



Tropical metacommunities along elevational gradients: effects of forest type and other environmental factors

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Elevational gradients provide a natural experiment for assessing the extent to which the structure of animal metacommunities is molded by biotic and abiotic characteristics that change gradually, or is molded by aspects of plant community composition and physiognomy that change in a more discrete fashion. We used a metacommunity framework to integrate species-specific responses to environmental gradients as an approach to detect emergent patterns at the mesoscale in the Luquillo Mountains of Puerto Rico. Elements of metacommunity structure (coherence, species turnover and range boundary clumping) formed the basis for distinguishing among random, checkerboard, Gleasonian, Clementsian, evenly spaced and nested patterns. Paired elevational transects (300–1000 m a.s.l.) were sampled at 50 m intervals to decouple underlying environmental mechanisms: a mixed forest transect reflected changes in abiotic and biotic conditions, including forest type (i.e. tabonuco, palo colorado and elfin forests), whereas another transect reflected changes in environmental conditions but not forest type, as its constituent plots were located within palm forest. Based on distributional data (presence versus absence of species), the mixed forest transect exhibited Clementsian structure, whereas the palm forest transect exhibited quasi-Gleasonian structure. In contrast, the distribution of modes in species abundance was random with respect to the latent environmental gradient in the mixed forest transect and clumped with respect to the latent environmental gradient in the palm forest transect. Such contrasts suggest that the environmental factors affecting abundance differed in form or type from those affecting distributional boundaries. Variation among elevational strata with respect to the first axis of correspondence from reciprocal averaging was highly correlated with elevation along each transect, even though axis scores were not correlated between mixed forest and palm forest transects. This suggests that the identity of the environmental characteristics, or the form of response by the fauna to those characteristics, differed between the two elevational transects. Despite the proximity of the transects, the patchy configuration of palm forest, and the pervasive distribution of the dominant palm species, the relative importance of abiotic variables and habitat in structuring gastropod metacommunities differed between transects, which is remarkable and attests to the sensitivity of metacommunity structure to environmental variation.

The role of environmental gradients in molding the structure of ecological communities has been a topic of considerable importance in ecology for decades (Whittaker 1956, 1975, Terborgh 1971, Scheiner and Willig 2005). Perhaps the most famous debate centered on the opposing views of Clements (1916) and Gleason (1926). The former held that suites of species evinced similar responses to environmental gradients, resulting in the formation of distinct communities that could be distinguished as a consequence of compositional unity in space, with the termini of species distributions concentrated at the spatial periphery of each community. In contrast, the latter held that species responded to environmental gradients in idiosyncratic manners, so that compositional unity was not pervasive and range termini were distributed randomly in space. A number of alternative configurations of species ranges (i.e. metacommunity structures) along environmental gradients

have been identified subsequently, including checkerboard (Diamond 1975), nested (Patterson and Atmar 1986), and evenly spaced (Tilman 1982) distributions. More specifically, strong interspecific competition can produce tradeoffs that manifest as distributions that are more evenly spaced along environmental gradients than expected by chance (Tilman 1982). Alternatively, strong competition can result in checkerboard patterns if pairs of species with mutually exclusive ranges (Diamond 1975) occur independently of other such pairs. Finally, species-poor communities may form nested subsets of increasingly species-rich biotas (Patterson and Atmar 1986) along an environmental gradient, with predictable patterns of species loss associated with variation in species-specific characteristics (e.g. dispersal ability, habitat specialization, tolerance to abiotic conditions). In contrast to these distinctive structures, random metacommunities occur

when species distributions are not associated in a significant way with a common latent environmental gradient (i.e. a preponderance of species does not form coherent distributions with regard to a latent gradient).

Most investigations of metacommunity structure have evaluated whether empirical data support one of these configurations rather than a random pattern (e.g. nested vs random), without simultaneously assessing multiple alternative or competing hypotheses (Hylander et al. 2005, Bloch et al. 2007). Such approaches suffer from an inflated declaration of random patterns. For example, in testing for nested distributions, a non-significant outcome could arise from a truly random structure, but could also arise as a consequence of other non-nested patterns that were not the focus of analysis (e.g. Gleasonian, Clementsian, checkerboard or evenly spaced patterns).

Metacommunities

A metacommunity is a group of local communities that are connected via dispersal (Hanski and Gilpin 1991). The concept focuses on the emergent structure of a group of interconnected sites, and shifts the focus from patterns at local scales to patterns across mesoscales, and from mechanisms that primarily operate locally to those that operate at any of a number of scales (Leibold 2011). In this context, the metacommunity perspective of Leibold and Mikkelsen (2002), including recent amplifications (Presley et al. 2010), provided a comprehensive quantitative framework for distinguishing among competing hypotheses concerning the nature of biotic structure along environmental gradients. Compared to other analytical approaches to study metacommunities, this comprehensive framework is unique in simultaneously evaluating multiple competing hypotheses that represent

different organizational models (e.g. Clementsian, Gleasonian, nested, checkerboard, evenly spaced, and random structures). In concert, a hierarchical analysis (Fig. 1) of coherence, species turnover, and range boundary clumping – the three elements of metacommunity structure – discriminates among six idealized patterns of species distribution (Leibold and Mikkelsen 2002) and their quasi-structures (Presley et al. 2010).

Coherence indicates that species distributions in a metacommunity are molded by a common environmental gradient. If the occurrences of species are not defined by the same environmental gradient, an attempt to order species along the same gradient will result in non-coherent distributions and the metacommunity will have random structure. If the environmental distributions of pairs of species are mutually exclusive, and independent of other such pairs, a metacommunity exhibits negative coherence, consistent with checkerboard distributions (reminiscent of, but not identical to, the concept first proposed by Diamond 1975). The remaining four structures exhibit positive coherence, and are distinguished via analyses of range turnover and range boundary clumping. In nested biotas, the distributions of species with smaller environmental ranges are contained within those of wider-ranging species (Patterson and Atmar 1986), resulting in less range turnover along the latent environmental gradient than is expected by chance (i.e. negative turnover). Clementsian, Gleasonian, and evenly-spaced distributions exhibit positive range turnover (i.e. more species turnover among sites than expected by chance); analysis of range boundary clumping is required to discriminate among them. Clumped range boundaries delineate discrete compartments (groups of species that replace other such groups along a gradient) that define Clementsian structure (Clements 1916). In Gleasonian structures, species distributions occur independently and idiosyncratically with respect to the latent environmental

