

A Complex Metacommunity Structure for Gastropods Along an Elevational Gradient

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ABSTRACT

The metacommunity framework integrates species-specific responses to environmental gradients to detect emergent patterns of mesoscale organization. Abiotic characteristics (temperature, precipitation) and associated vegetation types change with elevation in a predictable fashion, providing opportunities to decouple effects of environmental gradients *per se* from those of biogeographical or historical origin. Moreover, expected structure is different if a metacommunity along an elevational gradient is molded by idiosyncratic responses to abiotic variables (expectation = Gleasonian structure) than if such a metacommunity is molded by strong habitat preferences or specializations (expectation = Clementsian structure). We evaluated metacommunity structure for 13 species of gastropod from 15 sites along an elevational transect in the Luquillo Experimental Forest of Puerto Rico. Analyses were conducted separately for the primary axis and for the secondary axis of correspondence extracted via reciprocal averaging. The metacommunity exhibited quasi-Clementsian structure along the primary axis, which represented a gradient of gastropod species specialization that was unassociated with elevation. The secondary axis represented environmental variation associated with elevation. Along this axis, the metacommunity exhibited Clementsian structure, with specialists characterizing each of three suites of sites that corresponded to three distinct forest types. These forest types are associated with low (tabonuco forest), mid- (palo colorado forest), or high (elfin forest) elevations. Thus, variation among sites in species composition reflected two independent processes: the first decoupled from elevational variation and its environmental correlates, and the second highly associated with environmental variation correlated with elevation.

Key words: Clementsian distributions; coherence; environmental gradients; Gastropoda; Puerto Rico; rain forest; range boundary clumping; range turnover.

PATTERNS OF SPECIES RICHNESS ALONG ELEVATIONAL GRADIENTS have been studied extensively (*e.g.*, Whittaker 1956, Terborgh 1977, Olson 1994, Rahbek 1995, McCain 2005, Wiens *et al.* 2007, McCain 2009), with many considering patterns of species turnover along such gradients (*e.g.*, Whittaker & Niering 1965, Terborgh 1971, Mena & Vásquez-Domínguez 2005, Tattersfield *et al.* 2006). Considerably less work has assessed emergent patterns that result from changes in species composition along elevational gradients (Hoagland & Collins 1997, Hofer *et al.* 1999, Lobo & Halffter 2000). The metacommunity concept (Leibold *et al.* 2004) provides a framework that explicitly incorporates species identity and can be used to evaluate the organization of biotas along environmental gradients. In general, two complementary approaches have been used to evaluate patterns of spatial variation in species composition. One approach uses expectations of spatially mediated mechanistic models (Cottenie 2005) to understand mesoscale variation in site composition and considers the roles of patch dynamics, species sorting, mass effects, and neutrality (Leibold *et al.* 2004, Holyoak *et al.* 2005). Alternatively, a pattern-based approach evaluates characteristics of species distributions along environmental gradients that manifest as particular metacommunity structures

(*e.g.*, checkerboard, nested, evenly spaced, Gleasonian, or Clementsian patterns *sensu* Leibold & Mikkelsen 2002). In ecology and biogeography, recognition of patterns usually is a precursor to the identification of mechanistic bases that explain those patterns. Nonetheless, recent research on metacommunities has largely underplayed identification of spatial patterns based on species distributions and has proceeded directly to a search for structuring mechanisms.

Metacommunity structures represent patterns along a multi-dimensional continuum of possibilities. Historically, several structures (*e.g.*, nested subsets, checkerboards) have been identified to represent idealized expectations if a strong mechanism molds the distributions of a group of species (*e.g.*, taxon or guild). Clements (1916) described a structure comprising multiple communities, with sharp boundaries between communities and distinctive species composition of each community arising from a shared evolutionary history and inter-dependent ecological relationships. In contrast, Gleason (1926) described a structure based on species-specific responses to the environment, with coexistence resulting from chance similarities in requirements or tolerances. Strong interspecific competition may result in trade-offs that manifest as distributions that are more evenly spaced along environmental gradients than expected by chance (Tilman 1982). Alternatively, strong competition may result in checkerboard patterns produced by pairs of species

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with mutually exclusive ranges (Diamond 1975). If such mutually exclusive pairs occur independently of other such pairs, the metacommunity would exhibit a checkerboard structure. Finally, species-poor communities may form nested subsets of increasingly species-rich biotas (Patterson & 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). Although each of these structures originally was associated with particular mechanisms, in most cases multiple mechanisms may give rise to the same structure, and disentangling the relative contribution of each mechanism has been difficult.

