

Metacommunity structure of tropical forest along an elevation gradient in Puerto Rico

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Abstract: The development of metacommunity theory, which suggests that the diversity and composition of communities is influenced by interactions with other communities, has produced new tools for evaluating patterns of community change along environmental gradients. These techniques were used to examine how plant communities changed along elevation gradients in montane tropical forests. Two transects of 0.1-ha vegetation plots were established every 50 m in elevation in the mountains of eastern Puerto Rico. The transects ranged from 300 m to 1000 m asl and 400 m to 900 m. In each plot, all free-standing woody stems greater than 1 cm in diameter at 130 cm in height were marked, measured and identified. Additional data on three similar transects were taken from the literature. The upper or lower boundaries of species ranges were significantly clumped along all five transects. Coherence, a measure of the number of gaps in species distributions, was also significant across all transects, and three transects showed significant, albeit low, nestedness. Four sites had significant species turnover. These results suggest that metacommunity techniques can be useful in searching for patterns of community change present in montane tropical forests.

Key Words: coherence, elevation, metacommunity, montane communities, nestedness, Puerto Rico, species boundaries

INTRODUCTION

Broad interest in how plant communities change along environmental gradients was launched by the dispute between Clements (1916, 1936) and Gleason (1926) about whether such communities change sharply or continuously. Gleason's (1926) more continuous and individualist view has come to dominate ecological thinking, largely because of analyses of species distributions and boundaries in a variety of habitats (Austin 1985, Austin & Smith 1989, McIntosh 1967, 1975; Whittaker 1967). Despite this consensus, the structure of tropical montane plant communities along elevation gradients remains an area of active debate. A variety of older studies and reviews have argued that sharp ecotones between forest communities are common on tropical mountains, with relatively abrupt shifts in plant species composition and physiognomy (Grubb 1977, Grubb & Whitmore 1966, Richards 1952, 1996; Whitmore 1984). More recent studies have bolstered

this view, suggesting that sharp ecotones can occur because of shifts in underlying soils, sharp changes in humidity associated with persistent cloud cover, or differences in disturbance histories (Fernandez-Palacios & de Nicolas 1995, Hemp 2006, Kitayama 1992, Woldu *et al.* 1989). In contrast, numerous studies have found evidence for more gradual changes in plant communities along tropical elevation gradients, with no evidence of discrete ecotones (Hamilton 1975, Lieberman *et al.* 1996, Lovett 1996, 1998; Vázquez & Givnish 1998). Ashton (2003) provides one intermediate view between these two perspectives, concluding that the abruptness of community transitions may depend on which types of transitions (e.g. between lower montane forest to upper montane forest) are being studied.

The development of metacommunity theory has provided new tools for addressing how tropical montane forests vary with elevation (Holyoak *et al.* 2005, Leibold *et al.* 2004). The metacommunity perspective stresses that communities are connected, and that their diversity and composition can be influenced by interactions with neighbouring communities through dispersal or migration (Leibold *et al.* 2004). Plant communities along an elevation gradient are clearly a metacommunity,

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as they can potentially exchange species through dispersal.

In this study, the metacommunity structure of tropical montane forests was examined following the methods of Hoagland & Collins (1997) and Leibold & Mikkelsen (2002). These approaches use aspects of species distributions along environmental gradients as a way of assessing the broader metacommunity structure and discriminating between alternative, hypothetical species patterns (Hoagland & Collins 1997, Leibold & Mikkelsen 2002).

Hoagland & Collins (1997) proposed a family of models based on three quantifiable features of species distributions along a gradient: (1) the clustering of species boundaries; (2) the clustering of the modes of species abundances; and (3) the nestedness of species distributions, which measures the extent to which species-poor sites are subsets of species-rich sites. In this approach, a metacommunity is examined for the presence or absence of each of these three features. Leibold & Mikkelsen (2002) suggested a similar approach that assessed metacommunity structure using three indices. The first, coherence, is a measure of the number of gaps, or embedded absences, within the distribution of a species along a gradient. A species with many absences in its range has a less coherent distribution than one with no gaps. The second index used by Leibold & Mikkelsen (2002) is species turnover, which is a count of the number of times species replace each other along the gradient. This index measures the extent to which species appear to be 'avoiding' each other along a gradient. Species turnover is also the inverse of nestedness (Leibold & Mikkelsen 2002). The third index is the clustering of species boundaries, which is also used by Hoagland & Collins (1997). Both methods provide a way of comparing the structure of metacommunities from different sites.

This study had two objectives. The first was to apply these metacommunity techniques to determine how montane forest communities change along elevation gradients and to describe in more detail how these transitions were occurring. Data for this objective came from two elevation transects of 0.1-ha plots established in the Luquillo Mountains of eastern Puerto Rico. The second objective was to see if any patterns observed in the current study were also apparent in earlier studies from the literature. Any similarities may mean that the same factors are structuring montane tropical forests across regions.

METHODS

Study area

The Luquillo Experimental Forest (LEF) (18° 19.6'N, 65° 49.4'W) is located in eastern Puerto Rico and is ideal for this study because the flora is well-known, the sites are relatively accessible, and the history of human

disturbance in the area has been extensively documented (Brown *et al.* 1983). The LEF covers 11,330 ha and ranges in elevation from 100 to 1075 m asl (Brown *et al.* 1983; Figure 1). At 350 m, temperatures average 24.5 °C in September, the warmest month, and 21.0 °C in January, the coolest (Brown *et al.* 1983). At 1051 m temperatures are, on average, about 4.5 °C lower (Brown *et al.* 1983). Mean annual precipitation increases with elevation from about 2300 mm at 100 m to 4700 mm at 700 m but then declines to 3600 mm at 1051 m (Brown *et al.* 1983). At all elevations rainfall averages more than 100 mm every month of the year. Precipitation is also higher on the north-facing, windward side of the mountains than on the south-facing, leeward side (Weaver 1991). At upper elevations, the forest is frequently enveloped by clouds, reducing mean annual solar radiation to approximately 63% of nearby coastal areas (Briscoe 1966).

