

DIVERSITY AND DISTRIBUTION PATTERNS OF GROUND-DWELLING ARTHROPODS  
IN THE SANTA CATALINA MOUNTAINS, ARIZONA

by

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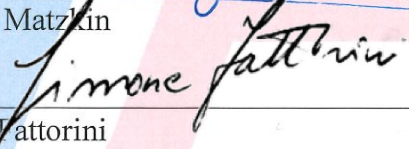
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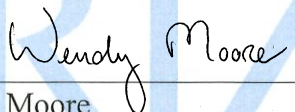
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Final approval and acceptance of this dissertation is contingent upon the candidate's submission of the final copies of the dissertation to the Graduate College.

I hereby certify that I have read this dissertation prepared under my direction and recommend that it be accepted as fulfilling the dissertation requirement.

  
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## ABSTRACT

Mountains, with their rapid climatic and topographic variations along elevational gradients, offer ideal settings for investigating general patterns and factors associated with species diversity. While some common patterns and factors associated with species diversity may emerge across different systems, taxonomic groups are expected to exhibit differences along the same environmental gradient due to their distinct ecological requirements. However, relatively few studies have simultaneously examined multiple taxonomic groups within the same system, and it remains unclear whether commonalities exist in how species diversity varies with elevation and key environmental factors. In the Santa Catalina Mountains, elevational patterns of species richness were found to vary in different ground-dwelling arthropod groups. In line with this finding, combinations of different environmental factors are associated with variation in species richness in different ground-dwelling arthropods, suggesting that different taxonomic groups might not respond in the same way to the same environmental gradient. At the same time, average temperature and temperature range explained most of the variation in species richness in most groups, highlighting their predictive value in some but not all ground-dwelling arthropod groups.

According to the climatic variability hypothesis, species range extent and distribution are determined by the climatic fluctuations a species can tolerate. Along gradients of climatic variability, species adapted to stable conditions are expected to not survive in areas with greater climatic fluctuations, and therefore present smaller range extents. In contrast, species inhabiting more variable climates are predicted to have broader range extents, as they can tolerate both climatically variable and stable regions. Since climatic variability generally increases with elevation, species range extents are expected to increase with elevation, a pattern known as Rapoport's rule. Based on Rapoport's rule, species richness is also expected to decline with increasing climatic variability, and consequently with elevation, since climatic specialists are gradually filtered out at higher elevations. Here, the validity of Rapoport's corollaries is explored by establishing the relationship between species range extent, species richness, elevation, and climatic variability in different groups of ground-dwelling arthropods on the Santa Catalina Mountains. Although species range extent seemingly increases with increasing climatic variability as expected by the climatic variability hypothesis, this pattern does not result in elevational patterns of species range extent and species richness concordant with Rapoport's rule.

Contrary to species richness, variation in community structure is consistent across ground-dwelling arthropod groups. Pure turnover is the dominant component of beta diversity for all taxa, as beta diversity mostly varies according to biome identity along this elevational gradient. In line with this finding, environmental distances, but not geographic distances, correlate with turnover and overall beta diversity in all taxa, possibly suggesting that local environmental factors play a key role in shaping communities characterized by distinct species. This similarity in community structure and variation along environmental distance is further highlighted in Canonical Correspondence Analysis (CCA), where average temperature emerges as the main factor associated with patterns in community composition across all taxa. Based on these observations, we propose that environmental distance and average temperature might serve as a

shared proxy for community structure differences across various arthropod groups in the Santa Catalina Mountains, and potentially other ranges within the Madrean Sky Island Archipelago.

## CHAPTER 1

### INTRODUCTION

#### 1.1 Species diversity patterns and the Santa Catalina Mountains

Biodiversity is not evenly distributed spatially and understanding what drives its spatial patterns is a fundamental topic in ecology and biogeography (Gaston 2000, Peters et al. 2016, Szewczyk and McCain 2016). Studying species diversity patterns is not only important to understand how ecological dynamics (e.g., species interactions and effects of environmental conditions) shape communities and ecosystems (Leibold et al. 2004), but also to model their future changes in response to global climate change and other anthropogenic disturbances, which is essential to determine appropriate conservation measures (Gaston 2000, Bellard et al. 2012, Longino and Branstetter 2019).

The latitudinal gradient is one of the most pervasive and longest studied spatial patterns of diversity on Earth. An increase in species diversity from the poles to the midlatitudes or equator has been observed and studied in a variety of taxa for over two centuries, with only a few notable exceptions within some clades (Gaston 2000, Jablonski et al. 2017, Beaugrand et al. 2020). While most of these studies focus on plants and vertebrates, spatial patterns in species diversity have also been examined in other taxa such as bacteria, algae, protozoans, mollusks, parasitic worms, and some arthropods (for an extensive reference list, see Fattorini 2022). Since von Humboldt (Humboldt and Bompland 1807), it has been well known that parallelisms exist between latitudinal and elevational gradients, driven by similar responses of ecosystems to changes in climatic conditions (Fattorini et al. 2019). Like latitudinal gradients, species diversity also decreases with elevation in response to changes in climatic conditions. However, climatic factors change more rapidly from lower to higher elevations than from lower to higher latitudes (Lomolino 2001). For example, the average annual temperature on land decreases by about 1 °C with every 200 m increase in elevation and 1°C with each one degree increase in latitude (Montgomery 2006). This makes it possible to investigate how diversity responds to variation in climatic conditions on a much smaller scale than along latitudinal gradients (Körner 2007, Fattorini et al. 2020, Mantoni et al. 2021). In addition to climate, many other environmental parameters that influence animal life vary with elevation, such soil characteristics and vegetation structure (Fattorini et al. 2019; Moradi et al. 2020). Therefore, elevational gradients may represent ideal systems to understand how patterns of species diversity vary in response to environmental parameters and their influence on ecosystem functionality (Fattorini 2014, Sun et al. 2020, Mantoni et al. 2021, Muluvhahothe et al. 2021, Liu et al. 2022).

Understanding patterns of species diversity and their drivers along elevational gradients also has important implications for the conservation of terrestrial biodiversity (Fattorini et al. 2020). Despite representing only 25% of all land area, mountains host a third of terrestrial plant diversity and account for numerous endemic and rare species, making them biodiversity hotspots and important targets for conservation priorities (Körner 2004, 2007, Rahbek et al. 2019, Fattorini et al. 2020). Part of this diversity is represented by high elevation species locally adapted to cooler climates and particularly vulnerable to global warming (Poloni et al. 2022). Lowland species can find refuges on mountains from anthropic disturbance and climate change

(Poloni et al. 2022). Furthermore, mountains support lowland biodiversity by contributing to about half of the lowland river flow from snowmelt (Fattorini et al. 2020).

One of the world's biodiversity hotspots is the Madrean Sky Island Archipelago of the southwestern United States and northwestern Mexico (Mittermeier et al. 2004). This archipelago spans the Cordilleran Gap between North America's Rocky Mountains and Sierra Madre Occidental and includes about 65 mountain ranges. Because of the "sea" of dryland that divides them, the term "sky islands" was coined to describe how these isolated mountains resemble insular systems (Brusca and Moore 2013, Brusca et al. 2013). Along the elevation of the Madrean Sky Islands, there are over half of the North American species of birds, as well as the highest known diversity of ants, mammals, and reptiles for North America (Felger and Wilson 1994, Warshall 1994, Yanahan and Moore 2019). Because of its diversity, biogeographical history, and unique location, this region has attracted the interest of researchers for over a century. For example, the steep succession of plant communities on the Santa Catalina Mountains inspired Forest Shreve (1915) to explore changes in vegetation and the climatic factors underlying these changes. In his work, he eloquently wrote:

*"The journey from the base to the summit of the Santa Catalina Mountains brings to the eyes of the observer a constantly changing panorama of vegetation. New types of plants are constantly being encountered with increase of altitude, while types already familiar are being left behind."*

The Santa Catalina Mountains not only offer a range of climatic changes from lower to higher elevations that parallel those observed traveling from Mexico to Canada (Brusca and Moore 2013), but also a succession of eight biomes (desert scrub, desert grassland, oak-grassland, oak woodland, chaparral, pine-oak woodland, pine forest, and mixed conifer forest) (Moore et al. 2013, Yanahan and Moore 2019), which represents a clear parallelism between latitudinal and elevational gradients and an opportunity to study ecosystem dynamics in diverse community assemblages on a much smaller geographic scale.

In addition to the dramatic climatic and vegetation changes that can occur along elevation gradients, the position and biogeographic history of mountain ranges can increase the diversity and complexity of their fauna and flora. For example, some mountains are cross-roads between different biomes (e.g., the Alps contain elements from nearby Mediterranean and temperate forest biomes), or they can act as migratory routes during geo-climatic events (e.g., the North-South migration of species through South American mountain systems during the Pliocene) (Fattorini et al. 2020). This is also the case for the Madrean Sky Island Archipelago, which straddles temperate, subtropical and tropical climatic zones, and biogeographical regions, including the Rocky Mountains and Sierra Madre Occidental ranges, and the Chihuahuan and Sonoran deserts. Furthermore, this mountain archipelago has historically undergone profound faunal and floristic range shifts. For example, the end of the last glacial and start of the current interglacial phase coincided with the northward shift of species, as well as isolation of temperate species at higher montane elevations (Warshall 1944, Brusca and Moore 2013).

Most research on the spatial distribution of biodiversity focuses on taxonomic diversity. Taxonomic diversity (TD) studies the variety of taxa and how it changes over space and time (e.g., species richness and abundance along environmental gradients). It is usually divided into



alpha, beta, and gamma components, which respectively describe the diversity of taxa in a given assemblage (alpha), changes in taxa composition between assemblages (beta), and cumulative diversity across assemblages (gamma) (Magurran 2004, Borges et al. 2020). For my research, I will explore the alpha and beta taxonomic diversities of ground-dwelling arthropods of the Santa Catalina Mountains and test different mechanistic hypotheses previously proposed to explain spatial distributions of biodiversity. As mentioned above, mountains of the Madrean Sky Island Archipelago offer the perfect opportunity to examine the role of environmental factors in shaping current variations in species diversity as well as the different ways communities/biomes interact with one another along the elevation gradient. Furthermore, although much has been done to describe the fauna and flora of the Santa Catalina Mountains, the discovery and description of new species in the area is far from being complete (i.e., in our unpublished studies I have found about 10% of all US ant species on a single mountain of this mountain archipelago). Concurrently, recent studies have highlighted that this incredible diversity is undergoing important shifts in elevation because of global climate change (e.g., as temperatures rise and precipitation decreases, many species are shifting upward in elevation) (Brusca et al. 2013, Yanahan and Moore 2019). If the current trends of global climate change are not alleviated, a dramatic shift and extirpation of present-day high-elevation biotic communities will occur (Yanahan and Moore 2019). I will especially focus on patterns of diversity in arthropods that, despite their prevalence in the terrestrial realm (e.g., insects have about a million described species and about 5.5 million undescribed species; Stork 2018), have not been well investigated in comparison to smaller taxonomic groups such as plants and vertebrates along latitudinal and elevational gradients (Stork 2018, Fontanilla et al. 2019, Fattorini 2022).

Meyer et al. (2015) published the first investigation of ground-dwelling arthropod assemblages along two full elevation gradients of these mountains. To assess the diversity and distribution of ground-dwelling arthropods, 66 sampling sites were identified in recognizable plant biomes along the elevation gradients on the southern and northern sides of the Santa Catalina Mountains. They sampled ground-dwelling arthropods for two weeks in the spring (pre-monsoon season) and two weeks in the summer (post-monsoon season) of 2011. At each of the 66 sampling sites, they set 10 pitfall traps arranged 10 m apart along a 100 m transect line, resulting in 660 samples in each season. Beetles (Coleoptera), spiders (Araneae), grasshoppers and crickets (Orthoptera), and millipedes and centipedes (Myriapoda) were sorted to species, curated, and deposited in the University of Arizona Insect Collection. Meyer et al. (2015) analyzed these taxa to investigate differences in ground-dwelling arthropods composition among biomes by using permutation-based hypothesis testing (ANOSIM analyses). Focusing on community composition, they found that each plant biome on the Santa Catalina Mountains hosts different communities of beetles, spiders, orthopterans, and myriapods.

My dissertation builds upon this work by utilizing the arthropod specimens and data from this study, along with Formicidae, to explore patterns and variables associated with different components of taxonomic diversity across various ground-dwelling arthropod groups in the Santa Catalina Mountains.

## 1.2 Dissertation Format

The format of this dissertation follows the guidelines found in Article IV of the University of Arizona Dissertation Formatting Guide, which outlines details for manuscript-based dissertations. The following chapter contains brief descriptions of the manuscripts prepared during the current research. Each manuscript is included in an appendix of this dissertation. These manuscripts are prepared for submission to peer-reviewed journals and are formatted according to the guidelines of *Ecography*.

## CHAPTER 2

### THE CURRENT STUDY

This chapter summarizes the manuscripts developed during the current study on patterns and environmental factors influencing taxonomic diversity in the ground-dwelling arthropods of the Santa Catalina Mountains. It includes the titles, authors, and a brief description of each manuscript.

#### 2.1 Greater climatic variability is associated with higher, rather than lower, species richness in ground-dwelling arthropods along elevational gradients.

Davide Bergamaschi, Simone Fattorini, Kim Franklin, Wallace M. Meyer III, and Wendy Moore

Variations in species richness along elevational gradients have been examined in relation to both spatial constraints and environmental variables leading to an array of hypotheses as to what factors best predict species richness patterns. Here, we explore these questions by investigating patterns of species richness of ground-dwelling arthropod groups on a mountain range in the Madrean Sky Island Archipelago of the Southwest. We use a multi-model approach to determine what factors best explain variation in species richness in various taxonomic groups and to see whether those factors are consistent across taxonomic scales. Multi-model selection and multiple regression analyses revealed that species richness across different arthropod groups is associated with a unique combination of environmental factors. Our results contribute to a growing body of research indicating that temperature (both average temperature and temperature range) plays a key role in affecting species richness in montane systems. However, contrary to classic ecological hypotheses and results from other study systems, we find that greater climatic variability (as measured by temperature range) was associated with higher species richness, suggesting that species in this region are adapted to variable climates. Our results point to the complexity of species richness patterns and caution against over-generalizing across taxa or systems, emphasizing the need for further research into the environmental factors that influence biodiversity at different scales. Further studies that consider these factors across multiple taxa will help refine our understanding of biodiversity patterns in montane ecosystems and beyond.

#### 2.2 Relationships between climatic variability, species range extent and species richness are inconsistent with Rapoport's rule

Davide Bergamaschi, Simone Fattorini, and Wendy Moore

According to the climatic variability hypothesis, species range extent and distribution are determined by the climatic fluctuations a species can tolerate. Along gradients of climatic variability, species adapted to stable conditions are expected to have smaller range extents, as they may not survive in areas with greater climatic fluctuations. In contrast, species inhabiting more variable climates are predicted to have broader range extents, as they can tolerate both climatically variable and stable regions. Since climatic variability generally

increases with elevation, species range extents are expected to increase with elevation, a pattern known as Rapoport's rule. Based on Rapoport's rule, species richness is also expected to decline with increasing climatic variability, and consequently with elevation, since climatic specialists are gradually filtered out at higher elevations. Here, we explored whether species range extents of different groups of ground-dwelling arthropods on the Santa Catalina Mountains vary along an elevational gradient in accordance with Rapoport's rule and the climatic variability hypothesis. Ground-dwelling arthropods were collected across 66 locations and climatic variability was quantified for each location as thermal variability. Elevational range extents were calculated for each species, as well as the maximum climatic variability experienced by each species at any given location. Then, we studied how climatic variability varies with elevation and the relationship between species range extent and maximum climatic variability, as well as species range extent with elevation. Contrary to expectations, we found that climatic variability declined with increasing elevation in this system. While species range extent was generally positively correlated with the maximum climatic variability experienced by each species, it did not covary with elevation. Moreover, species with small ranges were not restricted to climatically stable environments, and instead, occurred throughout the elevational gradient. These results suggest that while species in more climatically unstable environments tend to have broader ranges, species with small ranges are distributed across the entire gradient. As a result, variation in species range and variation in species richness are decoupled: an average increase in species extent does not imply that communities in more unstable environments are simply subsets of those in more stable environments. In fact, we found that specialists (species with small ranges) are not concentrated in climatically stable environments. These results suggest that climatic variability favors species with broader ranges as they are more tolerant, but species with small ranges may occur throughout, possibly because their niches are restricted by non-climatic factors (e.g., biotic interactions).

### 2.3 Pure turnover, rather than nestedness, drives beta diversity of ground-dwelling arthropod communities in the Santa Catalina Mountains.

Davide Bergamaschi, Simone Fattorini, and Wendy Moore

Mountains, with their rapid climatic and topographic variations along elevational gradients, provide ideal settings for exploring general patterns and environmental factors associated with community structure. Variation in community composition along these gradients is shaped by environmental and spatial differences, with species turnover often considered the main factor generating community dissimilarity. However, some studies have also proposed a "filtering" effect, where communities may not consist of entirely different species but rather represent nested subsets of one another. The Santa Catalina Mountains, part of the Madrean Sky Island Archipelago, are home to an extraordinary diversity of ground-dwelling arthropods. Recent surveys have documented over 400 species on this single "Sky Island," raising the question of how this diversity is distributed across elevational gradients and what environmental factors are associated with variations in community structure. While previous research has observed variation in beta diversity across different ground-dwelling arthropod taxa influenced by biome and seasonal changes in the same system, the extent to which these patterns are shaped by environmental or spatial distances and the relative contributions of

species turnover and nestedness remain unclear. In this study, we investigate the community structure of different ground-dwelling arthropods groups in the Santa Catalina Mountains by partitioning beta diversity into turnover and nestedness components. We examine how these components relate to environmental and geographic distances across communities, and we identify key environmental factors associated with community structure through Canonical Correspondence Analysis. Our results reveal that species turnover rather than nestedness plays a predominant role in shaping community composition. Environmental distance emerges as a significant factor associated with community structure across all arthropod taxa, whereas geographic distance plays a minimal role in some groups. Notably, temperature significantly explains variations in community composition across all ground-dwelling arthropods, underscoring its potential role as a key environmental factor influencing community structure in this montane system. Despite differences in ecological roles and dispersal capabilities of the arthropod taxa considered, our findings hint at the importance of environmental gradients, particularly temperature and its covariates, in influencing species replacement along elevational gradients and shaping arthropod communities. This research contributes to our understanding of community dynamics in montane ecosystems, emphasizing the contribution of species turnover to overall beta diversity and the role of environmental conditions in producing variation in community composition.

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## APPENDIX A

### GREATER CLIMATIC VARIABILITY IS ASSOCIATED WITH HIGHER, RATHER THAN LOWER, SPECIES RICHNESS IN GROUND-DWELLING ARTHROPODS ALONG ELEVATIONAL GRADIENTS

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**Title:** Greater climatic variability is associated with higher, rather than lower, species richness in ground-dwelling arthropods along elevational gradients.

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## **ABSTRACT**

Variations in species richness along elevational gradients have been examined in relation to both spatial constraints and environmental variables leading to an array of hypotheses as to what factors best predict species richness patterns. Here, we explore these questions by investigating patterns of species richness of ground-dwelling arthropod groups on a mountain range in the Madrean Sky Island Archipelago of the Southwest. We use a multi-model approach to determine what factors are associated with species richness in various taxonomic groups and to see whether those factors are consistent across taxonomic scales. Multi-model selection and multiple regression analyses revealed that species richness in different arthropod groups are associated with a unique combination of environmental factors. Our results contribute to a growing body of research indicating that that temperature (both average temperature and temperature range) is strongly associated with species richness in montane systems. However, contrary to classic ecological hypotheses and results from other study systems, we find that greater climatic variability (as measured by temperature range) was associated with higher species richness, suggesting that species in this region are adapted to variable climates. Our results point to the complexity of species richness patterns and caution against over-generalizing across taxa or systems, emphasizing the need for further research into the environmental factors that influence biodiversity at different scales. Further studies that consider these factors across multiple taxa will help refine our understanding of biodiversity patterns in montane ecosystems and beyond.

**KEYWORDS:** Species richness, elevation, sky islands, ground-dwelling arthropods, Myriapoda, Insecta, Araneae, Orthoptera, Coleoptera, Staphylinidae, Carabidae, Tenebrionidae, Formicidae

## **1 | INTRODUCTION**

Elevational gradients are widely used in ecological research due to their broad variations in abiotic conditions over relatively short distances (Körner 2007, Fattorini et al. 2019, Moradi et al. 2020). Most studies of elevation gradients have investigated the association between environmental factors and elevational changes in species richness to facilitate identification of

key factors explaining biodiversity patterns along these gradients. Although taxonomic groups often exhibit distinct responses to environmental gradients, synthesis of this research has led to the identification of recurrent patterns in some taxa, like a decline in species richness with increasing elevation or a mid-peak at intermediate elevations (McCain and Grytnes 2010, Guo et al. 2013). However, elevational gradient studies typically focus on a single taxon, and it remains unclear whether findings are applicable to multiple taxa with differing ecological requirements (Peters et al. 2016).

Relatively few studies have explored commonalities in variation of species richness and influential environmental factors across multiple taxa along the same elevational gradient (Duan et al. 2016, Peters et al. 2016, Vetaas et al. 2019). Based on these studies, different patterns may emerge within the same elevational gradient for different taxonomic groups. However, it has been suggested that this discrepancy among patterns tends to be reduced when considering broad and more ecologically inclusive groups, where species richness usually declines with increasing elevation (Peters et al. 2016).

Variations in species richness along elevational gradients have been examined in relation to both spatial constraints and environmental variables leading to an array of hypotheses as to what factors best predict species richness patterns. One such hypothesis is the mid-domain effect (Colwell et al. 2004; Colwell 2008; Prillwitz and Blasius 2020). This hypothesis suggests that the observed mid-elevation peak in species richness could result from neutral processes rather than being driven by specific environmental factors. Essentially, it proposes that if species with different range extents are stochastically distributed along the elevation gradient, you would expect to find more species at intermediate elevations simply due to chance alone. Environmentally driven hypotheses include: (1) the ambient energy hypothesis, which predicts species richness increases with increasing environmental energy, most commonly thermal energy, as warmer climates are more physiologically tolerable than colder climates (Turner et al. 1987, Currie et al. 2004); (2) the water availability hypothesis, which predicts species richness increases with water availability through its positive effect on biomass, which in turn increases richness (Hawkins et al. 2003, Rodríguez et al. 2005); (3) the habitat heterogeneity hypothesis, which predicts species richness increases with habitat heterogeneity as it provides higher diversity of niches (MacArthur and MacArthur 1961), and finally; (4) climatic fluctuation filtering, a corollary of Rapoport's hypothesis, which predicts species richness declines with increasing climatic variability since few generalists species that are able to cope with larger climatic fluctuations (Stevens 1992; Sanders 2002; Fernández and Vrba 2005; Fattorini 2014; Pintor et al. 2015).

