Relating species richness to the structure of continuous landscapes: alternative methodological approaches

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Abstract. Numerous studies have focused on the relationship between landscape structure and plant diversity based on the patch-mosaic landscape paradigm, by deriving structural data from classified images. Since the use of discrete classes poses limitations for predicting biodiversity patterns in complex, low human-impacted ecosystems, two alternative methods have been used to analyze changes of landscape attributes in a continuum: moving-window metrics and surface metrics (image texture). Here, we compare these two approaches for predicting richness of all plant species, legume species, legume trees, legume shrubs, legume forbs, and legume climbers across a tropical landscape in Mexico, based on the records of vascular plants in 250 10 × 10 m plots. Multiple regression and variance partitioning methods were used to analyze the effects of the two landscape descriptors (moving-window and surface metrics), scale (400- and 200-m moving-window sides), and space (based on the extraction of principal coordinates of neighbor matrices’ vectors) on species richness. The predictive power of all metrics was relatively small for total species richness, but generally higher for legume species. For legume forbs, surface metrics-based models indicated a direct association between species richness and landscape homogeneity. Moving-window metrics were highly sensitive to the biological group and to spatial scale, likely due to a leftover effect of image classification procedures. Conversely, surface metrics were more independent from scale and taxonomy. Attempts to predict species richness in highly diverse, low human-impacted tropical ecosystems more rapidly and accurately should better rely on surface metrics rather than on moving-window metrics, in line with the continuous landscape paradigm.

Key words: image texture; landscape metrics; landscape pattern; Leguminosae; moving-window metrics; principal coordinates of neighbor matrices’ vectors; plant diversity; spatial scale; species richness; surface metrics; tropical dry forest; variance partitioning.
INTRODUCTION

The interplay between landscape structure and plant diversity is a key topic of landscape ecology (Uuemaa et al. 2009, Walz 2011, Schindler et al. 2013, Amici et al. 2015). Several theoretical models have provided useful insights into this relation, for example, those based on island biogeography (MacArthur and Wilson 1967), spatial heterogeneity (Tilman and Pacala 1993), dispersal potential (Hubbell 2001), negative conspecific interactions (Janzen 1970, Connell 1971), productivity (Tilman 1982), disturbance (Levin and Paine 1974), and metapopulation theories (Levins and Culver 1971). Despite important differences among these models, all share a common tenet: A landscape pattern should match an ecological process. This notion has prompted numerous studies, encompassing a wide array of geographic regions, environments, scales, biomes, taxonomic groups, and gradients of naturalness. Despite such ample variety of conditions, the majority of studies are based on the patch-mosaic landscape paradigm (Forman 1995), deriving their structural data from a classified satellite image.

The use of discrete landscape classes poses severe limitations for predicting biodiversity patterns in complex natural systems (Southworth et al. 2004, Stickler and Southworth 2008, St-Louis et al. 2009). Landscape properties within a class are presumed to be homogeneous; thus, this approach tends to overlook important information for species with irregular distributions (Palmeirim 1988). Inherent image classification errors related to highly heterogeneous systems may mask the actual composition and configuration of the landscape (Wagner and Fortin 2005). Moreover, in ecosystems with broad ecotones the arbitrary delineation of boundaries between landscape classes may lead to flawed image classification. Also, a given classification scheme may not necessarily represent the spatial organization of the relevant ecological requirements of all species being examined. Therefore, some studies have emphasized the importance of visualizing the gradual changes of landscape attributes across the surface (Cihlar 2000, McGarigal and Cushman 2005) by using either of two divergent approaches: moving-window metrics and surface metrics. The moving-window approach provides a continuous representation of the landscape starting from a classified image, which is expected to reflect the species’ perception of landscape structure. Thus, instead of analyzing the whole landscape pattern, this method quantifies local landscape patterns, emulating the way in which species may experience it (McGarigal and Cushman 2005). In turn, the surface metrics approach allows one to analyze local patterns in the spatial variation of pixels (i.e., texture) in a raw unclassified image (Petrou and García-Sevilla 2006, Márquez Flores 2008). These local patterns are indicative of landscape complexity at various scales (McGarigal et al. 2009) following the principle that links vegetation heterogeneity with the spatial variability of its remotely sensed signal (Rocchini et al. 2004, 2010, Farina 2006, Malhi and Román-Cuesta 2008, Gallardo-Cruz et al. 2012, Block et al. 2016).