The soils in the LEF are derived from volcanoclastic sediments, except in one area where a quartz diorite intrusion is present (Sieders 1971; Figure 1). Volcanoclastic sediments weather to dense clays (Ultisols), whereas soils derived from diorite are sandier (Beinroth 1982). With increasing elevation, soils typically become saturated and have a higher carbon content but lower bulk density along with reduced concentrations of phosphorus and iron (McGroddy & Silver 2000, Silver *et al.* 1999). McGroddy & Silver (2000) attributed much of the variation in soil characteristics to frequent anaerobic periods at higher elevations.

The LEF has been managed by the U.S. Forest Service since 1917. Recent human disturbance peaked in the 1930s when logging and farming occurred at lower elevations (García-Montiel & Scatena 1994, Thompson *et al.* 2002). Minor harvesting for timber management and charcoal production continued at low elevations until the 1970s (García-Montiel & Scatena 1994, Zimmerman *et al.* 1994). There were no obvious signs of human disturbance at any of the sites in this study.

Hurricanes are the most important form of natural disturbance in Puerto Rico, with high winds causing extensive direct damage to the vegetation and the accompanying rainfall leading to landslides, especially at upper elevations (Scatena & Larsen 1991, Walker *et al.* 1991, Zimmerman *et al.* 1994). Hurricane Hugo made landfall in north-east Puerto Rico in September 1989, and Hurricane Georges hit south-eastern Puerto Rico in September 1998, 3 y before this study. No attempt was made to specifically assess the influence of hurricanes on forest structure with elevation. However, none of the study sites showed signs of recent landslides or extensive canopy damage.

Plots

Foster *et al.* (1999) analysed photos of the LEF taken in 1936, during the period of greatest human disturbance to

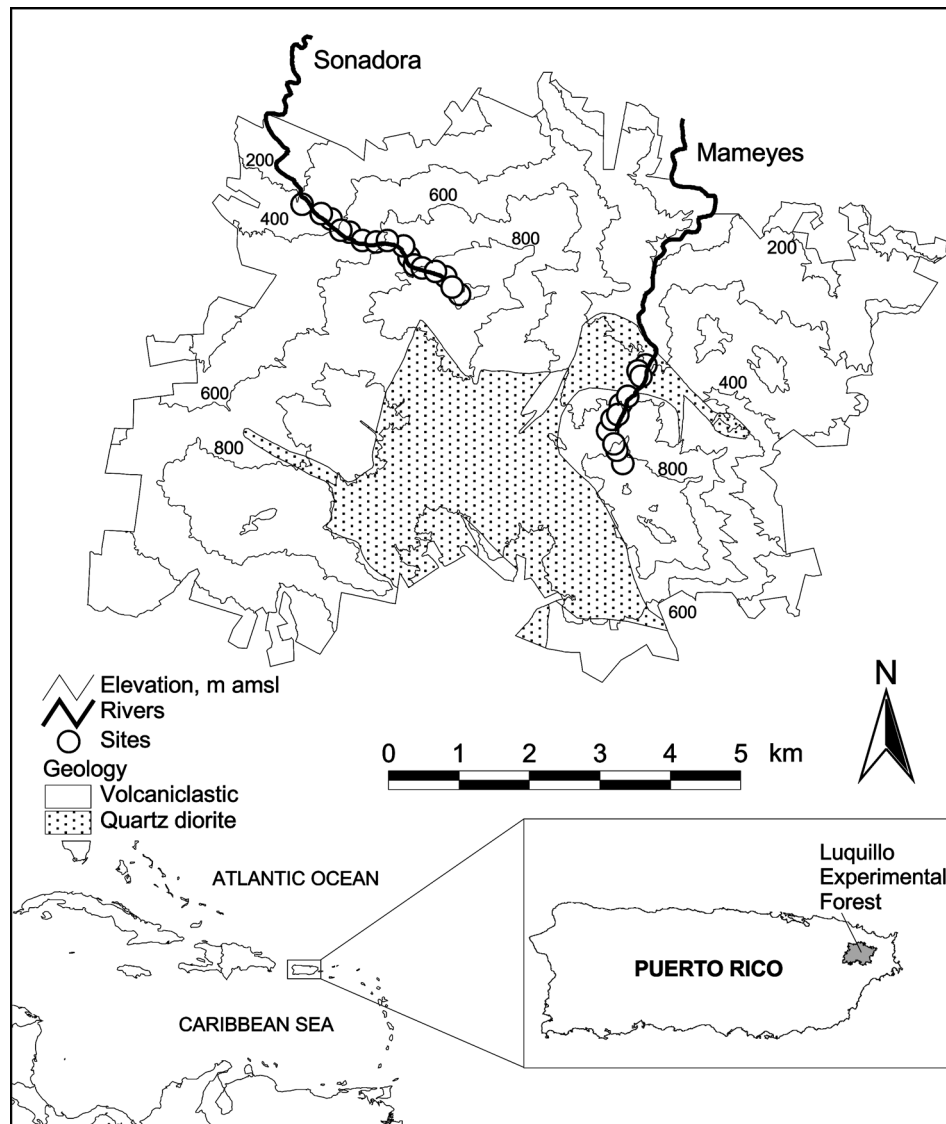


Figure 1. Luquillo Experimental Forest, Puerto Rico. Points indicate the locations of the permanent vegetation plots in the watersheds of the Sonadora and Mameyes Rivers.

the forest and classified areas by forest type and per cent cover. Based on these assessments, sites for the plots were selected from areas that were in the 80–100% cover class in 1936 and were not considered secondary forest or were otherwise obviously disturbed.