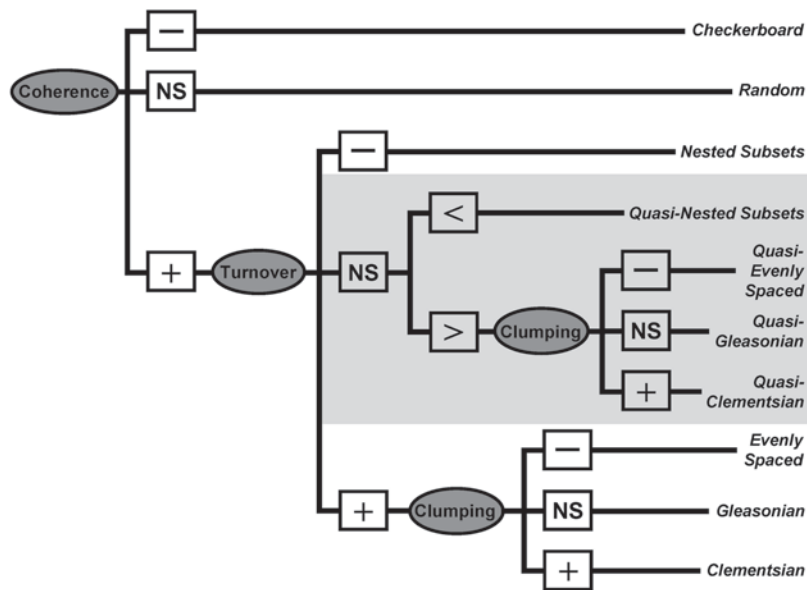


Figure 1. A diagrammatic representation (after Presley et al. 2010) of the combinations of distributional characteristics (elements of metacommunity structure in shaded ovals) that differentiate among six idealized metacommunity structures and four quasi-structures (in shaded area) that are associated with four of the idealized structures. Results that are consistent with particular structures are within circles (+ = positive significance, NS = non-significance, - = negative significance). For non-significant analyses of turnover, < indicates that observed number of replacements was less than the average number based on randomizations and > indicates that observed number of replacements was greater than the average number based on randomizations.

gradient (Gleason 1926). Hyper-dispersed range boundaries (negative boundary clumping) along the latent gradient are indicative of an evenly-spaced structure (Tilman 1982). Quasi-structures (Presley et al. 2010) arise when the direction of species turnover (a non-defining element of community structure) is consistent in sign (direction) but not in magnitude (significance) with predictions associated with a particular pattern (shaded area of Fig. 1).

Elevational gradients

Elevational gradients are useful for assessing environmental characteristics to which species respond because changes in elevation result in predictable and appreciable variation in plant species composition and structure, as well as in abiotic (e.g. temperature, precipitation) factors (Fig. 2). Although the degree of variation in temperature that accompanies changes in elevation differs depending on geographic and topographic particulars, temperature decreases 6.5°C on average for every 1-km increase in elevation (i.e. the moist adiabatic lapse rate). Moreover, variation in species composition is less likely to arise because of historical contingency (i.e. effects of multiple species pools or multiple sources of colonization) along elevational gradients compared to latitudinal gradients or gradients associated with large island systems (e.g. Caribbean islands). Consequently, mountain systems facilitate a relatively uncompromised focus on ecological rather than biogeographic mechanisms when studying environmental gradients.

Although elevational changes in abiotic characteristics and associated vegetation are predictable, they differ in the form of their variation. Abiotic characteristics generally change in a gradual, but not necessarily linear fashion with elevation (Barry 1992, Whiteman 2000), whereas floral associations often have more-or-less discrete boundaries recognized as habitat types, forest types, or life zones (Kessler 2000, Hemp

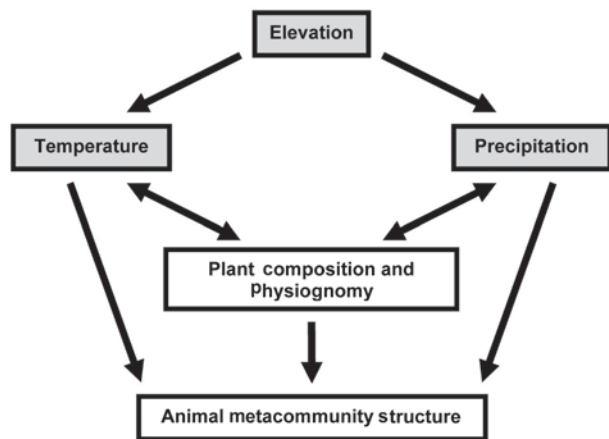


Figure 2. A conceptual model illustrating how biotic and abiotic characteristics that are affected by elevation can interact indirectly, via plant species composition and physiognomy for example, or directly, via temperature and precipitation, for example, to affect animal metacommunity composition and structure. In addition to direct effects (e.g. habitat and food resources) on animal metacommunities, plant species composition and physiognomy may affect animal metacommunities by modifying local microclimates (hence the bi-directional arrows).

2006). Because habitat specialization and responses to abiotic characteristics are important in defining the ranges of animal species, the structure of a metacommunity is contingent on the dominant mechanism that molds animal species distributions. If habitat boundaries are more-or-less discrete, metacommunities along elevational gradients that are molded by habitat preferences or specializations should include multiple species with range boundaries that are coincident with those of the habitats (i.e. range boundary clumping) and should evince Clementsian structure. Conversely, if species-specific tolerances to abiotic characteristics that change gradually with elevation are idiosyncratic, then metacommunities molded by responses to abiotic characteristics should have Gleasonian structure.

