Are landscape attributes a useful shortcut for classifying vegetation in the tropics? A case study of La Amistad International Park

Alexandre K. Monro[1,2], **Nadia Bystriakova**[1,4] (iD), and **Frank González**[3]

[1] Identification and Naming Department, The Royal Botanic Gardens, Kew, TW9 3AE, UK

[2] Department of Life Sciences, The Natural History Museum, Cromwell Road, London, SW7 5BD, UK

[3] Laboratorio de Ecología Urbana, Universidad Estatal a Distancia, San José, 474-2050, Costa Rica

ABSTRACT

Effective vegetation classification schemes identify the processes determining species assemblages and support the management of protected areas. They can also provide a framework for ecological research. In the tropics, elevation-based classifications dominate over alternatives such as river catchments. Given the existence of floristic data for many localities, we ask how useful floristic data are for developing classification schemes in species-rich tropical landscapes and whether floristic data provide support for classification by river catchment. We analyzed the distribution of vascular plant species within 141 plots across an elevation gradient of 130 to 3200 m asl within La Amistad National Park. We tested the hypothesis that river catchment, combined with elevation, explains much of the variation in species composition. We found that annual mean temperature, elevation, and river catchment variables best explained the variation within local species communities. However, only plots in high-elevation oak forest and Páramo were distinct from those in low- and mid-elevation zones. Beta diversity did not significantly differ in plots grouped by elevation zones, except for low-elevation forest, although it did differ between river catchments. None of the analyses identified discrete vegetation assemblages within mid-elevation (700–2600 m asl) plots. Our analysis supports the hypothesis that river catchment can be an alternative means for classifying tropical forest assemblages in conservation settings.

Abstract in Spanish is available with online material.

Key words: beta diversity; community data analysis; Costa Rica; elevation zones; high-elevation oak forest; Panama; river catchment; Talamanca Mountains; vegetation classification.

Effective vegetation classification schemes support conservation (Lindenmayer *et al.* 2008, Evens & Keeler-Wolf 2014) and provide a framework for ecological research (ESA Vegetation Classification Panel 2015). Conservation planning in the tropics requires choices about how to assess, classify, and monitor biodiversity (Margules & Pressey 2000, Ferrier 2002). Floristic assemblages or classes have long been recognized as useful for assessing biodiversity and the identification of floristic units is often the first step in this process (Humbold & Bonpland 2008). Devictor *et al.* (2010) suggest that, together with taxonomic (floristic) diversity, phylogenetic and functional diversity should also be considered because they better meet conservation needs. In tropical forests, landscape-scale mapping and identification of floristic diversity patterns are challenging (Kessler 2000, Sundqvist *et al.* 2013); achieving adequate sample coverage in species-rich and structurally diverse landscapes is difficult (Homeier *et al.* 2010).

In data-poor locations, conservation planning may have to rely on vegetative classifications generated using remotely collected data. Remote collection may be more efficient than collecting detailed floristic data, given the relationships between floristic

composition, environmental gradients (*e.g.*, Franklin 1995, Vazquez & Givnish 1998, Guisan & Zimmermann 2000, Ferrier 2002), and beta diversity (Givnish 1999). At the scale of protected areas or national parks, one could also base classifications on river catchments, topography, or other geographical landscape features (Syrbe *et al.* 2013, Warren *et al.* 2014, Walz 2015). Where floristic data exist, landscape attributes may represent a valuable source of data for classifying species assemblages. Classifications based on geographical landscape frequently rely on elevation in combination with evapotranspiration potential or substrate (Tosi 1969, 1971, Tuomisto *et al.* 2002), whereas river catchment is rarely used. A long-standing confrontation between niche-based and dispersal-based theories affects the theoretical context of contrasting classifications by elevation zones and river catchment (Hubbell 2001). In addition to isolation by distance, river catchment (or watershed) might limit dispersal by creating a natural barrier in the form of a ridge, for example. In the tropics, contribution of geographic distance to floristic variation is roughly constant (20–30%), while contribution of the environment varies more (10–40%; Chave 2008). The distribution of Panamanian tree species appears to be determined more by dispersal limitation than by environmental heterogeneity, with the environment alone (*i.e.*, rainfall, topography, and soil properties) explaining

10–12% of the floristic variation; space alone, 22–27%; and the interaction between the two, 13–18% (Chust *et al.* 2006).

Using a floristic survey carried out in Central America's La Amistad International Park (PILA), we explored the correlations between species composition and environmental (climate, elevation) and spatial (river catchment) factors, asking: (1) to what extent does elevation in general, and pre-defined elevation zones in particular, explain variation in species composition across sites? (2) How does beta diversity change when species are grouped by elevation and river catchment area? (3) How sensitive are the answers to our sampling methods?

METHODS

Study area.—PILA is part of the La Amistad Biosphere Reserve and World Heritage Site, a complex and heterogeneous ecosystem that includes indigenous reserves, protected areas, and management units across two countries, Costa Rica and Panama (Autoridad Nacional del Ambiente 2004, Borge 2004). At the regional level, PILA represents the second largest state-controlled park and forms the core of the third largest biosphere reserve in Central America. UNESCO declared PILA a World Heritage Site in 1983 and listed it as a Binational property on the World Heritage List in 1991.

PILA comprises 401,000 ha (Fig. S1) of a biodiversity-rich landscape (Davis *et al.* 1997, Borge 2004) with ca 3100 species of vascular plants (Monro *et al.* in press). PILA exhibits a rainfall gradient which ranges from 2000 to 2500 mm on the Pacific slopes and 4000 to 6000–7000 mm on the Caribbean slopes (Herrera 1986, Autoridad Del Ambiente 2004, Borge 2004). Temperatures range from freezing or several degrees below freezing above 3100 m asl (Cerro Fábrega, Monro *pers. obs.*) to +36 °C at sea level (Tosi 1971). Approximately 85% of PILA is at an elevation of 1000 m or more, with 32% at or above 2000 m elevation.

