

Mid-elevational Peaks in Diversity of Ground-dwelling Arthropods with High Species Turnover on the Colorado Plateau

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Abstract

Patterns of biodiversity along elevational gradients elucidate how climate shapes biological communities and help predict ecosystem responses to environmental change. Arid elevational gradients are particularly interesting because temperature limitations at high elevations and precipitation limitations at low elevations cause mid-elevation peaks in diversity. Ground-dwelling arthropods form highly diverse communities but few studies document elevational patterns of their full diversity. Here we investigate the elevational patterns of ground-dwelling arthropods in northern Arizona on the Colorado Plateau, an arid and understudied region in the United States. We sampled seven sites along an elevation gradient from 1,566 to 2,688 m corresponding to a difference of 6.5°C average annual temperature and 620 mm average annual precipitation. We captured 16,942 specimens comprising 169 species, mostly ants and beetles, and discovered a new ant species. First- and second-order elevation terms significantly correlated to multiple measures of arthropod α and β diversity. Arthropod abundance, richness, and Shannon-Wiener diversity index peaked at mid-elevations, with functional groups (i.e., omnivores, predators, detritivores, and herbivores) showing similar patterns. Community composition varied significantly across the gradient, correlated with changes in elevation, and was driven by shifts of ants dominating low- to mid-elevations, to beetles dominating high-elevations. Dissimilarity among sites was driven by high species turnover with 59% of species exclusive to a single site, whereas nestedness among sites was low except at the lowest elevation site. High rates of turnover and elevation-dependent communities suggest that ground-dwelling arthropods are highly vulnerable to environmental change, particularly at lower elevations in arid regions.

Key words: insects, climate, nestedness, altitude, diversity

A long-standing issue in ecology are the causes of diversity patterns along elevational gradients. Generally, species richness in local communities declines with increasing elevation as temperatures decrease (Hillebrand 2004, Rahbek 2005, Kraft et al. 2011, Peters et al. 2016). Yet alternative patterns in α -diversity patterns have been observed: peaks at mid-elevations (e.g., Terborgh 1977, McCain and Grytnes 2001, Rowe et al. 2015), declines at mid-elevation (e.g., Zhang et al. 2016), and increases with elevation (e.g., Sanders et al. 2003). These alternative patterns are typical of arid gradients, where precipitation decreases at lower elevations. Precipitation, along with temperature, adds stressors on the low end of arid gradients which drives community patterns, typically causing mid-elevations to have favorable climates and high diversity (Supriya et al. 2019). Community composition patterns (i.e., β -diversity) also change along elevational gradients as species are lost or gained (i.e., nestedness) or replaced by

other species (i.e., turnover), but similar to α -diversity, these patterns can be highly idiosyncratic across taxa and regions (e.g., Jacquemyn et al. 2007, Bishop et al. 2015, Paknia and Rajaei 2015, Nunes et al. 2016, da Silva et al. 2018, Noriega and Realpe 2018). Nonetheless, nestedness and turnover patterns are informative of more subtle processes that affect species composition, which can give a more detailed glimpse of climate relationships with communities along elevational gradients (Sanders and Rahbek 2012, Kraft et al. 2011).

Ground-dwelling arthropod communities are highly diverse and omnipresent in terrestrial ecosystems, mainly belonging to the ‘brown’ food web. Brown food webs are strongly regulated by temperature and limited by precipitation, the two main drivers of arthropod community change along elevational gradients (Hodkinson 2005). However, high diversity and cryptic habitats of ground-dwelling arthropods has largely limited our understanding

of brown food webs (Behan-Pelletier and Newton 1999), and most elevational studies only examine portions of ground-dwelling arthropod communities (e.g., ants; Smith et al. 2014, Andersen 1997, Sanders et al. 2003, or carabid beetles; Maveety et al. 2011). Studies suggest that most arthropods prefer warm climates with richness declining with increasing elevation and latitude (Hodkinson 2005); on the other hand, dry conditions should limit richness at low elevations. Limitations at the dry (low) and cold (high) ends of arid gradients should result in mid-elevation peaks of α -diversity (Supriya et al. 2019). However, few elevational studies examine the full range of ground-dwelling insect taxa or attempt to partition β -diversity of this community into nestedness and turnover components.

In this study, we describe the diversity patterns of ground-dwelling arthropods along an elevational gradient on the southern Colorado Plateau, an arid region in the southwestern United States. The dominant vegetation along this gradient can be grouped by life zones (Merriam 1898) which have been used to characterize bird (e.g., Bock and Webb 1984) and bee communities (McCabe et al. 2019) but are untested for ground-dwelling arthropods. We used this framework of life zones along the elevational gradient to examine: 1) how patterns of α - and β -diversity change across elevation and 2) how ground-dwelling arthropods organize within and across life zones. We predicted that α -diversity would peak at mid-elevation, limited at the low end by dry conditions and at the high end by cold temperatures. We also predicted that patterns of β -diversity would follow, with sites on the extreme ends of the gradient more dissimilar and potentially nested as a result of environmental filtering. Like many arid regions, the southwestern United States is particularly vulnerable to changes in climate (Elias et al. 2018), thus documenting these patterns will help our understanding of subsequent changes to these ecosystems (Sundqvist et al. 2013).

Methods

Study Sites

We sampled seven sites along an elevational gradient spanning 1,566 to 2,688 m in northern Arizona. This region spans four life zones: desert grassland, pinyon-juniper, ponderosa, and mixed conifer, and sites are part of the Southwestern Experimental Garden Array (SEGA). Hereafter we refer to these sites collectively as the 'SEGA' gradient and each site by its elevation (Fig. 1, Supp. Table 1 [online only]). The SEGA gradient differs markedly in vegetation which peaks in species richness and ground cover at mid-elevations (sites have been extensively surveyed, detailed here www.sega.nau.edu). In short, xeric grasslands (site: 1,566 m) transfer to open woodlands in pinyon-juniper (sites: 1,930 m, 2,056 m), then to monotypic pine stands in ponderosa with interspersed meadows (sites: 2,179, 2,200, 2,276 m), and finally dense spruce-fir-aspen stands in mixed conifer (site: 2,688 m). More mid-elevational sites are available on SEGA as these life zones (pinyon-juniper and ponderosa) occupy larger areas of land in our region. All sites are a) located within lands managed by the National Forest Service or Bureau of Land Management, b) generally undisturbed and remote, c) share similar grazers (e.g., cattle, elk, pronghorn antelope, and deer), and d) were recently fenced (1–2 yr prior) excluding grazers at the time of our sampling. The climates of these sites have been extensively documented through on-site weather stations and satellite monitoring. 30-year means of annual temperature ranges from 6.5°C to 13°C, and precipitation from 152 to 772 mm. Elevation strongly and negatively correlated with mean annual temperature ($r = -0.97$, $R^2 = 0.79$, $P < 0.001$) and positively with mean annual precipitation ($r = 0.92$, $R^2 = 0.92$, $P < 0.001$) across the SEGA gradient.

