Chapter 10
Communities of Small Terrestrial Arthropods Change Rapidly Along a Costa Rican Elevation Gradient

M. Alex Smith, Connor Warne, Kate Pare, Sarah Dolson, Elyssa Loewen, Kelsey Jones, Megan McPhee, Lauren Stitt, Lauren Janke, Rebecca M. Smith, Heather Coatsworth, Alexandre M. M. C. Loureiro, Angel Solis, Carlos F. Viquez, Josephine Rodriguez, Jose Fernandez-Triana, Michael J. Sharkey, James Whitfield, Alejandro Masís, María Marta Chavarría, Roger Blanco, Felipe Chavarria, Eugenie Phillips-Rodríguez, Roberto Fernández, Dunia Garcia, Guillermo Pereira, Harry Ramirez, Manuel Pereira, Winnie Hallwachs, and Daniel H. Janzen

10.1 Elevational Gradients

The abundance and diversity of life changes with elevation. Indeed, because of the interactions between climate and elevation that produce environmental heterogeneity (Körner 2004, 2007), mountains are hotspots for diversity (Rahbek et al. 2019a). Numerous specific mechanisms have been proposed to explain why changes in diversity would track changes in elevation, including area, geometric constraints,

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M. A. Smith (✉) · K. Pare · M. McPhee · L. Stitt · A. M. M. C. Loureiro
Department of Integrative Biology, University of Guelph, Guelph, ON, Canada
e-mail: salex@uoguelph.ca; laurenstitt@loyalistcollege.com; a.loureiro@uoguelph.ca

C. Warne
Department of Integrative Biology, University of Guelph, Guelph, ON, Canada

School of Environmental Sciences, University of Guelph, Guelph, ON, Canada
e-mail: cwarne@uoguelph.ca

S. Dolson
Department of Integrative Biology, University of Guelph, Guelph, ON, Canada

Department of Biology, University of Ottawa, Ottawa, ON, Canada
e-mail: sdols079@uottawa.ca

E. Loewen
Department of Integrative Biology, University of Guelph, Guelph, ON, Canada

Department of Biology, University of Regina, Regina, SK, Canada

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and abiotic factors such as temperature and precipitation. Perhaps the simplest of those mechanisms is the species-area relationship. Larger areas at the base of a mountain have more space for immigration and evolution in ecological and evolutionary time-scales than do the smaller areas towards the peak (Rosenzweig 1995). In the absence of other changes along an elevational gradient, the species-area relationship predicts greater diversity in the larger downslope habitats than in the smaller upslope peaks. Another possible explanation is the geometric constraints (or the mid-domain effect [Colwell et al. 2004]), which predict diversity peaks at mid-elevations through the greatest accumulation of overlapping elevational ranges. The mid-domain effect is essentially a null model (Colwell et al. 2005) and the lack of independence between other factors may demonstrate support for this model (e.g. if area and ideal habitat peak at mid-elevations, it would produce the same pattern) (Currie and Kerr 2008). Diversity-elevation patterns have been mechanistically linked to abiotic factors such as temperature and precipitation. Changing levels of precipitation across elevation could drive changes in animal abundance and diversity if they change plant diversity or productivity (Antonelli et al. 2018). Precipitation

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K. Jones
Department of Integrative Biology, University of Guelph, Guelph, ON, Canada

Department of Biological Sciences, University of Alberta, Edmonton, AB, Canada
e-mail: kljones1@ualberta.ca

L. Janke
Department of Integrative Biology, University of Guelph, Guelph, ON, Canada

Graduate Department of Forestry John H. Daniels Faculty of Architecture, Landscape, and Design University of Toronto, Toronto, ON, Canada

R. M. Smith
Department of Integrative Biology, University of Guelph, Guelph, ON, Canada

Department of Environmental Studies, University of Victoria, Victoria, BC, Canada
e-mail: rebeccasmith@uvic.ca

H. Coatsworth
Department of Integrative Biology, University of Guelph, Guelph, ON, Canada

Department of Infectious Diseases and Immunology, University of Florida,
Gainesville, FL, USA
e-mail: h.coatsworth@ufl.edu

A. Solis
Department of Integrative Biology, University of Guelph, Guelph, ON, Canada

Departamento de Historia Natural, Museo Nacional de Costa Rica, Santo Domingo de Heredia, Costa Rica, Museo Nacional de Costa Rica, Santo Domingo, Costa Rica

