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ORIGINAL ARTICLE

Variation in biodiversity and abundance of functional groups of arthropods along a tropical elevational gradient in Puerto Rico

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Abstract

Elevational gradients represent platforms for exploring the effects of environmental variation on biodiversity. The environmental correlates of these spatial gradients are likely to be modified during the Anthropocene, as species respond to global change drivers including warming and increased frequency of extreme events. We quantified variation in the abundance of four functional groups of canopy arthropods (i.e., folivores, sap-suckers, detritivores, and predators), as well as in aspects of biodiversity on each of six host-plant species along two elevational transects in the Luquillo Mountains of Puerto Rico: a mixed forest transect, traversing tabonuco, palo colorado, and elfin forests, and a palm forest transect, comprising only patches dominated by sierra palm (*Prestoea acuminata*). We expected gradients in arthropod abundance and biodiversity to be host-tree specific, and for gradients on palm to differ between transects due to a combination of mechanisms associated with host selection, rescue effects, habitat structure, and source pool dynamics. In general, abundance and biodiversity declined with elevation. The ways in which abundance declined with increasing elevation was contingent on host tree identity and on arthropod functional group, whereas all aspects of biodiversity declined with elevation in consistent manners regardless of host tree identity or transect. Similarly, turnover (beta components of biodiversity between sequential elevational strata) did not differ between transects. Decreases in productivity with increasing elevation may be responsible for gradients in abundance or biodiversity. However, host-specific and functional group-specific gradients suggest that elevational effects manifest differently depending on tree species identity and resource bases that are consumer specific.

KEYWORDS
canopy arthropods, Caribbean, folivory, insect-plant interactions, macroecology, montane forests, sierra palm

1 | INTRODUCTION

Aspects of global change, including warming (e.g., Brown et al., 2022; Shi et al., 2021), increased frequency and intensity of extreme weather events such as cyclonic storms and droughts (Habibullah et al., 2021; Maxwell et al., 2019), and altered composition and configuration of landscapes via anthropogenic activities (Presley et al., 2019; Scott et al., 2001; Vitousek et al., 1997), increasingly threaten biodiversity in ecosystems throughout the world. As a consequence, concerns about the Earth's sixth mass extinction, especially as they relate to loss of ecosystem services (Cardinale et al., 2006; Smale et al., 2019), have arisen in both popular and scientific venues (Ceballos et al., 2015). Within this context, it has become critical to characterize spatial patterns of biodiversity, understand the mechanisms that give rise to them, and employ that understanding to inform conservation and management of natural resources.

1.1 | Elevational gradients

Elevational gradients represent an important environmental platform (Garten Jr. et al., 1999; González et al., 2013) for studying the effects of climate change on the spatial organization of populations, communities, and metacommunities (Grytnes & McCain, 2007; Körner, 2003; McCain & Grytnes, 2010; Presley & Willig, 2023). Areas with high elevational relief are often regional or global hot spots of biodiversity (Körner, 2007), stimulating much ecological and biogeographic research along elevational gradients, as recently considered in a Special Feature in *Frontiers of Biogeography* (Vetaas, 2021). Montane regions experience steep gradients in temperature and moisture, with temperature declining and precipitation increasing as elevation increases, comparable to the changes that accompany increasing latitude. However, montane gradients are spatially condensed compared to latitudinal gradients, with the same temperature change occurring across a 1000-m increase in elevation as occurs over a 550-km increase in latitude (Montgomery, 2006). Hence, the range of habitat conditions that occur over a wide latitudinal gradient occur on a smaller spatial scale in montane areas, potentially making montane ecosystems sensitive indicators of environmental changes and their effects on biodiversity dynamics (Elsen et al., 2018; Willig & Presley, 2019).

As global climate warms, species distributions are expected to shift toward higher latitudes or higher elevations, within the constraints of precipitation change (Franklin et al., 1992; Freeman et al., 2018; Schowalter, 2022). Because of their greater specialization and more restricted geographic ranges compared to temperate counterparts, tropical organisms should respond more strongly to environmental changes along elevational gradients (González & Lodge, 2017; Janzen, 1967; Rapoport, 1982; Tedersoo et al., 2014). The rapid rate of change in environmental characteristics within relatively short distances along elevational gradients can provide insights into the mechanisms that determine species distributions and community assembly (Cantrell et al., 2013; Richardson & Richardson, 2013; Terborgh, 1971; Whittaker, 1960; Willig et al., 2013), which can then be contrasted over time (Moritz et al., 2008; Rowe, 2007; Schowalter et al., 2005), over space (Dunn et al., 2009; Schowalter et al., 2005; Wiens et al., 2006; Willig & Lyons, 1998), or among taxa (Presley et al., 2012). Because responses along elevational gradients may occur more quickly than those along latitudinal gradients, elevational responses may be useful in predicting responses along analogous latitudinal gradients, at least where mountain ranges are not too isolated to represent longer latitudinal gradients. Nonetheless, elevational domains are smaller and in closer geographic proximity to each other compared to equivalent latitudinal domains representing similar environmental attributes. Consequently, mass effects associated with dispersal tend to enhance the homogenization of species composition along elevational gradients compared to their latitudinal counterparts. Similarly, the smaller area of elevational domains compared to their equivalent latitudinal domains, would decrease the number of domain specialists if effective population sizes are less than the minimum sizes needed to maintain positive growth rates, thereby decreasing the heterogeneity of species composition along gradients of elevation compared to those associated with latitude.

1.2 | Luquillo Mountains

The Luquillo Mountains in Puerto Rico rise to 1075 m in elevation, presenting gradients of climate and vegetation change that extend through five life zones from subtropical moist forest to lower montane rain forest (Ewel & Whitmore, 1973). A sequence of plant assemblages occurs along this gradient from mid-elevation (200–600 m asl) tabonuco forest through palo colorado forest (600–900 m) to elfin woodland (900–1075 m). In addition, palm forest (i.e., patches dominated by *Prestoea acuminata* [sierra palm]) is a naturally fragmented forest type that can occur at all elevations on steep slopes with wet soils. Importantly, this palm is quite common throughout the Luquillo Mountains, even in nonpalm forests. As a consequence of elevational variation in climatic, biogeochemical, and plant characteristics, the abundance and biodiversity of many groups of heterotrophs, including vertebrates (Campos-Cerqueira et al., 2017), invertebrates (Richardson & Richardson, 2013; Willig et al., 2013), and microbes (e.g., Cantrell et al., 2013), vary along this montane gradient as well.