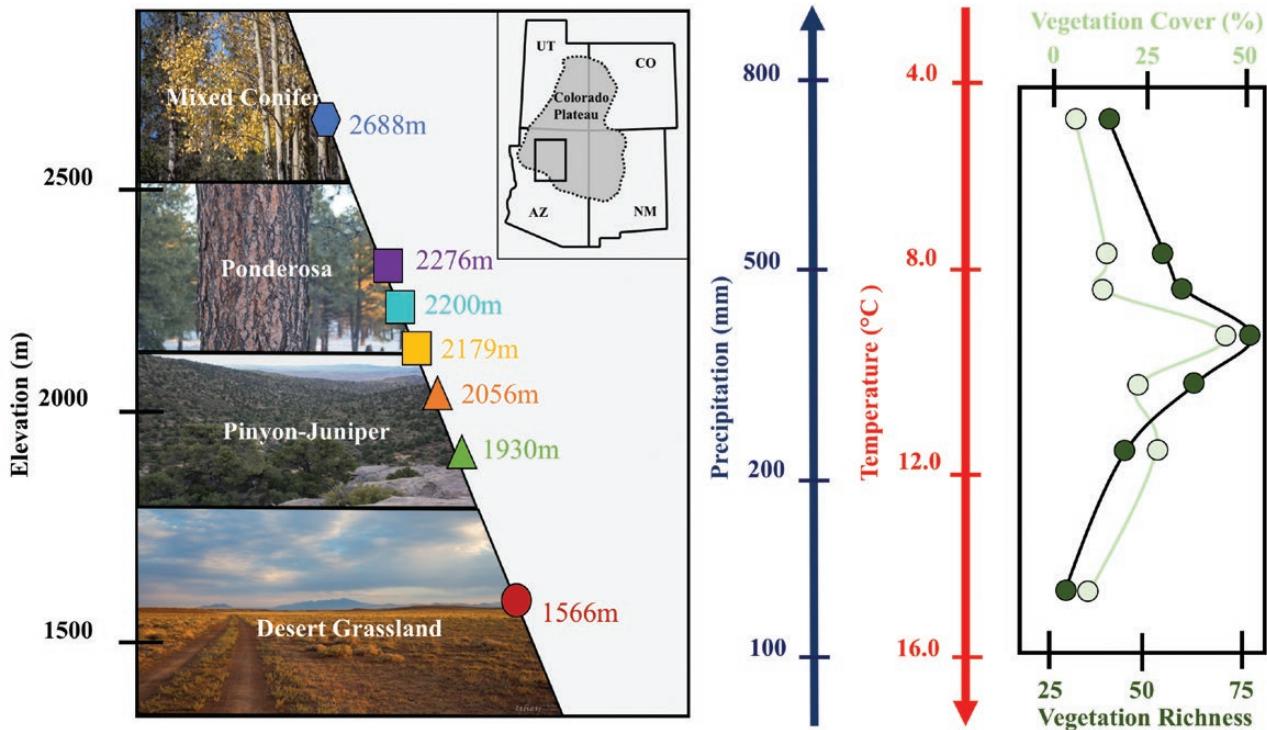


Fig. 1. Elevational gradient sites (color) in four life zones (shape) in northern Arizona on the Colorado Plateau. Scales of mean annual temperature and precipitation, along with vegetation cover percent and richness are also shown for each site (Supp. Table 1 [online only], data available at www.sega.nau.edu).

Sampling

At each site, we placed two parallel 100 m transects in undisturbed land at least 20 m from fencing and 10 m apart from one another. At sites with multiple habitat types (i.e., meadows and forests at sites in pinyon-juniper and ponderosa life zones), transects were positioned to encompass both habitats types. Along each transect, we placed 10 pitfall traps 10 m apart ($n = 20$ for each site). Pitfall traps are widely used to sample ground-dwelling arthropods and are considered robust for sampling ants (Andersen 1991, 2002) and ground-beetles (Andersen 1995), among other groups. Pitfall traps consisted of a long borosilicate glass tube measuring 32 mm in diameter and 200 mm long. These traps are large enough to sample most arthropods (*Eleodes obscurus* was our largest collected specimen at ~25 mm length). We fitted these into a 25 cm long PVC sleeve, filled tubes with ~100 mm of propylene glycol, and set traps flush to the ground. We wired a PVC pitfall top to each sleeve to prevent dilution or overfill from precipitation. We choose this trap design due to key advantages over larger diameter traps: a) lower evaporation rates mean they can be left out longer (our sampling period was 15-days), b) they are less likely to capture or have preservative consumed by nontarget vertebrate species, and c) they are more likely to sample litter dwelling species that rarely surface due to lids that sit low allowing litter crawlers to enter without exposure to sunlight (Higgins et al. 2014).

We synchronously sampled sites for 15 days starting 17 July 2014. We sorted 134 samples (six traps were lost to flooding) at Northern Arizona University, and identified and curated specimens at the Colorado Plateau Museum of Arthropod Biodiversity. We counted but excluded from analysis several groups as either these groups were not ground-dwelling [Diptera, Lepidoptera, parasitic Apocrita (Hymenoptera)] or taxonomic resources were nonexistent (mites). We were able to identify and include immature spiders and hemimetabolous insect specimens. We identified 69.4% of individuals and 57.4% of taxa to species, and the remaining we assigned to morphospecies, with the help of specialists (Supp. Table 2 [online only]), voucher specimens at <https://scan-bugs.org/portal/> and <https://bugguide.net>). Morphospecies designations indicate less taxonomic certainty but are necessary when working with the many taxonomically unresolved groups of ground-dwelling arthropods. We assigned morphospecies designations with specialist help and hereafter use ‘species,’ ‘richness,’ and ‘diversity’ to refer to taxa. We also assigned species to functional groups (i.e., omnivore, detritivore, predator, or herbivore). All ants were omnivores and vice versa, while other functional groups were composed of multiple taxa.

Data Analysis

We performed all analyses on a) the entire ground-dwelling arthropod community and b) three abundant functional groups (i.e., omnivores, detritivores, and predators), to test whether trophic roles differed as a function of elevation. We do not report herbivore results here because most were singleton specimens and were likely by-catch due to our sampling method (see Supp material [online only] for analyses of subgroups herbivores and beetles). We conducted all analyses in R.3.6.2. (R-script in Supp. File 1 [online only]).