C. F. Viquez
Heredia, Costa Rica, National System of Conservation Areas (SINAC), San Jose, Costa Rica

J. Rodriguez
Department of Natural Sciences, University of Virginia, Wise, VA, USA
e-mail: jjr5x@uvawise.edu

can increase with elevation (McCain and Grytness 2010), though in the tropics, this pattern can be extremely variable. Temperature changes with elevation, often in a linear fashion called the lapse rate (Barry 2008), and this change is a frequent predictor of diversity and abundance. Combining the effect of temperature and precipitation through time, Janzen (1967) made the observation that where these abiotic conditions are less variable (low seasonality) as in the neotropics (Myster in press), communities should be characterised by high turnover with increasing elevation. Because of this stability, neotropical species should be characterised by narrow physiological tolerances and experience large costs of dispersal across climatic gradients, resulting in low gene flow among populations, and high rates of allopatric speciation across that elevational gradient (Smith 2018).

Janzen's observations produced a mini-industry of ecological inquiry in the following 50+ years (Ghalambor et al. 2006; Sheldon et al. 2018b). This is perhaps not surprising considering that since von Humboldt's famous recounting of his exploration of Ecuadorian mountains, elevational gradients have intrigued biologists – in particular for how rapidly the animal and plant species changed as one moved up or down slope. The apparent vertical stacking of species' ranges results in a situation where one might expect ranges that span hundreds of kilometres across latitude or longitude to reach across only hundreds of vertical metres. Janzen's 1967 "mountain passes" observation was that the particularly dense strata along tropical elevational gradients were likely due to the relative stability (compared to temperate

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J. Fernandez-Triana
Canadian National Collection of Insects, Arachnids and Nematodes, Agriculture and
Agri-Food Canada, Ottawa, ON, Canada

M. J. Sharkey
The Hymenoptera Institute, Redlands, CA, USA
e-mail: msharkey@uky.edu

J. Whitfield
School of Integrative Biology, University of Illinois Urbana-Champaign, Urbana, IL, USA
e-mail: jwhitfie@illinois.edu

A. Masís · M. M. Chavarría · F. Chavarria
Area de Conservacion Guanacaste, Liberia, Costa Rica
e-mail: amasis@acguanacaste.ac.cr; mmchava@acguanacaste.ac.cr;
fchava@acguanacaste.ac.cr

R. Blanco
Programa de Investigacion, Area de Conservacion Guanacaste, Liberia, Costa Rica
e-mail: rblanco@acguanacaste.ac.cr

E. Phillips-Rodríguez · R. Fernández
Guanacaste Dry Forest Conservation Fund, Sector Santa Rosa, Área de Conservación
Guanacaste, Liberia, Costa Rica

D. Garcia · G. Pereira · H. Ramirez · M. Pereira
Programa Parataxónomos, Area de Conservacion Guanacaste, Liberia, Costa Rica

W. Hallwachs · D. H. Janzen
Department of Biology, University of Pennsylvania, Philadelphia, PA, USA
e-mail: whallwac@upenn.edu; djanzen@sas.upenn.edu

elevational gradients) of abiotic factors. Densely packed and rapidly changing ranges have bestowed tropical mountains with some of the greatest diversity on the planet (Antonelli et al. 2018; Rahbek et al. 2019a; Perrigo et al. 2020). Tropical mountains are thus home to an enormous proportion of global diversity, much of it endemic to these elevational "islands" (Myers et al. 2000; Rahbek et al. 2019a), because they can act as both a pump (or a cradle) for novel diversity (Chown and Gaston 2000; Camacho et al. 2021) or a museum for diversity to persist within, or retreat to, as habitat shrinks (Rahbek et al. 2019b), or all of the above.

As with many ecological phenomena, much of what is known about how diversity changes along elevation is known through, or extrapolated from, vertebrates. In a series of influential meta-analyses, Dr. Christy McCain described four predominant patterns, varying in frequency across vertebrate taxa: with increasing elevation (i) decreasing diversity; (ii) low-elevation plateau in diversity; (iii) low-elevation plateaus with mid-elevation peaks; and (iv) unimodal mid-elevational peak in diversity. Birds tended to be equally distributed amongst the trends (McCain 2009). Reptiles predominantly declined with elevation (McCain 2010). Small mammals displayed either mid-elevational diversity peaks (nonvolant; McCain 2005), or a combination of decreasing and mid-elevational peaks (bats; McCain 2007).