Because all species in a community rarely respond to the identical suite of environmental characteristics, empirical structures at best only approximate particular idealizations. As a result, identification of best-fit structures for empirical metacommunities is often difficult, especially without objective criteria to assess the correspondence of empirical data with each of the possible idealizations. Leibold and Mikkelsen (2002) developed a set of objective criteria and a rigorous quantitative approach to simultaneously test the correspondence of an empirical structure to each of a number of hypothetical idealizations of species distribution. Using the same analytical approach, Presley *et al.* (2010) expanded this conceptual framework into a comprehensive approach for evaluation of metacommunity structures. This approach combined an evaluation of three characteristics of species distributions (coherence, range turnover, and range boundary clumping) to identify which hypothetical idealization best approximates an empirical structure. Each non-random structure assumes that species distributions are molded by a combination of biotic interactions (*e.g.*, competition, habitat associations) and responses to abiotic factors (*e.g.*, temperature, rainfall) that vary among sites and constitute an environmental gradient. Moreover, the primary mechanisms that define each idealized structure are unique (Clements 1916, Gleason 1926, Diamond 1975, Tilman 1982, Patterson & Atmar 1986), allowing analyses to simultaneously distinguish among multiple competing hypotheses.

ELEVATION.—Because environmental characteristics (*e.g.*, temperature, precipitation, vegetational composition) to which species respond change with elevation in predictable fashions, elevational gradients are useful platforms from which to address issues of metacommunity structure. In addition, along elevational gradients much environmental variation in abiotic factors can occur in a relatively small geographic area. More specifically, for temperatures above freezing, a 4.9°C decrease occurs for every 1 km increase in elevation (the moist adiabatic lapse rate; Jacobson 2005). To achieve similar variation in climate along latitudinal gradients, approximately 6.5° of latitude outside of the tropics are required to achieve variation associated with a 1 km change in elevation. As a result, ecological studies of biodiversity or species composition along latitudinal gradients may be confounded by historical contingency, such as the existence of multiple species pools or multiple sources of colonization, making the relative contribution of ecological and historical factors unclear. This is particularly important at large spatial scales, where ecological and biogeographic mechanisms

can give rise to similar patterns, and disentangling the relative contribution of each is difficult. For example, latitudinal gradients in species richness likely result from some combination of ecological (*e.g.*, species–area relationships, species–energy relationships, environmental predictability) and evolutionary–historical (*e.g.*, environmental stability, evolutionary time, differential evolutionary speed) mechanisms; however, predictions based on each type of mechanism are the same (increasing richness with decreasing latitude) and disentangling the relative contribution of each is difficult (Rhode 1992, Willig 2000, Willig *et al.* 2003). Variation in species composition is less likely to arise because of historical contingency along elevational gradients than along latitudinal gradients. Consequently, these systems facilitate an uncompromised focus on ecological mechanisms.

Although elevational changes in abiotic characteristics and associated vegetation are predictable, they differ in form. Abiotic characteristics generally change in a gradual fashion with elevation, whereas vegetation associations often have more-or-less discrete boundaries between habitat types or life zones (*e.g.*, Terborgh 1971, Brown *et al.* 1983). Because habitat specializations or responses to abiotic characteristics are important in defining ranges of species, the structure of a metacommunity is contingent on the mechanism that molds species distributions. If habitat boundaries are more-or-less discrete, metacommunities along elevational gradients that are molded by habitat preferences or specializations should evince Clementsian distributions with species having range boundaries that are clumped and coincident with those of the habitats. Conversely, if abiotic characteristics change gradually with elevation, and if species-specific tolerances to abiotic characteristics are idiosyncratic, then metacommunities molded by responses to abiotic characteristics should have Gleasonian distributions. We used the analytical approach of Leibold and Mikkelsen (2002) and the conceptual framework of Presley *et al.* (2010) to evaluate the relative importance of habitat associations and of abiotic characteristics on species distributions and emergent metacommunity structure of terrestrial gastropods along a tropical environmental gradient.

METHODS

STUDY AREA.—The Luquillo Experimental Forest (LEF) comprises 11,300 ha in northeastern Puerto Rico (Fig. S1), and is a Man and the Biosphere Reserve (Franklin 1977) as well as a site in the National Science Foundation's Long-Term Ecological Research Network (Hobbie *et al.* 2003). Three forest types (tabonuco, palo colorado, and elfin) occur in the Luquillo Mountains in association with elevational zones (Brown *et al.* 1983), whereas a fourth forest type (Palm Forest) occurs at all elevations and occupies poorly drained soils. Research was conducted along an elevational gradient in the Sonadora River watershed in the LEF, where a permanent transect was established (Barone *et al.* 2008). The transect spanned 700 m of elevation (from 300 to 1000 m asl) was on the northwest facing slope on clayey soils, and included tabonuco, palo colorado, and elfin forests.