Gastropod fauna

Terrestrial gastropods are taxonomically diverse and numerically abundant in many ecosystems, making them useful species for biogeographic and macroecological studies, including those focusing on community or metacommunity structures (Steinitz et al. 2005, Stanisci et al. 2007, Clements et al. 2008, Wronski and Hausdorf 2010). Moreover, terrestrial gastropods, like non-marine mollusks in general, are suffering from global declines and are in need of scientifically informed conservation action and management (Lydeard et al. 2004). Consequently, there is considerable urgency to understand mesoscale variation in gastropod diversity and the factors that affect it. In addition, gastropods are ectothermic and constrained in distribution and behavior by desiccation stress (Cook 2001). They cannot quickly escape desiccation associated with higher temperature and lower humidity because they are not particularly vagile. Consequently, this fauna evinces a suite of attributes that suggest differential responses to spatial variation in habitat or microclimate that might be reflected in metacommunity structure along elevational gradients where dramatic environmental changes occur over relatively small spatial extents (Tattersfield et al. 2001, Liew et al. 2010).

Objectives

We used a comprehensive metacommunity approach (Leibold and Mikkelsen 2002, Presley et al. 2010) to evaluate the form of terrestrial gastropod metacommunity organization along two parallel environmental gradients: one that comprises distinctive plant communities and one that represents a single plant community. In so doing, we assess the relative importance of habitat associations versus variation in other environmental characteristics on animal species distributions and their emergent metacommunity structures. We also assessed the extent to which the environmental variation that molds gastropod distribution is related to elevation.

Material and methods

Study area

The Luquillo Experimental Forest (LEF) comprises 11300 ha in northeastern Puerto Rico (Fig. 3). It is a

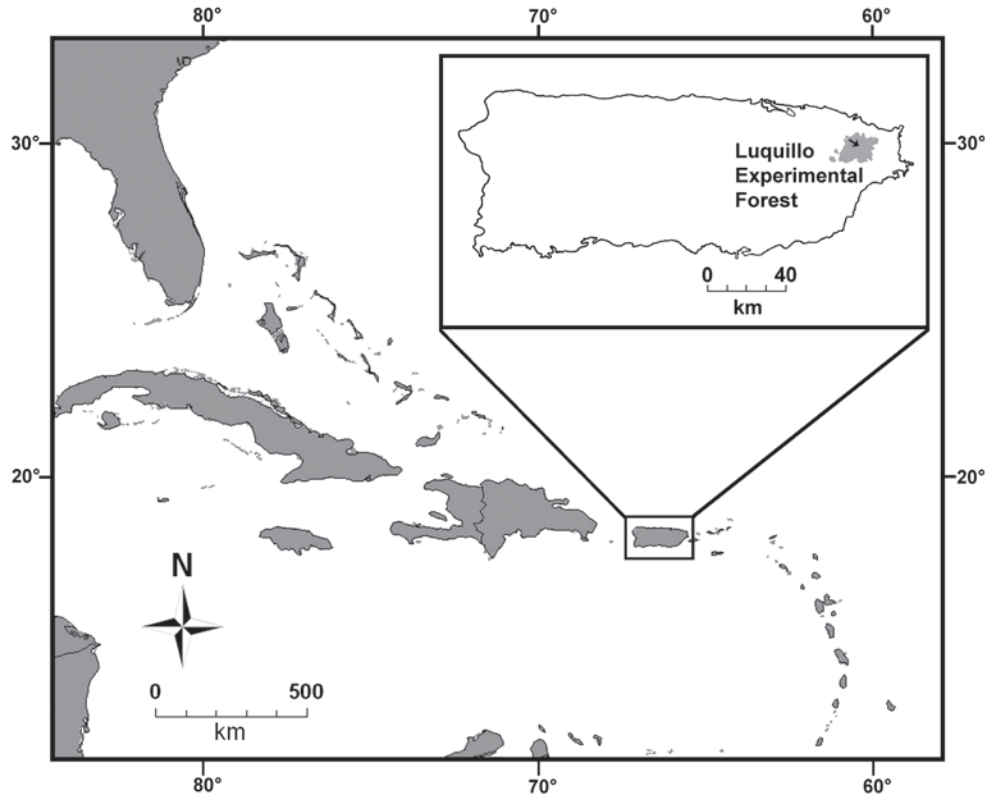


Figure 3. Map of the Caribbean showing the location, size, and shape of Puerto Rico as well as the location of the Luquillo Experimental Forest (LEF) on the island. Within the LEF, an arrow indicates the location and length of the elevational transect; the arrow head indicates the high elevation end of the transect ($18^{\circ}18'32''\text{N}$, $65^{\circ}47'46''\text{W}$) whereas the arrow base indicates the low elevation end of the transect ($18^{\circ}19'23''\text{N}$, $65^{\circ}49'12''\text{W}$).

Man and the Biosphere Reserve as well as a site in the National Science Foundation's Long-Term Ecological Research network. Three forest types (tabonuco, palo colorado and elfin) occur in the LEF in association with elevational zones, whereas a fourth forest type (palm forest) occurs at all elevations and occupies well drained soils that are dominated by sierra palm (*Prestoea acuminata*). In general, forest types were defined by the presence and abundance of plant species (e.g. trees, shrubs, epiphytes), as well as by the physiognomy of the vegetation (Wadsworth 1949, Brown et al. 1983). Research was conducted along two parallel elevational transects in the Sonadora River watershed (Barone et al. 2008). Each transect extended between 300–1000 m a.s.l., and was on the northwest-facing slope on clayey soils. One transect included tabonuco, palo colorado and elfin forests (hereafter mixed forest transect), whereas the other included only sites that were heavily dominated by *P. acuminata* (hereafter palm forest transect).

Tabonuco forest occurs at elevations between 200–600 m a.s.l., and is the most extensive and best studied portion of the LEF (Reagan and Waide 1996). It is a subtropical wet forest according to the Holdridge classification system (Brown et al. 1983) and is characterized by a dominant hardwood species, *Dacryodes excelsa* (Burseraceae). Other common trees of the tabonuco forest canopy include *Manilkara bidentata*, *Sloanea berteriana*, *Guarea guidonia* and *P. acuminata* (Odum and Pigeon 1970). Canopy height is >20 m, with emergent trees up to 35 m. Rainfall in tabonuco forest is substantial, averaging 346 cm year^{-1} (McDowell and Estrada-Pinto

1988). Humidity is consistently high, and little seasonal or diurnal variation occurs in temperature (Odum and Pigeon 1970). Mean annual temperature in tabonuco forest is 23°C , with monthly temperatures ranging between 21 – 25°C .