We have learned much from vertebrate-described patterns of macroecology. However, most organisms are invertebrates, most of these are arthropods, most of these are insects and most of these are unknown to science (Odegaard 2006; Basset et al. 2012). This enormous taxonomic impediment frames how incompletely we understand the relationship between diversity and elevation for the most diverse taxonomic group (terrestrial arthropods), in the most species-rich regions (the tropics). While there are examples of insect taxa for which we have a good taxonomic understanding (including moths – [Beck et al. 2017], and some beetle taxa such as the Carabidae [Zou et al. 2014]), for most taxa, we simply do not have the data and elevation-diversity patterns are inferred or unclear. This is most prevalent in the tropics, where, up to 90% of taxa may await formal description (Raven et al. 2021). In spite of the impediment of their enormous diversity; when diversity and elevation relationships of different insects has been investigated we have seen all of mid-elevational peaks, declines, and increases (McCoy 1990). Brehm et al. (2007) found much variation within moth taxa along a Costa Rican elevational transect with many following a mid-elevational peak. Janzen found many arthropod taxa showed mid-elevation peaks in diversity and abundance in Costa Rica (Janzen 1973) and Venezuela (Janzen et al. 1976). He postulated that this was due to a higher number of consumable small niches of plants because days were warm enough days for full photosynthesis, but colder nights so that the plants did not burn off what they made in the day. This has likely long been the cause of higher agricultural yields at mid-elevations in the tropics and was suggested to him by old agricultural discussions and considerations of plant metabolism.

Faced with this uphill battle through the morass of diversity and underfunded and unappreciated taxonomy, in many cases, we resort to a strategy of surrogacy, where a better known or understood taxon is considered to predict and hold for the unknown species or taxa. Unfortunately, efforts to use patterns elucidated for these surrogate umbrella taxa have often failed to predict and explain patterns of less charismatic organisms (Fiedler et al. 2008; Peters et al. 2016).

10.2 Expectations in the Study of High Elevation Tropical Forest Communities: Past and the Future

In temperate environments, high elevation localities are often thought to experience greater variation in abiotic conditions and therefore, high-elevation taxa are expected to show greater physiological tolerances (Mamantov et al. 2021). However, along tropical mountains, as in Costa Rica's Área de Conservación Guanacaste (ACG), the greatest variability in abiotic factors occurs in the low elevation dry forest. Here, forests may experience months with no appreciable precipitation and then effectively become rain forests during the wet season. In fact, the arthropod species in high-elevation tropical environments, such as cloud forests, are often thought to be specialised to the invariably cold and wet conditions found there. Thus, while diversity often declines with elevation, such specialisation can lead to disproportionately high biodiversity per unit area in high-elevation environments.

While high elevation cloud forest may have lower biodiversity than associated areas downslope, they also likely host higher biodiversity than one would expect based on area and history alone. Furthermore, selection for lineages able to survive in the prevalent cold-wet conditions may result in environmental filtering of the species present in a community resulting in a pattern of phylogenetic clustering (e.g. Smith et al. 2014). This is to be expected if biological feature (or function) and phylogeny were coupled (Faith 2018) such that taxa from a restricted part of the phylogeny possessed some (suite of) morphological or physiological trait(s) that fostered their success in the hostile environment. How well supported is this reasonable initial assumption of functional and phylogenetic coupling? What is known regarding how insects and arthropods tolerate extreme high and low temperatures?

Counter to this expectation for greater physiological tolerance in high vs. low variability environments, a recent and exhaustive meta-analysis found that thermal tolerance did not vary with elevation for terrestrial ectotherms (Sunday et al. 2019). However, in truth, our current conclusions about "ectotherms" or "insects" to date are in no way complete, and although the literature may contain statements regarding macroecological trends for insects or arthropods, these may be misleading due to various taxonomic biases of what taxa have been described (large-bodied) and where (the global North). Indeed, when global data are synthesised, these evident biases are apparent. For example, large meta-analyses regarding how ectotherms are affected by elevation (Freeman et al. 2018; Sunday et al. 2019) show this literature bias towards species living in the global north and toward certain taxa. Estimates of one common measure of thermal tolerance (in this case of high temperature extremes or CT_{max}) were dominated by studies on one taxon; ants (Sunday et al. 2019). There were 185 cases of thermal tolerance (CT_{max}) associated with elevation for terrestrial arthropods, and of these, 123 (66%) were from species of ants. Since these data were derived from one taxon where the individuals tested are not the unit of selection (in social species, the colony is also the unit of selection) a bias is introduced. Although there have been several comprehensive reviews of late, it is important to note there were fewer than 150 reports regarding insect range changes with elevation and of these, 2/3rds were moth species from one study and no study occurred in the neotropics (Freeman et al. 2018).