PILA originally comprised a number of regional and national vegetation classifications that differed in the number of classes and the elevations used to delimit them (Holdridge 1967, Holdridge *et al.* 1971, Tosi 1969, Gómez 1986, Davis *et al.* 1997, Central American commission for Environment and Development 2016, Kappelle *et al.* 2002, Zamora 2008). Monro *et al.* (2009) generated the first unified vegetation zone map for PILA based on plant species assemblages and elevation: (1) *low-elevation forest* (LEF), below 700 m; (2) *mixed forest in transition to low-elevation forest* (MFTLEF), 701–1200 m; (3) *mixed forest in transition to cloud forest* (MFTCF), 1201–1600 m; (4) *cloud forest* (CF), 1601–2100 m; (5) *low-elevation oak forest* (LEOF), 2101–2600 m; (6) *high-elevation oak forest* (HEOF), 2601–3100 m; and (7) *Páramo*, 3101–3500 m. Elevation zone ranges were congruent with those identified by Davis *et al.* (1997) except that the single montane belt was split into two zones, LEOF and HEOF, to reflect differences in species composition (Kappelle & Zamora 1995, M.O., *pers. obs.*).

The dataset.—We conducted sampling between 2003 and 2009. Data collection in the area is constrained by access, requiring us to focus our sampling on areas within a two-day hike from the nearest road and on two sites for which we secured funding for helicopter access. At each site, all vascular plant taxa were sampled at each of 10–20 points, for a total of 141 sample points across nine field sites (Fig. S1 and Table S1). Sampling locations were not evenly represented across elevations, with most sampling points at mid-elevation sites (MFTLEF, MFTCF, and CF; 35–37 points per elevation band) and fewest sampling points in the lowest (LEF) and highest (LEOF, HEOF, and Páramo) elevation bands (5–13 per elevation band).

We recorded all species we found in 6–8 h within a 50-m radius of the sampling point (total sampling = *ca.* 2468 person hours from area of 110.7 ha). We sampled the canopy, understory, and ground layer. This approach offers an advantage over fixed-size sampling plots by balancing site comparability with the need to comprehensively record biodiversity; the time ordinarily spent demarcating plots is instead spent collecting data. In each plot, we recorded the identity of canopy trees and their reproductive status. Finally, we documented the river catchment for each sample plot.

For each plot, we extracted the values of annual mean temperature, °C (ANMT), and average annual precipitation, mm (ANP), from Worldclim dataset (Hijmans *et al.* 2005). We calculated the values of several landscape attributes for each plot using ArcGIS (ArcGISv. 10.2.2, 1999–2014 Esri Inc.): orientation of slope (Aspect); slope, degrees (Slope); and river catchment area (Catchment Area). We chose the first two variables because of the study area's pronounced elevation gradient and complex terrain; we chose river catchment because of the potential influence on vegetation (Costa *et al.* 2005). Aspect was incorporated as a categorical variable with nine levels: Flat, North, North-East, East, South-East, South, South-West, West, and North-West. Five Catchment Areas (La Estrella, Rio Changuinola, Rio Sixaola, Banano, and Terraba) were incorporated as levels of a categorical variable. We assigned each plot to one of the seven elevation zones defined by Monro *et al.* (2009).

Statistical analyses.—We carried out all analyses using packages *base* and *vegan* in R Version 3.1.2 (R Foundation for Statistical Computing).

Assessing relationships between environmental gradients and species assemblages across sites.—To identify putative natural gradients and how they influenced species composition, we carried out detrended correspondence analysis, DCA (Hill & Gauch 1980), implemented as function *decorana* and fitted environmental vectors into community ordination using function *envfit*. To identify potential discontinuities along elevation gradient, we carried out Correspondence Analysis, CCA (Ter Braak 1986), using elevation as a factor with seven levels corresponding to elevation zones (see Introduction). We built the maximal CCA model with all variables (Aspect, Catchment Area, Elevation, Slope, ANMT, and ANP). All correlations between environmental variables were below 0.5. We analyzed marginal effects when each term was eliminated from the model using ANOVA with 199 permutations.

QUANTIFYING CHANGES IN BETA DIVERSITY WITH ELEVATION WHEN SPECIES ARE GROUPED BY ELEVATION AND RIVER CATCHMENT AREA.—We used the approach proposed by Jari Oksanen (Ramos-G. *et al.* 2016) to quantify beta diversity (Anderson *et al.* 2006). In this method, the index of dissimilarity based on the Arrhenius species–area model is defined as $S = cX^Z$, where X is the size of the site and c and z are estimated parameters (Ramos-G. *et al.* 2016). Function *betadiver* finds the value of z, which gives the steepness of the species area curve and is a measure of beta diversity; the fewer species the plots share, the steeper the curve (Ricotta *et al.* 2002). To assess how beta diversity changed along the elevation gradient and between river catchments, we first grouped sites by elevation zones and then by river catchments. For each factor, we analyzed beta diversity separately and applied Tukey's honest significant difference test (Tukey's HSD) to identify significant pairwise differences.

ASSESSING POTENTIAL BIASES IN OUR RESULTS DUE TO SAMPLING EFFORT.—To identify potential sources of bias in this dataset, we visually compared two frequency distributions: 1) the area of PILA (represented by the number of 1 × 1 km grid squares) and 2) the sampled area (represented by the number of plots) along altitudinal, temperature, and precipitation gradients. Greater discrepancy between the corresponding pairs of frequency distributions would suggest that the sample is not representative of the greater population, which could undermine the results of statistical analyses. We built histograms using function *hist* showing density distributions of the area of PILA, and the area of sampling plots, along the environmental gradients specified above. We then carried out Shapiro–Wilk normality test (Royston 1982) using function *shapiro.test*. If sampling effort adequately represented species richness of PILA, then the species accumulation curve (SAC) would flatten out after an initial exponential increase (Gotelli & Colwell 2001). To test this hypothesis, we built a species accumulation curve by randomly adding samples from the species pull to the accumulation curve and then plotting the mean of these permutations using *specaccum* function (method = "random", permutations = 1000).