Community Modeling

We analyzed ground-dwelling arthropod metacommunity responses to elevation using multivariate generalized linear models (GLMs) with function *manyglm* in R-package ‘mvabund’ (Wang et al. 2012). *Manyglm* fits a single GLM to each species, providing global estimates of significance while controlling for multiple testing. We compared models for 1) null patterns ($y = a$), 2) linear patterns of

abundance with elevation ($y = a + bx$), and 3) quadratic patterns indicating mid-elevation peaks [$(y = a + cx^2)$ or $(y = a + bx + cx^2)$] (Werenkraut and Ruggiero 2014), with both Poisson and negative binomial distributions. We included pitfall trap as a random effect in all models to account for potential spatial dependencies. We selected the best models by comparing Akaike information criterion which suggested a negative binomial distribution (AIC, Supp. Table 3). We determined the significance of predictor terms in the best-fitting models with analysis of deviance tests (function *anova.manyglm*).

α -Diversity

We evaluated patterns of α -diversity [richness, abundance, and Shannon-Wiener (SW) diversity index] along the elevational gradient by comparing mixed effect models. We calculated linear mixed models (LMMs) for normally distributed variables richness and SW diversity index using function *lmer* in R-package ‘lmer’ (Bates et al. 2015). We calculated generalized linear mixed models (GLMMs) for abundance data using R-function *glmer* (Bates et al. 2015). For abundance GLMMs, we choose either Poisson or negative binomial distributions by comparing AIC. Similar to the *manyglm* analysis, we compared models of 1) null patterns ($y = a$), 2) linear patterns of abundance with elevation ($y = a + bx$), and 3) quadratic patterns indicating mid-elevation peaks [$(y = a + cx^2)$ or $(y = a + bx + cx^2)$] (Werenkraut and Ruggiero 2014), all with pitfall trap as a random effect. Prior to analysis, we scaled elevation terms. We selected the best models by comparing AIC and performing likelihood ratio tests using maximum likelihood (Supp. Table 4 [online only], Leingartner et al. 2014).

β -Diversity

To determine whether species assemblages followed life zone patterns similar to other communities (e.g., vegetation (Bock and Webb 1984) and bee communities (McCabe et al. 2019), we used ordination techniques to test site groupings. We used a Bray-Curtis distance metric displaying the two axes that explained the most variation on square root-transformed abundance data (McCune and Grace, 2002). We visualized results via multi-dimensional scaling (MDS) plots. We used permutational analysis of variance (PERMANOVA, permutations = 9,999) to test site grouping followed by pairwise comparisons (Supp. Table 5 [online only]). We then fitted environmental variables to ordinations and used permutations to test significance (permutations = 999). We did ordination analyses with the R-packages *vegan* (Oksanen et al. 2017) and *ecodist* (Goslee and Urban 2007).

To determine patterns of turnover and nestedness among sites, we partitioned β -diversity of arthropod-occurrences into incidence-based turnover (β_{ju}) and nestedness (β_{jne}) components (Baselga and Orme 2012) and abundance-based turnover ($\beta_{BC,BAL}$) and nestedness ($\beta_{BC,GRA}$) components (Baselga 2017) using R-package *betapart*. In this method, incidence-based β -diversity is decomposed by subtracting Simpson index of dissimilarity (accounting only for species turnover, (β_{ju})) from Jaccard index of dissimilarity (accounting for total β_{JAC}) yielding nestedness (β_{jne}). For abundance-based data, Bray-Curtis dissimilarity indices (β_{BC}) are decomposed similarly into β -diversity into turnover ($\beta_{BC,BAL}$) and nestedness ($\beta_{BC,GRA}$). We performed analyses for all taxa together, and separately for each functional group.

Results

In total, we captured 16,942 specimens comprising 169 species (Supp. Table 2 [online only]). Species accumulation curves

approached an asymptote for all sites indicating sufficient sampling [Supp. Fig. 1 [online only]]. Ants (Formicidae) and beetles (Coleoptera) were the most numerous ground-dwelling arthropods both in abundance (ants 48.1% and beetles 29.0% of individuals, Fig. 2A) and richness (beetles 39.6% and ants 17.8% of species, Fig. 2A). Their abundance was followed by arachnids minus mites (3.2% of individuals, 16.0% of species; hereafter referred to as ‘arachnids’) and springtails (Collembola, 12.9% of individuals, 2.3% of species). Hereafter referred to as ‘others’, the remaining groups of insects were from various insect orders (e.g., Orthoptera (2.7% of individuals, 4.7% of species) and Hemiptera (0.8% of individuals, 8.9% of species), among others, Supp. Table 2 [online only]). Functionally, 16.6% of species and 48.1% of individuals were omnivores (composed entirely of ants), 37.3% of species and 20.4% of individuals were predators, 26.0% of species and 30.1% of individuals were detritivores, and 19.5% of species and 1.4% of individuals were herbivores (Fig. 2B).

Beetles were dominant both in abundance and richness at the two higher elevation, forested sites (Fig. 3). At low- to mid-elevations, beetles were low in abundance but high in richness. Ant abundance peaked at ~80% of individuals at mid-elevation sites; ant species made up ~25–33% of richness for most sites. Arachnids were low in abundance, but typically made up 5–10% of site richness. Collembola were low in richness, but had high abundance at the low elevation site making up ~60% of individuals. Functional groups were fairly consistently split among species across sites: herbivores were ~5–10% of species, detritivores ~30–35% of species, predators 15–25% of species, and omnivores ~20–35% of species. However, functional groups were

more varied among abundance: herbivores and predators were ~5% of individuals in low- and mid-elevation sites but increased to ~25–35% at high elevation sites, detritivores were ~10–25% of individuals at most sites but dominated the lowest elevation site at ~60% of individuals, and omnivores dominated mid-elevation sites at ~60–80% of individuals but were lower in abundance at low- and high-elevation sites.

Community Modeling

Models with the best fit to arthropod metacommunity data included first- and second-order elevation terms (Supp. Table 3 [online only]). Analysis of deviance indicated significant effects of both terms (elevation, Deviance [Dev] = 1471, Pr (>Dev) = 0.001, elevation², [Dev] = 20,188, Pr (>Dev) = 0.001). Similar patterns were found when functional groups were modeled separately, except for omnivores (i.e., ants), which best fit to only the second-order elevation term (Supp. Table 3 [online only]).

α -Diversity

Arthropod abundance showed a stronger (positive) linear relationship with elevation (Fig. 4A). However, both species richness and Shannon-Wiener diversity index showed stronger quadratic rather than linear or null relationships with elevation (Fig. 4B and C). In general, the lowest and highest elevation sites had the lowest α -diversity, while mid-elevation sites had the highest α -diversity. Richness and abundance of all functional groups were lowest at low elevation, with most groups peaking at mid-elevations except detritivores which increased exponentially with elevation (Fig. 4D–I).

