

Population, community, and metacommunity dynamics of terrestrial gastropods in the Luquillo Mountains: a gradient perspective

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Elevational variation in the Luquillo Mountains creates strong environmental gradients that affect the abundance and distribution of species. Moreover, the geographic mappings of these environmental gradients will likely shift as a consequence of global climate change, subsequently altering patterns of biodiversity. Because they are taxonomically diverse, numerically abundant, responsive to anthropogenic and natural disturbances, and potentially keystone heterotrophs (detritivores, herbivores, and carnivores), terrestrial gastropods represent a model taxon for exploring variation in biodiversity. As a consequence, we synthesize extant knowledge and execute new analyses to explore spatial and environmental variation in multiple aspects of gastropod biodiversity at the population (total abundance as well as abundance of each of 14 species), community (richness, evenness, dominance, rarity, diversity), and metacommunity levels. Mean elevational range size of species increased with increasing elevation, but provided only weak support for the elevational extension of Rapoport's rule. The abundances of most species varied with elevation, and did so in a consistent manner along mixed forest (tabonuco – palo colorado – elfin forest) and palm forest transects. Similarly, community level aspects of biodiversity varied with elevation in a consistent manner in both mixed forest and palm forest transects. Moreover, variation among sites in species composition was similar regardless of whether the ordination was based on incidence (i.e. presence versus absence of species) or abundance (double square root transformed density). This was true for the mixed forest as well as for the palm forest transects. In addition, variation among sites in composition was correlated with elevation. Finally, based on analyses of coherence, range turnover, and boundary clumping, metacommunity structure along the mixed forest transect was Clementsian, whereas along the palm forest transect it was quasi-Gleasonian. Population- and community-level attributes of biodiversity changed gradually, and paralleled variation in total gastropod abundance and net primary productivity in general. Similar mechanisms (more individuals hypothesis or passive sampling) explain both elevational variation and the differences between mixed forest and palm forest transects. Moreover, the higher abundances of gastropods in palm-dominated forest patches is a likely mechanism contributing to differences between metacommunity organization in the mixed forest and palm forest transects.

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Gradients of biodiversity are of considerable theoretical interest as they relate to both spatial and environmental variability (Scheiner and Willig 2005, Colwell 2011, Fox et al. 2011). Elevational gradients in particular provide a powerful test bed in which to examine patterns and processes related to many aspects of biodiversity (Whittaker 1956, 1960, 1965, Whittaker and Niering 1965, Terborgh 1971, 1977, Rahbek 1995, Hoagland and Collins

1997, Hofer et al. 1999, Lobo and Halffter 2000, McCain 2005, 2007a, b, 2009a, Tattersfield et al. 2006). Dramatic variation in a variety of important environmental drivers (e.g. solar insolation or available energy, temperature, and precipitation) is characteristic of elevational gradients. Because this variation occurs over relatively short geographic extents, ecological mechanisms, rather than biogeographical or historical mechanisms, likely mold biotic

responses. This contrasts greatly with latitudinal gradients of biodiversity, in which considerably greater geographic distances are necessary to produce comparable variation in environmental drivers, and where it is much more difficult to disentangle ecological from biogeographical and historical mechanisms (Willig 2000, Willig et al. 2003). Most studies of elevational variation in aspects of biodiversity have focused on gradients of species richness or patterns of metacommunity organization; elevational gradients of species range size or other community level aspects of biodiversity (e.g. species evenness, diversity, dominance or rarity) have enjoyed considerably less attention (Brown et al. 1996, Colwell 2011), even though the latter can vary independently of each other (Stevens and Willig 2002, Wilsey et al. 2005). All of these aspects of biodiversity have received renewed attention because the predicted changes in climate that are associated with greenhouse gas emissions promise to manifest early and most strongly in polar regions or at upper elevations, especially in tropical environs (Franklin et al. 1992, Körner 2007, Colwell et al. 2008, Malhi et al. 2010). Moreover, each of these patterns of biodiversity arises as a consequence of the way in which species distributions respond to salient environmental and spatial gradients (Brown et al. 1996, Sexton et al. 2009).

Elevational gradients of biodiversity

The generalization that species richness declines with increasing elevation enjoyed popular (Brown and Gibson 1983, Begon et al. 1990) and somewhat uncritical support because it mirrored the latitudinal gradient of species richness and because it was promulgated in a number of foundational treatises of modern ecology, including both empirical (Kikkawa and Williams 1971 for New Guinea, Terborgh 1971, 1977 for Peru) and theoretical (MacArthur 1972) perspectives. More recent studies, especially those that are synthetic, control for area and sampling biases, or are based on meta-analyses, suggest that a monotonic decrease in richness with elevation is far from universal and for some taxa may be rare (Rahbek 1995, McCain 2005). Moreover, such studies suggest that empirical patterns are likely driven by a suite of factors, rather than by a single overarching mechanism.

Recent research on aspects of biodiversity that weight richness by measures of importance (e.g. abundance, biomass, frequency of occurrence), such as species evenness, dominance, diversity, and rarity, have documented considerable variability among aspects in responses to gradients of latitude (Stevens and Willig 2002, Willig et al. 2003) and productivity (Wilsey et al. 2005, Vance-Chalcraft et al. 2010). The theory of such gradients is at an early stage of maturation (*sensu* Pickett et al. 1994) and ripe for development based on the detection of recurrent patterns or linkage to established mechanisms.

Elevational gradients of species range size

Prior to the late twentieth century, little research concerned elevational gradients of species range size (for a summary, see MacArthur 1972). Rapoport's rule (the hypothesis that latitudinal ranges of plants and animals are generally smaller at lower latitudes than at high latitudes) was applied to the elevational domain by Stevens (1989) as it was hypothesized that similar mechanisms molded both elevational and latitudinal gradients. This catalyzed a significant increase in the interest in and focus on patterns of range size on mountains (Dunn et al. 2007, McCain 2009a, b, Alexander et al. 2011). More specifically, the extension of Rapoport's rule to elevation (i.e. elevational range sizes of species increase with increasing elevation) was based on the assumption that individuals living at higher elevations experience a wider amplitude of environmental conditions during their lifetimes than do individuals living at lower elevations (Merriam 1894, Adams et al. 1920), resulting in adaptations to an increasing range of environmental conditions with greater elevation. Nonetheless, a broad diversity of methodological, empirical, and conceptual concerns has been expressed about both incarnations of Rapoport's rule, and its relationship to gradients of species richness remains controversial (Rahbek 1995, Lyons and Willig 1997, Taylor and Gaines 1999, Sizling et al. 2009).

Elevational patterns of metacommunity organization

A metacommunity comprises multiple sites (i.e. putative communities) that are connected to each other via the dispersal of species among them (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 multiple spatial scales (Leibold 2011). Although the term only recently appeared in the lexicon of ecology, many themes related to metacommunities emerged in one of the most famous debates that centered on the opposing views of Clements (1916) and Gleason (1926) concerning the structure of communities along environmental gradients. Clements posited that groups of species respond similarly to environmental gradients, resulting in the formation of distinct communities that could be distinguished as a consequence of compositional unity, with the termini of species distributions concentrated at the spatial periphery of each compartment or community (i.e. the community-unit theory). In contrast, Gleason maintained that species responded to gradients in idiosyncratic manners, so that range termini were distributed randomly and distinctive communities were not identifiable with respect to underlying environmental gradients (i.e. the individualistic hypothesis). From

theoretical and empirical perspectives, Terborgh (1971) further developed many of these ideas in his studies of the elevational gradient of metacommunity organization for the avifauna in the Vilcabamba Mountains of Peru. More recently, a number of other configurations of species ranges (i.e. metacommunity structures) with respect to environmental gradients have been identified, including checkerboard (Diamond 1975), nested (Patterson and Atmar 1986), and evenly spaced (Tilman 1982) structures. Although each of these structures originally was associated with a particular mechanism, in most cases multiple mechanisms can give rise to the same structure, and disentangling the relative contribution of each mechanism to metacommunity structure can be challenging.

Although elevational changes in abiotic characteristics and associated vegetation are predictable, they differ in the form of their variation. Edaphic conditions may change abruptly at stratigraphic boundaries, but other abiotic characteristics generally change in a gradual and potentially non-linear fashion with elevation (Barry 1992, Whiteman 2000). In contrast, floral associations along elevational gradients typically have more or less discrete boundaries that are recognized as habitat types or life zones (Kessler 2000, Hemp 2006). The extent and location of faunal ranges may be defined by habitat specializations or by responses to abiotic characteristics. The identity of dominant mechanisms will likely determine the structure of a metacommunity. Habitat boundaries along elevational gradients are more-or-less discrete, therefore animal metacommunities along these gradients that are molded by habitat preferences or specializations should include multiple species with range boundaries that are coincident with ecotones, resulting in Clementsian structure. Conversely, if species-specific tolerances to abiotic characteristics that change gradually with elevation structure animal metacommunities, then distributions should more closely approximate a Gleasonian ideal. Habitat distributions in the Luquillo Experimental Forest (LEF) provide a unique opportunity to disentangle the relative contributions of habitat type and abiotic characteristics to metacommunity structure along elevational gradients.

Luquillo Mountains of Puerto Rico

The Luquillo Mountains arise from the coastal plain of northeastern Puerto Rico (Fig. 1), with a maximum elevation of 1338 m (Picó 1974). Significant changes in climatic conditions attend this elevational variation, including increases in precipitation and solar insolation, as well as decreases in temperature (Picó 1974, Birdsey and Weaver 1982). These broad climatic gradients overlay topographic variability (i.e. summit, slope, swale, and valley) and geomorphic heterogeneity (volcaniclastic versus quartz diorite substrates) to produce a tapestry of conditions to which species respond over ecological and evolutionary time

(Lugo et al. 2012, Waide and Willig 2012). Although precipitation is substantial throughout the year, a modestly less wet period (hereafter the dry season) typically extends from January to April (Brown et al. 1983).

Like the rest of the Caribbean Basin, Puerto Rico is subject to numerous tropical storms and hurricanes (Landsea et al. 1999), with over 2000 hurricanes recorded in the Caribbean islands from 1851 to 2010 <<http://hurricane.csc.noaa.gov/hurricanes/>>. These large-scale disturbances considerably alter spatial dynamics with regard to abiotic conditions, especially those related to temperature and moisture, by effecting extensive defoliation, initiating tree falls and branch falls, and inducing the formation of landslides (Guariguata 1990, Larsen et al. 1999). Indeed, the structure and function of many aspects of the Luquillo Mountains are disturbance-mediated characteristics (Walker et al. 1991, 1996, Lugo and Waide 1993, Willig et al. 2011a, Brokaw et al. 2012).

Forest types

The classical perspective is that three forest types (tabonuco, palo colorado, and elfin) occur in the LEF in association with elevational zones, whereas a fourth forest type (palm) occurs at all elevations (Wadsworth 1949, Brown et al. 1983, Weaver and Gould 2013; Fig. 1). In general, forest types are defined by the dominant large plant species (e.g. trees, shrubs, epiphytes), as well as by physiognomy of the vegetation. Tabonuco forest occurs at elevations up to 600 m, and is the most extensive and best studied portion of the LEF (Reagan and Waide 1996). It is characterized by a dominant hardwood species, *Dacryodes excelsa* (Burseraceae). Palo colorado forest begins at 600 m, the cloud condensation point, and occurs up to 900 m. This forest type is named after the colorado tree, *Cyrilla racemiflora*, the most common large tree at these elevations. Elfin forest occurs on the summits of mountains in the LEF and on windward ridges above 900 m. The three most common species are an herb (*Pilea krugii*), a semi-woody plant (*Wallenia yunqueensis*), and a woody canopy tree (*Calyco-gonium squamulosum*). Palm forest occurs throughout the elevational gradient in the Luquillo Mountains. It occurs on steep slopes and wet soils that are dominated strongly by the sierra palm *Prestoea montana*. Its distribution is fragmented and patchy, as it is interspersed within each of the other forest types in the LEF.