Autocorrelation is the lack of independence between pairs of observations at given distances in time and space, a common issue in ecological data (Legendre 1993). Presence of autocorrelation in our dataset would suggest non-independent samples, leading to potential invalidation of our statistical analysis (Hurlbert 1984). To estimate the degree of spatial autocorrelation in species richness data, we used Moran's I coefficient (Legendre and Legendre 1998). We used package *pgirmess* to build correlograms of the species richness data in 100 distance classes.

RESULTS

We recorded 8306 individuals of 2117 species. The 2117 species observed at the 141 plots belong to 178 different vascular plant families (Table S2), among which the most species rich were Piperaceae (147 spp), Rubiaceae (144), Melastomataceae (110), Araceae (106), and Asteraceae (71). Some of the most common families (Table S2) showed a steady decline in per-plot number of records along the elevation gradient, with the highest per-plot number of records in LEF (Figs. S2–S5), while the decline in per-plot number of records with elevation was irregular (Figs. S6–S9) in the other families. The most widespread species were the early successional tree species, *Cecropia angustifolia* (observed at 61 of 141 sample points) and *Hampea appendiculata* (observed at 46 sample points), and the ground story herb / epiphyte *Anthurium microspadix* (observed at 45 sample points).

TO WHAT EXTENT DO ENVIRONMENTAL GRADIENTS IN GENERAL, AND PRE-DEFINED ELEVATION ZONES IN PARTICULAR, EXPLAIN VARIATION IN SPECIES ASSEMBLAGES ACROSS SITES?—DCA revealed high gradient length (13.7 standard deviations along DCA1), indicating that a few species occupied both ends of the gradient (Table S3). The first and second ordination axes explained the variation within the dataset well, as indicated by high eigenvalues (0.70 and 0.55, respectively, Table S3). The first axis involved elevation and ANMT, indicating that the observed differences in species composition were largely due to the changes in temperature and altitude. The second axis was related to ANP, indicating that rainfall strongly influenced species composition. All environmental variables were highly significant except for Slope (Table S4 and Figs. S10 and S11). According to CCA, all selected environmental variables except for Aspect and ANP influenced species community structure (Table S5). After selection by permutation test for marginal effects of terms, we built a minimal adequate CCA model with four untransformed variables (Catchment Area, Elevation Band, Slope, and ANMT); the model explained 12.0% of variation (Table S6). Along the principal axis of ordination (CCA1), the only discontinuity was between the sites (plots) in HEOF and Páramo versus those in the low- and mid-elevation zones (Figs. 1 and S12). The second cluster of plots showed a strong trend (CCA2) with a progression of elevation zones from low to high. This gradient appeared to be related to the differences in annual precipitation as shown by DCA, despite the lack of significance of ANP in the CCA model (Fig. S10).

HOW DOES BETA DIVERSITY CHANGE WITH ELEVATION WHEN SPECIES ARE GROUPED BY ELEVATION AND RIVER CATCHMENT AREA?—Beta diversity differed significantly between LEF and all other zones (Fig. 2 and Table S7). Beta diversity also differed significant between HEOF and three other zones (MFTLEF, MFTCF, and CF), but not between HEOF and the neighboring zones (LEOF and Páramo). All pairwise differences in beta diversity of species grouped by river catchment were significant except for two pairs: Terraba-Banano and Sixaola-Changuinola (Fig. 3 and Table S8).

ASSESSING POTENTIAL BIASES IN OUR RESULTS DUE TO SAMPLING EFFORT.—Our SAC did not approach a plateau (Fig. S13), suggesting that sample effort was insufficient for generating a comprehensive species list. A checklist for PILA (Monro *et al.*, in press), which documents ca. 3080 species, supports this conclusion.

Visual analyses of the frequency distributions revealed that the areas of high elevation (2000–3000 m of altitude) were
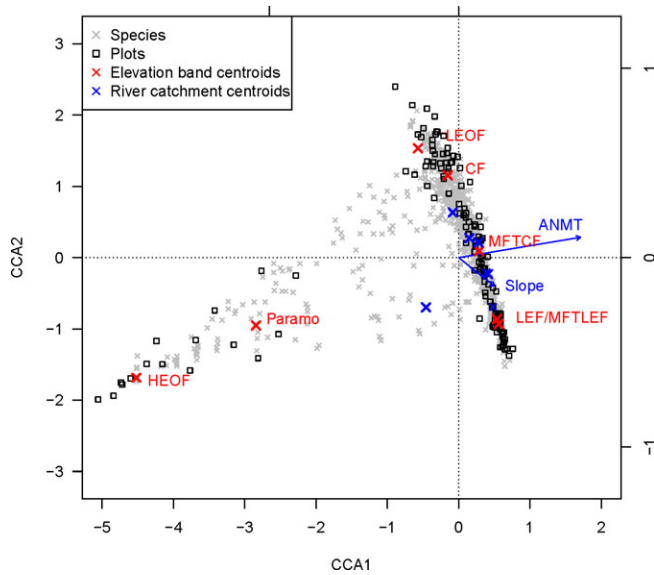
FIGURE 1. CCA ordination diagram for species showing the first two ordination axes. Elevation zones: low-elevation forest (LEF), below 700 m; (2) mixed forest in transition to low-elevation forest (MFTLEF), 701–1200 m; (3) mixed forest in transition to cloud forest (MFTCF), 1201–1600 m; (4) cloud forest (CF), 1601–2100 m; (5) low-elevation oak forest (LEOF), 2101–2600 m; (6) high-elevation oak forest (HEOF), 2601–3100 m; (7) Páramo, 3001–3500 m. The plots in HEOF and Páramo were separated by CCA from those in the low- and mid-elevation zones.
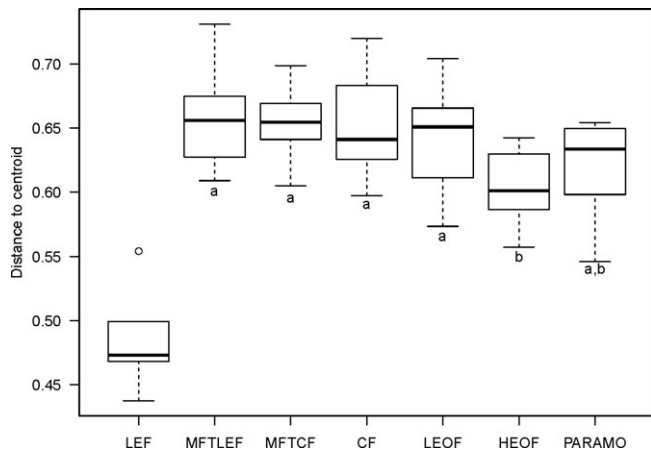
FIGURE 2. Species beta diversity in plots grouped by elevation zones. Beta-diversity analysis is based on the species presence/absence data in individual plots. Not significantly different (at 0.05 level of confidence) comparisons are indicated by the same letters. Elevation zones as in Fig. 1.