Despite the widely accepted idea that gradual variation is pervasive in natural landscapes, it is still uncertain which of these two methodological approaches is more powerful to relate landscape structure and plant diversity, and thus which one will more efficiently advance our understanding of the diversity–landscape relationship. Our main goal was to provide a comprehensive answer to these questions both by comparing the results from these two approaches and by incorporating into the analysis additional relevant sources of variation, namely evolutionary constraints (taxonomy), convergent ecological responses (growth form), spatial scale (extent), and space (i.e., autocorrelation patterns). We did this in a highly complex semi-natural landscape, where plant diversity is very high (Pérez-García et al. 2010).

First, we related landscape structure, derived from both methods, to six sets of plant species: all species, legume species, legume trees, legume shrubs, legume forbs, and legume climbers. We focused on legumes because of their high richness in the area, wide distribution across plant communities, and general prevalence in tropical dry landscapes (Trejo and Dirzo 2002, Pérez-García et al. 2012). This procedure revealed potential landscape associations driven by taxonomic affinities or growth form. Second, for each plant set we examined the effect of changing scale (i.e., extent) on the direction and strength taken by this relationship (Storch and Gaston...
To this end, we used two window sizes to describe both highly localized and medium-range landscape variations. Finally, we measured the dependence on space of species richness of these plant groups in the study landscape (Fortin and Dale 2005, Dormann et al. 2007). This final step allowed us to assess the relative contributions of space and landscape descriptors to the spatial distributions of species using spatial variables and variance-partitioning methods. The relative contributions of these two factors have been seldom assessed in studies relating landscape structure and species richness. While the potential of space to explain a considerable proportion of species-diversity variation is presently recognized (Legendre 1993, Legendre and Legendre 2000), its role has been neglected by most studies that have related species variability to landscape descriptors.

**METHODS**

**Study area**

The study area is the seasonally dry tropical landscape in Nizanda, Mexico (16°39.49′ N, 95°0.66′ W), which covers about 64 km² with an elevation range from 100 to 700 m a.s.l. Mean annual temperature is 27.6 °C and total average annual rainfall is 900 mm, with a rainy season between May and October. Five plant communities display an intricate spatial arrangement across the landscape (Fig. 1): savanna, sub-deciduous forest, semi-evergreen forest, and xerophytic vegetation, all embedded in a matrix of tropical dry forest (Lebrija-Trejos 2001, Gallardo-Cruz et al. 2005, 2009, 2010, Pérez-García et al. 2004, López-Olmedo et al. 2006, 2007, Pérez-García et al. 2009). According to the index of naturalness proposed by Machado (2004), this landscape may be classified as a category 8, subnatural system.

**Plant diversity assessment**

Plant diversity was assessed through a survey based on a stratified random design in which each plant community was randomly sampled proportionally to its area. A total of 250 plots (10 × 10 m) were distributed as follows: 116 in tropical dry forest, 47 in savanna, 38 in xerophytic vegetation, 26 in semi-evergreen forest, and 23 in sub-deciduous forest. All plots were located using a GPS (global positioning system) unit, avoiding areas affected by human activities. In each plot, we recorded the presence of all vascular plant species. We constructed six species-richness sets: total species, all legumes, and four legume groups defined by growth form. Species-richness values were tested for normality and homoscedasticity, and transformed when needed.

**Remotely sensed data and image processing**

We used a high-resolution satellite image (Quickbird; pixel size = 2.6 m) to calculate the moving-window and surface metrics. The scene was acquired at the end of the rainy season to reduce cloud cover and to ensure the presence of foliage in the canopy. The original image was geometrically and atmospherically corrected to surface reflectance following Krause (2005).