The 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 aspects of biodiversity and metacommunity structure (Steinitz et al. 2005,

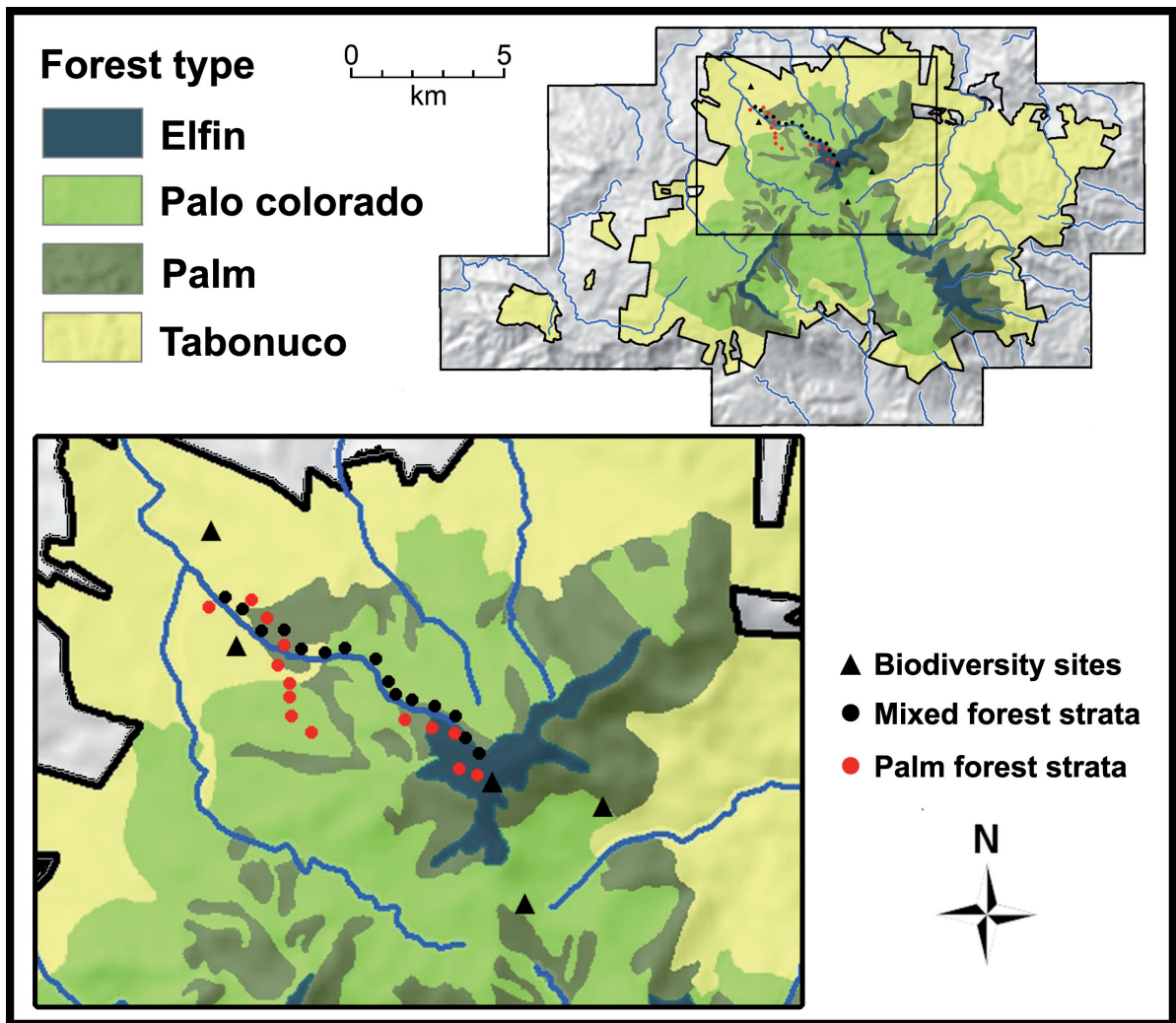


Figure 1. Map (modified from McDowell et al. 2012) of the Luquillo Experimental Forest, Puerto Rico, showing the distribution of major forest types in the LEF, and locations of study sites for three elevational transects within the LEF. In the fine grained study, the mixed forest transect (black dots) had 15 elevational strata from 300 m to 1000 m, the palm forest transect (red dots) had 14 elevational strata that occurred every 50 m of elevation (except for 750 m) from 300 to 1000 m. In the coarse grained study, the elevational transect (triangles) had five strata that occurred every 200 m of elevation from 200 to 1000 m. Major rivers are indicated by blue lines.

Stanisic et al. 2007, Clements et al. 2008, Wronski and Hausdorf 2010, Presley et al. 2011, Willig et al. 2011b). Moreover, terrestrial gastropods, like non-marine mollusks in general, are suffering global declines and require science-informed conservation action and management (Lydeard et al. 2004). Consequently, considerable urgency exists for understanding mesoscale variation in gastropod biodiversity and the factors that affect it. In addition, gastropods are ectothermic and constrained in distribution and behavior by desiccation stress (Russell-Hunter 1983, Cook 2001). They cannot quickly escape desiccation associated with higher temperature and lower humidity because they are not particularly vagile. In conclusion, the suite of attributes characterizing this fauna suggest that there would

be species-specific responses to spatial variation in habitat or microclimate that might be reflected in elevational gradients, where dramatic environmental changes occur over relatively small spatial extents (Tattersfield et al. 2001, Aubry et al. 2005, Chiba 2007, Liew et al. 2010).

Forty-four species of terrestrial gastropod are recorded from the LEF (Garrison and Willig 1996); however, only 26 of these species forage above the leaf litter, and most are rare (Table 1). Gastropods in the LEF are well understood taxonomically (Garrison and Willig 1996), and habitat associations of some species are well documented (Cary 1992, Willig et al. 1998). Habitat use by gastropods in the LEF spans a gradient from species that occur almost exclusively on soil, leaf litter, rocks, and fallen dead wood (e.g.

A. alticola, *M. croceum*, *P. portoricensis*) to those that occur almost exclusively on live vegetation (e.g. *G. nigrolineata*, *P. acutangula*); however, the majority of species commonly occur on litter, as well as on live vegetation (Table 1). In general, particular species of gastropod do not maintain strong associations with particular species of plant; however, they may select particular trees based on size and bark texture (Heatwole and Heatwole 1978). Competition among species of gastropod in the LEF has little effect on growth rates or abundances (Bloch and Willig 2009, 2011). Nocturnal habits, thick shells, and noxious secretions represent effective defenses against predation (Heatwole and Heatwole 1978).

Goals

We synthesize new data along with information in the literature to better understand spatial dynamics of multiple aspects of biodiversity for terrestrial gastropods in the Luquillo Mountains. Nonetheless, our approach is not comprehensive. Rather, we focus on gradients of biodiversity (i.e. species range size, abundance, composition, richness, evenness, dominance, diversity and rarity), as well as patterns of metacommunity structure, that emerge as a consequence of elevational variation in abiotic and biotic characteristics.

Focal studies

Elevational gradients in aspects of gastropod biodiversity were studied based on two different experimental designs, each at different locations in the Luquillo Mountains and each at different times with respect to hurricane impacts. The earlier study (for details, Alvarez 1997) was more coarse grained in that only five elevational strata were surveyed from 200 to 1000 m, at 200 m intervals, whereas the latter study (for details, Presley et al. 2011 and Willig et al. 2011b) was more fine grained and restricted to the Sonadora River watershed, where elevational strata were surveyed from 300 to 1000 m, at 50 m intervals. Only the salient features of these studies are described here.

To minimize alteration of plots in both studies, substrates were disturbed as little as possible during the search for gastropods. This approach excluded small, litter-dwelling species from consideration. This issue is problematic when attempting a complete taxonomic inventory of a region (Cameron and Pokryszko 2005) because most individuals and taxa dwell in the leaf litter in many terrestrial gastropod assemblages (Tattersfield 1996, Barker and Mayhill 1999, Schilthuizen and Rutjes 2001, Nekola 2005). In contrast to such gastropod assemblages, 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). Consequently,

the assemblage under consideration in each focal study 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. Unless otherwise specified, statistical analyses were executed using R (R Development Core Team 2009).

Coarse grained study

Elevational strata were established at 200 m (Highway 186), 400 m (near El Verde Field Station), and 600 m (at Highway 191), as well as along the service road to the communication towers on El Yunque at 800 m, and 1000 m (Fig. 1). When possible, each stratum comprised thirty sites (6 × 6 m square quadrats), equally representing three categories of canopy openness (i.e. 0–10% openness, 11–20% openness, and 21–30% openness) based on densiometer readings. Only two canopy openness categories (0–10 and 11–20%) were present at 200 and 400 m, reducing total number of quadrats in the study to 130.

Sites with canopy openness > 10% were uncommon in the study area; therefore, these quadrats were established in any suitable location. Quadrats in closed-canopy forest (openness ≤ 10%) were selected based on randomly generated directions and distances (between 12 and 20 m) from the center of a quadrat with more open canopy. Each quadrat was searched for terrestrial gastropods from the leaf litter to a height of 3 m between 19:00 and 04:00 h. Each quadrat was surveyed twice during the dry season (March–April 1993) and twice during the wet season (June–August 1993). All elevations were surveyed once before any elevation was surveyed for a second time during a particular season.

Variation in species range size

For each gastropod species, range size was estimated as its elevational extent between 200 and 1000 m. This is an underestimate for low elevation species that may extend further into the lowlands of the island. Elevational gradients in range size were quantified by calculating the mean elevational range size of all species that occur at a particular stratum with elevation. Two factors argue against use of statistical inference in these analyses: the non-independence of data points and the small number of elevational strata.

Variation in population-level aspects of biodiversity

For each species of gastropod, elevational variation in site abundance was evaluated taking into account the effects of season (wet versus dry) and canopy openness (0–10% openness versus 11–20% openness) via a repeated measures (season) two-way (elevation and openness) analysis of variance (Program MANOVA, SPSS 1990). The absence

Table 1. Foraging location, guild, and shell size for gastropods that occur in the Luquillo Experimental Forest of Puerto Rico.

Order	Family	Species	Foraging location*	Guild**	Mean shell size***	Maximum shell size***
Mesogastropoda						
Cyclophoridae						
		<i>Megalomastoma croceum</i>	SL	G	20.5†	30
		<i>Megalomastoma verruculosum</i>	L	G	10.2†	
Pomatiidae						
		<i>Chondropoma riisei</i>	V	G	12.4†	
		<i>Chondropoma yunquei</i>	V	G	13.0†	
Neritoida						
Helicinidae						
		<i>Alcadia alta</i>	V	G	4.8	10
		<i>Alcadia striata</i>	V	G	9.1	20
Stylommatophora						
Amphibulimidae						
		<i>Caeotis nigrolineata</i>	V	G		
Clausiliidae						
		<i>Nenia tridens</i>	LV	G	25.6	29
Euconulidae						
		<i>Guppya gundlachi</i>	L	G	2.5†	
		<i>Habroconus ernsti</i>	LV	G	2.8†	
Haplotrematidae						
		<i>Austroselenites alticola</i>	L	C	20.5†	25
Helminthoglyptidae						
		<i>Cepolis squamosa</i>	LV	G	14.3	25
		<i>Cepolis musicola</i>	LV	G	6.0†	15
Limacidae						
		<i>Deroceras laeve</i>	L	G		
Oleacinidae						
		<i>Oleacina glabra</i>	V	C	24.3	30
		<i>Oleacina interrupta</i>	V	C	23.2†	
		<i>Oleacina playa</i>	V	C	22.1	35
Pleurodontidae						
		<i>Pleurodonte caracolla</i>	LV	G	41.5	80
		<i>Pleurodonte marginella</i>	LV	G	32.5†	45
		<i>Polydontes acutangula</i>	V	G	35.5	65
		<i>Polydontes lima</i>	V	G	25.5†	35
		<i>Polydontes luquillensis</i>	LV	G	32.9	
Pupillidae						
		<i>Pupisoma minus</i>	V	G	1.5†	

Table 1. Continued.

Order	Family	Species	Foraging location*	Guild**	Mean shell size***	Maximum shell size***
		<i>Pupisoma dioscoricola</i>	V	G	1.5†	
		<i>Vertigo hexodon</i>	LV	G	1.7†	
	Sagdididae					
		<i>Hyalosagda selenina</i>	LV	G	4.7†	
		<i>Platysuccinea portoricensis</i>	LV	G	18.8†	25
		<i>Yunquea denselirata</i>	L	G	4.0†	
	Subulinidae					
		<i>Lamellaxis gracilis</i>	L	G	5.5†	10
		<i>Lamellaxis micra</i>	L	G	4.0†	
		<i>Leptinaria unilamellata</i>	L	G	8.3†	
		<i>Obeliscus terebraster</i>	L	G	28.3†	30
		<i>Obeliscus swiftianus</i>	L	G	8.0†	
		<i>Obeliscus hasta</i>	L	G	17.1†	
		<i>Opeas alabastrinum</i>	L	G		
		<i>Opeas pumilum</i>	L	G	4.5†	
		<i>Subulina octona</i>	L	G	14.0†	15
	Thysanophoridae					
		<i>Thysanophora plagiptycha</i>	L	G	2.5†	
	Zonitidae					
		<i>Nesovitrea subhyalina</i>	LV	G		
		<i>Glyphyalinia indentata</i>	L	G	5.0†	
		<i>Striatura meridionalis</i>	V	G	1.4†	
		<i>Zonitoides arboreus</i>	L	G	4.1†	
	Systelommatophora					
	Veronicellidae					
		<i>Diplosolenodes occidentalis</i>	LV	G	NA	

* Foraging locations: S, soil; L, litter and debris; V, live vegetation (Garrison and Willig 1996).

** Guild categories: C, carnivore; G, grazers of algae, fungi, or detritus.

*** Mean diameter (mm) of shell for heliciform species or mean length of shell for non-heliciform species (Alvarez 1997).

† Only available measurement from a single 'representative' individual (Van Der Schalie 1948).

of more open sites (21–30% openness) at lower elevations (200 and 400 m) prevented inclusion of that openness category in statistical analyses.

Variation in community-level aspects of biodiversity

Mean species richness, evenness (Pielou's J index [Pielou 1966]), and diversity (Shannon's index [Pielou 1975]) were estimated for sites within categories of season (wet and dry), canopy openness (1–10 and 11–20%) and eleva-

tion (200, 400, 600, 800, and 1000 m). For each index separately, mean data were subjected to a doubly repeated measures (season within combinations of canopy openness and elevation) analysis of covariance without replication.