under-represented while the highest elevation range (above 3000 m of altitude) was over-represented (Fig. S14); the areas with ANMT below 17.5°C were under-represented and the areas with ANMT above 25°C were over-represented (Fig. S15); the areas with rainfall below 2500 mm and above 3750 mm were under-represented while those above 3000 mm were over-
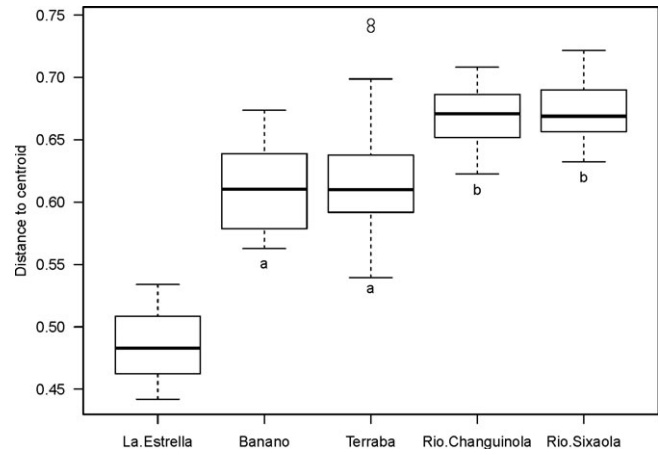

FIGURE 3. Species beta diversity in plots grouped by river catchments. Beta-diversity analysis is based on the species presence/absence data in individual plots. Not significantly different (at 0.05 level of confidence) comparisons are indicated by the same letters. Elevation zones as in Fig. 1.

represented (Fig. S16). Global values of spatial autocorrelation measured by Moran's I for species richness were different from zero (Table S9), suggesting the presence of spatial structure at the scale of the analyses.

DISCUSSION

We found that floristic studies can yield valuable classificatory information but at the scale of PILA (4000 km^2), elevation and river catchment provide a pragmatic classification that is meaningful with respect to community composition and species diversity. With respect to whether grouping by elevation or river catchment better explains variation in species composition and beta diversity, elevation was the abiotic variable that best accounted for variation in species composition and taxon diversity. River catchment was subservient to elevation in this respect. Elevation and river catchment (Monro *et al.* 2009) are practical classificatory tools because they are easy and economical to map. The inclusion of river catchment provides alignment with watershed management as an approach to resource management (Dixon & Easter 1986).

IS IT BETTER TO CLASSIFY VEGETATION IN PILA BY ELEVATION OR RIVER CATCHMENT.—Our floristic dataset supported the classification of PILA into four classes: Páramo, HEOF, mid-elevation zones (LEOF, CF, MFTCF, and MFTLEF), and LEF; apart from LEF, the classes did not differ in beta diversity. For the broad mid-elevation class, we suggest using environmental gradients combined with edaphic, hydrological/river catchment area and historical data to generate discrete classes that are informative with respect to, but not based on, direct biodiversity observations. Although forest community structure varies with changes in edaphic conditions (Clark & Clark 2000, Tuomisto *et al.* 2002), in the case of PILA, insufficient data on soils exist to support its

inclusion in a classification. Historical features, such as the presence of glaciers, are congruent with patterns recovered in the biodiversity data (discrete break at 3100 m) and represent an appropriate surrogate. We do not know, however, of any historical features that could be applied to the montane forest class; river catchment may be a good classifier for this elevation range.

SPECIES COMMUNITIES IN PILA AND THEIR CLASSIFICATION.—Surprisingly, most studies of plant diversity across elevation gradients in the tropics do not attempt to classify by species composition but rather by species richness or species turnover (beta diversity) (see Sanchez *et al.* 2013, Krömer *et al.* 2013 etc.). Our ordination confirmed that selected environmental variables, including elevation, explain 12% of the total variation in species composition. Our analysis supports the classification of PILA into four elevation classes rather than the seven proposed by Monro *et al.* (2009). These four classes are low-elevation forest (below 700 m asl), montane forest (between 700 and 2600 m asl), high-elevation oak forest (between 2600–3100 m asl), and the shrub- and herb-dominated Sub-Páramo (above 3100 m asl). Our results combine the 700–2600 m elevation zone into a single class and support the distinction of high-elevation oak forest (HEOF), which shows greatest affinity with the neighboring shrub- and herb-dominated Sub-Páramo vegetation.