**Landscape descriptors: moving-window metrics**

The initial step to compute these metrics is to identify ecological units homogeneous in structure, function, and disturbance regimes based on the plant communities and land use types present at the site (Forman and Godron 1986, Yoshida and Tanaka 2005). Accordingly, we performed a supervised object-oriented classification (Blaschke and Hay 2001) using Definiens Professional (version 5.0.6.2, Definiens AG, Munich, Germany). Our aim was to identify the above-mentioned five plant communities (depicted in Fig. 1), while keeping the distinction between them and the areas where the natural vegetation was cleared for agriculture and cattle raising. This classification was based on the shape and color properties of groups of pixels (objects). Additional details of this procedure can be found in Benz et al. (2004). With the categorical map, we calculated 12 class- and landscape-level metrics (Table 1) using a moving-window approach in FRAGSTATS (ver. 4, University of Massachusetts, Amherst, Massachusetts, U.S.A., www.umass.edu/landeco/research/fragstats/fragstats.html). With this technique, a window moves across the classified image one cell at a time, calculating the selected metric within the window and returning that value to the center cell. From the resultant surface, each cell synthesizes the structure of the landscape within the window (McGarigal and Cushman 2005). From
these surfaces, we extracted the corresponding metric values for the central pixel of the 250 sampling plots. The effect of scale was analyzed using square windows with sides of 400 and 200 m (sensu Goodchild 2001). These geographic dimensions improve the spatial analysis of plant diversity related to autocorrelation patterns in the region (Gallardo-Cruz et al. 2010).

**Landscape descriptors: surface metrics**

The analysis of a digital surface may be approached through the use of image texture, which refers to the spatial arrangement of the pixel values within a digital image (Haralick 1979, Irons and Petersen 1981, Márquez Flores 2008). This property was analyzed using second-order texture metrics that consider the spatial relations between groups of two neighboring pixels within a given window (Petrou and Garcia-Sevillia 2006). The calculation of second-order metrics involves the construction of gray-level co-occurrence matrices (GLCMs), which contain the co-occurrence probability of pixel values for pairs of pixels in a given direction and distance. To create such matrices, we used a spatial distance of one pixel, four directions (0°, 45°, 90°, 135°), and 64 gray levels. A GLCM was built for each direction, and from each matrix, a texture measurement was calculated using four formulas (Haralick 1979, Table 2). Finally, the texture measurements of each direction were averaged to obtain a single spatially invariant texture metric. These metrics were calculated using a moving-window approach for three data layers: the red (RED; 0.63–0.69 µm) and infrared (IR; 0.76–0.90 µm)

![Image](image_url)
This index does not saturate under dense canopy conditions and incorporates two empirical parameters ($C_1 = 6$, $C_2 = 7.5$), the blue channel for atmospheric correction, and sensitivity minimization of soil background reflectance variation ($G = 2.5; L = 1$; Gao et al. 2000).

From the 12 resulting texture surfaces (three layers and four metrics), we extracted the value for each one of the 250 plots. To analyze the effect of scale, the entire procedure was performed using square windows with sides of 400 and 200 m. The procedure was programmed in ENVI 4.5/IDL (version 7.0, ITT Visual Information Solutions, Boulder, Colorado, U.S.A.).

Spatial analysis
Ecologists are increasingly paying attention to the role of space in determining floristic turnover in a landscape; this does not imply that space as such is the driving force of these changes, but rather a surrogate to many ecological and geographical processes that are spatially structured themselves (Kareiva 1994, Tuomisto et al. 2003, Gallardo-Cruz et al. 2010). The spatial dependence of species richness across the landscape was analyzed using the “principal coordinates of neighbor matrices” method (PCNM; Borcard and Legendre 2002). Principal coordinates of neighbor matrices is based on a principal coordinate analysis of a truncated geographical distance matrix between sampling sites. The method creates a set of explanatory spatial variables (i.e., PCNM vectors) with structures at all scales encompassed by the samples data matrix. To generate the PCNM vectors, we (1) created an Euclidean distance matrix based on the geographical distances between sites, (2) replaced in this matrix those distances greater than the largest distance between adjacent sites with an arbitrary large number (Borcard et al. 2004), (3) performed a principal coordinate analysis on the modified distance matrix, and (4) retained the principal coordinate axes that correspond to positive eigenvalues. The method produced 112 PCNM vectors, among which 29 had positive and significant autocorrelation values ($P < 0.001$, Moran’s test). These were retained as the set of explanatory space variables to determine their statistical relation with the response (i.e., species richness) variables.