From September 2001 to July 2002, we established two transects of permanent vegetation plots in the watersheds of the Sonadora and Mameyes Rivers in the LEF. The Sonadora watershed faces north-west and has clayey soils, whereas the Mameyes runs northward and has sandier soils below 550 m and clayey soils above (Figure 1). Each 0.1-ha vegetation plot was 50 × 20 m, with the long side perpendicular to the slope. Plots were placed every 50 m in elevation. The coordinates and elevation for the plots were determined using a GPS unit (Trimble TDC 1, Trimble Co., Sunnyvale, CA, USA). All of the plots were located on the main slope of the mountain and out of ravines formed by

rivers. No effort was made to avoid gaps in the canopy, intermittent streams or other variations in the forest, but no plot included a permanent stream. The highest plot on each transect was determined by the elevation at the top of each watershed, and the lowest plots were limited by disturbed areas further down the mountains.

In each plot, all free-standing woody stems at least 1.0 cm in diameter at 130 cm in height were permanently tagged and identified. The flora of the LEF is well-known, and botanists from the University of Puerto Rico confirmed identifications of rare species.

Gradient analysis

Species distributions along the transects were evaluated following procedures outlined in Hoagland & Collins (1997) and Leibold & Mikkelsen (2002). We analysed

the clustering of the upper and lower boundaries of species ranges and the clustering of modes of species abundances with the G-test (Sokal & Rohlf 1995). The number of boundaries or modes observed in each plot was compared with an expected number derived from the number of species in each plot. We used this approach (rather than Morisita's index employed by Hoagland & Collins, 1997) because plots with more species would be expected to have more boundaries and modes, all else being equal, and this allowed us to test for the presence of clusters while controlling for differences in species richness. We evaluated the clustering of upper and lower species boundaries separately, since the locations of boundaries may be affected by different factors. We also assumed that species present in the highest plots were not at their upper boundaries, and that those in the lowest plots were not at their lower boundaries, and thus they were not included in the analysis.

The nestedness of species distributions along each transect was calculated using the method of Wright & Reeves (1992), as recommended by Hoagland & Collins (1997). This involves the calculation of two metrics, N_c and C . The former is a measure of the number of times the presence of a species at a site accurately predicts its presence at sites with more species. If sites were perfectly nested, the species from each site is a subset of the next most diverse site. Since the size of N_c is positively related to the number of species and sites, Wright & Reeves (1992) devised a standardized measure C , or relative nestedness index, that ranges from 0, where nestedness is not different from random, to 1, for perfect nestedness. Negative values of C can occur when nestedness is less than expected from random. Wright & Reeves (1992) suggest evaluating the significance of either C or N_c with Cochran's Q statistic.

We followed Leibold & Mikkelsen (2002) in evaluating species turnover, which can be determined from the number of species replacements in a site by species matrix. A replacement occurs when two species have distributions that are offset by one plot. This result is compared with a null model in which species ranges are rearranged at random across the sites. Significance is determined by comparing the number of replacements in the data matrix after ordination by reciprocal averaging with the expected number based on 200 iterations. If fewer replacements than expected are found, then the distribution is highly nested (Leibold & Mikkelsen 2002).

In the approach of Leibold & Mikkelsen (2002), coherence is measured in an ordinated species-by-site matrix by counting the number of embedded absences or times that a species is absent within its range. The more holes there are in the range of a species across a series of plots, the less coherent is its distribution. To determine if this number of absences is unexpectedly large or small, a comparison is made of the actual

number of embedded absences with an expected number based on 200 iterations of a null model. In each iteration of the null model, the matrix of species by sites is rearranged at random, re-ordinated, and the number of embedded absences is counted (Leibold & Mikkelsen 2002). Significance is evaluated by comparing the number of embedded absences in the ordinated data with the expected number based on the null model.

Comparison with other transects

We analysed data from three previously published studies on tropical montane vegetation gradients. In the first, Lieberman *et al.* (1996) established a transect on Volcan Barva in north-east Costa Rica that consisted of eleven 1-ha plots at irregular intervals from 100–2600 m asl. Unlike the present study, the Volcan Barva census had a minimum stem size of 10 cm dbh and included woody lianas. We used data from Appendix 1 of Lieberman *et al.* (1996). In the second study, Kappelle *et al.* (1995) set up two transects in Chirripó National Park in southern Costa Rica. These transects consisted of 0.05-ha plots every 100 m in elevation in mature *Quercus* forests. In the plots, the canopy cover of all trees, shrubs, herbs and bryophytes was estimated for each species. In our analysis of Kappelle *et al.* (1995) we used data from the 'Atlantic' transect (from their Table 4a), which ranged from 2000–3100 m in elevation. In the third study, Vázquez & Givnish (1998) established 0.1-ha study sites, consisting of ten 0.01-ha circular plots from 1500–2500 m in the Sierra de Manantlán Biosphere Reserve in Jalisco, Mexico. Presence/absence data of all vascular plants were recorded in each plot, and all woody stems greater than 2.5 cm dbh were measured. A complete summary of the data by species is not provided, limiting the analyses to the clustering of species boundaries using numbers derived from their Table 1 and Figure 3.

RESULTS

Sonadora and Mameyes transects

Fifteen 0.1-ha plots were set up along the Sonadora transect, which ranged in elevation from 300–1000 m. A total 6562 stems of 99 species were marked. The Mameyes transect included 11 plots from 400–900 m, with 5799 stems of 77 species. (Details on stem density and basal area will be published elsewhere.) Across both transects, a total of 13 stems of three non-native species were identified. These species were excluded from the analyses. In addition, the analyses did not include 54 native species with four or fewer stems, including 30 species represented by a single individual.

Table 1. P values from the gradient analysis for the clustering of upper and lower boundaries of species ranges, modes of species abundances, the degree of nestedness, species turnover and coherence. The Sonadora and Mameyes transects were located in eastern Puerto Rico (present study); the Volcan Barva transect was in north-eastern Costa Rica (Lieberman *et al.* 1996), the Chirripó transect was in central Costa Rica (Kappelle *et al.* 1995); and the Sierra de Manantlán transect was in south-west Mexico (Vázquez & Givnish 1998). n.a. = data not available.