Cloud condensation begins at 600 m a.s.l. Palo colorado forest begins at this point and occurs up to 900 m a.s.l. This forest type is named after the colorado tree (*Cyrtilla racemiflora*), the most common large tree at these elevations. Other common tree species of palo colorado forest include *Calycogonium squamulosum*, *Ocotea spathulata*, *Micropholis garcinifolia*, and *M. chrysophylloides* (Brown et al. 1983). Canopy height is <15 m, with lower and more dense branching than in tabonuco forest, making distinction of the canopy and sub-canopy difficult. Palo colorado forest has more vines, epiphytes, herbaceous plants, and a thicker surface network of roots than does tabonuco forest, as well as increased rainfall (mean annual rainfall is 470 cm). Mean annual temperature is 21°C , with mean monthly temperatures that range between 19 – 23°C .

Elfin forest occurs on the summits of mountains in the LEF and on windward ridges above 900 m a.s.l. Its canopy is only 2–3 m tall and comprises short, twisted trees and shrubs. The three most common species are a herb (*Pilea krugii*), a semi-woody plant (*Wallenia yunqueensis*), and a woody canopy tree (*Calycogonium squamulosum*). Surface roots cover the forest floor and constitute 60% of the total forest floor biomass (Lyford 1969). Epiphytes and epiphytic algae cover most woody plants (Weaver 1972). Mean annual rainfall is 360 cm, with monthly rainfall varying from 30 to 60 cm and a relative

humidity always above 95%. Mean monthly temperatures range between 16–20°C (Brown et al. 1983).

Palm forest occurs throughout the elevational gradient in the Luquillo Mountains. It occurs on steep slopes and wet soils that are strongly dominated by *P. acuminata*. Its distribution is fragmented and patchy, as it is interspersed within all of the life zones of the LEF. The canopy of palm forest is <15 m, does not support an extensive subcanopy stratum, and harbors few herbaceous plants, vines, or epiphytes in the understory. At mid-elevational (~750 m a.s.l.) floodplains, it is the most productive forest type (Waide et al. 1998) in the Luquillo Mountains. Although pure palm forest did not exist at all elevations in the Sonadora watershed, over 80% of canopy trees at each site selected for the palm forest transect were *P. acuminata* (and 95% at most sites), thereby assuring minimal elevational changes in vegetation structure and composition.

Study organisms

Forty-four species of terrestrial gastropods are recorded from the LEF (Garrison and Willig 1996); however, only 26 of these species forage above the leaf litter, and most are rare or uncommon. Gastropods in the LEF are well understood taxonomically (Garrison and Willig 1996). They span the broad elevational gradient in the LEF (Alvarez 1997), and exhibit species-specific demographic responses with respect to small scale (tree fall gaps; Alvarez and Willig 1993) and broad scale (human land use and hurricanes; Willig and Camilo 1991, Secrest et al. 1996, Willig et al. 2007) disturbances. Moreover, the habitat associations of some species are well documented (Cary 1992, Willig et al. 1998).

Field methods

Each transect (i.e. mixed forest and palm forest) comprised elevational strata spaced at 50-m elevational increments between 300–1000 m a.s.l.; however, the Sonadora watershed did not contain a sufficiently large patch of palm forest at the 750 m elevational stratum. Consequently, the mixed forest transect comprised 15 strata and the palm forest transect comprised 14 strata. In the mixed forest transect, plots were arranged in a 0.1-ha rectangle (50 × 20 m) comprising 10 circular plots (3 m radius) configured in 2 parallel rows, each containing 5 evenly-spaced plots with 10 m between plot centers. Rectangular strata were aligned with their long axes perpendicular to the Sonadora River. Because the elevational distribution and size of palm forest patches were variable, palm forest strata were located within 1 km of the corresponding stratum in mixed forest, and always within the Sonadora watershed. By necessity, the configuration of plots within strata of palm forest was more variable than in mixed forest. Nonetheless, plots within a stratum of palm forest were always contiguous, with a maximum distance between centers of the most distant plots being less than 58.3 m (mean = 43.6 m, SD = 6.07 m). This is comparable to the situation along the mixed forest transect, where 41.2 m was the maximum distance between plot centers within a stratum.

Gastropods on each plot were sampled 3 times during the summer (wet season) of 2008. Sampling was conducted

at night (20:00–04:00) to coincide with peak activity of gastropods (Heatwole and Heatwole 1978, Willig et al. 1998). Each time a plot was surveyed, two people searched all available surfaces (e.g. soil, litter, rock cover, vegetation, debris) up to a height of approximately 3 m for 15 min or until all substrates had been completely searched, whichever was longer. All gastropods were identified to species in the field. To minimize the effects of sampling sequence on elevational patterns, sampling was not repeated at any one elevation until after the entire gradient was sampled.

To minimize alteration of long-term study plots, substrate was disturbed as little as possible during the search for gastropods. This method limits the inference space of the study, potentially excluding small, litter-dwelling species from consideration. In many terrestrial gastropod assemblages, most individuals and taxa dwell in the leaf litter (Tattersfield 1996, Barker and Mayhill 1999, Schilthuizen and Rutjes 2001, Nekola 2005), which can be problematic when attempting a complete taxonomic inventory of a region (Cameron and Pokryszko 2005). In contrast, the gastropod fauna of the LEF comprises many large and arboreal taxa, and density of gastropods in litter samples typically is quite low (Richardson et al. 2005). In addition, estimates of population density by visual enumeration (minimum number known to be alive) correlate strongly with mark–recapture estimates of density, at least for two of the arboreal species (*Caracolus caracolla* and *Nenia tridens*), suggesting that such estimates adequately reflect changes in relative density over time or space (Bloch 2004). Consequently, our inference space was constrained to include only macro-individuals that emerged above the leaf litter (Liew et al. 2010 used a similar approach), an assemblage for which we are confident that our visual sampling method was appropriate.

Quantitative analyses

Metacommunity structure of terrestrial gastropods along a latent environmental gradient was determined separately for mixed forest and palm forest transects using the methodology of Leibold and Mikkelsen (2002) and Presley et al. (2010). These analyses used presence–absence data for strata (i.e. data were pooled from all ten plots to characterize each stratum). We supplemented these analyses with approaches based on abundance.