The PCNM method was performed using the spacemakeR library (Dray et al. 2006) in R (R Foundation for Statistical Computing, Vienna, Austria).

Table 1. Abbreviations and description for the 12 moving-window metrics used in the analysis.

| Moving-window metric                                      | Abbreviation | Description                                      |
|-----------------------------------------------------------|--------------|--------------------------------------------------|
| Largest patch index                                       | LPI          | Percentage of total landscape area covered by the largest patch |
| Shannon’s diversity index                                 | SHDI         | Quantifies landscape diversity                   |
| Total core area                                            | TCA          | Sum of the core areas in the landscape           |
| Percentage of landscape                                   | Pland        | Proportional abundance of each patch type in the landscape |
| Total edge contrast index                                  | TECI         | Measures the contrast along all edges across the landscape |
| Area-weighted mean patch size                              | AreaAM       | A relative measure of mean patch size           |
| Area-weighted edge contrast index                          | EconAM       | An area-weighted amount of contrast along the patch perimeter |
| Area-weighted largest patch index                          | LPIAM        | An area-weighted measure of the percentage of total landscape area covered by the largest patch |
| Mean area-weighted proximity index                         | ProxAM       | A relative measure of patch isolation and fragmentation of the corresponding patch type within a specified neighborhood |
| Mean area-weighted similarity index                        | SimiAM       | An area-weighted measure of patch isolation under a landscape mosaic perspective. This index considers the size and proximity of all patches, regardless of class, whose edges are within a specified search radius of the focal patch |
| Perimeter/area ratio                                       | ParaAM       | Measures shape complexity                       |
| Standard deviation of perimeter/area ratio                 | ParaSD       | Measure of absolute variation of shape complexity |

† AM, area-weighted mean, which is equal to the sum across all patches in the landscape of the corresponding patch metric values, multiplied by the proportional abundance of the patch. AM metrics provide a landscape-level measure of landscape structure.
Table 2. Abbreviations, formulas, and descriptions of the four surface metrics derived from the gray-level co-occurrence matrix (GLCM).

| Surface metric | Abbreviation and formula | Description |
|----------------|--------------------------|-------------|
| Mean           | MEAN = \( \sum_{i,j=0}^{N-1} iP_{ij} \) | Mean of the probability values from the GLCM. It is directly related to the image spectral heterogeneity |
| Variance       | VAR = \( \sum_{i,j=0}^{N-1} (i - MEAN)^2 \) | Measure of the global variation in the image. Large values denote high levels of spectral heterogeneity |
| Correlation    | COR = \( \sum_{i,j=0}^{N-1} \frac{p_{ij} - (i - MEAN)(j - MEAN)}{VAR} \) | Measure of the linear dependency between neighboring pixels |
| Second moment  | SM = \( \sum_{i,j=0}^{N-1} p_{ij}^2 \) | Measure of the order in the image. It is related to the energy required for arranging the elements in the system |

Notes: \( P_{ij} \) is the \((i, j)\) element of the GLCM and represents the probability of finding the reference pixel value \(i\) in combination with a neighbor pixel value \(j\). Note that \( \sum_{i} P_{ij} = 1 \).

**Effects on species diversity**

Multiple regression and variance partitioning methods were used to analyze the effects of landscape and space (PCNM vectors) on species diversity. The procedure involved four stages. First, by using multiple regressions we fitted models between a species-diversity variable (the six sets of plant species) and one set of landscape data (either 12 moving-window metrics or 12 surface metrics). These models represent the variation explained exclusively by landscape data \((a)\) plus the variation explained jointly by landscape data and space \((b)\); in other words, this first model represents \(a + b\) (Fig. 2). Second, a multiple regression model using the selected set of space variables was fitted to the dependent variables. This second model represents spatially dependent variation \((c)\) plus the variation explained jointly by landscape data and spatial dependence \((b)\); that is, this second model represents \(b + c\) (Fig. 2). Third, the total amount of variation explained \((a + b + c)\) was calculated by combining the two previous multiple regression models into a global regression model using exclusively significant variables. All multiple regression analyses were implemented using forward selection in SPSS. Finally, variance partitioning was performed to determine the relative importance of landscape variables \((a = (a + b + c) - (b + c))\), spatial structure \((c = (a + b + c) - (a + b))\), and shared variation \((b = (a + b + c) - (a) - (c))\) on species diversity (Borcard et al. 2004).

