

The spatial configuration of taxonomic biodiversity along a tropical elevational gradient: α -, β -, and γ -partitions

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Abstract

Biodiversity at larger spatial scales (γ) can be driven by within-site partitions (α), with little variation in composition among locations, or can be driven by among-site partitions (β) that signal the importance of spatial heterogeneity. For tropical elevational gradients, we determined the (a) extent to which variation in γ is driven by α - or β -partitions; (b) elevational form of the relationship for each partition; and (c) extent to which elevational gradients are molded by zonation in vegetation or by gradual variation in climatic or abiotic characteristics. We sampled terrestrial gastropods along two transects in the Luquillo Mountains. One passed through multiple vegetation zones (tabonuco, palo colorado, and elfin forests), and one passed through only palm forest. We quantified variation in hierarchical partitions (α , β , and γ) of species richness, evenness, diversity, and dominance, as well as in the content and quality of litter. Total gastropod abundance linearly decreased with increasing elevation along both transects, but was consistently higher in palm than in other forest types. The gradual linear decline in γ -richness was a consequence of opposing patterns with regard to α -richness (monotonic decrease) and β -richness (monotonic increase). For evenness, diversity, and dominance, α -partitions and γ -partitions evinced mid-elevational peaks. The spatial organization of gastropod biodiversity did not mirror the zonation of vegetation. Rather, it was molded by: (a) elevational variation in productivity or nutrient characteristics, (b) the interspersed palm forest within other forest types, and (c) the cloud condensation point acting as a transition between low and high elevation faunas.

Abstract in Spanish is available with online material.

KEYWORDS

diversity, dominance, evenness, Gastropoda, hierarchical partitioning of diversity, Puerto Rico, richness, tropical montane forest

1 | INTRODUCTION

Understanding the spatial organization of biodiversity is necessary for determining the scales at which mechanisms operate to generate variation in the identity and abundances of species. Consequently, the manners in which the hierarchical configuration of biodiversity

varies with respect to environmental or geographic gradients have attracted much attention (e.g., Gering, Crist, & Veech, 2003; Higgins, 2010; Summerville, Boulware, Veech, & Crist, 2003; Wagner, Wildi, & Ewald, 2000; Wilsey, 2010), with a recent surge in attention to β -diversity (Mori, Isbell, & Seidel, 2018) because of its potential relationship with multifunctionality of ecosystems. Importantly,

patterns of biodiversity are often scale-dependent (e.g., Jackson & Fahrig, 2014; Scheiner et al., 2000), highlighting the role of spatial compartmentalization in heterogeneous landscapes. Biodiversity at larger spatial scales (γ) can be driven by within-site diversity (α -partitions), if little compositional variation characterizes communities (Cornell, Karlson, & Hughes, 2007; Gering & Crist, 2002; Pegg & Taylor, 2007), or biodiversity can be driven by among-site variation (β -partitions) that signal the importance of spatial heterogeneity at landscape or regional spatial scales (Belmaker, Ziv, Shashar, & Connolly, 2008; Erős, 2007; Stendera & Johnson, 2005). The contributions of α - or β -partitions to γ are largely dependent on the nature of environmental variation within a domain of interest (Freestone & Inouye, 2006) and the ways in which different species respond to spatial variation in the environment.

1.1 | Elevational gradients

Montane environments provide powerful test beds for the examination of patterns and processes that mold spatial patterns of biodiversity (e.g., Cisneros et al., 2014; González, Willig, & Waide, 2013; McCain, 2009; Terborgh, 1971; Whittaker, 1956; Willig & Presley, 2016). Dramatic variation in environmental drivers (e.g., solar insolation, temperature, precipitation) occurs over relatively short geographic extents, such that ecological mechanisms, rather than biogeographic or historic 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, making it more difficult to disentangle ecological from biogeographic or historic mechanisms (Willig, Kaufman, & Stevens, 2003; Willig & Presley, 2013). Elevational gradients of biodiversity have received renewed attention because predicted changes in climate promise to manifest first and most strongly at high latitudes and elevations, especially in tropical environs (Colwell, Brehm, Cardelús, Gilman, & Longino, 2008; Dirnbock, Essi, & Rabitsch, 2011; González et al., 2013; Malhi et al., 2010). This may be particularly true to the extent that tropical species have evolved in environments with less intra-annual variability in climatic conditions, leading to narrow niche breadths than in their extratropical counterparts (Janzen, 1967).

1.2 | Gastropods in the Luquillo Mountains

Terrestrial gastropods are taxonomically diverse and numerically abundant heterotrophs that fill important roles as detritivores, herbivores, and carnivores, making them useful for biogeographic, macroecological, or conservation study (e.g., Bloch, Higgins, & Willig, 2007; Clements et al., 2008; Stanisci, Cameron, Pokryszko, & Nekola, 2007). In addition, gastropods are ectothermic, constrained in distribution and behavior by desiccation stress (Cook, 2001), and not particularly vagile. Consequently, this fauna evinces the necessary attributes to study the effects of spatial variation in habitat, abiotic characteristics, and climate on biodiversity along elevational gradients.

Elevational gradients are useful for assessing environmental characteristics to which species respond because changes in elevation result in predictable and appreciable variation in plant species composition and structure, as well as in abiotic factors (e.g., temperature, precipitation, N-content, or N to C ratio). Although elevational changes in abiotic characteristics and associated vegetation are predictable, they differ in the form of their variation. Climatic characteristics, as well as abiotic factors associated with productivity (e.g., N-content or N to C ratio), generally change in a gradual, but not necessarily linear fashion with elevation (Waide, Zimmerman, & Scatena, 1998; Whiteman, 2000), whereas floral associations often have more or less discrete boundaries recognized as habitat types, forest types, or life zones (e.g., Hemp, 2006; Kessler, 2000). Because habitat specialization and responses to abiotic characteristics are important in defining the ranges of animal species, the spatial organization of biodiversity is contingent on the dominant mechanism that molds animal species distributions. The differences in the form of elevational variation in abiotic factors and vegetation offer an opportunity to disentangle the effects of these potential structuring mechanisms. If habitat preferences or specializations determine hierarchical structure of biodiversity along elevational gradients, then communities within a vegetation type should exhibit low among-site variation (i.e., low β -diversity), with high β -diversity among vegetation types. In contrast, if the spatial structure of biodiversity is driven by species-specific tolerances to abiotic characteristics that change gradually with elevation, then β -diversity among elevations within a vegetation type should be no different than β -diversity among vegetation types.

1.3 | Objectives and hypotheses

We explore the extent to which environmental characteristics mold patterns of taxonomic biodiversity of terrestrial gastropods along a tropical elevational gradient by quantifying the hierarchical compartmentalization (α -, β -, and γ -partitions) of species richness, evenness, diversity, and dominance, along two parallel transects, one passing through three elevationally stratified forest types (tabonuco, palo colorado, and elfin) and one passing only through palm forest. In addition, we determine the form and parameterization of elevational gradients of each hierarchical partition along each transect. Finally, we evaluate the effects of elevation and transect on litter nutrient content, which may represent an alternative driver of spatial structure of biodiversity for terrestrial gastropods along elevational gradients.