Transect	Upper boundaries	Lower boundaries	Modes	Nestedness	Species turnover	Coherence
Sonadora	< 0.001	0.98	0.70	0.005	< 0.001	< 0.001
Mameyes	0.015	0.92	0.15	0.005	< 0.001	< 0.001
Volcan Barva	< 0.001	0.10	0.03	< 0.001 [†]	0.009	< 0.001
Chirripó	0.075	0.004	0.82	< 0.001	< 0.001	< 0.001
Sierra de Manantlán	0.020	0.0002	n.a.	n.a.	n.a.	n.a.

[†]Volcan Barva transect was significantly anti-nested.

The uphill boundaries of species distributions were significantly clustered on both the Sonadora and Mameyes transects (Table 1, Figure 2). On the Sonadora, the upper boundaries formed three distinct peaks at 500, 700 and 900 m, suggesting discontinuities in the forest community immediately above those elevations. On the Mameyes, only one distinct cluster was present, at 850 m, with smaller peaks at 700 and 750 m. In contrast, the lower boundaries of species ranges were not significantly clustered on either the Sonadora or the Mameyes. Overall, there were fewer lower boundaries than upper boundaries, as many species continued further down the mountain than our lowest plots.

Though the modes of species abundances fluctuated considerably across plots, they were not significantly clustered along either transect (Table 1). The patterns seen in the modes largely reflected differences in species number across the plots.

Species distributions were significantly nested for both transects, suggesting that the species composition of species-poor plots were subsets of species-rich plots (Table 1). In practice, species richness declined with elevation, meaning that the composition of high-elevation plots had some species from the species-rich lower-elevation plots. However, the relative nestedness index values for both transects were rather low ($C = 0.20$ for the Sonadora transect; $C = 0.22$ for the Mameyes) and may be attributed to the presence of a few widespread species being present in most of the plots.

Species turnover was also significant for both transects (Table 1). There was a tendency for the ranges of species to be offset from one another, at least when compared to a null model. Another interpretation of this result is that there was enough change in species composition in the plots that the sites with fewer species were not simply subsets of the more species-rich plots – that the sites were anti-nested (Table 1).

Species distributions along both transects were also significantly coherent (Table 1). This indicates that there were fewer embedded absences, or gaps in the species

distributions, than expected from randomly generated models.

Other tropical montane transects

For the Volcan Barva transect (Lieberman *et al.* 1996), the upper boundaries were significantly clustered, though the lower boundaries were not (Table 1, Figure 3). Clusters of upper boundaries occurred at 750 m and 1000 m and again at 2000 m. The 750-m cluster coincides with a shift in the sampling increment from 200 m to 250 m, though it seems unlikely that an additional 50 m in elevation would in itself result in a more than doubling of the number of upper boundaries. Modes of species abundances were also significantly clustered, with a peak at the 300-m plot and a distinct depression at the 1500-m plot.

The relative nestedness index for this transect was negative ($C = -0.15$), indicating anti-nested distributions. This result is congruent with the measure of species turnover, which found that the actual number of replacements in species distributions was higher than expected, again indicating anti-nestedness (Table 1). Finally, the species distributions on the Volcan Barva transect were significantly coherent (Table 1).

Unlike the previous transects, plant species on the Chirripó transect (Kappelle *et al.* 1995) had significantly clustered lower boundaries, but the upper boundaries were not clustered (Table 1, Figure 4). Modes were not significantly clustered. Species distributions were significantly nested, though as with the other transects the level of nestedness was low ($C = 0.10$). The measure of species turnover found that species replacements were significantly higher than expected by chance, again indicating anti-nestedness.

Finally, the Sierra de Manantlán transect (Vázquez & Givnish 1998) showed significant clustering of both upper and lower boundaries of species distributions, though the clustering of the lower boundaries was more pronounced (Figure 5).

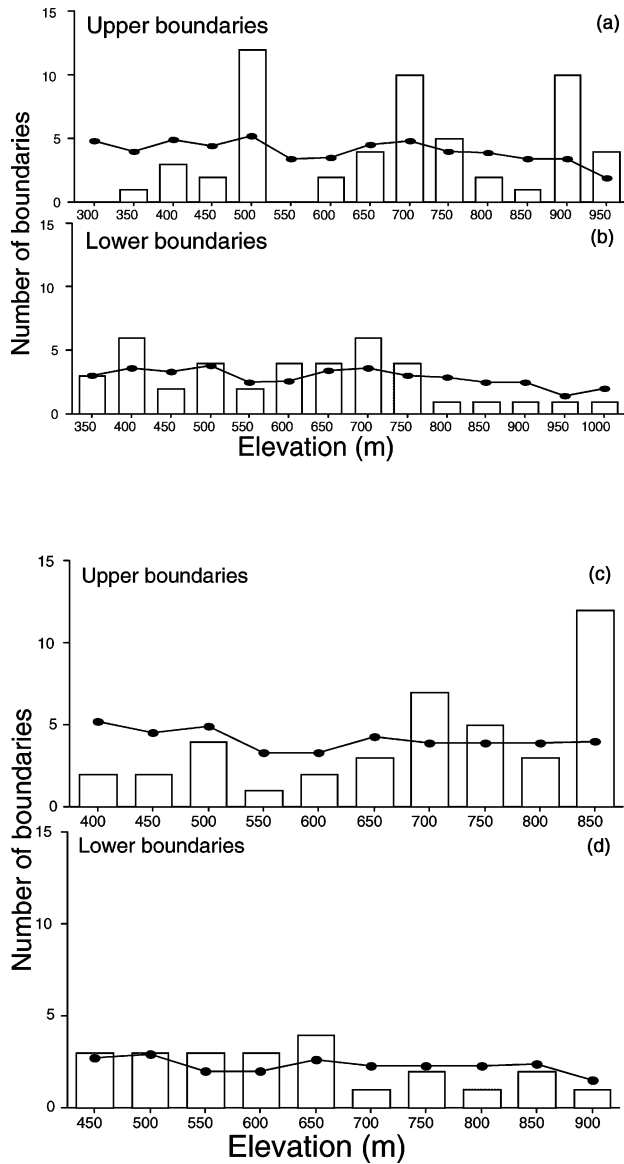


Figure 2. Number of species having upper or lower boundaries in plots along the Sonadora (a & b) and the Mameyes (c & d) transects. For both transects, upper boundaries were significantly clustered, while lower boundaries were not. Lines on the figures indicate the expected number of boundaries based on the number of species in the plot and the total number of boundaries.