**Results**

**Overall floristic assessment**

A total of 1001 vascular plant species were recorded in the 250 100-m² sampling plots distributed across the landscape. Of these, 119 species (12%) were members of Leguminosae. Additional important plant families were Asteraceae with 73 species, Euphorbiaceae (48), Rubiaceae (41), Poaceae (40), Convolvulaceae (32), Bignoniaceae (31), Malpighiaceae (24), Malvaceae (23), Acanthaceae (21), and Polygonaceae (20). A small fraction of species (54; 5%) remained undetermined, but none of them belonged to any of the most speciose families.

The distribution of legumes by growth form was uneven. Nearly half of all legumes were trees (51 species; 42.9%). Forbs and shrubs accounted for 22.7% (27 species) and 16.8% (20 species), respectively. Climbers were the least represented group (8.4%, 10 species).

**Prediction of total plant species richness**

The capacity to predict total species richness based on landscape descriptors was very limited, as no single combination of predictive factors (Table 3) produced \( R^2 \) values > 0.20 (Fig. 3). The highest \( R^2 \) corresponded to the full models incorporating both landscape and space variables \((a + b + c)\), with the largest \( R^2 \) obtained from the use of moving-window metrics for the 400-m scale (0.161). Individual contributions of the two main factors, namely landscape data \((a)\) and space variables \((c)\), to total variance were relatively small (Fig. 3A, B). In the case of landscape structure, the largest significant \((P < 0.05)\) contribution came from moving-window metrics for the 400-m scale (0.030), while for space the largest value was produced by surface metrics-based models, also for the 400-m scale (0.098).

The predictive variables retained in the models constructed for the entire flora were not the same for the two spatial scales in the case of surface..
Fig. 2. Venn diagram representing the partition of the variance of the response variable \(Y\) (species richness) between two sets of explanatory variables, namely landscape data (a) and space (c). The variance jointly explained by landscape data and space is represented by (b) in the diagram. The rectangle represents the total variance in \(Y\).

Table 3. Standardized coefficients for linear regression models based on moving-window metrics (MWM) for predicting species diversity in six plant sets (all species, legume species, legume trees, legume shrubs, legume forbs, and legume climbers).

| MWM  | All species | Legume species | Legume trees | Legume shrubs | Legume forbs | Legume climbers |
|------|-------------|----------------|--------------|---------------|-------------|----------------|
|      | Scale 1    | Scale 2        | Scale 1      | Scale 2       | Scale 1     | Scale 2        | Scale 1    | Scale 2        | Scale 1    | Scale 2        | Scale 1    | Scale 2        |
| LPI  | 0.091       | 0.161          | 0.276        | 0.278         | 0.169       | 0.197          | 0.264     | 0.288          | 0.467      | 0.498          | 0.225      | 0.271          |
| SHDI | 0.263       | ...            | ...          | ...           | 0.257       | ...            | 0.381     | 0.358          | 0.419      | 0.684          | 0.156      | ...            |
| AreaAM | ...     | ...            | ...          | ...           | 0.531       | ...            | 0.381     | 0.358          | 0.235      | ...            | 0.279      | ...            |
| EconAM | ...      | 0.185          | ...          | ...           | 0.725       | ...            | 0.899     | ...            | 0.156      | ...            | 0.330      | ...            |
| LPIAM | 4.542      | 0.542          | 2.054        | 0.673         | 0.235       | ...            | 0.235     | ...            | 0.279      | ...            | 0.279      | ...            |
| TCA  | ...        | ...            | ...          | ...           | 0.235       | ...            | 0.235     | ...            | 0.279      | ...            | 0.279      | ...            |
| ParaAM | ...     | ...            | ...          | ...           | 0.266       | ...            | 0.266     | ...            | 0.266      | ...            | 0.266      | ...            |
| ParaSD | ...    | 0.175          | 0.162        | 0.248         | 0.175       | ...            | 0.175     | ...            | 0.175      | ...            | 0.175      | ...            |
| PlanD | ...       | ...            | ...          | ...           | ...         | ...            | 0.235     | ...            | 0.235      | ...            | 0.235      | ...            |
| ProxAM | ...    | ...            | ...          | ...           | 0.235       | ...            | 0.235     | ...            | 0.235      | ...            | 0.235      | ...            |
| SimiAM | ... | ...          | ...          | ...           | ...         | ...            | ...       | ...            | ...        | ...            | ...        | ...            |
| TECI | ...        | ...            | ...          | ...           | ...         | ...            | ...       | ...            | ...        | ...            | ...        | ...            |