Tabonuco forest occurs at elevations below 600 m, and is the most expansive and best studied portion of the LEF (Reagan &

Waide 1996, Brokaw *et al.* 2011). It is a subtropical wet forest according to the Holdridge classification system (Ewel & Whitmore 1973), 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 *Prestoea acuminata* (Odum & Pigeon 1970, Lawrence 1996). Canopy height is > 20 m, with emergent trees up to 35 m. Rainfall is substantial, averaging 346 cm/yr (McDowell & Estrada-Pinto 1988). Humidity is consistently high, and little seasonal or diurnal variation occurs in temperature (Odum & Pigeon 1970).

Cloud condensation occurs at 600 m in the LEF. Palo Colorado forest begins at this elevation and continues to 900 m. This forest type is named after the Colorado Tree (*Cyrilla racemiflora*), which is the most common large tree in this elevational zone. Other common tree species include *Calycogonium squamulosum*, *Ocotea spathulata*, *Micropholis garcinifolia*, and *Micropholis chrysophylloides* (Brown *et al.* 1983). Canopy height is < 15 m, with lower and denser branching than in tabonuco forest, making distinction of the canopy and subcanopy difficult. Palo Colorado forest supports more vines, epiphytes, herbaceous plants, and a thicker surface network of roots compared with tabonuco forest.

Elfin forest occurs on the summits of mountains and on windward ridges above 900 m in the LEF. Its canopy is 2–3 m tall and comprises short, twisted trees, and shrubs. The three most common plant species are a herb (*Pilea krugii*), a semi-woody plant (*Wallenia yunquensis*), and a woody canopy tree (*C. squamulosum*). Surface roots cover the forest floor and constitute 60 percent of the total forest floor biomass (Lyford 1969). Epiphytes and epiphytic algae cover most woody vegetation (Weaver 1972). Mean monthly rainfall varies from 30 to 60 cm, and relative humidity always is above 95 percent. Mean monthly temperatures range from 16°C to 20°C (Brown *et al.* 1983).

STUDY ORGANISMS.—Terrestrial gastropods are taxonomically diverse and numerically abundant in many ecosystems, making them useful for studies of community or metacommunity structure. In addition, gastropods are ectothermic, constrained in distribution and behavior by desiccation stress (Russell-Hunter 1983, Cook 2001), and are not particularly vagile. Consequently, this fauna has the necessary attributes to study the effects of spatial variation in habitat and microclimate on metacommunity structure along elevational gradients that evince environmental changes over relatively small spatial extents. Forty-four species of terrestrial gastropod are recorded from the LEF (Garrison & Willig 1996); however, only 26 of these forage above the leaf litter, and most are rare or uncommon. Gastropods in the LEF are well understood taxonomically (Garrison & Willig 1996), and respond to small-scale (Alvarez & Willig 1993) and to broad-scale (Willig & Camilo 1991, Secrest *et al.* 1996, Bloch & Willig 2006, Willig *et al.* 2007) disturbances. Habitat associations of some species are well understood (Cary 1992, Alvarez & Willig 1993, Willig *et al.* 1998). Habitat use by gastropods in the LEF spans a gradient from those that occur almost exclusively on soil, leaf litter, rocks, and fallen dead wood (*e.g.*, *Austroselenites alticola*, *Megalomastoma croceum*, *Platysuccinea porto-*

ricensis) to those that occur almost exclusively on live vegetation (*e.g.*, *Gaeotis nigrolineata*, *Polydotes acutangula*); however, the majority of species commonly occur on soil and associated substrates, as well as on live vegetation. In general, particular species of gastropod are not associated with particular species of plant, but *Caracollus caracolla* does select trees based on size and bark texture (Heatwole & Heatwole 1978). Competition among species of gastropod in the LEF has little effect on growth rates or abundances (Bloch & Willig 2009, Bloch & Willig 2010). Nocturnal habits, thick shells, and noxious secretions represent effective defenses against predation (Heatwole & Heatwole 1978).

FIELD METHODS.—The Sonadora transect comprised 15 elevational strata from 300 to 1000 m at 50 m elevational increments. At each stratum, a 0.1 ha (50 m by 20 m) study area was established. Within each study area, ten circular plots (3 m radius) were configured in two parallel rows, each containing five evenly spaced plots with 10 m between plot centers. Each study area was aligned with its long axis perpendicular to the elevational gradient.