However exhaustive, and needed, analyses like Sunday et al. (2019) and Freeman et al. (2018) are, from the perspective of the terrestrial invertebrate they are only as comprehensive or predictive as the existing data allow. Indeed, one of the stated goals for the publication of such synthetic datasets like GlobalTherm is to call attention to the gaps such that we can identify and fill them (Bennett et al. 2018). Tropical terrestrial invertebrates represent such a gap. To understand how thermal tolerance changes with elevation requires more data and testing of those taxa about which we know the least. Our intent is not to criticise the authors of syntheses. We acknowledge the dearth of information for the majority of life which share their planet with us. But best to minimise such generalisations when so much remains unknown – and to resolve the so-called "taxonomic impediment" is critical to this problem. How insects will respond across elevation during climate change (or other perturbations such has drought, landslides, entomological or food pandemics, etc.) is largely not understood. In part, this is because of the scale of the problem – it is not possible to yet be comprehensive when insect diversity is overwhelmingly large and perhaps as little as 10% of species are described (Raven et al. 2021). In this slice of the world's biodiversity, using transparent proxies for formally described species hypotheses, such as DNA barcodes, may provide the greatest benefit.

Janzen's observation that mountain passes act "higher" in the tropics than their elevation would suggest, and that therefore there are predictable differences between tropical and temperate elevational gradients prompted much ecological inquiry in the intervening years (Ghalambor et al. 2006; Sheldon et al. 2018a). One example involved changes in aquatic insects across elevation in Ecuador and Colorado (Polato et al. 2018; Smith 2018). Aquatic insect species may change more rapidly than terrestrial species because they may be limited by lower oxygen levels in warm water temperatures more rapidly than terrestrial insects would be by air temperatures changes (Shah et al. 2020). Furthermore, arthropods in the terrestrial environment may be able to move in space (e.g. microhabitats such as deeper in leaf litter, etc.) to avoid these fluctuations and buffer them from the warming (Antão et al. 2020; Shah et al. 2020). However, terrestrial arthropods will be exposed to more rapid temperature fluctuations in air than in water, and so we might expect them to be more dramatically affected than aquatic systems. Because of these competing processes, it is unclear whether the patterns observed in aquatic insects will be as strong, or evident, for the diverse and abundant taxa in the forest leaf-litter.

Here we describe our ongoing work within this taxonomic impediment amongst terrestrial arthropods of the forests (and principally the leaf litter of those forests) in a neotropical hotspot of global biodiversity and conservation – the Área de Conservación Guanacaste (ACG) in northwestern Costa Rica (Janzen and Hallwachs

2016). We describe results of this work gathered in more than a decade of sampling this biodiversity using DNA barcodes as a preliminary identification of the units of diversity by including it with what is known about ecology and morphology. Interim names are a necessary step since most of the taxa we work with have no formal scientific name. We will begin by describing the ACG terrestrial environment along three volcanoes in broad strokes (to do this description justice would require many large volumes alone) followed by temperature and precipitation data collected in the past decade along one of the specific elevation gradients present within the park: Volcan Cacao.

10.3 Case Study: Elevation Gradients on the Volcanoes of the Área de Conservación Guanacaste (Costa Rica)

Área de Conservación Guanacaste (ACG) in northwestern Costa Rica is a 169,000 hectare UNESCO World Heritage Preserve that, in addition to a 43,000 hectare marine area, has a terrestrial environment that contains several isolated stratovolcanoes that create elevational gradients from sea-level to ~1800 m. Along these volcanoes, ACG contains 11 Holdridge life zones (Holdridge 1967). Upslope from the Pacific Ocean, the principal changes are from tropical dry forest to rain forest and then to cloud forest (Fig. 10.1). Of course, within these elevation gradients, there are multiple anthropogenic gradients in and around ACG associated with a long history of human habitation, including farming and ranching (Janzen and Hallwachs 2016, 2020). In ACG, there is no páramo, although in some cases (such as the active

Fig. 10.1 The ACG contains 11 Holdridge life and as you move upslope from the Pacific Ocean, the principal changes you would observe is a change from tropical dry forest to rain forest and then to cloud forest. We captured these high-resolution panoramic images (GigaPans) in our field work across this ~1500 m elevational gradient. Dry forest (near the Area Administrativa in late April): http://gigapan.com/galleries/10092/gigapans/207958, Rain forest (1200 m elevation in late April): http://gigapan.com/galleries/10092/gigapans/207933, Cloud forest (1500 m elevation in late November): http://www.gigapan.com/galleries/6817/gigapans/94235. This images and others are included in a gallery of multiple sites through time is here: http://www.gigapan.com/galleries/10092