Similarly to variation in patterns of species richness, these hypotheses have received variable support depending on the taxonomic group considered, the ecological breadth of the group, and the mountain system concerned (Zellweger et al. 2016, Peters et al. 2016). For instance, ambient energy is expected to explain most of the variance in taxonomically inclusive communities (e.g., at higher taxonomic levels where species richness tends to decline with elevation in response to decline in ambient energy) (Buckley et al. 2010; Hurlbert and Stegen 2014, Peters et al. 2016). Based on this theoretical framework, broader taxonomic groups including more distantly related taxa are more likely to include species with different ecologies, allowing them to exploit a wider range of niches and the full range of available energy within a system ("energy optimum");

Hurlbert and Stegen 2014). In contrast, narrow taxonomic groups that include closely related taxa with similar ecologies tend to show unique species richness patterns and responses due to niche conservatism, which limits full exploitation of the available ambient energy (i.e., narrower taxonomic groups work within an “energy sub-optimum”; Buckley et al. 2010; Hurlbert and Stegen 2014). Empirical evidence of this pattern was found on Mount Kilimanjaro, where temperature was the primary factor explaining variation in species richness when examining the entire fauna and flora, while distinct combinations of environmental factors best explained the variation in species richness of different subclades (Peters et al. 2016).

In the present study, we explore patterns of species richness and the value of environmental variables, including temperature (ambient energy), humidity (water availability), terrain ruggedness (habitat heterogeneity), and temperature range (Rapoport’s hypothesis), as well as geometric constraints (mid-domain effect) in predicting the variation of species richness of ground-dwelling arthropods in the Santa Catalina Mountains (Arizona, USA). This mountain range is within the Madrean Sky Island Archipelago, a global biodiversity hotspot (Mittermeier et al. 2004), and is transversed by two roads from the base to the top, making it a convenient and accessible place to study species distribution and variation of species richness along elevational gradients. The mountain ranges within the Madrean Sky Island Archipelago are isolated from one another by low elevation “seas” of desert, whereas the ranges can harbor up to eight distinct plant biomes. Floristically, the climatic shift from desert to mixed conifer forests is like that seen by travelling from Mexico to Canada (Whittaker and Niering 1965, Rahbek 1995, Moore et al. 2013, Brusca et al. 2013, Brusca and Moore 2013, Yanahan and Moore 2019). We conducted analyses on a wide array of taxonomic groups (including millipedes, spiders, ants, beetles, and grasshoppers and crickets). This approach allowed us to investigate whether the environmental factors associated with diversity differed among the taxonomic groups. We also conducted analyses on both broad and narrow taxonomic groups (Table 1) to determine if the factors associated with diversity were consistent across the taxonomic scale.

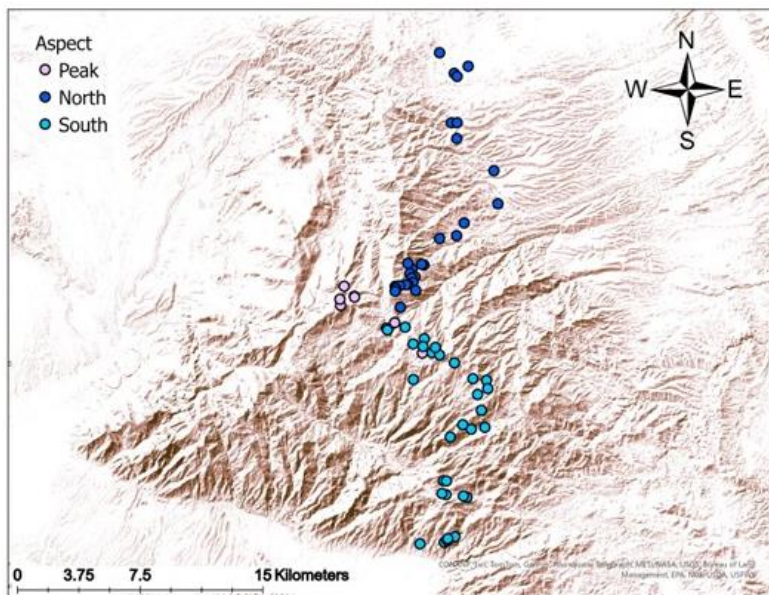
## **2 | METHODS**

### **2.1 | Study area**

The Santa Catalina Mountains near Tucson, AZ, USA are part of the Madrean Sky Island region that spans the Cordilleran Gap between the Rocky Mountains/Colorado Plateau and the Sierra Madre Occidental. These Sky Island mountains are characterized by a sequence of biomes (biome stacking) along their elevational gradients from approximately 900 to 2800 m, offering an example of the parallelism between latitudinal and elevational gradients (Brusca et al. 2013). In the Santa Catalina Mountains, the following biomes can be found from the lowland (about 900 m) to the mountain top (2791 m elevation): Desert Scrub, Desert Grassland, Oak-Grassland, Oak Woodland, Pine-Oak Woodland, Chaparral, Pine Forest, Mixed Conifer Forest (Moore et al. 2013, Yanahan and Moore 2019). The region has two rainy seasons, in the winter from December through February and in the summer from July through September. Summer rains that are part of the North American Monsoon system account for half the annual precipitation (Douglas et al. 1993, Meyer et al. 2015).

### **2.2 | Arthropod sampling and processing**

Data used for this study were derived from the material collected during an extensive biodiversity survey carried out in 2011 as part of the Arizona Sky Island Arthropod Project based at the University of Arizona (Moore et al. 2013). Sampling and specimen processing methods have been previously described in detail (Meyer et al. 2015) and are summarized again here. Ground-dwelling arthropods were sampled from 66 100-meter transects distributed along two elevational gradients in the Santa Catalina Mountains. Transects were located on the southern and northern slopes of the mountains to encompass the large variation in slope and aspect, as well as in biomes, occurring in the study area from 1045 m to 2777 m (Figure 1). Along each transect, 10 pitfall traps were placed 10 m apart from one another (Supplementary Material Figure S1). Each trap consisted of a 150 ml test tube (3.2 cm diameter) half filled with propylene glycol that was inserted into a protective PVC sleeve buried in the ground with a PVC rain shield. The PVC sleeve was left in place throughout the study to enable repeat sampling from the same locations. Traps were active for 14 consecutive days in two periods: pre-monsoon (May 5-19) and post-monsoon (September 1-15) 2011 (Supplementary Material Table S1). At the end of each 14-day collecting period, the content of each pitfall trap was collected, placed in 80% ethanol, and stored at -20°C.



**Figure 1.** Hillshade map of the Santa Catalina Mountains and the 66 transect locations on the higher peaks (purple dots) and along its southern (light blue dots) and northern (blue) slopes. Hillshades were derived from a 1/3 arc-second DEM from US Geological Survey.

Adults of Myriapoda, Araneae, Orthoptera, Coleoptera, and Formicidae were sorted to putative species. Species names were assigned, when possible, while the remainder were identified to genus and assigned a morphospecies number. While data from specimens of Myriapoda, Araneae, Orthoptera and Coleoptera were also included in a previous study (Meyer et al. 2015), the ants (Formicidae) are included in the present study for the first time. Voucher specimens are pinned, labeled, and deposited in the University of Arizona's Insect Collection (<https://uaic.arizona.edu/>).

The final dataset included 74,310 specimens and 449 species/morphospecies (Table 1). To study variation in patterns of species richness and the taxonomic scalability of these patterns, we analyzed data for 10 taxonomic groups separately. All 449 species were included in our analyses of “all ground-dwelling arthropods”, and subsets of these species were also included in less inclusive datasets (Table 1). Species lists of Myriapoda, Araneae, Orthoptera and Coleoptera were published by Meyer et al. (2015), and a species list of the ants (Formicidae) is provided in Supplementary Material (Table S2).

**Table 1.** Taxon group names, composition, and species richness of the ten groups analyzed in this study. Groups are listed from most to least inclusive, such that each group includes taxa nested beneath it.

1	All ground-dwelling arthropods	449
2	Araneae	101
3	Myriapoda	16
4	Insecta	332
5	Orthoptera	25
6	Formicidae (Hymenoptera)	117
7	Coleoptera (3 families below + 107 other spp.)	190
8	Carabidae	21
9	Staphylinidae	25
10	Tenebrionidae	37

### 2.3 | Sampling coverage and species richness

Before analyses, we quantified sample coverage (Chao and Jost 2012) for all 10 taxonomic groups (Table 1) with the package iNEXT 3.0.1 (Hsieh et al. 2016) in R 4.4.2. Sampling coverage estimates were consistently very high (mean > 0.8, S.D < 0.17, mode > 0.9 in most cases). Consequently, we calculated species richness at each site as the observed cumulative number of species/morphospecies for each transect from the yield of all 10 traps across both sampling seasons (see Supplementary Material Table S1).

### 2.4 | Spatial constraint of living on a mountain

To explore the mid-domain effect, we used the species richness expected by a mid-domain model as a predictor of the observed species richness, with a positive correlation in line with a mid-domain effect. To calculate mid-domain values, we divided the elevational gradient into 36 vertical bands of 50 m. Based on their elevation, transects were assigned to one 50 m band between 1000 m and 2800 m (e.g. 1000-1050, 1050-1100 etc.). Then, we calculated the range extent of each ground-dwelling arthropod species as the maximum elevation of the highest band minus the minimum elevation of the lowest band in which they occurred. In this way, for an individual species, the minimum range extent possible is 50 m while the maximum is 1800 m. Finally, empirical range extents were randomly reshuffled along the elevational gradient and species richness values expected under the mid-domain model were calculated as the mean total number of ranges overlapping in each elevational band across 1000 permutations using the range shuffle function in the R package rangemodelR 1.0.4 (Marathe 2016) in R 4.4.2. This package

enables testing for both hard and soft boundaries on species distributions (Wang and Fang 2012). Hard boundaries represent spatial or environmental limits that cannot be traversed by species, while soft boundaries can be transversed. In this study, the peak of the mountain is an obvious hard boundary for ground-dwelling arthropods. On the other hand, the lowest boundary (1000 m) is not the lowest elevation found in the surrounding lowlands. Therefore, we set 1000 m as a soft boundary and 2800 m as a hard boundary.

## **2.5 | Environmental variables**

### **2.5.1 | Temperature and humidity**

Average temperature and humidity were used, respectively, as measures of ambient energy and water availability in this system. Log-Tag HAXO-8 temperature and humidity recorders were placed above the soil/litter (2 cm) at the center of each transect and covered with a plastic shield. We used measurements taken between May 7<sup>th</sup> (2011) to May 6<sup>th</sup> (2012) every 30-minutes to calculate averages of temperature and humidity for each transect separately. Missing 30-minute data due to recorder malfunction were imputed using the inverse-distance weighting interpolation (Workneh et al. 2024) with the Spatial Analyst extension in ArcGIS Pro 3.1.3 (ESRI 2016). For this analysis, we used the default power value = 2 (Maleika 2020, Fattorini et al. 2023). Finally, we calculated the average temperature and humidity recorded from throughout the year for each transect separately.

### **2.5.2 | Rapoport's hypothesis**

For each transect, we defined climatic variability as the difference between the mean temperature of the warmest and coldest month.

### **2.5.3 | Habitat-heterogeneity**

Habitat heterogeneity was evaluated in terms of how jagged or flat the terrain was. To this end, we used the terrain ruggedness index proposed by Riley et al. (1999), which uses differences in elevation between adjacent grid cells in a digital elevation model. The terrain ruggedness index was calculated with the Arc Hydro Toolset in ArcGIS Pro 3.1.3 (ESRI 2016) using 1/3 arc-second digital elevation model (10 m resolution) (U.S. Geological Survey 2024). Terrain ruggedness index values were then extracted within a 100 m diameter circle and averaged for each transect. The center of each circle was georeferenced with a Garmin 62S GPS and used as the starting geographic coordinates of each transect.

## **2.6 | Statistical analyses**

To describe patterns of species richness along elevation in this system, we used a LOESS regression approach with the package ggplot 3.5.1 in R 4.4.2.

We used two steps to investigate the degree to which species richness is associated with the spatial and environmental factors.

First, we used multi-model selection approach. As different combinations of factors may best predict species richness in different groups, multi-model inference allowed us to account for both model and parameter estimate uncertainties (Burnham and Anderson 2002, 2004). Models included every possible combination and number of factors and were evaluated, and subsequently selected, based on their corrected Akaike Information Criterion (AICc) scores. We selected models that had the lowest AICc scores and were equally supported ( $\Delta AIC \leq 2$  from the best model's AICc score). We computed coefficients and significance levels for each factor by using conditional model averaging.

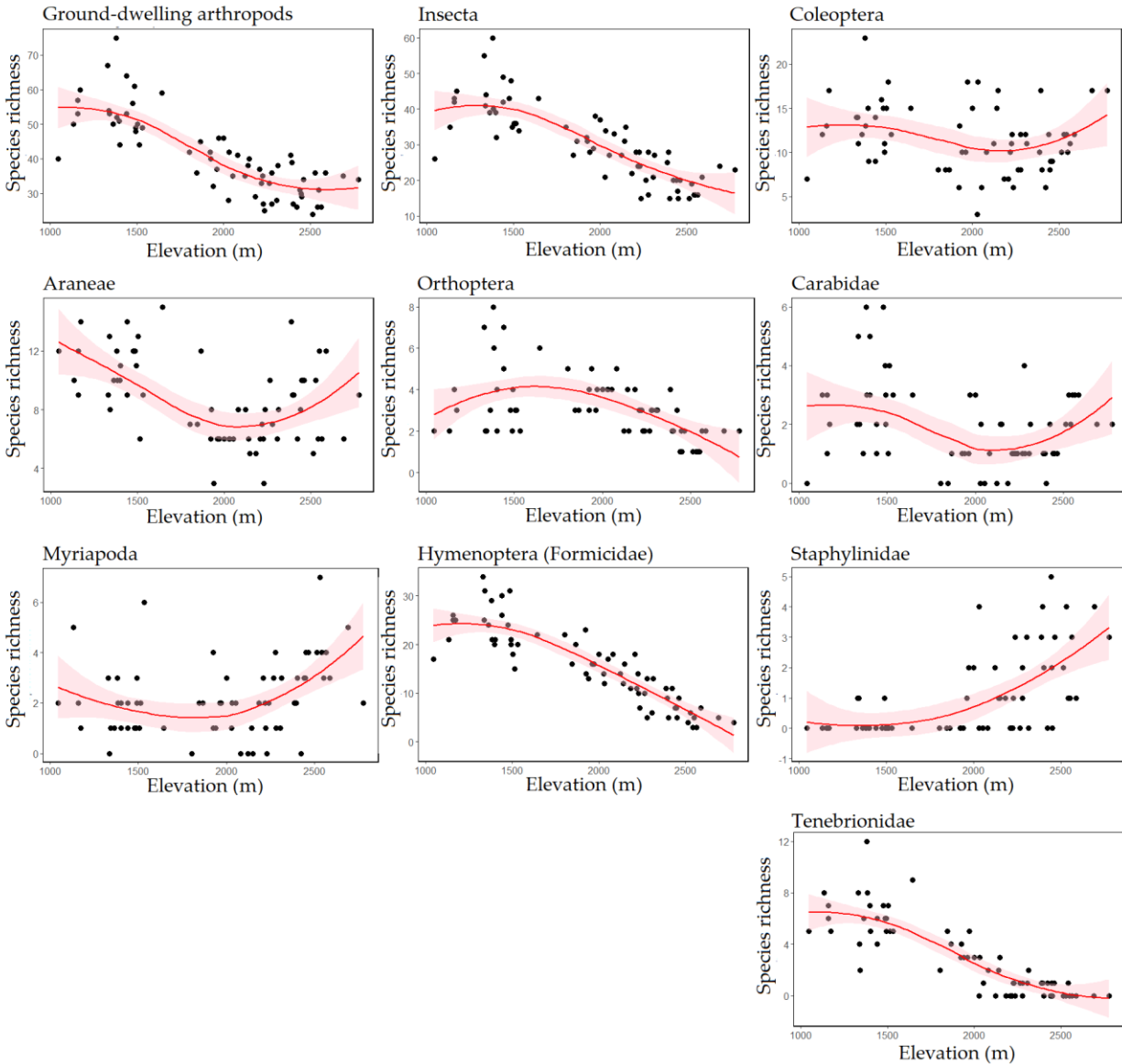
Second, we ran a multiple regression analysis focusing on individual models for each group that included only explanatory variables deemed conditionally significant. This approach allowed us to further evaluate the importance of each explanatory variable based on its significance and parameter estimates, as well as to assess the predictive power of these models in explaining variation in species richness for each taxonomic group. Multi-model selection and averaging were carried out using the R package MuMIn 1.48.4 (Bartoń 2024) in R 4.4.2.

Before analyses, explanatory and response variables were ln-transformed. As species richness and environmental variables typically present non-linear relationships (Austin 1980), ln-transformations were used to improve linearity (see Supplementary Material, Figures S2 and S3). In addition, we z-transformed values of richness and those variables that were deemed conditionally significant before running the multiple regression analysis to compare parameter estimates as standardized coefficients (beta coefficients). To calculate Pearson correlation coefficients and relative p values, and to draw charts, the package psych 2.4.6.26 (Revelle 2024) was used in R 4.4.2.

### **3 | RESULTS**

Although the relationship between richness and elevation varied among taxa, some recurrent patterns were apparent (Figure 2). Araneae and Myriapoda showed U-shaped patterns, with a strong decline of species richness at around 2000-2200 m (Araneae) or 1500-2000 m (Myriapoda). A similar U-shaped pattern was also observed in Coleoptera and Carabidae, although it was preceded by a plateau at lower elevations. Ground-dwelling arthropods, Insecta, Formicidae, and Tenebrionidae showed a plateau in species richness at lower elevations followed by a decline in species richness with increasing elevation. The Orthoptera showed a distinctly hump-shaped pattern, while Staphylinidae richness increased with elevation.





**Figure 2.** Patterns of elevational species richness for individual taxa: Variation in species richness along elevation for all ground-dwelling arthropods, as well as for Araneae, Myriapoda, Insecta, Orthoptera, Formicidae, Coleoptera, Carabidae, Staphylinidae, and Tenebrionidae. Each point represents the cumulative species richness at each transect, while the curves and shaded areas indicate LOESS regressions and their associated standard errors.

Results of the multi-model selection are presented in Table 2 and results of the multiple linear regression are presented in Table 3. Mid-domain effect was not supported as an important factor in predicting species richness in this system, except for Orthoptera. Average temperature and temperature range explains most of the variation in species richness in most taxa. With the exception of Staphylinidae (for which a negative association with average temperature was found), the relationship between species richness and both average temperature and temperature range was positive. The variation in species richness in most groups is associated with different combinations of factors. The coefficient of variation of individual models was low for most

groups and moderately high ( $R^2 > 0.6$ ) only for all ground-dwelling arthropods, Insecta, Tenebrionidae, and Formicidae. Finally, none of the factors were significantly associated with species richness of Carabidae (see Supplementary Material Table S3 and S4).

**Table 2.** Regression coefficients estimated with multi-model selection (conditional averages) for the ground-dwelling arthropod groups considered in this study. “Number of models” represents the number of models included in each conditional estimate (the best models with lowest AICc and  $\Delta AIC \leq 2$ ). Other values represent the average conditional parameter estimates calculated for each factor. Cells with positive and significant coefficients are in black, cells with negative and significant coefficients are in red. Number of asterisks denote  $p < 0.001$  ‘\*\*\*’,  $p < 0.01$  ‘\*\*’, and  $p < 0.5$  ‘\*’. Empty cells represent factors that were not included among the selected models.

Taxon	Number of models	Mid-domain effect	Average temperature	Average humidity	Temperature range	Terrain ruggedness
Arthropoda	2	-0.21*	0.69***	0.23	0.73**	
Araneae	7	-0.22	0.67***	-0.89**	0.58	-0.10
Myriapoda	3	-0.40*	0.27	-0.45		.35**
Insecta	2	-0.22*	0.97**	0.62*	0.92**	
Orthoptera	10	0.48*	0.98	1.22	1.08	0.20
Formicidae	8	0.21	1.52***	0.64	1.01*	-0.10
Coleoptera	3	-0.50**	0.21		1.48**	0.05
Carabidae	6	0.12	0.24	-0.26		-0.20
Staphylinidae	5	-0.10	-1.30***		-0.61	-0.14
Tenebrionidae	3	-0.38	2.18***	0.76	1.62*	0.21*

**Table 3.** Standardized regression coefficients (beta coefficients) and model  $R^2$  from multiple linear regressions including only explanatory variables found to be important in the multi-model selection (based on conditional averages) for the ground-dwelling arthropod groups considered in this study. Cells with positive and significant coefficients are in black, cells with negative and significant coefficients are in red. Number of asterisks are for  $p < 0.001$  ‘\*\*\*’,  $p < 0.01$  ‘\*\*’, and  $p < 0.5$  ‘\*’. All shown models were significant ( $p < 0.01$ ). Carabidae are not present as no variable was retained in the multimodel selection procedure. Empty cells are for explanatory variables that were not found important in the multi-model selection (based on conditional averages) and therefore they were not included in this analysis.

Taxon	Multi $R^2$	Mid-domain effect	Average temperature	Average humidity	Temperature range	Terrain ruggedness
Arthropoda	0.66	-0.28*	0.71***		0.36**	
Araneae	0.16		0.04	-0.37*		
Myriapoda	0.27	-0.30*				0.36**
Insecta	0.74	-0.24*	0.94***	0.27*	0.33**	
Orthoptera	0.35	0.60***				
Formicidae	0.83		0.65***		0.31***	
Coleoptera	0.15	-0.46*			0.57**	

Staphylinidae	0.45	-0.67***		
Tenebrionidae	0.8	0.75***	0.24**	0.14*

#### 4 | DISCUSSION

Our study reveals distinct patterns and key environmental variables associated with elevational variation in species richness across multiple groups of ground-dwelling arthropods. Except for Orthoptera (grasshoppers, crickets, and katydids), we found no evidence that the mid-domain effect explains species richness patterns in the ground-dwelling arthropod groups we examined (Tables 2 and 3). In particular, the influence of geometric constraints was rejected in all ground-dwelling arthropods, Myriapoda, Insecta, and Coleoptera. This suggests that for these groups, patterns of species richness are not simply due to the geometric constraint of living on a mountain, but instead some environmental and/or biotic factors influence their species richness. Species richness patterns in Orthoptera may be largely influenced by the mid-domain effect as our results suggest, however, there are other likely biotic factors that also might explain this result, which we did not test. Notably, grasslands, the preferred habitat of orthopterans (Miao et al. 2018, Poniatowsky et al. 2024), also peaks at mid elevations on these mountains. The effect of geometric constraints on species elevational distribution and diversity is a debated topic (Colwell et al. 2004). Its importance and effect have been mixed across different studies encompassing different taxa such as ants, gastropods, small mammals, birds and plants (Kessler 2000, Sanders 2002, McCain 2004, Baur et al. 2014). Furthermore, a previous study carried out across multiple taxa on Mount Kilimanjaro also did not find a pervasive role of geometric constraints in explaining species diversity across different taxonomic scales (Peters et al. 2016).