If climatic factors (e.g., temperature or precipitation) or abiotic factors (e.g., N-content or N to C ratio) that are related to productivity primarily mold elevational variation in gastropod biodiversity, then patterns should be continuous in nature and indistinguishable between transects. In contrast, if variation in plant community composition primarily molds elevational variation in gastropod biodiversity, patterns along the two transects should be different (i.e., compartmentalized along the mixed forest transect and continuous along the palm forest transect). Moreover, spatial variability

of gastropod assemblages at small (within an elevation) and large (among elevations) spatial scales should be less along the palm forest transect than along the mixed forest transect because variation in vegetation at small and large scales is less in palm forest than within or among the other forest types.

2 | METHODS

2.1 | Study area

The Luquillo Experimental Forest (LEF) is a Man and the Biosphere Reserve within the Luquillo Mountains of Puerto Rico (Supporting Information Figure S1a) and a site in the National Science Foundation's Long-Term Ecological Research network (Brokaw et al., 2012). Traditionally, tabonuco, palo colorado, and elfin forests are recognized as elevational zones in the Luquillo Mountains (Brown, Lugo, Silander, & Liegel, 1983; McDowell et al., 2012), with a fourth forest type dominated by sierra palm (*Prestoea acuminata*) and occurring as patches within other forest types at all elevations (hereafter palm forest).

Tabonuco forest occurs at elevations below 600 m. It is a subtropical wet forest, with a canopy height that is >20 m and emergent trees up to 35 m. Average annual rainfall is 346 cm, and mean temperature is 23°C, with little seasonal or diurnal variation (Odum & Pigeon, 1970). Cloud condensation begins at 600 m, marking the replacement of tabonuco forest by palo colorado forest, which extends to 900 m, has a canopy <15 m and has low and dense branching that supports more vines, epiphytes, and herbaceous plants, than does tabonuco forest. Mean annual rainfall is 470 cm, and mean annual temperature is 21°C. Elfin forest occurs above 900 m, has short, twisted trees and shrubs, and a low canopy (3 m). Epiphytes and epiphytic algae cover most woody vegetation. Mean annual rainfall is 360 cm, relative humidity is >95%, and mean annual temperature is 18°C (Brown et al., 1983). Palm forest occurs on steep slopes and wet soils throughout the elevational gradient. Its distribution is fragmented, as it is interspersed as patches within each of the other three forest types. Palm forest does not support an extensive subcanopy and harbors few shrubs, herbaceous plants, vines, or epiphytes in the understory. Throughout the gradient, palm forest is generally more productive than are other forest types at the same elevation (Richardson, Richardson, & Soto-Adames, 2005; Weaver & Murphy, 1990).

Research was conducted along two parallel elevational transects in the Sonadora River watershed (Willig et al., 2011) along the northwest-facing slope, from 18.32°N and 65.82°W at 300 m asl to 18.31°N and 65.79°W at 1,000 m asl. One included tabonuco, palo colorado, and elfin forests (hereafter mixed forest transect), whereas the other included only sites that were dominated by *P. acuminata* (hereafter palm forest transect). Over 80% of canopy trees at each stratum in the palm forest transect were *P. acuminata* (>95% at most sites), ensuring minimal elevational changes in vegetation structure or composition along that transect.

2.2 | Field methods

Each transect comprised elevational strata spaced at 50 m elevational increments from 300 m to 1,000 m asl; however, the Sonadora watershed did not contain a sufficiently large patch of palm forest at the 750 m elevation. Consequently, the mixed forest transect included 15 strata and the palm forest transect included 14 strata (Supporting Information Figure S1b). At each stratum, ten 3-m radius circular plots were established, resulting in 150 and 140 total plots for the mixed forest and palm forest transects, respectively. Strata from different transects occurring at the same elevation were always <1 km apart, and usually within 200 m or each other. Gastropods were sampled from each plot of each transect three times during the wet season of 2008. To minimize the effects of sampling sequence on elevational patterns, surveys were not repeated at any stratum until all strata along a transect were sampled the same number of times. The abundance of each species of gastropod was represented by the minimum number known alive during the survey period (Willig, Presley, Bloch, & Alvarez, 2013).

Terrestrial gastropods in the LEF are primarily herbivores and detritivores that rely on the production and decomposition of nutrient-rich plant materials (Garrison & Willig, 1996). These gastropods forage primarily on the surfaces of live and dead plant materials in, on, and above the leaf litter, up to a height of a few meters. Consequently, the amount and quality of available leaf litter are reflective of resource availability (i.e., productivity) for terrestrial gastropods. Litter was collected from one randomly chosen 0.5 m by 0.5 m quadrat (0.25 m²) within each sample plot, air-dried to constant mass, and weighed. Three plots from each elevational stratum were randomly chosen for analysis of litter nutrient content and quality. Each litter sample was separated into leafy and woody materials. See Supporting Information Appendix S1 for detailed methods for nutrient analysis.

2.3 | Quantification and partitioning of biodiversity

Biodiversity was quantified via species richness (number of observed species) and three metrics that represent distinct aspects of abundance-weighted biodiversity: Shannon diversity (Magurran, 1988), Camargo's evenness (Camargo, 1993), and Berger-Parker dominance (Berger & Parker, 1970). Each metric was expressed as Hill numbers to estimate "true" biodiversity (Jost, 2006). Importantly, Hill numbers for all metrics are on the same scale (i.e., from 1 to species richness) and greater values connote greater biodiversity for all metrics, including dominance (i.e., high values for dominance expressed as Hill numbers indicate low numerical dominance and high biodiversity).

Separately for each transect and for each biodiversity metric, we partitioned total biodiversity (γ) into within (α) and among (β) partitions using a multiplicative model (Jost, 2007) for a hierarchical sampling design. Partitioning involved three spatial scales: plot, elevational stratum, and transect. At the smallest spatial scale, α_{plots} was the average biodiversity of plots within strata along a transect,

and β_{plots} was the average number of compartments (i.e., a group of plots with similar species composition that is distinct from other such groups) within elevational strata in a transect. At the mid-sized spatial scale, α_{strata} was the average biodiversity of strata (plots were pooled within each stratum) and β_{strata} was the number of elevational compartments along a transect. At the largest spatial scale, γ_{transect} estimated biodiversity of an entire transect. The two β -partitions reflect different sources of heterogeneity along a transect: β_{plots} reflects the average number of distinct microhabitats within a stratum, and β_{strata} reflects the number of distinct elevational zones along the gradient. The complete multiplicative model for partitioning of biodiversity for each transect is given by:

$$\gamma_{\text{transect}} = \alpha_{\text{plots}} \times \beta_{\text{plots}} \times \beta_{\text{strata}}$$

To determine whether empirical values of hierarchical partitions of biodiversity differed from those produced by random processes (Higgins, 2010), we conducted simulations based on two different concepts, transect-level versus stratum-level species pools, reflecting gradient-wide and local processes, respectively. In each case, individuals were randomly selected from a species pool with replacement and allocated to plots with a constraint that simulated and empirical numbers of individuals in a plot were equal. In the transect-level approach, a single species pool comprised data from all plots from each transect, thereby assuming that individuals can colonize plots with equal efficacy from any elevation along a particular transect. In the stratum-level approach, the species pool for each stratum was unique, comprising only those individuals from the 10 plots at that stratum, thereby assuming that individuals can only colonize plots from a restricted elevational domain. For each combination of transect and species pool, we conducted 1,000 simulations to create an expected distribution of hierarchical partitions for each metric of taxonomic biodiversity as the basis to evaluate deviations from expectations. To evaluate whether the transect-level species pools differed between mixed and palm forest, we conducted two contingency g -tests (Sokal & Rohlf, 1995), one in which species were paired between transects based on their order in a rank abundance distribution and one in which species were paired between transects based on taxonomic identity. Partitioning of biodiversity was conducted in MATLAB 7.8.0.347.