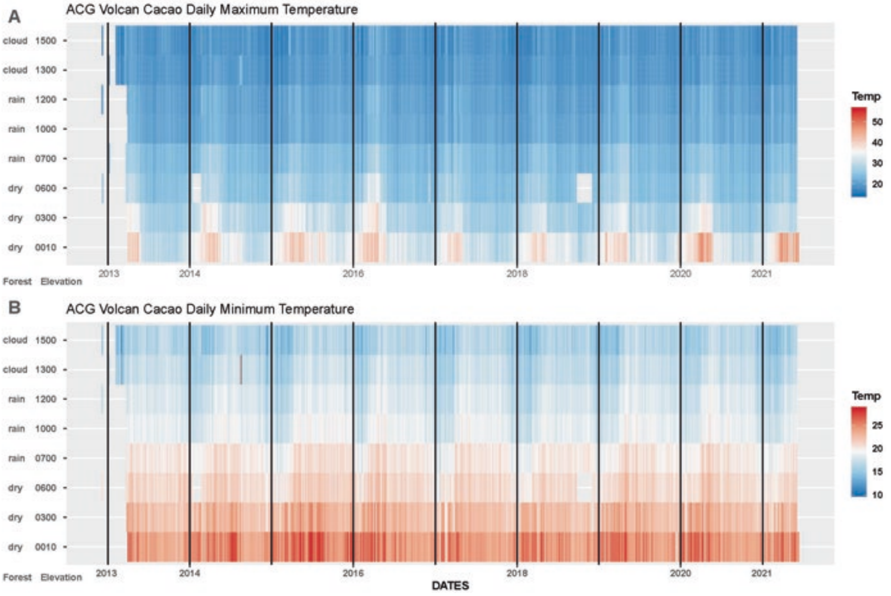

Fig. 10.2 Elevational Warming Stripes through time and space: this is a plot of more than two million temperature recordings at eight elevations across the Volcan Cacao elevational gradient in ACG between December 2012 and June 2021. At each location, temperature dataloggers recorded the temperature each 15 minutes. The maximum and minimum of these daily 96 recordings at each elevation is presented at a vertical bar along the x-axis that coloured according to the temperature scale bar for each panel. Going from left to right through time, you can see the evident seasonality of hot temperatures associated with the dry season and the comparative cooler temperatures in the rainy season. Going up the y-axis, in the mid-high elevation sites, moving from left to right through time, you can see the comparative stability in maximum temperatures

volcano Rincon de la Vieja), there are areas near the peak of the volcano that are without forest owing to recent eruptions. There is no classical "tree line" largely because the "trees" are eventually replaced with shrubs with increasing elevation.

While an ecologist working on temperate mountains may expect that high elevation communities experience the greatest variation in abiotic conditions like temperature and precipitation. However, on the ACG volcanoes, it is the low-elevation seasonal dry forest that has the greatest annual and daily variation in temperature and precipitation compared to the (historically – pre-climate change) stable cool and wet of the high elevation cloud forest (Fig. 10.2).

The forests that are vertically stratified across the ACG elevational gradient looked markedly different during the time that many of its extant resident species likely evolved or moved there as the high elevation glaciers retreated perhaps 20,000–30,000 years ago. The region has been subject to tens of thousands of years of violent volcanic change – some of which would have led to the eradication of whatever forests and communities were there previously. For example, a powerful explosion ~1.5 million years ago, where the Rincon de la Vieja volcanic complex stands today, filled a lake and destroyed forests that that had extended from Nicaragua to the city of Liberia (Janzen and Hallwachs 2020). The modern day volcanoes (Volcan Rincon de la Vieja, Cacao, and Orosi) emerged roughly 50,000, 30,000, and 20,000 years ago, respectively (Janzen and Hallwachs 2020). Forests colonised these emerging and cooling slopes during periods of Pleistocene cooling (Janzen and Hallwachs 2016). During these times, the cloud forest that we see today, restricted to the very highest elevations of the volcanoes, likely extended all the way to their base and connected them (Ramirez-Barahona and Eguiarte 2013). The massive diversity of life that calls these gradients home today would only have had a chance to evolve in situ if their speciation occurred >1.5 million years ago – and since then, their home was volcanically razed to the ground and re-erected. It is more useful to consider that the taxa we observe today have, by and large, arrived from elsewhere. Niche diversification across elevation would certainly have played a role in this long-term diversification – but the diversity of live resident here is the product of multiple processes (Antonelli 2022).