The best-fit pattern of metacommunity structure for each transect was determined using three characteristics of species distributions (coherence, species range turnover, and boundary clumping) from an ordinated presence–absence matrix. Each matrix was ordinated via reciprocal averaging, which simultaneously optimizes the proximity of sites with similar species composition and the proximity of species with similar distributions in the ordinated space. Reciprocal averaging is appropriate for identifying patterns in response to gradients because similarity in species-specific distributions determines the position of sites along the axis of correspondence (i.e. a latent environmental gradient) without a priori knowledge of the particular factors that govern species responses (Gauch et al. 1977, Leibold and Mikkelsen 2002).

A null model that constrained column totals (site richness) to equal the observed totals and that had equal row probabilities (species occurrences) was chosen a priori because it has

a desirable combination of type I and type II error properties when applied to small matrices (i.e. those with fewer than 30 species and sites), and creates a biologically realistic null space in which the number of species at each site is fixed, but the number of sites at which a species occurs is random (Presley et al. 2009, Presley and Willig 2010). For each transect, 1000 randomly generated matrices were created and subjected to reciprocal averaging. Embedded absences in each randomly generated matrix were counted and used to create a null distribution. A z-test based on the mean and variance of the null distribution was used to determine significance. A metacommunity was considered significantly and positively coherent if the likelihood due to chance of having fewer embedded absences than observed was $\leq \alpha/2$ (i.e. a two-tailed test). A metacommunity was considered significantly and negatively coherent if the likelihood due to chance of having more embedded absences than observed was $\leq \alpha/2$.

Species range turnover was evaluated for each coherent metacommunity. To quantify turnover, the number of times one species was replaced by another between each possible pair of sites was counted in the ordinated empirical matrix. To ensure that the number of replacements was an accurate estimate of species turnover along the latent environmental gradient, species ranges were made coherent by filling in embedded absences prior to analysis, as recommended by Leibold and Mikkelsen (2002). To determine significance, the empirical number of replacements was compared to a null distribution of such replacement values created from 1000 matrices that contained randomly shifted species ranges (Leibold and Mikkelsen 2002). A metacommunity exhibited positive species turnover when the likelihood of randomly generating more replacements than observed was $\leq \alpha/2$; a metacommunity exhibited negative species turnover when the likelihood of randomly generating fewer replacements than observed was $\leq \alpha/2$.

Structures consistent with both positive coherence and positive turnover were distinguished from each other via analysis of range boundary clumping. Morisita's index (I) measures the clumping of species distributional boundaries by counting the number of terminal boundaries at each stratum (Hurlbert 1990). Significance was determined via a χ^2 goodness of fit test that compared the observed distribution of range boundaries to an expected uniform distribution. Range boundaries that occurred at random have a Morisita's index of ~ 1.0 and a non-significant χ^2 test. Index values > 1.0 with a significant χ^2 test indicate clumped boundaries, whereas index values < 1.0 with a significant χ^2 test indicate hyper-dispersed boundaries.

We followed Presley et al. (2010) and recognized quasi-structures (shaded area of Fig. 1). More specifically, if range turnover was non-significant, but the amount of sample turnover was less than the average number from randomly generated matrices, we considered the metacommunity to be quasi-nested. In contrast, if range turnover was non-significant, but the amount of sample turnover was more than the average number from randomly generated matrices, we considered the metacommunity to be quasi-evenly spaced, quasi-Gleasonian, or quasi-Clementsian, if the amount of boundary clumping was significantly less than, indistinguishable from, or significantly more than that expected by chance, respectively.

The distribution of modes in species abundance provides complementary insights about the structure of metacommunities, when coupled with the framework of Leibold and Mikkelsen (2002). More specifically, clumped range boundaries indicate that species exhibit similar degrees of tolerance along a latent environmental gradient, whereas clumped modes of abundance indicate that species have similar optima along that gradient. Consequently, the dispersion of modes was evaluated via a statistical assessment and a mode clustering index (MC) in which $MC < 1.0$ indicates evenly spaced modes, $MC > 1.0$ indicates clustered modes, and $MC \sim 1.0$ indicates randomly distributed modes (Poole and Rathcke 1979). This analysis was conducted separately for each transect. In addition, we tested if mean abundance differed between mixed and palm forest using a paired t-test (Sokal and Rohlf 1995) for each species, as well as for the fauna as a whole. We evaluated whether the overall direction of difference in mean abundance between transects was consistent among species (i.e. did one forest type consistently harbor greater abundances of species than another) using a binomial test (Sokal and Rohlf 1995).

To determine if elevation was associated with the latent environmental gradient as defined by reciprocal averaging, a Spearman rank correlation was conducted between site component scores and elevation in m for each transect. To determine if the elevational structure of the metacommunities were similar in palm and mixed forest transects, Spearman rank correlations were performed between axis scores of strata paired by elevation.

Analyses of coherence, species range turnover, and range boundary clumping were performed in Matlab 7.5.0.342, release 2007b (script files for Matlab are available for download at www.tarleton.edu/~higgins/EMS.htm). Component scores for sites along primary axes as defined by reciprocal averaging were obtained using the simple correspondence analysis option in Mini-Tab 15.1.30.0. Spearman rank correlations were conducted in R ver. 2.9.0. We used an α -level of 0.05 for all analyses.

Results

A total of 16 species of gastropods were documented during surveys of the elevational strata (15 species on the mixed forest transect based on 15 strata, where *Obeliscus terebraster* was absent and 15 species on the palm forest transect based on 14 strata, where *Cepolis musicola* was absent). The mixed-forest transect comprised 119 occurrences (53% matrix fill) whereas the palm forest transect comprised 124 occurrences (59% matrix fill). Percent of total inertia associated with the primary axis of correspondence in the analysis by reciprocal averaging was 26.8% and 32.3% in mixed forest and in palm forest, respectively.

Metacommunity structure

The metacommunity of each transect exhibited strong and significant positive coherence along the latent environmental gradient as defined by reciprocal averaging (Table 1). This indicates that the distributions of most species were determined by variation along a common latent environmental

Table 1. Results of analyses of coherence, species range turnover, range boundary clumping, and mode clumping for tropical gastropods along two elevational transects (mixed forest and palm forest) in the Luquillo Experimental Forest of Puerto Rico. Significant results ($p \leq 0.05$) are bold. Abs = no. of embedded absences, Rep = no. of replacements, SD = standard deviation, MC = mode clumping index.