Our failure to recover many discrete vegetation classes using taxonomic composition across the species-rich and physiognomically complex 700–2600 m elevation range is consistent with previous studies of tropical forest (Lieberman *et al.* 1996, Vazquez & Givnish 1998, Hartshorn 2000, Bach & Gradstein 2011). The lack of discontinuity in species composition across an elevation gradient might reflect taxon composition, at species or family ranks, changing continuously with elevation due to an absence of well-defined environmental breaks (Kessler 2000, Bach & Gradstein 2011, Sundqvist *et al.* 2013). Kessler (2000) also suggests that it is harder to detect environmental discontinuities in tropical forest at low-to-mid elevations because of their taxon richness and complexity. The basis for species assemblages remains unclear (Austin 2002) and our fragmented knowledge of species interdependence and turnover in tropical forests makes it difficult to capture assemblages at any particular point in time.

Despite difficulties in detecting discrete species assemblages across this extensive mid-elevation range, elevation classes continue to be proposed as frameworks for both conservation planning (Davis *et al.* 1997, Hartshorn 2000) and investigating diversity patterns (Rahbek 1995, 2005, Grytnes & McCain 2007, Willinghöfer *et al.* 2012, Sundqvist *et al.* 2013). This is likely for pragmatic reasons; elevation subdivisions are unambiguous and economical to apply, there is complete coverage, and they can be replicated globally (Lomolino 2001, McCain 2009). Sundqvist *et al.* (2013) also suggest that, to better predict community and ecosystem responses to climate change, there is a need for studies that observe how multiple contrasting taxa respond to elevation along the same gradient.

Our recovery of distinct forest assemblages at the 700–2600 and 2600–3100 m asl ranges corroborates the results of previous studies. For example, Lieberman *et al.* (1996) found no discontinuities across an elevational transect on the nearby Volcan Barva in Costa Rica (range 30–2600 m asl), while Bach and Gradstein (2011) found discontinuity only at the 3000/3050 interface (Bolivian Andes, range 1700–3400 m asl).

Discontinuity in species turnover and field observations supported our recovery of the distinct taxon assemblage at the 2600–3100 m asl range; although *Quercus* dominates the forest canopy across the 2100–3100 m asl range, its taxon composition differs significantly. While not suggested by broader regional classifications (Holdridge 1967, Holdridge *et al.* 1971, Davis *et al.* 1997, Hartshorn 2000), the subdivision of the 2101–3100 elevation range was also suggested by Kappelle and Van Uffelen (2006). The CCA for species (Fig. 1) suggests that HEOF is more similar to Páramo and that LEOF is more similar to the mid-elevation forest. Most noticeable was the substitution of some families in the ground story from one class to the other. Kappelle *et al.* (1995) and our data both showed substitution of Rubiaceae and Gesneriaceae terrestrial shrubs in LEOF by Ericaceae and Asteraceae terrestrial shrubs in HEOF (Figs. S2–S9). For example, we observed a transition from 42 Rubiaceae and 15 Gesneriaceae terrestrial shrub species in LEOF to one and zero species in HEOF. We also found that Rubiaceae diversity was maintained, but that it shifted from shrubby to herbaceous taxa. Kappelle *et al.* (1995) suggested that these changes in family composition in oak forest are a consequence of decreasing canopy height combined with lower air temperature and an increasing prevalence of strong winds. Our observations of forest with a canopy of 35 m at 2900 m asl (AM, pers. obs) do not wholly support such a scenario. An alternative explanation may be that HEOF represents areas recently derived from Páramo vegetation and that taxonomic affinity reflects some Páramo species persisting in HEOF. During the last glacial maximum, Páramo would have occupied the HEOF elevation rage. As glaciers receded and disappeared ca 10 KYA (Horn 1993), it would have been colonized by the tree species dominant in the adjacent HEOF (*Quercus* spp., *Vaccinium* spp., *Schefflera* spp., etc.) with shade-tolerant species remaining (*e.g.*, *Hymenophyllum fucoides*, *Macleania rupestris*, *Viburnum costaricanum*).

In addition to recovering four discrete species assemblages, we recovered river catchment as an important variable in CCA and in beta-diversity analysis. While river catchment has been demonstrated to influence species assemblages for understory herbs in lowland tropical forest at the scale of 100 km^2 (Costa *et al.* 2005), our work documents that river catchment influences entire vascular plant assemblages in the tropics at the scale of 1000 km^2. This finding warrants further research and may provide evidence of a synergy between land-use and conservation planning whereby catchment areas could represent effective spatial units for both (Chan *et al.* 2006, Pressey *et al.* 2007).

SAMPLING EFFORT AND POTENTIAL BIAS.—In the case of diversity-rich and data-poor systems, data collection costs are high and available funds low. The main limitation of the sampling design used in this study was the non-random distribution of sample

points due to logistical constraints and an attempt to sample all major catchment areas. A more appropriate sample design could have been achieved using a helicopter, at an approximate cost of US$20K per point and US$2.8 m in total.

After assessing potential biases in our results due to sampling effort, we concluded that the answers to the first (to what extent does elevation in general, and pre-defined elevation zones in particular, explain variation in species composition across sites?) and second (how does beta diversity change when species are grouped by elevation and river catchment area?) research questions were likely influenced by sampling effort. The dataset inadequately represented the annual mean temperature and annual mean precipitation gradients, although the distribution of elevation was close to that within the study area (Figs. S14–S16). The sample points are clustered in nine localities; this likely resulted in pseudo-replication or potential invalidation of the results of our statistical analysis (Hurlbert 1984). To test this assumption, we calculated Moran's I (Moran 1950) within the species richness dataset; the observed value of autocorrelation was significantly different from zero, suggesting presence of spatial structure at the scale of the data analysis. If we had confidence in plot abundance scores, hierarchical models would have been an appropriate tool to deal with pseudo-replication (Ross *et al.* 2012). Confidence in plot data would also enable testing the outcomes of constrained ordination; several random subsets of the community data would have been ordinated to see whether the basic patterns remain stable (Wilson 1981). The species area curve (Fig. S13) suggests that total sample effort and sample effort at each point were insufficient; this study recovered only 69% of documented occurrences (Monro *et al.* 2009). In addition, we probably underestimated the numbers of twiners and lianas in the lower-elevation zones because of the logistic challenges of recording high canopy species. Inadequate sampling within individual plots undermines species richness, biodiversity, and ordination analyses, as well as the results of floristic analysis within the elevation zones. Without further validation of the dataset by additional fieldwork, it is impossible to estimate the predictive power of abundance scores or evaluate the soundness of the statistical analyses.