On smaller, or isolated mountains or volcanoes, as occur in ACG, the transition from rain forest to cloud forest appears at lower elevations compared to larger massifs farther south in Costa Rica due to the so called Massenerhebung Effect (Grubb 1971) (also called the mountain mass elevation effect [Flenley 1995], mountain elevation effect [McCain 2005], or Merriam Effect [Martin 1963]). Here, forest types typically seen at higher elevations on large mountains occur at lower elevations on isolated peaks (like ACG stratovolcanoes) due to the reduced capacity to reflect heat and that block the prevailing moisture laden winds than a smaller mountain has compared to a larger mountain (range) and the subsequent formation of clouds at these lower elevations. One consequence of the climate crisis is that the time covered in clouds, that any mountain would have experienced historically, will be reduced (the "lifting cloud base hypothesis" – [Pounds et al. 1999]), whereas the base height of orographic clouds formation will increase (Lawton et al. 2016) – an effect is particularly pronounced on small, isolated mountains in northwestern Costa Rica (Karmalkar et al. 2008). Indeed, the proportions of times that the peaks of the ACG volcanoes are observed to be imbedded in clouds has reduced dramatically in the past two decades (Janzen and Hallwachs 2020). Because of the high rate of endemicity in cloud forest taxa (Still et al. 1999), this consequence of the climate crisis has a dramatically negative effect on endemic biological diversity (Freeman et al. 2018) – preceded ironically by an increase in diversity as downslope taxa from the rain and dry forest move upward as occurs in numerous taxa (Warne et al. 2020; Edwards et al. in review).

A brief aside about the terms, "elevation" and "altitude." Altitude is vertical distance between two points not in contact. Elevation is the vertical distance between a point on the land's surface and a reference point (i.e. sea level) and so our data are elevational, not altitudinal. See Körner (2007) and McVicar and Körner (2013) for a concise explanation of the difference between altitude and elevation as it pertains to ecologists.

10.3.1 Sampling Leaf Litter Arthropods and Temperature Along Elevation Gradients on the Volcanoes of the Área de Conservación Guanacaste (Costa Rica)

To capture and quantify elevational, seasonal, and temporal changes in temperature and precipitation, we initiated air temperature measurements in ACG across the Volcan Cacao elevation gradient in late 2012 – and after some technical difficulties – all monitoring sites were active by March 2013. We measured air temperature using Hobotemp HOBO 64 K Pendant (Waterproof) Data Loggers and the HOBO Rain Gauge (Metric) RG3M Data Loggers set to record air temperature (every 15 minutes) and precipitation. Each monitoring site hosts two dataloggers (set on a tree trunk approximately 1 metre off the ground) in case one experiences battery failure. While there were some small interruptions (for example, at the 600 m site, both dataloggers failed for a period in 2018), these eight sites have been continuously monitoring air temperature since early 2013, resulting in >2.6 million data points over ~3500 days. These dataloggers are not contained within a solar radiation shield, but the setup at each elevation was comparable. Thus, comparisons of specific temperatures to other elevational gradients may be difficult (as direct solar radiation may cause intense microclimatic spikes), but do permit comparisons between these monitoring sites along this gradient and through time. To display the trends across elevation and through time, we adapted the "Warming Stripes" approach pioneered by Ed Hawkins (Hawkins 2018) into a vertical mountain of space, time, and temperature. For each day and each elevation, we determined the average maximum and minimum temperatures. These were then plotted through time on the x-axis where each day is a vertical bar, and across elevation on the y-axis (labelled with elevation and forest type). The shade of the daily vertical bar represents the temperature (deeper blue = colder and deeper red = hotter). The resulting visualisation (Fig. 10.2) captures the elevational, seasonal, and temporal trends in daily maximum and minimum temperature. For example, consider the dry season–rainy season periodicity in the dry forest up to ~600 m elevation. At these low elevation localities, the dry season extends from ~November to mid-May, which is reflected in the deep red the daily bars of the daily maximum temperature (Fig. 10.2a). The daily minimum temperatures show the trend during the rainy season of cooler conditions associated with the return of the rain (Fig. 10.2b). At the rain forest localities (~700–1200 m), there is reduced seasonality in the daily maximum temperatures, although one can see a slight increase in the daily maximum temperature during the dry season. The lower elevation rain forest locations bear much similarity to the down slope dry forests with respect to the daily minimum temperature – they do not cool off proportionally as much from the heat of the day (Fig. 10.2b). The cloud forest locations (1300 and 1500 m) show the low temperatures and limited variability in daily minimum or maximum temperature that still characterise these high elevation/high precipitation and low temperature forests.