DISCUSSION

The analyses of five vegetation transects from four neotropical sites showed that tropical montane forests have considerable metacommunity structure, though there was some variation in this structure across sites. All five transects showed significant clustering of species boundaries, though the patterns differed. Three transects had clustering of upper boundaries but not lower, one transect exhibited the reverse pattern, and the final had clustering of both upper and lower boundaries. Such

boundary clusters have been reported previously from a variety of temperate habitats. For example, Auerbach & Shmida (1993) compared the ranges of plant species on Mt. Hermon, Israel, with a null model and found that clustering was more common for upper boundaries than lower ones. Shipley & Keddy (1987), using an analysis of deviance, demonstrated that wetter and drier boundaries of species distributions were independently clustered along a marsh in Quebec, Canada. Hoagland & Collins (1997), in their analysis of wetland vegetation transects, reported significantly clustered species boundaries in about 25% of their 41 transects. Finally, using data from the literature, Leibold & Mikkelsen (2002) analysed 29 transects and found that 11 had highly significant clumping of species boundaries, including half of the six transects along temperate zone altitudinal gradients.

The causes of upslope and downslope species boundaries are not necessarily the same (Auerbach & Shmida 1993, Pielou & Routledge 1976). Upper boundaries (or those at the more physiologically stressful

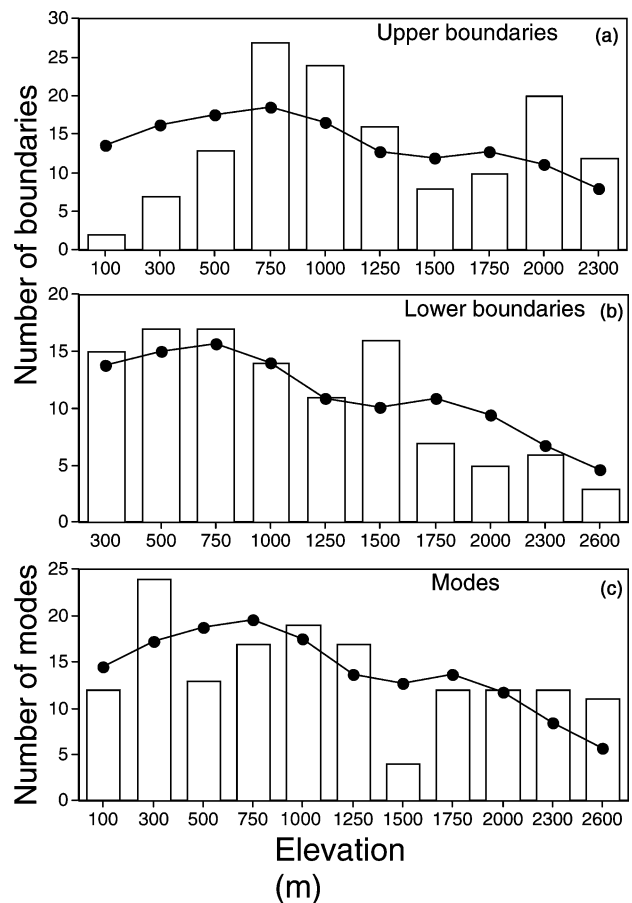


Figure 3. Clustering of upper boundaries (a), lower boundaries (b) and modes of species abundance (c) for the elevation transect along Volcan Barva, Costa Rica. Data are from Lieberman *et al.* (1996). The upper boundaries and modes are significantly clustered, while the lower boundaries are not.

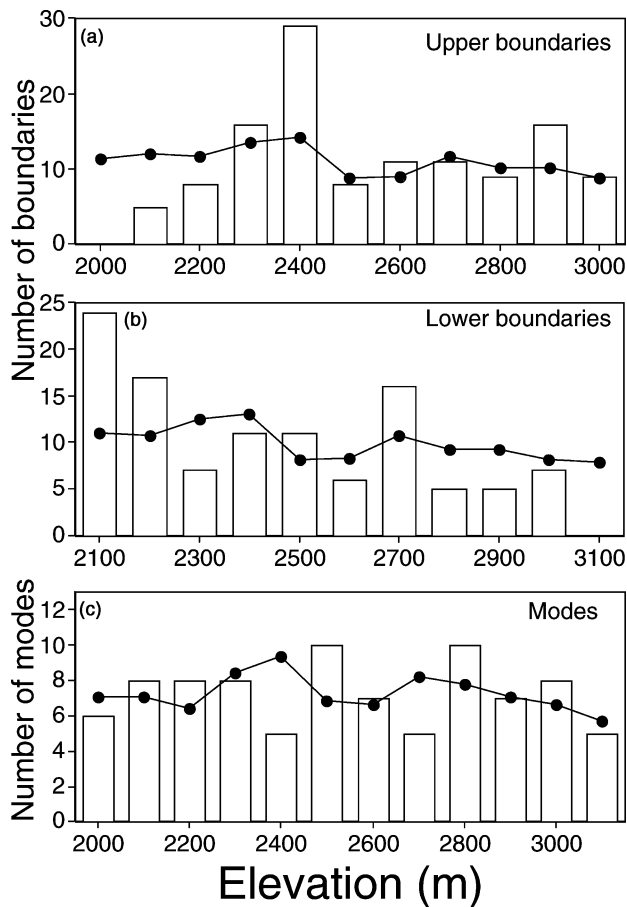


Figure 4. Clustering of upper boundaries (a), lower boundaries (b) and modes of species abundance (c) for the elevation transect in the Chirripó National Park, Costa Rica. The bars represent the actual numbers of species, and the lines represent the expected number. Data are from Kappelle *et al.* (1995).