2.4 | Elevational gradients

At the focal scale of elevational strata, we used a comprehensive statistical approach to evaluate gradients in hierarchical attributes of each of four components of biodiversity, in total abundance of gastropods, and in each of six nutrients that reflect litter content or quality. More specifically, we conducted a hierarchical partitioning of biodiversity for each elevational stratum (i) separately according to the relationship:

$$\gamma_{\text{stratum } i} = \alpha_{\text{plots } i} \times \beta_{\text{plots } i}$$

These partitions of biodiversity for species richness, evenness, diversity, and dominance, as well as plot scale data for total

gastropod abundance, and plot scale data for estimates of nutrient content and quality, informed assessments of elevational gradients in a comparable manner.

Effects of linear and quadratic representations of elevation (E and E^2), transect (T), and their interactions ($T \times E$ and $T \times E^2$) were tested via multivariable analysis of covariance (ANCOVA), with transect as a model I factor (i.e., a fixed treatment effect) and representations of elevation as a continuous variable. Thereafter, we conducted polynomial regression, followed by linear regressions if quadratic terms were not significant or MOS tests (Mitchell-Olds & Shaw, 1987) when quadratic terms were significant. In doing so, we characterize the form and parameterization of elevational gradients and contrast them between transects in a manner consistent with the results from multivariable ANCOVA. In the case of nonlinear relationships, the MOS test distinguishes monotonic relationships from those with humps or troughs. All statistical tests were executed in R 3.2.2, and we adopted an overall convention of significance at an α -level of 0.05, but also considered marginally significant results ($0.10 \geq p > 0.05$) when discussing general patterns.

To evaluate the effects of variation in gastropod abundance on elevational gradients in each hierarchical partition of each component of biodiversity, we conducted multivariable ANCOVA with abundance (A), linear and quadratic representations of elevation (E and E^2), transect (T), and their interactions ($T \times E$ and $T \times E^2$) as explanatory characteristics. Differences between ANCOVA results that did or did not account for variation in abundance suggest the extent to which elevational patterns in biodiversity result from elevational variation in abundance.

3 | RESULTS

3.1 | Species pools

The species pool for the mixed forest transect comprised 15 species and 3,949 individuals. The species pool for the palm forest transect comprised 15 species and 5,973 individuals. The rank abundance distributions of the two species pools were indistinguishable (contingency test: $g = 17.72$, $df = 15$, $p = 0.278$), whereas the species abundance distributions of the two pools (Figure 1) were significantly different (contingency test: $g = 23.35$, $df = 15$, $p = 0.045$). Nonetheless, species composition was similar between transects in two important ways: (a) transects shared 14 species, with each transect having 1 unique, rare species (*Cepolis musicola* along the mixed forest transect and *Obeliscus terebraster* along the palm forest transect); and (b) the same four species (*Caracolis caracolla*, *Nenia tridens*, *Platysuccinea portoricensis*, and *Gaeotis nigrolineata*) were most abundant and comprised >96% of all individuals along each transect (Figure 1).

3.2 | Biodiversity partitioning

The patterns of spatial partitioning and hierarchical structure were quite similar for mixed forest and palm forest transects (Table 1).

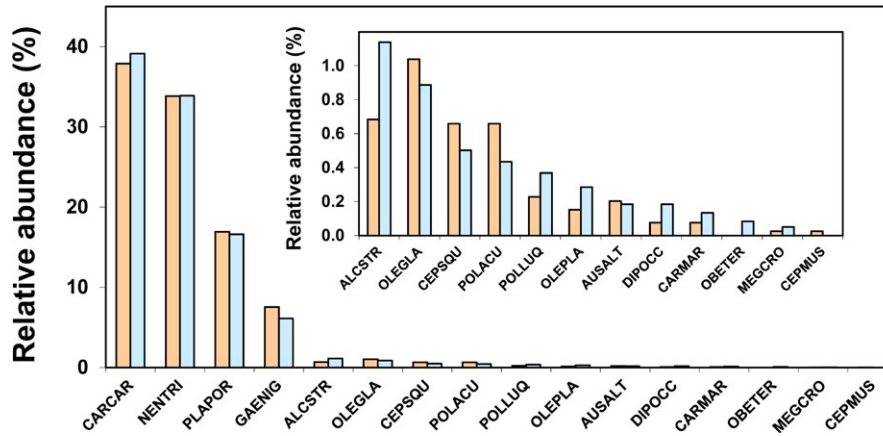


FIGURE 1 Species abundance distributions of terrestrial gastropods for mixed forest (orange bars) and palm forest (blue bars) transects from the Luquillo Mountains of Puerto Rico. Order of species was determined from the combined data for both transects. The gray insert provides enhanced resolution of relative abundances of rare species. Abbreviations for gastropod species are as follows: ALCSTR, *Alcaldia striata*; AUSALT, *Austroselenites alticola*; CARCAR, *Caracolus caracolla*; CARMAR, *Caracolus marginella*; 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*; POLACU, *Polydotes acutangula*; and POLLUQ, *Polydotes luquillensis*

More specifically, α_{plots} and α_{strata} for each metric were less than that produced by random allocation of individuals from the stratum- or transect-level species pools, except in the cases of species richness for α_{strata} . In contrast, β_{plots} for each metric was greater than that produced by random allocation of individuals from the stratum- or transect-level species pools, except for dominance. Species pool effects were most pronounced for β_{strata} in that

empirical metrics generally did not differ from random expectation based on stratum-level pools, but were greater than expected based on transect-level pools. Neither species pool nor transect affected the direction of deviation from random expectation for γ , but empirical values were less than expected due to chance for evenness and diversity, and indistinguishable from chance for dominance.

TABLE 1 Estimates of α , β , and γ for each of four biodiversity metrics (I) for gastropods from elevational transects in the Sonadora watershed of the Luquillo Experimental Forest

Diversity component	Species richness			Camargo evenness			Shannon diversity			Berger-Parker dominance		
	I	Pool		I	Pool		I	Pool		I	Pool	
		S	T		S	T		S	T		S	T
Mixed forest												
α_{plots}	3.64	<	<	2.35	<	<	2.42	<	<	1.77	<	<
β_{plots}	2.18	>	>	1.17	>	>	1.33	>	>	1.07	>	<@
α_{strata}	7.93	>	<	2.75	<@	<	3.21	<	<	1.90	<	<
β_{strata}	1.89	ns	>	1.34	ns	>	1.43	ns	>	1.55	ns	>
γ	15			3.67	<	<	4.58	<	<	2.96	ns	ns
Palm forest												
α_{plots}	4.33	<	<	2.54	<	<	2.76	<	<	1.90	<	<
β_{plots}	2.05	>	>	1.20	>	>	1.26	>	>	1.10	>	ns
α_{strata}	8.86	>	<	3.04	<@	<	3.48	<	<	2.10	<@	<
β_{strata}	1.69	<	>	1.24	ns	>	1.33	ns	>	1.52	ns	>
γ	15			3.77	<	<	4.64	<	<	3.18	ns	ns

Note. Analyses were conducted using stratum-level (S) and transect-level (T) species pools (see text for details). Significance ($p \leq 0.05$) is indicated by < for components that are less than expected by chance and by > for components that are greater than expected by chance. Marginal significance ($0.05 < p \leq 0.10$) is denoted by @. Confidence intervals for γ diversity of species richness are biased, as simulations cannot result in more species than those that exist in the data set; statistical interpretations were not conducted in this case.