1.3 | Sierra palm as a model system

The abundance and biodiversity of arthropods on *P. acuminata* likely depend on the community context within which a host plant exists (Figure 1). According to the Resource Concentration Hypothesis (Futuyma & Wasserman, 1980; Kareiva, 1983), heterotrophs should be more abundant in patches of concentrated host resources than in patches with sparser host resources because foraging individuals are more likely to find hosts that are close together. In palm forest, most arthropods on *P. acuminata* likely colonize from other sierra palms (green circles in Figure 1) that are in close proximity. Although other host species can be a source of colonists (pink circle in Figure 1), because they are rare or distant compared to other *P. acuminata* individuals in palm forest, they likely have a lesser effect on abundance or biodiversity of arthropod assemblages on *P. acuminata*. Because the cumulative abundance of *P. acuminata* in a plot is relatively large, the size of the overall habitat those individuals represent is large and the distance to other *P. acuminata* host individuals is relatively small. This

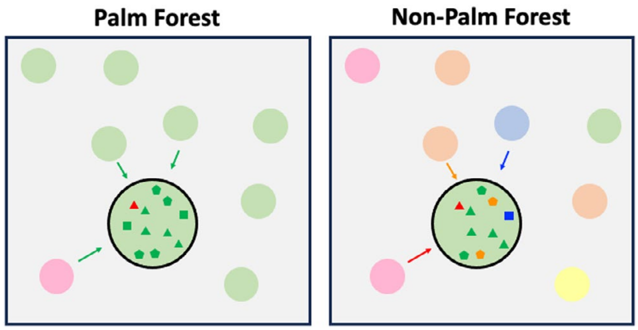

FIGURE 1 Graphic illustration of the effect of forest context (palm forest versus nonpalm forest) on the abundance and biodiversity at the species level of arthropods on *Prestoea acuminata* host trees. Circles represent host trees and colors (green, red, orange, yellow) represent different species of trees. The focal host tree (green, *P. acuminata*) is indicated by a circle with a bold black perimeter. The sizes of the circles are irrelevant, except that the size is enlarged for the focal tree to facilitate visualization of the nature of the arthropod assemblage that has colonized it. Within the large circle representing the host tree, the combination of symbol shapes and colors represent different species of arthropod, with symbol color indicating the source (host species) of colonists.

predisposes the focal host individual to support greater abundances of species that are adapted to live on this host species. In contrast, because fewer sierra palm individuals coexist in close proximity in nonpalm forests, biodiversity of arthropods should be low on individual hosts because the pool of potential colonist species is low. This effect could be exacerbated if arthropod species exhibit high host specificity (i.e., if arthropods can effectively colonize a limited number of available host plant species). In a nonpalm forest, arthropods on *P. acuminata* may predominantly colonize from nonpalm host species. This results in a greater biodiversity of arthropods than would be expected in a more homogeneous palm forest. [Correction added on 16 December 2024, after first online publication: In the preceding sentence, text 'a' has been changed to 'biodiversity' in this version.] Conversely, the abundance of arthropods on the focal host individual could be low because some of the arthropod species from nonpalm sources would be unable to persist or reproduce on a nonpreferred host (habitat filtering), the size of the palm habitat is relatively small (area effect in island biogeography), and the distance to other *P. acuminata* host individuals is relatively large (distance effect in island biogeography). Consequently, on hosts plants paired by elevation but in different forest types, we expect mean abundance to be greater but mean biodiversity to be lower on *P. acuminata* hosts from palm forest compared to those from nonpalm forest (resource concentration hypothesis—Futuyma & Wasserman, 1980; Kareiva, 1983).

1.4 | Objectives

Our goals were to evaluate the effects of elevation and host tree identity on aspects of arthropod assemblages associated with the canopies of understory tree species in the Luquillo Mountains. In general, we expected (1) the abundance and biodiversity of arthropods to decline with increasing elevation in a host-specific manner, and (2) elevational variation in the abundance and biodiversity of palm-associated arthropods to differ between palm forest and mixed forest transects. Moreover, we expected the abundance of arthropods to be greater on palms within palm forest than on palms within other forest types because of mechanisms related to host selection behavior (Futuyma & Wasserman, 1980; Kareiva, 1983; Schowalter, 2022), habitat area (Rosenzweig, 1995), and rescue effects (Brown & Kodric-Brown, 1977). In contrast, we expected the biodiversity of arthropods on palms within palm forest to be lower than the biodiversity of arthropods on palms within other forest types because of mechanisms associated with habitat heterogeneity (Tscharntke et al., 2012) and source pool dynamics (Lessard et al., 2012). Finally, we expected turnover of arthropod community composition on palms to be greater along the mixed forest transect than along the palm forest transect because of the influence of the greater diversity and abundance of nonpalm tree species in tabonuco, palo colorado, or elfin forests.

2 | MATERIALS AND METHODS

2.1 | Site description

The Luquillo Experimental Forest (LEF) is a Long-Term Ecological Research site within El Yunque National Forest (18°19.6′N, 65°49.4′W) in eastern Puerto Rico (Brown et al., 1983). The LEF is managed by the U.S. Forest Service, comprises 11,330 ha, and ranges in elevation from 100 to 1075 m asl (Brown et al., 1983). Historical temperatures at 350 m asl average 24.5°C during the warmest month (September), and 21.0°C during the coolest month (January). At 1051 m asl historical temperatures average about 4.5°C cooler than at 350 m asl (Brown et al., 1983). Mean annual precipitation increases with elevation from ~2300 mm at 100 m to ~4700 mm at 700 m, but then declines to ~3600 mm at 1051 m (Brown et al., 1983). Precipitation at all elevations averages more than 100 mm every month of the year, but typically is 2-fold greater during the wet season (May–December) than during the dry season (January–April). At higher elevations, the forest is frequently enveloped by clouds, reducing mean annual solar radiation by approximately 47%, compared to nearby coastal areas (Briscoe, 1966).

The Sonadora stream channel begins at ~1000 m asl within El Toro Wilderness Area and continues downslope until it meets the Río Espirito de Santo, which is just outside the LEF (<250 m asl). Two transects (mixed-forest and palm forest) were established that parallel the Sonadora stream channel, with plots at 50-m elevational intervals from 300 m to 1000 m asl within the Sonadora drainage basin. These transects facilitate efforts to distinguish between the effects of plant assemblage composition and variation in the abiotic environment along the elevational gradient

(Willig et al., 2011, 2013; Willig & Presley, 2019). The mixed forest transect comprised 15 elevational strata whereas the palm forest transect comprised only 14 strata; a forest patch dominated by *P. acuminata* did not occur in the Sonadora Watershed at 750 m asl. The average distance between adjacent strata on the mixed forest transect was 0.23 km (minimum, 0.15 km; maximum, 0.32 km) and was similar to the average distance between adjacent strata on the palm forest transect, which was 0.19 km (minimum, 0.05 km; maximum, 0.29 km). The mean distance between strata on different transects but at the same elevation was 0.32 km (minimum, 0.03 km; maximum, 0.96 km). The upper boundaries of plant species distributions formed three distinct peaks at 500, 700, and 900 m asl, suggesting discontinuities in the forest immediately above those elevations (Barone et al., 2008). Accordingly, we selected predominant understory tree species from four zones in the mixed-forest plots: 300–550 m (*Miconia prasina* and *Psychotria berteriana*), 600–700 m (*Croton poecilanthus*, *M. prasina*, *P. berteriana*), 750–850 m (*Calycogonium squamulosum*, *Miconia sintenisii*, and *P. berteriana*) and 900–1000 m (*M. sintenisii* and *P. berteriana*). *Prestoea acuminata* was sampled from all strata, except from the 550–750 m range on the palm forest transect due to limited access.

