made. Therefore, the possible variety of statistically reasonable predictor combinations could lead to different conclusions about the relationship of species diversity and habitat indicators. We chose those models with the lowest prediction error and subsequently discussed the ecological meaning of these models using the most important predictors.

We used the *autopls* package in R (Schmidlein et al., 2012), which implements a variable selection to reduce the size of the set of predictor variables. At the same time, the variable selection reduces computation time, and improves both model performance

and interpretability (Andersen and Bro, 2010). This optimization procedure was based on a filter combining significance of predictors estimated by jackknifing and variable importance in the projection (VIP). The VIP scores are based on the weighted sums of the absolute regression coefficients across the number of latent vectors (Chong and Jun, 2005).

Following our proposed aims, we fitted models for species richness and the two NMDS axes characterizing species turnover to compare their performance using the leave-one-out (LOO) validated  $R^2$ . For all models, we tested the regression residuals for spatial autocorrelation using Moran’s I with a neighborhood of five neighbors, but we did not find a significant autocorrelation of the residuals in any of the models ( $p < 0.05$ ). To identify both the most important predictors for each model and an overall trend among species richness and turnover, we used VIP values as a measure of predictor importance, and regression coefficients as a measure of predictor influence (Chong and Jun, 2005). In general, special emphasis is put on the VIP values greater than one, since the average of squared VIP scores equals one (Mehmood et al., 2012). However, to consider a model-specific VIP cutoff and to facilitate the interpretation of predictor variables, we placed emphasis on all VIP scores greater than the third quartile of all VIP observations in each model.

## 3. Results

### 3.1. Species diversity measures

In general, the composition of species along NMDS axes is often related to species richness. However, we found significant correlations only between species richness and NMDS I for pyraloid moths ( $r = 0.82$ ,  $p < 0.01$ ) and a correlation between species richness and NMDS II for ants ( $r = 0.66$ ,  $p < 0.01$ ).

Since the three moth taxa were sampled on the same plots, we were able to test for correlations between diversity measures of these taxa. Measures of species richness showed no significant correlations between moth taxa, but correlations were found for NMDS I ( $r > |0.95|$  in all three cases;  $p < 0.01$ ) and for NMDS II ( $r > |0.81|$ ;  $p < 0.01$ ).

### 3.2. Predictive power of diversity models

The predictability of species richness highly varied among taxa, ranging from 4% of explained variance for arctiinae moths to 78% for ants (Table 4). When image textures from a different window size (3 pixels  $\times$  3 pixels; 18 m  $\times$  18 m) were used as additive predictors (Table 5 in Appendix A), the predictive power of species richness of trees and birds increased significantly from 12% to 22% and from 13% to 27%, respectively. In contrast to species richness, the models of NMDS I showed universally high LOO-validated  $R^2$  values for all six taxa, ranging from 0.64 (birds) to 0.98 (trees; Table 4). NMDS II showed more variation in model performance among taxa than NMDS I, and ranged from 33% of explained variance for trees to 74% for pyraloid moths (Table 4).

### 3.3. Predictor importance and influence

The species richness of both pyraloid moths and ants increased with decreasing DEM values and, in addition, that of ants increased with increasing ‘entropy’ texture of ARI, while that of pyraloid moths increases with decreasing ‘mean’ texture of ARI (Fig. 2). By contrast, DEM was not included in the models of geometrid moths and arctiinae moths, and it showed low importance in the models of trees and birds (VIP values  $<$ 3rd quartile, Fig. 2). The species richness of these taxa increased with increasing ‘mean’ and ‘entropy’ texture metrics. Tree species richness was negatively associated

**Table 4**

Results of partial-least squares regressions with implemented backward selection and leave-one-out (LOO) cross validation for the three diversity measures and all studied taxa using a set of spatial predictors (n = 12).