In line with different taxonomic groups exhibiting different responses to the same environmental gradient (Guo et al. 2013), patterns of species richness along the elevational gradient of the Catalina Mountains varied across ground-dwelling arthropods. However, five basic patterns can be broadly recognized in this system: a U-shaped pattern, a U-shaped pattern preceded by a plateau at lower elevations, a hump-shaped pattern, an increase in species richness with increasing elevation, and a decline in species richness with increasing elevation preceded by a plateau at lower elevation. The variety of patterns encountered is in line with the results of a previous study exploring multiple animal and plant groups along the elevation gradient of Mount Kilimanjaro, where patterns of species richness largely varied among different taxa (Peters et al. 2016). Also consistent with this study where patterns of species richness converged to monotonically declining along elevation from narrow to broad taxonomic groups, we found that declining patterns characterized broad taxonomic groups like ground-dwelling arthropods and Insecta, although preceded by a plateau at lower elevations. Declining with or without plateau and hump-shaped patterns are commonly found in biodiversity research on mountains (McCain and Grytnes 2010). The monotonic decline has been explained with reference to increasingly harsher conditions, while a mix of mutually non-exclusive hypotheses (mid-domain effect and presence of intermediate, optimal environmental conditions, such as moderate temperatures, higher moisture levels, and higher habitat diversity) have been proposed for hump-shaped patterns (Colwell et al. 2004, McCain and Grytnes 2010, Fattorini 2014, Peters et al. 2016). The decline in species richness observed for Formicidae, Tenebrionidae, Insecta, and ground-

dwelling arthropods in general suggests that for these groups environmental conditions become harsher with elevation. However, we also found two unexpected patterns: an increase of species richness with elevation in Staphylinidae and an overall U-shaped pattern for Myriapods, Araneae, Carabidae and Coleoptera in general. These results indicate that: (1) Staphylinidae react in the opposite way to the environmental conditions that influence species richness in Formicidae, Tenebrionidae, Insecta and ground-dwelling arthropods in general, and (2) Myriapods, Araneae, Carabidae and Coleoptera in general form two distinct broad communities of species associated with lower and higher elevation habitats possibly as a result of complex responses to multiple environmental factors.

In our system we found higher average temperature to be positively associated with species richness for most groups. This is consistent with the oft-cited ambient energy hypothesis that predicts regions with higher average temperatures tend to have more available energy for organisms and therefore support a greater number of species. Indeed, the ambient energy hypothesis is considered by many to be the best explanation for patterns in species richness at broader and more ecologically inclusive taxonomic levels (Buckley et al. 2010; Hurlbert and Stegen 2014, Peters et al. 2016). We discovered one exception to this trend for Staphylinidae, for which colder average temperatures were associated with higher species richness, which could explain their increasing diversity with increasing elevation. These findings are consistent with other studies in which staphylinids have higher species richness in colder, more mesic environments (Dolson et al. 2021).

To be clear, our study does not attempt to identify causal mechanisms driving patterns of species richness, but rather attempts to determine which environmental factors are associated with species richness. The important distinction is that the actual drivers may only be correlated with the best environmental factors we identified. For example, primary productivity is known to correlate with average temperature (O'Brien 2006), and it may be that high primary productivity actually drives high species richness of ground dwelling arthropods, or a myriad of other factors that we did not test. Like almost all studies of this nature, what we are looking for in this study are the best proxies for predicting high species richness rather than the drivers of species richness.

Perhaps the most surprising and interesting result of our study was the numerous positive associations involving temperature range (Tables 2 and 3). We used temperature range as a proxy for the Rapoport's hypothesis, which predicts species richness will decline with increasing climatic variability due to the limited ability of specialists to cope with climatic fluctuations (Stevens 1992; Sanders 2002; Fernández and Vrba 2005; Fattorini 2014; Pintor et al. 2015). Based on this explanation, species richness should increase with declining climatic variability, as a more climatically stable environment should favor the persistence of both climatic specialists, adapted to this favorable condition, and climatic generalists (Stevens 1989, 1992). However, in our system we found the opposite to that predicted by Rapoport's rule. Elevations with greater temperature ranges (higher climatic variability) tended to have increased species richness (Table 3).

Measures of habitat heterogeneity and water availability were associated with variation in species richness in only a few groups (see Tables 1 and 2). Specifically, species richness in

Tenebrionidae and Myriapoda was positively associated with terrain ruggedness (topographic heterogeneity), while increased humidity was associated with higher species richness in Insecta. In particular, habitat heterogeneity, albeit supported, had a smaller effect size compared to average temperatures. This limited importance of habitat heterogeneity, compared to other factors, is not unusual. Previous studies have often found habitat heterogeneity to play a secondary role relative to climatic conditions in explaining species richness variation across different taxa (Field et al. 2009; Ramos et al. 2021). Since most studies that focused on habitat heterogeneity were conducted on vertebrates and in areas impacted by anthropogenic disturbance (Tews et al. 2004), our results contribute to understanding whether the secondary role of habitat heterogeneity applies to invertebrates and across different ecological systems.

The limited association between species richness and average humidity was an unexpected finding in our study. In general, mountain areas characterized by aridity at lower elevations may show a reduced species richness at lower elevations due to harsh conditions (Whittaker and Niering 1965, Brown and Lomolino 1998, Di Biase et al. 2021). In the Madrean Sky Island System, mountain ranges are surrounded by a “sea” of desert and thus species richness is expected to be negatively affected by extreme temperatures and water scarcity. For example, it has been observed that the breeding season of several taxa in this region is triggered by water availability during the monsoon season and winter rains (Phillips and Comus 2000). For this reason, we would have expected a central role of humidity to influence patterns of species richness. However, this was not the case. In our study, average humidity was associated with species richness when aggregating Insecta, but not when aggregating all ground-dwelling arthropods. However, precipitation was significantly positively associated with the species richness of ground-dwelling arthropods on the nearby Colorado Plateau of northern Arizona (Uhey et al. 2020). That study, however, is substantially different from ours in that it focused on higher elevation communities (between 1900 and 2200 m) that may be inhabited by species less adapted to arid conditions. The prevalence of xeric species adapted to the aridity of lower elevations on the Santa Catalina Mountains may explain our results. In particular, this might explain the negative association between Araneae and humidity in this system. Since spiders effectively cope with hot and dry climatic conditions (e.g., Cloudsley-Thompson, 1983), spider communities of the study area most likely include many species locally adapted to desert conditions (see Phillips and Comus 2000). Alternatively, the negative association between spiders and humidity may result from the periodical flooding occurring in this region during the monsoon season, since spiders are negatively affected by flooding (Uetz et al. 1979).

Our results show that species richness in different arthropod taxa is associated with different environmental factors, revealing the risk of drawing generalizations based on only one or a few taxa. Furthermore, although most taxa do show a positive relationship between species richness and average temperature, temperature range was also an important factor in predicting variation of species richness at broad taxonomic scale (i.e., ground-dwelling arthropods). As a result, our study suggests caution in generalizing responses of species richness across both narrow and broad taxonomic scales, as these responses may vary depending on the study system rather than representing a universal rule. Additionally, the unique responses observed for each group in this study underscore the importance of carefully selecting surrogate species when monitoring habitats in montane ecosystems.

While our study encompasses a broad range of taxa, it specifically focuses on the ground-dwelling arthropod fauna. As such, our findings may not be applicable to the entire arthropod community of the study area. For instance, although our research indicates that ground-dwelling spiders are negatively impacted by humidity, this may not hold true for the arboreal spider species in the region. Flooding associated with increased rainfall, as experienced during the monsoon season in our system (Lytle and White 2007), is a major challenge for desert species (Cloudsley-Thompson, 1983) and was found to negatively affect ground dwelling spider diversity (Uetz et al. 1979), but arboreal species might not be as affected.

Finally, the unexpected association between climatic variability and species diversity in our system is worth investigating further. Studies aimed at testing Rapoport's hypothesis often involve examining the relationship between species' elevational range (which is assumed to reflect the breadth of their climatic niche of the species) and elevation, with no direct analysis of climatic variability (Pintor et al. 2015). As climatic variability generally increases with elevation (Stevens 1989, Stevens 1992), it would offer a mechanistic explanation for Rapoport's hypothesis. Future studies investigating this relationship in the Santa Catalina Mountains could provide insights into the surprisingly frequent positive association between climatic variability and species richness in this system.

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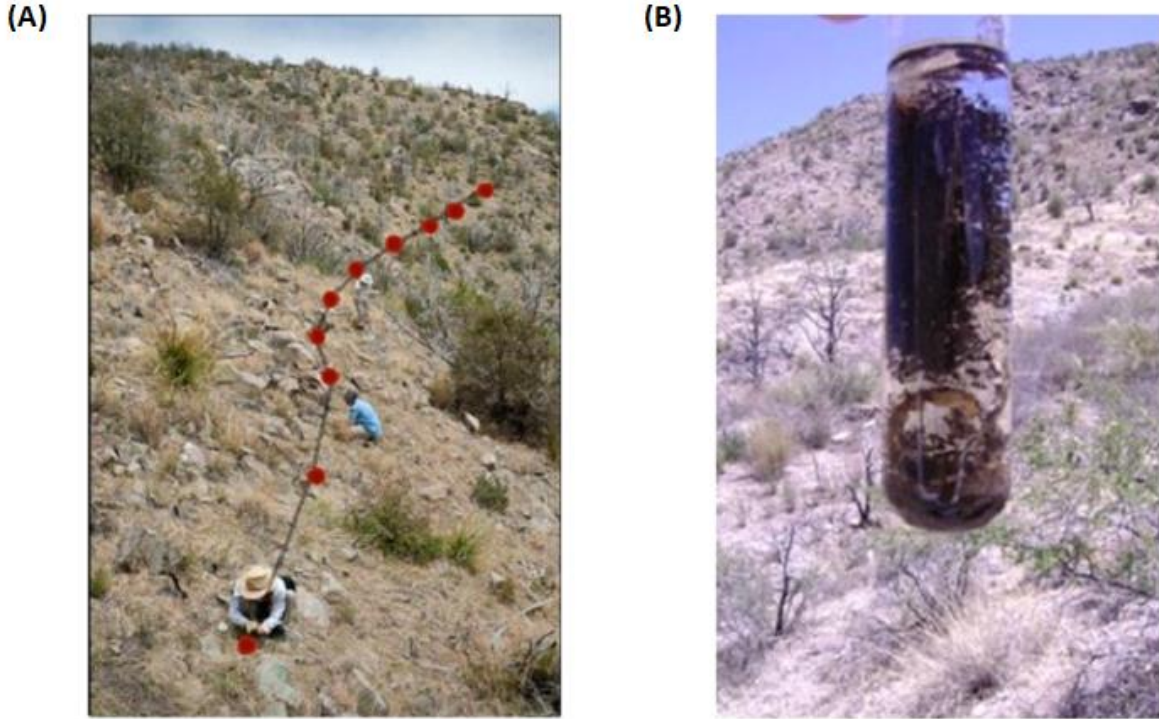
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**Supplementary Materials**

**Figure S1.** A, one 100 m transect established for this study. Red dots indicate the approximate location of a single pitfall trap. One trap was set every 10 m along the transect. B, one pitfall trap half filled with propylene glycol the yield of arthropods at the end of a two-week sampling period.



**Table S1.** Sampling effort for different sampling units. In this study, species richness for each site was calculated as the cumulative yield of all traps per transect across both sampling seasons. The number of traps that were used in this study after removing traps destroyed or flooded are in brackets.

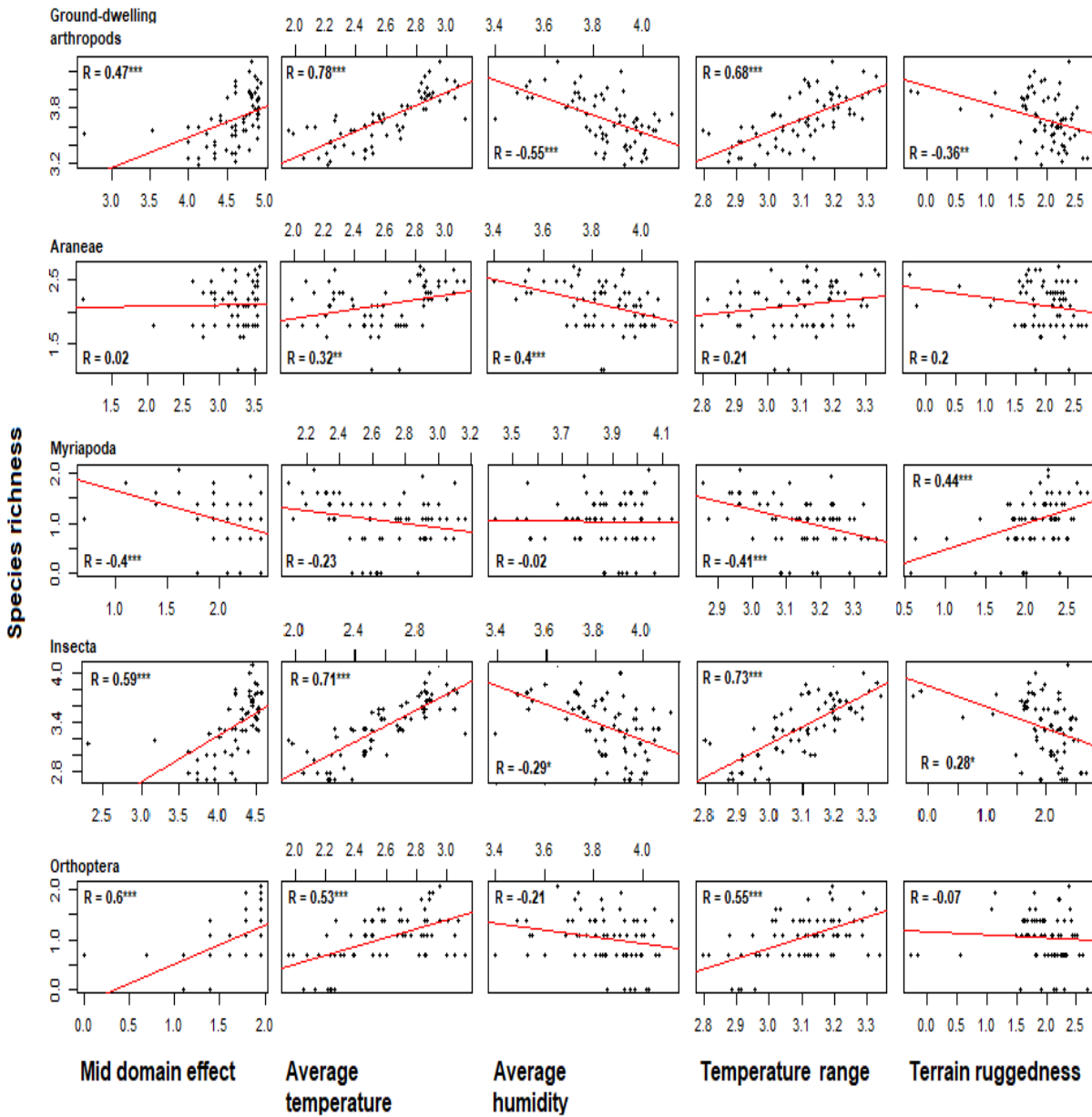
	<b>Pre-monsoon</b> May 5-19, 2011	<b>Post-monsoon</b> September 1-15, 2011	<b>Total</b>
Number of 100 m transects with 10 traps each	66	66	132
Total number of traps	660 [648]	660 [609]	1320 [1257]

**Table S2. Formicidae - species list**

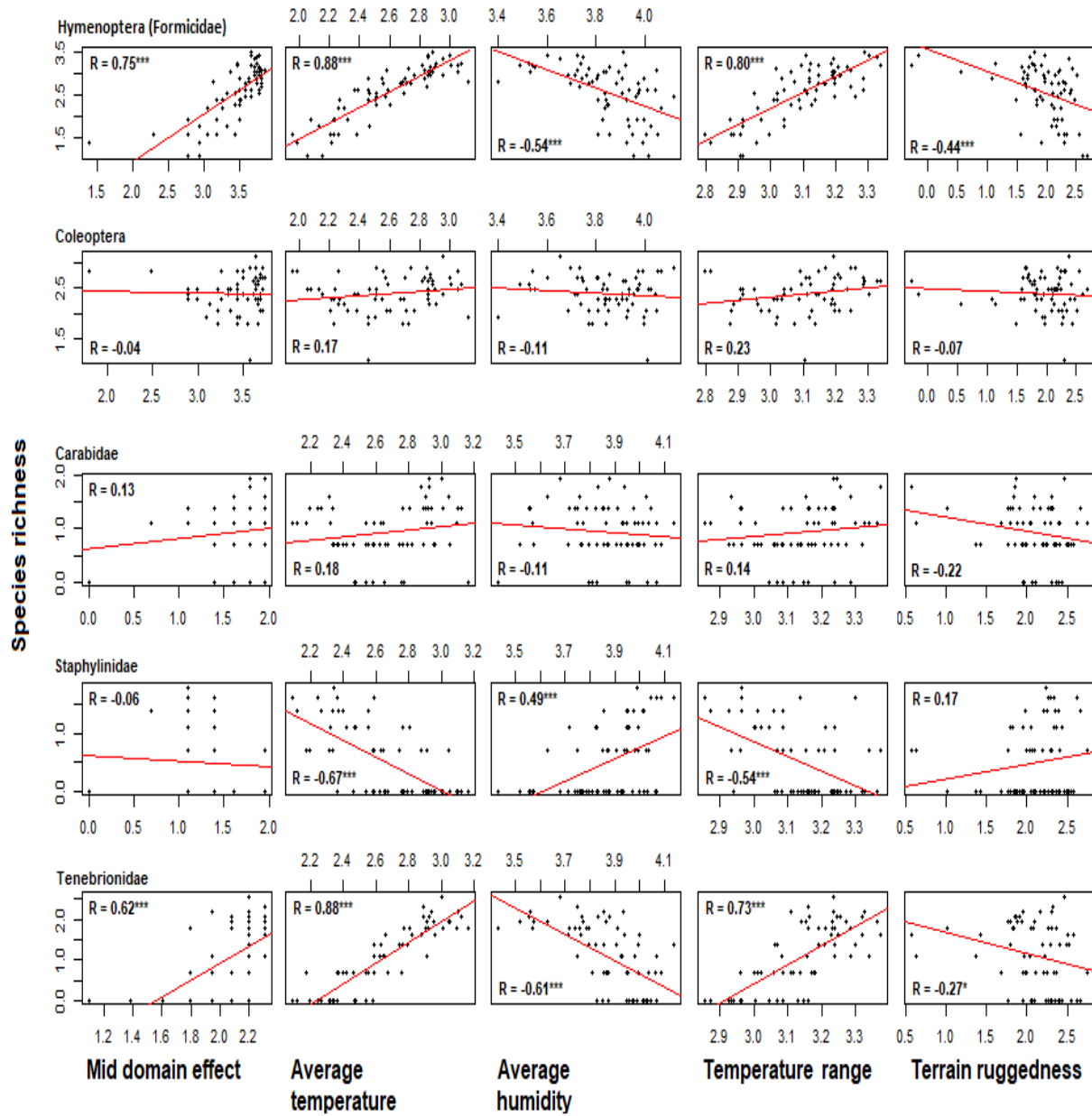
<i>Aphaenogaster_albisetosa</i>	<i>Lasius_pallitarsus</i>	<i>Pheidole_sp7</i>
<i>Aphaenogaster_punctaticeps</i>	<i>Lasius_sitiens</i>	<i>Pheidole_sp8</i>
<i>Aphaenogaster_texana</i>	<i>Lasius_subumbratus</i>	<i>Pheidole_sp9</i>

<i>Brachymyrmex_depilis</i>	<i>Leptothorax_sp1</i>	<i>Pheidole_sp10</i>
<i>Camponotus_festinus</i>	<i>Liometopum_apiculatum</i>	<i>Pheidole_sp12</i>
<i>Camponotus_fragilis</i>	<i>Liometopum_luctuosum</i>	<i>Pheidole_sp 13</i>
<i>Camponotus_mina</i>	<i>Monomorium_spp</i>	<i>Pheidole_titanus</i>
<i>Camponotus_modoc</i>	<i>Myrmecocystus_mendax</i>	<i>Pheidole_xerophila</i>
<i>Camponotus_ocreatus</i>	<i>Myrmecocystus_mexicanus</i>	<i>Pogonomyrmex_apache</i>
<i>Camponotus_sp1</i>	<i>Myrmecocystus_mimcus</i>	<i>Pogonomyrmex_barbatus</i>
<i>Camponotus_cf_sansabeanus</i>	<i>Myrmecocystus_navajo</i>	<i>Pogonomyrmex_desertorum</i>
<i>Camponotus_vafer</i>	<i>Myrmecocystus_placodops</i>	<i>Pogonomyrmex_huachucanus</i>
<i>Camponotus_vicinus</i>	<i>Myrmica_az02</i>	<i>Pogonomyrmex_imberbicus</i>
<i>Crematogaster_browni</i>	<i>Myrmica_striolagaster</i>	<i>Pogonomyrmex_pima</i>
<i>Crematogaster_colei</i>	<i>Myrmica_sp1</i>	<i>Polyergus_breviceps</i>
<i>Crematogaster_dentinodis</i>	<i>Myrmica_tahoensis</i>	<i>Prenolepis_imparis</i>
<i>Crematogaster_depilis</i>	<i>Myrmica_wheeleri</i>	<i>Solenopsis_amblychila</i>
<i>Crematogaster_emeryana</i>	<i>Neivamyrmex_nigrescens</i>	<i>Solenopsis_aurea</i>
<i>Crematogaster_isolata</i>	<i>Neivamyrmex_opacithorax</i>	<i>Solenopsis_spp</i>
<i>Crematogaster_opuntiae</i>	<i>Neivamyrmex_texanus</i>	<i>Solenopsis_xyloni</i>
<i>Crematogaster_smithi</i>	<i>Nylanderia_terricola</i>	<i>Stenamma_californicum</i>
<i>Crematogaster_torosa</i>	<i>Nylanderia_vividula</i>	<i>Stenamma_chiricahua</i>
<i>Cyphomyrmex_flavidus</i>	<i>Odonotmachus_clarus</i>	<i>Stenamma_huachucanum</i>
<i>Cyphomyrmex_wheeleri</i>	<i>Pheidole_bicarinata</i>	<i>Stenamma_snellingi</i>
<i>Dorymyrmex_bicolor</i>	<i>Pheidole_cerebrosior</i>	<i>Strumagenys_sp1</i>
<i>Dorymyrmex_az02</i>	<i>Pheidole_desertorum</i>	<i>Strumagenys_sp2</i>
<i>Dorymyrmex_az03</i>	<i>Pheidole_diversipilosa</i>	<i>Tapinoma_sessile</i>
<i>Dorymyrmex_insanus</i>	<i>Pheidole_gilvescens</i>	<i>Temnothorax_andrei</i>
<i>Forelius_mccooki</i>	<i>Pheidole_hyatti</i>	<i>Temnothorax_neomexicanus</i>
<i>Forelius_pruinosus</i>	<i>Pheidole_marcidula</i>	<i>Temnothorax_pergandei</i>
<i>Formica_aserva</i>	<i>Pheidole_obtusospinosa</i>	<i>Temnothorax_nitens</i>
<i>Formica_densiventris</i>	<i>Pheidole_rhea</i>	<i>Temnothorax_rugulatus</i>
<i>Formica_gnava</i>	<i>Pheidole_sciophila</i>	<i>Temnothorax_sp1</i>
<i>Formica_neogagates</i>	<i>Pheidole_spadonia</i>	<i>Tetramorium_hispidum</i>
<i>Formica_occulta</i>	<i>Pheidole_peripilosa</i>	<i>Tetramorium_spinosum</i>
<i>Formica_az04</i>	<i>Pheidole_sp2</i>	<i>Trachymyrmex_arizonensis</i>
<i>Hypoconerops_opacior</i>	<i>Pheidole_sp3</i>	<i>Trachymyrmex_desertorum</i>
<i>Hypoconerops_sp1</i>	<i>Pheidole_sp4</i>	
<i>Lasius_alienus</i>	<i>Pheidole_sp5</i>	
<i>Lasius_az01</i>	<i>Pheidole_sp6</i>	

**Figure S2.** Linear regression models describing the relationship between the natural logarithm of species richness for ground-dwelling arthropods as a whole, Myriapoda, Insecta, Araneae, and Orthoptera and the natural logarithm of the environmental factors. For each relationship Pearson correlation coefficient ( $r$ ) and significance ( $p < 0.001$  ‘\*\*\*’,  $p < 0.01$  ‘\*\*’,  $p < 0.5$  ‘\*’) are reported.