2.2 | Arthropod sampling and classification

In June 2017, trees were sampled by hand-bagging branches within 3 m of the forest floor, following a well-established protocol (Schowalter & Chao, 2021). A 50-l plastic bag was quickly slipped over an accessible branch of a randomly chosen tree of each species (if present), the branch was clipped, and the bag was sealed. Branches were usually ~50 cm in length and no more than 1 cm in diameter at the point of excision.

This sampling technique typically undersamples highly mobile arthropods (e.g., bees, wasps, flies). However, this technique is particularly useful for representing the density and biomass of resident invertebrates that feed over periods of weeks to months on resources associated with the sampled plant, and that have the greatest effect on foliage turnover and nutrient flux (Blanton, 1990; Majer & Recher, 1988). Alternative sampling techniques often yield more species and individuals, but branch bagging yields greater abundances of species that characterize particular plants (Blanton, 1990; Majer & Recher, 1988). We emphasize that our objective was not to represent arthropod biodiversity of the forest exhaustively, but rather to evaluate the responses of arthropod assemblages on particular tree species to environmental gradients associated with elevation.

All arthropods in each sample were identified to the lowest possible taxonomic level. Most taxa were identified to genus or family by the senior author, using collections at El Verde Field Station, or by systematics colleagues at Louisiana State University. Many taxa could not be accurately named due to a lack of reference material and were sorted into “morphospecies” (hereafter species). Based on morphological characteristics or autecological information about taxa, specimens were classified into one of four functional groups: folivores, sap-suckers, detritivores, or predators. Foliage from samples was pressed and dried at 50°C to constant weight to provide a measure of sample mass for use as a covariate in quantitative analyses. In addition, the percent of leaf area missing (LAM) from foliar samples was estimated visually. Although this metric is not an accurate measure of folivore consumption because of expansion of holes as leaves grow (Lowman, 1984) and does not account for consumption by sap-suckers, it does reflect folivore effect on leaf area index and penetration of light and precipitation through the canopy (Schowalter et al., 2011). Following the recommendations of Fauth et al. (1996), we refer to the collection of arthropods from a host tree as an “assemblage” rather than a “community”, because the focal group is restricted to species within a single clade (Arthropoda) that co-occur in time and space, rather than all species, regardless of clade, that co-occur in time and space (i.e., a community). Similarly, we refer to the suite of arthropods within a functional group that co-occurs in time and space as an “ensemble” rather than a local guild because the focal group is restricted to functionally similar species within a single clade (Arthropoda) that co-occur in time and space, rather than all species that are functionally similar, regardless of clade, that co-occur in time and space (i.e., a local guild).

2.3 | Quantitative analyses

For each sample, we quantified the abundance of each of the four functional groups based on the sum of the number of individuals in all morphospecies assigned to a particular functional group. We quantified total abundances as the sum of the abundances of all species regardless of affiliation with functional groups. In addition, we quantified six measures of taxonomic biodiversity: species richness, and a variety of measures that are sensitive to species abundances, including Shannon diversity (Pielou, 1966), Camargo evenness (Camargo, 1993), Berger-Parker dominance (Berger & Parker, 1970), and two measures of rarity. Local rarity was defined as the number of species in a sample whose relative abundance in that sample was less than $1/S_s$, where S_s is the number of species in the sample. In contrast, global rarity was defined as the number of species in a sample whose relative abundance in the species pool (sum of all individuals from all samples) was less than $1/S_T$, where S_T is the number of species in the species pool. Importantly, any species can be rare locally, whereas the identities of the rare taxa based on global rarity are the same for all samples. In addition to taxonomic biodiversity, in which species represent the focal entity, we quantified ensemble biodiversity, in which functional groups were the focal entity for analyses. From this perspective, we quantified the same six measures of biodiversity used at the species level. Each metric of biodiversity based on species or ensembles was expressed as a Hill number (Jost, 2006). Importantly, Hill numbers for all metrics are on the same scale (i.e., from 1 to species richness for taxonomic biodiversity, and from 1 to the number of functional groups for ensemble biodiversity) with greater values connoting greater biodiversity for all metrics, including dominance (i.e., high values for dominance expressed as Hill numbers indicate low dominance and high biodiversity).

The selected metrics of biodiversity have a long history of use and were chosen because they characterize nuanced aspects of the shape of species abundance distributions or ensemble abundance distributions (e.g., Stevens & Willig, 2002; Willig & Presley, 2019). Because of their mathematical bases, these metrics are predisposed to be correlated with each other if the shapes of species abundance distributions are similar among communities. Nonetheless, their empirical associations need not be significant. Using Pearson product–moment correlations, we quantified the associations between all possible pairs of biodiversity metrics, and did so separately at the level of species and at the level of ensemble. Analyses were executed for canopy arthropods from the mixed forest transect regardless of host tree identity, and for canopy arthropods from *P. acuminata* regardless of transect.

For samples from the mixed forest transect, we conducted an analysis of covariance (ANCOVA) to decompose the effects of elevation and host tree identity, while controlling for variation in sample mass, on the abundance of each functional group, total abundance, each metric of biodiversity at the species level, and each metric of biodiversity at the ensemble level. For arthropod samples from *P. acuminata*, we conducted an ANCOVA to decompose the effects of elevation and transect (mixed forest versus palm forest), while controlling for variation in sample mass, on the abundance of each functional group, each metric of biodiversity at the species level, and each metric of biodiversity at the ensemble level. A parallel set of analyses was conducted to evaluate elevational variation in LAM. For samples from the mixed-forest transect, a fully factorial model evaluated the effects of elevation, host tree identity, and folivore abundance on patterns of LAM along the elevational gradient. For samples from *P. acuminata*, a fully factorial model evaluated the effects of elevation, transect, and folivore abundance on patterns of LAM on this particular tree species.

Analyses of biodiversity and LAM used Gaussian error distributions and were conducted using the *lm* and *anova* functions in the stats package in R (R Core Team, 2023). Analyses of abundance used negative binomial distributions via the glm.nb function from the mass library (Venables & Ripley, 2002) because these data were counts and prone to zero inflation. Analyses restricted to the mixed forest transect removed variation associated with sample mass before analyzing the effects of elevation (covariate), host tree identity (factor), or their interaction on abundances or metrics of biodiversity. Similarly, analyses restricted to samples from *P. acuminata* removed variation associated with sample mass before analyzing the effects of elevation (covariate), transect (factor), and their interaction on abundances or metrics of biodiversity.