At each plot, gastropods were surveyed four times during the wet season (July) of 2007. Sampling was conducted at night (2000–0400 h) to coincide with peak activity of gastropods (Heatwole & Heatwole 1978, Willig *et al.* 1998). During each survey, all available surfaces (*e.g.*, soil, litter, rock cover, vegetation, debris) up to a height of approximately 3 m were inspected for gastropods. All gastropods were identified to species in the field. To minimize the effects of survey sequence on elevational patterns, sampling was not repeated at any one elevation until after the entire gradient was surveyed.

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 & Mayhill 1999, Schilthuisen & Rutjes 2001, Nekola 2005). In contrast, the gastropod fauna of the LEF comprises many large and arboreal or semi-arboreal taxa, and density as well as richness of gastropods in litter samples, typically are quite low (Richardson *et al.* 2005). In contrast, estimates of population density by visual enumeration correlate strongly with mark-recapture estimates for two of the arboreal species (*C. caracolla* and *Nenia tridens*), suggesting that such estimates adequately reflect changes in density over time or space (Bloch 2004). Consequently, our inference space was constrained to include only individuals that occur on or above the leaf litter, an assemblage for which we are confident that our visual sampling method was appropriate.

QUANTITATIVE ANALYSES.—Metacommunity structure was determined for the primary and secondary axes of correspondence (Presley *et al.* 2009) using three characteristics of species distributions (coherence, turnover, and boundary clumping) from an ordinated presence-absence matrix. Each matrix was ordered via reciprocal averaging, which optimizes the simultaneous proximity of sites with similar species compositions and the proximity of species with

similar environmental distributions. Reciprocal averaging is appropriate for identifying patterns in response to gradients because species occurrences determine the position of sites along the axis of correspondence (*i.e.*, latent environmental gradient) without a priori knowledge of the particular factors that govern the response of each species (Gauch *et al.* 1977, Gauch 1982, Leibold & Mikkelsen 2002).

In general, species occur within a range of environmental characteristics and at all suitable locations within that range (*i.e.*, no holes should exist in the fundamental niche of a species). This continuity of environmental response is termed coherence (Leibold & Mikkelsen 2002). For a metacommunity to exhibit coherence, two things must be true. First, species occurrences must be a function of environmental characteristics that differ among sites and that represent a latent gradient of environmental variation for the metacommunity; this latent gradient is a composite of abiotic and biotic environmental characteristics to which species respond. Second, a majority of species must respond to the same latent gradient. Coherence was assessed by comparing the number of embedded absences (*i.e.*, absences that have at least one presence toward each extreme in a row or a column) in the matrix to a distribution of embedded absences produced by a null model (Leibold & Mikkelsen 2002).

For each analysis of coherence, 1000 randomly generated matrices were created using a null model that constrained site richnesses to equal observed values and that had equiprobable species occurrences. This null model creates a biologically realistic null space for evaluation of coherence (Presley *et al.* 2009, 2010). Each randomly generated matrix was subjected to reciprocal averaging.

Embedded absences of the randomly generated matrices were counted and used to create a null distribution, and a z -test based on the mean and variance of that null distribution was used to determine significance. A metacommunity was considered significantly and positively coherent if the likelihood of having fewer embedded absences than expected was $\leq \alpha/2$ (a two-tailed test). A metacommunity was considered significantly and negatively coherent if the likelihood of having more embedded absences than expected was $\leq \alpha/2$. Negative coherence is characteristic of checkerboards, whereas positive coherence is characteristic of 12 coherent structures (Fig. 1). Nonsignificant coherence indicates random structure, and suggests that the distributions of most species are not shaped by the same environmental gradient.

To quantify turnover, the number of times one species was replaced by another for each possible pair of sites was counted in the empirical matrix. A replacement between two species occurs when the range of Species A extends beyond that of Species B at one end of the gradient and the range of Species B extends beyond that of Species A at the other end of the gradient. To determine significance, the observed number of replacements was compared with a null distribution of replacement values created from 1000 matrices that contained randomly shifted species ranges. Significantly negative turnover is indicative of nested distributions. Significant positive turnover is indicative of Gleasonian, Clementsian, or evenly spaced structures. Nonsignificant turnover is characteristic of quasi-structures (Presley *et al.* 2010), with nonsignificant negative turnover indicative of quasi-nested structures and nonsignificant positive turnover indicative of quasi-Gleasonian, quasi-Clementsian, or quasi-evenly spaced structures (Fig. 1).