CONCLUSION

At the scale of protected areas and national parks, our floristic dataset identifies elevation as a better classifier of vegetation than river catchment with respect to species composition and diversity. River catchment is, however, identified as having some classificatory power. Combining elevation and river catchment may help align vegetation classification with watershed management and better support the sustainable use of natural resources.

ACKNOWLEDGMENTS

DATA AVAILABILITY

Data available in the Dryad Repository: https://doi.org/10.5061/dryad.424b2 (Monro *et al.* 2017), and the Figshare Digital Repository: (https://doi.org/10.6084/m9.figshare.4964849.v1).

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

TABLE S1. *Description of the nine field sites.*

TABLE S2. *Information on families.*

TABLE S3. *Results of DCA performed on species matrix.*

TABLE S4. *Direction cosines and squared correlation coefficients of the vectors and factors fitted into species community ordination.*

TABLE S5. *Results of the permutation test for marginal effects of terms in the species model.*

TABLE S6. *Minimal adequate CCA model for species.*

TABLE S7. *Results of the Tukey HSD test for beta diversity of species grouped by elevation zones.*

TABLE S8. *Results of the Tukey HSD test for beta diversity of species grouped by River Catchment.*

TABLE S9. *Global values of spatial autocorrelation measured by Moran's I for species richness data.*

FIGURE S1. Map of the study area.

FIGURE S2–S6. Altitudinal distribution for Rubiaceae (Fig. S2); Araceae (Fig. S3); Arecaceae (Fig. S4); Gesneriaceae (Fig. S5); Asteraceae (Fig. S6).

FIGURE S7–S9. Altitudinal distribution for Solanaceae (Fig. S7): Ericaceae (Fig. S8); Urticaceae (Fig. S9).

FIGURE S10–S12. Graphical representation of the results of DCA performed on species community dataset.

FIGURE S13. Species accumulation curve.

FIGURE S14–S16. Histograms showing density distributions of the area of PILA.

LITERATURE CITED

ANDERSON, M. J., K. E. ELLINGSEN, AND B. H. MCARDLE. 2006. Multivariate dispersion as a measure of beta diversity. Ecol. Lett. 9: 683–693.

AUSTIN, M. P. 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. Ecol. Model. 157: 101–118.

AUTORIDAD NACIONAL DEL AMBIENTE. 2004. Plan de Manejo del Parque Internacional La Amistad/Corredor Biológico Mesoamericano del Atlántico Panameño. Autoridad Nacional del Ambiente, Panamá.

BACH, K., AND S. R. GRADSTEIN. 2011. A comparison of six methods to detect altitudinal belts of vegetation in tropical mountains. Ecotropica 17: 1–13.

BORGE, C. C. 2004. Plan de Manejo Parque Internacional La Amistad Talamanca [Versión Final]. SEDEr, The Nature Conservancy, Parks in Peril, USAID, Ministerio del Ambiente y Energía, San José, Costa Rica.

CENTRAL AMERICAN COMMISSION FOR ENVIRONMENT AND DEVELOPMENT. 2016. http://www.ccad.ws/antecedentes.html, accessed June 16, 2006, the Ecomapas Project, http://www.inbio.ac.cr/ecomapas/ecomapas/ecomapas.html, last accessed January 5, 2016.

CHAN, K. M. A., M. R. SHAW, D. R. CAMERON, E. C. UNDERWOOD, AND G. C. DAILY. 2006. Conservation planning for ecosystem services. PLoS Biol. 4: e379.

CHAVE, J. 2008. Spatial variation in tree species composition across tropical forests: pattern and process. In W. P. Carson, and S. A. Schnitzer (Eds.). Tropical forest community ecology, pp. 11–30. Wiley-Blackwell, Oxford, UK.

CHUST, G., J. CHAVE, R. CONDIT, S. AGUILAR, S. LAO, R. PÉREZ, AND J. FRANKLIN. 2006. Determinants and spatial modeling of tree β-diversity in a tropical forest landscape in Panama. J. Veg. Sc. 17: 83–92.

CLARK, D. B., AND D. A. CLARK. 2000. Landscape-scale variation in forest structure and biomass in a tropical rain forest. Forest Ecol. Manag. 137: 185–198.

COSTA, F. R., W. E. MAGNUSSON, AND R. C. LUIZAO. 2005. Mesoscale distribution patterns of Amazonian understorey herbs in relation to topography, soil and watersheds. J. Ecol. 93: 863–878.

DAVIS, S. D., V. H. HEYWOOD, O. HERRERA-MACBRYDE, J. VILLA-LOBOS, AND A. HAMILTON. (eds.). 1997. Centres of plant diversity: A guide and strategy for their conservation. Volume 3: The Americas. IUCN Publications Unit, Cambridge, UK.

DEVICTOR, V., D. MOUILLOT, C. MEYNARD, F. JIGUET, W. THUILLER, AND N. MOUQUET. 2010. Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: the need for integrative conservation strategies in a changing world. Ecol. Lett. 13: 1030–1040.

DIXON, J. A., AND K. W. EASTER. 1986. Integrated watershed management: an approach to resource management. In K. W. Easton, J. A. Dixon, and M. M. Hufschmidt (Eds.). Watershed resources management: An integrated framework with studies from Asia and the pacific, pp. 3–16. Westview Press, Honolulu, Hawaii.