For canopy arthropod assemblages on *P. acuminata*, we estimated turnover (β component of biodiversity based on an additive model; Gering et al., 2003) between sequential elevational strata along each transect. We then compared their magnitudes between transects using a paired *t*-test via the *t*-test function in the stats package in R (R Core Team, 2024). We did so separately for Hill-transformed values of richness, diversity, evenness, dominance, local rarity, and global rarity based on species and based on ensembles. Because not all strata along each transect were sampled, analyses were restricted to sequential pairs of strata that were sampled along both transects (i.e., turnover between 300 m and 350 m, 350 m and 400 m, 400 m and 450 m, 450 m and 500 m, and 800 m and 850 m) to employ a more powerful paired statistical design.

3 | RESULTS

The power to detect significant effects in this study, especially those involving interactions, is diminished by (1) the small number of individual trees at each stratum that represent particular host species, (2) the restricted elevational range of host species, and (3) interspecific differences in the elevational extent of host species in the Luquillo Mountains. Individual insect taxa were not sufficiently abundant for analyses. Nonetheless, detected effects must be strong to overcome the limitations associated with issues of statistical power.

3.1 | Mixed forest transect

Elevational variation in total abundance depended on host species (Table 1, Figure 2). Moreover, the nature of the relationship between abundance and elevation differed among functional groups. The abundance of detritivores and folivores varied with elevation in a consistent manner, regardless of host tree species (Table 1). In contrast, elevational variation in abundance of predators and sap-suckers depended on host species (Table 1). Regardless of these heterogeneous results, total abundance as well as abundance of each of the functional groups, except for predators, declined with increasing elevation.

All pairs of metrics of biodiversity were significantly and highly correlated at the species-level (*R* ranging from .413 to .928) and at the ensemble level (*R* ranging from .581 to .994) for the mixed forest transect (Table S1). Elevational variation in each of six aspects of biodiversity at the species level and at the ensemble level was consistent regardless of host species identity (Table 1). In general, biodiversity declined with increasing elevation (Figure 3).

Elevational gradients of LAM on the mixed forest transect were contingent on host tree identity, but were not affected by folivore abundances (Figure 2; Table 2). LAM on *M. prasina* ($p = .015$) and *M. sintenisii* ($p = .051$) increased with increasing elevation, LAM on *P. brachiata* ($p = .065$) decreased with increasing elevation, and LAM on *P. acuminata* exhibited no relationship with elevation ($p = .664$).

3.2 | Palms along the mixed forest and palm forest transects

Total abundance on palm hosts decreased significantly with elevation in indistinguishable ways along both transects (Table 3,

TABLE 1 Results from generalized linear models with negative binomial error terms (analyses of abundance) or with Gaussian error terms (analyses of biodiversity) that decompose the effects of elevation and host tree identity on total arthropod abundance, abundance of each of four guilds, six aspects of biodiversity at the species level, or six aspects of biodiversity at the ensemble level while controlling for sample mass. Plant hosts were restricted to those from along the mixed forest transect.

	Sample mass (df = 1)		Elevation (df = 1)		Host tree (df = 5)		Elevation × host tree (df = 5)	
	χ^2 or F	*p*	χ^2 or F	*p*	χ^2 or F	*p*	χ^2 or F	*p*
Abundance (S, N)								
Detritivore abundance (9, 31)	.41	.522	14.02	**<.001**	11.15	**.049**	7.96	.159
Folivore abundance (5, 24)	6.44	**.011**	33.60	**<.001**	6.25	.283	5.77	.330
Predator abundance (10, 121)	5.39	**.020**	43.64	**<.001**	513.38	**<.001**	67.49	**<.001**
Sap-sucker abundance (7, 110)	1.75	.186	.38	.537	70.54	**<.001**	18.32	**.003**
Total abundance (38, 307)	27.68	**<.001**	99.38	**<.001**	325.18	**<.001**	183.76	**<.001**
Species biodiversity								
Species richness	.09	.770	19.54	**<.001**	.80	.561	1.44	.245
Shannon diversity	.01	.935	13.32	**.001**	.41	.835	1.51	.222
Camargo evenness	.16	.690	10.69	**.003**	.45	.812	1.26	.310
Berger-Parker dominance	.60	.445	5.69	**.025**	.39	.848	1.23	.323
Global rarity	.00	.985	10.76	**.003**	.79	.564	1.38	.265
Local rarity	1.07	.312	19.42	**<.001**	1.06	.406	1.06	.406
Ensemble biodiversity								
Guild richness	.21	.649	26.92	**<.001**	1.03	.419	2.07	.103
Shannon diversity	.01	.942	21.53	**<.001**	.43	.825	1.83	.144
Camargo evenness	.07	.795	18.53	**<.001**	.53	.752	1.77	.156
Berger-Parker dominance	.23	.639	13.62	**.001**	.67	.652	1.37	.268
Global rarity	1.66	.210	27.55	**<.001**	1.37	.270	1.20	.338
Local rarity	.01	.912	33.17	**<.001**	.70	.626	.93	.479

Note: Analyses with negative binomial error terms use χ^2 as a test statistic, whereas analyses with Gaussian error terms use *F* as a test statistic. Significant ($p \leq .05$) results are bold.

Abbreviations: df, degrees of freedom; *N*, number of individuals; *S*, number of species of invertebrate.

Figure 4). Similarly, detritivore abundance on palm hosts decreased significantly with elevation but did not differ between transects. Neither predator abundance nor sap-sucker abundance on palm hosts was associated with elevation, transect, or their interactions. In contrast, elevational variation in abundance of folivores on palm hosts differed between transects (Table 3). Generally, abundance declined with increasing elevation (Figure 4).

All pairs of biodiversity metrics were significantly and highly correlated at the species-level (*r* ranging from .558 to .995) and at the ensemble level (*r* ranging from .523 to .992) for analyses based on palm hosts regardless of transect (Table S2). Elevational variation in each of six aspects of biodiversity at the species level and at the ensemble level (Table 3) was consistent regardless of transect (Table 1). Regardless of metric, biodiversity declined with increasing elevation (Figures 5, S2). LAM on *P. acuminata* was not affected by elevation, transect, or folivore abundance (Table 2; Figures 3, S1).

Turnover between sequential elevational strata did not differ between transects ($p > .217$). This was true regardless of biodiversity metric for both species- and ensemble-based considerations (Table 4).