end of the gradient) may be more likely to result from abiotic factors, while lower boundaries may result from competition (Auerbach & Shmida 1993, Hamilton & Perrott 1981). If this suggestion proves correct, abiotic factors in general may be more likely to generate clusters of species boundaries as well, as a single factor or a group of correlated factors could simultaneously limit the distribution of many species. These abiotic factors could include one or repeated disturbances, which can have a significant effect in some montane forests (Arriaga 2000, Martin *et al.* 2007). For example, Martin *et al.* (2007) showed that fires and related abiotic factors could lead to an abrupt boundary between monodominant pine forest and diverse cloud forest on mountains in the Dominican Republic.

For vegetation along the Sonadora and Mameyes transects, fog levels could be influencing the upslope distribution of species. In the LEF, a persistent cloud base often reaches down to between 550–650 m (Baynton 1968). These elevations correspond roughly to a cluster of upper boundaries observed at 500 m on the Sonadora

transect (though not on the Mameyes transect). Grubb (1971; see also Grubb & Whitmore 1966) hypothesized that fog can lead to transitions between forest types on tropical mountains, arguing that frequent fogs can result in higher soil water content and reductions in mineralization and nutrient supply. Studies by Silver *et al.* (1999) and McGroddy & Silver (2000) documented similar ecosystem effects of fog in the LEF. Thus, fog may indirectly limit the upward distribution of species adapted to more aerobic soil conditions found in lowland forests. Which factors, including fog, influence the clustering of species boundaries at the other sites, remains unclear.

All transects showed significant coherence. How common coherence is in metacommunities remains unclear, as the technique is still relatively new. Fontaneto *et al.* (2005) found that moss-dwelling rotifer communities in Italy were significantly coherent in sites along a stream. Likewise, Kusch *et al.* (2005) observed consistent coherence in Lepidoptera communities across different forest patches in Luxembourg. Leibold & Mikkelsen (2002) analysed 35 vegetation transects from the literature and determined that over half were significantly coherent, including seven of eight altitudinal gradients. These results, along with the current study,

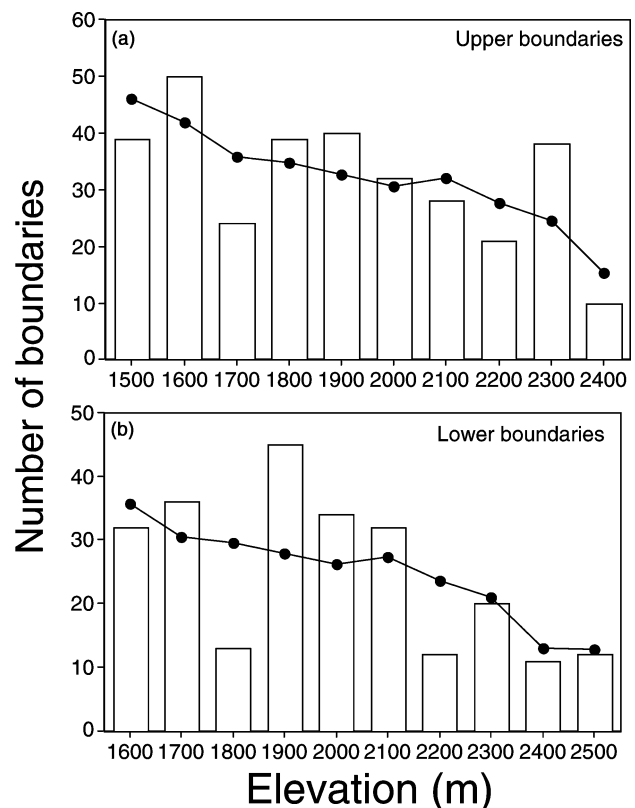


Figure 5. Clustering of upper (a) and lower (b) boundaries for an elevation transect in the Sierra de Manantlán, Jalisco, Mexico. The bars represent the actual numbers of species, and the lines represent the expected number. Data are from Vázquez & Givnish (1998).

make it appear that elevation gradients are especially likely to show coherence.

The ecological processes generating coherence have not been fully examined, but Leibold & Mikkelsen (2002) argue that coherence suggests that the structure of metacommunities may be dominated by a single axis of variation. The use of ordination before the analysis for coherence maximizes the importance of this axis of variation for each transect. Species that show incoherence after the ordination are responding to different underlying factors. For example, gap specialists in a mature forest dominated by shade-tolerant species would likely have incoherent distributions. A transect or metacommunity with high levels of incoherence could occur in a very heterogeneous landscape where different factors (such as substrate, climate and disturbance regime) are variable. In addition, species that are strongly dispersal-limited are less likely to make it to all suitable sites along the gradient, and so any metacommunity with many dispersal-limited species should show lower coherence. The high levels of coherence found in the transects in this study may indicate that most species are responding to the factors generating the primary axis of variation and that dispersal limitation was not an important factor determining metacommunity structure.

The use of reciprocal averaging as a means of ordination in the method of Leibold & Mikkelsen (2002) may explain the apparent contradiction between the nestedness and species turnover results. The ordination rearranged the order of the plots according to their scores on the first ordination axis, so that those with the most similar species list are adjacent in the data matrix. When species turnover is calculated, this approach increases the number of turnovers. Leibold & Mikkelsen (2002) favour ordination before the evaluation of the data because data on environmental variables may be lacking or the appropriate data may not have been collected. In effect, the species composition along each transect is used to reflect the underlying (if unknown) gradient.