Boundary clumping	+	Clementsian	Quasi-Clementsian	Quasi-nested clumped species loss	Nested clumped species loss
	NS	Gleasonian	Quasi-Gleasonian	Quasi-nested stochastic species loss	Nested stochastic species loss
	-	Evenly spaced	Quasi-evenly spaced	Quasi-nested hyperdispersed species loss	Nested hyperdispersed species loss
		+	NS (>)	NS (<)	-
		Turnover			

FIGURE 1. Twelve coherent metacommunity structures defined by range turnover and boundary clumping (modified from Presley *et al.* 2010). Significant positive results, +; significant negative results, -; nonsignificant clumping, ns; nonsignificant turnover but with more replacements than the average number in randomly generated metacommunities, ns (>); nonsignificant turnover but with fewer replacements than the average number in randomly generated metacommunities, ns (<).

TABLE 1. Results of analyses of coherence, range turnover and boundary clumping for tropical gastropods in the Luquillo Experimental Forest of Puerto Rico. Analyses were performed separately for the primary and secondary axes of correspondence. Significant results ($P \leq 0.05$) are bold. Abs, number of embedded absences; Rep, number of replacements; SD, standard deviation.

Axis	Inertia	Coherence				Range turnover				Boundary clumping		
		Abs	<i>P</i>	Mean	SD	Rep	<i>P</i>	Mean	SD	Morisita's index	<i>P</i>	Metacommunity structure
Primary	0.34	26	< 0.001	48	4.5	263	0.362	186	83.6	2.167	0.011	Quasi-Clementsian
Secondary	0.25	40	0.001	53	4.0	153	0.024	60	41.1	2.320	0.047	Clementsian

Coherent structures with positive turnover were distinguished via analysis of range boundary clumping (Fig. 1). Similarly, three forms of species loss for nested or for quasi-nested structures were distinguished via analysis of boundary clumping. Morisita's index (I) measures the clumping of species distributional boundaries by counting the number of terminal boundaries at each site. Significance was determined via a χ^2 Goodness-of-Fit test that compared the observed distribution of range boundaries with an expected flat distribution. Range boundaries that occurred at random have $I \sim 1.0$ and are consistent with Gleasonian, quasi-Gleasonian, or stochastic species loss in nested or in quasi-nested structures. An $I > 1.0$ with a significant χ^2 test indicates clumped boundaries and is consistent with Clementsian, quasi-Clementsian, or clumped species loss in nested or in quasi-nested structures. An $I < 1.0$ with a significant χ^2 test indicates hyper-dispersed boundaries and is consistent with evenly spaced, quasi-evenly spaced, or hyper-dispersed species loss in nested or in quasi-nested structures (Fig. 1). Additional details of the analytical and conceptual approaches appear elsewhere (Leibold & Mikkelsen 2002; Presley *et al.* 2009, 2010).

To determine if elevation was associated with the primary or secondary latent environmental gradients as defined by reciprocal averaging, a Spearman's rank correlation was conducted between elevation and the correspondence scores for sites, separately for each axis. The degree of correspondence (not the same as the amount of explained variation) associated with each axis is reflected by its inertia. 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 <http://www.tarleton.edu/~higgins/EMS.htm>). Correspondence scores for primary axes as defined by reciprocal averaging were obtained using the simple correspondence analysis option in Minitab 15.1.30.0. Spearman's rank correlations were conducted in R (R Development Core Team 2009). An α of 0.05 was used for all analyses.

RESULTS

Fifteen species of gastropod were documented during surveys of the elevational transect (Table S1). Only two individuals were recorded for each of two species, *Lamellaxis gracilis* and *Vaginulus occidentalis*. For autecological reasons, these species are difficult to document using our survey methods, making it unlikely that the data accurately reflected the ranges of these species. As a result, we did not include either in analyses of metacommunity structure. The degree of cor-

respondence (percent of total inertia) achieved along the primary and secondary axes of ordination were 34 percent and 25 percent, respectively (Table 1).

The metacommunity exhibited strong positive coherence along each axis (Table 1), indicating that two strong latent gradients existed for gastropods. Along the primary axis, species distributions exhibited nonsignificant positive turnover and positive boundary clumping, consistent with quasi-Clementsian structure. Along the secondary axis, species distributions exhibited significant positive turnover and significant positive boundary clumping, consistent with Clementsian structure.

Rank order of component scores of elevational strata along the primary latent environmental gradient was not correlated with elevation ($\rho = 0.104$, $P = 0.712$). In contrast, rank order of component scores of elevational strata along the secondary latent environmental gradient was very highly significantly correlated with elevation ($\rho = -0.889$, $P < 0.001$).