Notes: See Table 1 for abbreviations and description of the 12 moving-window metrics (MWM) shown. Values in bold on the first row correspond to \(R^2\) obtained for the full models (a + b + c). Only significant coefficients (\(P < 0.05\)) are shown.
metrics (Table 3). Conversely, in the case of texture-based models there were two variables common to both models (REDVAR and REDSM; Table 4).

Prediction of all-legume species richness

Full models predicting all-legume species richness (Tables 3 and 4) had a considerably higher predictive capacity, with $R^2$ values generally twice as large as the previous ones (Fig. 4). Surface metrics models for the two spatial scales analyzed had $R^2$ values $>0.30$. Compared to models based on moving-window metrics, surface metrics models gained relatively larger contributions from the landscape component and smaller ones from the spatial component.

Modeling for all-legume species richness based on surface metrics showed that only perimeter-area ratio (ParaAM) was retained in the models for both spatial scales. Conversely, four variables were common to the two full texture models $(a+b+c)$, namely IRMEAN, IRSM, REDMEAN, and EVIMEAN (Tables 3 and 4).

Prediction of legume species richness by growth form

Moving-window and surface full models $(a+b+c)$ predicting legume species richness by growth form showed a variable behavior, with cases of both larger and smaller $R^2$ values than full models predicting all-legume species richness (Fig. 4). Particularly noticeable was the increase in the predicting ability of models for species richness of legume forbs, with $R^2$ values $>0.45$ for both spatial scales in the case of moving-window metrics models, and $>0.50$ for both spatial scales regarding surface metrics models. Full models for trees, shrubs, and forbs based on moving-window metrics had higher $R^2$ values when constructed for the larger scale (400 m), and the same pattern was true for most surface metrics models, except for the model predicting forb species richness.

The partitioning of full-model $R^2$ values into components for the four growth form groups of legumes revealed that in most cases, the contributions of space variables accounted for a larger proportion of total explained variance (Fig. 4). However, the model predicting legume tree richness based on moving-window metrics at the 400-m scale, and the models for the two spatial scales constructed to predict legume forb richness using surface metrics showed that the contribution of the landscape structure component $(a)$ was always more than twice as large as the spatial component $(c)$, as seen in their $R^2$ values: legume trees moving-window metrics $= 0.041$ vs. $0.014$ (400-m scale); and legume forbs surface metrics $= 0.249$ vs. $0.098$ (200-m scale) and $0.185$ vs. $0.078$ (400-m scale).

In modeling forb species richness based on surface metrics, the variables included in models constructed for the two spatial scales were IRMEAN, REDMEAN, REDVAR, and EVIMEAN (Table 4). In turn, the model predicting tree species richness based on moving-window metrics at the 400-m scale retained Largest patch index (LPI), Shannon’s diversity index (SHDI), Area-weighted mean patch size (AreaAM),
Table 4. Standardized coefficients for linear regression models based on surface metrics for predicting six species-diversity sets (all species, legume species, legume trees, legume shrubs, legume forbs, and legume climbers).