The metacommunity techniques used in this study suggest that there was considerable structure along each of these transects, and that in all cases there were elevations where the forest community changed relatively rapidly. For the transects taken from the literature, this conclusion contradicts the authors' own, suggesting that the techniques used for analysing transects can influence whether patterns are detected. For example, Lieberman *et al.* (1996) in the Volcan Barva transect used a detrended correspondence analysis and compared the axis 1 scores of 20 × 20-m subplots of each plot with altitude. The axis 1 scores increase smoothly with elevation, suggesting no distinctive ecotones along the transect. In contrast, the community changes noted in this study, such as the clustering of upslope boundaries at particular elevations, show that sometimes the change in species composition

can be substantial, despite this apparent absence of ecotones. The 2000-m plot in the Volcan Barva transect had 55 species (Lieberman *et al.* 1996). Twenty of these were at their upper limit along the transect, meaning that over a third of the species appear to drop out before the next plot, at 2300 m. In contrast, the 1500-m plot had 74 species (Lieberman *et al.* 1996) and only eight, or about 11%, were at their upper limit. Whether the first of these changes would constitute an ecotone is unclear. However, this and the other transects examined clearly show distinctive shifts in species composition with elevation.

The ultimate utility of the techniques used here remains to be seen, since some of the types of analyses are relatively new. They do, however, provide another way to look for patterns of species composition along transects, and they allow for the ready comparison across transects and sites. The search for common patterns should help to understand more fully the mechanisms operating on tropical montane forests.

This study shows that tropical montane forests exhibit considerable metacommunity structure. Some structural features, such as coherence, were present in all the forests examined, whereas others, such as the clumping of upper and lower species boundaries, differed across the forests. The presence of metacommunity structure in all the sites suggests that one or more factors may strongly influence woody plant distributions across tropical mountains, but what these factors are and how they act remains to be determined.

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LITERATURE CITED

ARRIAGA, L. 2000. Types and causes of tree mortality in a tropical montane cloud forest of Tamaulipas, Mexico. *Journal of Tropical Ecology* 16:623–636.

- ASHTON, P. S. 2003. Floristic zonation of tree communities on wet tropical mountains revisited. *Perspectives in Plant Ecology, Evolution and Systematics* 6:87–104.
- AUERBACH, M. & SHMIDA, A. 1993. Vegetation change along an altitudinal gradient on Mt. Hermon, Israel – no evidence for discrete communities. *Journal of Ecology* 81:25–33.
- AUSTIN, M. P. 1985. Continuum concept, ordination methods, and niche theory. *Annual Review of Ecology and Systematics* 16:39–61.
- AUSTIN, M. P. & SMITH, T. M. 1989. New model for the continuum concept. *Vegetatio* 83:35–47.
- BAYNTON, H. W. 1968. Ecology of an elfin forest in Puerto Rico. 2. Microclimate of Pico del Oeste. *Journal of the Arnold Arboretum* 49:419–430.
- BEINROTH, F. H. 1982. Some highly weathered soils of Puerto Rico. I. Morphology, formation, and classification. *Geoderma* 27:1–74.
- BRISCOE, C. B. 1966. *Weather in the Luquillo Mountains of Puerto Rico*. Institute of Tropical Forestry Research Paper ITF-3. Institute of Tropical Forestry, Rio Piedras.
- BROWN, S., LUGO, A. E., SILANDER, S. & LIEGEL, L. 1983. *Research history and opportunities in the Luquillo Experimental Forest*. General Technical Report No. SO-44. U. S. Department of Forestry, Southern Experiment Station, New Orleans. 132 pp.
- CLEMENTS, F. E. 1916. *Plant succession: an analysis of the development of vegetation*. Carnegie Institute of Washington, Washington. 512 pp.
- CLEMENTS, F. E. 1936. Nature and structure of the climax. *Journal of Ecology* 24:252–284.
- FERNANDEZ-PALACIOS, J. M. & DE NICOLAS, J. P. 1995. Altitudinal pattern of vegetation variation on Tenerife. *Journal of Vegetation Science* 6:183–190.
- FONTANETO, D., MELONE, G. & RICCI, C. 2005. Connectivity and nestedness of the meta-community structure of moss dwelling bdelloid rotifers along a stream. *Hydrobiologia* 542:131–136.
- FOSTER, D. R., FLUET, M. & BOOSE, E. R. 1999. Human or natural disturbance: landscape-scale dynamics of the tropical forests of Puerto Rico. *Ecological Applications* 9:555–572.
- GARCÍA-MONTIEL, D. C. & SCATENA, F. N. 1994. Effect of human activity on the structure and composition of a tropical forest in Puerto Rico. *Forest Ecology and Management* 63:57–78.
- GLEASON, H. A. 1926. Individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club* 53:7–26.
- GRUBB, P. J. 1971. Interpretation of the “Massenerhebung” effect on tropical mountains. *Nature* 229:44–45.
- GRUBB, P. J. 1977. Control of forest growth and distribution on wet tropical mountains: with species reference to mineral nutrition. *Annual Review of Ecology and Systematics* 8:83–107.
- GRUBB, P. J. & WHITMORE, T. C. 1966. Comparison of montane and lowland rain forest in Ecuador. II. The climate and its effects on the distribution and physiognomy of the forests. *Journal of Ecology* 54:303–333.
- HAMILTON, A. C. 1975. Quantitative analysis of altitudinal zonation in Uganda forests. *Vegetatio* 30:99–106.
- HAMILTON, A. C. & PERROTT, R. A. 1981. Study of altitudinal zonation in the montane forest belt of Mt. Elgon, Kenya/Uganda. *Vegetatio* 45:107–125.
- HEMP, A. 2006. Continuum or zonation? Altitudinal gradients in the forest vegetation of Mt. Kilimanjaro. *Plant Ecology* 184:27–42.
- HOAGLAND, B. W. & COLLINS, S. L. 1997. Gradient models, gradient analysis, and hierarchical structure in plant communities. *Oikos* 78:23–30.
- HOLYOAK, M., LEIBOLD, M. A. & HOLT, R. D. 2005. *Metacommunities: spatial dynamics and ecological communities*. University of Chicago Press, Chicago. 520 pp.
- KAPPELLE, M., VAN UFFELEN, J.-G. & CLEEF, A. M. 1995. Altitudinal zonation of montane *Quercus* forests along two transects in Chirripó National Park, Costa Rica. *Vegetatio* 119:119–153.
- KITAYAMA, K. 1992. Altitudinal transect study of the vegetation on Mount Kinabalu, Borneo. *Vegetatio* 102:149–171.
- KUSCH, J., GOEDERT, C. & MEYER, M. 2005. Effects of patch type and food specializations on fine spatial scale community patterns of nocturnal forest associated Lepidoptera. *Journal of Research on the Lepidoptera* 38:67–77.
- LEIBOLD, M. A. & MIKKELSON, G. M. 2002. Coherence, species turnover, and boundary clumping: elements of meta-community structure. *Oikos* 97:237–250.
- LEIBOLD, M. A., HOLYOAK, M., MOUQUET, N., AMARASEKARE, P., CHASE, J. M., HOOPEES, M. F., HOLT, R. D., SHURIN, J. B., LAW, R., TILMAN, D., LOREAU, M. & GONZALEZ, A. 2004. Metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* 7:601–613.
- LIEBERMAN, D., LIEBERMAN, M., PERALTA, R. & HARTSHORN, G. S. 1996. Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica. *Journal of Ecology* 84:137–152.
- LOVETT, J. C. 1996. Elevational and latitudinal changes in tree associations and diversity in the Eastern Arc mountains of Tanzania. *Journal of Tropical Ecology* 12:629–650.
- LOVETT, J. C. 1998. Continuous change in Tanzanian moist forest tree communities with elevation. *Journal of Tropical Ecology* 14:719–722.
- MARTIN, P. H., SHERMAN, R. E. & FAHEY, T. J. 2007. Tropical montane forest ecotones: climate gradients, natural disturbance and vegetation zonation in the Cordillera Central, Dominican Republic. *Journal of Biogeography* 34:1792–1806.
- MCGRODDY, M. & SILVER, W. L. 2000. Variations in belowground carbon storage and soil CO₂ flux rates along a wet tropical climate gradient. *Biotropica* 32:614–624.
- MCINTOSH, R. P. 1967. The continuum concept of vegetation. *Botanical Review* 33:130–187.
- MCINTOSH, R. P. 1975. H. A. Gleason – ‘individualistic ecologist’ 1882–1975: his contribution to ecological theory. *Bulletin of the Torrey Botanical Club* 102:253–273.
- PIELOU, E. C. & ROUNTLEDGE, R. D. 1976. Salt marsh vegetation: latitude gradients in the zonation pattern. *Oecologia* 24:311–321.
- RICHARDS, P. W. 1952. *Tropical rain forest: an ecological study*. (First edition). Cambridge University Press, Cambridge. 450 pp.
- RICHARDS, P. W. 1996. *Tropical rain forest: an ecological study*. (Second edition). Cambridge University Press, Cambridge. 599 pp.
- SCATENA, F. N. & LARSEN, M. C. 1991. Physical aspects of Hurricane Hugo in Puerto Rico. *Biotropica* 23:317–323.
- SHIPLEY, B. & KEDDY, P. A. 1987. Individualistic and community-unit concepts as falsifiable hypotheses. *Vegetatio* 69:47–55.