**Figure S3.** Linear regression models describing the relationship between the natural logarithm of species richness for Formicidae, Coleoptera, Staphylinidae, Carabidae, and Tenebrionidae the natural logarithm of the environmental factors. For each relationship Pearson correlation coefficient ( $r$ ) and significance ( $p < 0.001$  ‘\*\*\*’,  $p < 0.01$  ‘\*\*’,  $p < 0.5$  ‘\*’) are reported.



**Table S3.** Conditional average estimates from multi-model inference. MDE = mid-domain effect, T\_mean = Average temperature, H\_mean = Average humidity, T\_range = Temperature range, TRI = Terrain ruggedness

Ground-dwelling arthropods					
	Estimate	SE	Adj. SE	z value	Pr(> z )
(Intercept)	0.32391	0.85049	0.86414	0.375	0.70778
MDE	-0.2125	0.08538	0.08703	2.442	0.01462 *
T_mean	0.69486	0.15935	0.16194	4.291	1.78E-05 ***
H_mean	0.23159	0.26112	0.2664	0.869	0.38467
T_range	0.72652	0.26651	0.27169	2.674	0.00749 **

Araneae					
	Estimate	SE	Adj. SE	z value	Pr(> z )
(Intercept)	4.72664	1.95991	1.97417	2.394	0.01665 *
MDE	-0.21684	0.15932	0.16133	1.344	0.17892
T_mean	0.66993	0.1813	0.18485	3.624	0.00029 ***
H_mean	-0.88949	0.26638	0.27149	3.276	0.00105 **
T_range	0.57536	0.48061	0.48725	1.181	0.23767
TRI	-0.10253	0.07711	0.0786	1.304	0.19207

Myriapoda					
	Estimate	SE	Adj. SE	z value	Pr(> z )
(Intercept)	1.4749	1.3027	1.315	1.122	0.26205
MDE	-0.3964	0.1535	0.1562	2.537	0.01118 *
T_mean	0.2734	0.2484	0.2534	1.079	0.28057
H_mean	-0.453	0.3563	0.3634	1.247	0.21248
TRI	0.3458	0.1064	0.1085	3.186	0.00144 **

Insecta					
	Estimate	SE	Adj. SE	z value	Pr(> z )
(Intercept)	-3.0054	1.5755	1.5915	1.888	0.05896 .
H_mean	0.6211	0.3011	0.3072	2.022	0.04322 *
MDE	-0.2241	0.106	0.1081	2.072	0.03823 *
T_mean	0.9692	0.2993	0.3021	3.208	0.00134 **
T_range	0.9177	0.3092	0.3153	2.91	0.00361 **

Orthoptera					
	Estimate	SE	Adj. SE	z value	Pr(> z )
(Intercept)	-5.6351	3.8454	3.8711	1.456	0.1455
MDE	0.4797	0.238	0.2413	1.988	0.0468 *
T_mean	0.978	0.5852	0.5899	1.658	0.0973 .
H_mean	1.2159	0.6224	0.6325	1.922	0.0546 .
T_range	1.0781	0.652	0.6635	1.625	0.1042
TRI	0.1961	0.1029	0.1049	1.869	0.0617 .

Hymenoptera (Formicidae)					
	Estimate	SE	Adj. SE	z value	Pr(> z )
(Intercept)	-6.05359	2.02042	2.04239	2.964	0.00304 **
MDE	0.20881	0.12899	0.13141	1.589	0.11206
T_mean	1.51935	0.34222	0.34585	4.393	0.0000112 ***
H_mean	0.64332	0.40363	0.41125	1.564	0.11775
T_range	1.01197	0.46654	0.47434	2.133	0.03289 *
TRI	-0.10291	0.06943	0.07077	1.454	0.14591

Coleoptera					
	Estimate	SE	Adj. SE	z value	Pr(> z )
(Intercept)	-0.6521	1.17171	1.19344	0.546	0.58479
MDE	-0.50151	0.18836	0.19199	2.612	0.009 **
T_mean	0.20844	0.21514	0.21942	0.95	0.34214
T_range	1.48353	0.50548	0.51483	2.882	0.00396 **
TRI	0.05472	0.08805	0.08981	0.609	0.5423

Carabidae					
	Estimate	SE	Adj. SE	z value	Pr(> z )
(Intercept)	1.122	0.8802	0.8897	1.261	0.207
MDE	0.1185	0.1904	0.1941	0.61	0.542
T_mean	0.238	0.2181	0.2221	1.071	0.284
H_mean	-0.2628	0.3981	0.4059	0.647	0.517
TRI	-0.1966	0.1182	0.1204	1.632	0.103

Staphylinidae					
	Estimate	SE	Adj. SE	z value	Pr(> z )
(Intercept)	4.51675	1.25384	1.26902	3.559	0.000372 ***
MDE	-0.09734	0.13308	0.13568	0.717	0.473145
T_mean	-1.30214	0.23175	0.23572	5.524	< 2e-16 ***
T_range	-0.61148	0.66687	0.67931	0.9	0.368037
TRI	-0.13709	0.11654	0.11875	1.154	0.248323

Tenebrionidae					
	Estimate	SE	Adj. SE	z value	Pr(> z )
(Intercept)	-10.2188	2.41721	2.44769	4.175	2.98E-05 ***
MDE	-0.38179	0.27439	0.27951	1.366	0.172
T_mean	2.18048	0.37849	0.38326	5.689	1.00E-08 ***
H_mean	0.75875	0.60478	0.61723	1.229	0.219
T_range	1.61789	0.61664	0.62826	2.575	0.01 *
TRI	0.21379	0.0978	0.09976	2.143	0.0321 *



**Table S4.** Models included in the multi-model conditional average for each taxonomic group. The combination of factors included for each model is provided in the first column for each group. Environmental factors are coded based on the numbers in “Environmental predictor term code”. For each model, number of parameters (df), log-likelihood (logLik), delta AICc (delta), and the probability of the model being the best model (weight) are provided.

Environmental predictor term code	
Average humidity	1
Mid domain effect	2
Average temperature	3
Temperature range	4
Terrain ruggedness	5

Ground-dwelling arthropods					
	df	logLik	AICc	delta	weight
234	5	28.19	-45.37	0	0.69
1234	6	28.61	-43.79	1.58	0.31

Araneae					
	df	logLik	AICc	delta	weight
1	3	-17.92	42.23	0	0.23
124	5	-15.94	42.89	0.66	0.16
15	4	-17.12	42.9	0.67	0.16
23	4	-17.23	43.12	0.89	0.15
12	4	-17.57	43.8	1.57	0.1
125	5	-16.4	43.8	1.57	0.1
14	4	-17.67	43.99	1.76	0.09

Myriapoda					
	df	logLik	AICc	delta	weight
25	4	-37.35	83.35	0	0.43
125	5	-36.5	84	0.65	0.31
235	5	-36.71	84.42	1.07	0.25

Insecta					
	df	logLik	AICc	delta	weight
1234	6	19.31	-25.21	0	0.69
34	4	16.12	-23.59	1.61	0.31

Orthoptera					
	df	logLik	AICc	delta	weight
245	5	-28.73	68.47	0	0.17
1235	6	-27.82	69.07	0.6	0.13
135	5	-29.12	69.24	0.77	0.12
24	4	-30.45	69.56	1.09	0.1
1345	6	-28.09	69.61	1.14	0.1
123	5	-29.48	69.97	1.5	0.08
2345	6	-28.28	69.98	1.51	0.08
12345	7	-27.13	70.2	1.73	0.07
2	3	-31.95	70.29	1.82	0.07
23	4	-30.84	70.34	1.88	0.07

Formicidae					
	df	logLik	AICc	delta	weight
134	5	-1.88	14.76	0	0.18
2345	6	-0.77	14.96	0.2	0.17
234	5	-2.05	15.11	0.35	0.15
1345	6	-1.08	15.57	0.81	0.12
1234	6	-1.17	15.76	1	0.11
12345	7	-0.05	16.02	1.26	0.1
34	4	-3.82	16.29	1.52	0.09
1235	6	-1.45	16.33	1.57	0.08

Coleoptera					
	df	logLik	AICc	delta	weight
24	4	-18.83	46.32	0	0.53
234	5	-18.34	47.67	1.35	0.27
245	5	-18.63	48.26	1.93	0.2

Carabidae					
	df	logLik	AICc	delta	weight
5	3	-45.79	97.98	0	0.3
(Null)	2	-47.48	99.15	1.18	0.17
3	3	-46.46	99.31	1.34	0.15
35	4	-45.44	99.53	1.56	0.14
15	4	-45.57	99.79	1.81	0.12
25	4	-45.59	99.84	1.86	0.12

Staphylinidae					
	df	logLik	AICc	delta	weight
3	3	-39.73	85.84	0	0.36
35	4	-39.14	86.94	1.09	0.21
34	4	-39.45	87.55	1.7	0.15
23	4	-39.45	87.56	1.71	0.15
345	5	-38.42	87.84	1.99	0.13

Tenebrionidae					
	df	logLik	AICc	delta	weight
345	5	-25.76	62.52	0	0.46
2345	6	-24.91	63.23	0.71	0.32
12345	7	-24.05	64.03	1.51	0.22

## APPENDIX B

### RELATIONSHIPS BETWEEN CLIMATIC VARIABILITY, SPECIES RANGE EXTENT AND SPECIES RICHNESS ARE INCONSISTENT WITH RAPOPORT'S RULE

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and editing (equal); Wendy Moore: Data curation (equal), Writing – review and editing (equal),  
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**Title:** Relationships between climatic variability, species range extent and species richness are inconsistent with Rapoport's rule

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## **ABSTRACT**

According to the climatic variability hypothesis, species range extent and distribution are determined by the climatic fluctuations a species can tolerate. Along gradients of climatic variability, species adapted to stable conditions are expected to have smaller range extents, as they may not survive in areas with greater climatic fluctuations. In contrast, species inhabiting more variable climates are predicted to have broader range extents, as they can tolerate both climatically variable and stable regions. Since climatic variability generally increases with elevation, species range extents are expected to increase with elevation, a pattern known as Rapoport's rule. Based on Rapoport's rule, species richness is also expected to decline with increasing climatic variability, and consequently with elevation, since climatic specialists are gradually filtered out at higher elevations. Here, we explored whether species range extents of different groups of ground-dwelling arthropods on the Santa Catalina Mountains vary along an elevational gradient in accordance with Rapoport's rule and the climatic variability hypothesis. Ground-dwelling arthropods were collected across 66 transects and climatic variability was quantified for each location as thermal variability. Elevational range extents were calculated for each species, as well as the maximum climatic variability experienced by each species at any given transect. Then, we examined how climatic variability varies with elevation and the relationship between species range extent and maximum climatic variability, as well as species range extent with elevation. Contrary to expectations, we found that climatic variability actually declined with increasing elevation in this system. While species range extent was generally positively associated with the maximum climatic variability experienced by each species, it did not covary with elevation. Moreover, species with small ranges were not restricted to climatically stable environments, and instead occurred throughout the elevational gradient. These results suggest that while species in more climatically unstable environments tend to have broader ranges, species with small ranges are distributed across the entire gradient. As a result, variation in species range and variation in species richness are decoupled: an average increase in species extent does not imply that communities in more instable environments are simply subsets of those in more stable environments. In fact, we found that specialists (species with small ranges) are not concentrated in climatically stable environments. These results suggest that climatic variability favor species with broader ranges as they are more tolerant, but species with small ranges may occur throughout, possibly because their niches are restricted by non-climatic factors (e.g., biotic interactions).

**KEYWORDS:** Climatic variability, Rapoport's rule, elevation, species range extent

## 1 | INTRODUCTION

Understanding the variation in species range extent and its drivers along elevational gradients has been a central focus in ecology and conservation for over three decades (Stevens 1992, McCain and Knight 2013, Pintor et al. 2015). In mountainous regions, which are home to diverse species and high levels of endemism, species range extent has been a key metric for studying ecological patterns and assessing conservation risks (Fattorini et al. 2020). For example, the relationship between species range extent and climatic factors offers valuable insights into species climatic niche breadths and their potential responses to climate change (Wiens et al. 2010, McCain and Knight 2013). Furthermore, range extent serves as an important indicator of extinction vulnerability, particularly for endemic species with small distributions (McCain and Colwell 2011, Wang et al. 2023).

Based on the climatic variability hypothesis, the range extent of a species along an elevational gradient depends on changes in climatic variability (Janzen 1967, Stevens 1989, 1992). Regions characterized by higher climatic variability will select for species that can withstand a wide range of climatic conditions (i.e., climatic generalists) and can inhabit both climatically stable and climatically unstable areas. On the other hand, climatically stable regions will host climatic specialists that are locally adapted to these conditions, as well as climatic generalists (Pintor et al. 2015). If this scenario is supported, two outcomes are expected along a climatic variability gradient. First, since climatic specialists are constrained to regions with lower climatic variability and climatic generalists can inhabit a wide variety of conditions, species range extents should be wider in climatic generalists than in specialists (Stevens 1989). Second, species range extents should increase with increasing climatic variability as climatic variable regions are exclusively inhabited by climatic generalists with wide range extents (Stevens 1989).

Climatic variability is usually expected to increase with increasing elevation (Stevens 1992). As a result, species range extents are expected to increase with increasing elevation, in accordance with the climatic variability hypothesis (Stevens 1992). This pattern, which suggests broader species ranges at higher elevations, is also known as Rapoport's rule (Stevens 1989, 1992). Rapoport's rule further posits that as climatic specialists are progressively filtered out by the harsher conditions at higher elevations, species diversity should decline along the climatic variability gradient (Stevens 1989, 1992). This elevational pattern in species range extent and diversity has been observed across various terrestrial and aquatic taxa, such as insects, arachnids, gastropods, fungi, and plants (Sanders 2002, Almeida-Neto et al. 2006, Hausdorf 2006, Risba and Schroeder 2006, Ogwu et al. 2019, Chen et al. 2022, Schifani et al. 2024). However, various studies have also highlighted the limitations of Rapoport's rule, suggesting that it is not a universally applicable pattern (McCain and Knight 2013). In some cases, for instance, species range extents do not increase with increasing elevation, even when species diversity declines along the same gradient (Risba and Schroeder 2006, McCain and Knight 2013, Feng et al. 2016, Macek et al. 2021).

In other cases, species range extent increases with elevation, but this pattern is not always accompanied by the expected unimodal decline in species diversity along the same gradient (e.g., Sanders 2002, Zhou et al. 2019). These empirical findings are particularly interesting, as they suggest that while climatic variability may still influence the distribution of climatic specialists

and the extent of their ranges, the corollary proposed by Rapoport’s rule (i.e., that species diversity declines with increasing elevation due to a climatic variability gradient) may not be a universal consequence of this distribution. Thus, elevational variation in species ranges and richness may be decoupled. Moreover, relatively few studies have quantified climatic variability along elevational gradients (Pintor et al. 2015), making it difficult to evaluate this scenario and determine if climatic variability might influence distribution and extent of species ranges without producing a decline in species richness along the same gradient.

On the Santa Catalina Mountains, part of the Madrean Sky Island Archipelago and biodiversity hotspot (Moore et al. 2013), climatic variability (temperature range) has been found to be an important factor correlated with species richness of a diverse assemblage of ground-dwelling arthropods (Bergamaschi et al. A). These included Formicidae (Hymenoptera), Tenebrionidae (Coleoptera), all Coleoptera, Insecta (including Formicidae, Coleoptera, Orthoptera), and different ground-dwelling arthropods as a whole (including Formicidae, Coleoptera, Orthoptera, Araneae, and Myriapoda) (Bergamaschi et al. in prep). However, contrary to the predictions of Rapoport’s rule (Stevens 1989), species richness increases with increasing climatic variability (Bergamaschi et al. in prep). Since species ranges and richness may be decoupled (e.g., Sanders 2002, Zhou et al. 2019), it is still possible that climatic variability acts on species ranges as postulated by Rapoport’s rule, even when species diversity does not vary according to this rule.

In this study, we examine the putative influence of climatic variability on species range extents in ground-dwelling arthropods along the elevational gradient of the Santa Catalina Mountains. We begin by exploring the classical expectation that climatic variability (measured as temperature range) increases with elevation. Next, we investigate the potential role of climatic variability in shaping species distributions and extent of species ranges by estimating the association between maximum climatic variability experienced by each species and their range extents. In this context, we explore two key questions: (1) whether climatic variability influences species range extent and distribution, even when species diversity does not seem to follow Rapoport’s rule, and (2) whether other ecological processes might be distinctly associated with the variation in species range extent along this gradient.

## 2 | METHODS

### 2.1 | Quantitative sampling and specimen processing

We use the extensive quantitative dataset of ground-dwelling arthropods previously described and analyzed in Meyer et al. (2015) and Bergamaschi et al. (in prep). In this study, we explore five groups in which Bergamaschi et al. (in prep) found species richness to be positively associated with climatic variability (Table 1).

Table 1. Taxon group names, composition, and species richness of the five groups analyzed in this study. Groups are listed from most to least inclusive, such that each group includes taxa nested underneath them. These five groups are the subset of taxa for which species richness was positively associated with temperature range (climatic variability) in Bergamaschi et al. (in prep).

1	All ground-dwelling arthropods	449
-	Araneae	101

-	Myriapoda	16
2	Insecta	332
-	Orthoptera	25
3	Formicidae (Hymenoptera)	117
4	Coleoptera (3 families below + 107 other spp.)	190
-	Carabidae	21
-	Staphylinidae	25
5	Tenebrionidae	37

## 2.2 | Species range extent

To determine the extent of species ranges, the elevational gradient was divided into 36 vertical bands 50 meters wide, spanning from 1000 to 2800 meters (i.e., 1000-1050 m, 1050-1100 m, etc.). Data from sampling sites belonging to the same band were pooled. Then, the extent of each species' range was calculated as the difference between the maximum elevation of the highest band and the minimum elevation of the lowest band where the species was found. Consequently, species ranges varied from a minimum of 50 meters (difference between two adjacent bands) to a maximum of 1800 meters (difference between the highest and the lowest bands of the gradient).

## 2.3 | Estimating the climatic tolerance of a species

As described in Bergamaschi et al. (in prep), we estimated climatic variability of each transect as the mean ground temperature differences between the warmest and coldest month measured between May 7<sup>th</sup> (2011) and May 6<sup>th</sup> (2012). We then used a method developed by Pintor et al. 2015 to estimate maximum annual variability to evaluate the climatic tolerance of each species. First, we identified all the transects from which a given species was collected. Then, we chose the climatic variability value of the most variable transect and used that value as the estimate of the climatic tolerance for that species. For instance, if a species occurred in three different transects, we used the climatic variability measure of the most variable transect as a measure of climatic tolerance for that species. This value served as our measure of maximum climatic variability, similar to the maximum annual variability used in Pintor et al. (2015).

## 2.3 | Climatic variability vs Elevation

Before testing the climatic variability hypothesis, we investigated the variation of climatic variability along the elevational gradients. We used the Pearson correlation coefficient to evaluate the relationship between climatic variability and elevation.

## 2.4 | Analyses

### *Species range extent*

We investigated the variation in mean species range extent across elevational bands by using a method proposed by Stevens (Stevens 1989). This method is often used to explore patterns of variation in species range across elevational gradients (Stevens 1989, 1992, McCain and Knight 2013, Pintor et al. 2015, Mumladze et al. 2017, Zhou et al. 2019). As climatic variability

typically increases with elevation, according to Rapoport's rule, the mean range extent is also expected to increase, as climatic specialists are gradually filtered out by unstable conditions.

We calculated the mean and standard deviation of species range extents for each of our five taxonomic groups for each elevational band. Then, we looked for a correlation between mean species range extent and elevation using Spearman correlation coefficient.