Species diversity measures	Taxonomic group	R <sup>2</sup>	LOO R <sup>2</sup>	No. of latent vectors	No. of predictors
Species richness	Trees	0.30	0.12	2	8
	Pyraloidea	0.84	0.72	4	7
	Geometridae	0.75	0.57	4	5
	Arctiinae	0.40	0.04	2	7
	Ants	0.85	0.78	2	10
	Birds	0.33	0.13	1	4
NMDS I	Trees	0.99	0.98	7	9
	Pyraloidea	0.96	0.94	2	2
	Geometridae	0.96	0.90	3	8
	Arctiinae	0.97	0.89	6	12
	Ants	0.94	0.89	4	7
	Birds	0.78	0.64	3	9
NMDS II	Trees	0.41	0.33	2	3
	Pyraloidea	0.95	0.74	6	8
	Geometridae	0.94	0.71	9	12
	Arctiinae	0.78	0.64	2	8
	Ants	0.74	0.63	2	9
	Birds	0.59	0.45	2	7

with the TPI and positively associated with the ‘entropy’ statistics of the NIR band (Fig. 2).

Since NMDS I and II are based on ordinations, the direction of predictor influence is arbitrary. NMDS I of all taxa except ants was predicted by DEM; for pyraloid moths, DEM and TPI were the only predictors (Fig. 2). NMDS I of bird species was also predicted by SLOPE and the texture ‘correlation’ of ARI, whereas NMDS I of trees, geometrid moths, and arctiinae moths was also predicted by additional ‘mean’ and ‘entropy’ texture statistics. For trees, NMDS II was predicted by TPI, while DEM and ‘mean’ and ‘entropy’ texture statistics together predicted NMDS II of ants (Fig. 2). NMDS II of all ectotherms animals was predicted by ‘entropy’ texture metrics of NDVI.

#### 4. Discussion

Our models revealed considerable variation in the ability of habitat indicators to predict species richness across the six taxa studied. Four out of six taxa were predicted by RS texture metrics, largely independent of elevation. Our models also revealed the high predictability of species turnover assessed by NMDS ordination of all six taxa. A combination of elevation and taxon-specific texture metrics explained species turnover along an elevational gradient, and texture metrics, particularly ‘entropy’ texture metrics, explained species turnover along more subtle, local changes in habitat structure.

##### 4.1. Species richness and elevation

Considering the well-documented response of ectotherms to temperature (e.g., McCain and Grytnes, 2010), it is not surprising that the number of species of pyraloid moths and ants decreased with increasing elevation. Consequently, elevation is a good proxy for the thermal gradient (Fries et al., 2009), but also precipitation and water logging increase (Beck and Kottke, 2008; Fries et al., 2014) and soil fertility and N availability decrease with increasing elevation (Wolf et al., 2011). In comparison with PLS regression models using ‘topography only’ as predictor variables (Table 6 in Appendix A), topography would suffice to explain species richness of pyraloid moths, and models for ants slightly benefited from the inclusion of additional texture metrics. In combination with elevation, textural information provided further facets of the environment to model additional variance in species richness, such as ‘entropy’ statistics of ARI for ants. ARI accounts for the accumula-