DISCUSSION

In general, analyses of metacommunity structure are restricted to a single axis (Leibold & Mikkelsen 2002, Presley *et al.* 2009 and sources therein). Nonetheless, the distribution of each species is defined by a suite of biotic and abiotic characteristics, which collectively define the niche (Chase & Leibold 2003). Consequently, it is not surprising that entire groups of species evince responses to multiple axes of ecologically important variation. As a result, examination of structure along multiple gradients should be a regular component of exploratory analyses of metacommunity structure (Presley *et al.* 2009). Such an approach helps to ensure a thorough understanding of structure along environmental gradients as well as the relative contribution of structuring mechanisms. A common criticism of interpretations of ecological data based on multiple axes extracted via reciprocal averaging or similar ordination procedures (*e.g.*, principal components analysis) is that they can produce 'arch' or 'horseshoe' effects, with the secondary axis representing a quadratic distortion of the primary axis and not reflecting a true biological aspect of the data (Gauch 1982). These distortions often result from the primary axis being molded by shared presences and by the secondary axis being molded by shared absences along the same environmental gradient. No arch effect was evident for gastropods in the LEF (Fig. 2), suggesting that the secondary axis of correspondence was independent of the primary axis, and that

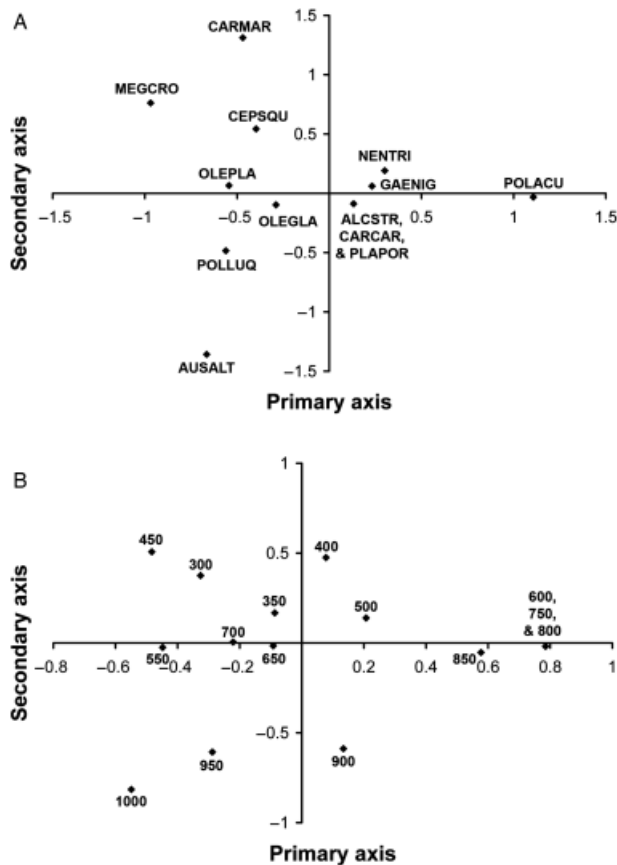


FIGURE 2. (A) Positions of each species of gastropod with respect to the primary and secondary axes of ordination derived via reciprocal averaging; and (B) positions of each elevational stratum with respect to the primary and secondary axes of ordination derived via reciprocal averaging. Abbreviations for gastropod species (panel A) are: ALCSTRI, *Alcaldia striata*; AUSALT, *Austroselenites alticola*; CARCAR, *Caracolis caracolla*; CARMAR, *Caracolis marginella*; CEPSQU, *Cepolis squamosa*; GAENIG, *Gaeotis nigrolineata*; MEGCRO, *Megalomastoma croceum*; NENTRI, *Nenia tridens*; OLEGLA, *Oleacina glabra*; OLEPLA, *Oleacina playa*; PLAPOR, *Platysuccinea portoricensis*; POLACU, *Polydontes acutangula*; POLLUQ, *Polydontes luquillensis*. Numerical values (panel B) represent elevation in meters.

patterns associated with each axis likely represent responses to different and independent aspects of the environment.