4 | DISCUSSION

Because of concerning projections about the effects of global change on the biota, increasing attention to the protection of elevational gradients in montane regions may be required for effective conservation action (e.g., Elsen et al., 2018). The details of the required conservation action may depend on the nature of empirical gradients of abundance,

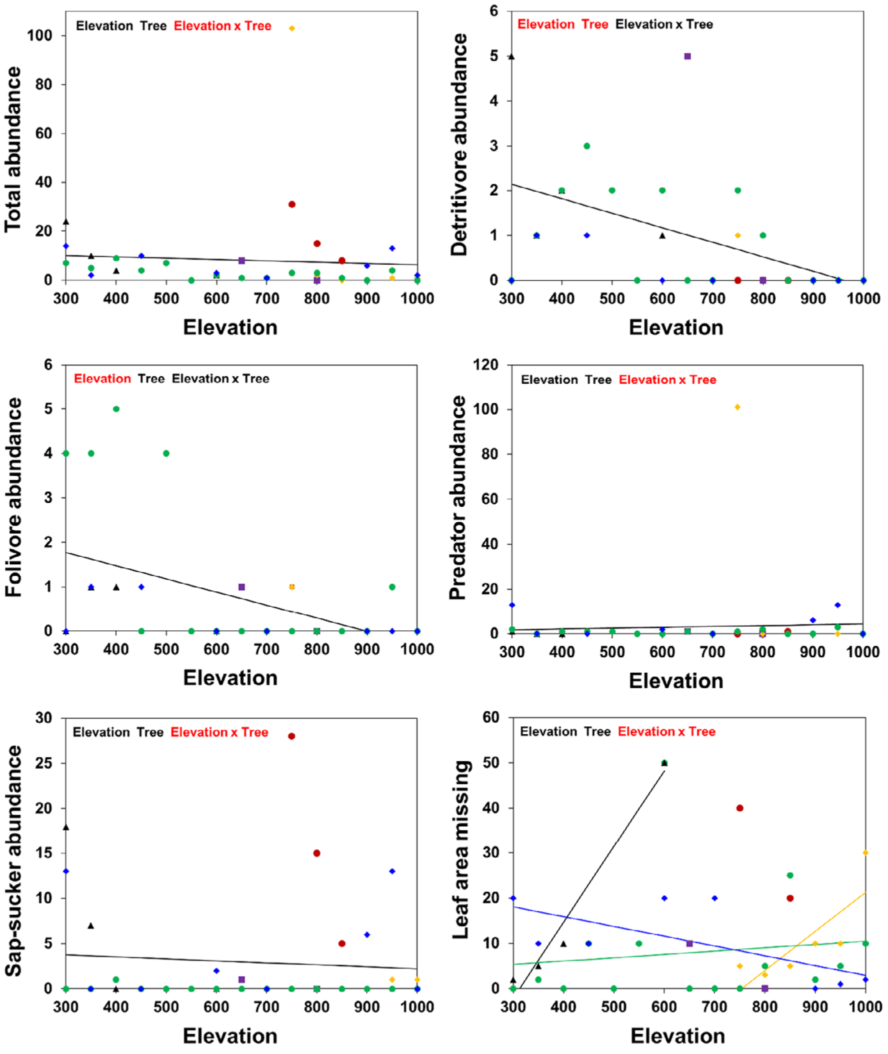

FIGURE 2 Elevational gradients in abundance of canopy arthropods and in leaf area missing (LAM) along the mixed forest transect in the Luquillo Mountains of Puerto Rico, including total arthropod abundance and the abundance of each of four functional groups. Symbols represent a single sample from particular host tree species within each elevational stratum: *Calycogonium squamulosum*, red circles; *Croton poecilanthus*, purple squares; *Miconia prasina*, black triangles; *Miconia sintenisii*, yellow diamonds; *Prestoea acuminata*, green circles; *Psychotria brachiata*, blue diamonds. Solid black lines represent best-fit linear regression models based on all samples. For models with significant interactions, best-fit regression lines were plotted for each host tree species, with line colors matching the symbol color for the respective host tree species. Significance of factors from generalized linear mixed-effects models (Table 1) for elevation, tree species, and interactions between elevation and tree species are indicated by red letters (black letters represent nonsignificant terms).

which for arthropods include: (1) monotonic decreases with increasing elevation, (2) mid-elevational peaks, (3) monotonic increases with increasing elevation (including those with asymptotes or plateaus), (4) mid-elevational troughs, and (5) no discernable patterns (Supriya et al., 2019). To some extent, such disparate empirical gradients likely arise because of variation in latitudinal contexts, differences in the elevational extents, differences in environmental characteristics at the base of mountains (e.g., aridity, humidity), differences in substrate identity from which arthropods were collected (e.g., ground, leaves, air), or variation in sampling methodologies, including sample effort and number of sites per gradient (Supriya et al., 2019). Fortunately, inter-ensemble comparisons of variation in abundances or biodiversity within the Luquillo Mountains from our work are not subject to such critiques, although comparisons of our results with those from other studies would involve the same interpretative constraints.

4.1 | Elevational gradients

Our results support the hypothesis that arthropod abundance and richness decline with increasing elevation. These results are consistent with studies along elevational gradients elsewhere (e.g., Röder et al., 2017; Sohn et al., 2019; Zhao et al., 2023).

A number of mechanisms have been advanced to account for elevational variation in biodiversity, including considerations of climate, space, evolutionary history, and biotic interactions (Grytnes & McCain, 2007). Unfortunately, consensus is elusive as to whether a dominant cause exists or its identity, especially given the variety of forms (e.g., monotonic declines, unimodal) that patterns along gradients exhibit for a diversity of taxa (plants, vertebrates, invertebrates) in a variety of geographic contexts (tropical, temperate, and xeric habitats) throughout the world (McCain & Grytnes, 2010) and the confounding of harsher climate with declining area for gradients in both latitude and elevation (Terborgh, 1973). Nonetheless, variation in climatic characteristics (e.g., temperature and precipitation) that affect primary production are often considered to play an important role. Primary productivity decreases with increasing elevation in the Luquillo Mountains (Harris et al., 2013; Weaver & Murphy, 1990), as does the concentration of essential nutrients in leaf necromass (Willig & Presley, 2019). Heterothermic organisms, such as arthropods, are sensitive to variation in temperature, and their