### *Climatic variability*

To investigate the climatic variability hypothesis, we began by examining its fundamental assumption for which the extent of a species range increases with the maximum climatic variability it experiences. In particular, we explored the association between mean maximum climatic variability per range extent and species range extent in all five groups using Spearman's rank correlation coefficient.

Then we explored whether (1) species with narrower range extents are more frequently found in more climatically stable areas than expected by chance alone, and (2) larger range extents are inherently more likely to include regions with greater climatic fluctuations (Pintor 2015). We compared the observed maximum climatic variability measures for each species with those expected based on a random distribution of species range extents across the climatic variability gradient.

We did so by using a method like that proposed by Pintor et al. (2015). First, for each species, we counted the number of transects where it occurred. Then, we randomly re-sampled the same number of occurrences for each species along the entire climatic variability gradient (66 transects) and repeated this process 100 times to create a null distribution of climatic variability values. This approach simulated a scenario where species occurrences were not influenced by climatic variability but instead were randomly distributed along the elevational gradient of the Santa Catalina Mountains.

We then compared the observed maximum climatic variability for each species to the null distribution, and the proportion of null values above the observed maximum was calculated. We hypothesized that species with narrow range extents would tend to occur in more stable climates, resulting in a higher proportion of null values exceeding their observed maximum climatic variability and that species with larger range extents would naturally show greater climatic variability by chance, leading to a lower proportion of null values exceeding their observed maximum. The relationship between the proportion of null values above the observed maximum and species range extent was analyzed using Spearman's rank correlation coefficient.

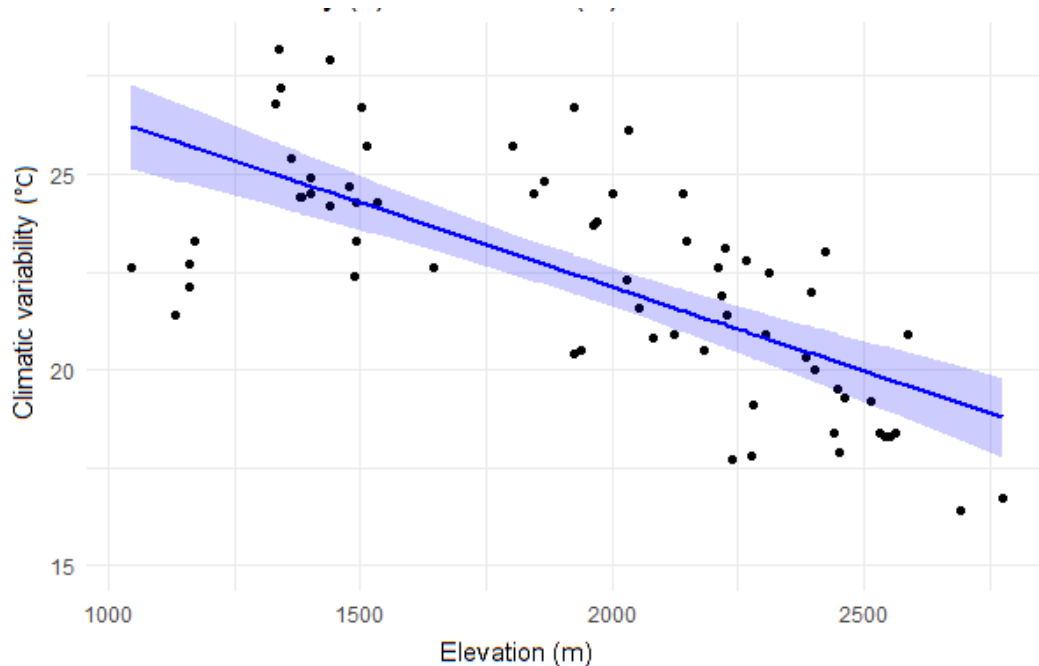
We also counted the total number of species with the smallest range extents (i.e., 50 m) and we calculated the proportion of species within this group whose observed maximum climatic variability was found to be  $\leq 95$  simulations out of 100 in our null distribution. Similar to Pintor et al. (2015), we reasoned that if most species with small range extents fell into this group, we could conclude that small ranged species are indeed distributed preferentially in more climatically stable areas, as predicted by the climatic variability hypothesis.

All analyses were separately carried out for Formicidae (Hymenoptera), Tenebrionidae (Coleoptera), Coleoptera, Insecta (including Formicidae, Coleoptera, Orthoptera), and all ground-dwelling arthropods (including Formicidae, Coleoptera, Orthoptera, Araneae, and Myriapoda). All analyses were conducted in R 4.4.2 with the R package ‘stats’ (R Core Team 2024).

### 3 | RESULTS

#### 3.1 | Climatic variability, species range extent and elevation

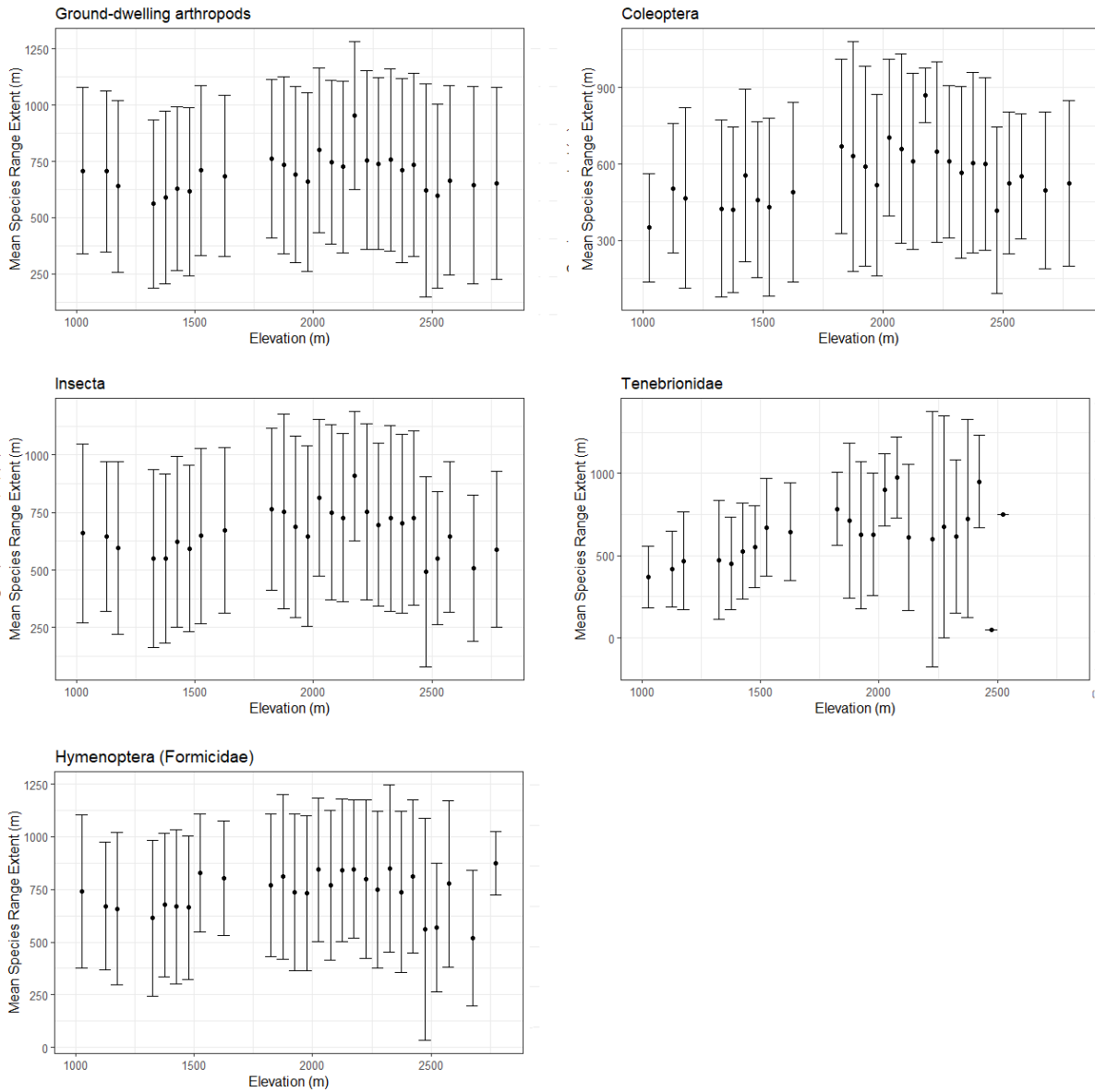
Temperature range declined with increasing elevation ( $r = -0.71$ ,  $p < 0.001$ , Figure 1). On the Santa Catalina Mountains, lower elevations experience higher annual temperature fluctuations than higher elevations (Figure 1).



**Figure 1.** Climatic variability (°C) calculated as the difference between the average temperature of the warmest and the coldest months, plotted against elevation (OLS regression,  $R^2 = 0.50$ ,  $p < 0.001$ ).

No clear relationship between mean species range extent (m) and elevation (m) was found in the majority of taxa (ground-dwelling arthropods:  $r_s = 0.17$ ,  $p = 0.403$ ; Insecta:  $r_s = 0.02$ ,  $p = 0.918$ ; Coleoptera:  $r_s = 0.34$ ,  $p = 0.082$ , and Formicidae:  $r_s = 0.22$ ,  $p = 0.268$ ) (Figure 2). Mean species range extent (m) was, however, positively correlated with elevation in Tenebrionidae ( $r_s = 0.52$ ,  $p = 0.01$ ). In this group, mean species range extent increased with increasing elevation across all gradient except for one elevational band: 2450-2500 m.

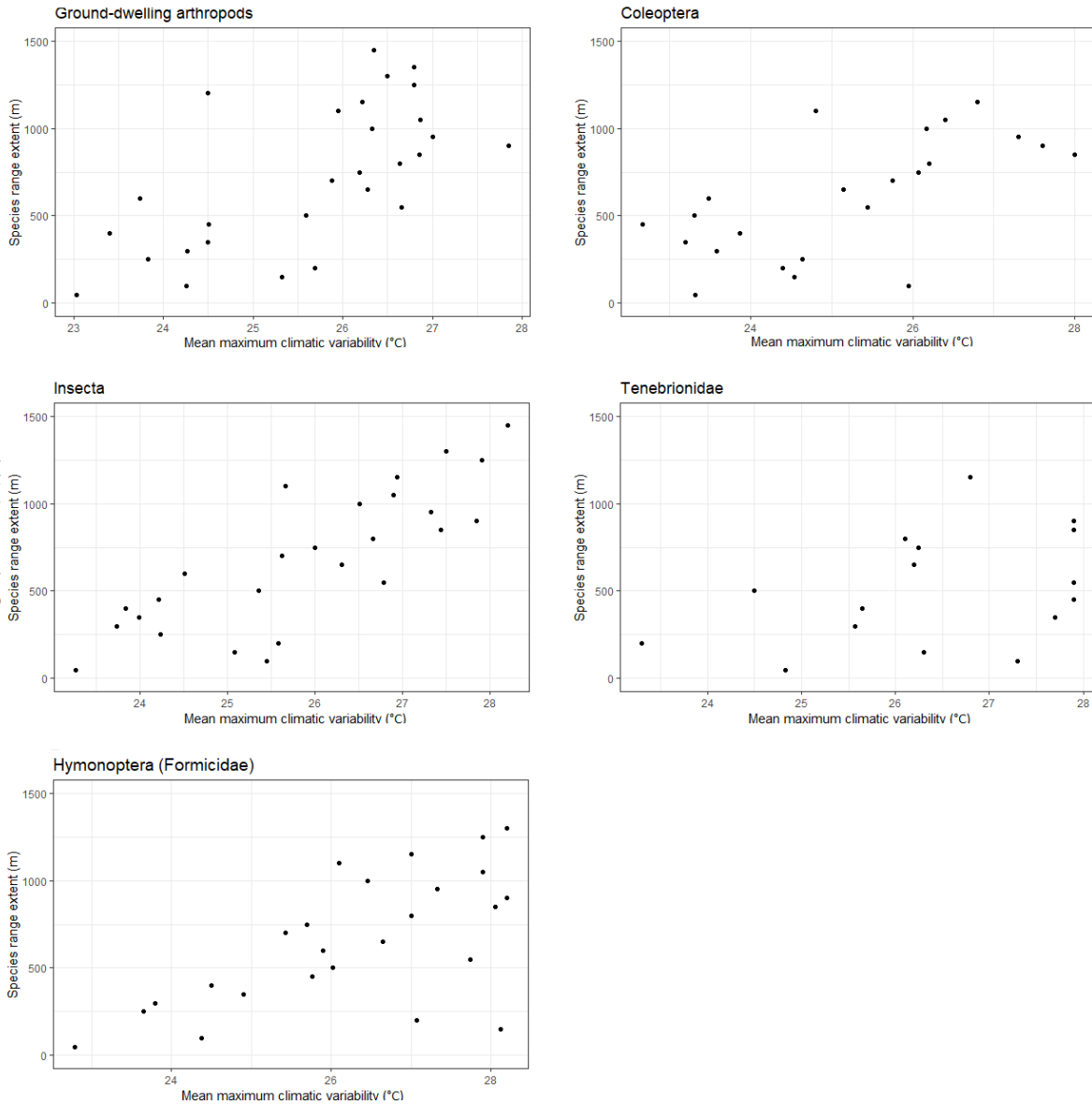




**Figure 2.** Mean species range extent (m) against elevation (m). A significantly ( $p < 0.05$ ) positive correlation (Spearman rank correlation coefficient) was found only for Tenebrionidae (see text). Whiskers indicate standard deviation. Except for Tenebrionidae ( $r_s = 0.52$ ,  $p = 0.01$ ), no significant association was found (ground-dwelling arthropods:  $r_s = 0.17$ ,  $p = 0.403$ ; Insecta:  $r_s = 0.02$ ,  $p = 0.918$ ; Coleoptera:  $r_s = 0.34$ ,  $p = 0.082$ ; and Formicidae:  $r_s = 0.22$ ,  $p = 0.268$ ).

### 3.2 | Mean maximum climatic variability and species range extent

Mean maximum climatic variability ( $^{\circ}\text{C}$ ) was correlated with variation of species range extent (m) across all groups except for Tenebrionidae (ground-dwelling arthropods:  $r_s = 0.58$ ,  $p < 0.001$ ; Insecta:  $r_s = 0.86$ ,  $p < 0.001$ ; Coleoptera:  $r_s = 0.68$ ,  $p < 0.001$ ; Tenebrionidae:  $r_s = 0.41$ ,  $p = 0.117$ ; and Formicidae:  $r_s = 0.64$ ,  $p < 0.001$ ) (Figure 3).

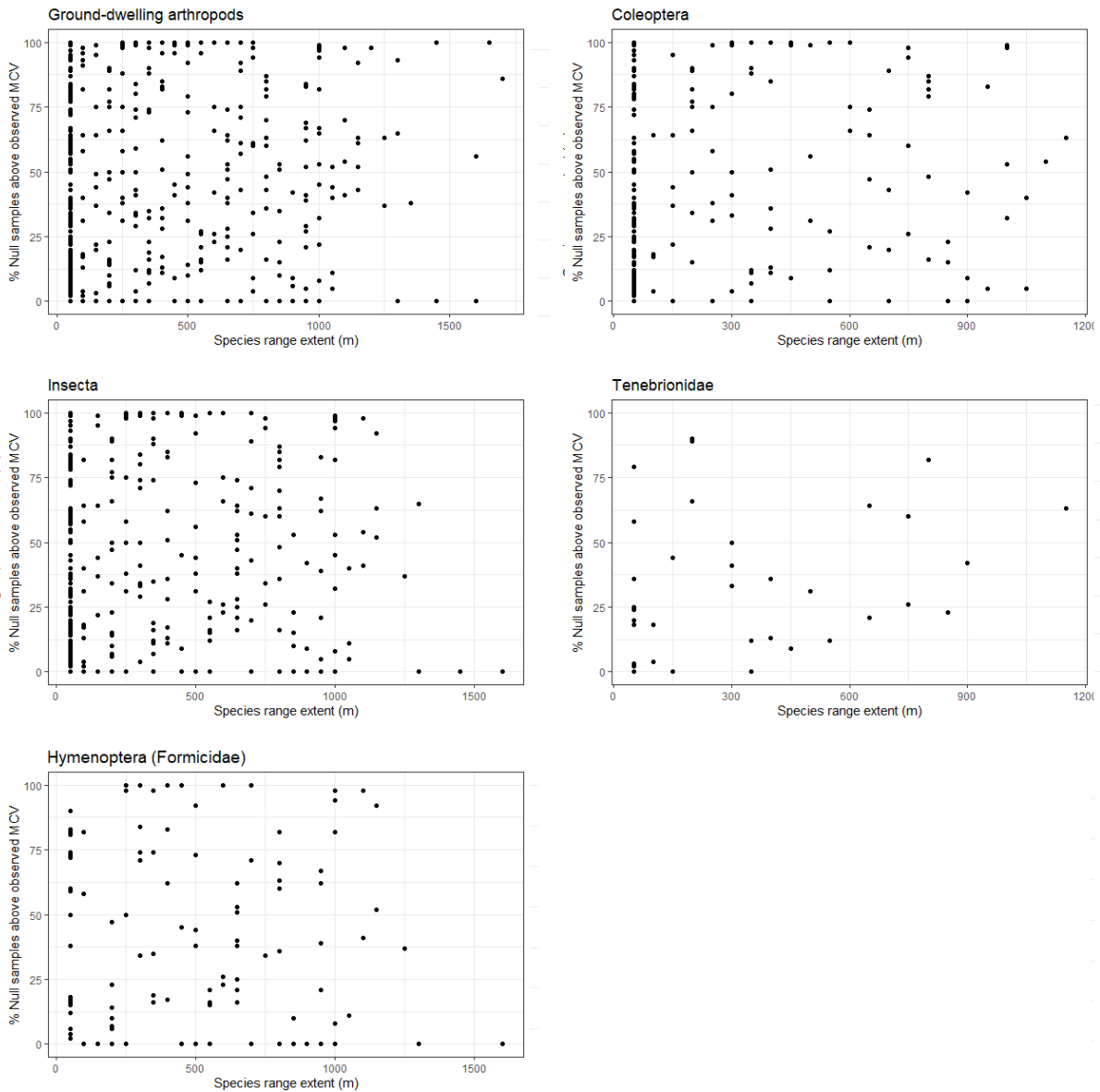


**Figure 3.** Mean maximum climatic variability ( $^{\circ}\text{C}$ ) based on elevational species range extent (m). The most variable climatic variability measure across all transects was recorded for each species and plotted against the species elevational range extent. Significantly ( $p < 0.05$ ) positive correlations (Spearman rank correlation coefficient) were found in all cases except for Tenebrionidae (ground-dwelling arthropods:  $r_s$

= 0.58,  $p < 0.001$ ; Insecta:  $r_s = 0.86$ ,  $p < 0.001$ ; Coleoptera:  $r_s = 0.68$ ,  $p < 0.001$ ; Tenebrionidae:  $r_s = 0.41$ ,  $p = 0.117$ ; and Formicidae:  $r_s = 0.64$ ,  $p < 0.001$ ).

### **3.3 | Species range extent and proportion of null values above observed maximum climatic variability**

No correlation was found between species range extent (m) and proportion of null values above observed maximum climatic variability measures in Formicidae (Formicidae  $r_s = -0.05$ ,  $p = 0.61$ ), Tenebrionidae ( $r_s = 0.28$ ,  $p = 0.097$ ), Insecta ( $r_s = 0.05$ ,  $p = 0.412$ ) and ground-dwelling arthropods ( $r_s = 0.06$ ,  $p = 0.205$ ) (Figure 3). In line with these findings, the majority of small ranged species in these groups did not occur in climatically most stable environments (ranging between 0 and 5%, Table 2). Contrary to our prediction that the proportion of null values in species with small ranges would be higher than in those with large ranges, we found a positive correlation between species range extent (m) and the proportion of null values exceeding the observed maximum climatic variability in Coleoptera ( $r_s = 0.16$ ,  $p = 0.027$ ). In line with this result and similar to the other groups, most species with narrow ranges were not located in climatically stable environments, with only 7% found in such areas (Table 1).



**Figure 4.** Species range extent (m) against % null values above the observed maximum climatic variability. This percentage represents the number of times that null maximum climatic variability was higher than the observed across 100 iterations in which occurrences for each species were randomly shuffled across transects. If smaller ranged species are preferentially found in climatic stable areas and larger ranged species are found in more climatic unstable areas by chance alone, the % of null values should decline from smaller to larger range extents. Significantly ( $p < 0.05$ ) positive correlations (Spearman rank correlation coefficient) were only found for Coleoptera (ground-dwelling arthropods:  $r_s = 0.06$ ,  $p = 0.205$ ; Insecta:  $r_s = 0.05$ ,  $p = 0.412$ ; Coleoptera:  $r_s = 0.16$ ,  $p = 0.027$ ; Tenebrionidae ( $r_s = 0.28$ ,  $p = 0.097$ ); and Formicidae  $r_s = -0.05$ ,  $p = 0.61$ ).

**Table 1.** The number of species with a narrow range extent (i.e., 50 m) whose observed maximum climatic variability was found to be  $\leq 95$  simulations out of 100 in our null model computation. If the majority of species with narrow ranges fell into this group, we can conclude that they are indeed distributed preferentially in more climatically stable areas as predicted by the climatic variability hypothesis (see Pintor et al. 2015).

Number of species with small range extents (50 m)

	Total number	# in climatically stable areas	% in climatically stable areas
Ground-dwelling arthropods	142	7	4.9
Insecta	114	6	5.3
Hymenoptera (Formicidae)	20	0	0.0
Coleoptera	86	6	7.0
Tenebrionidae	11	0	0.0

#### 4 | DISCUSSION

Contrary to the classical assumption that climatic variability increases with elevation (Stevens 1992), we found that lower elevations exhibit greater temperature fluctuations compared to higher elevations in the Santa Catalina Mountains.

Also, although we found a positive correlation between species range extent and maximum climatic variability in groups such as ground-dwelling arthropods, Insecta, Coleoptera, and Formicidae, we did not find a positive relationship between species mean range extent and elevation across most taxa. In contrast, for Tenebrionidae, the pattern was reversed: species range extent increased with elevation, but no significant relationship was found between maximum climatic variability and range extent in this group. When we accounted for random expectations using a null model, the observed deviations from the null distribution did not support the predictions of the climatic variability hypothesis. Only a few species were found in climatically more stable environments, while the majority presented different climatic niche breadth varying from climatically stable to unstable. Similarly, no clear association was found when comparing the deviation from the null maximum climatic variability distribution across smaller and larger ranged species. This latter result may explain why mean species range extent does not increase/decline with increasing elevation, as narrow ranged species are distributed throughout the elevational gradient.