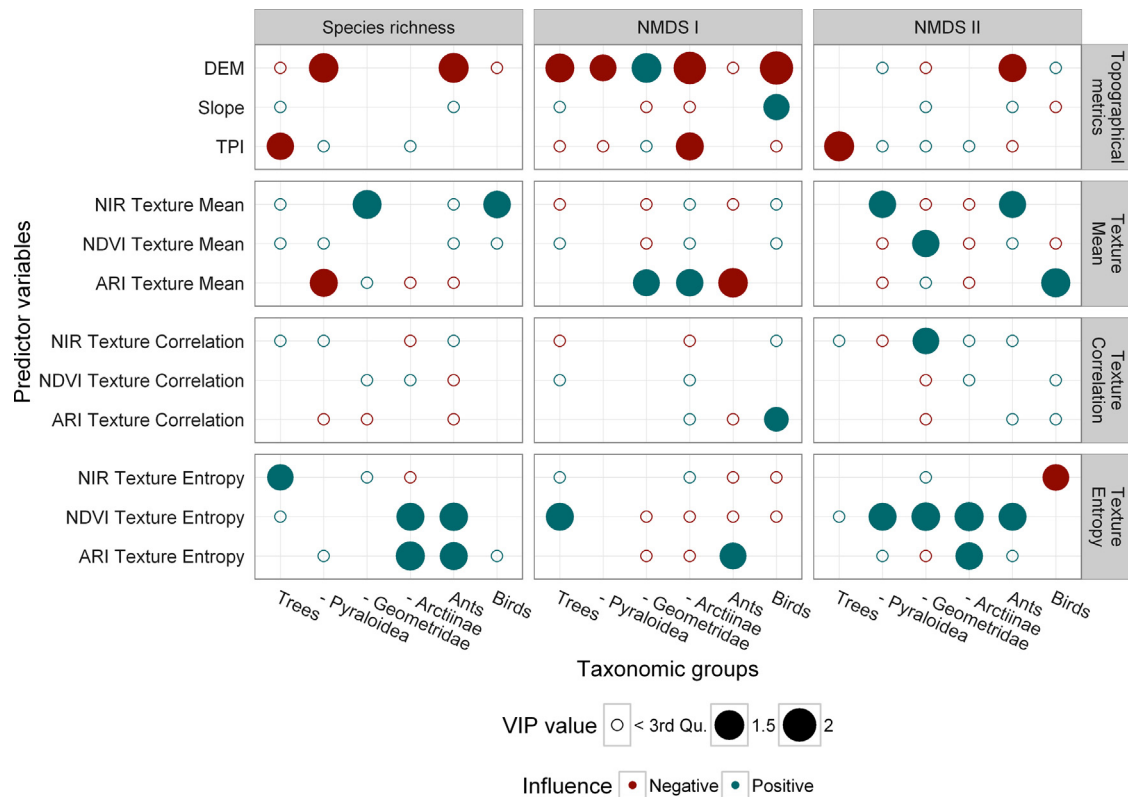
tion of anthocyanin pigments in leaves (Gitelson et al., 2001; Sims and Gamon, 2002). Anthocyanin pigments are generally higher in senescent leaves but occur also as protection against herbivory mostly in young leaves (Karageorgou and Manetas, 2006), and might protect against UV radiation (Caldwell, 1981; Steyn et al., 2002). Generally, tropical mountain regions have high UV-B levels, which increase with altitude and canopy openness (Flenley, 2011). ‘Entropy’ statistics account for the degree of disorder (Haralick, 1979) and thus high values of ‘entropy’ ARI depict a higher vegetation heterogeneity somehow related to anthocyanin pigments in canopy leaves. In addition, ‘entropy’ ARI decreased with a higher C/N ratio in plant tissues ( $r = -0.55$ ,  $p < 0.01$ ; Table 4 in Appendix A), which is a proxy for N availability in forest soils that is related to nutrient use efficiency of plants (Wolf et al., 2011). Therefore, this texture metric might be an important indicator of nutritional quality of foliage for herbivores.

##### 4.2. Species richness and habitat structure

Species richness of trees, geometrid and arctiinae moths, and birds showed no significant response to elevation, and models using ‘topography only’ as predictor variables were weak or even failed to explain the variability of species richness (Table 6 in Appendix A). This indicates that information from topography cannot predict the diversity of these taxa successively, which confirms the findings regarding species richness of geometrid moths in Brehm et al. (2016).

Species richness of trees, geometrid moths, arctiinae moths and birds was better predicted by textural predictors, such as ‘mean’ NIR for geometrid moths and birds, and ‘entropy’ NDVI/ARI for arctiinae moths. For our study area, Pearson correlations suggested that ‘mean’ and ‘entropy’ texture metrics were equal or even more highly related to site-based forest productivity data ( $r = 0.40–0.78$ ,  $p < 0.01$ ) than topographical metrics ( $r = 0.38–0.64$ ,  $p < 0.01$ ; Table 4 in Appendix A). We suppose that ‘entropy’ statistics of the NIR band and NDVI thus depict a high diversity of vegetation types. This habitat heterogeneity, which is probably related to a high structural complexity in ravine forests or forest edges, might support more coexisting species.

Particularly the predictability of geometrid moths that explains 57% of species richness should be noted because earlier studies that assessed only the effects of temperature or elevation revealed much less predictive power ( $\max(|r|) = 0.29$ ;  $p > 0.24$ , Brehm et al., 2016;  $R^2 = 0.0243$ ,  $p > 0.488$ , Fiedler et al., 2008). As suggested in Stein et al.



**Fig. 2.** Variable importance in projection (VIP) values for all models and input predictors as scaled circles. VIP values greater than the third quartile of all VIP values in the corresponding model are considered significant; circle size is scaled according to the corresponding VIP value. The size of VIP values below the third quartile of VIP observations is fixed and indicated by open circles. Direction of predictor influence was extracted from regression coefficients and is indicated by color.