ESA Vegetation Classification Panel. 2015. How can a national vegetation classification help ecological research and management? Front. Ecol. Environ. 13: 185–186.

EVENS, J., AND T. KEELER-WOLF. 2014. Vegetation mapping is essential in conserving rare desert plant species and plant communities. Fremontia 42: 11–14.

FERRIER, S. 2002. Mapping spatial pattern in biodiversity for regional conservation planning: where to from here? Sys. Biol. 51: 331–363.

FRANKLIN, J. 1995. Predictive vegetation mapping: geographic modelling of biospatial patterns in relation to environmental gradients. Prog. Phys. Geog. 19: 474–499.

GIVNISH, T. J. 1999. On the causes of gradients in tropical tree diversity. J. Ecol. 87: 193–210.

GÓMEZ, L. D. 1986. Vegetación y Clima de Costa Rica, Vol. 1. Universidad Estatal A Distancia, San José, Costa Rica.

GOTELLLI, N. J., AND R. K. COLWELL. 2001. Quantifying biodiversity: procedures and pitfalls in measurement and comparison of species richness. Ecol. Lett. 4: 379–391.

GRYTNES, J. A., AND C. M. MCCAIN. 2007. Elevational trends in biodiversity. In S. Levin (Ed.). Encyclopaedia of biodiversity, pp. 1–8. Elsevier, New York, NY.

GUISAN, A., AND N. E. ZIMMERMANN. 2000. Predictive habitat distribution models in ecology. Ecol. Modell. 135: 147–186.

HARTSHORN, G. S. 2000. Tropical and subtropical vegetation of Mesoamerica. In M. G. Barbour, and W. D. Billings (Eds.). North American terrestrial vegetation, pp. 623–660. Cambridge Universtiy Press, Cambridge, UK.

HERRERA, W. 1986. Clima de Costa Rica. Editorial Universidad Estatal a Distancia (UNED), San Jose, Costa Rica.

HIJMANS, R. J., S. E. CAMERON, J. L. PARRA, P. G. JONES, AND A. JARVIS. 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25: 1965–1978.

HILL, M. O., AND H. G. GAUCH. 1980. Detrended correspondence analysis: an improved ordination technique. Vegetatio 42: 47–58.

HOLDRIDGE, L. R. 1967. Life zone ecology. Tropical Science Centre, San Jose, Costa Rica.

HOLDRIDGE, L. R., W. C. GRENKE, W. H. HATHEWAY, T. LIANG, AND J. A. TOSI. 1971. Forest environments in the tropical life zone. Pergamon Press, Oxford, UK.

HOMEIER, J., S.-W. BRECKLE, S. GÜNTER, R. T. ROLLENBECK, AND C. LEUSCHNER. 2010. Tree diversity, forest structure and productivity along altitudinal and topographical gradients in a species-rich ecuadorian montane rain forest. Biotropica 42: 140–148.

HORN, S. P. 1993. Postglacial vegetation and fire history in the Chirripó Páramo of Costa Rica. Quat. Res. 40: 107–116.

HUBBELL, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, NJ.

HUMBOLD, A., AND E. BONPLAND. 2008. Essay on the geography of plants. The University of Chicago Press, Chicago and London.

HURLBERT, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54: 187–211.

KAPPELLE, M., M. CASTRO, H. ACEVEDO, P. CORDERO, L. GONZÁLEZ, E. MÉNDEZ, AND H. MONGE. 2002. A rapid method in ecosystem mapping and monitoring as a tool for managing Costa Rican ecosystem health. In D. J. Rapport, W. L. Lasley, D. E. Rolston, N. O. Nielsen, C. O. Qualset, and A. B. Damania (Eds.). Managing for healthy ecosystems, pp. 449–457. Lewis Publishers, Boca Raton, FL.

KAPPELLE, M., J.-G. V. UFFELEN, AND A. M. CLEEF. 1995. Altitudinal zonation of montane quercus forests along two transects in Chirripó National Park, Costa Rica. Vegetatio 119: 119–153.

KAPPELLE, M., AND J. G. VAN UFFELEN. 2006. Altitudinal zonation of montane oak forests along climate and soil gradients in Costa Rica. In M. Kappelle (Ed.). Ecology and conservation of neotropical montane Oak forests, pp. 39–54. Springer, Berlin, Heidelberg.

KAPPELLE, M., AND N. ZAMORA. 1995. Changes in woody species richness along an altitudinal gradient in Talamancan montane Quercus forests, Costa Rica. In S. P. Churchil, H. Balslev, E. Forero, and J. L. Luteyn (Eds.). Biodiversity and conservation of Neotropical montane forests, pp. 135–148. New York Botanical Garden Press, Bronx, NY.

KESSLER, M. 2000. Altitudinal zonation of Andean cryptogam communities. J. Biogeogr. 27: 275–282.

KRÖMER, T., A. ACEBEY, J. KLUGE, AND M. KESSLER. 2013. Effects of altitude and climate in determining elevational plant species richness patterns: a case study from Los Tuxtlas, Mexico. Flora 208: 197–210.

LIEBERMAN, D., M. LIEBERAMN, R. PERALTA, AND G. S. HARTSHORN. 1996. Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica. J. Ecol. 84: 137–152.

LINDENMAYER, D. B., R. J. HOBBS, R. MONTAGUE-DRAKE, J. ALEXANDRA, A. BENNETT, M. BURGMAN, P. CALE, A. CALHOUN, V. CRAMER, P. CULLEN, D. DRISCOLL, L. FAHRIG, J. FISCHER, J. FRANKLIN, Y. HAILA, M. HUNTER, P. GIBBONS, S. LAKE, G. LUCK, C. MACGREGOR, S. MCIN- TYRE, R.