Habitat	Species richness	Coherence			Species turnover			Boundary clumping			Mode clumping			Metacommunity structure	
		Elevational strata	Abs	p	Mean	SD	Rep	p	Mean	SD	Morisita's index	p	MC		p
Mixed forest	15	15	46	< 0.001	68	5.9	304	0.022	156	64.8	1.733	0.035	0.844	0.596	Clementsian
Palm forest	15	14	35	< 0.001	54	5.1	279	0.072	157	68.0	1.077	0.370	2.410	0.002	Quasi-Gleasonian

gradient within mixed forest as well as within palm forest. In the mixed forest, the metacommunity evinced significant and positive species turnover, as well as significant boundary clumping, consistent with Clementsian structure (Fig. 1). Nonetheless, modes in abundance were distributed at random along the same latent environmental gradient (Table 1). In palm forest, species turnover was non-significant but positive, and boundary clumping non-significant, consistent with quasi-Gleasonian structure (Fig. 1). However, the modes of abundance were clumped in the palm forest (Table 1), an unexpected pattern if species distributions are idiosyncratic and abundance distributions are Gaussian along the latent environmental gradient.

Rank order of axis scores for the strata along the latent environmental gradient was correlated significantly with elevation for the mixed forest transect ($n = 15$, $\rho = -0.63$, $p = 0.011$), as well as for the palm forest transect ($n = 14$, $\rho = -0.600$, $p = 0.026$). Nonetheless, axis scores for mixed forest were not correlated significantly with those for palm forest ($\rho = 0.396$, $p = 0.161$) when matched by stratum (750 m stratum in mixed forest was excluded from analyses because a paired site in palm forest was lacking).

Mean abundance in palm forest was significantly greater than mean abundance in mixed forest for three species at the 0.05 level (*C. caracolla*, *N. tridens* and *P. portoricensis*) and for an additional three species (*A. striata*, *O. playa* and *V. occidentalis*) at the 0.10 level, as well as for the fauna as a whole (Table 2). Even more remarkable, the direction of difference in mean abundance was consistent for all 15 species (greater in palm than in mixed forest), the likelihood of which is quite small due to chance alone (binomial test, $p < 0.001$).

Discussion

Along each transect, terrestrial gastropods responded to environmental variation in the Luquillo Mountains (i.e. distributions were coherent). Nonetheless, the differences in environmental characteristics between elevational transects gave rise to different metacommunity structures in mixed forest versus palm forest. Consistent with metacommunities molded by habitat preferences or specializations, gastropod metacommunity structure was Gleasonian in the palm forest transect and Clementsian in the mixed forest transect (Table 1, Fig. 4). Along the palm forest transect, where tree species composition and physiognomy were relatively invariant, elevational variation in abiotic and biotic characteristics produced a latent environmental gradient to which gastropod species responded in an idiosyncratic and independent fashion. Thus, the way in which elevation molds the distribution of gastropod species is consistent with a Gleasonian structure (Table 1, Fig. 4B). When this elevational variation in biotic and abiotic characteristics was overlain by zonal differences in tree species composition and physiognomy, as along the mixed forest transect, gastropod species formed a Clementsian metacommunity, in which two compartments (Fig. 4A, Table 1) were distinguishable, and consistent with the distinction between elfin or cloud-dominated forest and other mountain rainforests as a group (palo colorado and tabonuco forest). Thus, the way in which elevation molds

Table 2. Mean abundance per stratum of each snail species that occurred in both transects as well as the total mean abundance of the entire gastropod fauna, percent change in abundance between mixed forest and palm forest, and results (mean difference in abundance, t statistic, and p-value) of paired t-tests with observations paired by stratum. Results that were significant ($p \leq 0.05$) or that were marginally significant ($0.10 \geq p > 0.05$) are bold. *Obeliscus terebraster* was absent from the mixed forest transect. *Cepolis musicola* was absent from the palm forest transect.

Gastropod species	Mean abundance		% change in abundance	Paired t-test		
	Mixed	Palm		\bar{d}	t	p-value
<i>Alcaldia striata</i>	1.86	4.86	162	3.00	-1.99	0.068
<i>Austroselenites alticola</i>	0.57	0.79	38	0.21	-0.59	0.568
<i>Caracolus caracolla</i>	106.50	167.00	57	60.50	-2.33	0.037
<i>Caracolus marginella</i>	0.21	0.57	167	0.36	-0.69	0.504
<i>Cepolis squamosa</i>	1.86	2.14	15	0.29	-0.41	0.689
<i>Gaeotis nigrolineata</i>	20.57	26.14	27	5.57	-0.71	0.490
<i>Megalomastoma croceum</i>	0.07	0.21	200	0.14	-1.47	0.165
<i>Nenia tridens</i>	93.79	144.50	54	50.71	-2.25	0.043
<i>Oleacina glabra</i>	2.71	3.79	39	1.07	-1.00	0.338
<i>Oleacina playa</i>	0.43	1.21	183	0.79	-1.86	0.085
<i>Platysuccinea portoricensis</i>	44.64	70.86	59	26.21	-3.06	0.009
<i>Polydotes acutangula</i>	1.79	1.86	4	0.07	-0.10	0.925
<i>Polydotes luquillensis</i>	0.64	1.57	144	0.93	-0.67	0.517
<i>Vaginulus occidentalis</i>	0.21	0.79	267	0.57	-1.85	0.088
Entire fauna	91.95	142.09	55	50.14	-3.09	0.009

the distribution of gastropod species and their resultant organization into metacommunities is dynamic.

Mixed forest gradient

The Clementsian structure along the mixed forest transect was complex. The environmental distribution of many species spanned >90% of the strata along the gradient (taxa designated by gray in Fig. 4A). Nonetheless, a few species occurred only at the upper end of the latent environmental gradient (i.e. *Austroselenites alticola*, *Megalomastoma croceum*, *Polydotes luquillensis*), and a few species occurred only at the lower end of the latent environmental gradient (i.e. *Caracolus marginella*, *Cepolis musicola*). An expansive transition zone, representing ~ a third of the latent environmental gradient, harbored only widely-distributed species. All of the species with distributions primarily at the upper end of the latent environmental gradient enjoyed their highest abundances there as well. Finally, most of the species that were ubiquitous exhibited mid-gradient modes in abundance at or near the transition zone between compartments in the metacommunity. A similar analysis of snail distributions along the same elevational transect in 2007 detected a Clementsian pattern as well (Presley et al. 2011), suggesting that this metacommunity structure is stable, at least over the short-term. Finally, the rank order of elevational strata based on gastropod distributions (this study) was significantly correlated ($p = 0.58$, $p = 0.022$) with the rank order of elevational strata based on tree distributions (Barone et al. 2008), corroborating the contention that forest zonation strongly influences gastropod distributions along the mixed forest transect.