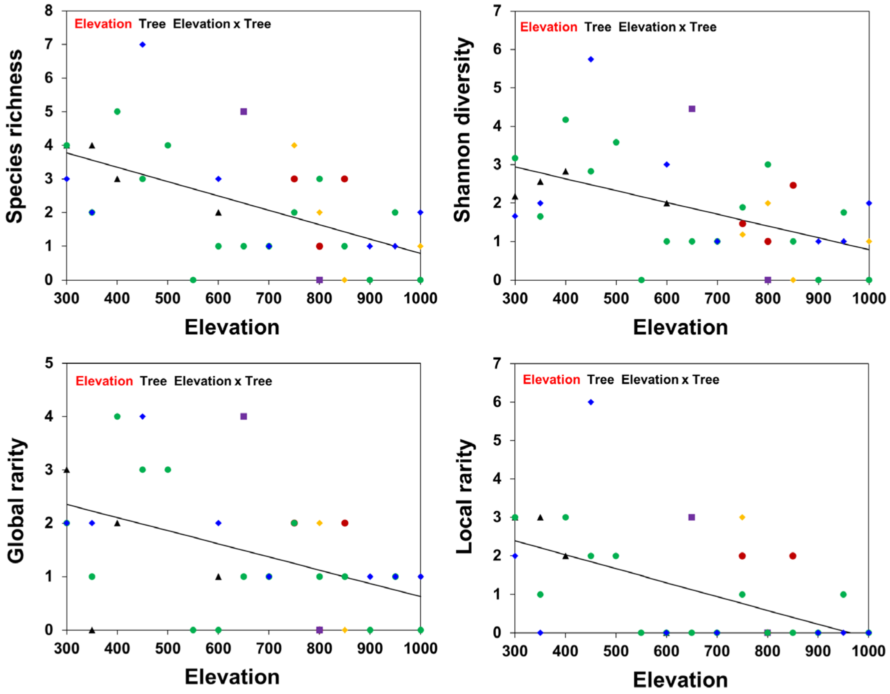

FIGURE 3 Elevational gradients in biodiversity of canopy arthropods at the species level along the mixed forest transect in the Luquillo Mountains of Puerto Rico as represented by each of six metrics: Species richness, Shannon diversity, global rarity, and local rarity. Symbols represent individual samples from particular host tree species within each elevational stratum: *Calycogonium squamulosum*, red circles; *Croton poecilanthus*, purple squares; *Miconia prasina*, black triangles; *Miconia sintenisii*, yellow diamonds; *Prestoea acuminata*, green circles; *Psychotria brachiata*, blue diamonds. Solid black lines represent best-fit linear regression models based on all samples. Significance of factors from generalized linear mixed-effects models (Table 1) for elevation, tree species, and interactions between elevation and tree species are indicated by red letters (black letters represent nonsignificant terms).

TABLE 2 Results from generalized linear models with Gaussian error terms that decompose the effects of elevation, host tree identity, and folivore abundance along the mixed forest transect on leaf consumption, or the effects of elevation, transect, and folivore abundance on leaf area missing for samples from *Prestoea acuminata* along mixed or palm forest transects.

Mixed forest transect				*Prestoea acuminata* along both transects			
	Df	F	p		Df	F	p
Elevation	1	.351	.561	Elevation	1	.192	.667
Host tree species	5	.588	.710	Transect	1	1.440	.248
Folivore abundance	1	2.553	.128	Folivore abundance	1	2.412	.140
Elevation × Host	4	3.976	**.018**	Elevation × Transect	1	.343	.566
Elevation × Folivore	1	.034	.855	Elevation × Folivore	1	.003	.959
Host × Folivore	4	1.414	.270	Transect × Folivore	1	.166	.690
3-way interaction	2	.035	.966	3-way interaction	1	.045	.835

Note: Significant ($p \leq .05$) results are bold.

abundance and diversity typically decline as temperature declines (Schowalter, 2022; Zhao et al., 2023). Some groups may show peak abundance at intermediate elevations, perhaps reflecting opposing gradients in temperature and predator abundance (Toko et al., 2023). Nevertheless, we correctly predicted that abundance and biodiversity of canopy arthropods would decrease with increasing elevation, as it does for a number of other groups of organisms (e.g., plants, microbes, gastropods, arthropods, vertebrates) in the Luquillo Mountains (Barone et al., 2008; Campos-Cerqueira et al., 2017; Cantrell et al., 2013; Ewel & Whitmore, 1973; O'Meara & Yee, 2024; Richardson & Richardson, 2013; Schaus et al., 2023; Willig et al., 2011, 2013; Willig & Presley, 2019). In the absence of manipulative experiments, the ultimate cause of elevational variation in aspects of biodiversity remains inconclusive.

We expected ecosystems at lower elevation to support more individuals than ecosystems at higher elevation because conditions become harsher, with lower productivity and diversity of resources. This pattern has been observed for gastropods and ground-dwelling arthropods along these same transects (O'Meara & Yee, 2024; Schaus et al., 2023; Willig & Presley, 2019), with variation in abundance linked to elevational variation in the quantity and quality of leaf litter. Because heterotherms require external heat sources to support metabolic activity, colder temperatures at higher elevations filter intolerant individuals, especially in tropical faunas with little opportunity to develop cold tolerance. Furthermore, plant productivity typically declines with decreasing temperatures, limiting resource availability to support arthropod food webs (e.g., Schowalter, 2022).

TABLE 3 Results from generalized linear models with negative binomial error terms (analyses of abundance) or general linear models with Gaussian error terms (analyses of biodiversity) that decompose the effects of elevation and transect (mixed forest versus palm forest) on total arthropod abundance, abundance of each of four guilds, each six aspects of biodiversity at the level of species, or each of six aspects of biodiversity at the level of ensemble while controlling for sample mass. The focal host tree was restricted to *Prestoea acuminata* along both palm forest and mixed forest transects.

	Sample mass		Elevation		Transect		Elevation × transect	
	(df = 1)		(df = 1)		(df = 1)		(df = 1)	
	χ^2 or *F*	*p*	χ^2 or *F*	*p*	χ^2 or *F*	*p*	χ^2 or *F*	*p*
Abundance (S, N)								
Detritivore abundance (8, 18)	3.82	.051	4.41	**.036**	.21	.651	1.89	.170
Folivore abundance (3, 24)	5.49	**.019**	22.09	**<.001**	5.39	**.020**	6.20	**.013**
Predator abundance (9, 21)	1.85	.173	.85	.357	.01	.937	.00	.974
Sap-sucker abundance (1, 2)	2.98	.085	1.75	.185	.84	.358	.32	.574
Total abundance (27, 76)	.30	.586	16.41	**<.001**	.12	.727	.16	.692
Species biodiversity								
Species richness	.12	.736	14.78	**.001**	.31	.584	.17	.687
Shannon diversity	.08	.775	14.08	**.001**	.65	.431	.56	.465
Camargo evenness	.07	.791	14.01	**.001**	1.03	.322	.98	.335
Berger-Parker dominance	.00	.958	10.13	**.005**	1.39	.252	1.72	.206
Global rarity	.07	.790	11.44	**.003**	.03	.872	.22	.644
Local rarity	.45	.510	10.48	**.004**	.10	.758	.00	.954
Ensemble Biodiversity								
Guild richness	.00	.969	17.89	**<.001**	.30	.588	.08	.782
Shannon diversity	.01	.916	18.76	**<.001**	.59	.451	.27	.608
Camargo evenness	.06	.810	19.74	**<.001**	1.22	.284	.58	.455
Berger-Parker dominance	.49	.494	20.79	**<.001**	1.65	.215	.90	.355
Global rarity	.00	.965	26.39	**<.001**	.21	.649	.01	.942
Local rarity	.57	.458	5.71	**.027**	.19	.666	.14	.711

Note: Analyses with negative binomial error terms use χ^2 as a test statistic, whereas analyses with Gaussian error terms use *F* as a test statistic. Significant ($p \leq .05$) results are bold.

Abbreviations: df, degrees of freedom; *N*, number of individuals; *S*, number of species of invertebrate.

Variation among sites in the cumulative abundance of individuals can give rise to variation in aspects of biodiversity. The linkage exists for statistical and biological reasons as detailed in the Theory of Random Placement (Coleman et al., 1982) and the More Individuals Hypothesis (Srivastava & Lawton, 1998). Nonetheless, empirical evidence suggests that the form of the elevational relationship is scale sensitive (Willig & Presley, 2019). Gradients in abundance and biodiversity will likely be more distinct in regions with steeper or longer gradients in elevation.