Mac Nally, A. Manning, J. Miller, H. Mooney, R. Noss, H. Possingham, D. Saunders, F. Schmiegelow, M. Scott, D. Sim-Berloff, T. Sisk, G. Tabor, B. Walker, J. Wiens, J. Woinarski, and E. Zavaleta. 2008. A checklist for ecological management of landscapes for conservation. Ecol. Lett. 11: 78–91.

Lomolino, M. 2001. Elevation Gradients of Species-Density: Historical and Prospective Views. Global Ecology and Biogeography 10: 3–13.

Margules, C. R., and R. L. Pressey. 2000. Systematic conservation planning. Nature 405: 243–253.

McCain, C. M. 2009. Global analysis of bird elevational diversity. Global Ecol. Biogeogr. 18: 346–360.

Monro, A. K., N. Bystriakova, and F. González. 2017. Data from: Are landscape attributes a useful shortcut for classifying vegetation in the Tropics? A case study of La Amistad International Park. Dryad Digital Repository. https://doi.org/10.5061/dryad. 424b2

Monro, A. K., O. Chacón, N. Zamora, N. Brown, F. González, D. Santamaría, and M. Correa. 2009. Zonas de Biodiversidad del Parque Internacional La Amistad (PILA) Costa Rica - Panama. The Natural History Museum, London and Instituto Nacional de Biodiversidad, Santo Domingo de Herencia, Universidad de Panama, Panama City, FL.

Monro, A. K., F. González, D. Santamaría, O. Chacón, A. Rodríguez, D. Solano, N. Zamora, and M. Correa. In press. A first checklist to the vascular plants of La Amistad International Park (PILA), Costa Rica Panama. Phytotaxa 2017.

Moran, P. A. P. 1950. Notes on Continuous Stochastic Phenomena. Biometrika 37: 17–23.

Pressey, R. L., M. Cabeza, M. E. Watts, R. M. Cowling, and K. A. Wilson. 2007. Conservation planning in a changing world. Trends Ecol. Evol. 22: 583–592.

Rahbek, C. 1995. The elevational gradient of species richness: a uniform pattern? Ecography 18: 200–205.

Rahbek, C. 2005. The role of spatial scale and the perception of large-scale species richness patterns. Ecol. Lett. 8: 224–239.

Ramos-G., J., A. V. Rodríguez-T., L. B. Flores-C., F. N. Rivera-O., M. S. Vásquez-M., A. Ponce-M., and E. T. Wang. 2016. Diversity of fungal endophytes from the medicinal plant *Dendropanax arboreus* in a protected area of Mexico. Ann. Microbiol. 66: 991–1002.

Ricotta, C., M. L. Carranza, and G. Avena. 2002. Computing β-diversity from species-area curves. Basic Appl. Ecol. 3: 15–18.

Ross, B. E., M. B. Hooten, and D. N. Koons. 2012. An accessible method for implementing hierarchical models with spatio-temporal abundance data. PLoS ONE 7: e49395.

Royston, J. 1982. An Extension of Shapiro and Wilk's W Test for Normality to Large Samples. Journal of the Royal Statistical Society. Series C (Applied Statistics) 31(2): 115–124. doi:10.2307/2347973.

Sanchez, M., F. Pedroni, P. V. Eisenlohr, and A. T. Oliveira-Filho. 2013. Changes in tree community composition and structure of Atlantic rain forest on a slope of the Serra do Mar range, southeastern Brazil, from near sea level to 1000 m of altitude. Flora 208: 184–196.

Sundqvist, M. K., N. J. Sanders, and D. A. Wardle. 2013. Community and ecosystem responses to elevational gradients: processes, mechanisms, and insights for global change. Ann. Rev. Ecol. Evol. Sys. 44: 261–280.

Syrbe, R.-U., E. Michel, and U. Walz. 2013. Structural indicators for the assessment of biodiversity and their connection to the richness of avifauna. Ecol. Ind. 31: 89–98.

Ter Braak, C. J. F. 1986. Canonical correspondence analysis: a new eigenvecor technique for multivariate direct gradient analysis. Ecology 67: 1167–1179.

Tosi, J. A. 1969. Mapa ecológico, República de Costa Rica: según la clasificación de zonas de vida del mundo de L. R. Holdridge. Centro de Ciencias Tropicales, San José, Costa Rica.

Tosi, J. A. 1971. Zonas de vida: Una base ecológica para las investigaciones silvícolas e investigación forestal en la República de Panamá. United Nations Development Programme-Food and Agriculture Organization of the United Nations, Technical Report.

Tuomisto, H., K. Ruokolainen, A. D. Poulsen, R. C. Moran, C. Quintana, G. Canas, and J. Celi. 2002. Distribution and diversity of pteridophytes and Melasomataceae along edaphic gradients in Yasuni National Park, Ecuadorian Amazonia. Biotropica 34: 516–533.

Vazquez, J. A., and T. J. Givnish. 1998. Altitudinal gradients in tropical forest composition, structure and diversity in the Sierra de Manantlan. J. Ecol. 86: 999–1020.

Walz, U. 2015. Indicators to monitor the structural diversity of landscapes. Ecol. Model. 295: 88–106.

Warren, D. L., M. Cardillo, D. F. Rosauer, and D. I. Bolnick. 2014. Mistaking geography for biology: inferring processes from species distributions. Trends Ecol. Evol. 29: 572–580.

Willinghöfer, S., D. Cicuzza, and M. Kessler. 2012. Elevational diversity of rainforest herbs: when the whole is less than the sum of its parts. Plant Ecol. 213: 407–418.

Wilson, M. V. 1981. A statistical test of the accuracy and consistency of ordinations. Ecology 62: 8–12.

Zamora, N. 2008. Unidades fitogeográficas para la clasificación de ecosistemas terrestres en Costa Rica. Recursos Naturales y Ambiente 54: 14–20.