Fine grained study

Research was conducted along two parallel elevational transects in the Sonadora River watershed (Fig. 1). Each

transect extended from 300 to 1000 m, and was on the northwest-facing slope on clayey soils (Picó 1974). One transect included tabonuco, palo colorado, and elfin forests (hereafter mixed forest transect), whereas the other included only sites that were heavily dominated by the sierra palm (hereafter, palm forest transect). The mixed forest transect comprised 15 elevational strata from 300 to 1000 m at 50-m elevational increments. An analogous design characterized the palm forest transect, except that no area of palm-dominated forest existed at 750 m in the Sonadora watershed; therefore, the palm forest transect comprised only 14 elevational strata.

Ten circular plots (3 m radius) were established at each elevational stratum in each transect. Gastropods were sampled from each plot of the mixed forest transect four times during the wet season of 2007, and from each plot of each transect three times during the wet season of 2008. Analyses were conducted separately for each year. Sampling was conducted at night (20:00–04:00 h) 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 surfaces (e.g. soil, litter, rock cover, vegetation, debris) up to a height of approximately 3 m until all substrates had been completely searched or for 15 min, whichever was longer. All gastropods were identified to species in the field. To minimize effects of sampling sequence on elevational patterns, sampling was not repeated at any stratum until after the entire gradient was sampled.

Variation in population-level aspects of biodiversity

For each species of gastropod, as well as for total abundance, elevational variation in plot abundance was evaluated taking into account the effects of transect (mixed forest and palm forest) via an analysis of covariance (transect as factor; elevation as covariate). In this context, a significant transect \times elevation interaction suggests that elevational variation in environmental characteristics operates differently in the two transects. In addition, least squares analysis between abundance and elevation were executed separately for each species and for the combined fauna on each transect.

Variation in community-level aspects of biodiversity

Species richness, evenness (Camargo's index [Camargo 1995]), diversity (Shannon's index), dominance (Berger-Parker index [Berger and Parker 1970]) and rarity (the number of species at a stratum whose proportional abundance at that stratum was less than the inverse of species richness [Stevens and Willig 2002]) were estimated separately for each plot within each stratum for each transect. For each community-level index of biodiversity, elevational variation was evaluated taking into account the effects of transect (mixed forest and palm forest) via an analysis

of covariance (transect as factor; elevation as covariate). In this context, a significant transect \times elevation interaction suggests that elevational variation in environmental characteristics operates differently in the two transects. In addition, simple linear regressions between each index and elevation were executed separately for each transect.

Metacommunity analysis

Following well-established quantitative methods (Leibold and Mikkelsen 2002, Presley et al. 2009, 2010), we determined the best-fit structure for a metacommunity for mixed forest and palm forest transects by estimating three characteristics of species distributions: coherence, species range turnover, and range boundary clumping (Fig. 2, 3). This approach is based on three objective criteria to test the correspondence of an empirical structure to each of a number of hypothetical idealizations (Fig. 2) of species distribution along a latent environmental gradient (Leibold and Mikkelsen 2002, Presley et al. 2010). Each non-random structure assumes that species distributions are molded by a combination of biotic interactions (e.g. competition, habitat associations) or responses to abiotic factors (e.g. temperature, rainfall) that vary among sites and constitute an environmental gradient.

Prior to analysis, an incidence (presence-absence) 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. Ordination axes represent latent environmental gradients to which the biota responds. In general, species occur within a range of each environmental characteristic and should be able to exist at all suitable locations within such ranges (i.e. no holes should exist in the niche of a species). This continuity of range along a gradient is termed coherence (Leibold and Mikkelsen 2002). For an entire metacommunity to exhibit coherence, the distributions of a preponderance of species must be molded by the same latent environmental gradient. Such metacommunities will have one of 12 possible coherent structures (Fig. 3), which are distinguished by combinations of species range turnover and range boundary clumping (Presley et al. 2010). To quantify turnover, the number of times one species replaced another along a latent environmental gradient was counted in the empirical matrix for each possible pair of sites. 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. Morisita's index (I) measures the clumping of species distributional boundaries at each site. Significance was determined via a χ^2 goodness-of-fit test that compared the observed distribution of range boundaries to an expected flat distribution. To determine if elevation was associated with the latent environmental gradient as defined by re-

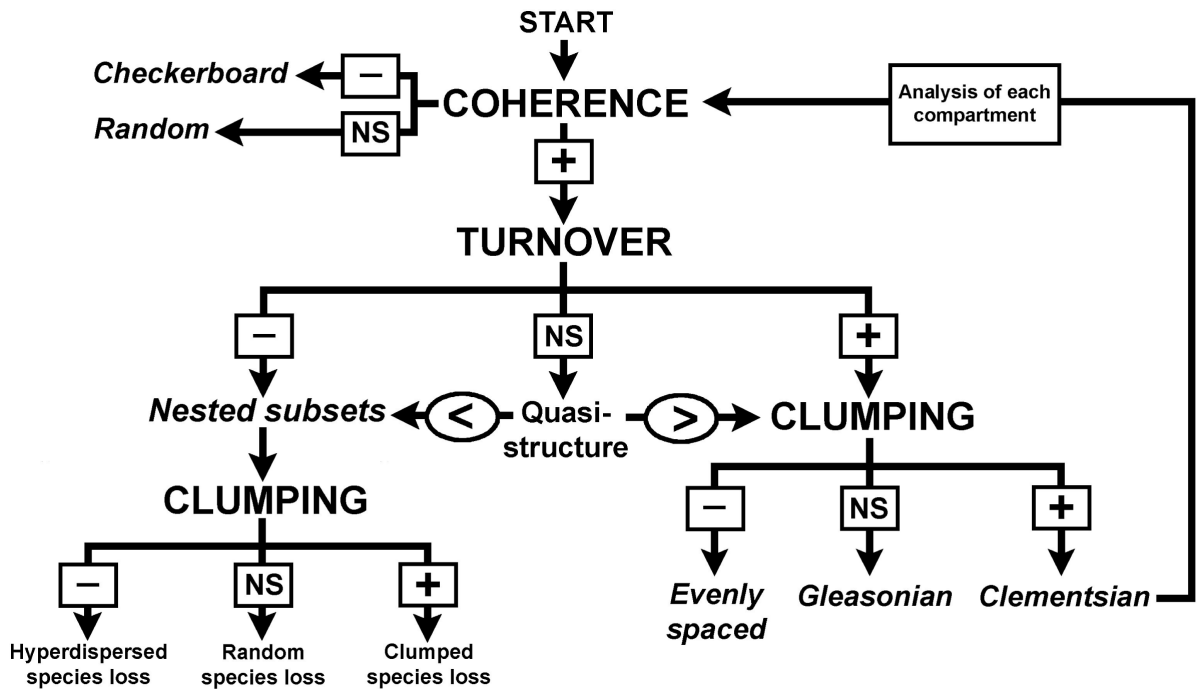


Figure 2. Diagrammatic representation of the conceptual approach for determination of best-fit metacommunity structure via analysis of coherence, range turnover, and range boundary clumping and combinations of results that are consistent with each of six idealized structures (Leibold and Mikkelson 2002), three patterns of species loss for nested subsets, six quasi-structures, and structures of compartments within Clementsian distributions. Boxes designate statistical results; ovals indicate direction of non-significant turnover (from Presley et al. 2010).

reciprocal averaging, a Spearman rank correlation was conducted between stratum scores and elevation in meters for each transect.

Variation in species composition

We used PROXIMITIES (SPSS 15.0.0) to create pair-wise similarity values for each pair of elevational strata for each elevational transect. Similarity of species composition for elevational strata based on incidence data was estimated based on a geometric mean using Ochiai's index. Similarity of gastropod communities at elevational strata based on abundance data was estimated using Euclidean distances. For each analysis, the resultant stratum by stratum matrix of compositional similarity was subjected to analysis by classical non-metric multidimensional scaling (MDS) for ordinal data (Schiffman et al. 1981, Young 1981) using ALSCAL (SPSS 15.0.0). MDS is a non-parametric analog of principal components analysis that facilitates the visualization of inter-stratum similarity and delineation of groups of strata with similar species composition based on incidence or abundance. To quantify the extent to which particular species contributed to stratum differences from the MDS based on Euclidean distances, we calculated the Spearman rank correlation between abundances of each species and stratum scores for each axis separately. To de-

termine if the rank order of sites along the first dimension produced via MDS was similar for analyses based on incidence and abundance data, a Spearman rank correlation was conducted between stratum scores.

Results

Species range size

Mean elevational range of species increased with elevation (Fig. 4). Nonetheless, the elevational rate of increase in range size was quite low (17 m per 100 m), with the smallest mean range size (646 m) at 200 m and at 400 m, and the largest mean range size (760 m) at 800 m and at 1000 m. Three phenomena contributed to this pattern. First, four species were restricted to lower elevations (*P. marginella*, *C. squamosa*, *N. tridens*, and *D. occidentalis*). Second, only one species was restricted to higher elevations (i.e. *P. luquillensis*). Finally, most of the fauna (9 of 14 species) was ubiquitous, occurring throughout the elevational gradient. At best, the observed increase in range size with elevation in the absence of statistical inference provides only the weakest of support for the elevational extension of Rapoport's rule (Stevens 1992).

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 3. Twelve coherent metacommunity structures defined by combinations of species range turnover and range boundary clumping. Quasi-structures are shaded. Significant positive results, +; significant negative results, -; non-significant clumping, NS; non-significant turnover but with more replacements than the average number in randomly generated metacommunities, NS (>); non-significant turnover but with fewer replacements than the average number in randomly generated metacommunities, NS (<). Modified from Presley et al. (2010).

Elevational variation in population-level aspects of biodiversity

Coarse grained study

In both wet and dry seasons, mean abundances varied greatly among species within elevational strata (Table 2). Moreover, the abundances of most species (9 of 10) differed among elevational strata (Table 3). Five species differed with elevation in the same manner regardless of season or canopy openness (i.e. *A. alticola* [maximum at 1000 m], *N. tridens* [maximum at 600 m], *O. glabra* [maximum at 400 m], *P. acutangula* [maximum at 400 m], and *P. luquillensis* [maximum at 1000 m]). The way in which abundance differed among elevational strata depended on season for four species (*A. alta* [maximum at 200 m], *C. squamosa* [maximum at 200 m], *G. nigrolineata* [maximum at 400 m], and *P. caracolla* [maximum at 200 m]). Finally, the way in which abundance differed with elevation was complex for *P. portoricensis* (maximum at 600 m), and contingent on the interaction between season and openness category.

Fine grained study

The abundances of most species varied significantly with elevation (Table 4). Elevational variation in abundance

was consistent, regardless of transect, for 9 species (6 at the 0.05 alpha level and 3 at the 0.10 alpha level) and differed with transect for two species. The abundances of three species did not vary significantly with elevation. For

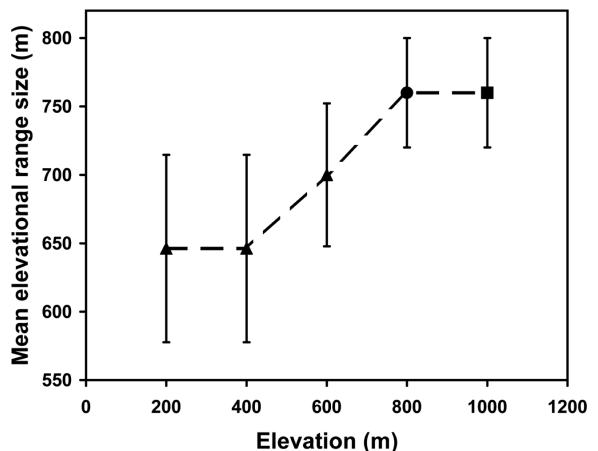


Figure 4. Relationship between mean elevational range size (± 1 SE) and elevation for 14 species of gastropod from the Luquillo Experimental Forest, Puerto Rico (coarse grained study; after Alvarez 1997). Symbols indicate elevationally defined forest types: triangles (\blacktriangle), tabonuco forest; circles (\bullet), palo colorado forest; and squares (\blacksquare), elfin forest.

Table 2. Mean density (\pm 1 standard deviation) for each of 14 species and 3 estimates of mean biodiversity of gastropods along an elevational gradient in the Luquillo Experimental Forest during the dry season and during the wet season (coarse grained study; after Alvarez 1997). Descriptive statistics are based on 30 sites (36 m²) for 600, 800, and 1000 m elevations (all 3 canopy opening categories) and are based on 20 sites (36 m²) for 200 and 400 m elevations (excluding canopy opening > 20%).