4.2 | Gradients of abundance-weighted metrics of biodiversity

The ways in which abundance biodiversity varies with elevation have not been well established from theoretical or empirical perspectives. Nonetheless, we expect some abundance-weighted metrics (e.g., diversity, local rarity) whose magnitudes are related to species richness to be strongly molded by elevation in a manner similar to that of species richness. Analyses from the mixed forest transect corroborate the decline in all five abundance-weighted measures of biodiversity with increasing elevation, whether the focus is on species or on ensembles (Table 1 and Figure 2). Similarly, analyses of data from palm hosts corroborate declines in abundance-weighted measures of biodiversity with increasing elevation, whether the focus is on species or ensembles (Table 3, Figures 3, S1). In the aftermath of Hurricane Maria, which occurred after our data were collected, common species of ants became more abundant compared to prehurricane conditions; this effect was greatest at lower elevations (O'Meara & Yee, 2024). This suggests that large-scale disturbances can temporarily affect elevational gradients in abundance as well as in abundance-weighted aspects of biodiversity, by creating conditions that are favorable to

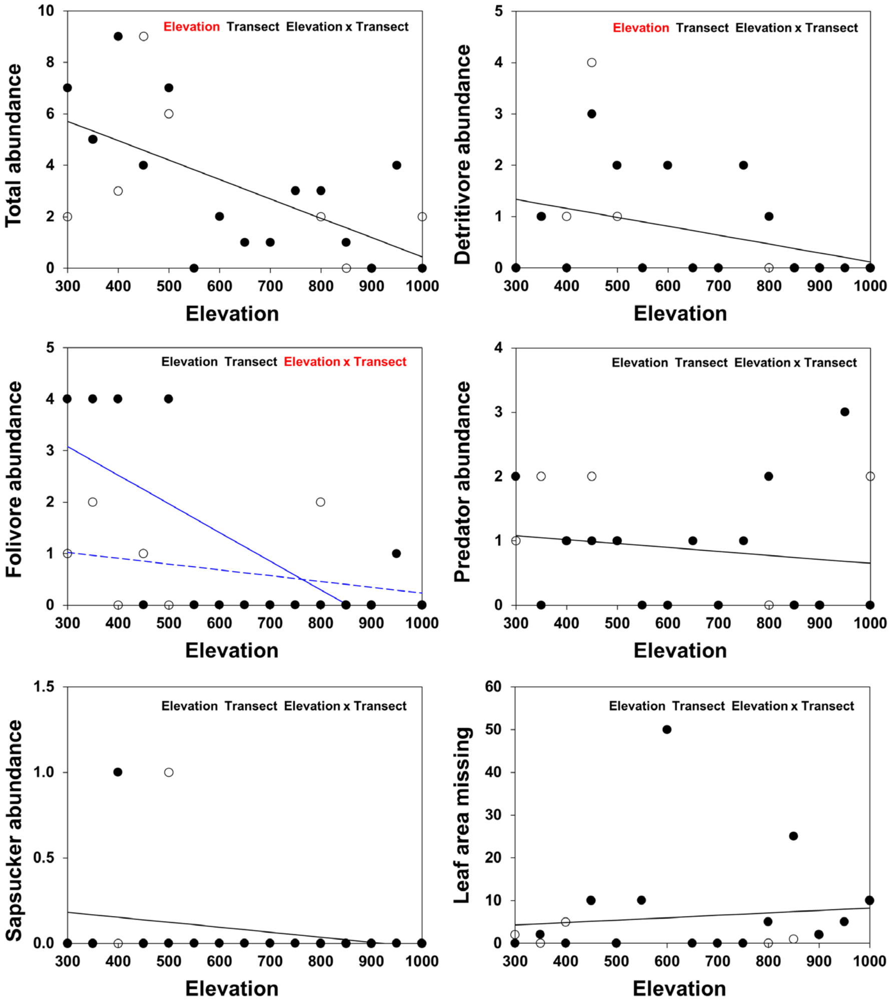

FIGURE 4 Elevational gradients in canopy arthropod abundance and in leaf area missing (LAM) from Sierra Palm (*Prestoea acuminata*) hosts along the mixed forest and palm forest transects in the Luquillo Mountains of Puerto Rico, including total arthropod abundance and the abundance of each of four functional groups. Symbols represent single samples from *P. acuminata* within each elevational stratum: Mixed-forest transect, filled circles; palm forest transect, open circles. Solid black lines represent best-fit linear regression models based on all samples unless a significant transect effect exists, in which case linear regression models were conducted separately for each transect with solid and dashed blue lines representing mixed and palm forest transects, respectively. Significance of factors from generalized linear mixed-effects models (Table 3) for elevation, transect, and interactions between elevation and transect are indicated by red letters (black letters represent nonsignificant terms).

common species (which likely are generalists), but not for rare species (which likely are specialists). In this case, the increased abundances of common species would reduce biodiversity at lower elevations more than at higher elevations, possibly changing the direction, strength, or shape of elevational gradients of biodiversity.

4.3 | Gradients in folivory

We expected LAM to decline with increasing elevation because folivore abundance, as well as total abundance and biodiversity, declined with increasing elevation. However, empirical results were more complicated (Figures 2 and 4). LAM on *P. acuminata* was unrelated to folivore abundance, elevation, transect, or their interactions. Similarly, LAM was unrelated to the abundance of folivores along the mixed forest transect but did vary with elevation in a host-specific manner.

Previous studies generally documented increases in LAM with elevation. More specifically, leaf damage from herbivorous insects in Nepal (Paudel et al., 2021), insect herbivory in Spain (Galmán et al., 2019), and leaf damage from insects in South Korea (Sohn et al., 2019) all increased with increasing elevation. Critically, these elevational increases in herbivory occurred whether herbivore abundances increased (Paudel et al., 2021) or decreased (Sohn et al., 2019). This elevational increase in leaf damage likely is associated with slower temperature-mediated growth rates as elevation increases (Coomes & Allen, 2007; Rapp et al., 2012).

4.4 | Effects of host tree species

Arthropod abundance could differ among host species in one of two ways: (1) consistent differences among host species regardless of elevation or (2) differences among host species that are contingent on elevation. This latter scenario was observed in the Luquillo Mountains (Table 1). This is consistent with earlier studies (e.g., Schowalter et al., 2021) and likely reflects variation in nutritional quality and defensive chemistry among tree species (Schowalter, 2022), as well as the ways in which these factors respond to environmental attributes associated with elevation (Galmán et al., 2019; Paudel et al., 2021; Sohn et al., 2019).