These >2 million data points, are the raw data for lapse rates for daily maximum, minimum, and average temperature (Fig. 10.3). The expected change of average

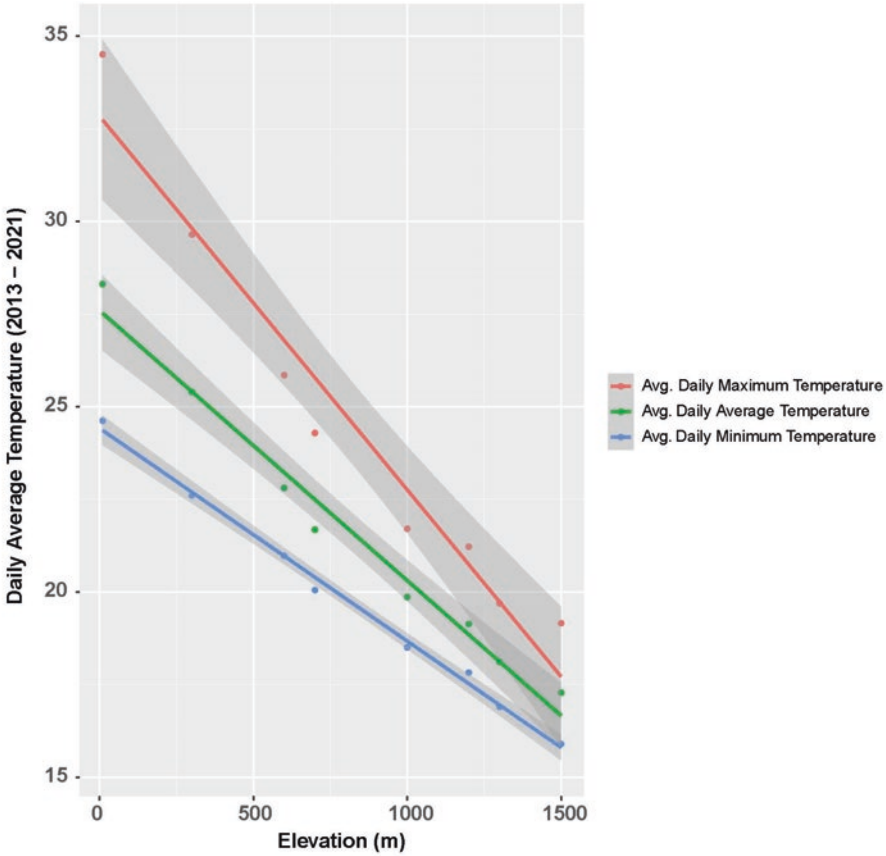

Fig. 10.3 Lapse rate for daily average (green), maximum (red), and minimum (blue) temperature across the Volcan Cacao elevation gradient. Calculated between March 2013 and June 2021, the average temperature changes 0.73 °C with 100 m elevational change, the average daily maximum temperature changes 1.0 °C with every 100 m change in elevation, and the daily average minimum changes 0.57 °C with every 100 m of elevational change

temperature is 0.7 °C/100 m elevation for the daily average, 1 °C change/100 m in daily maximum, and 0.5 °C/100 m for the daily minimum.

These vertical and seasonal changes, have all been recorded in the hottest decade that Costa Rica has endured since the start of the twentieth century. Hawkins' warming stripes for Costa Rica (https://showyourstripes.info/c/centralamerica/costarica) display this pattern dramatically. The elevational patterns from this 9-year period would have been even more pronounced if we had been able to capture the previous records with this precision. As we move farther into the climate-crisis, we are seeing more seasonality in the low-elevation dry forests (longer hot dry conditions as were evident during the 2015/2016 El Nino event) and an increased frequency with which this pulsing seasonality extends upslope into today's rain and cloud forest. When