| Surface metric | All species | Legume species | Legume trees | Legume shrubs | Legume forbs | Legume climbers |
|----------------|-------------|----------------|--------------|--------------|--------------|----------------|
|                | 200 m 400 m| 200 m 400 m    | 200 m 400 m  | 200 m 400 m  | 200 m 400 m  | 200 m 400 m    |
| IRENG          | 0.141 0.152 | 0.307 0.303    | 0.205 0.214  | 0.299 0.316  | 0.593 0.529  | 0.170 0.188    |
| IRENG          | ... −0.265  | ... −0.278     | ... −0.247   | ... −0.208   | ... −0.254   | ... −0.135     |
| IRSM           | −0.182 ...  | −0.278 −0.807  | −0.247 −0.308| −0.254 −0.858| ... ...       | ... ...        |
| IRMEAN         | ... ...     | ... −0.869 −0.685| −0.214 ...   | −0.727 ...   | −1.129 −0.933| ... ...        |
| REDVAR         | 0.173 0.331 | ... 0.197      | ... 0.311    | ... 0.153    | ... ...      | ... ...        |
| REDMEAN        | 0.169 0.198 | ... 0.156      | ... 0.311    | ... 0.153    | ... ...      | ... ...        |
| REDCORR        | ... ...     | ... ...        | ... −0.237   | ... −0.124   | ... ...      | ... ...        |
| EVIENG         | ... −1.507  | −1.147 ...     | −1.460 ...   | −1.921 −1.709| −0.938 ...   | ... ...        |
| EVIMean        | ... ...     | ... 0.769      | ... 0.555    | ... ...      | ... ...      | ... ...        |
| EVICORR        | ... ...     | ... −0.159     | ... 0.186    | ... 0.164    | ... ...      | ... ...        |

Notes: See Table 2 for abbreviations, formulas, and descriptions of surface metrics. Values in bold on the first row correspond to $R^2$ obtained for the full models ($a + b + c$). Only significant coefficients ($P < 0.05$) are shown.

Area-weighted largest patch index (LPIAM), and Mean area-weighted similarity index (SimiAM; Table 3).

Consistency of variable inclusion in the models

Tables 3 and 4 show important inconsistencies, both in the identity of landscape variables included in the models for the different plant groups and the two spatial scales and in the signs of their coefficients. In fact, no single moving-window or surface variable was included across all models.

In the case of moving-window variables, LPI excelled over all others in terms of its relevance, as it was the only one included in more than half of the models (eight models). Next to it, only AreaAM, LPIAM, ParaAM, and SimiAM appeared in five models. At the opposite end, no model included total core area (TCA). A very conspicuous pattern among these variables is that their coefficients are rather inconsistent concerning their signs; a clear example of this is LPI, as this variable had three cases of negative coefficients vs. five cases of positive ones. However, only ParaAM had negative coefficients in all five models. Perhaps such inconsistencies reflect a lack of coordination between the behaviors of species belonging to different growth form categories, as these have different ways of relating to the environment. Yet, future research should focus on this issue in order to provide more definite conclusions. Finally, all these variables were highly sensitive to changes in the spatial scale: No single model pair for any plant group included the same or nearly the same variables for the prediction of species richness.

In general, the set of surface variables showed a more consistent behavior than moving-window variables regarding their inclusion in the different models and the signs of their coefficients. For example, five of them appeared in at least five (but in no more than seven) models (IRENG, IRSM, REDMEAN, REDVAR, EVIENG). More importantly, these variables were almost totally consistent in the signs of their coefficients, except for REDVAR. Likewise, the spatial scale of analysis had a smaller effect on the models involving surface variables, as there were 12 cases of the same variable being included in the two models predicting species richness of a given plant group for both spatial scales. This pattern was particularly evident in the case of all legumes, and to a lesser extent, of legume forbs.

Discussion

The largest proportion of the Earth’s biota is strongly concentrated in tropical regions, both
humid and seasonally dry (Chave 2008). Therefore, any attempt to accurately predict species richness of tropical systems by using surrogates is warranted, particularly considering the large time and financial costs involved in the assessment of such diversity directly on the terrain (Gillespie et al. 2006, Hernandez-Stefanoni 2006, Hernandez-Stefanoni et al. 2011). Therefore, the relatively low predictive capacity of the full models constructed for the entire flora of Nizanda based on moving-window and surface variables, and for the two spatial scales, seems at first glance disappointing. Being realistic, perhaps one should expect a higher predictive power only for systems characterized by a smaller biodiversity (Krauss et al. 2004, Block et al. 2016), while moderate predictive capacities may be the norm with increasing levels of regional diversity (Torras et al. 2008). Thus, for a highly diverse landscape such as Nizanda, it may be unreasonable to expect much higher $R^2$ values than ours. This hindrance is related to the plethora of individual responses displayed by all species concurring in a given landscape, many of which are neither linear nor Gaussian. Without such variety of responses, the coexistence of many of those species would be impossible, as predicted by niche differentiation models (Tilman 1982, Tilman and Pacala 1993). An example of the difficulties in modeling community diversity attributes in highly diverse systems is provided by Solórzano et al. (2017), carried out in the tropical dry forest of the same locality, who showed that no single model constructed for several diversity attributes had a significantly better goodness-of-fit than expected at random. In clear contrast, when we applied the same methodological approach in a less diverse landscape (a
mountainous temperate region of central Mexico), the modeling of species richness was more successful (Block et al. 2016).