(2014), habitat heterogeneity might be more important for certain herbivores than climatic or topographical heterogeneity since different clades of moth species have developed distinct biological features to cope with environmental factors such as temperature (Braga and Diniz, 2015). By contrast, arctiinae moths comprise a speciose clade of which a large amount of caterpillar species are not classical herbivores as they feed on dead or withered leaves or epiphylls (Bodner et al., 2015; Seifert et al., 2016). Therefore, it is not surprising that neither topographical nor texture metrics as proxies for habitat heterogeneity (dominated by tree crowns) were able to model the species richness of arctiinae moths successfully.

Although the predictability of species richness of trees and birds was low, we showed that it significantly increased when texture metrics of multiple window sizes were used (Table 5 in Appendix A), as recommended by Mairota et al. (2015) to match the approximate scale of activity (e.g., home ranges) among species of the targeted taxonomic group. Birds were sampled only along a short stretch of the elevational gradient (700 m; Fig. 1), which might cause a higher dependence of species richness on habitat heterogeneity than on topography. However, general patterns of bird species richness remain unclear because of contrasting results obtained in tropical forests along elevational gradients, ranging from increasing bird species richness with higher habitat heterogeneity (Wallis et al., 2016b), to decreasing species richness with increasing elevation (Jankowski et al., 2013), to a hump-shaped relationship between elevation and species richness (Herzog et al., 2005).

Our models of tree species richness were associated with negative TPI values that represent locations that are on average lower in elevation than its surrounding and that have lower values of 'correlation' NDVI, which indicated areas of uniform NDVI values. Thus, in accordance with Werner and Homeier (2015), higher tree

species richness might occur in valleys where the canopy is higher and denser (= high leaf area index) representing higher soil nutrient availability compared to upper slopes and ridges. The low to moderate predictive power of tree species richness found in this study and in earlier studies that assessed multi-spectral RS metrics (e.g., Fricker et al., 2015) lead to the need for information on more subtle variance in either habitat characteristics or the spectral response of woody plant species in the canopy. Variables derived from RS information with higher spectral resolution, as recommended by Asner and Martin (2011), have been successfully used to model tropical tree alpha-diversity (Féret and Asner, 2014; Schäfer et al., 2016). For example, Vaglio Laurin et al. (2014) have shown that hyperspectral data explain up to 84.9% of the alpha-diversity of upper canopy trees in a West African forest, whereas common vegetation indices yield poor results. We therefore propose that pigment-related hyperspectral data would be more successful in modeling tree species richness than habitat heterogeneity assessed with image texture metrics.

#### 4.3. Species turnover along environmental gradients

Models for species turnover showed far higher predictive power among all taxa than models for species richness. The scores along the first NMDS axis were strongly associated with elevation. By contrast, the scores of the second NMDS axis showed a response to the elevational gradient only for ants. Species have evolved specific adaptations to climatic zones that influence their distribution (Angilletta Jr., 2009; for ants, e.g., Bishop et al., 2015; for geometrid moths, e.g., Brehm et al., 2003; for other moths species, e.g., Fiedler et al., 2008). Thus, it is not surprising that the elevational gradient is crucially important for the compositional change (Guerin et al., 2013). It is obvious that other factors besides elevation influenced



the composition and turnover of the investigated assemblages, but our results underline the importance of elevation for shaping an important part of species turnover of almost all taxa, from primary producers to herbivores, detritivores, and predators.

The scores of the second dimension of NMDS ordination (for ants, the first NMDS axis) indicated a change in species composition predicted by texture metrics that characterize local habitat heterogeneity. Assemblages of all taxonomic groups of moths and ants changed with primary productivity and habitat heterogeneity ('entropy' NDVI), or in the case of arctiinae moths, with variation in ARI, which is related to the C/N ratio in understory plant tissues. This might explain the small-scaled compositional change in species assemblages along forest edges or glades to forests with a higher canopy cover, as observed in the study area for a range of organisms (Brehm et al., 2003; Hilt et al., 2006; Hilt and Fiedler, 2006; Wallis et al., 2016b). Thus, the second ordination axis appears to account for compositional variation of communities along a habitat structural gradient, largely independent of elevation.