Palm forest gradient

The palm forest metacommunity exhibited Gleasonian structure (Table 1). Again, the distribution of many species spanned >90% of the strata along the gradient (taxa

designated by gray shading in Fig. 4B). In addition, nearly half of the species occurred at a larger proportion of strata in the palm forest metacommunity than in the mixed forest metacommunity (i.e. *Alcaldia striata*, *Austroselenites alticola*, *Megalomastoma croceum*, *Oleacina glabra*, *O. playa*, *Polydotes acutangula*, *Vaginulus occidentalis*). In the absence of appreciable variation in tree species composition or physiognomy in palm forest, gastropod species exhibit broader distributions along the gradient, and do so in idiosyncratic and independent fashions, giving rise to a Gleasonian structure.

Considerations of abundance

Importantly, metacommunity structure, as defined by Leibold and Mikkelson (2002) and Presley et al. (2010), is sensitive only to the presence or absence of species, not to variation in abundance along the ranges of species. Thus, the metacommunity approach provides only partial insight about the structure of the fauna along the gradient. Variation in the abundances of each species, as well as differences between matched elevational strata from the mixed and palm forest transects provides complementary insights about biotic structure.

Each species, as well as the gastropod fauna as a whole, enjoyed greater abundances in strata from palm forest than in strata from mixed forest (Table 2). This suggests that when controlling for elevation, palm forest is more productive than mixed forest, at least with respect to limiting resources that are critical for gastropods. The greater productivity in palm forest might also account for its higher species richness of gastropods when controlling for elevation (paired t-test, $t = 2.74$, $p = 0.017$). Indeed, a number of mechanisms, including neutral or random processes, could give rise to this difference in richness between strata along these transects (Scheiner and Willig 2005). A manipulative experiment or syntopic measurements of a number of environmental characteristics along each transect would be necessary to resolve the mechanistic bases of the observed trends in composition and richness.

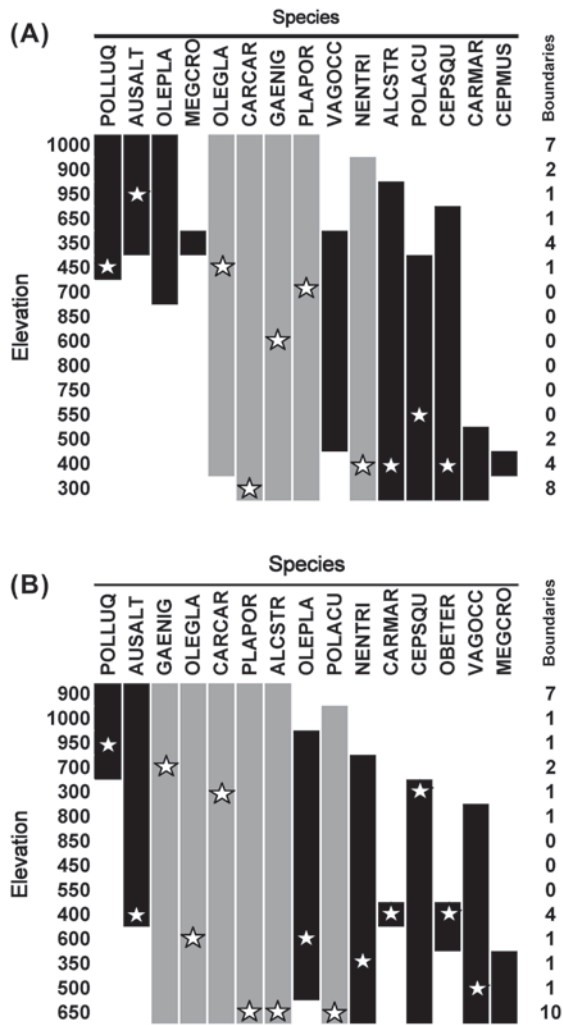


Figure 4. Terrestrial gastropod distributions along latent environmental gradients from two transects in the Luquillo Experimental Forest of Puerto Rico: (A) mixed forest transect, and (B) palm forest transect. Shaded bars represent the distributions of species along a latent environmental gradient as derived via reciprocal averaging (light shading identifies ubiquitous species with distributions at all or all but one stratum; dark shading identifies restricted range species whose distributions contribute to empirical metacommunity structure). Modes of abundance for each species along each transect are indicated with stars (modes were not determined for species whose abundances were always either 0 or 1 for strata). Number of range boundaries that occurred at each elevational stratum is listed to the right of each metacommunity. Abbreviations for gastropod species are: ALCSTR = *Alcaldia striata*, AUSALT = *Austroelenites alticola*, CARCAR = *Caraculus caracolla*, CARMAR = *Caraculus marginella*, CEPMUS = *Cepolis musicola*, CEPSQU = *Cepolis squamosa*, GAENIG = *Gaeotis nigrolineata*, MEGCRO = *Megalomastoma croceum*, NENTRI = *Nenia tridens*, OBETER = *Obeliscus terebraster*, OLEGLA = *Oleacina glabra*, OLEPLA = *Oleacina playa*, PLAPOR = *Platysuccinea portoricensis*, POLACU = *Polydontes acutangula*, POLLUQ = *Polydontes luquillensis*, VAGOCC = *Vaginulus occidentalis*.

Application of spatially-mediated models (Cottenie 2005) to evaluate the relative importance of mechanisms such as patch dynamics, species sorting, mass effects, and neutrality (Holyoak et al. 2005) require a priori identification and measurement of the salient environmental factors to which

the fauna respond along each transect. Nonetheless, distinguishing the role of spatial variation versus environmental variation would be particularly difficult in the context of the Luquillo Mountains, as elevation is a one-dimensional spatial gradient that gives rise to variation in multiple environmental characteristics, making it difficult to decompose their unique contributions to the variation among sites in species composition.