Species abundance	Dry season					Wet season				
	200	400	600	800	1000	200	400	600	800	1000
<i>Alcadia alta</i>	0.10 \pm 0.31	0.00 \pm 0.00	0.00 \pm 0.00	0.13 \pm 0.43	0.03 \pm 0.18	1.15 \pm 1.35	0.00 \pm 0.00	0.07 \pm 0.25	0.13 \pm 0.35	0.03 \pm 0.18
<i>Alcadia striata</i>	0.00 \pm 0.00	0.20 \pm 0.52	0.20 \pm 0.61	0.07 \pm 0.25	0.37 \pm 0.85	0.05 \pm 0.22	0.25 \pm 0.64	0.43 \pm 1.33	0.10 \pm 0.31	0.37 \pm 0.61
<i>Austroselenites alticola</i>	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00	0.03 \pm 0.18	0.13 \pm 0.35	0.05 \pm 0.22	0.00 \pm 0.00	0.00 \pm 0.00	0.03 \pm 0.18	0.07 \pm 0.25
<i>Cepolis squamosa</i>	0.25 \pm 0.55	0.25 \pm 0.79	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00	1.10 \pm 1.92	0.45 \pm 1.05	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00
<i>Diplosolenodes occidentalis</i>	0.00 \pm 0.00	0.00 \pm 0.00	0.03 \pm 0.18	0.00 \pm 0.00	0.00 \pm 0.00	0.05 \pm 0.22	0.15 \pm 0.49	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00
<i>Gaeotis nigrolineata</i>	0.40 \pm 0.88	4.35 \pm 7.63	3.30 \pm 6.67	5.10 \pm 5.27	0.27 \pm 0.52	0.25 \pm 0.55	2.60 \pm 2.33	1.40 \pm 3.05	1.73 \pm 2.89	0.03 \pm 0.18
<i>Nenia tridens</i>	0.05 \pm 0.22	1.00 \pm 1.41	1.37 \pm 2.50	0.00 \pm 0.00	0.00 \pm 0.00	0.30 \pm 1.34	1.25 \pm 1.21	1.83 \pm 3.17	0.00 \pm 0.00	0.00 \pm 0.00
<i>Oleacina playa</i>	0.10 \pm 0.31	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00	0.10 \pm 0.31	0.05 \pm 0.22	0.00 \pm 0.00	0.00 \pm 0.00	0.03 \pm 0.18
<i>Oleacina glabra</i>	0.05 \pm 0.22	0.10 \pm 0.31	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00	0.25 \pm 0.44	0.45 \pm 0.76	0.13 \pm 0.43	0.07 \pm 0.25	0.07 \pm 0.25
<i>Platysuccinea portoricensis</i>	0.05 \pm 0.22	0.20 \pm 0.89	0.23 \pm 0.50	0.20 \pm 0.48	0.13 \pm 0.35	0.85 \pm 1.39	0.65 \pm 1.60	0.83 \pm 0.79	0.73 \pm 0.91	0.53 \pm 1.22
<i>Pleurodonte caracolla</i>	8.35 \pm 4.93	1.60 \pm 2.44	1.47 \pm 1.78	0.47 \pm 1.50	0.00 \pm 0.00	16.75 \pm 10.93	4.50 \pm 6.29	2.20 \pm 2.09	0.67 \pm 1.03	0.03 \pm 0.18
<i>Pleurodonte marginella</i>	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00	0.10 \pm 0.31	0.05 \pm 0.22	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00
<i>Polydontes acutangula</i>	0.05 \pm 0.22	0.35 \pm 0.59	0.27 \pm 0.52	0.33 \pm 0.61	0.03 \pm 0.18	0.30 \pm 0.47	0.60 \pm 1.23	0.33 \pm 0.80	0.53 \pm 0.97	0.00 \pm 0.00
<i>Polydontes luquillensis</i>	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00	0.40 \pm 0.62	0.00 \pm 0.00	0.00 \pm 0.00	0.07 \pm 0.25	0.20 \pm 0.55	0.53 \pm 0.82
Community-level aspects of biodiversity										
Species richness	1.60 \pm 0.75	2.35 \pm 1.42	2.00 \pm 1.11	1.60 \pm 0.77	1.65 \pm 1.10	3.10 \pm 1.52	3.65 \pm 1.79	2.83 \pm 1.26	1.93 \pm 1.17	2.38 \pm 1.60
Shannon diversity	0.12 \pm 0.13	0.34 \pm 0.19	0.23 \pm 0.19	0.13 \pm 0.16	0.11 \pm 0.17	0.25 \pm 0.12	0.43 \pm 0.21	0.37 \pm 0.17	0.23 \pm 0.20	0.12 \pm 0.19
Pielou's J index (evenness)	0.63 \pm 0.18	0.85 \pm 0.21	0.88 \pm 0.16	0.79 \pm 0.15	0.92 \pm 0.10	0.63 \pm 0.21	0.91 \pm 0.10	0.92 \pm 0.12	0.89 \pm 0.16	0.93 \pm 0.07

Table 3. Results (p-values) of repeated measures (season) two-way analyses of variance that evaluate changes in abundance for 11 species of gastropod in response to elevation and canopy openness (course grained study; after Alvarez 1997). Significant results ($p \leq 0.05$) are bold. Significance of factors or interactions was not interpreted if they appear as components within significant higher order interactions (Sokal and Rohlf 1995).

	Elevation	Openness	Season	Higher order interactions			
	(E)	(O)	(S)	E × O	E × S	O × S	E × O × S
<i>Alcadia alta</i>	< 0.001	1.000	0.005	0.960	< 0.001	0.792	0.999
<i>Alcadia striata</i>	0.165	0.403	0.084	0.204	0.806	0.384	0.698
<i>Austroselenites alticola</i>	0.046	0.389	0.425	0.308	0.389	0.425	0.914
<i>Cepolis squamosa</i>	< 0.001	0.065	0.038	0.256	0.034	0.368	0.761
<i>Gaeotis nigrolineata</i>	< 0.001	0.930	< 0.001	0.252	0.021	0.594	0.875
<i>Nenia tridens</i>	< 0.001	0.613	0.171	0.810	0.775	0.844	0.949
<i>Oleacina glabra</i>	0.007	0.550	0.001	0.903	0.177	0.268	0.252
<i>Platysuccinea portoricensis</i>	0.503	0.154	< 0.001	0.414	0.485	0.013	0.029
<i>Pleurodonte caracolla</i>	< 0.001	0.149	< 0.001	0.783	< 0.001	0.134	0.188
<i>Polydotes acutangula</i>	0.035	0.038	0.250	0.067	0.261	0.005	0.103
<i>Polydotes luquillensis</i>	0.001	0.735	0.026	0.599	0.199	0.652	0.935

species with consistent elevational variation, abundances decreased with increasing elevation. A consistent mean difference in abundance between transects characterized 5 species. In contrast, the abundances of only two species differed between transects in a way that depended on elevation. The abundances of 7 species were indistinguishable between transects. Nonetheless, the sample mean of abundance was always higher in the palm forest transect than in the mixed forest transect (Willig et al. 2011b). Finally, the way in which elevation affected total abundance differed between transects (Table 4). Total abundance decreased more rapidly with elevation on the palm forest transect than on the mixed forest transect (Fig. 5F).

Elevational variation in community-level aspects of biodiversity

Coarse grained study

In general, all attributes of biodiversity varied with elevation and did so in a consistent fashion, that is, without interaction with canopy openness or season (Table 5). Nonetheless, the direction of the association differed among attributes (i.e. evenness increases with increasing elevation, whereas richness, diversity, dominance, and rarity decrease with increasing elevation; Fig. 5). More specifically, mean richness declined significantly with elevation ($p = 0.001$); season had a consistent additive effect ($p = 0.018$) in that richness in the wet season was higher than in the dry season. This seasonal difference is most likely a consequence of behavioral differences in activity rather than a reflection of true changes in aspects of biodiversity,

per se. In contrast, mean evenness increased significantly with elevation ($p = 0.002$); neither canopy openness nor season affected variation. Diversity is a composite attribute (richness weighted by abundance); consequently, it reflects the combined effects of richness and evenness. Because richness decreases and evenness increases with elevation, diversity may have only a weak relationship to elevation. In fact, mean diversity declined with elevation weakly compared to richness (i.e. it only approaches significance; $p = 0.096$), as variation in Shannon diversity is more strongly affected by variation in richness than by variation in the abundances of particular species (Boyle et al. 1990).

Fine grained study

Elevational variation in each community-level aspect of biodiversity was significant and independent of transect (Table 4). Moreover, all community-level aspects of biodiversity that differed between transects (richness, diversity, and rarity) did so in a consistent way, regardless of elevation (Table 4, Fig. 5).

Mesoscale patterns along elevational gradients

Elevation was correlated with correspondence scores on the secondary axis for strata along the mixed forest transect in 2007 ($\rho = -0.889$, $p < 0.001$), with correspondence scores on the primary axis for strata along the mixed forest transect ($\rho = -0.63$, $p = 0.011$) in 2008; and with correspondence scores on the primary axis for strata along the palm forest transect ($\rho = -0.600$, $p = 0.026$) in 2008. In

Table 4. Results (p-values) of analyses of covariance that evaluate the effects of transect (mixed forest versus palm forest) and elevation on population-level and community-level aspects of biodiversity for gastropods from the Luquillo Experimental Forest of Puerto Rico. Transect was a factor, elevation was a covariate, and plots within each stratum was a random factor. Results of least squares analyses illustrate how species abundance or aspects of biodiversity respond to changes in elevation (per 100 m) separately for each elevational transect. Significant results ($p \leq 0.05$) are bold.

	ANCOVA			Mixed forest transect		Palm forest transect	
	Transect	Elevation	Transect × Elevation	Slope	r ²	Slope	r ²
Species abundance							
<i>Alcadiā striata</i>	0.001	0.049	0.625	-0.052	0.045	-0.031	0.005
<i>Austroselenites alticola</i>	0.041	0.017	0.026	-0.052	0.045	-0.002	0.000
<i>Cepolis squamosa</i>	0.588	< 0.001	0.635	-0.088	0.101	-0.104	0.097
<i>Diplosolenodes occidentalis</i>	0.105	0.199	0.873	-0.009	0.021	-0.012	0.004
<i>Gaeotis nigrolineata</i>	0.115	0.007	0.340	-0.333	0.056	-0.159	0.009
<i>Megalomastoma croceum</i>	0.282	0.095	0.758	-0.004	0.013	-0.006	0.009
<i>Nenia tridens</i>	< 0.001	< 0.001	0.094	-3.459	0.461	-4.394	0.388
<i>Oleacina glabra</i>	0.147	0.938	0.243	-0.018	0.005	0.021	0.005
<i>Oleacina playa</i>	0.019	0.448	0.222	0.004	0.002	-0.016	0.009
<i>Platysuccinea portoricensis</i>	< 0.001	< 0.001	0.257	0.996	0.166	0.673	0.065
<i>Pleurodonte caracolla</i>	< 0.001	< 0.001	0.128	-4.869	0.453	-6.000	0.420
<i>Pleurodonte marginella</i>	0.459	0.091	0.445	-0.011	0.027	-0.028	0.011
<i>Polydontes acutangula</i>	0.844	0.092	0.480	-0.034	0.020	-0.014	0.003
<i>Polydontes luquillensis</i>	0.140	0.005	0.002	-0.005	0.001	0.091	0.072
Total abundance	< 0.001	< 0.001	0.042	-7.874	0.521	-9.997	0.507
Community-level aspects of biodiversity							
Species richness	< 0.001	< 0.001	0.293	-0.351	0.262	-0.275	0.158
Shannon diversity	< 0.001	< 0.001	0.118	-0.062	0.111	-0.032	0.045
Camargo evenness	0.978	< 0.001	0.796	0.053	0.133	0.057	0.240
Berger–Parker dominance	0.111	0.004	0.912	0.015	0.023	0.014	0.038
Rarity	< 0.001	< 0.001	0.414	-0.230	0.165	-0.180	0.109

contrast, scores for the primary axis of correspondence (i.e. the primary latent environmental gradient) for mixed forest in 2007 were not correlated with elevation ($p = 0.104$, $p = 0.712$). In each year, the mixed forest metacommunity exhibited Clementsian structure for the axis that was correlated with elevation (secondary axis for 2007 and primary axis for 2008), whereas the palm forest metacommunity exhibited quasi-Gleasonian structure along the primary axis associated with elevation (Table 6). Mean abundance was significantly greater in palm forest than in mixed forest for three species (*P. caracolla*, *N. tridens*, and *P. portoricensis*) and for the fauna as a whole at the 0.05 level, and for an additional three species (*A. striata*, *O. playa*, and *D. occidentalis*) at the 0.10 level (Willig et al. 2011b). Moreover, the direction of difference in mean abundance was consistent

for all 15 species (higher in palm than in mixed forest), the likelihood of which due to chance alone is quite small (Binomial test, $p < 0.001$).