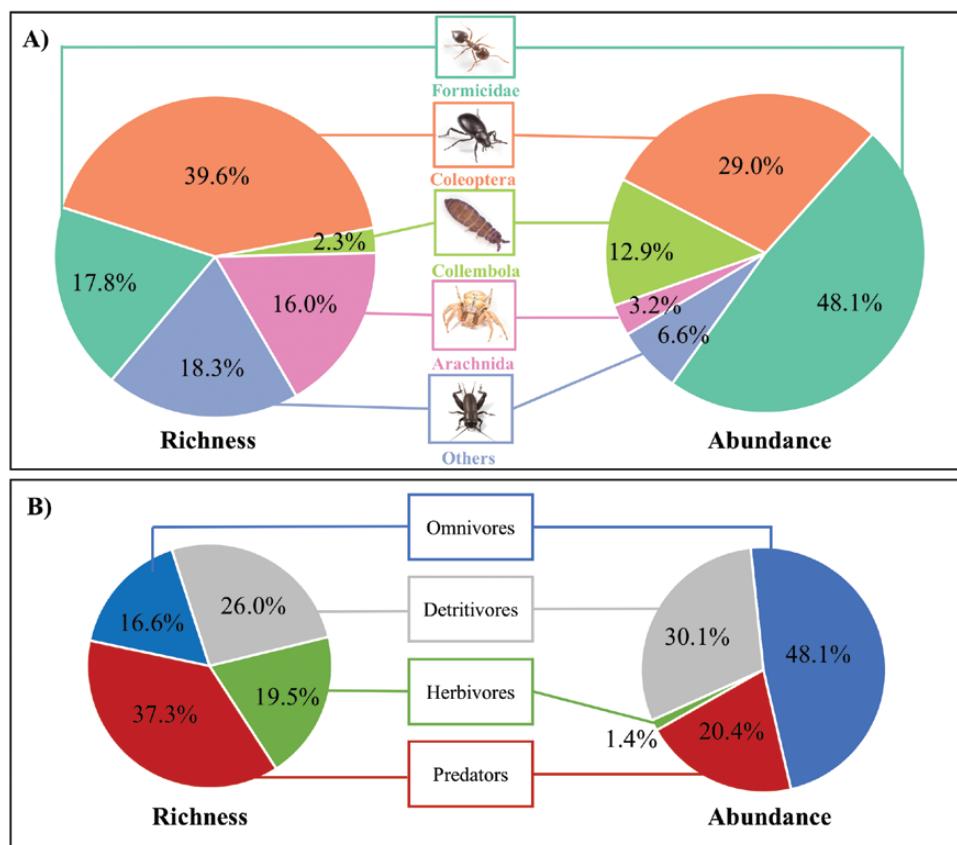


Fig. 2. Richness and abundance compositions. A) the most numerous ground-dwelling arthropod groups (both number of species and individuals), and B) the most numerous functional groups of ground-dwelling arthropods.

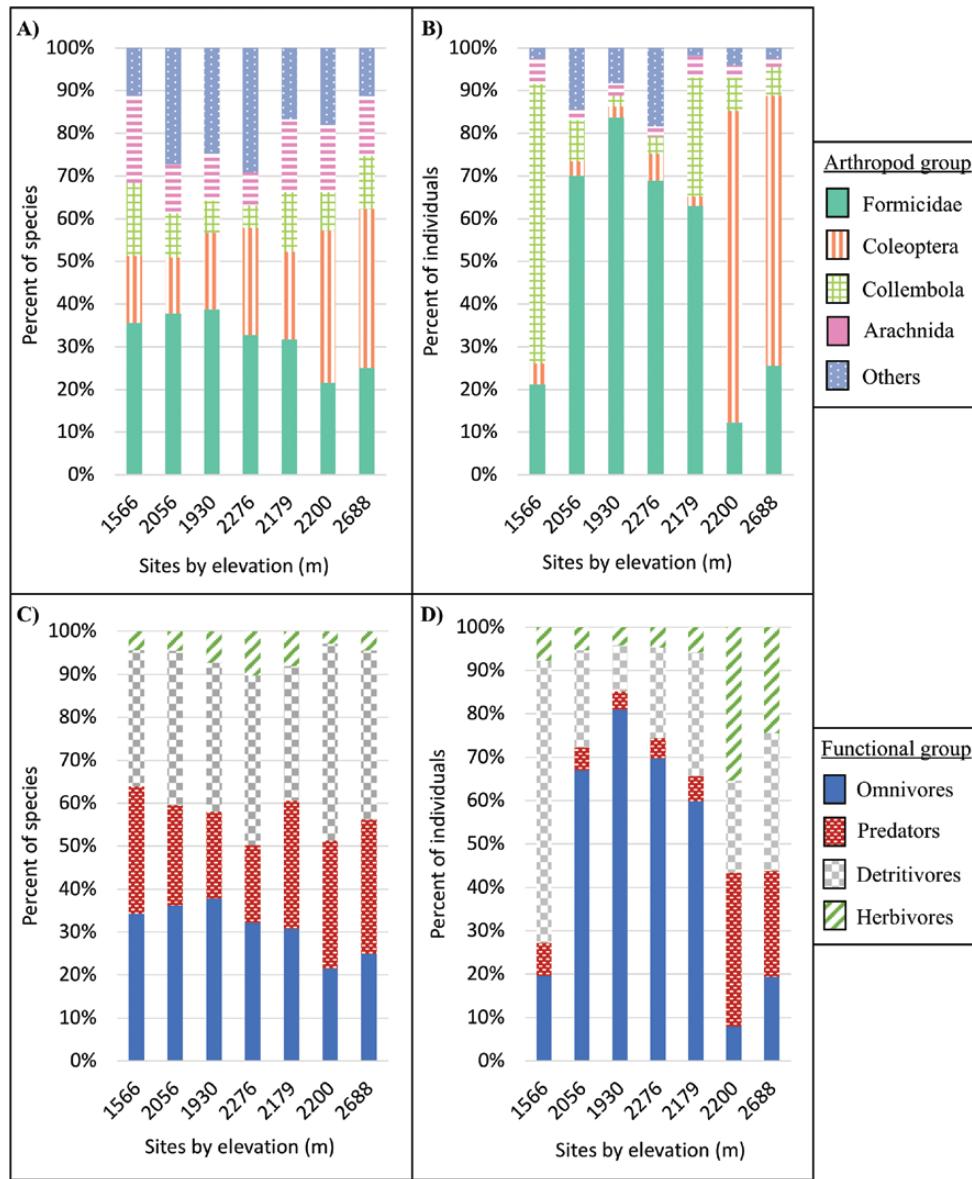


Fig. 3. Composition of arthropods across sites. A) Percent of species and B) percent of individuals by major ground-dwelling arthropod groups across elevational sites, and C) percent of species and D) percent of individuals by functional groups.