Turnover among plots within strata (β_{plots_i}) was greater than turnover among strata (β_{strata_i}) for species richness. In contrast, turnover among strata (β_{strata_i}) was greater than turnover among plots within a stratum (β_{plots_i}) for metrics of biodiversity that are sensitive to species abundance. These patterns characterized both the mixed forest and palm forest transects (Table 1).

3.3 | Elevational gradients of biodiversity

Total gastropod abundance declined linearly and at the same rate with increasing elevation along both transects, and was consistently greater in palm than in non-palm forest (Table 2, Figure 2). Elevational gradients in partitions of taxonomic biodiversity were quite variable (Figure 3a–l), including four patterns: (a) no association, (b) monotonic and linear, (c) monotonic and nonlinear, and (d) quadratic with a hump. Differences between transects were rare (i.e., α_{plots_i} for richness [Figure 3a], α_{plots_i} for diversity [Figure 3g]) and never arose from interactions with linear ($T \times E$) or quadratic ($T \times E^2$) representations of elevation (Table 2).

For species richness (Figure 3c), $\gamma_{\text{stratum}_i}$ decreased with increasing elevation in the same manner along both transects (coincident lines). This was a consequence of opposing patterns for α_{plots_i} (monotonically decreasing; Figure 3a) and β_{plots_i} (monotonically increasing; Figure 3b).

For metrics sensitive to variation in abundance (Figure 3d–l), elevational gradients in α_{plots_i} or $\gamma_{\text{stratum}_i}$ were always hump-shaped, whereas elevational patterns of β_{plots_i} were variable: hump-shaped for evenness; positive and linear for diversity; and no relationship

for dominance. Moreover, variation in abundance had few effects on the responses of partitions of biodiversity to elevation (Supporting Information Table S1). Differences between transects for α_{plots_i} for richness and α_{plots_i} for diversity (Table 2) were mostly related to differences between transects in total gastropod abundance. Moreover, the linear elevational response of α_{plots_i} for diversity (Table 2, Figure 3g) becomes a quadratic response when accounting for variation in abundance. In part, this is somewhat trivial as the p -value for the quadratic component approached significance ($p = 0.051$) in the analysis that did not account for variation in abundance (Table 2) and was significant ($p = 0.031$) in the analysis that accounted for variation in abundance (Supporting Information Table S1).

3.4 | Elevational gradients of litter nutrients

In general, the amount of litter as well as nutrient content and quality declined monotonically with increasing elevation (Table 3), although the form of the decline depended on the identity of the nutrient and transect (Supporting Information Figure S2). Most characteristics of litter content (i.e., N, Mg, P, or K) or quality (i.e., N:C, Mg:C, or P:C) decreased in a linear fashion with increasing elevation and did so in an indistinguishable manner along mixed forest and palm forest transects. Although none of the main or interactive effects of elevation or transect on C were significant, a consistent effect of elevation approached significance ($p = 0.092$), suggesting a linear decrease with increasing elevation. The P:C linearly decreased with increasing elevation at indistinguishable rates along both transects, but ratios were consistently higher along the palm forest compared to the

TABLE 2 Results of multivariable analysis of covariance evaluating the effects of elevation and transect on hierarchical components of each of four metrics of gastropod biodiversity as well as on total gastropod abundance

Diversity component	Elevation	Elevation ²	Transect	Elevation × transect	Elevation ² × transect
Abundance	<0.001	0.057	0.002	0.293	0.242
Richness					
α_{plots_i}	<0.001	0.018	0.016	0.636	0.256
β_{plots_i}	0.092	0.023	0.141	0.525	0.277
$\gamma_{\text{stratum}_i}$	0.003	0.579	0.207	0.719	0.196
Evenness					
α_{plots_i}	0.075	<0.001	0.075	0.717	0.789
β_{plots_i}	0.023	0.007	0.555	0.637	0.162
$\gamma_{\text{stratum}_i}$	0.701	<0.001	0.198	0.575	0.774
Diversity					
α_{plots_i}	0.018	<0.001	0.049	0.547	0.812
β_{plots_i}	<0.001	0.051	0.136	0.507	0.242
$\gamma_{\text{stratum}_i}$	0.815	<0.001	0.222	0.677	0.677
Dominance					
α_{plots_i}	0.084	<0.001	0.130	0.667	0.563
β_{plots_i}	0.880	0.079	0.552	0.543	0.796
$\gamma_{\text{stratum}_i}$	0.184	<0.001	0.136	0.518	0.960

Note. Significant results ($p \leq 0.05$) are bold.

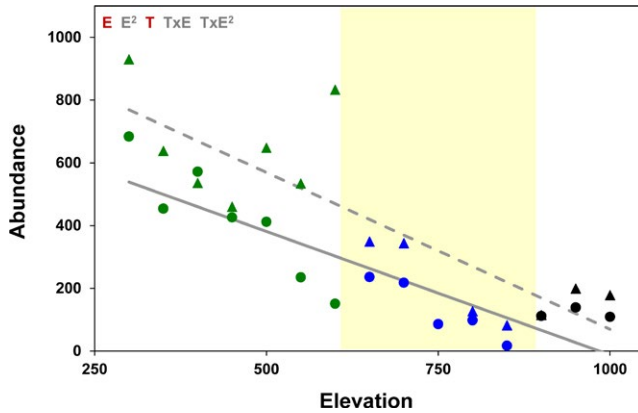


FIGURE 2 Elevational gradients in abundance of terrestrial gastropods along mixed forest (circles, solid gray line) and palm forest (triangles, dashed gray line) transects in the Luquillo Mountains. Green, blue, and black symbols represent elevational zones associated with tabonuco, palo colorado, and elfin forest, respectively. Symbols represent cumulative abundance from ten plots within each stratum; lines represent best-fit polynomial models. Significance of factors from multivariable analysis of covariance (Table 2) for elevation (E), quadratic representation of elevation (E^2), transect (T), and interactions between transect and linear ($T \times E$) or quadratic ($T \times E^2$) representations of elevation are indicated by red letters (gray letters represent non-significant terms). Yellow-shaded area represents the elevational range of palo colorado forest, with white areas to the left and right representing tabonuco and elfin forest, respectively

mixed forest transects (i.e., parallel lines). The K:C varied with elevation in a consistent monotonic fashion regardless of transect (i.e., ratios decreased with increasing elevation in an accelerating fashion). Although Ca and Ca:C declined monotonically with increasing elevation, the form of the decrease differed between transects: an accelerating decline was along the palm forest transect and a linear decline was along the mixed forest transect (Supporting Information Figure S2).