AN AXIS OF SPECIALIZATION.—In an analysis of metacommunity structure along a strong environmental gradient, such as that typical of elevational gradients, we expected that the primary axis of correspondence would represent a response to environmental variation that was correlated strongly with elevation. In many previous analyses, this expectation was satisfied, including for analyses of multiple taxa from the LEF, including trees, anoles, stream macroinvertebrates, birds, spiders, and invertebrates that inhabit bromeliads (S. Presley unpubl. data). If an axis of correspondence represents elevation, sites are ordered primarily according to elevation and species are ordered primarily according to the portion of the gradient on which they specialize (*i.e.*, low-elevation specialists

occur at one end of the gradient, high-elevation specialists occur at the other end of the gradient, and specialists on intermediate elevations as well as widely distributed species occur in intermediate areas). Consequently, it is noteworthy that the primary axis of correspondence for gastropods did not represent an elevational gradient in environmental variation (Fig. 2B). Rather, the primary axis reflected a dichotomy between species that did not occur at mid-elevations (*i.e.*, high- or low-elevation specialists) at one end of the gradient and species that did occur at mid-elevations at the other end of the gradient. More specifically, species characteristic of higher (≥ 900 m) or of lower (≤ 500 m) elevations had negative scores on the primary axis, whereas species that occurred throughout the transect or that occurred only at mid-elevations had positive scores (Fig. 2A). This dichotomy resulted in quasi-Clementsian structure, with one group of sites characterized by many high or low elevational specialists and another group of sites that harbored primarily wide-ranging species. This grouping of high and low-elevation specialists, as well as high and low elevational strata, at the same end of the latent environmental gradient was unexpected.

Along the elevational transect in the LEF, *Caracolis marginella*, *Cepolis squamosa*, and *M. croceum* were low-elevation specialists; *A. alticola* was a high-elevation specialist; *Oleacina glabra* and *Oleacina playa* were pervasive at high and at low elevations, but were infrequent at mid-elevations; occurrences of *Polydontes luquillensis* were scattered along the gradient; *Alcaldia striata*, *C. caracolla*, *G. nigrolineata*, *N. tridens*, and *P. portoricensis* occurred throughout the transect; and *P. acutangula* was restricted to mid-elevations (Table S1). These elevational associations of species were similar to those reported previously from eastern Puerto Rico (Heatwole & Heatwole 1978, Alvarez 1997).

Two species of snails (*O. glabra* and *O. playa*) that prey on other snail species occurred at elevation strata below 600 m and above 900 m, but were absent from most of the mid-elevations that are characterized by palo colorado forest. These apparent disjunct spatial distributions likely caused the unexpected association of high- and low-elevation specialists along the primary axis. Unfortunately, little autecological knowledge about *Oleacina* is available to explain this phenomenon. The elevational zone where *Oleacina* were largely absent is characterized by palo colorado forest; however, a forest type dominated by sierra palm (*P. acuminata*) that is restricted to steep, wet slopes, and patches of regenerating forest created by treefalls or landslides occurs throughout this elevational range. *Oleacina playa* and *O. glabra* were found commonly between 600 and 900 m on a nearby parallel transect that was restricted to palm dominated forest (M. Willig unpubl. data), indicating that Palm Forest may act as a dispersal conduit for these species that otherwise appear to have a disjunct spatial distribution along the elevational transect. Many species of snail (*e.g.*, *Alcaldia alta*, *A. striata*, *C. squamosa*, *G. nigrolineata*, *N. tridens*, *Subulina octona*) on which *Oleacina* may prey are associated with sierra palm (Alvarez 1997), possibly because tissues of these trees are high in calcium (Sánchez *et al.* 1997). Consequently, species of *Oleacina* do occur along the entire elevational gradient, but not along the particular transect sampled for this study. Mid-elevational strata of the transect had the least amount of leaf litter or decomposing vegetation as well as the least amount of soil moisture (C. Bloch & B. Klingbeil pers. obs.), which typically is correlated with litter

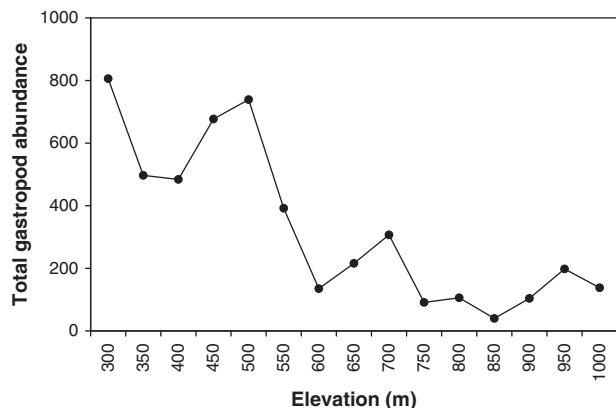


FIGURE 3. Total gastropod abundance along an elevational transect in the Luquillo Experimental Forest, Puerto Rico.