β -Diversity

β -Diversity showed strong elevational patterns, where sites grouped separately. All three explanatory variables were significant: elevation, mean annual temperature, and precipitation (Fig. 5). Sites within the same life zone shared close proximity and aligned along axis one according to elevation.

All functional groups showed similar trends across elevation: a) significant site grouping, b) sites within the same life zone shared close proximity and aligned along axis according to elevation, and c) elevation, precipitation, and temperature were significant explanatory variables (Fig. 6). Omnivores and predators both had overlap of mid-elevation sites, with high and low elevation sites mostly separate; detritivores had overlap of mid-elevation sites into low elevation.

Turnover Across Elevation

Ground-dwelling arthropod communities showed high dissimilarity among sites and strong patterns of turnover along the elevational gradient (Fig. 7, Supp. Table 5 [online only]). Dissimilarity

among sites was over 50% for all incidence-based and over 60% for all abundance-based site comparisons. This was largely driven by turnover: incidence-based turnover (β_{inc}) averaged 67.0% compared to 4.8% for nestedness (β_{ne}), and abundance-based turnover ($\beta_{\text{BC,BAL}}$) averaged 80.8% compared to 7.6% for nestedness ($\beta_{\text{BC,GRA}}$). High turnover indicates that the number of shared species among sites was low: 59.2% (100/169) of species were exclusive to one site, 16.0% (27/169) to two sites, 10.1% (17/169) to three sites, 5.3% (9/169) to four sites, and 4.7% (8/169) to five sites (Supp. Table 2 [online only]). Four species (*Ceuthophilus lamelliceps* Rehn (Orthoptera: Rhaphidophoridae), *Monomorium cyaneum* Wheeler (Hymenoptera: Formicidae), a morphospecies of *Seira Lubbock* (Entomobryomorpha: Entomobryidae) and a morphospecies of *Xysticus*) occurred at six of seven sites, and four species (*Eleodes extricatus*, a morphospecies of Staphylinidae in the subfamily Aleocharinae, a morphospecies of *Solenopsis* Westwood (Hymenoptera: Formicidae) in the fugax group and a morphospecies of *Sminthuridae*) occurred in all seven sites. Comparison of elevational pairs (i.e., each site and its immediately adjacent uphill

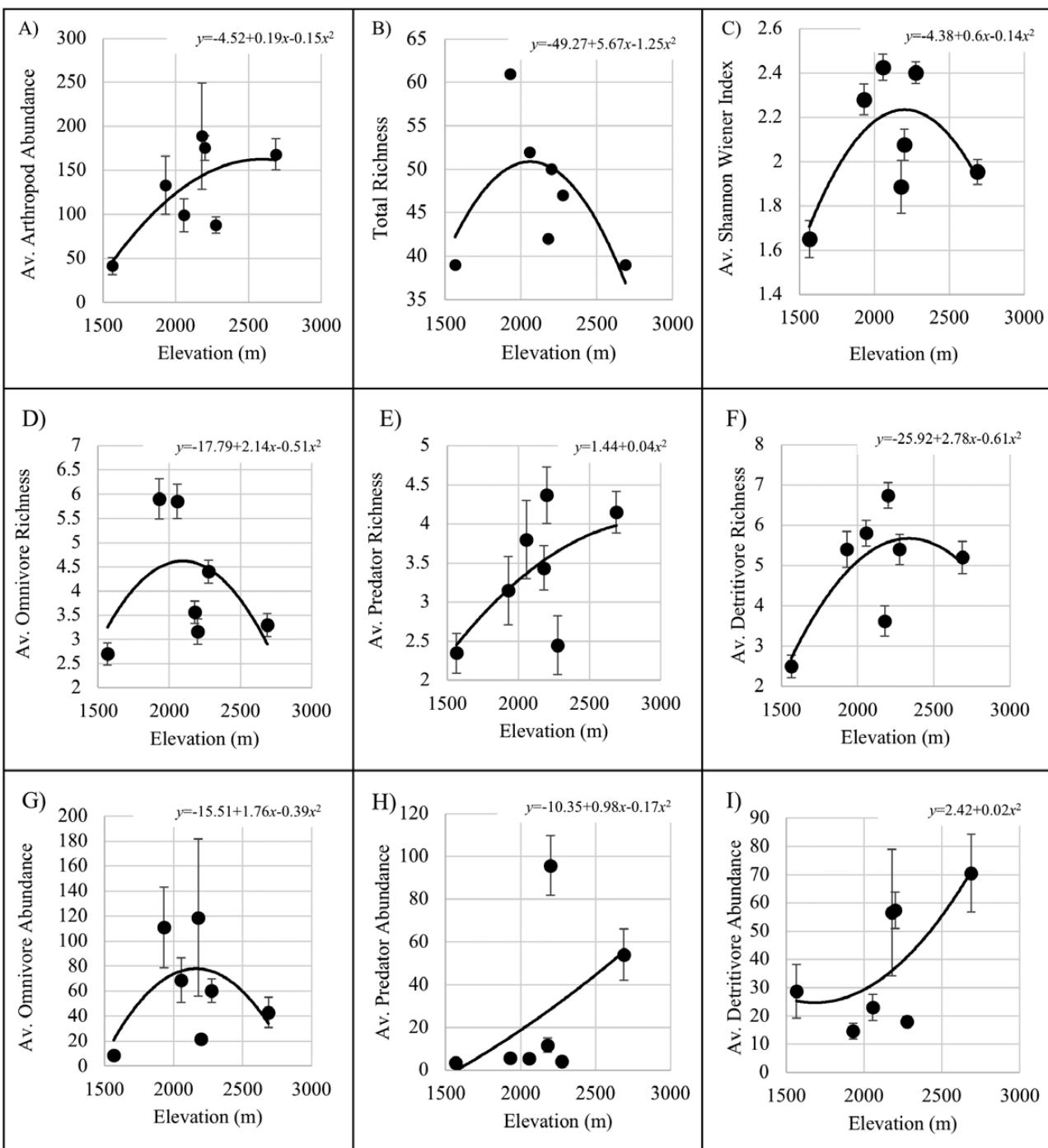


Fig. 4. Elevational α -diversity patterns of A) average abundance, B) total richness, and C) average Shannon-Wiener diversity index, D) omnivore richness, E) predator richness, F) detritivore richness, G) omnivore abundance, H) predator abundance, and I) detritivore abundance (model details: Supp. Table 4 [online only]).

neighbor) show that along the elevational gradient nestedness was low except for the lowest elevation site. This site was partially nested ($\beta_{jne} = 16.0\%$, $\beta_{BC,GRA} = 38.6\%$, Fig. 7) because the abundance and richness of this site was low (Fig. 4).