Thus, our findings question the logic of Rapoport's rule: while variation in species extents increases with climatic instability (as postulated by Rapoport's rule), this does not translate into a

decrease in species richness (as predicted under Rapoport's rule) as previously observed in this system (Bergamaschi et al. in prep). In other words, although our data are consistent with the premises underlying Rapoport rules, they did not support the consequences of these premises.

This decoupling between the distribution of ranges and species richness originates from the behavior of species of restricted ranges, which, in contrast with the climatic variability hypothesis, are not confined to the most stable environments. Thus, climatic variability seems to act in a more complex way than expected: unstable environments may select for species with broader ranges, but species with small ranges are not confined to more climatically stable environments.

Elevation is often used as a proxy for climatic variation, since many climatic factors vary with elevation (Fattorini et al. 2022). For instance, temperature generally decreases predictably with elevation, making it a convenient covariate in studies where direct measurements of climatic variables are unavailable (Körner 2007, Longino et al. 2014). Similarly, as climatic variability is *a priori* assumed to increase with elevation (Stevens 1992, Pintor 2015), many studies have examined patterns of species range extent along elevation or their elevational midpoints without directly quantifying the underlying climatic variability gradient (Pintor et al. 2015).

Consequently, when species range extent has been found to increase with elevation, this has typically been attributed to the broader climatic niche breadth of high-elevation species, which are thought to tolerate a wider range of climatic conditions and therefore inhabit larger areas (e.g., Zhou et al. 2019, Chen et al. 2022). However, this is not always the case, as our study demonstrates, since climatic variability can vary inversely with elevation. Thus, in light of our results, we argue that direct climatic measurements are essential to investigate the true role of climatic variability in shaping species distributions and range extent.

Our finding that the mean species range extents did not increase with elevation in ground-dwelling arthropods, Insecta, Coleoptera, and Formicidae is not uncommon, as a positive relationship has been observed in a limited number of taxa (Ribas and Schroeder 2006, McCain and Knight 2013, Pintor et al. 2015, Feng et al. 2016, Chen et al. 2022). Actually, it was not observed in many vertebrates, including bats, birds, frogs, and non-volant small mammals (McCain and Knight 2013). In the context of our system, the lack of patterns consistent with an increase in species ranges with elevation is particularly unsurprising, as climatic instability, which is assumed to be the driver of the variation in species range extent, does not increase with elevation. However, unlike Stevens' (1989, 1992) conclusions, the absence of an increase in species average extent with elevation does not necessarily negate a possible role of climatic variability in shaping species range extents (Pintor et al. 2015, Beck et al. 2016, Mumladze et al. 2017). For example, moths in the Swiss Alps and snails and plants in the Greater and Lesser Caucasus, though not displaying Rapoport's effects, show patterns that align with the climatic variability hypothesis (Beck et al. 2016, Mumladze et al. 2017). Our analysis of the correlation between maximum climatic variability and species range extent in these mountains suggests a similar situation. In fact, while we do not observe Rapoport's effects in most groups, we find that climatic variability is still associated with species range extent in a manner consistent with the climatic variability hypothesis. Specifically, in ground-dwelling arthropods, Insecta, Coleoptera, and Formicidae, range extent increases with the maximum climatic variability experienced by each species along the elevational gradient.

Interestingly, had Rapoport's effects been an inevitable consequence of climatic variability influencing species range distributions, given the correlation between climatic variability and elevation observed in our system, we would expect to find a relationship between species range and elevation, although an inverse one (i.e., a decline in mean range extent with increasing elevation,). However, this is not the case, further suggesting that the effects of climatic variability on range extents do not automatically translate into elevational patterns in species extent and richness. This also helps to explain the observed inconsistency of Rapoport's effects across different ecological systems (e.g., McKay and Knight 2013). The key to understanding this inconsistency lies in the behavior of species with small ranges.

Although we found a correlation between maximum climatic variability and species range extent, our comparison with null expectations did not produce the expected outcomes under the climatic variability hypothesis. Specifically, contrary to Rapoport's rule, species with smaller range extents in the Santa Catalina Mountains are not preferentially distributed in more climatically stable areas. This raises the question of what other factors might influence species range extent and the distribution of ground-dwelling arthropods in this region.

While climatic variability remains one of the most widely recognized drivers of species range and distribution (Mumladze et al. 2017), it is possible that it can operate in directions opposite to what we anticipated. For instance, extreme temperature fluctuations have recently been proposed to work contrary to Stevens' (1989) hypothesis, constraining species' elevational ranges when fluctuations exceed species' thermal limits (Gallou et al. 2023). Additionally, the climatic variability hypothesis does not account for the potential role of biotic interactions like predation and competition in shaping the realized niche of species. In fact, environmental factors and biotic interactions can interact in complex ways, influencing the co-occurrence of climatic specialists and generalists, and thereby limiting their potential range extent along environmental gradients (Chen et al. 2024). For instance, competition has recently been associated with species distribution and elevational ranges of lowland and highland plants in the Swiss Alps and the realization of narrow range extents of birds in tropical mountains (Freeman et al. 2022, Lyu and Alexander 2022). Lastly, in line with our comparison to null expectations, the distribution of ground-dwelling arthropods along this gradient may not be significantly influenced by abiotic or biotic interactions, but instead could follow a random distribution constrained by the elevational geometry of the mountain (see Colwell et al. 2004 for a rationale). Paradoxically, the only group which showed a positive correlation between range extent and elevation (as predicted by Rapoport's rule) were the Tenebrionidae, whose ranges, however, were not associated with climatic variability (which should be the generator of the elevational pattern). This suggests that the observed elevational pattern in tenebrionid range extent should derive from some other cause. As tenebrionids are, in general, very speciose in arid environments with many species inhabiting deserts (Ragionieri et al. 2023), this result might be explained by the presence of many specialists (species with restricted ranges) in low elevation (climatically highly variable) areas.

Our findings suggest that elevational patterns in species distribution and range extent cannot always be interpreted using the classic theoretical framework of the climatic variability hypothesis and Rapoport's rule. First, the absence of Rapoport's pattern in species extents with elevation does not necessarily imply that climatic variability does not influence species range extent. Typically, climatic variability is expected to increase with elevation, but our results

challenge this assumption, revealing instances where opposite patterns occur. Furthermore, even when an association between climatic variability and species range extent is observed, it does not always produce an inverse Rapoport's pattern along the elevational gradient. Second, while a positive correlation between climatic variability and species range extent is observed, it does not necessarily imply that species range extent varies in line with the climatic niche breadth of the species, as predicted by the climatic variability hypothesis. After controlling for null expectations, we found that ground-dwelling arthropods with smaller range extents are not necessarily confined to more climatically stable environments. Instead, they occur throughout the elevational gradient of the Santa Catalina Mountains. Our study suggests that communities of more instable environments are composed of species with broader ranges, but species with small ranges occur through the whole gradient. As a result, variation in species range and variation in species richness are decoupled: an average increase in species extent does not imply that communities of more instable environments are simply subsets of those of more stable environments. In fact, we found that specialists (species with small ranges) are not concentrated in climatically stable environments. These results suggest that climatic variability favor species with broader ranges as they are more tolerant, but species with small ranges may occur throughout, possibly because their niches are restricted by non-climatic factors (e.g., biotic interactions) or as a consequence or chance alone.



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## APPENDIX C

### PURE TURNOVER, RATHER THAN NESTEDNESS, DRIVES BETA DIVERSITY OF GROUND-DWELLING ARTHROPOD COMMUNITIES IN THE SANTA CATALINA MOUNTAINS

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Conceptualization (lead), Methodology (equal), Formal analysis (supporting), Writing – review  
and editing (equal); Wendy Moore: Data curation (equal), Writing – review and editing (equal),  
Funding Acquisition (lead), Supervision (lead).

**Title:** Pure turnover, rather than nestedness, drives beta diversity of ground-dwelling arthropod communities in the Santa Catalina Mountains.

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## **ABSTRACT**

Mountains, with their rapid climatic and topographic variations along elevational gradients, provide ideal settings for exploring general patterns and environmental factors associated with community structure. Variation in community composition along these gradients is shaped by environmental and spatial differences, with species turnover often considered the dominant driver of community dissimilarity. However, some studies have also proposed a "filtering" effect, where communities may not consist of entirely different species, but rather represent nested subsets of one another. The Santa Catalina Mountains, part of the Madrean Sky Island Archipelago, are home to an extraordinary diversity of ground-dwelling arthropods. Recent surveys have documented over 400 species on this single "Sky Island," raising the question of how this diversity is distributed across elevational gradients and what environmental factors is associated with variations in community structure. While previous research has observed variation in beta diversity across different ground-dwelling arthropod taxa influenced by biome and seasonal changes, the extent to which these patterns are shaped by environmental or spatial distances, and the relative contributions of species turnover and nestedness, remain unclear. In this study, we investigate the community structure of different ground-dwelling arthropods groups in the Santa Catalina Mountains by partitioning beta diversity into turnover and nestedness components. We examine how these components relate to environmental and geographic distances across communities, and we identify key variables associated with variation in community structure through Canonical Correspondence Analysis. Our results reveal that species turnover, rather than nestedness, plays the predominant role in shaping community composition. Environmental distance emerges as a significant influence on community structure across all arthropod taxa, with geographic distance playing a minimal role in some groups. Notably, temperature significantly explained variations in community composition across all ground-dwelling arthropods, underscoring its potential role as a key environmental variable influencing community structure in this montane system. These findings hint at the importance of environmental gradients, particularly temperature and its covariates in driving species replacement along elevational gradients and shaping arthropod communities, despite differences in ecological roles and dispersal capabilities of the species involved. This research contributes to our understanding of community dynamics in montane ecosystems, emphasizing the contribution of species turnover to overall beta diversity and the role of environmental conditions in producing variation in community composition.

**KEYWORDS:** Beta diversity, turnover, nestedness, ground-dwelling arthropods, environmental distance, geographic distance

## 1 | INTRODUCTION

Studying variation in species composition among assemblages across spatial or environmental gradients offers insights into the processes influencing community assembly (Petchey and Gaston 2006; Münkemüller et al. 2011; Swenson 2014; Cadotte and Tucker 2017). According to theory, variation in species assemblages can arise from both environmental sorting and neutral dynamics (Hubbell 2001, Svenning et al. 2011, Kraft et al. 2015). Environmental factors, such as climatic conditions, play a crucial role in shaping community assembly by favoring species with different ecological niches, thereby influencing beta diversity patterns. Conversely, according to neutral theories, variation in species composition can be a consequence of differences in dispersal abilities among species (Svenning et al. 2011). Although both differences in ecological niches and neutral dynamics may contribute to generating patterns of beta diversity, disentangling their relative importance is far from a trivial task.

Baselga (2010) identified two additive components into which total beta diversity can be partitioned: pure turnover and nestedness. Pure turnover occurs when species are replaced by other species (from one locality to another), whereas nestedness represents a spatial pattern in which less diverse communities are partial subsets of other communities with more species. Along an environmental gradient, environmental sorting may lead to nestedness patterns by progressively filtering species from a common species pool into smaller communities (environmental filtering), or environmental sorting may lead to turnover patterns, by creating conditions that different species can exploit (environmental replacement) (Qian et al. 2005, Cadotte and Tucker 2017, Menegotto et al. 2019). Under neutral scenarios, differences in dispersal capabilities may result in variations in nestedness or turnover, and lead to a distance-decay pattern in beta diversity, where dissimilarities between communities correlate with geographic distance (Hubbell 2001, Soininen et al. 2007, Morlon et al. 2008). In this context, investigating the predictive value of environmental and geographic differences in estimating variation in overall beta diversity, turnover, and nestedness components might hint at the underlying processes influencing community structure (Qian et al. 2005, Svenning et al. 2011, Cadotte and Tucker 2017, Fattorini 2022, Yuan et al. 2022, Yao et al. 2023).

Beta diversity partitioning in turnover and nestedness components and its response to environmental and spatial gradients may vary depending on the environment and the taxonomic groups examined (Chesters et al. 2019). In mountainous regions, climate changes rapidly with elevation, thus creating heterogeneity in conditions, essentially niches, that species can occupy, resulting in distinct community compositions across different elevations (Svenning et al. 2011, Nunes et al. 2016). For instance, various ground-dwelling arthropod groups, such as dung beetles and ants, exhibit community structures primarily shaped by turnover along elevational gradients (Nunes et al. 2016, da Silva et al. 2018, Flores et al. 2018, Uhey et al. 2021). Simultaneously, nestedness is also thought to contribute to overall beta diversity in more climatically extreme environments, such as those found at higher elevations (Paknia and Rajaei 2015, Nanda et al. 2021). As climatic conditions become increasingly harsh with elevation (e.g., colder temperatures), more climate-tolerant species from lower elevations are expected to colonize these higher-elevation environments (Stevens 1989). If differences between communities are completely attributable to nestedness, communities at one elevation would be subsets of those

found at lower elevations. In line with this scenario, nestedness was found to be an important component of community composition at higher elevations in some taxa, like macrolichens and moths, although this pattern is not universally observed across different mountainous ranges (Paknia and Rajaeai 2015, Nanda et al. 2021).

Research on other components of taxonomic diversity along elevational gradients has revealed predictable variations in species diversity depending on the taxonomic level examined (Buckley et al. 2010; Hurlbert and Stegen 2014, Peters et al. 2016). For example, species richness in broad taxonomic groups including a variety of ecologically diverse species tends to vary with ambient energy, while narrow and more specialized groups exhibit different environmental responses due to their ecological differences (Buckley et al. 2010; Hurlbert and Stegen 2014). Following this expectation, for instance, species richness in broad and more ecologically diverse groups like Insecta might always be expected to vary based on the same environmental variables (e.g., ambient energy), whereas in a smaller, ecologically specialized groups like Tenebrionidae and Staphylinidae, variation in species richness might vary depending on different environmental variables. However, relatively few studies have examined multiple taxonomic groups together in terms of beta diversity and its components, such as turnover and nestedness (Fattorini 2011; Menegotto et al. 2019; Fontana et al. 2020; Uhey et al. 2021). As a result, our understanding of how beta diversity varies with environmental and geographic factors based on taxonomic coverage remains limited.

A notable exception is the work by Meyer et al. (2015) that examined ground-dwelling arthropod assemblages along an elevational gradient in the Santa Catalina Mountains, Arizona. Their study revealed significant variations in community structure across different biomes and seasons, with notable differences in arthropod communities in some cases. While this research provided valuable insights into the influence of biomes and seasonal shifts on community structure, it did not specifically address the turnover and nestedness components of beta diversity, nor did it explore the environmental and geographic factors associated with these patterns. Consequently, the underlying mechanisms influencing beta diversity, particularly how turnover and nestedness are related to ecological differences and dispersal abilities, remain unclear. This raises the question of whether and how environmental factors are linked to the replacement or filtering of species across communities, and how these patterns vary across taxa with different ecological characteristics.

In this study, we examine how different taxonomic groups of ground-dwelling arthropods relate to: (1) the variation of overall beta diversity ( $\beta_{sor}$ ) and its turnover ( $\beta_{sim}$ ) and nestedness ( $\beta_{nes}$ ) components; (2) the association of beta diversity ( $\beta_{sor}$ ,  $\beta_{sim}$ , and  $\beta_{nes}$ ) with environmental and geographic differences between communities; and (3) the variation of community structure along individual environmental factors. This exploration involves different ground-dwelling arthropod taxa: Myriapoda, Araneae, Orthoptera, Coleoptera, Formicidae (Hymenoptera), and Insecta (including Orthoptera, Coleoptera, and Formicidae). Within Coleoptera, we further examined our hypotheses at the family level, focusing on three families: Carabidae, Staphylinidae, and Tenebrionidae. In addition, we selected for this study environmental factors that are usually associated with taxonomic diversity in a variety of groups. These include measures of ambient energy (measured as average temperatures), water availability (measured as average humidity), climatic variability (measured as temperature range), and habitat heterogeneity (measured as

terrain ruggedness) (MacArthur and MacArthur 1961, Turner et al. 1987, Stevens 1989, Hawkins et al. 2003).

If taxonomic level relates to differences in community structure and community's association with environmental and geographical factors, we anticipate that the contributions of turnover and nestedness to overall beta diversity will differ across taxonomic groups based on their ecological needs and dispersal capabilities. Additionally, overall beta diversity, along with its turnover and nestedness components, should correlate differently to environmental and geographical dissimilarities between communities. Specifically, if community assembly varies similarly to other components of taxonomic diversity, we might expect broader and more ecologically inclusive groups (i.e., ground-dwelling arthropods or Insecta) to primarily correlate with measures of ambient energy. In contrast, community structure of narrower and more ecologically specialized taxonomic groups (e.g., Tenebrionidae, Formicidae, and Staphylinidae) may show distinct associations with environmental and geographic variables in line with their unique ecological characteristics (Buckley et al. 2010; Hurlbert and Stegen 2014; Peters et al. 2016).

Based on these considerations, we formulate the following predictions related to the two contrasting hypotheses that communities are more structured by environmental conditions or neutral dynamics:

1. Under a neutral dynamics scenario, we expect that inter-site geographical distances demonstrate stronger associations with community composition than environmental differences.
2. Under a non-neutral dynamics scenario, we expect that inter-site environmental differences demonstrate stronger associations with community composition than geographical distance.

Under a non-neutral scenario, environmental sorting may be due to either environmental filtering or environmental replacement. In the first case, we expect variation in community structure to be mostly explained by its nestedness component, while in the second case pure turnover should be predominant.

Finally, we explore whether the association between different environmental variables vary or remain similar among taxa. In this case, we recognize two alternative scenarios upon which to build future explorations:

3. Variation in community composition varies depending on taxonomic level and ecological differences among taxa. We expect that narrow and more ecologically specialized taxonomic levels present idiosyncratic association with different environmental variables, while broader taxonomic and more ecologically inclusive levels will be uniformly associated with the same environmental variables.
4. Variation in community composition does not reflect taxonomic level and ecological differences. Contrary to patterns observed in other components of taxonomic diversity (e.g., species richness in this system, see Bergamaschi et al. A), variation in community



composition may be more tightly constrained by environmental factors and produce similar responses across taxa, even those with distinct ecological traits. In this context, our findings could be especially valuable for eventual prediction of community structure based on environmental and geographic differences across communities. These insights may be applicable to other similar fauna within the Madrean Sky Island Archipelago, helping to inform conservation priorities for this unique and diverse region.

## 2 | METHODS

### 2.1 | Study area, sampling and sample processing

Building upon the work of Meyer et al. (2015), we use an extensive dataset of ground-dwelling arthropods and add data on the Formicidae collected in the same traps, to investigate variations in beta diversity in relation to environmental and geographical factors along the elevational gradient of the Santa Catalina Mountains (Arizona, USA). The study area, sampling, and sample processing are described in Meyer et al. (2015).

### 2.2 | Beta diversity

Variation in community composition across sampling sites was analyzed using Baselga's (2010) partitioning of overall beta diversity expressed by the Dice-Sørensen's coefficient ( $\beta_{sor}$ ) comprising the pure turnover ( $\beta_{sim}$ ) and nestedness ( $\beta_{nes}$ ) components:

$\beta_{sor} = \beta_{sim} + \beta_{nes}$ , where  $\beta_{sor}$  is calculated as:

$$\beta_{sor} = (b + c)/(2a + b + c),$$

with "a" being the number of species shared between two communities, and "b" and "c" the number of species unique to one or the other community, respectively (Koleff et al. 2023).

Simpson's coefficient ( $\beta_{sim}$ ) is a measure of pure turnover (replacement), not influenced by species nestedness, and it is calculated as:

$$\beta_{sim} = \min(b,c)/(a + \min(b,c)),$$

where "a", "b" and "c" are the same as in the Dice-Sørensen's coefficient (Simpson 1943, Lennon et al. 2001).

When species richness is the same between communities, "b" and "c" are equal and any differences in species composition are attributable to turnover. When species richness varies between communities, dissimilarity between communities may arise from species loss or species filtering. These processes cause a nested pattern between communities, where species composition in a community is at least partially a nested subset of species from a larger community. The nestedness-resultant dissimilarity is the difference between  $\beta_{sor}$  and  $\beta_{sim}$ , and can be calculated as:

$$\beta_{nes} = (\max(b,c) - \min(b,c)) / ((2a + \min(b,c) + \max(b,c)) * a / (a + \min(b,c))).$$

$\beta_{sor}$ ,  $\beta_{sim}$  and  $\beta_{nes}$  were calculated using species occurrences data across sampling sites with the R package *recluster* (Dapporto et al. 2013, R Core Team 2024).

### 2.3 | Environmental and geographical distances

To explore the association between environmental and geographical distances on species composition across sites, we adopted Tuomisto and Ruokolainen's (2006) distance approach based on correlation of pairwise beta diversity values (calculated as  $\beta_{sor}$ ,  $\beta_{sim}$  and  $\beta_{nes}$ ) with inter-site geographical and ecological distances. To calculate environmental distances, we used measures of temperature, humidity, climatic variability, and topographic heterogeneity previously found to be associated with taxonomic alpha and beta diversity in arthropods in other systems (Baselga 2010, Svenning et al. 2011, Peters et al. 2016, Marathe et al. 2021, Silvestre et al. 2021, Fattorini et al. 2024). In particular, we used average temperature, average humidity, temperature range, and terrain ruggedness index calculated for each site (see Bergamaschi et al. in prep). Since these variables use different units, we first standardized each factor as Z-scores (after standardization, each factor will present mean 0 and standard deviation 1). Subsequently, we calculated environmental distances between sites as Euclidean distances (Fattorini et al. 2014). Z-scores and Euclidean distances were calculated in R 4.4.2 (R Core Team 2024). Finally, the starting point of each sampling site was georeferenced, and the corresponding geographic coordinates were used to calculate geographic distances between sites in ArcGIS Pro 3.1.3 (ESRI 2016).

### 2.4 | Analyses

To investigate inter-site relationships due to overall turnover and nested beta diversity, we used non-metric multi-dimensional scaling (NMDS). NMDS is an ordination technique that can be used to find a two-dimensional configuration of sites that best reflects their relationships based on dissimilarity measures (Moulopied et al. 2022, Fattorini et al. 2024). In this analysis, a measure of "stress" based on Procrustean analysis was used to evaluate the level of distortion between different configurations and the dissimilarity matrix. For an easier visualization, in the final configuration, the axis with the highest variance was standardized between 0 and 1, and the other axis was rescaled based on the first axis. Finally, we colored each site in the ordination plot according to their biome, and we labeled each point with their elevation. In this way, we tried to investigate how dissimilarities in community composition align with biome and elevation differences across sites.