Along each transect, terrestrial gastropods responded strongly to environmental variation (i.e. distributions were highly coherent). Nonetheless, the differences in variation of environmental characteristics between the mixed forest transect and the palm forest transect gave rise to distinct structures for each metacommunity. Consistent with forest type being of primary importance to structuring metacommunities, gastropods in mixed forest exhibited Clementsian structure each year and those in palm forest exhibited Gleasonian structure (Table 6). Tree species composition and physiognomy were relatively invariant along the palm forest transect, and elevational

variation in abiotic and non-flora related biotic characteristics produced a latent environmental gradient to which gastropod species responded in an idiosyncratic and independent fashion, resulting in Gleasonian structure (Fig. 6B). When zonal differences in tree species composition

and physiognomy along the mixed forest transect were combined with elevational variation in biotic and abiotic characteristics, as in the mixed forest transect, gastropods formed a Clementsian structure in which upper and lower elevational compartments were distinguishable (Fig. 6A)

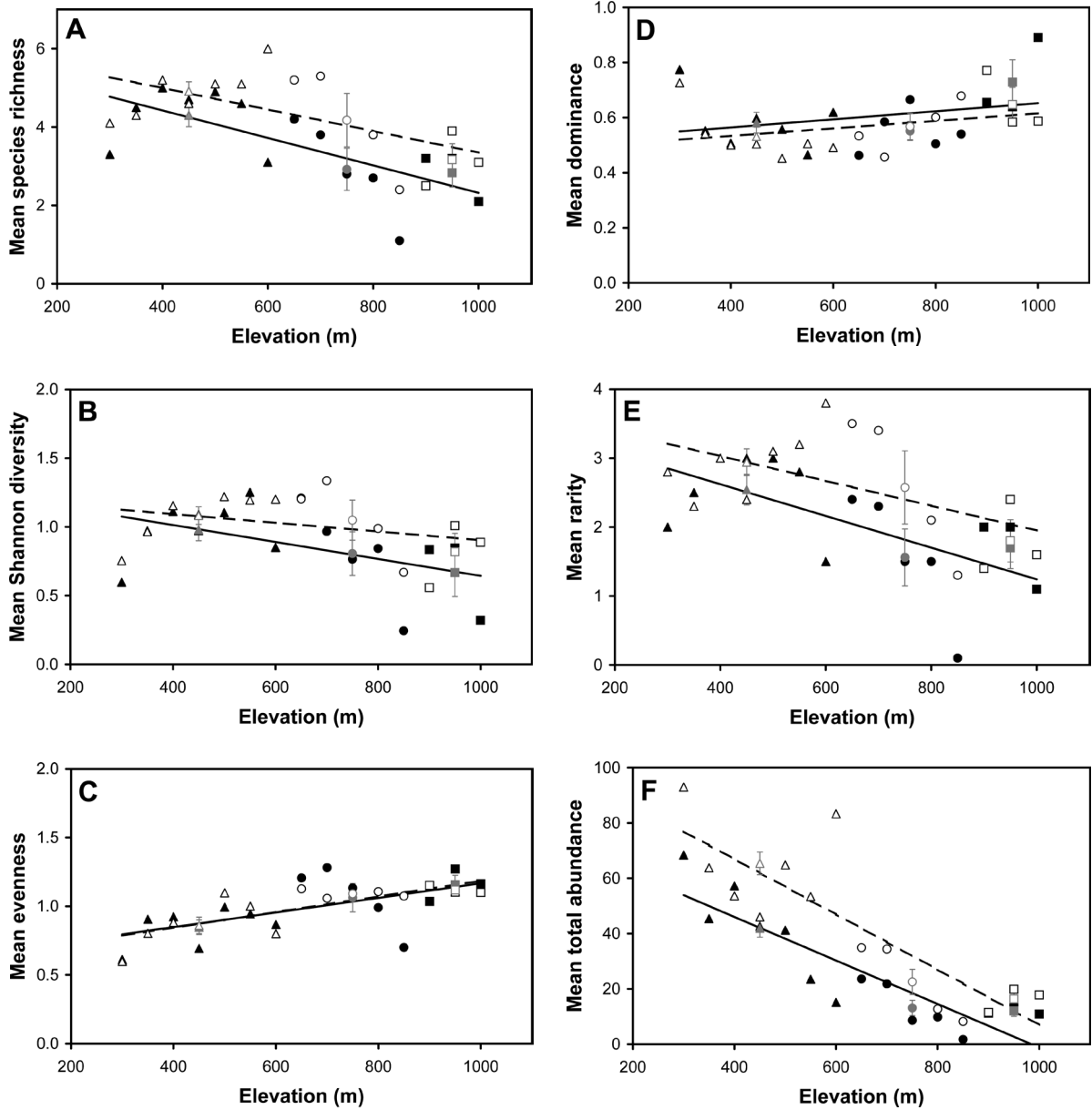


Figure 5. Relationship between elevation and the mean of each of five community-level aspects of biodiversity and total gastropod abundance along two transects (mixed forest and palm forest) in the Luquillo Mountains (fine grained study). (A) Species richness; (B) Shannon diversity; (C) Camargo evenness; (D) Berger–Parker dominance; (E) rarity; and (F) total abundance. Data for the mixed forest transect are indicated by filled black symbols, with the best fit linear relationship indicated by a dashed line. Symbols indicate elevationally defined forest zones: triangles (▲), tabonuco forest; circles (●), palo colorado forest; and squares (■), elfin forest zones. Mean and standard errors of biodiversity components for each forest type are indicated by grey symbols and vertical error bars, and are centered on the abscissa at the mean elevation of the plots in each forest type.

Table 5. Results (p-values) of doubly repeated measures (season within combinations of canopy openness and elevation) analyses of covariance without replication that evaluate effects of elevation, canopy openness, and season on species richness, Shannon diversity, and evenness (Pielou's J index) of gastropods in the Luquillo Mountains (course grained study; after Alvarez 1997). Significant ($p \leq 0.05$) results are bold.

	Elevation	Openness	Season	Higher order interactions			
	(E)	(O)	(S)	E × O	E × S	O × S	E × O × S
Species richness	0.001	0.186	0.018	0.420	0.059	0.261	0.878
Shannon diversity	0.096	0.156	0.278	0.445	0.844	0.556	0.611
Evenness	0.002	0.340	0.613	0.720	0.834	0.613	0.952

and consistent with the distinction between elfin forest and other forest types as a group (palo colorado and tabonuco forest).

Mixed forest gradient

The environmental distribution of many species spanned > 90% of the strata along the elevational gradient (taxa with distributions designated by gray bars in Fig. 6). Nonetheless, some species occurred only at the upper (i.e. *A. alticola*, *M. croceum*, *P. luquillensis*) or lower (i.e. *P. marginella*, *C. musicola*) end of the latent environmental gradient. All of the species with distributions primarily at the upper end of the latent environmental gradient attained their highest abundances there as well. The rank order of elevational strata based on gastropod distributions was significantly correlated ($\rho = 0.58$, $p = 0.022$) with the rank order of elevational strata based on tree distributions from this same transect (Barone et al. 2008), corroborating the contention that forest zonation strongly influences

gastropod distributions along the mixed forest transect. Indeed, the mixed forest metacommunity exhibited three discernable groups of elevational strata: those below 550 m, those above 850 m, and those between 550 and 850 m, inclusive (Presley et al. 2011, Willig et al. 2011b). These three elevational groupings 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).

Palm forest gradient

The palm forest metacommunity exhibited quasi-Gleasonian structure (Table 6). Again, the distribution of many species spanned > 90% of the strata along the gradient (taxa with distributions designated by gray bars in Fig. 6B). In addition, over half of the species occurred at a larger proportion of strata in the palm forest metacommunity than in the mixed forest metacommunity (i.e. *A. striata*, *A. alticola*, *M. croceum*, *O. glabra*, *O. playa*, *P. acutangula*, and

Table 6. Results of analyses of coherence, range turnover, and boundary clumping for tropical gastropods in the Luquillo Mountains of Puerto Rico (fine grained study; after Presley et al. 2011, Willig et al. 2011b). For the mixed forest transect in 2007, analyses were performed separately for primary and for secondary axes of correspondence. Significant results ($p \leq 0.05$) are bold. Abs, number of embedded absences; Rep, number of replacements; SD, standard deviation.

Year	Transect	Coherence				Range turnover				Boundary clumping		Metacommunity structure
		Abs	p	Mean	SD	Rep	p	Mean	SD	Morisita's index	p	
2007												
Mixed forest												
	Primary	26	< 0.001	48	4.5	263	0.362	186	83.6	2.167	0.011	Quasi-Clementsian
	Secondary	40	0.001	53	4.0	153	0.024	60	41.1	2.320	0.047	Clementsian
2008												
Mixed forest												
	Primary	46	< 0.001	68	5.9	304	0.022	156	64.8	1.733	0.035	Clementsian
Palm forest												
	Primary	35	< 0.001	54	5.1	279	0.072	157	68.0	1.077	0.370	Quasi-Gleasonian

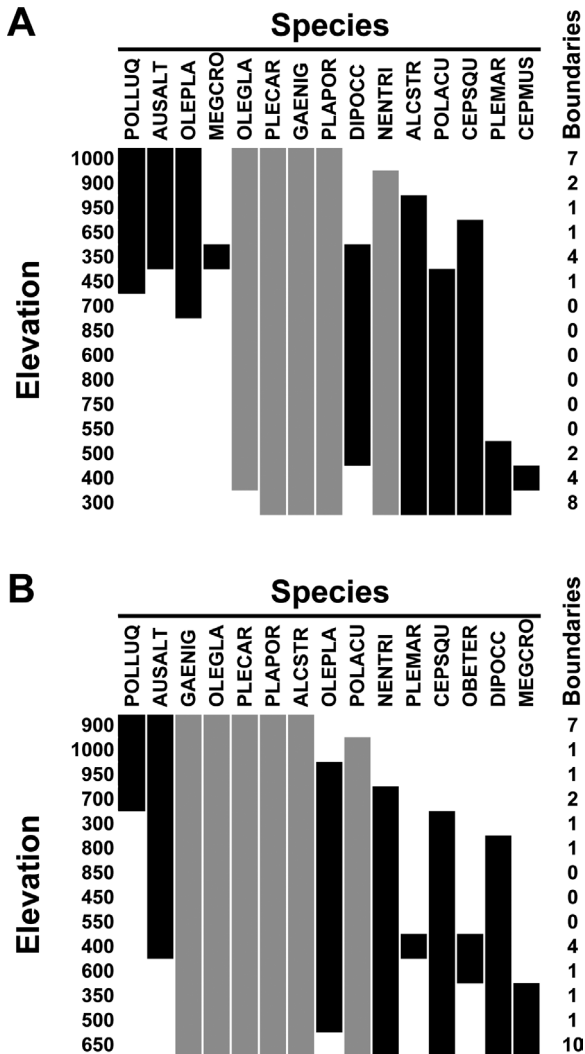


Figure 6. Terrestrial gastropod distributions along latent environmental gradients from two transects (fine grained study) in the Luquillo Mountains of Puerto Rico: (A) mixed forest transect, and (B) palm forest transect. Shaded bars represent the distributions of species along a latent environmental 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). Number of range boundaries that occurred at each elevational stratum is listed to the right of each metacommunity. Abbreviations for gastropod species are: ALCSTR, *Alcudia striata*; AUSALT, *Austroselenites alticola*; CEPMUS, *Cepolis musicola*; CEPSQU, *Cepolis squamosa*; DIPOCC, *Diplosolenodes occidentalis*; GAENIG, *Gaeotis nigrolineata*; MEGCRO, *Megalomastoma croceum*; NENTRI, *Nenia tridens*; OBETER, *Obeliscus terebraster*; OLEGLA, *Oleacina glabra*; OLEPLA, *Oleacina playa*; PLAPOR, *Platysuccinea portoricensis*; PLECAR, *Pleurodonte caracolla*; PLEMAR, *Pleurodonte marginella*; POLACU, *Polydontes acutangula*; POLLUQ, *Polydontes luquillensis*.

D. occidentalis). In the absence of appreciable variation in tree species composition or physiognomy in palm forest, gastropod species exhibited broader distributions along the gradient, and did so in idiosyncratic and independent fashions, giving rise to a quasi-Gleasonian structure. Each species had greater abundance in elevational strata from palm forest than in comparable strata from mixed forest (Willig et al. 2011b). In addition, species richness of gastropods at elevational strata was greater in palm forest than in mixed forest (Willig et al. 2011b). These results suggest that, when controlling for elevation, palm forests are more productive for gastropods than are other forest types in the LEF.

Elevational variation in species composition

Variation among sites in species composition (Fig. 7) was similar regardless of whether the ordination was based on incidence (i.e. presence versus absence of species) or abundance (double square root transformed density). This was true for the mixed forest (dimension 1: $\rho = 0.648$; $p = 0.014$; Fig. 7A, B) as well as for the palm forest (dimension 1: $\rho = 0.547$, $p = 0.045$; Fig. 7D, E) transects. Moreover, variation among sites was correlated with elevation in all four situations (mixed forest: incidence [$\rho = -0.674$, $p = 0.010$] and abundance [$\rho = -0.969$, $p < 0.001$]; palm forest: incidence [$\rho = -0.499$, $p = 0.072$] and abundance [$\rho = -0.829$, $p < 0.001$]). This suggests that views of faunal organization based on incidence mimic those based on abundance with similar elevational controls. Variation among strata in the mixed forest transect (Fig. 7C) was significantly affected by variation in abundances of 7 species (*A. striata*, *C. squamosa*, *G. nigrolineata*, *N. tridens*, *P. acutangula*, *P. caracolla*, and *P. portoricensis*). Similarly, variation among strata in the palm forest transect (Fig. 7F) was significantly affected by variation in abundances of 7 species (*A. striata*, *C. squamosa*, *N. tridens*, *O. glabra*, *P. caracolla*, and *P. luquillensis*). The species with the strongest effects on the first dimension of ordination were quite comparable in both transects (i.e. *C. squamosa*, *N. tridens*, and *P. caracolla*), except for the inclusion of *P. portoricensis* in the mixed forest transect and *P. luquillensis* in the palm forest transect.