Ground-dwelling arthropod functional groups showed different patterns of dissimilarity across the elevational gradient. Herbivores had the highest dissimilarity (average $\beta_{JAC} = 95.4\%$, $\beta_{BC} = 95.3\%$, Supp. Table 5 [online only]) followed by predators (average $\beta_{JAC} = 83.3\%$, $\beta_{BC} = 90.7\%$), omnivores (average $\beta_{JAC} = 70.2\%$, $\beta_{BC} = 89.5\%$), and lastly detritivores (average $\beta_{JAC} = 66.2\%$,

$\beta_{BC} = 75.9\%$). Average turnover was roughly 5–30 times higher than nestedness for all functional groups (Supp. Table 4 [online only]). However, both omnivores and predators showed nested patterns for abundance-based dissimilarity at mid-elevational sites (Fig. 8).

Discussion

Patterns of ground-dwelling arthropod diversity along elevational gradients have been relatively undescribed for most taxa, particularly in arid regions. We found strong patterns of species turnover across

elevation, with α -diversity peaking at mid-elevations consistent with predictions for arid regions, and consistent with patterns of diversity in plant communities. Arthropod community composition was unique at each location along the gradient, with groupings similar to Merriam's (1898) life zone concept. These elevational patterns are consistent with those of arid climates where communities are shaped by temperature and precipitation (Miranda et al. 2011, Chen et al. 2015, Harrison et al. 2020).

Ground-dwelling arthropod communities are extremely diverse and can change both seasonally and annually (Pan et al. 2015). Like many elevational studies, our results also come with the caveat that single sites may not fully represent the inherent species variation found at that elevational band. While species accumulation curves suggest we sampled most of the diversity at each site,

our single sampling period likely missed some seasonal and/or rare species. Our main purpose was to characterize the elevational patterns of dominant arthropod groups, providing a baseline for future work in this understudied region. We repeated our analyses without singleton species and some nontarget taxa, and found no change in any significant trend (Supp. File 2 [online only]). This suggests that rare species had little effect on elevational patterns of our ground-dwelling arthropod communities, indicating that our results should be viewed as reflective of broad elevational patterns of dominant taxa.

There are various mechanisms behind elevational patterns in diversity that involve ecological, climatic, geographic, and historical hypotheses (Rahbek 1995). Multiple abiotic and biotic factors that are spatially structured along elevational gradients can affect ground-dwelling arthropods: temperature, precipitation, partial pressures of both O_2 and CO_2 , ultraviolet radiation, primary productivity, available geographic area, and interspecific interactions. Furthermore, gradient edges are more likely to experience climatic disturbances (i.e., flooding or drought at low elevations, glaciation at high, Rohde 1992). Our study cannot separate these mechanisms, but these patterns strongly suggest the influence of climate.

In addition to climate, vegetation is likely an influential driver of the elevational patterns we observed, which in this system ranged from open-desert to mixed-conifer forests. These habitat differences can be highly influential in determining arthropod communities (Uhey et al. 2020a) and may have contributed to differences among these sites, especially at mid-elevations where both meadows and forests can occur at the same elevation. Mammalian grazing can also affect arthropods via effects on vegetation (Torma et al. 2019), and it is important to note that grazing was recently (1–2 yr prior to our sampling) excluded from the sites in this study which may influence our results. While we cannot separate vegetation and climate effects in this study, we have shown that climate is likely the stronger of the two drivers for ground-dwelling arthropods on elevation gradients

Fig. 5. Nonmetric scaling ordination of ground-dwelling arthropod communities in different elevational gradient sites (colors) in four different life zones (shape). Significant secondary correlations of environmental variables are shown as proportional arrows: elevation ($R^2 = 0.79, P < 0.001$), mean annual temperature ($R^2 = 0.75, P < 0.001$), and precipitation ($R^2 = 0.86, P < 0.001$). All sites group separately (PERMANOVA: $F = 33.78, P > 0.001$), with sites from the same life zone in close proximity along axis one.

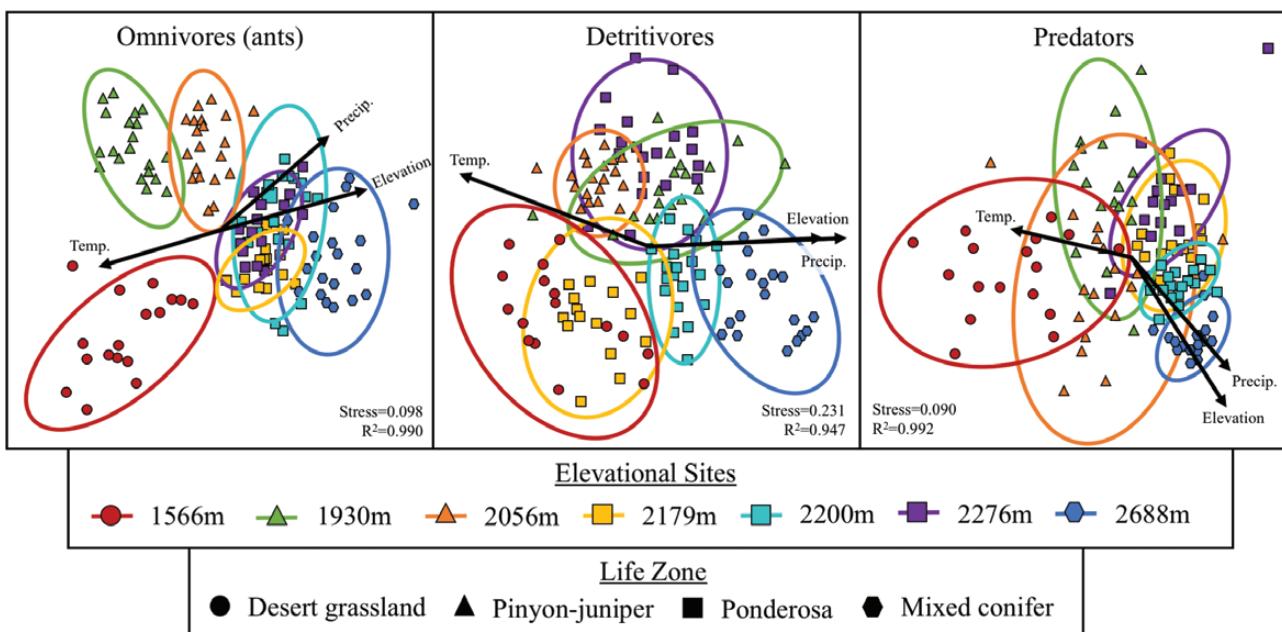


Fig. 6. Nonmetric scaling ordination of ground-dwelling arthropod functional groups in different elevational gradient sites (colors) in four different life zones (shape). Significant secondary correlations of environmental variables (Supp. Table 5 [online only]) are shown as proportional arrows: elevation, mean annual temperature, and precipitation. All sites group separately for all functional groups (Supp. Table 5 [online only]).