## 5. Conclusions

Indicator applications differed among both the taxa and diversity measures studied owing to distinct variation in patterns of species distribution. Species richness models of trees, geometrid moths, and birds highly benefited from integrating RS-based texture metrics. By contrast, topographical metrics sufficiently modeled species richness of pyraloid moths and ants. Models of species turnover can be constructed across taxonomic groups with far higher predictability than models of species richness. The two ordination axes effectively separated compositional change along the elevational gradient (NMDS I) from more subtle, changes in habitat structure, which were surrogated by RS-based texture metrics (NMDS II). However, we have to stress that the interpretation of causal relationships between RS texture metrics and species diversity is sometimes difficult and that field based inventories are still necessary to calibrate RS proxies. In addition, airborne RS missions are often not repeated and thus lack a temporal aspect, which is essential for recurrent monitoring. We therefore recommend to obtain habitat indicators from upcoming missions of satellites with a fine to moderate spatial and temporal resolution (e.g., Sentinel-2 mission; Drusch et al., 2012), which would allow the generation of cloud-free composites for different time spans. Hence, textural information derived from future satellite missions as habitat indicators would allow monitoring species diversity of a range of taxa successively in space and time.

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## Appendix A.

**Table A1**

Number of rarefied and extrapolated samples of tree and moth species covering 70% of the asymptotic richness. Sum of each row reveal the total number of samples.

Taxonomic group	No. of samples using rarefied species richness	No. of samples using extrapolated species richness	No. of samples using observed species richness
Trees	28	21	1
Pyraloidea	20	0	0
Geometridae	20	0	0
Arctiinae	18	2	0

**Table A2**

Stress values for the first two dimensions of NMDS ordinations.

Taxonomic group	1 Dimension	2 Dimensions
Trees	0.136	0.080
Pyraloidea	0.101	0.071
Geometridae	0.098	0.057
Arctiinae	0.140	0.080
Ants	0.207	0.118
Birds	0.330	0.171

**Table A3**

Texture statistics derived from gray-level co-occurrence matrices calculated from optical metrics (see Table 1). For the moving window approach that shifts in all directions, one window size was considered within the core analysis (3 pixels × 3 pixels). Image texture metrics derived from an additional window size (17 pixels × 17 pixels) to cope with different habitat scales of all taxonomic groups was used for a second model (Table 5 in Appendix A).

Texture statistics	Equation
Mean	$ME = \sum_{i,j=0}^{N-1} (p_{i,j})$
Entropy	$EN = \sum_{i,j=0}^{N-1} p_{i,j} (-\ln p_{i,j})$
Correlation	$CC = \sum_{i,j=0}^{N-1} p_{i,j} \left[ \frac{(i-ME)(j-ME)}{\sqrt{VA_i VA_j}} \right]$

\*With  $p_{i,j} = \frac{1}{N^2} \sum_{i,j=0}^{N-1} V_{i,j}$ , where  $V_{i,j}$  is the value in cell  $i, j$  and  $N$  is the number of rows or columns.

**Table A4**

Pearson correlation coefficients of habitat indicators and tree growth parameters. For all derived habitat indicators, we performed a correlation analysis with tree growth parameters derived from a plot-based inventory (Homeier et al., unpublished). Pearson's correlation coefficients depended on different numbers of samples. Data on stem diameter at breast height, above ground biomass increment (AGBi), and a measure of aboveground net primary production (NPPa; combination of AGBi and leaf litter production) were collected, and tree species were sampled ( $n = 50$ ). In addition, we measured the C/N ratio of leaves in understory plants and sampled ant species ( $n = 27$ ). Significant correlation coefficients are highlighted in bold. DEM, Digital elevation model; SLOPE, slope in degrees; TPI, topographical position index; NIR, near-infrared band; NDVI, normalized difference vegetation index; ARI, anthocyanin reflectance index.