Discussion

Although the elevational gradient in the Luquillo Mountains is relatively compact (sea level to < 1400 m), as is the extent of gastropod data collections (200–1000 m), considerable variation in biodiversity arises as a consequence of associated environmental gradients in abiotic and biotic characteristics. Moreover, elevational patterns of population and community level components of biodiversity are similar in the coarse grained and fine grained studies. This

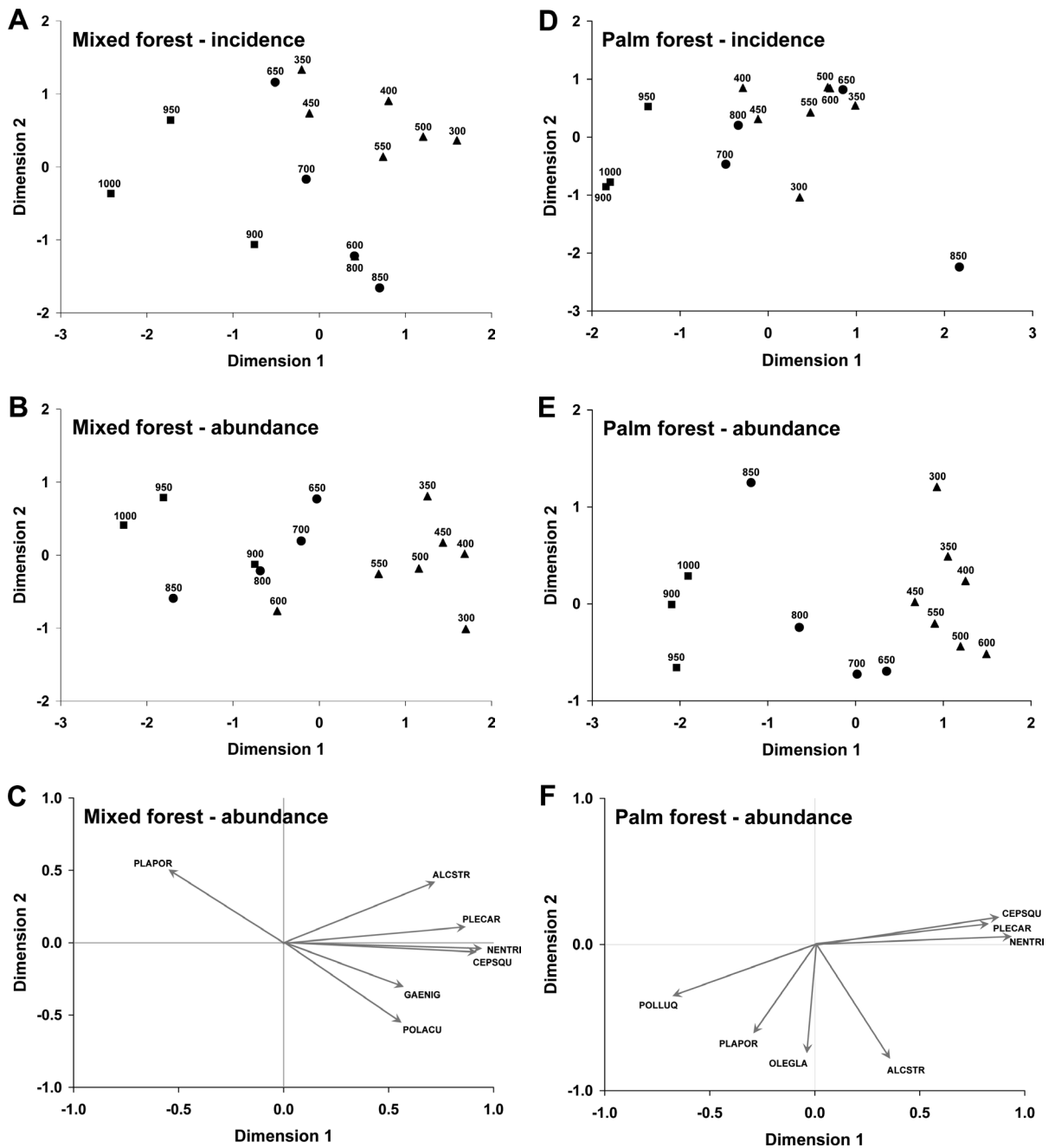


Figure 7. Relationships among elevational strata (numbers represent elevation in m) for each transect (fine gained study) based on gastropod species composition using non-metric multidimensional scaling (MDS; Young 1981). Analyses were conducted separately based on species incidence ((A) mixed forest transect [stress = 0.171]; (D) palm forest transect [stress = 0.142]) or abundance ((B) mixed forest transect [stress = 0.087]; (E) palm forest transect [stress = 0.102]). Correlations of species abundances with dimensions 1 and 2 from the corresponding MDS are shown ((C) mixed forest transect; (F) palm forest transect) for species whose abundance was significantly correlated with site scores for at least one axis. Symbols indicate elevationally defined forest zones: triangles (▲), tabonuco forest; circles (●), palo colorado forest; and squares (■), elfin forest zones.

suggests that consequences arising from differences in spatial scale (i.e. focus or extent of sampling sensu Scheiner et al. 2000) or time (1993 [4 yr after Hurricane Hugo] for the coarse grained study, and 2007–2008 [18–19 yr after Hurricane Hugo and 9–10 yr after Hurricane Georges] for the fine scaled study) had only minor impacts on general patterns.

For each community-level attribute of gastropod biodiversity in the Luquillo Mountains, the rates of elevational change are the same in palm forest and mixed forest transects (Table 4, Fig. 5). Moreover, the best fit lines representing the relationships are coincident for evenness (Fig. 5C). These patterns are explicable in light of additional observations. First, each gastropod species (Willig et al. 2011b), as well as the fauna as a whole (Fig. 5E), reach higher abundances in strata from the palm forest transect compared to the mixed forest transect. Second, total abundance of gastropods as well as the abundances of most species individually (Table 4, Fig. 5E), decrease with increasing elevation. From the perspectives of gastropods, these trends suggest that spatial variation in productivity (among elevational strata or between palm and non-palm forest) accounts for spatial variation in components of biodiversity.

Spatial dynamics of components of biodiversity are driven by productivity

Gastropod species richness, diversity, and rarity of strata from palm forest are consistently higher than in corresponding elevational strata in other forests, and decrease with increasing elevation (Fig. 5A, B, E). This may arise because important nutrients for snail metabolism and shell growth, such as nitrogen, phosphorous, calcium, potassium and magnesium, that are generally higher in litter from palm dominated areas compared to litter from non-palm dominated areas at the same elevation, and because these same nutrients generally decrease with increasing elevation from tabonuco to palo colorado to elfin forest (Richardson et al. 2005). If these factors contribute to higher snail abundances in palm versus mixed forest strata, and to higher snail abundance in lower versus higher elevational forests (Fig. 5F), then the more individuals hypothesis or passive sampling (Coleman et al. 1982, Srivastava and Lawton 1998, Scheiner and Willig 2005) may account for higher biodiversity in those aspects sensitive to variation in species number.

Elevational variation in species evenness and dominance (Fig. 5C, D) is not so simply associated with the variation in the number of individuals from a mechanistic perspective, although the correlative associations are clearly strong. As elevation increases, total abundance decreases (Fig. 5F) as does species richness (Fig. 5A), in part because of the loss of rare species (Fig. 5E). This is consistent with the hypothesis that increasing productivity (total above ground

net primary production [$\text{tons ha}^{-1} \text{yr}^{-1}$] and tree litterfall [$\text{tons ha}^{-1} \text{yr}^{-1}$] from elfin (3.7, 3.1) to palo colorado (7.6, 6.8) to tabonuco (10.5, 8.6) forest (Weaver and Murphy 1990, Weaver 1994) should support more populations at higher densities, such that taxa are less likely to suffer local extinction. In a straight forward manner, this results in higher richness and higher rarity in sites with higher productivity, and consequently these sites should and do have lower evenness (Fig. 5C). At the same time, the loss of species from low productivity sites (i.e. higher elevations) should allow the relative abundances of the remaining taxa to increase, effecting an increase in dominance, as was observed as well (Fig. 5D).

Comparison with elevational studies of other biotas in northeastern Puerto Rico

Elevational gradients in species richness have been examined for a variety of biotas in the mountainous regions of northeastern Puerto Rico. Elevational patterns of species richness are taxon specific including monotonic decreases, monotonic increases, modal relationships, and invariant patterns. Species richness declines with elevation for tree species (Waide et al. 1998), litter invertebrates along a mixed forest transect (Richardson et al. 2005), and gastropods along both mixed forest and palm forest transects (this study). In contrast, species richness increases with elevation for earthworms (Gonzalez et al. 2007) and attains mid-elevational peaks for invertebrates that inhabit bromeliads (Richardson and Richardson 2013) and for vascular epiphytes and vines (Brown et al. 1983). Finally, elevational variation in species richness is flat for litter invertebrates along a palm forest transect (Richardson et al. 2005). These different patterns could emerge as a consequence of a variety of factors including considerations of scale (focus and extent), sampling design (analyses of forest types rather than elevations, per se), analytical approaches, and the niche characteristics of biotas and the salient environmental characteristics to which they respond.

The research by Richardson et al. (2005) is of particular interest, as it was designed to separate the effects of forest type (tabonuco [330–500 m] versus palo colorado [750–780 m] versus elfin forest [820–1000 m]), from those associated with elevation, on community components of biodiversity of litter invertebrates. To do so, they examined paired palm and non-palm sites that correspond in elevation to each forest type. They detected a decline in richness from tabonuco to palo colorado to elfin forest in non-palm plots, but remarkably similar species richness in palm plots regardless of elevational position. In addition, they found higher compositional similarity between palm plots from different elevational forests than between non-palm plots from those same elevational forests. These results suggested that changes in plant species composition among forest types contributed to differences in invertebrate biodiversity

as a consequence of differences in physicochemical properties of litter rather than being a direct consequence of temperature or rainfall. In contrast, our results across multiple elevational strata documented parallel patterns (and sometimes coincident patterns) of elevational changes in biodiversity in both palm (palm forest transect) and non-palm (mixed forest transect) areas. Also in contrast, we detected correlated patterns of elevational change in species composition along the mixed forest transect and the palm forest transect (e.g. compare Fig. 7A and D as well as Fig. 7B and E), with the spatial variation in abundances of the three common snail species (*C. squamosa*, *N. tridens*, and *P. caracolla*) contributing significantly to the elevational patterns (Fig. 7C, F). We conclude that gradual changes in environmental characteristics, including the elevational decrease in net primary productivity (Waide et al. 1998) in the Luquillo Mountains, rather than the vegetative composition of the forest per se, played a dominant role in determining elevational trends (i.e. slopes) in gastropod biodiversity, but that differences between transects in vegetative characteristics caused consistent differences in mean values (additive effects) for biodiversity characteristics.

Differences between the conclusions of Richardson et al. (2005) for litter invertebrates, and our conclusions for terrestrial gastropods, could arise because of methodological differences between our studies. More likely, the autecological characteristics of litter invertebrates tie them to particular physicochemical attributes of the litter in which they live, while terrestrial gastropods are less tied to such characteristics. Rather, many gastropod species in the Luquillo Mountains are habitat generalists, generalist foragers, or both. Consequently, patterns of biodiversity are more closely tied to factors affecting productivity and the abundances of species, which then accounts (via passive sampling or the more individuals hypothesis) for differences between palm and non-palm areas as well as differences among elevational strata.

Structuring mechanisms in metacommunities

The terrestrial gastropods included in this analysis 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). A recent analysis of floral metacommunity structure from the mixed forest transect found significant clumping of range boundaries for species of woody plants (Barone et al. 2008). The fact that gastropods from the mixed forest transect exhibited similar metacommunity structure to that of the plants from the same transect indicates that plant species composition may be an important determinant of gastropod species distributions or that similar energetic constraints affect plant and gastropod species.

Microclimate (e.g. temperature, humidity) and soil characteristics (e.g. texture, moisture, nutrient content,

and 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 abiotic characteristics change gradually and predictably with elevation in the LEF (Brown et al. 1983). In addition, terrestrial gastropods generally exhibit species-specific tolerances to environmental variation in abiotic and biotic characteristics (Riddle 1983). Variation in forest type was absent from the palm forest transect. In the absence of such variation, abiotic factors may be the primary determinant of species distributions. Such a metacommunity should exhibit positive or random range turnover and randomly distributed range boundaries that are characteristic of Gleasonian and quasi-Gleasonian structures, respectively. The quasi-Gleasonian structure for gastropods along the palm forest transect is consistent with a metacommunity that is structured primarily by responses to elevational variation in abiotic characteristics. 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 abiotic and biotic features.

In general, microclimate (temperature, humidity) and soil characteristics (texture, moisture, nutrient content, mineral content) are more important determinants of terrestrial gastropod distributions than are associations with particular plant species (Cook 2001). 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 (Boycott 1934, Beyer and Saari 1977, Ondina et al. 2004). Some environmental characteristics change gradually and predictably with elevation, whereas others are more patchy and heterogeneous in distribution (Brown et al. 1983). Moreover, tolerance to variation in abiotic factors generally is a species-specific characteristic of terrestrial gastropods (Riddle 1983). For these reasons, we expected gastropods in the LEF to exhibit Gleasonian structure regardless of changes in plant composition. The gastropod species in the LEF are 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 and Mayhill 1999, Schilthuizen and Rutjes 2001, Ondina et al. 2004, Nekola 2005, Tattersfield et al. 2006). For many reasons, being more arboreal may increase the relative importance of vegetation in determining gastropod distributions in the LEF, compared to variation in soil characteristics or abiotic conditions. First, vegetation replaces soil or leaf litter as the primary substrate for arboreal gastropods. Second, vegetation helps to reduce evaporation and maintain sufficiently humid conditions for gastropods, which are susceptible to desiccation stress. Third, particular plant species and assemblages are associated with particular soil types and soil characteristics (Brown et al. 1983); there-

fore, 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 health.