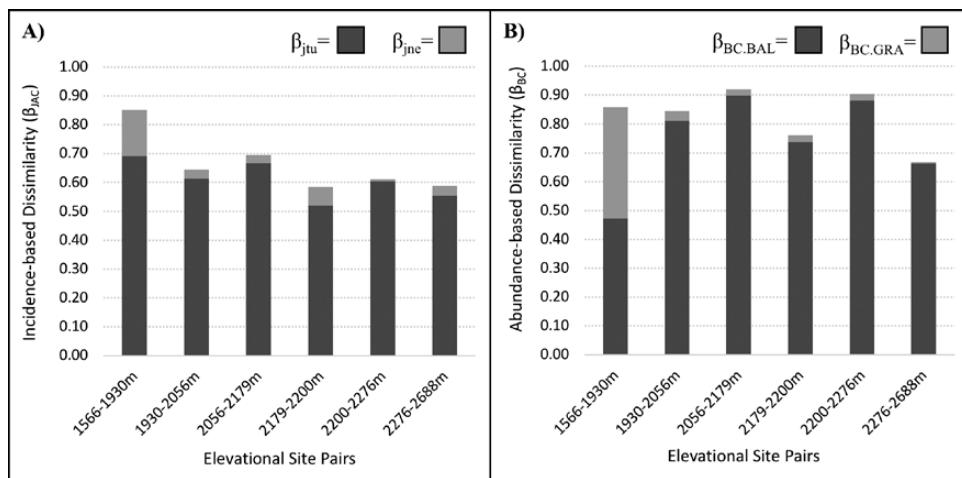


Fig. 7. Dissimilarity analysis (β -diversity) of ground-dwelling arthropods partitioned into A) incidence-based turnover (β_{jtu}) and nestedness (β_{jne}), and B) abundance-based turnover ($\beta_{BC,BAL}$) and nestedness ($\beta_{BC,GRA}$) of elevational site pairs (i.e., each site and its immediately adjacent uphill site).

in this region (Uhey et al. 2020a,b), consistent with other arid systems (Sanders et al. 2007, Supriya et al. 2019).

Ground-dwelling arthropods are highly thermophilic and sensitive to precipitation making temperature and precipitation the most likely drivers of their elevational distributions (Supriya et al. 2019). The mid-elevational peaks in richness we found suggest environmental filters of low temperature at high elevations and low precipitation at low elevations, as other studies on arid gradients have found both globally (reviewed by Supriya et al. 2019) and in similar arid regions of the southwestern United States (Andersen 1997, Sanders et al. 2003, Meyer et al. 2015). We have shown that precipitation and temperature are strong drivers of ant community composition along elevational gradients (Uhey et al 2020a) and ground-dwelling arthropods in pinyon-juniper woodlands (Uhey et al 2020b), both of which underscore the importance of environmental filters.

Elevational Variation in Turnover and Nestedness

Studies that examine turnover and nestedness are becoming more frequent (Soininen et al. 2018), but along elevational gradients remain sparse and largely limited in taxonomic scope (Jacquemyn et al. 2007, Bishop et al. 2015, Paknia and Rajaei 2015, Nunes et al. 2016, da Silva et al. 2018, Noriega and Realpe 2018). Turnover was the main β -diversity component in this study indicating that communities along the gradient are not subsets of each other but rather unique assemblages. Over half of the observed species were endemic to single sites; community composition largely conformed to the life zone concept (Merriam 1898). Our results suggest that ground-dwelling arthropods may further partition elevational ranges within life zones, as even sites in the same life zones were significantly distinct from one another. These results are similar to those of Meyer et al. (2015) who observed that ground-dwelling arthropod communities in 'sky island' mountains of southern Arizona were grouped by the similar biome concept. McCabe et al (2019) found that pollinators along elevational gradients grouped by life zone as well. These findings suggest that distinctive ground-dwelling arthropod assemblages along elevational gradients are similar to vegetation and other animal communities.

Patterns of high turnover among communities are commonly a result of competitive exclusion and/or niche specialization (Baselga 2010), although many other factors may be at play in this system such as canopy (or lack thereof), litter type, resources

for specialists, etc. In the case of environmental filtering, dispersal limitation and species coexistence through use of different micro-habitats often contribute to beta patterns (Kraft et al. 2015). Yet, competitive exclusion, dispersal limitations, habitat type, and resource availability are closely tied to climate, especially along elevational gradients (Albrecht et al. 2018). Elevational turnover patterns and the affinity of many ground-dwelling arthropods to narrow elevation bands (Sanders et al. 2003, Supriya et al. 2019) again suggest climate as an overarching driver of these patterns.

Nestedness indicates smaller subsections of larger communities and is more likely to increase where α -diversity decreases (Baselga 2010). Most studies that examine elevational patterns of turnover and nestedness find turnover to be high, except in some cases where high-elevation sites are nested indicating temperature filtering (Jacquemyn et al. 2007, Bishop et al. 2015, Paknia and Rajaei 2015, Nunes et al. 2016, da Silva et al. 2018, Noriega and Realpe 2018). In contrast, we found nestedness at low elevation, likely reflecting limitation imposed by reduced precipitation at the lowest site. However, these nested patterns were only evident in abundance-based analyses, suggesting that the arthropod community at the lowest elevation site is a subset of the more abundant (but not necessarily richer) higher elevation communities. On arid gradients, nestedness likely increases on gradient edges due to temperature and precipitation filters (Flores et al. 2018). At the high elevation end of the gradient, on the other hand, we did not observe the temperature limitation that we expected: nestedness values at high elevations were low. We speculate that the strongest effects of temperature may exist beyond the elevational range of this study, as we did not sample subalpine or alpine life zones.