Habit indicators	Pearson correlation coefficient			
	Stem size	AGBi	NPPa	C/N ratio
DEM	<b>0.38*</b>	<b>-0.64*</b>	<b>-0.64*</b>	0.41
SLOPE	0.28	0.13	0.29	-0.46
TPI	-0.20	0.28	0.13	0.41
NIR mean	-0.32	<b>0.59*</b>	<b>0.78*</b>	-0.08
NDVI mean	<b>-0.40*</b>	<b>0.62*</b>	<b>0.75*</b>	-0.19
ARI mean	0.11	0.09	0.33	0.24
NIR correlation	-0.22	0.19	0.27	-0.31
NDVI correlation	0.07	0.04	-0.11	-0.44
ARI correlation	-0.03	-0.01	0.03	-0.39
NIR entropy	-0.36	<b>0.58*</b>	<b>0.74*</b>	0.19
NDVI entropy	<b>-0.49*</b>	<b>0.64*</b>	<b>0.56*</b>	-0.42
ARI entropy	-0.32	0.35	0.13	<b>-0.55*</b>

\*p < 0.01



**Table A5**

Results of partial-least square regressions with implemented backward selection and leave-one-out cross validation (LOO) for geometrid moths and birds using additional 'mean' and 'entropy' texture statistics derived from a second moving window of 3 pixels × 3 pixels (18 m × 18 m), which resulted in 18 predictors in total. All resulting models included texture statistics from the additional smaller window after backward selection. LOO R<sup>2</sup> values higher than those in Table 4 are in bold.

Species diversity measures	Taxonomic group	R <sup>2</sup>	LOO R <sup>2</sup>	No. of latent vectors	No. of predictors
Species richness	Trees	0.49	<b>0.22</b>	5	9
	Pyraloidea	0.77	0.48	2	11
	Geometridae	0.75	0.57	2	8
	Arctiinae	0.38	<b>0.09</b>	2	12
	Ants	0.80	0.74	2	10
	Birds	0.61	<b>0.27</b>	5	9
NMDS I	Trees	0.99	0.98	7	10
	Pyraloidea	0.94	0.87	2	12
	Geometridae	0.96	<b>0.93</b>	2	13
	Arctiinae	0.96	<b>0.93</b>	2	10
	Ants	0.94	0.90	4	10
	Birds	0.80	<b>0.68</b>	3	11
NMDS II	Trees	0.42	0.29	3	6
	Pyraloidea	0.89	<b>0.82</b>	2	9
	Geometridae	0.79	0.62	2	7
	Arctiinae	0.83	<b>0.72</b>	2	11
	Ants	0.82	<b>0.75</b>	3	7
	Birds	0.66	<b>0.53</b>	2	8

**Table A6**

Results of partial least-squares regressions predicting taxa diversities using (1) only topographical metrics (DEM, SLOPE, and TPI) as predictors and (2) both topographical and spectral (NIR, NDVI, ARI) metrics. Because of the low dimension of predictors, we omitted the backward selection and chose two latent vectors for all models. The LOO (pseudo-) R<sup>2</sup> values are calculated as  $1 - SSE/SST$ , where  $SST$  is the corrected total sum of squares of the response, and  $SSE$  is the sum of squared errors for cross-validated predictions. Negative LOO R<sup>2</sup> values indicate an inability of the models (on average) to explain any of the variability in investigated taxa diversity among sample plots. DEM, Digital elevation model; SLOPE, slope in degrees; TPI, topographical position index; NIR, near-infrared band; NDVI, normalized difference vegetation index; ARI, anthocyanin reflectance index.

Species diversity measures	Taxonomic group	Topographical metrics only		Topographical and spectral metrics	
		R <sup>2</sup>	LOO R <sup>2</sup>	R <sup>2</sup>	LOO R <sup>2</sup>
Species richness	Trees	0.20	0.08	0.22	0.10
	Pyraloidea	0.82	0.77	0.79	0.71
	Geometridae	0.02	-0.68	0.64	0.51
	Arctiinae	0.11	-0.27	0.11	-0.41
	Ants	0.80	0.75	0.81	0.77
	Birds	0.15	-0.01	0.16	-0.11
NMDS I	Trees	0.98	0.98	0.98	0.98
	Pyraloidea	0.96	0.94	0.95	0.93
	Geometridae	0.96	0.94	0.96	0.93
	Arctiinae	0.93	0.86	0.95	0.92
	Ants	0.21	-0.03	0.87	0.82
	Birds	0.74	0.7	0.74	0.65
NMDS II	Trees	0.34	0.26	0.07	-0.05
	Pyraloidea	0.04	-0.87	0.52	0.30
	Geometridae	0.01	-0.86	0.30	-0.01
	Arctiinae	0.06	-0.86	0.41	0.07
	Ants	0.61	0.51	0.65	0.58
	Birds	0.01	-0.2	0.01	-0.15

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