In the Luquillo Mountains, three ensemble-specific responses were documented: (1) host species identity affected the abundance of predators and sap-suckers, but effects were contingent on elevation; (2) host species identity affected the abundance of detritivores

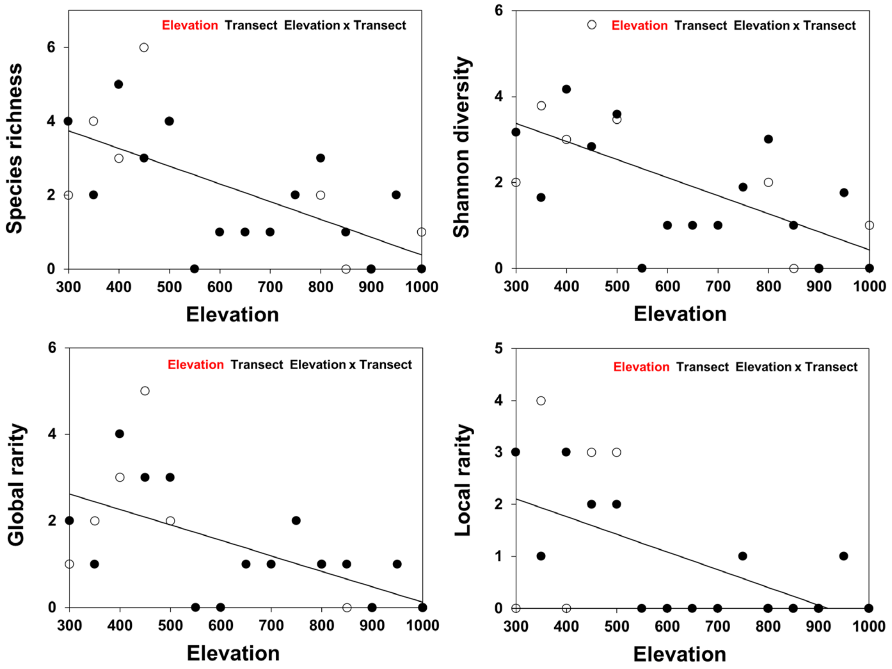

FIGURE 5 Elevational gradients in biodiversity of canopy arthropods at the species level from Sierra Palms (*Prestoea acuminata*) hosts along the mixed forest and palm forest transects in the Luquillo Mountains of Puerto Rico as represented by each of four metrics of biodiversity: Species richness, Shannon diversity, global rarity, and local rarity. Symbols represent single samples from *P. acuminata* within each elevational stratum: Mixed-forest transect, filled circles; palm forest transect, open circles. Solid black lines represent best-fit linear regression models based on all samples. Significance of factors from generalized linear mixed-effects models (Table 3) for elevation, transect, and interactions between elevation and transect are indicated by red letters (black letters represent nonsignificant terms).

TABLE 4 Paired *t*-tests comparing turnover (β component of biodiversity based on an additive model) between sequential elevational strata on the mixed forest and palm forest transects.

Type of beta diversity	df	*t*	*p*
Species biodiversity			
Species richness	5	−0.250	.542
Shannon diversity	5	−0.664	.247
Camargo evenness	5	−0.521	.318
Berger-Parker dominance	5	−0.201	.601
Global rarity	5	0.000	1.000
Local rarity	5	0.333	.363
Ensemble biodiversity			
Guild richness	5	0.417	.259
Shannon diversity	5	−0.149	.657
Camargo evenness	5	0.050	.798
Berger-Parker dominance	5	0.353	.217
Global rarity	5	0.083	.611
Local rarity	5	0.167	.576

Note: Separate analyses were executed for richness, diversity, evenness, dominance, local rarity, and global rarity based on species as well as ensembles. See text for details.

in a consistent way, regardless of elevation; and (3) host species identity did not affect differences in abundance of folivores. The interactions between host species and elevation suggests that responses of host tree species to elevation may affect their suitability for associated arthropods, or that abiotic correlates of elevation may enhance or diminish the ability of consumers to exploit particular resources that are host-specific in nature.

The ways in which the abundances of different ensembles respond to host species identity is not well understood, but it is known that such responses depend on host-specific concentrations of phytochemicals whose production is related to growing conditions (Schowalter, 2022). Tree species within genera or individuals within species can have significantly different phytochemical profiles (e.g., Coley et al., 2018; Genung et al., 2012) that affect herbivore attraction, survival, or LAM. Concentrations of various defensive chemicals can be affected by environmental variation, including that caused by disturbance (Hunter & Forkner, 1999; Mopper et al., 2004; Nunes et al., 2019). Of particular relevance to folivorous arthropods along tropical elevational gradients is that peroxidase, cinnamyl alcohol-dehydrogenase, and lignin concentrations can increase with wind exposure (Cipollini Jr., 1997), and that concentrations of gallic acid and flavenoid aglycone can decrease and increase, respectively, with increased exposure to UVB radiation (Rousseaux et al., 2004).

4.5 | Effects of forest type

Our results did not support the prediction that palms in palm forests would have greater arthropod abundance than would palms in other forest types. Folivores did show a significant elevation by transect interaction; however, folivore abundance was greater on palms in mixed-forest plots, contrary to our hypothesis, suggesting that abundance may be sensitive to factors such as the abundance and diversity of arthropods on surrounding tree species (Figures 5, S2). Importantly, because palm patches are relatively small and imbedded within a matrix of other forest types, patterns of arthropod abundance and biodiversity are likely dominated by the more extensive forest types in the surrounding landscape. Nevertheless, the inclusion of palm patches in a palm transect provided a unique opportunity to control the effects of host species × elevation interactions.

We expected that elevational turnover of the arthropod assemblage on palms would be greater along the mixed forest transect than along the palm forest transect. This assumed that changing plant species composition along the mixed forest transect would enhance turnover of canopy arthropods on *P. acuminata*. Contrary to that expectation, turnover between sequential elevational strata did not differ between transects for any of the metrics of biodiversity based on species or based on ensembles (Table 4). The lack of significance could result from ecological or statistical phenomena that are not mutually exclusive. The low power associated with small sample sizes would result in the lack of significance. Alternatively, palms might strongly filter potential colonists regardless of the abundance or identity of other host taxa, and the insects that they harbor or the abundance of *P. acuminata* in all forest types might create similar colonist species pools regardless of transect. Likely all three considerations contribute to empirical patterns.

4.6 | Prospects for the future

Our results are consistent with previous studies, indicating that declines in canopy arthropod abundance and richness with increasing elevation represent a characteristic pattern regardless of variation in host-plant species composition. As global temperatures rise, we expect that the ranges of arthropods will shift to higher elevations to effectively track their fundamental niches, especially thermal requirements. Species at the highest elevations, in particular specialists, will likely disappear for a number of interrelated reasons. First, the thermal regime for arthropod taxa adapted to cooler temperatures at high elevations will no longer exist. Second, some species of host plant may become sufficiently rare or be extirpated, thereby reducing the abundance of critical resources. Third, high-elevation arthropods may face increased competitive pressure from species whose distributions expand upslope. These mechanisms will combine to create conditions within which maintaining minimum population sizes is a challenge for high-elevation arthropod species.

AUTHOR CONTRIBUTIONS

T.D.S. performed field research on LTER-designed plots; S.J.P., and M.R.W. analyzed data; and T.D.S., S.J.P., and M.R.W. wrote the paper.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.gqnk98sxs and https://portal.edirepository.org/nis/mapbrowse?packageid=knb-lter-luq.96.2410869.

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SUPPORTING INFORMATION

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

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