Most β -diversity patterns we observed were driven by turnover from omnivorous ants to predacious beetles, where ants dominated low- to mid-elevation sites and beetles dominated higher elevation sites. Similar patterns are noted for elevational gradients in the tropics (Olsen 1994). Dominant ant species are thermophilic, many preferring lower elevations (Andersen 1997); in hotter climates they may exclude many interspecific competitors. At the higher end of the gradient, the most common beetles were species of ground-beetles (family: Carabidae) which compete with ants for arthropod prey (Erwin and Adis 1982). Some speculate that reduced competition from ants allows ground-beetles and other arthropods to occupy more general habitats at higher elevations (Olson 1994). Most of

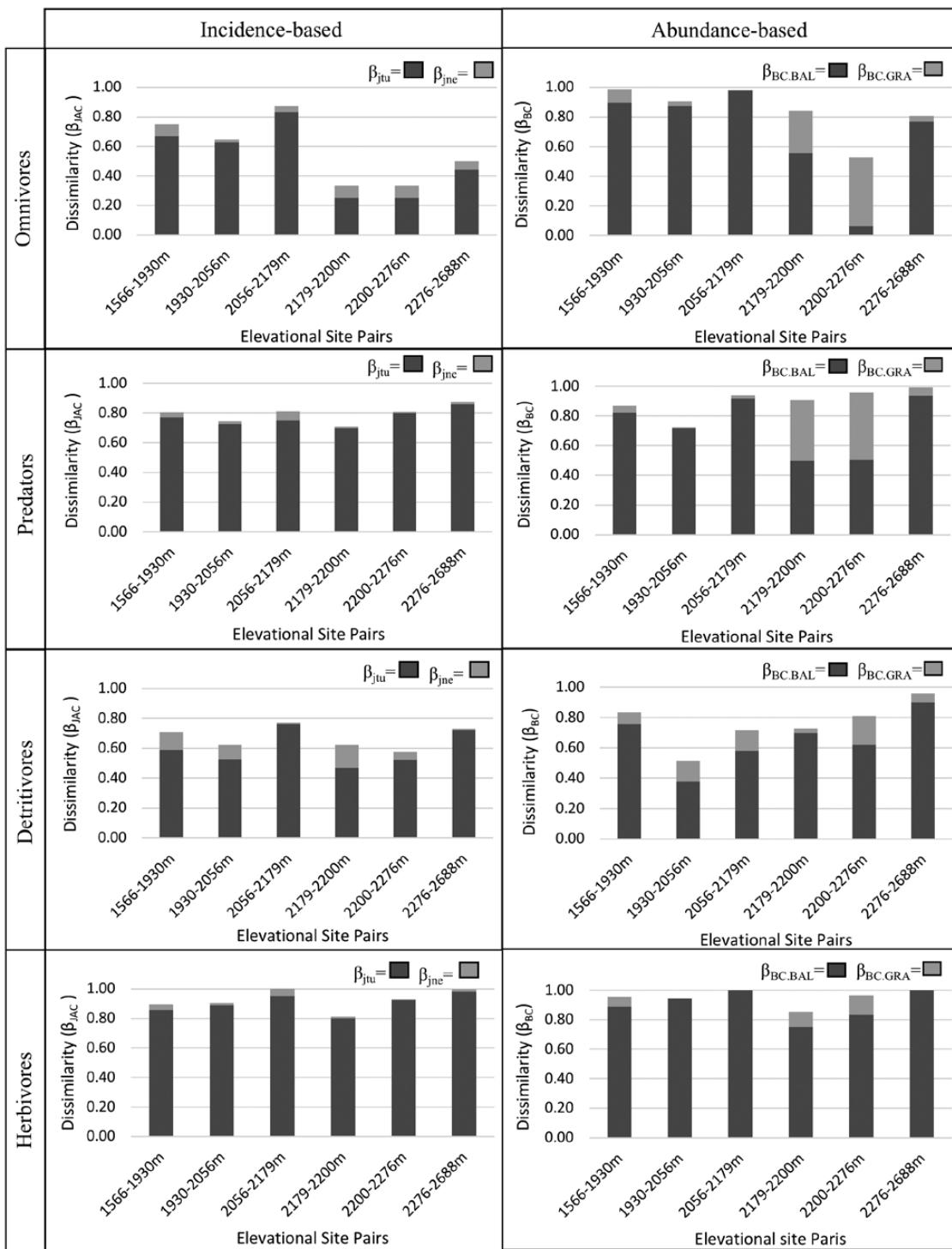


Fig. 8. Dissimilarity analysis (β -diversity) of ground-dwelling arthropod functional groups (rows) partitioned into incidence-based turnover (β_{jtu}) and nestedness (β_{jne}) in the first column, and abundance-based turnover ($\beta_{BC,BAL}$) and nestedness ($\beta_{BC,GRA}$) of elevational site pairs (i.e., each site and its immediately adjacent uphill site) in the second column.

the high-elevation beetles we observed were predators, driving the increase in predator abundance at high elevations.

Functional group differences in β -diversity showed variable patterns across elevation, indicating niches are differentially affected by elevation. Herbivores were highly dissimilar among sites compared to detritivores and omnivores. Herbivores are more likely to be specific to plant species compared to the more generalized diets

of detritivores and omnivores. Interestingly, predators and omnivores showed nested patterns between mid-elevational sites in the Ponderosa life zone. These patterns may signal temperature filtering for these groups at these elevations, or indicate habitat differences. Of course, our functional designations were simplistic with only four groups, as the functional roles of ground-dwelling arthropods are less-defined than other communities (e.g., riparian arthropods

(Kennedy et al. 2016), fish (Villéger et al. 2013), or birds (Mahoney et al. 2019)). Further partitioning arthropods into more defined functional groups may yield new insights into their elevational patterns.

Conclusion

Ground-dwelling arthropods communities strongly differed across elevation on the Colorado Plateau; these differences were likely driven by temperature and precipitation. The climate of this region is warming and drying; this favors vertical movement of communities to higher elevations (Minott and Kolb 2020). The high rates of turnover we observed suggest that competitive exclusion may be high (Baselga 2010), increasing the risk of local extinctions as species disperse to new elevations. In particular, increased temperature can increase dominant ant species which can destabilize insect communities (Diamond et al. 2016). Ants are predicted to become more dominant and occupy higher elevations as temperatures warm (Del Toro et al. 2015). However, the role of drought is much less understood than temperature making it difficult to predict how ground-dwelling insects will respond to climate change along arid gradients. Our results suggest that ground-dwelling arthropod assemblages are context-dependent making them highly vulnerable to environmental change, especially in lower arid elevations. Ours is the first study to document the elevational patterns of a wide-range of ground-dwelling arthropod taxa on the Colorado Plateau and we found many rarely documented taxa, including a new ant species (*Strumigenys superstes* (Hymenoptera: Formicidae), Booher and Uhey 2020). With the complexity of ground-arthropod biodiversity and the threat of climate change, we emphasize the need for further documenting elevational community patterns.

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