The initial NMDS configurations for Staphylinidae, Carabidae, and Tenebrionidae, using overall and turnover beta diversity, revealed the presence of a few sites that did not share any species with the majority. In the two-dimensional representations for overall and turnover dissimilarities these sites were far from any other, forcing the majority of sites to clump, despite their differing species compositions (Figure S1). Thus, to better elucidate relationships across the majority of sites, we excluded these outliers from the main NMDS representations of overall and turnover beta diversity for these families (Figure 2).

To assess which component of beta diversity, turnover or nestedness, explains most of the variation in overall dissimilarity for each taxon, we conducted two separate Mantel tests: one examining the correlation between  $\beta_{sor}$  and  $\beta_{sim}$  (to assess the importance of the turnover component), and the other between  $\beta_{sor}$  and  $\beta_{nes}$  (to assess the importance of nestedness component).

To gain insight into environmental and neutral processes in this system, we used partial Mantel tests to estimate the correlation between dissimilarities matrices built with  $\beta_{sor}$ ,  $\beta_{sim}$  and  $\beta_{nes}$ , and those representing environmental and geographical distances between sampling sites. Partial Mantel tests allow calculation of the correlation between a matrix “A” (e.g., overall beta diversity) and a matrix “B” (e.g., environmental distances), while accounting for the effect of matrix “C” (e.g., geographical distances) (Legendre and Legendre 2012, Fattorini 2014). The importance of environmental or geographical distances on components of beta diversity were assessed by running these analyses with either  $\beta_{sor}$ ,  $\beta_{sim}$  or  $\beta_{nes}$  as matrix A, and (i) environmental distances as matrix B and geographical distances as matrix C (to test the effect of the environment after partialling out that of geography: environmental sorting), and (ii) geographical distances as matrix B and environmental distances as matrix C (to test the effect of the spatial position after partialling out that of environment: neutral processes).

To further evaluate the association between individual environmental factors and species composition across sites, we ran canonical correspondence analyses (CCAs). CCA is a multivariate ordination technique that evaluates patterns of variation in community composition in relationship to multiple environmental factors. Those patterns that are best explained by the environment are then represented in an ordination plot to effectively visualize the relationships between community composition and the environmental factors (Ter Braak 1986). In the ordination plot, environmental factors are represented by arrows. The length of the arrow is directly related to the relative importance of each environmental factor in predicting variation in community composition. On the other hand, the direction of the arrow informs about the direction toward which the environmental factor increases. In addition, sites and/or species are represented by points whose position is informative about the variation in community composition that is associated with each environmental factor (Ter Braak 1986). Finally, the significance of each environmental factor in influencing the pattern in variation of community composition was tested using Monte Carlo permutations (1000 iterations) on a comprehensive model including all environmental factors.

NMDS, partial Mantel tests, and CCA analyses were performed in R 4.4.2 (R Core Team 2024) using the *vegan* 2.6-8 and *recluster* 2.9 packages (Dapporto et al. 2013, Oksanen et al. 2024). In all analyses, significance was set at  $\alpha = 0.05$ .

### **3 | RESULTS**

#### **3.1 | Species diversity**

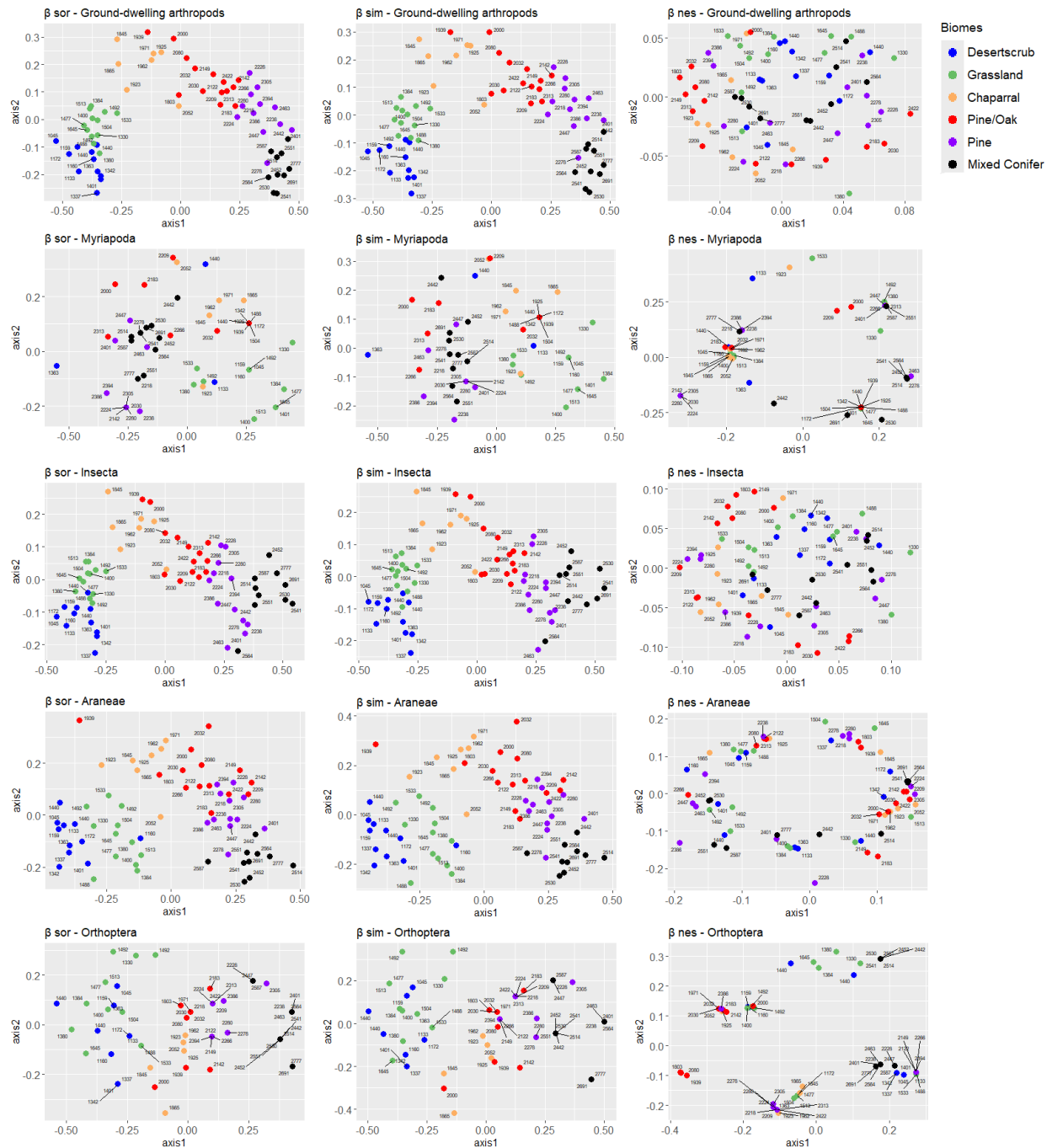
Our final dataset included 449 species/morphospecies of ground-dwelling arthropods comprising 101 Araneae, 16 Myriapoda, and 332 Insecta across 66 transects. Within Insecta, there were 25

Orthoptera, 117 Formicidae, and 190 Coleoptera (including 21 Carabidae, 25 Staphylinidae, 37 Tenebrionidae, and 107 other spp.). More details about sampling coverage and species diversity are provided in Bergamaschi et al. (in prep).

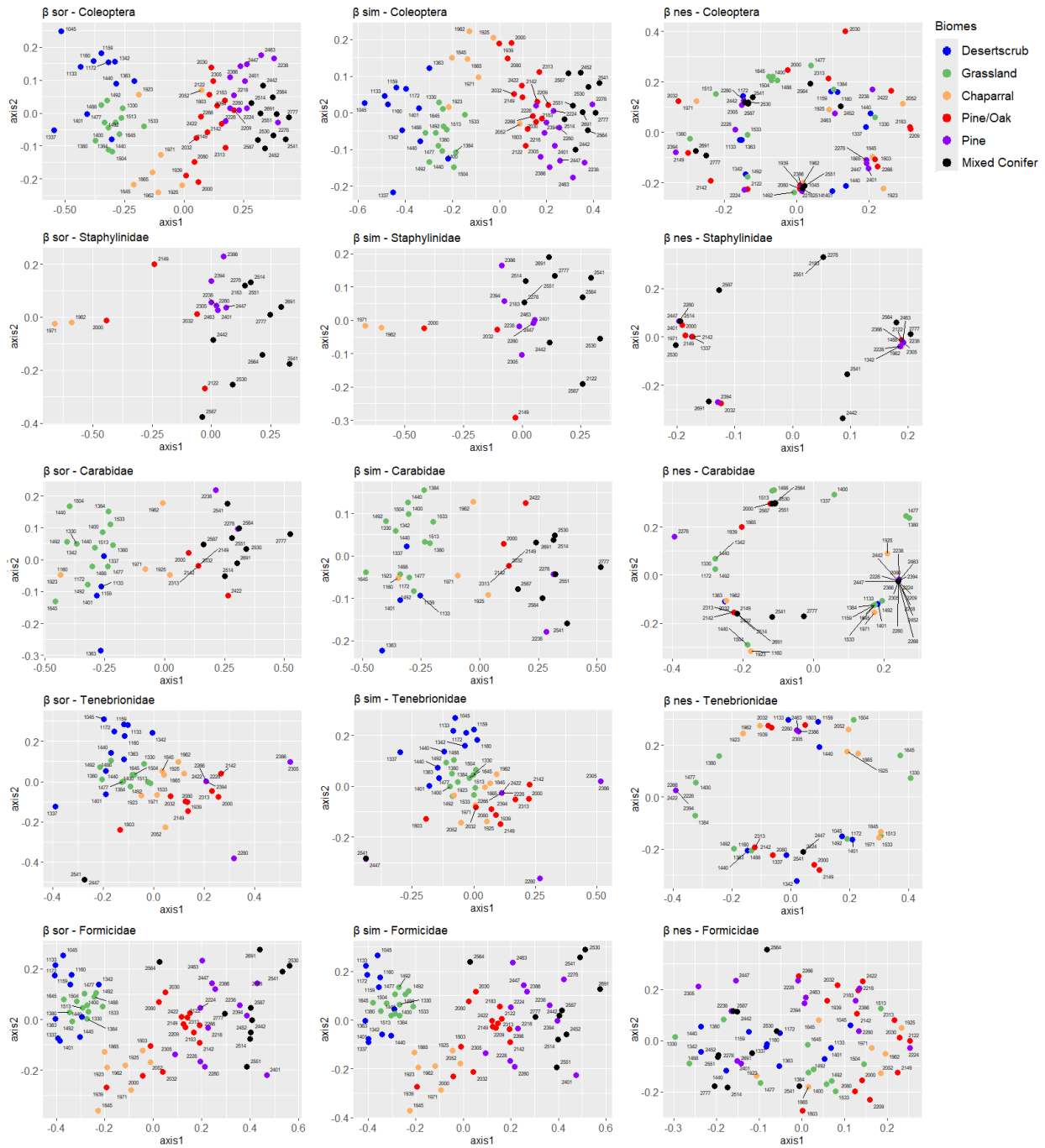
### 3.2 | Non-metric multi-dimensional scaling (NMDS)

NMDS configurations for overall beta diversity across different taxa tend to cluster according to biome affiliation and elevation. Similarly to Meyer et al. (2015), communities within the same biome and elevation are more similar to each other than to those from different biomes or elevations (Figures 1 and 2 -  $\beta_{sor}$ ). This pattern is particularly evident among Insecta, Araneae, and Coleoptera, where communities are clearly grouped by biome and progressively organized by elevation. However, overlaps can occur between biomes; for instance, desertscrub and grassland exhibited relatively similar communities, forming a distinct group in ants (Figure 2 -  $\beta_{sor}$ ). Additionally, pine/oak, pine, and mixed conifer biomes overlapped in Myriapoda, with desertscrub sites failing to form a distinct group in this taxon (Figure 1 -  $\beta_{sor}$ ). Grouping following biome and elevation is also visible in beetle families (Staphylinidae, Carabidae, and Tenebrionidae) after removing the few sites with unique species and high dissimilarity in community composition (compare Figure S1 including these sites and Figure 2). These patterns of overall dissimilarity are also observable in NMDS configurations of pure turnover ( $\beta_{sim}$ ), whereas NMDS configurations based on the nestedness contribution ( $\beta_{nes}$ ) did not reflect biome and elevation differences (Figures 1 and 2). These results indicate that environmental sorting is predominantly due to environmental replacement rather than to environmental filtering.

In summary, both overall and turnover dissimilarities displayed similar configurations across various taxa, highlighting distinct groupings based on biome and elevation from family to phylum. However, this structure became less pronounced in groups with fewer species, such as Myriapoda, Staphylinidae, Carabidae, and Tenebrionidae. Conversely, the nestedness component contributed to some variation in community composition between sites but did not align with biome and elevation characteristics. In general, however, these findings indicate a common response of different groups to the elevational gradient.



**Figure 1.** Results of non-metric multi-dimensional scaling (NMDS) for ground-dwelling arthropods as a whole, Myriapoda, Insecta, Araneae, and Orthoptera species composition using overall, turnover, and nestedness dissimilarities ( $\beta$ sor,  $\beta$ sim, and  $\beta$ nes). Dots represent different sampling sites. Biomes occurring on the Santa Catalina Mountains are represented by different colors, while labels describe the elevation (m) of each sampling site.



**Figure 2.** Results of non-metric multi-dimensional scaling (NMDS) for Coleoptera, Staphylinidae, Carabidae, Tenebrionidae, and Formicidae species composition using overall, turnover, and nestedness dissimilarities ( $\beta$  sor,  $\beta$  sim, and  $\beta$  nes). Dots represent different sampling sites. Biomes occurring on the Santa Catalina Mountains are represented by different colors, while labels describe the elevation (m) of each sampling site.

### 3.3 | Mantel and partial Mantel tests

Consistent with the similarity observed between overall and pure turnover NMDS ordination plots, Mantel tests indicated that pure turnover significantly explained most of the variance ( $R > 0.89$ ,  $p < 0.001$ ) in overall beta diversity across all taxa (Table 1). In contrast, nestedness was not identified as a significant component of overall beta diversity in this system, thus rejecting environmental filtering as an explanation of environmental sorting in favor of a role for environmental replacement.

When examining the correlation between beta diversity and environmental/geographical distances, relationships were similarly consistent across different taxa. After controlling for geographical distances, environmental distances emerged as the primary factor associated with variation in overall beta diversity and pure turnover for all taxa (Table 2). While geographical distances were also frequently associated with variation in overall beta diversity and pure turnover, the strength and frequency of significant associations was generally lower than for environmental distance for ground-dwelling arthropods as a whole, and also for Myriapoda, Araneae, Orthoptera, Coleoptera, and Carabidae. A similar pattern was observed for turnover dissimilarity, with the exception of Myriapoda, where no significant association was found between turnover and geographical distances. Finally, neither environmental nor geographical distances accounted for variation in species communities due to nested patterns. These results indicate that ground-dwelling arthropod communities are mostly structured by environmental factors across all taxa, while neutral dynamics played a subsidiary role in a minority of taxa.

**Table 1.** Results of Mantel tests of overall beta diversity against turnover and nestedness biogeographical distances for the ground-dwelling arthropods of the Santa Catalina Mountains. Significant  $p$  values ( $p < 0.05$ ) in bold.

Sørensen	Biogeographical distances			
	Simpson		Nestedness	
	$r$	$P$	$r$	$p$
Ground-dwelling arthropods	0.9919	<0.001	-0.4669	1
Araneae	0.9776	<0.001	-0.5858	1
Myriapoda	0.9223	<0.001	-0.5078	1
Insecta	0.9845	<0.001	-0.4525	1
Orthoptera	0.8995	<0.001	-0.3299	1
Hymenoptera (Formicidae)	0.9514	<0.001	-0.2943	1
Coleoptera	0.9636	<0.001	-0.5496	1
Staphylinidae	0.942	<0.001	-0.6232	1
Carabidae	0.9379	<0.001	-0.4901	1
Tenebrionidae	0.9061	<0.001	-0.4522	1

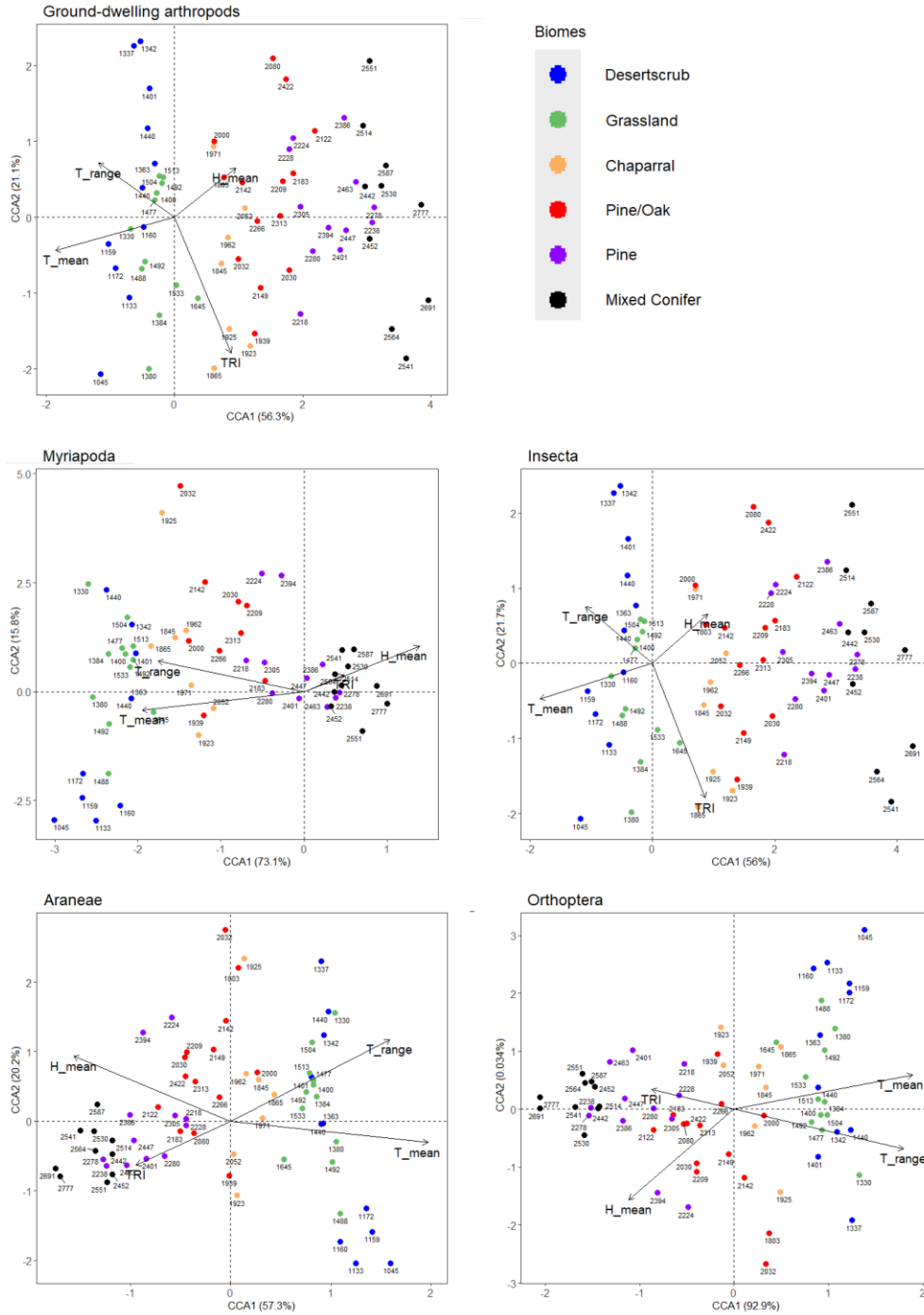
**Table 2.** Results of partial Mantel tests of biogeographical distances against environmental and geographical distances for the ground-dwelling arthropods of the Santa Catalina Mountains. Significant p values ( $p < 0.05$ ) in bold.