Comparison with elevational studies of gastropod biodiversity

Relatively few studies have explicitly examined terrestrial gastropod communities in the context of elevational gradients. These studies generally address relatively broad gradients at higher elevations than exist in the Luquillo Mountains (e.g. 570–4096 m in Malaysian Borneo; Liew et al. 2010). Nonetheless, a few comparisons are possible with respect to patterns of range sizes, assemblage structure, and biodiversity.

As in the Luquillo Mountains (Fig. 4, 6), many snail species occupying other elevational gradients have extensive elevational ranges. In Tanzania, mean elevational range of gastropod species was only 470 m (Tattersfield et al. 2006), but in New Mexico, the elevational ranges of many species spanned more than 600 m (Metcalf 1984), and in Kenya and Borneo, many species had ranges approaching or even exceeding 1000 m (Tattersfield et al. 2001, Liew et al. 2010). This was especially true of species occurring at lower elevations in Borneo, where ranges of a few species exceeded 2000 m (Liew et al. 2010).

Species richness of gastropods in the Luquillo Mountains declines with increasing elevation (Table 3, 4; Fig. 5A). This pattern was common in other mountainous areas such as Borneo (Liew et al. 2010), Kenya (Tattersfield et al. 2001), and southeastern France (Aubry et al. 2005), although the elevational gradients in these other studies extend into higher elevations than found in the Luquillo Mountains. In contrast, gastropod richness exhibited a mid-elevational peak in Tanzania (Tattersfield et al. 2006) and in the Organ Mountains of New Mexico (Metcalf 1984). In both cases, these mid-elevational peaks were at elevations at or above the maximum sampled in the Luquillo Mountains. Extension of sampling in the Luquillo Mountains into lowland forest (i.e. < 200 m) is necessary to reveal whether the observed linear decline is general (i.e. if richness in the lowlands is higher than that in tabonuco forest) or whether the observed linear decline represents the descending portion of a modal relationship (i.e. if richness is lower in the lowlands than in tabonuco forest). This is essentially an elevational variant of the pattern accumulation hypothesis for productivity (Gross et al. 2000, Scheiner et al. 2000). Assessment of this hypothesis is difficult in the context of Puerto Rico, as the lowlands are highly fragmented and modified by human activities.

Two studies report division of the gastropod fauna into distinct assemblages that correspond at least in part to transitions in vegetation structure or life zones, although the elevations at which this occurs and the proposed mechanisms differ. In southern New Mexico, snail

assemblages broadly correspond to vegetation zones that transition at approximately 2100–2400 m (Metcalf 1984). In montane forests of Tanzania, the faunal discontinuity occurs at approximately 1000 m (Tattersfield et al. 2006) and may reflect vegetation structure, rainfall patterns, and soil characteristics. In each of these studies, the majority of gastropods were small, litter-dwelling species; thus, vegetation characteristics may be important determinants of gastropod assemblage structure even for faunas that are not as dominated by arboreal species as are those in the Luquillo Mountains. A difference between high- and low-elevation faunas was also observed on Mount Kenya (Tattersfield et al. 2001), but the cause remains unclear.

Synthesis and future directions

In the Luquillo Mountains, many attributes of gastropod biodiversity and metacommunity organization arise as a consequence of spatial variation in environmental characteristics associated with productivity. Indeed, we have shown that variation in population and community level attributes of biodiversity change gradually, and parallel variation in total gastropod abundance and net primary productivity in general. These same mechanisms (more individuals hypothesis or passive sampling) explain both elevational variation and the differences between mixed forest and palm forest transects. Moreover, the higher abundances of gastropods in palm-dominated forest patches have been identified as a likely mechanism contributing to differences between metacommunity organization in the mixed forest and palm forest transects (Willig et al. 2011b).

Productive foci for future research should include linkages between particular environmental characteristics and various aspects of biodiversity in order to gain deeper mechanistic understanding of abiotic and biotic controls on forest structure. This requires the development of a synoptic network of sites at which suites of abiotic and biotic characteristics are measured in tandem. At the same time, fuller consideration of the effects of spatial heterogeneity on aspects of gastropod biodiversity would inform understanding of interactions between patch-generating phenomena, such as hurricanes and landslides, and local conditions that affect movement of individuals or source-sink dynamics (Willig et al. 2007). These approaches are particularly relevant to the future, as alterations in climatic characteristics and disturbance regimes associated with global change will likely alter the mapping of abiotic and biotic characteristics in geographic space, with profound consequences to the spatiotemporal dynamics of biodiversity.

Acknowledgements – 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 International 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 and the Univ. of Puerto Rico. Support for SJP and MRW was provided by the Center for Environmental Sciences and Engineering at the Univ. of Connecticut during preparation of this manuscript. Support for JAR was provided by the Ford Foundation. We thank D. Acosta, J. Blanco, I. Castro-Arellano, L. Cisneros, C. Curtis, C. Higgins, L. Jones, B. Klingbeil, N. Rivera, A. Schneider, R. Valentín, and J. Vose for their assistance in the field. The staff of El Verde Field Station in Puerto Rico provided valuable logistical support and field assistance. Finally, the clarity and content of the manuscript were improved as a consequence of three anonymous reviews.

References

- Adams, C. C. et al. 1920. Plants and animals of Mount Marcy, New York. I. – *Ecology* 1: 71–94.
- Alexander, J. M. et al. 2011. Assembly of nonnative floras along elevational gradients explained by directional ecological filtering. – *Proc. Natl Acad. Sci. USA* 108: 656–661.
- Alvarez, J. 1997. Patterns of abundance, species richness, habitat use and morphology in tropical terrestrial mollusks: effects of disturbance and elevation. – Unpubl. PhD thesis, Texas Tech Univ.
- Aubry, S. et al. 2005. Multi-scale altitudinal patterns in species richness of land snail communities in south-eastern France. – *J. Biogeogr.* 32: 985–998.
- Barker, G. M. and Mayhill, P. C. 1999. Patterns of diversity and habitat relationships in terrestrial mollusc communities of the Pukeamaru Ecological District, northeastern New Zealand. – *J. Biogeogr.* 26: 215–238.
- Barone, J. A. et al. 2008. Metacommunity structure of tropical forests along an elevational gradient in Puerto Rico. – *J. Trop. Ecol.* 24: 1–10.
- Barry, R. G. 1992. Mountain weather and climate. – Routledge.
- Begon, M. et al. 1990. *Ecology: individuals, populations and communities*, 2nd ed. – Blackwell.
- Berger, W. H. and Parker, F. L. 1970. Diversity of planktonic Foraminifera in deep sea sediments. – *Science* 168: 1345–1347.
- Beyer, W. N. and Saari, D. M. 1977. Effect of tree species on the distribution of slugs. – *J. Anim. Ecol.* 46: 697–702.
- Birdsey, R. A. and Weaver, P. L. 1982. The forest resources of Puerto Rico. – Resource Bulletin SO-85, US Dept of Agriculture.
- Bloch, C. P. and Willig, M. R. 2009. Effects of competition on size and growth rates of *Caracolus caracolla* (L.) in Puerto Rico. – *J. Molluscan Stud.* 75: 133–138.
- Bloch, C. P. and Willig, M. R. 2011. Density compensation suggests interspecific competition is weak among terrestrial snails in tabonuco forest of Puerto Rico. – *Caribb. J. Sci.*, in press.
- Boycott, A. E. 1934. The habitats of land Mollusca in Britain. – *J. Ecol.* 22: 1–38.
- Boyle, P. et al. 1990. A sensitivity analysis of nine diversity and seven similarity indices. – *J. Water Pollut. Contr. Fed.* 62: 749–762.
- Brokaw, N. V. L. et al. (eds) 2012. Disturbance and recovery in a tropical forest: long-term research in the Luquillo Mountains of Puerto Rico. – Oxford Univ. Press, in press.
- Brown, J. H. and Gibson, A. C. 1983. *Biogeography*. – Mosby.
- Brown, J. H. et al. 1996. The geographic range size: size, shape, boundaries and internal structure. – *Annu. Rev. Ecol. Syst.* 27: 597–623.
- Brown, S. et al. 1983. Research history and opportunities in the Luquillo Experimental Forest. – General Technical Report SO-44, US Dept of Agriculture.
- Camargo, J. A. 1995. On measuring species evenness and other associated parameters of community structure. – *Oikos* 74: 538–542.
- Cameron, R. A. D. and Pokryszko, B. M. 2005. Estimating the species richness and composition of land mollusc communities: problems, consequences and practical advice. – *J. Conchol.* 38: 529–547.
- Cary, J. F. Jr 1992. Habitat selection, home range, and population dynamics of *Caracolus caracolla* in the Luquillo Experimental Forest of Puerto Rico. – Unpubl. MS thesis, Texas Tech Univ.
- Chiba, S. 2007. Species richness patterns along environmental gradients in island land molluscan fauna. – *Ecology* 88: 1738–1746.
- Clements, F. E. 1916. Plant succession: an analysis of the development of vegetation. – Carnegie.
- Clements, R. et al. 2008. Using biogeographical patterns of endemic land snails to improve conservation planning for limestone karsts. – *Biol. Conserv.* 141: 2751–2764.
- Coleman, B. D. et al. 1982. Randomness, area and species richness. – *Ecology* 63: 1121–1133.
- Colwell, R. K. 2011. Biogeographical gradient theory. – In: Scheiner, S. M. and Willig, M. R. (eds), *The theory of ecology*. Univ. of Chicago Press, pp. 309–330.
- Colwell, R. K. et al. 2008. Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. – *Science* 322: 258–261.
- Cook, A. 2001. Behavioural ecology: on doing the right thing, in the right place at the right time. – In: Barker, G. M. (ed.), *The biology of terrestrial mollusks*. Oxford Univ. Press, pp. 447–487.
- Diamond, J. M. 1975. Assembly of species communities. – In: Cody, M. L. and Diamond, J. M. (eds), *Ecology and evolution of communities*. Harvard Univ. Press, pp. 342–444.
- Dunn, R. R. et al. 2007. When does diversity fit null model predictions? Scale and range size mediate the mid-domain effect. – *Global Ecol. Biogeogr.* 16: 305–312.
- Fox, G. et al. 2011. Theory of ecological gradients. – In: Scheiner, S. M. and Willig, M. R. (eds), *Theory of ecology*. Univ. of Chicago Press, pp. 283–307.
- Franklin, J. F. et al. 1992. Effects of global climate change on forests in northwestern North America. – In: Peters, R. L. and Lovejoy, T. E. (eds), *Global warming and biological diversity*. Yale Univ. Press, pp. 244–257.
- Garrison, R. W. and Willig, M. R. 1996. Invertebrates. – In: Reagan, D. P. and Waide, R. B. (eds), *The food web of a tropical rain forest*. Univ. of Chicago Press, pp. 183–245.
- Gleason, H. A. 1926. The individualistic concept of the plant association. – *Bull. Torrey Bot. Club* 53: 7–26.
- Gonzalez, G. et al. 2007. Earthworm communities along an elevation gradient in northeastern Puerto Rico. – *Eur. J. Soil Biol.* 43: S24–S32.
- Gross, K. L. et al. 2000. Patterns of species density and productivity at different spatial scales in herbaceous plant communities. – *Oikos* 89: 417–427.