Space has increasingly gained recognition among ecologists as a key variable in explaining the complex patterns of biological diversity on Earth (Kareiva 1994). Our study strongly supports this view, as the contribution of space (measured through the PCNM vectors) to total variance exceeded the contribution of landscape configuration in 21 out of 24 cases, regardless of the landscape descriptor or the spatial scale used for the analysis. The relative magnitude of the fraction of total variance corresponding to space (c) suggests the existence of some natural process capable of generating the observed spatial structure, even though no explanatory variable is presently available to account for it (Legendre and Legendre 2000, Borcard et al. 2004). The measurement of this fraction may become a valuable tool for landscape ecologists for the formulation of new hypotheses about these factors and processes. For example, one could reasonably argue that the plant species occurring in this landscape are subjected to strong dispersal limitations (Chave and Leigh 2002, Gallardo-Cruz et al. 2013). The overall consistencies among the variables included in the models and their signs lead to similar conclusions. We found that moving-window metrics are highly sensitive to the biological group under examination and to spatial scale (i.e., window size); such sensitivity is likely a leftover effect of the inability of image classification procedures to capture the internal heterogeneity of landscape patches. Despite significant attempts to tackle this shortcoming (McGarigal and Cushman 2005), it is important to recognize that these metrics are grounded on an artificial classification of an inherently continuous landscape. In contrast, surface metrics seem to have a more cohesive behavior, and to be more independent of these two factors of analysis, allowing a more rapid and accurate prediction of species richness.
Several reasons may help explain why surface metrics could be better landscape predictors than moving-window metrics, and better able to predict species richness, at least for legume forbs. As discussed previously, problems arise when any landscape descriptor is derived from an initial classification procedure of a satellite image. Thus, these problems are the consequence of treating a landscape with an intrinsically continuous heterogeneity as a collection of discrete units (Cihlar 2000). Clearly, this situation is not equally critical across the entire naturalness gradient, and one may expect anthropic landscapes to be less sensitive to this issue. We acknowledge the value of moving-window metrics as a proposal that recognizes this difficulty, yet classification errors are impossible to avoid. Moreover, our results also demonstrate that the proper selection of the moving-window size is crucial for the computation of these metrics. In this regard, McGarigal and Cushman (2005) suggest that window size should be appropriate to the scale at which the species (or process) senses the landscape. However, the use of moving-window metrics is limited when the response variable pertains to the community level (species richness in our case), because each species may have a different scale at which its response is maximum.

The use of surface metrics, however, is not totally problem-free. Its major strength rests on the fact that their derivation does not require the intermediate step of image classification and its burden of subjectivity. Yet, the challenge remains to find those metrics that best describe the heterogeneity of the remotely sensed signal. Also, we need to investigate further the effects of multiple factors that may alter the heterogeneity of an image, and ultimately the quantification of the many texture variables that have been described so far (Couteron et al. 2006, Barbier et al. 2010). Among them, the inclination angle of the scene, topography, season, cloud coverage, and other atmospheric conditions deserve more attention. Despite all these limitations, our study supports the idea that if future efforts are ever to predict more successfully species richness in highly diverse tropical systems with a high degree of naturalness, scientists should shift toward the use of the continuous landscape paradigm, as it better matches the nature of these systems.

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DATA AVAILABILITY

Data available from the Dryad Repository: https://doi.org/10.5061/dryad.vc51n47 (Gallardo-Cruz et al. 2018).