4 | DISCUSSION

Fundamental principles of ecology posit that all species have heterogeneous spatial distributions at multiple spatial scales, and the nature of that heterogeneity is species-specific as a result of intra- and inter-specific interactions as well as feedbacks between biotic and abiotic components of the environment (Scheiner & Willig, 2008, 2011). Montane settings provide a fertile testbed for addressing some of the most important ecological issues concerning the mechanisms that mold such variation. In the absence of manipulative experiments at large scales, it is impossible to identify causation with confidence, but the environmental gradients associated with elevation can provide considerable insight into questions that have been at the forefront of ecology for decades. Although previous research detected strong elevational gradients along palm and mixed forest transects in the Luquillo Mountains (Willig et al., 2013), it

suffered from three shortcomings. First, only linear responses were considered. Second, abundance-weighted metrics (evenness and diversity) were not transformed into Hill numbers. Third, analyses were restricted to the α -level (i.e., plot scale) and did not address variation at the γ -level (i.e., stratum scale). Herein, all three issues were addressed comprehensively, leading to more robust conclusions. We recognize that the geographic inference space of our research is limited to the Sonadora River watershed. Nonetheless, our results should be broadly applicable to other elevational gradients, especially those in the tropics for which environmental controls may be similar. Regardless, our extrapolations can be viewed as general hypotheses for examination in other geographic and environmental contexts.

4.1 | Abiotic versus biotic controls on biodiversity partitions

Based on elevational variation in plant species composition and physiognomy, spatial variability of gastropod assemblages among plots within elevational strata as well as among strata within transects should be less along the palm forest transect than along the mixed forest transect. Consequently, we would expect that (a) β_{plots} contributes more to γ along the mixed forest transect than along the palm forest transect; (b) β_{strata} contributes more to γ along the mixed forest transect than along the palm forest transect; and (c) the form of elevational gradients in $\alpha_{\text{plots } i}$, $\beta_{\text{plots } i}$, and $\gamma_{\text{stratum } i}$ will differ between transects for each component of biodiversity. An alternative set of hypotheses can be posed if climatic (i.e., temperature, precipitation, or humidity) and abiotic (i.e., nutrient content and quality of litter) considerations, which vary similarly along both transects (Table 3; Supporting Information Figure S2), mold spatial patterns of biodiversity. In that case, spatial variability of gastropod assemblages among plots within strata as well as among strata within transects should be similar along both transects. Consequently, we would expect that (a) β_{plots} contributes to γ similarly along both transects; (b) β_{strata} contributes to γ similarly along both transects; and (c) for each metric of biodiversity, the form of elevational gradients in $\alpha_{\text{plots } i}$, $\beta_{\text{plots } i}$, and $\gamma_{\text{stratum } i}$ will be similar for both transects.

Evidence based on the partitioning of biodiversity along elevational gradients provides support for the climatic or abiotic explanation for the spatial organization of gastropod biodiversity having priority over effects of vegetation. First, the magnitude of β_{plots} for each metric was quite similar for both transects (Table 1). Moreover, β_{plots} for each metric was generally greater than expected by random allocation of individuals regardless of species pool. Second, the magnitude of β_{strata} for both transects was similar for each component of biodiversity (Table 1). Moreover, β_{strata} for both transects was generally no different than that expected due to the random allocation of individuals from the stratum-level species pool and was always greater than expected due to the random allocation of individuals from the transect-level species pool. Third, transect effects were rare (i.e., 2 of 12 cases; $\alpha_{\text{plots } i}$ for richness and $\alpha_{\text{plots } i}$ for diversity) in general (Table 2) and absent when controlling for variation in total

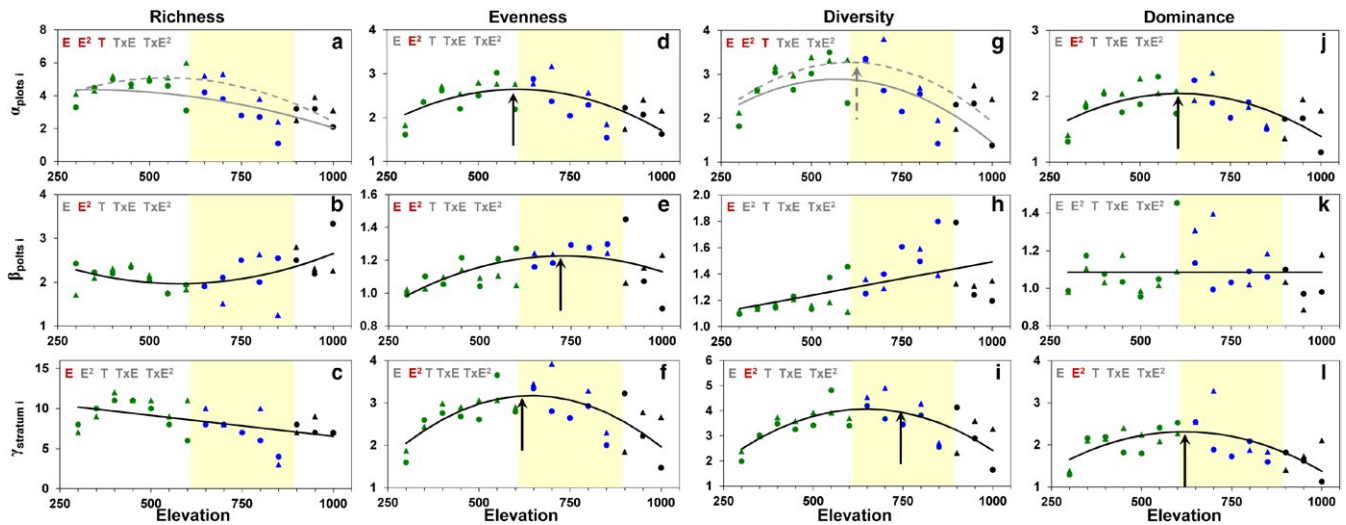


FIGURE 3 Elevational gradients of hierarchical partitions of components of biodiversity for terrestrial gastropods along mixed forest (circles) and palm forest (triangles) transects in the Luquillo Mountains. Green, blue, and black, symbols represent elevational zones associated with tabonuco, palo colorado, and elfin forest, respectively. Based on results from multivariable ANCOVAs, solid black lines represent best-fit models for both transects when simple or interactive effects of transect are not present; gray lines represent best-fit models for mixed forest (solid) and palm forest (dashed) transects separately, when simple or interactive effects of transect are present. Maxima are indicated by arrows for quadratic relationships with significant humps and correspond in color and form to the relationship with which they are associated. Significance of elevation (E), quadratic representation of elevation (E^2), transect (T), and interactions between transect and linear ($T \times E$) or quadratic ($T \times E^2$) representations of elevation are indicated by red letters (gray letters represent non-significant terms). Yellow-shaded area represents the elevational range of palo colorado forest, with white areas to the left and right representing tabonuco and elfin forest, respectively

gastropod abundance (Supporting Information Table S1). Moreover, even when present, transect effects did not involve interactions with linear or quadratic representations of elevation (i.e., the separate lines were parallel). Finally, none of the elevational gradients of $\alpha_{plots\ i}$ or $\gamma_{stratum\ i}$ for any component of biodiversity (Figure 3) along the mixed forest transect suggest discrete differences in biodiversity associated with tabonuco, palo colorado, or elfin forests.