- Guariguata, M. R. 1990. Landslide disturbance and forest regeneration in the upper Luquillo Mountains of Puerto Rico. – *J. Ecol.* 78: 814–832.
- Hanski, I. and Gilpin, M. 1991. Metapopulation dynamics: a brief history and conceptual domain. – *Biol. J. Linn. Soc.* 42: 3–16.
- Heatwole, H. and Heatwole, A. 1978. Ecology of the Puerto Rican camaenid tree-snails. – *Malacologia* 17: 241–315.
- Hemp, A. 2006. Continuum or zonation? Altitudinal gradients in the forest vegetation of Mt. Kilimanjaro. – *Plant Ecol.* 184: 27–42.
- Hoagland, B. W. and Collins, S. L. 1997. Gradient models, gradient analysis, and hierarchical structure in plant communities. – *Oikos* 78: 23–30.
- Hofer, U. et al. 1999. Spatial organization of a herpetofauna on an elevational gradient revealed by null model tests. – *Ecology* 80: 976–988.
- Kessler, M. 2000. Elevational gradients in species richness and endemism of selected plant groups in the central Bolivian Andes. – *Plant Ecol.* 149: 181–193.
- Kikkawa, J. and Williams, E. E. 1971. Altitude distribution of land birds in New Guinea. – *Search* 2: 64–65.
- Körner, C. 2007. The use of 'altitude' in ecological research. – *Trends Ecol. Evol.* 22: 569–574.
- Landsea, C. W. et al. 1999. Atlantic basin hurricanes: indices of climatic changes. – *Clim. Change* 42: 89–129.
- Larsen, M. C. et al. 1999. Slopewash, surface runoff and fine-litter transport in forest and landslide scars in humid-tropical steeplands, Luquillo Experimental Forest, Puerto Rico. – *Earth Surf. Process. Landforms* 24: 481–502.
- Leibold, M. A. 2011. The metacommunity concept and its theoretical underpinnings. – In: Scheiner, S. M. and Willig, M. R. (eds), *Theory of ecology*. Univ. of Chicago Press, pp. 163–183.
- Leibold, M. A. and Mikkelsen, G. M. 2002. Coherence, species turnover, and boundary clumping: elements of metacommunity structure. – *Oikos* 97: 237–250.
- Liew, T.-S. et al. 2010. The determinants of land snail diversity along a tropical elevational gradient: insularity, geometry and niches. – *J. Biogeogr.* 37: 1071–1078.
- Lobo, J. M. and Halffter, G. 2000. Biogeographical and ecological factors affecting the altitudinal variation of mountainous communities of coprophagous beetles (Coleoptera: Scarabaeoidea): a comparative study. – *Ann. Entomol. Soc. Am.* 93: 115–126.
- Lugo, A. E. and Waide, R. B. 1993. Catastrophic and background disturbance of tropical ecosystems at the Luquillo Experimental Forest. – *J. Biosci.* 18: 475–481.
- Lugo, A. E. et al. 2012. Ecological paradigms for the tropics: old questions and continuing challenges. – In: Brokaw, N. V. L. et al. (eds), *Disturbance and recovery in a tropical forest: long-term research in the Luquillo Mountains of Puerto Rico*. Oxford Univ. Press, in press.
- Lydeard, C. et al. 2004. The global decline of nonmarine mollusks. – *BioScience* 54: 321–330.
- Lyons, S. K. and Willig, M. R. 1997. Latitudinal patterns of range size: methodological concerns and empirical patterns for New World bats and marsupials. – *Oikos* 80: 292–304.
- MacArthur, R. H. 1972. *Geographical ecology: patterns in the distribution of species*. – Harper and Row.
- Malhi, Y. et al. 2010. Introduction: elevation gradients in the tropics: laboratories for ecosystem ecology and global change research. – *Global Change Biol.* 16: 3171–3175.
- McCain, C. M. 2005. Elevational gradients in diversity of small mammals. – *Ecology* 86: 366–372.
- McCain, C. M. 2007a. Area and mammalian elevational diversity. – *Ecology* 88: 76–86.
- McCain, C. M. 2007b. Could temperature and water availability drive elevational species richness patterns? A global case study for bats. – *Global Ecol. Biogeogr.* 16: 1–13.
- McCain, C. M. 2009a. Global analysis of bird elevational diversity. – *Global Ecol. Biogeogr.* 18: 346–360.
- McCain, C. M. 2009b. Vertebrate range sizes indicate that mountains may be 'higher' in the tropics. – *Ecol. Lett.* 12: 550–560.
- McDowell, W. H. et al. 2012. Geographic and ecological setting. – In: Brokaw, N. V. L. et al. (eds), *Disturbance and recovery in a tropical forest: long-term research in the Luquillo Mountains of Puerto Rico*. Oxford Univ. Press, in press.
- Merriam, C. H. 1894. Laws of temperature control and the geographic distribution of terrestrial animals and plants. – *Natl Geogr.* 6: 229–238.
- Metcalf, A. L. 1984. Distribution of land snails of the San Andres and Organ Mountains, southern New Mexico. – *Southwest. Nat.* 29: 35–44.
- Nekola, J. C. 2005. Geographic variation in richness and shell size of eastern North American land snail communities. – *Rec. West. Aust. Mus.* 68: 39–51.
- Ondina, P. et al. 2004. Relationships between terrestrial gastropod distribution and soil properties in Galicia (NW Spain). – *Appl. Soil Ecol.* 26: 1–9.
- Patterson, B. D. and Atmar, W. 1986. Nested subsets and the structure of insular mammalian faunas and archipelagos. – *Biol. J. Linn. Soc.* 28: 65–82.
- Pickett, S. T. et al. 1994. *Ecological understanding: the nature of theory and the theory of nature*. – Academic Press.
- Picó, R. 1974. *The geography of Puerto Rico*. – Aldine Publishing Company.
- Pielou, E. C. 1966. The measurement of diversity in different types of biological collections. – *J. Theor. Biol.* 13: 131–144.
- Pielou, E. C. 1975. *Mathematical ecology*. – Wiley.
- Presley, S. J. et al. 2009. Elements of metacommunity structure of Paraguayan bats: multiple gradients require analysis of multiple axes of variation. – *Oecologia* 160: 781–793.
- Presley, S. J. et al. 2010. A comprehensive framework for the evaluation of metacommunity structure. – *Oikos* 119: 908–917.
- Presley, S. J. et al. 2011. A complex metacommunity structure for gastropods along an elevational gradient. – *Biotropica* doi: 10.1111/j.1744-7429.2010.00727.x
- R Development Core Team 2009. R: a language and environment for statistical computing. – R Foundation for Statistical Computing, Vienna, Austria, <<http://www.R-project.org>>.
- Rahbek, C. 1995. The elevational gradient of species richness: a uniform pattern? – *Ecography* 18: 200–205.
- Reagan, D. P. and Waide, R. B. (eds) 1996. *The food web of a tropical rain forest*. – Univ. of Chicago Press.
- Richardson, B. A. and Richardson, M. J. 2013. Litter-based invertebrate communities in forest floor and bromeliad microcosms along an elevational gradient in Puerto Rico. – *Ecol. Bull.* 54: 101–116.

- Richardson, B. A. et al. 2005. Separating the effects of forest type and elevation on the diversity of litter invertebrate communities in a humid tropical forest in Puerto Rico. – *J. Anim. Ecol.* 74: 926–936.
- Riddle, W. A. 1983. Physiological ecology of land snails and slugs. – In: Russell-Hunter, W. D. (ed.), *The Mollusca*, Vol. 6, ecology. Academic Press, pp. 431–461.
- Russell-Hunter, W. D. 1983. Overview: planetary distribution of and ecological constraints upon the Mollusca. – In: Russell-Hunter, W. D. (ed.), *The Mollusca*, Vol. 6, ecology. Academic Press, pp. 1–27.
- Scheiner, S. M. and Willig, M. R. 2005. Developing unified theories in ecology as exemplified with diversity gradients. – *Am. Nat.* 166: 458–469.
- Scheiner, S. M. et al. 2000. Species richness, species–area curves and Simpson's paradox. – *Evol. Ecol. Res.* 2: 79–802.
- Schiffman, S. S. et al. 1981. Introduction to multidimensional scaling. – Academic Press.
- Schilthuizen, M. and Rutjes, H. A. 2001. Land snail diversity in a square kilometre of tropical rainforest in Sabah, Malaysian Borneo. – *J. Molluscan Stud.* 67: 417–423.
- Sexton, J. P. et al. 2009. Evolution and ecology of species range limits. – *Annu. Rev. Ecol. Evol. Syst.* 40: 415–436.
- Sizling, A. L. et al. 2009. Rapoport's rule, species tolerances, and the latitudinal diversity gradient: geometric considerations. – *Ecology* 90: 3575–3586.
- Sokal, R. R. and Rohlf, F. J. 1995. *Biometry: the principles and practice of statistics in biological research*, 3rd ed. – W. H. Freeman.
- SPSS 1990. *The SPSS base system user's guide*. – SPSS.
- Srivastava, D. S. and Lawton, J. H. 1998. Why more productive sites have more species: an experimental test of theory using tree-hole communities. – *Am. Nat.* 152: 510–529.
- Stanisic, J. et al. 2007. Forest snail faunas from S.E. Queensland and N.E. New South Wales (Australia): patterns of local and regional richness and differentiation. – *Malacologia* 49: 445–462.
- Steinitz, O. et al. 2005. Predicting regional patterns of similarity in species composition for conservation planning. – *Conserv. Biol.* 19: 1978–1988.
- Stevens, G. C. 1989. The latitudinal gradient in geographical range: how so many species coexist in the tropics. – *Am. Nat.* 133: 240–256.
- Stevens, G. C. 1992. The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. – *Am. Nat.* 140: 893–911.
- Stevens, R. D. and Willig, M. R. 2002. Geographical ecology at the community level: perspectives on the diversity of New World bats. – *Ecology* 83: 545–560.
- Tattersfield, P. 1996. Local patterns of land-snail diversity in a Kenyan rain forest. – *Malacologia* 38: 161–180.
- Tattersfield, P. et al. 2001. Land-snail faunas of afro-montane forests of Mount Kenya, Kenya: ecology, diversity and distribution patterns. – *J. Biogeogr.* 28: 843–861.
- Tattersfield, P. et al. 2006. Elevational variation in diversity and composition of land-snail faunas in a Tanzanian forest. – *Afr. J. Ecol.* 44: 47–60.
- Taylor, P. H. and Gaines, S. D. 1999. Can Rapoport's rule be rescued? Modeling causes of the latitudinal gradient of species richness. – *Ecology* 80: 2474–2482.
- Terborgh, J. 1971. Distribution on environmental gradients: theory and a preliminary interpretation of distributional patterns in the avifauna of the Cordillera Vilcabamba, Peru. – *Ecology* 52: 23–40.
- Terborgh, J. 1977. Bird species diversity on an Andean elevational gradient. – *Ecology* 58: 1007–1019.
- Tilman, D. 1982. Resource competition and community structure. *Monographs in population biology*. – Princeton Univ. Press.
- Van Der Schalie, H. 1948. The land and fresh water mollusks of Puerto Rico. – Misc. Publ. No. 70, Univ. of Michigan.
- Vance-Chalcraft, H. et al. 2010. Relationship between above-ground biomass and multiple measures of biodiversity in subtropical forest of Puerto Rico. – *Biotropica* 42: 290–299.
- Wadsworth, F. H. 1949. The development of the forest land resources of the Luquillo Mountains, Puerto Rico. – Unpubl. PhD thesis, Univ. of Michigan.
- Waide, R. B. and Willig, M. R. 2012. Conceptual overview: disturbances, gradients, and ecological response. – In: Brokaw, N. V. L. et al. (eds), *Disturbance and recovery in a tropical forest: long-term research in the Luquillo Mountains of Puerto Rico*. Oxford Univ. Press, in press.
- Waide, R. B. et al. 1998. Controls of primary productivity in a montane tropical forest: lessons for the Luquillo Mountains in Puerto Rico. – *Ecology* 79: 31–37.
- Walker, L. R. et al. 1991. Ecosystem, plant and animal responses to hurricanes in the Caribbean. – *Biotropica* 23: 313–521.
- Walker, L. R. et al. 1996. Long term responses of Caribbean ecosystems to disturbance. – *Biotropica* 28: 414–614.
- Weaver, P. L. 1994. Bano de Oro National Area, Luquillo Mountains, Puerto Rico. – General Technical Report SO-111, USDA Forest Service.
- Weaver, P. L. and Murphy, P. G. 1990. Forest structure and productivity in Puerto Rico's Luquillo Mountains. – *Biotropica* 22: 69–82.
- Weaver, P. L. and Gould, W. A. 2013. Forest vegetation along environmental gradients in northeastern Puerto Rico. – *Ecol. Bull.* 54: 43–66.
- Whiteman, D. 2000. *Mountain meteorology*. – Oxford Univ. Press.
- Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. – *Ecol. Monogr.* 26: 1–80.
- Whittaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. – *Ecol. Monogr.* 30: 279–338.
- Whittaker, R. H. 1965. Vegetation of the Santa Catalina Mountain, Arizona: a gradient analysis of the south slope. – *Ecology* 46: 429–452.
- Whittaker, R. H. and Niering, W. A. 1965. Vegetation of the Santa Catalina Mountain, Arizona: a gradient analysis of the south slope. – *Ecology* 46: 429–452.
- Willig, M. R. 2000. Latitude, common trends within. – In: Levin, S. (ed.), *Encyclopedia of biodiversity*. Academic Press, pp. 701–714.
- Willig, M. R. et al. 1998. Long-term monitoring of snails in the Luquillo Experimental Forest of Puerto Rico: heterogeneity, scale, disturbance, and recovery. – In: Dallmeier, F. and Comisky, J. (eds), *Forest biodiversity in North, Central, and South America and the Caribbean: research and monitoring*. Parthenon Press, pp. 293–322.
- Willig, M. R. et al. 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. – *Annu. Rev. Ecol. Evol. Syst.* 34: 273–309.

- Willig, M. R. et al. 2007. Cross-scale responses of biodiversity to hurricane and anthropogenic disturbance in a tropical forest. – *Ecosystems* 10: 824–838.
- Willig, M. R. et al. 2011a. Long-term dynamics of tropical walking sticks in response to multiple large-scale and intense disturbances. – *Oecologia* 165: 357–368.
- Willig, M. R. et al. 2011b. Tropical metacommunities and elevational gradients: disentangling effects of forest type from other elevational factors. – *Oikos* doi: 10.1111/j.1600-0706.2011.19218.x
- Wilsey, B. et al. 2005. Relationships among indices suggest that richness is an incomplete surrogate for grassland biodiversity. – *Ecology* 86: 1178–1184.
- Wronski, T. and Hausdorf, B. 2010. Diversity and body-size patterns of land snails in rain forests of Uganda. – *J. Molluscan Stud.* 76: 87–100.
- Young, F. W. 1981. A readable overview of nonmetric issues in the context of the general linear model and components and factor analysis. – *Psychometrika* 46: 357–388.