- SIEDERS, V. M. 1971. *Geologic map of the El Yunque quadrangle, Puerto Rico. Miscellaneous Geological Investigation I-658*. U.S. Department of the Interior, Geological Survey, Washington.
- SILVER, W. L., LUGO, A. E. & KELLER, M. 1999. Soil oxygen availability and biogeochemistry along rainfall and topographic gradients in upland wet tropical forest soils. *Biogeochemistry* 44:301–328.
- SOKAL, R. R. & ROHLF, F. J. 1995. *Biometry*. (Third edition). W. H. Freeman & Co. New York. 887 pp.
- THOMPSON, J., BROKAW, N., ZIMMERMAN, J. K., WAIDE, R. B., EVERHAM, E. M., LODGE, D. J., TAYLOR, C. M., GARCÍA-MONTIEL, D. & FLUET, M. 2002. Land use history, environment, and tree composition in a tropical forest. *Ecological Applications* 12:1344–1363.
- VÁZQUEZ, G. & GIVNISH, T. J. 1998. Altitudinal gradients in tropical forest composition, structure and diversity in the Sierra de Manantlán. *Journal of Ecology* 86:999–1020.
- WALKER, L. R., BROKAW, N. V. L., LODGE, D. J. & WAIDE, R. B. 1991. Ecosystem, plant and animal responses to hurricanes in the Caribbean. *Biotropica* 23:313–520.
- WEAVER, P. L. 1991. Environmental gradients affect forest composition in the Luquillo Mountains of Puerto Rico. *Interciencia* 16:142–151.
- WHITTAKER, R. H. 1967. Gradient analysis of vegetation. *Biological Reviews* 42:207–264.
- WHITMORE, T. C. 1984. *Tropical rain forests of the Far East*. (Second edition). Clarendon Press, Oxford. 352 pp.
- WOLDU, Z., FEOLI, E. & NIGATU, L. 1989. Partitioning an elevation gradient of vegetation from southeastern Ethiopia by probabilistic methods. *Vegetatio* 81:189–198.
- WRIGHT, D. H. & REEVES, J. H. 1992. On the meaning and measurement of nestedness of species assemblages. *Oecologia* 92:416–428.
- ZIMMERMAN, J. K., EVERHAM, E. M., WAIDE, R. B., LODGE, D. J., TAYLOR, C. M. & BROKAW, N. V. L. 1994. Responses of tree species to hurricane winds in subtropical wet forest in Puerto Rico: implications for tropical tree life histories. *Journal of Ecology* 82:911–922.