4.2 | Spatial linkages between abundance and production, nutrient content, and nutrient quality

Primary production (Weaver & Murphy, 1990), as well as litter production (i.e., $g\ L/m^2$), litter quality (i.e., N:C, P:C, K:C, Mg:C, or Ca:C), and litter nutrient concentrations (e.g., N, P, K, Mg, and Ca) that are essential for gastropod metabolism, decreases with increasing elevation

TABLE 3 Results of multivariable analysis of covariance evaluating the effects of elevation and transect on amount of litter, the quantity of nutrients in the litter, and the quality of the litter (i.e., ratio of nutrients to carbon)

	Elevation	Elevation ²	Transect	Elevation \times transect	Elevation ² \times transect
Amount of litter	0.035	0.908	0.434	0.405	0.777
Litter quantity (g/m^2)					
Carbon	0.092	0.713	0.335	0.550	0.836
Nitrogen	<0.001	0.575	0.882	0.427	0.711
Calcium	<0.001	0.503	0.323	0.665	0.016
Magnesium	<0.001	0.325	0.095	0.377	0.226
Phosphorus	<0.001	0.879	0.303	0.703	0.962
Potassium	<0.001	0.120	0.098	0.905	0.259
Litter quality (Nutrient to carbon ratio)					
Nitrogen	0.001	0.275	0.160	0.851	0.689
Calcium	<0.001	0.658	0.724	0.891	0.009
Magnesium	<0.001	0.335	0.228	0.553	0.083
Phosphorus	<0.001	0.916	0.043	0.994	0.979
Potassium	0.002	0.049	0.124	0.740	0.233

Note. Significant results ($p \leq 0.05$) are bold.

(Supporting Information Figure S2). In addition, differences between palm and non-palm forest have been documented previously in the Luquillo Mountains for C:N and Mg concentration at low elevations, C:N and concentration of P at mid-elevations, and for C:N as well as concentrations of N, K, P, and Mg at high elevations (Richardson et al., 2005). In the Sonadora River watershed, P:C in litter consistently differed between transects and was higher in palm than in non-palm forests (Table 3; Supporting Information Figure S2). In addition, the concentration of Ca and Ca:C in the litter declined with increasing elevation, linearly in non-palm forest and monotonically (saturating) in palm forest, without consistent differences between transects in either attribute (Table 3, Supporting Information Figure S2). Consequently, cumulative abundance of gastropods decreased in parallel linear manners along palm and mixed forest transects, with greater abundance along the palm than mixed forest transect at 13 of 14 elevations (Figure 2). Similarly, the abundance of most gastropod species declined with increasing elevation (Willig et al., 2013), with all species (Willig et al., 2011) enjoying higher abundances in palm than in non-palm forest (significantly so for seven of 14 species).

4.3 | The linkage between biodiversity and abundance

Variation among sites in the cumulative abundance of individuals can give rise to variation in aspects of biodiversity, especially those metrics that are sensitive to the number of species (i.e., species richness and Shannon diversity). The linkage exists for statistical and biological reasons as detailed in the Theory of Random Placement (Coleman, Mares, Willig, & Hsieh, 1982) and the More Individuals Hypothesis (Srivastava & Lawton, 1998). Thus, we might expect that (a) species richness and diversity would exhibit monotonic declines with increasing elevation; and (b) each metric would be higher in palm forest than in elevationally matched palm forest.

Empirical evidence in support of these ideas is equivocal and depends on focal scale. As expected for $\alpha_{\text{plots } i}$ of richness and diversity, magnitudes of metrics are greater in palm than in non-palm forest so that best-fit models are essentially parallel (Figure 3a,g). Moreover, the strong effects of transect (Table 2) weaken to non-significance if variation in abundance is “controlled” in analyses (Supporting Information Table S1). This supports the idea that passive sampling plays a role in molding spatial variation in biodiversity at small focal scales (e.g., plots). In contrast, elevational gradients of $\gamma_{\text{stratum } i}$ are coincident along both transects for richness and diversity, and in the latter case, the relationship is hump-shaped rather than monotonic (Figure 3c,i). Although spatial variation in $\gamma_{\text{stratum } i}$ of richness (Figure 3c) supports the idea that passive sampling molds elevational gradients, the coincidence of lines for $\gamma_{\text{stratum } i}$ of richness and diversity (Figure 3c,i) suggests that variation in abundance does not play as dominant or pervasive a role at the scale of strata. Similarly, elevational variation in $\alpha_{\text{plots } i}$ and $\gamma_{\text{stratum } i}$ for evenness (Figure 3d,f) and dominance (Figure 3j,l) fails to provide support for the contention that abundance molds patterns of biodiversity along the

gradient. Each partition for each component of biodiversity does not decline monotonically with increasing elevation, but instead evinces hump-shaped gradients. Moreover, differences between mixed forest and palm forest transects are not apparent for evenness or dominance.

The progressive loss of rare species (those with a proportional abundance $<1/S$, where S is species richness) between 350 m and 600 m asl may account for this discrepancy between empirical evidence and expectation. In the Luquillo Mountains, rare species dominate the gastropod fauna: ~20%–40% of species are rare at the level of plots; ~50%–70% of the species are rare at the stratum level; and ~75%–80% of the species are rare at the transect level. Moreover, at all spatial scales, there are more rare species in palm than in non-palm forest. Thus, the spatial dynamics of biodiversity are driven by stochastic features associated with dispersal among plots or strata, in combination with filtering mechanisms associated with niche attributes of species and the habitat characteristics at local sites.

4.4 | Do elevational gradients of biodiversity depend on component or scale?

For each component of gastropod biodiversity in the Luquillo Mountains, the form of the relationship does not differ appreciably between the focal scale of plots ($\alpha_{\text{plots } i}$) and strata ($\gamma_{\text{stratum } i}$). Species richness evinces the most distinctive differences: $\alpha_{\text{plots } i}$ decreases monotonically but not linearly with increasing elevation, whereas $\gamma_{\text{plots } i}$ decreases linearly with increasing elevation (Figure 3a,c). The form of elevational gradients in abundance-weighted metrics of biodiversity (evenness [Figure 3d,f], diversity [Figure 3g,i], and dominance [Figure 3j,l; scaled so that a larger index connotes higher biodiversity and low dominance]) are scale-independent: modal with peaks in mid-elevation forest. Thus, at the focal scales of plots (28.3 m²) and strata (1,000 m²), elevational gradients are quite similar in the Luquillo Mountains. Nonetheless, the nonlinear responses of metrics of biodiversity (especially those that weight species by their relative abundance) to elevation reaffirms the concern of assuming a constant rate of change in compositional turnover along environmental gradients, or basing comparisons among regions or taxa on a metric that assumes such invariance (Fitzpatrick et al., 2013).

Regardless of focal scale, elevational gradients in richness (monotonically decreasing) are quite different from those for abundance-weighted metrics (modal). This corroborates the contention that species richness is not an effective surrogate for other metrics of biodiversity and is often an incomplete surrogate for biodiversity in general. Similar differences in the form of environmental gradients associated with species richness and abundance-weighted metrics have been uncovered in a variety of situations (e.g., forest tree biodiversity and above ground production [Vance-Chalcraft, Willig, Cox, Lugo, & Scatena, 2010], grassland plant biodiversity and productivity [Wilsey, Chalcraft, Bowles, & Willig, 2005; Chalcraft, Wilsey, Bowles, & Willig, 2009]). In the Sonadora River watershed, the rise in evenness and diversity between

300 m and 600 m asl, and especially in tabonuco forest, despite the decline in species richness along those same elevations, is a consequence of the loss of rare species and a reduction in dominance at the level of plots and strata.