The distribution of modes in the abundance of species was random along the latent environmental gradient in the mixed forest transect (Table 1), an unexpected outcome to be associated with Clementsian structure (based on presence and absence of species). This suggests that the spatial distributions of abundance of many gastropod species were not Gaussian or symmetrical in nature. Most species whose distributions included the lower end of the latent environmental gradient had modes in abundance at low elevations, suggesting that their distributions represented lowland species that can persist up to all but the highest of elevations, where the most extreme environmental conditions occur (i.e. elfin forest). In contrast, modes in the abundance of species were clumped at the lower end as well as at the upper end of the latent environmental gradient (Fig. 4B) in palm forest, an unexpected outcome for a metacommunity with Gleasonian structure.

Structuring mechanisms

The gastropod species that compose these two metacommunities are largely arboreal, with the majority of their active time spent foraging on the surfaces of live or dead woody plants (Garrison and Willig 1996, Willig et al. 1998). As a result, forest type, as defined by tree species composition, may be a primary factor molding patterns of gastropod species distributions. Forest types in the LEF occur in elevational bands, with more-or-less distinctive ecotones marking the transition from one forest to another (Brown et al. 1983). Indeed, a recent analysis of metacommunity structure found significant clumping of range boundaries for trees in the LEF (Barone et al. 2008). Consequently, if gastropod metacommunity structure in the LEF primarily was molded by forest type, then structure along each transect should be distinct. Specifically, the metacommunity along the mixed forest transect should exhibit Clementsian structure with distinct groups of species associated with different forest types, and with species range boundaries that were clumped and coincident with forest ecotones. In contrast, the metacommunity along the palm transect should not exhibit Clementsian structure with compartments that are coincident with elevational limits typically associated with each forest type because forest composition changed little with elevation.

Microclimate (e.g. temperature, humidity) and soil characteristics (e.g. texture, moisture, nutrient content, mineral content, especially Ca, which is critical for shell growth) can be important determinants of terrestrial gastropod distributions (Boycott 1934, Ondina et al. 2004). Many of these characteristics change gradually and predictably with elevation (Brown et al. 1983). Moreover, tolerance to environmental variation generally is a species-specific characteristic of terrestrial gastropods (Riddle 1983). Therefore, if elevation-associated variation in the environment molds species distributions in the absence of multiple forest types, the

metacommunity should exhibit random (or positive) range turnover and randomly distributed range boundaries that are characteristic of Gleasonian distributions. This hypothesis was supported by empirical data from the palm forest transect. Moreover, the random and independent distribution of modes in abundance of gastropods along the mixed forest transect reflect such idiosyncratic responses to environmental variation as well. Taken together, these analyses suggest that the distribution of gastropods in the Luquillo Mountains is affected by two broad correlates of elevational variation: one related to forest type and one related to other biotic and abiotic features.

Noisy systems, complex systems

Although metacommunity structure was different between mixed forest and palm forest transects, appreciable complexity characterized each metacommunity, and patterns with respect to abundance did not mirror those based on presence and absence. Moreover, the correspondence between the latent environmental gradient and elevational position of strata was only modest, albeit significant, in each transect.

A number of factors could contribute to these two phenomena. First, elevation may not be a strong surrogate for environmental characteristics in disturbance-mediated environments, such as those in the Luquillo Mountains. A variety of disturbance events such as hurricanes, landslides, and tree falls can alter abiotic (e.g. temperature, light, humidity, soil characteristics) and biotic (plant species composition) conditions, creating considerable variation within a particular elevational domain, and diminishing the apparent correlation between environmental characteristics and elevation. Second, palm forest occurs as patches within tabonuco, palo colorado, and elfin forest, so that movement of gastropods among palm forest patches and between palm forest and any of the other forest types could be common (Cary 1992). Third, the defining tree species of palm forest (*P. acuminata*) is common in each of the three other forest types. Moreover, most gastropod species occur on sierra palms at all elevations in the Luquillo Mountains (Alvarez 1997), and palms are high in calcium, an essential nutrient for shell anabolism (Sánchez et al. 1997). The proximity of forest types and the ubiquitous distribution of sierra palms in all of them would tend to homogenize structure and increase the likelihood that source-sink dynamics could obscure differences between transects. Fourth, the presence of a single individual is all that is necessary to document the presence of a species. If particular species are rare throughout their elevational range, the stochastic presence or absence of that species would add considerable noise to observed patterns. Given the diversity of factors that would tend to homogenize species composition between elevational strata, it was remarkable that distinctive metacommunity structures could persist in close proximity within the same watershed, and in a disturbance-mediated ecosystem, where the environmental characteristics of sites change during secondary succession in response to tree falls, landslides, cyclonic storms, and human activities (Lugo and Waide 1993).

Mesoscale ecology and synoptic networks

Future research on mesoscale questions, such as those involving elevational gradients and metacommunities, should

explicitly link pattern and process if ecological understanding is to accelerate as rapidly as possible. This may require the deployment of synoptic networks that comprise sites at which species composition and relevant environmental characteristics are measured at scales relevant to the autecological and synecological characteristics of the targeted species. In this manner, both pattern-based (e.g. metacommunity structure sensu Leibold and Mikkelsen 2002, Presley et al. 2010) and mechanism-based (e.g. spatially-mediated mechanistic models sensu Cottenie 2005) approaches can be used in tandem to understand the likely environmental forces that structure biotas. Only with this knowledge in mind, can conservation action be directed at appropriate scales to protect particular combinations of coexisting species.

Acknowledgments – This research was facilitated by a grant (DEB-0218039) from the National Science Foundation to the Inst. of Tropical Ecosystem Studies, Univ. of Puerto Rico, and the Internat Inst. of Tropical Forestry as part of the Long-Term Ecological Research Program in the Luquillo Experimental Forest. Additional support was provided by the USDA Forest Service, the Univ. of Puerto Rico, and the Center for Environmental Sciences and Engineering at the Univ. of Connecticut. The staff of El Verde Field Station provided valuable logistical support in Puerto Rico. We thank L. Jones, N. Rivera and C. Curtis for assistance with field work.

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