Matrix correlation		Biogeographical distances					
Matrix A × Matrix B	Matrix C (controlling)	Sørensen		Simpson		Nestedness	
		<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>
<b>Ground-dwelling arthropods</b>							
Environmental distances	Geographic distance	0.6374	<b>&lt;0.001</b>	0.6379	<b>&lt;0.001</b>	-0.3283	1
Geographic distance	Environmental distances	0.07122	<b>0.013</b>	0.06958	<b>0.008</b>	-0.02032	0.682
<b>Araneae</b>							
Environmental distances	Geographic distance	0.479	<b>&lt;0.001</b>	0.4749	<b>&lt;0.001</b>	-0.2935	1
Geographic distance	Environmental distances	0.1455	<b>&lt;0.001</b>	0.1621	<b>&lt;0.001</b>	-0.1467	1
<b>Myriapoda</b>							
Environmental distances	Geographic distance	0.3121	<b>&lt;0.001</b>	0.3195	<b>&lt;0.001</b>	-0.2288	1
Geographic distance	Environmental distances	0.08505	<b>0.012</b>	0.05592	0.084	0.006786	0.427
<b>Insecta</b>							
Environmental distances	Geographic distance	0.6445	<b>&lt;0.001</b>	0.6379	<b>&lt;0.001</b>	-0.2951	1
Geographic distance	Environmental distances	0.03211	0.138	0.04692	0.081	-0.07347	0.98
<b>Orthoptera</b>							
Environmental distances	Geographic distance	0.5425	<b>&lt;0.001</b>	0.5104	<b>&lt;0.001</b>	-0.2141	1
Geographic distance	Environmental distances	0.106	<b>&lt;0.001</b>	0.1323	<b>0.007</b>	-0.1014	0.998
<b>Hymenoptera (Formicidae)</b>							
Environmental distances	Geographic distance	0.6004	<b>&lt;0.001</b>	0.5702	<b>&lt;0.001</b>	-0.1662	1
Geographic distance	Environmental distances	-0.0641	0.975	-0.02518	0.781	-0.07303	0.949
<b>Coleoptera</b>							
Environmental distances	Geographic distance	0.5438	<b>&lt;0.001</b>	0.5276	<b>&lt;0.001</b>	-0.3035	1
Geographic distance	Environmental distances	0.1504	<b>&lt;0.001</b>	0.1449	<b>&lt;0.001</b>	-0.07634	0.97
<b>Staphylinidae</b>							
Environmental distances	Geographic distance	0.3071	<b>&lt;0.001</b>	0.3022	<b>0.004</b>	-0.2181	0.997
Geographic distance	Environmental distances	0.07325	0.245	0.05912	0.305	-0.02231	0.551
<b>Carabidae</b>							
Environmental distances	Geographic distance	0.4155	<b>&lt;0.001</b>	0.4255	<b>&lt;0.001</b>	-0.2878	1
Geographic distance	Environmental distances	0.1771	<b>&lt;0.001</b>	0.1612	<b>&lt;0.001</b>	-0.06772	0.957
<b>Tenebrionidae</b>							
Environmental distances	Geographic distance	0.4334	<b>&lt;0.001</b>	0.3784	<b>&lt;0.001</b>	-0.1624	1
Geographic distance	Environmental distances	0.03198	0.276	0.07847	0.08	-0.1119	0.991

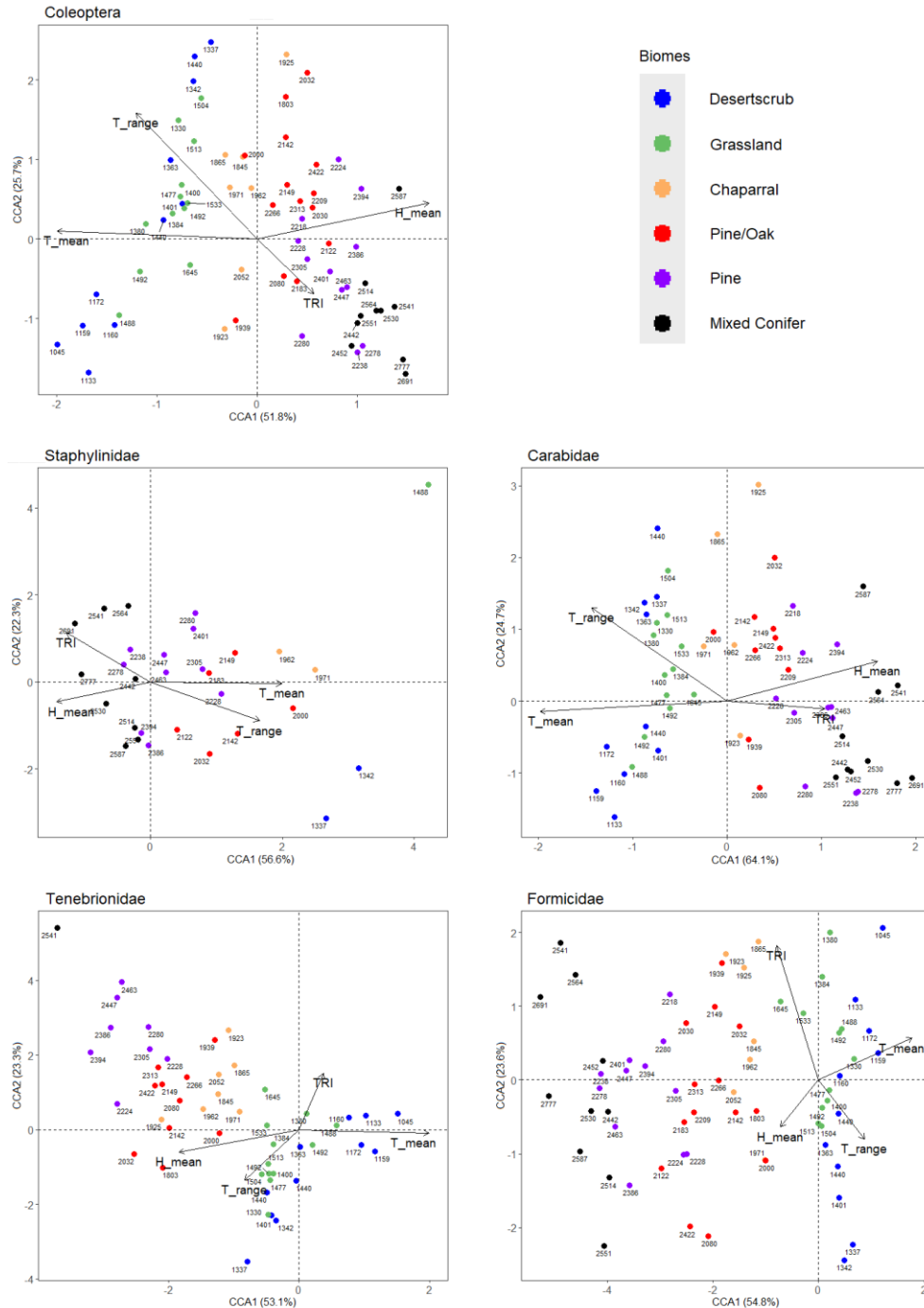
### 3.4 | Canonical correspondence analysis (CCA)



Patterns of variation in community composition associated with environmental variables, as well as the relationships between individual communities and environmental variables, were represented in CCA ordination plots (Figures 3 and 4). Overall, CCA explained a variable percentage of the variation in community composition for different taxa (from 12.2% for Formicidae to 35.4% in Orthoptera, Table 3). Within this variation, however, the first two canonical axes always explained most of the variation (>70% for all taxa). Average temperature (T\_mean) showed the most consistent association with variation in community composition across all the considered taxa (Table 3). Furthermore, the first canonical axis was always highly correlated with average temperature (factor score > |0.8|). Average temperature was particularly important in explaining species composition in desertscrub and grassland environments in all groups, in particular Myriapoda, Tenebrionidae, and Formicidae (Figures 3 and 4). Species composition in Araneae, Coleoptera, Orthoptera, and Carabidae was also significantly associated with temperature range (Tables 3 and 4). Overall, sites are still clustered based on biome identity, although some overlaps are still found in groups like Myriapoda and Staphylinidae. These results indicate that ground-dwelling arthropod communities are mostly structured by variation in temperature conditions, and possibly biome affiliation, across all taxa studied.



**Figure 3.** Canonical correspondence analysis (CCA) for ground-dwelling arthropods as a whole, Myriapoda, Insecta, Araneae, and Orthoptera. Dots represent different sampling sites. The pattern in variation of community composition that is best explained by the environmental variable is visualized in the ordination plot. Environmental variables are represented by arrows (T\_mean = average temperature, T\_range = temperature range, H\_mean = average humidity, and TRI = terrain ruggedness index), while sites are represented by dots colored and labeled accordingly to biome and elevation (m). Arrow length and direction indicates the relative importance of the association between a factor and variation in community composition and the direction of this relationship.



**Figure 4.** Canonical correspondence analysis (CCA) for Coleoptera, Staphylinidae, Carabidae, Tenebrionidae, and Formicidae. Dots represent different sampling sites. The pattern in variation of community composition that is best explained by the environment is visualized in the ordination plot. Environmental variables are represented by arrows (T\_mean = average temperature, T\_range = temperature range, H\_mean = average humidity, and TRI = terrain ruggedness index), while sites are represented by dots colored and labeled accordingly to biome and elevation (m). Arrow length and direction indicated the relative importance of the association between a factor and variation in community composition and the direction of this relationship.

**Table 3.** Results from canonical correspondence analysis for the influence of different environmental variables on community composition along the elevational gradients. Constrained variance explained by the CCA model and individual CCA axis are reported. F statistics and P-values (in parentheses) are shown for CCA model and individual factors (significant values are in bold). Significance was assessed using Monte Carlo permutation tests (1000 permutations).

Taxon	CCA model	CCA model	Eigenvalues - canonical axes				Proportion of constrained variance - canonical axes				Environmental factors significance - F, (P)			
			CCA1	CCA2	CCA3	CCA4	CCA1	CCA2	CCA3	CCA4	T_mean	T_range	H_mean	TRI
Ground-dwelling arthropods	0.134	<b>2.36 (0.001)</b>	0.828	0.311	0.248	0.085	0.563	0.211	0.168	0.057	<b>4.76 (0.001)</b>	1.69 (0.115)	1.23 (0.433)	1.78 (0.062)
Araneae	0.153	<b>2.76 (0.001)</b>	0.858	0.303	0.18	0.157	0.573	0.202	0.12	0.105	<b>6.23 (0.001)</b>	<b>2.27 (0.001)</b>	1.24 (0.116)	1.30 (0.089)
Myriapoda	0.225	<b>3.91 (0.001)</b>	0.787	0.17	0.065	0.054	0.731	0.158	0.06	0.05	<b>10.99 (0.001)</b>	2.34 (0.133)	1.27 (0.5)	1.06 (0.651)
Insecta	0.131	<b>2.31 (0.001)</b>	0.811	0.315	0.242	0.081	0.56	0.217	0.167	0.056	<b>4.57 (0.001)</b>	1.67 (0.134)	1.22 (0.431)	1.77 (0.073)
Orthoptera	0.354	<b>8.36 (0.001)</b>	0.758	0.028	0.019	0.011	0.929	0.034	0.023	0.014	<b>27.90 (0.001)</b>	<b>3.99 (0.016)</b>	0.77 (0.597)	0.80 (0.588)
Hymenoptera (Formicidae)	0.122	<b>2.11 (0.001)</b>	0.759	0.326	0.231	0.069	0.548	0.236	0.167	0.05	<b>3.85 (0.001)</b>	1.65 (0.120)	1.19 (0.424)	1.75 (0.077)
Coleoptera	0.142	<b>2.52 (0.001)</b>	0.904	0.449	0.252	0.14	0.518	0.257	0.145	0.08	<b>5.20 (0.001)</b>	<b>2.58 (0.001)</b>	0.98 (0.642)	1.30 (0.228)
Staphylinidae	0.147	<b>1.08 (0.019)</b>	0.841	0.331	0.178	0.135	0.566	0.223	0.12	0.091	<b>2.43 (0.001)</b>	0.77 (0.444)	0.48 (0.855)	0.64 (0.638)
Carabidae	0.169	<b>2.70 (0.001)</b>	0.892	0.344	0.13	0.027	0.641	0.247	0.093	0.019	<b>6.84 (0.001)</b>	<b>2.47 (0.005)</b>	0.46 (0.977)	1.05 (0.458)
Tenebrionidae	0.168	<b>2.22 (0.001)</b>	0.843	0.371	0.297	0.077	0.531	0.233	0.187	0.049	<b>4.69 (0.001)</b>	1.75 (0.124)	0.80 (0.641)	1.64 (0.096)

T\_mean = average temperature, T\_range = temperature range, H\_mean = average humidity, TRI = terrain ruggedness index

**Table 4.** Results from canonical correspondence analysis for the influence of different environmental variables on community composition along the elevational gradients. Factor scores indicating the correlation between individual environmental variables and CCA axis are reported.

Factor Scores	CCA1	CCA2	CCA3	CCA4	Factor Scores	CCA1	CCA2	CCA3	CCA4
<b>Ground-dwelling arthropods</b>					<b>Hymenoptera (Formicidae)</b>				
T_mean	-0.93	-0.219	-0.106	-0.276	T_mean	0.886	0.283	0.056	-0.363
T_range	-0.592	0.357	0.462	0.556	T_range	0.436	-0.4	-0.438	0.676
H_mean	0.476	0.326	-0.113	0.809	H_mean	-0.359	-0.317	0.209	0.852
TRI	0.439	-0.893	0.09	0.029	TRI	-0.397	0.91	-0.121	-0.014
<b>Araneae</b>					<b>Coleoptera</b>				
T_mean	0.988	-0.153	-0.009	0.015	T_mean	-0.999	0.05	-0.002	0.004
T_range	0.796	0.586	0.056	-0.141	T_range	-0.606	0.794	0.012	-0.043
H_mean	-0.786	0.467	-0.154	0.374	H_mean	0.857	0.226	0.226	-0.404
TRI	-0.474	-0.315	-0.773	-0.281	TRI	0.281	-0.343	-0.81	-0.383
<b>Myriapoda</b>					<b>Staphylinidae</b>				
T_mean	-0.974	-0.211	0.056	0.052	T_mean	0.996	-0.02	-0.04	-0.078
T_range	-0.879	0.347	0.075	0.317	T_range	0.828	-0.447	-0.297	0.162
H_mean	0.694	0.521	0.096	-0.487	H_mean	-0.711	-0.229	-0.635	-0.195
TRI	0.24	0.19	-0.759	-0.575	TRI	-0.637	0.564	-0.42	0.317
<b>Insecta</b>					<b>Carabidae</b>				
T_mean	-0.922	-0.238	-0.088	-0.292	T_mean	-0.992	-0.073	0.09	0.043
T_range	-0.545	0.378	0.455	0.595	T_range	-0.72	0.651	-0.228	0.077
H_mean	0.453	0.328	-0.147	0.816	H_mean	0.797	0.277	-0.378	0.38
TRI	0.431	-0.896	0.106	0.022	TRI	0.518	-0.055	0.763	0.382
<b>Orthoptera</b>					<b>Tenebrionidae</b>				
T_mean	0.946	0.298	0.085	-0.1	T_mean	0.996	-0.04	-0.066	0.036
T_range	0.897	-0.342	-0.083	0.268	T_range	-0.416	-0.67	-0.516	-0.334
H_mean	-0.558	-0.781	-0.116	-0.254	H_mean	-0.917	-0.297	-0.023	0.264
TRI	-0.436	0.17	-0.859	-0.21	TRI	0.188	0.76	-0.603	0.152

T\_mean = average temperature, T\_range = temperature range, H\_mean = average humidity, TRI = terrain ruggedness index

## 4 | DISCUSSION

This study reveals common patterns and environmental variables associated with the community structure of ground-dwelling arthropods in the Santa Catalina Mountains. Across ground-dwelling arthropod groups, the overall dissimilarity among communities mostly aligned with differences in biome and elevation across sites. Notably, pure turnover was the predominant component of this dissimilarity, significantly contributing to overall beta diversity measures. Furthermore, environmental distances explained most of the variation in community composition, surpassing geographical distances in both significance and explanatory power across multiple ground-dwelling arthropod groups. Notably, when examining individual environmental factors, average temperature was significant and explained most of the variance in community structure across all taxa. Overall, these results might hint to a role of environmental factors, particularly temperature, in influencing community structure by species replacement in this mountain range, despite obvious differences (such as trophic role and dispersal capability) among taxa. In addition, our findings collectively point to a scenario where community structure of ground-dwelling beetles does not follow neutral dynamics but is sensitive to variation in environmental characteristics that determine species replacements.

Our findings partially align with a previous exploration of this system, where ground-dwelling arthropod communities were separately analyzed before and after summer monsoon season (Meyer et al. 2015). By using Bray-Curtis similarity coefficient, an “abundance-based extension” of the Dice-Sørensen’s coefficient used in our study (Legendre and Legendre 2012, Baselga 2013), Meyer et al. (2015) found that species assemblages varied according to biome differences in ground-dwelling arthropods as a whole. Distinct differences between biomes were also found in Coleoptera and Araneae, although they were not consistent across all biomes and depended on seasonality. In contrast, Orthoptera and Myriapoda did not show important community variation across biomes (Meyer et al. 2015). Using NMDS ordination based on overall beta dissimilarities (Dice-Sørensen’s coefficient) across the whole sampling period, we found here that ground-dwelling arthropod communities still tend to distinctly cluster based on biome and changes in elevation. However, this pattern is not only evident in ground-dwelling arthropods as a whole, but also within Insecta, Araneae, and Coleoptera separately. In these taxa, communities are also arranged progressively from lower to higher elevation biomes, reflecting the characteristic biome stacking typical of the sky island mountains (Moore et al. 2013). Similar patterns are also observed in Myriapoda, Orthoptera, Staphylinidae, Carabidae, and Formicidae, although some overlap occurs between closely related biomes in these groups, a possibly lower resolution due to the smaller number of species involved.

When comparing overall beta diversity to its pure turnover and nestedness components, pure turnover emerged as the primary contributor to differences in ground-dwelling arthropod communities in the Santa Catalina Mountains. In NMDS ordination, using Simpson’s coefficient for pure turnover leads to community clustering that closely aligns with overall beta diversity. Similar to overall beta diversity, differences in community composition due to pure turnover corresponded to variations in biome and elevation across sites. In contrast, community ordination based on nestedness dissimilarity did not show a clear pattern. Moreover, individual Mantel tests revealed that pure turnover was the most important factor influencing overall beta diversity across all taxa, explaining most of its variation.

This dominant role of pure turnover in community structure has been proposed as a key factor in explaining the variation of terrestrial species richness in mountain regions (Svenning et al. 2011). According to this theoretical framework, mountains support a high diversity of species due to the variety of environmental conditions they encompass within a small geographical area (Svenning et al. 2011). As one traverses the elevational gradients, rapid topographic and climatic changes create a mosaic of diverse habitats that foster distinct species assemblages (i.e., high pure turnover) and, consequently, greater species diversity (Fattorini et al. 2019). In line with this theoretical scenario, pure turnover has been found to be the main contributor to community dissimilarities in a wide variety of tropical and temperate mountainous systems and taxa, including plants, birds, spiders, butterflies, grasshoppers, and ants (Mota et al. 2018, Li et al. 2019, Fontana et al. 2020, Nunes et al. 2016, 2017, Nunes et al. 2020). This pattern was also found in this study exploring the ground-dwelling arthropods of the Santa Catalina Mountains, a system characterized by high species diversity, over 400 species of myriapods, orthopterans, spiders, beetles, and ants, and a significant pure turnover between communities.

While pure turnover typically dominates community dissimilarity in mountainous systems, increasingly harsh environmental conditions can still determine some degree of nested community structure along elevational gradients. Higher elevation communities, for example, may include a nested subset of species from lower elevation if their physiological tolerance allows them to colonize harsher higher elevation environments (e.g. colder temperatures) (Stevens 1992, Paknia and Rajaeai 2015, Nanda et al. 2021). On the other hand, arid mountainous systems may also present similar environmental filtering at lower elevations, where increasing temperatures and declining water availability may be limiting for the physiological tolerance of different species (Brown and Lomolino 1998, Olano et al. 2013; Di Biase et al. 2021). In line with this expectation, ground-dwelling arthropods inhabiting the lower elevations of the Colorado Plateau were found to include species also found at higher elevation, possibly resulting from the increasing aridity characterizing lower elevations in this system (Uhey et al. 2021). Nevertheless, although the Santa Catalina Mountains are characterized by similar climatic extremes at both lower and higher elevations (e.g., water scarcity at lower elevations and extreme temperatures at both lower and higher elevations) (Whittaker and Niering 1965, Brown and Lomolino 1998, Moore et al. 2013), a nested pattern did not emerge from our analyses. NMDS ordination, indeed, does not show any clustering based on biome and elevation for lower and higher elevation communities as we would expect if nestedness was an important component of overall beta diversity at these elevations.

Overall and pure turnover were significantly associated with environmental distances across all taxa. This might suggest a role of climatic and topographic conditions in sorting species into distinct communities rather than merely filtering them from a common pool. A possible scenario that finds further support by the absence of a significant relationship between the nestedness component and either environmental or geographical distances (Table 2). Geographic distances, on the other hand, presented a smaller effect in explaining overall and pure turnover in ground-dwelling arthropods as a whole, or overall turnover in Myriapoda, Araneae, Orthoptera, Coleoptera, and Carabidae.

All these findings point to a scenario in which communities of ground-dwelling arthropods of the Catalina Mountains are more structured by differences in environmental conditions than neutral dynamics.

Previous research showed that temperature is an important factor in explaining beta diversity in different groups (Chesters et al. 2019). When exploring the individual role of different environmental factors on community structure, temperature was found the most important factor explaining this variation across all taxa. This might highlight an overarching influence of temperature on ecological dynamics, even among organisms with different ecological roles and dispersal abilities. Variation in community composition therefore does not follow predictions similarly to other components of taxonomic diversity. Differences in taxonomic level indeed do not result in idiosyncratic correlations to environmental variation, as we would expect by ecological differences in narrower taxonomic groups (see Chapter 1 of this dissertation and Peters et al. 2016).

Although we cannot infer causality from this observational study, we might still speculate about the role of the environment in influencing community structure in this system. On the Santa Catalina Mountains, temperature might act as a fundamental environmental filter, shaping community composition by affecting physiological and behavioral traits, such as metabolic rates, reproductive cycles, and survival thresholds. The dominance of temperature in influencing community composition, despite differences in trophic roles (e.g., predators like Carabidae vs. decomposers like Tenebrionidae) and dispersal capacities (higher in flying insects like ants and lower in flightless arthropods like myriapods), suggests that thermal tolerance and adaptability may be critical factors for survival and distribution across all these taxa.

Because temperature decreases with elevation, and many other factors covary with elevation creating a globally harsher environment for most animals (e.g., because of higher radiation, stronger winds, lower soil nutrients, less stable substrates, shorter plant growing seasons, lower productivity; Fattorini et al. 2020), temperature might act as a proxy for other variables that can influence species composition. For this reason, it is uncertain if the association between community dissimilarity and environmental distance results from a direct or indirect effect of environmental variables on ground-dwelling arthropod community structure.

Specific physiological constraints may limit certain species to distinct environmental conditions, and the environment would therefore directly select for specialists. For example, some arthropods like Chironomidae are renowned for their specific temperature developmental requirements, so much that their fossils are used for past climate condition inference (Eggermont and Heiri 2012). In contrast, environmental conditions may indirectly select for different specialists through their effect on vegetation structure (Stange and Ayres 2010, Chesters et al. 2019). Aligning with this “indirect” scenario, biomes on the Santa Catalina Mountains follow climatically structured elevation zones (Moore et al. 2013, Meyer et al. 2015) and present distinct vegetation structure that may influence the occurrence of arthropod species. Elements of vegetation like vertical and horizontal structure, flower density, and litter depth, which widely vary in this system, have been found important drivers of species diversity and composition in arthropods (Moses et al. 2020, Muluvhahote et al. 2021).



Pure turnover, rather than nestedness, influences beta diversity, suggesting that communities differ primarily through species replacement across sites, possibly due to the unique conditions of biomes/elevations. The finding that environmental distance is more strongly and consistently associated with community composition than geographical distance might hint to the importance of environmental filters over neutral dynamics. Temperature is a key variable influencing community composition, possibly acting as a direct filter and/or a proxy for other elevation-related environmental factors. In summary, our study shows that community dissimilarities in arthropod groups along an elevational gradient are primarily structured by species turnover and covary with environmental gradients, especially temperature. Furthermore, taxonomic level does not influence these results, and different groups show similar variation in community structure and similar environmental variables associated with community structure along this elevational gradient.

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**Supplementary Material**

**Figure S1.** The results of the non-metric multi-dimensional scaling (NMDS) analysis for Staphylinidae, Carabidae, and Tenebrionidae composition, based on overall and turnover dissimilarities ( $\beta_{sor}$  and  $\beta_{sim}$ ). In each case, a few outlier sites created an artificial over clustering of sites that do not truly resemble each other in terms of species compositions.