4.5 | Role of spatial variation in productivity and essential nutrients

Biodiversity–productivity relationships are scale-dependent (e.g., Chalcraft, Williams, Smith, & Willig, 2004; Mittelbach et al., 2001; Scheiner et al., 2000; Waide et al., 1999), and relationships of productivity with components of taxonomic biodiversity that weight species by relative abundance or relative biomass (e.g., species diversity, evenness, dominance) are not necessarily of the same form as those for species richness (e.g., Vance-Chalcraft et al., 2010; Wilsey et al., 2005). Our results are relevant to this controversy to the extent that elevation is a reasonable surrogate for productivity or that variation in litter amount, nutrient content, or nutrient quality is related to productivity in a monotonic fashion.

All abundance-weighted measures of taxonomic biodiversity evinced modal patterns at $\alpha_{\text{plots } i}$ and $\gamma_{\text{stratum } i}$ levels, with mid-elevational (=mid-productivity) peaks at or near the cloud condensation point, and did so along both mixed forest and palm forest transects (Figure 3d,f,g,i,j,l). The peaks likely arise because the cloud condensation point corresponds to (a) an appreciable decline in the relative abundances of two low-elevation dominants (*C. caracolla* and *N. tridens*); (b) an appreciable increase in relative abundances of the upper elevation dominant (*P. portoricensis*); and (c) the locus of highest relative abundances of *G. nigrolineata*. Consequently, these mid-productivity peaks in biodiversity arise due to a transition between species that dominate at lower or higher elevations and correspond to the transition between lower elevation and higher elevation gastropod assemblages based on species incidence along the mixed forest transect (Willig et al., 2011).

4.6 | Local versus regional mechanisms

A controversy exists regarding the use of spatial variation in β -partitions of biodiversity to understand mechanisms that underlie elevational or latitudinal gradients. Kraft, Comita, et al. (2012) and Kraft, Sanders, et al. (2012) quantified latitudinal and elevational changes in α -, β -, and γ -partitions of species richness for woody plants, and posited that random processes alone can give rise to these gradients of β -diversity, concluding that it is unnecessary to invoke variation in mechanisms of local community assembly along gradients of latitude or elevation. The approach of Kraft, Comita, et al. (2012) and Kraft, Sanders, et al. (2012) has been questioned from methodological and design perspectives (Qian, Wang, & Zhang, 2012; Tuomisto & Ruokolainen, 2012), with a re-analysis of data supporting the opposing conclusion (i.e., the β -partition of richness increased with increasing latitude after adjustment for gradient-wide variation in γ). Our use of stratum-level and transect-level species pools allows us to explore these issues for multiple metrics of taxonomic biodiversity with respect to elevation.

Variation among plots within strata reflects local spatial variation in microclimate and microhabitat, whereas variation among strata along a transect reflects elevational variation in biotic (e.g., productivity and forest type) and abiotic (e.g., climate and nutrients) characteristics. For each metric along each transect, the contributions of β_{plots} and β_{strata} to γ were similar (Table 1). This suggests that local environmental variation and elevational variation in the environment contributed similarly to γ , a surprising effect given the dramatic climatic gradient and the differences between transects in the plant communities that they comprise.

Species filtering at the plot and stratum level has a similar effect on each transect, with significantly smaller empirical values of α_{plots} and α_{strata} than would be expected given a random selection of individuals from either stratum-level or transect-level species pools (Table 1). These results support the perspective that local and regional mechanisms together affect the number, identity, and abundances of species along both transects (in contrast to the conclusions of Kraft, Comita, et al. (2012) and Kraft, Sanders, et al. (2012)).

4.7 | Environmental complexity and homogenization

Biogeographic and ecological phenomena likely contribute to the hierarchical organization of gastropod biodiversity, including elevational gradients. Island faunas are depauperate compared to their mainland counterparts, and often contain a preponderance of generalist species (e.g., Angerbjörn, 1985; Scott, Clegg, Blomberg, Kikkawa, & Owens, 2003). Hurricane-prone environments that have persisted for millennia, like the LEF, may also select for more generalist niche characteristics in its fauna (e.g., Waide, 1991; Williams, 1969). The extent to which these phenomena are true would diminish the contributions of β -partitions of biodiversity to elevational domains (γ) along either palm or mixed forest transects.

Sierra palm is ubiquitous in the Luquillo Mountains in both palm and non-palm forests (Brown et al., 1983; McDowell et al., 2012), and is an important substrate or food source for gastropods (Garrison & Willig, 1996; Willig et al., 1998). Moreover, palm forest interdigitates with the other forest types along the gradient. These attributes of the flora tend to diminish gastropod compositional variation among strata along the mixed forest transect and enhance similarity between strata of the same elevation on different transects. In addition, disturbance events such as tree falls, landslides, and hurricanes may alter the mapping of ecological space onto geographic space, and these effects may persist as legacies for decades (Waide & Willig, 2012; Willig et al., 2007), thereby diminishing the strength of spatial gradients or the extent to which spatial gradients such as elevation can represent surrogates for particular environmental gradients (e.g., productivity).

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DATA AVAILABILITY

Data are permanently deposited in the Luquillo LTER Data Catalog: <https://luq.lter.network/datacatalog> (Data Set ID 171: <https://luq.lter.network/data/luqmetadata171>).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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SUPPORTING INFORMATION

The spatial configuration of taxonomic biodiversity along a tropical elevational gradient: α -, β -, and γ -partitions

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APPENDIX S1 - Detailed methods for nutrient analyses

Woody portions of each sample were pulverized using a mortar and pestle and then a Scienceware Micro-mill. Leafy portions of each sample were homogenized using a mortar and pestle, and a subsample of this material was transferred to the Micro-mill for pulverization. Wood and leaf samples were analyzed separately for 6 nutrients: carbon, nitrogen, calcium, magnesium, phosphorus, and potassium. Results from woody and leafy materials were combined to estimate the overall content (g/m^2) of nutrients in the litter. Quality of the litter was expressed as the ratio of the mass of each nutrient (“X”) to the mass of carbon (using the convention “X:C”).

Nutrient content of litter samples was determined by the Environmental Chemistry Laboratories of the Center for Environmental Sciences and Engineering at the University of Connecticut (<https://cese.uconn.edu/>). Carbon and nitrogen contents were quantified using the USEPA Method 440. A 2 g homogenate was dried overnight in a drying oven, a 2 mg subsample was weighed onto the solid tin combustion capsule, and placed into a Perkin Elmer® (Norwalk, CT) 2400 CHN analyzer. Metal content was quantified using a Perkin Elmer 7300DV Dual View Inductively Coupled Plasma Optical Emission Spectrometer according to established protocols (Environmental Protection Agency 2000). Approximately 0.2 g of the sample was removed, homogenized, and placed into a hot block tube. Trace metal grade hydrochloric (3.6 mL) and nitric (1.2 mL) acids were added to each tube and placed in the hot block, and refluxed for 3 hours at 95 °C. Samples were cooled and brought up to a final volume of 25 ml with DI water. Standard quality assurance procedures were employed, including analysis of initial and

continuing calibration checks and blanks, duplicate samples, preparation blanks, post digestion spiked samples, and laboratory control samples.