depth. The lack of soil moisture and detritus may combine to decrease survivorship of gastropods during hotter, drier periods and may reduce the amount of forage for some species of snails, many of which commonly feed on dead plant material (Heatwole & Heatwole 1978, Garrison & Willig 1996, Alvarez 1997). Indeed, these portions of the transect harbored the lowest total abundance of gastropods (Fig. 3), despite being covered by forest that is much more productive than the elfin forests that are characteristic of higher elevations. *Oleacina* may be affected by this condition directly via decreased survivorship, as well as indirectly via a decrease in prey abundance. Because *Oleacina* occurred at each extreme of the elevational transect, it is unlikely that *Oleacina* distributions are defined by variation in abiotic factors associated with elevation. Rather, reduction in habitat quality for gastropods created an environmental gradient in which habitats present at higher and lower elevations were more similar in quality for some gastropod species than either was to the intervening elevational strata, thereby creating an unexpected environmental gradient along the primary axis of correspondence.

THE ELEVATIONAL GRADIENT.—The secondary axis of correspondence was highly correlated with elevation, with three discernable groups occurring along this axis: strata below 550 m had positive scores, strata above 850 m had negative scores, and strata between 550 and 850 m, inclusive, had scores approximating zero (Fig. 2B). These three elevational groups were closely associated with the elevational zones traditionally defined as tabonuco (< 600 m), palo colorado (600–900 m), and elfin (> 900 m) forests (Brown *et al.* 1983). Gastropod composition at strata associated with elfin forest was highly distinct from that of lower elevation forests (Fig. 2B). In contrast, differences between strata associated with tabonuco forest and with palo colorado forest were less distinct.

This assemblage of gastropods is largely arboreal, with the vast majority of active individuals occurring on the surfaces of live or dead woody plants, including fallen logs and leaf litter (Garrison & Willig 1996, Willig *et al.* 1998). As a result, tree species composition of forests in the LEF has the potential to mold patterns of gastropod distribution. Primary forest types in the LEF, which are defined by tree species composition and physiognomy, 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 woody plants in the LEF (Barone *et al.* 2008). Consequently, if gastropod metacommunity structure in the LEF primarily was molded by forest type, the metacommunity would 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 concert, the Clementsian structure associated with elevation (Table 1; Fig. 2B), and the proximity of changes in species composition with recognized ecotones between forest types support the hypothesis that habitat preferences or specializations are more important in defining gastropod distributions than are species-specific responses to abiotic variation associated with elevation.

CONCLUDING REMARKS.—Microclimate (temperature, humidity) and soil characteristics (texture, moisture, nutrient content, mineral content) can be important determinants of terrestrial gastropod distributions (Cook 2001). These factors typically are more important than associations with particular plant species. Vegetation primarily influences gastropod populations and assemblages indirectly by altering microclimate or by providing habitat structure and resources, rather than through direct species-specific effects of plants on snails (*e.g.*, Boycott 1934, Beyer & Saari 1977; Ondina & Mato 2001). Some of these environmental characteristics change gradually and predictably with elevation, whereas others are more patchy and heterogeneous in distribution (Brown *et al.* 1983). Moreover, tolerance to environmental variation generally is a species-specific characteristic of terrestrial gastropods (Riddle 1983 and sources therein). For these reasons, we expected gastropods in the LEF to exhibit Gleasonian structure. The gastropod assemblage in the LEF is more arboreal than are the well-studied gastropod assemblages on which our expectations were based (Boycott 1934, Riddle 1983, Russell-Hunter 1983, Tattersfield 1996, Barker & Mayhill 1999, Schilthuisen & Rutjes 2001, Ondina *et al.* 2004, Nekola 2005, Tattersfield *et al.* 2006). For many reasons, being more arboreal may increase the relative importance of foliage in determining gastropod distributions in the LEF, compared with variation in soil characteristics or abiotic conditions. First, vegetation replaces soil or leaf litter as the primary substrate for arboreal gastropods. Second, in wet forests, vegetation helps to reduce evaporation and maintain sufficiently humid conditions. Third, particular plant species and assemblages are associated with particular soil types and soil characteristics (Brown *et al.* 1983); therefore, plant species may be indicators of habitat quality to the extent that they indicate the presence of minerals (especially calcium) that are important to gastropod metabolism. This situation resulted in a Clementsian structure for the gastropod metacommunity that was defined primarily by elevational changes in forest type.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *Abundances for each species and for all gastropods for each elevational stratum along a transect in the Sonadora watershed in the Luquillo Experimental Forest of Puerto Rico.*

FIGURE S1. Map of the Caribbean showing the location, size, and shape of Puerto Rico as well as the location of the Luquillo Experimental Forest (LEF).

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