Environmental Protection Agency (2000) EPA method 6010C (SW-846): inductively coupled plasma-atomic emission spectrometry. Revision 3. Washington, D.C.

TABLE S1. Results of multivariable analysis of covariance evaluating the effects of elevation, abundance, and transect on hierarchical components of each of four metrics of gastropod biodiversity. Significant results ($P \leq 0.05$) are bold.

Diversity component	Elevation		Abundance	Transect	Elevation ² x transect	
	Elevation	Elevation ²			transect	x transect
Richness						
$\alpha_{\text{plots } i}$	< 0.001	0.007	< 0.001	0.441	0.233	0.233
$\beta_{\text{plots } i}$	0.093	0.023	0.200	0.355	0.443	0.199
$\gamma_{\text{stratum } i}$	0.003	0.576	0.080	0.746	0.513	0.318
Evenness						
$\alpha_{\text{plots } i}$	0.077	< 0.001	0.096	0.301	0.584	0.966
$\beta_{\text{plots } i}$	0.017	0.005	0.036	0.452	0.983	0.321
$\gamma_{\text{stratum } i}$	0.707	< 0.001	0.646	0.223	0.623	0.812
Diversity						
$\alpha_{\text{plots } i}$	0.016	< 0.001	0.031	0.324	0.363	0.906
$\beta_{\text{plots } i}$	< 0.001	0.035	0.008	0.965	0.216	0.489
$\gamma_{\text{stratum } i}$	0.819	< 0.001	0.529	0.306	0.687	0.670
Dominance						
$\alpha_{\text{plots } i}$	0.087	< 0.001	0.201	0.336	0.583	0.455
$\beta_{\text{plots } i}$	0.877	0.073	0.397	0.193	0.746	0.542
$\gamma_{\text{stratum } i}$	0.193	< 0.001	0.650	0.142	0.585	0.971

FIGURE S1. The Luquillo Mountains of Puerto Rico extend from 100 m to 1075 m asl and include the Luquillo Experimental Forest (Panel A). Three elevationally delimited forest types occur in the Luquillo Mountains: tabonuco forest (300–600 m), palo colorado forest (600–900 m), and elfin forest (> 900 m). A fourth forest type, palm forest, has a patchy distribution and occurs at all elevations. Two transects, each comprising a sequence of elevational strata from 300–1000 m at 50 m intervals, were established in the Sonadora River watershed of the Luquillo Mountains (Panel B). A mixed forest transect passed through tabonuco, palo colorado, and elfin forests (blue, green, and orange dots, respectively) and a parallel palm forest transect contained only patches of sierra palm forest (black dots).

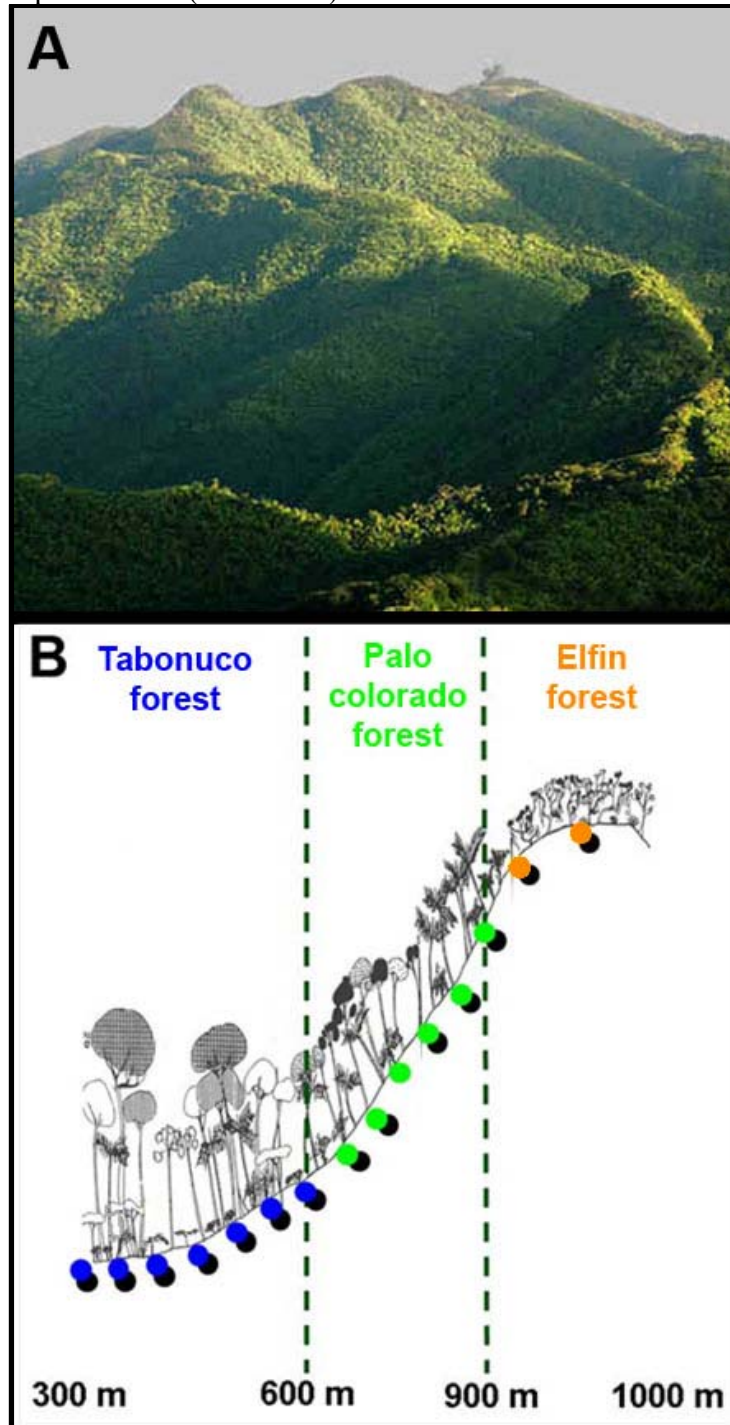


FIGURE S2. Elevational gradients in litter amount, nutrient content (g/m^3) of litter, or nutrient quality (nutrient to carbon ratio) of litter along elevational transects in the Luquillo Mountains. Circles and triangles represent averages from 3 plots within each stratum for mixed forest or palm forest transects, respectively. Green, blue, and black indicate elevational zones associated with tabonuco, palo colorado, and elfin forests, respectively. Significance of factors from multivariable analysis of covariance (Table 3) for transect (T), elevation (E), quadratic representation of elevation (E^2), and interactions between transect and linear ($T \times E$) or quadratic ($T \times E^2$) representations of elevation are indicated by red letters (gray letters represent non-significant terms). Lines represent best-fit models from polynomial or linear regressions as indicated by multivariable analysis of covariance (Table 3). Black lines represent best-fit models for both transects combined (i.e., no consistent effect of transect or interactive effect of transect with linear or quadratic representations of elevation). Gray solid or gray dashed lines represent best-fit models for mixed forest or palm forest transects, respectively, and indicate significant differences between transects.