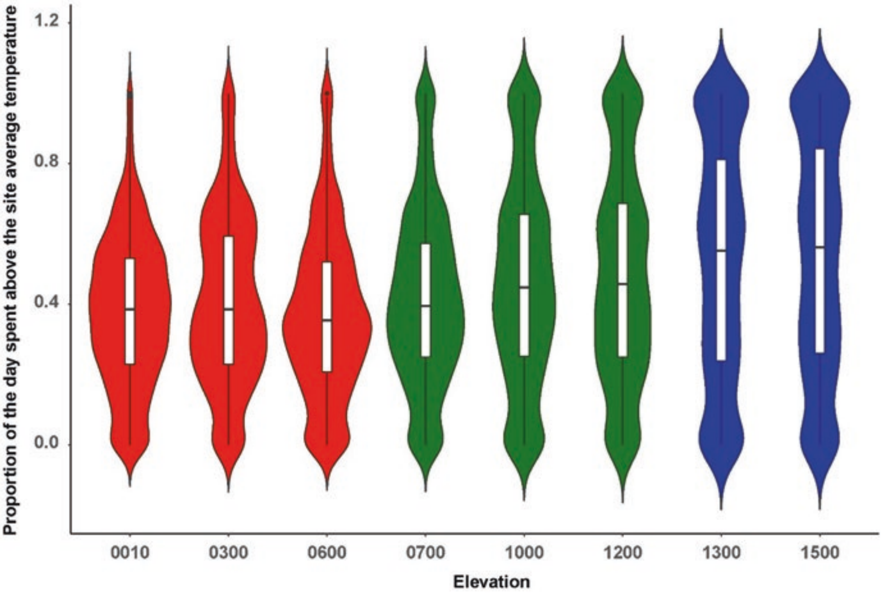

Fig. 10.4 The proportion of the day, at each site, that the temperature recorded was above the average daily temperature for that site. Cloud forest locations (blue), while cooler, with lower average temperatures – spend a greater proportion of the day above that average. Thus, while they are colder, they exist near a tipping point that makes them more vulnerable to coming changes associated with the climate crisis (increasing heat and dryness)

DHJ arrived in Liberia in 1963 the dry season was roughly 4 months long – and today it is six. A foreshadowing was during the 2015/2016 El Nino event. During this severely dry period, daily maximum temperatures, much hotter than average, can be seen leaking into the rain and cloud forest, while in addition, the expected cooling of the dry forest never occurred.

One additional way to consider the stability and therefore climate change vulnerability of the high-elevation forests in ACG is to examine the proportion of the day that each site spends above its average temperature (Fig. 10.4). The pattern is that the hot dry forests spend less than half the day above the site average, while the colder and wetter cloud forest sites spend much more of the day above the average. This is driven by the marked diurnal temperature spikes in the dry forest in the dry season, and the comparative diurnal stability in the cloud forest in the same months. The forest is on a precipice – cloud forest average temperatures are already being exceeded and the coming regularity of spikes and dryness will only serve to accelerate the rate at which these forests surpass historic average values – and in doing so – likely remove habitat for their species.

The patterns of precipitation collected using the tipping bucket rain gauge RG3M remain to be analysed. In the interim, we present a single temporal snapshot (March to September 2013) of data across the elevational gradient to demonstrate the marked differences in amounts of precipitation that each site receives during the last 3 months of the dry season and the first 3 months of the rainy season. While incomplete, we prefer this to using the WorldClim (Fick and Hijmans 2017) data because the ACG elevational gradient is steep enough that several sites occur within the same grid square of the WorldClim dataset and as such, sites that experience marked differences in precipitation would be lumped together.

The standardised sampling regime of the ACG leaf-litter organisms has been detailed elsewhere (Smith et al. 2014) and is covered in detail in the associated supplementary material (Appendix ECOG-00631 at http://www.ecography.org/readers/appendix). Briefly, we have adjusted the ALL ant protocol (Agosti and Alonso 2000) to be carried out by a single person. At each sample elevation, a representative 50 m long transect is actively sampled for 1–2 hours while six pairs of bait and pitfall traps collect for 5 hours. Three 0.5 m^2 samples of leaf litter are sifted and collected in the field using a Davis sifter, and that siftate is then placed in a mini-Winkler for approximately 48 hours. Each site has a Townes-style Malaise trap (Townes 1972) that runs continuously throughout the year and its insects collected weekly. The result is a standardised and replicated combination of six different collection methods that have been ongoing since 2008. While the protocol was initiated with the goal of sampling ants – it is efficient at collecting many leaf-litter taxa, and in the intervening 12–15 years, we have taken every available opportunity to sort, categorise, image, and DNA barcode other exemplar taxa of the leaf-litter including rove beetles (Staphylinidae: Coleoptera), spiders (Araneae: Arachnida), springtails (Collembola: Hexapoda), and pillbugs (Isopoda: “Crustacea”). In addition, we have included in this analysis one group of parasitoid wasps (Microgastrinae, Braconidae, Hymenoptera) that were captured exclusively using Townes style Malaise traps (Townes 1972) within a subset of the same gradient (300–1500 m) and at the same locations (Rodriguez 2009).

To better understand the distributions, causes, and consequences of biodiversity and elevation in the tropics, we used these resilient and standardised collection methods across the ACG elevational gradient multiple times per year intensively (and continuously throughout the year for the Malaise trap method). However, most of the tens of millions of species of multi-cellular animal on the planet weigh less than a gram, are less than a centimetre long, have never been sampled and are not named; so, conducting pragmatic or theoretical biodiversity science within this kind of taxonomic impediment is at best difficult, at worst, impossible. Certainly, without names and methods to identify samples, future comparisons across localities will be impossible. Indeed, names are critical to nearly all downstream biology (Patterson et al. 2010). Therefore, to identify and describe species, we augmented traditional taxonomic methods by DNA barcoding (Smith 2012) the samples collected here. Samples from the six taxa we include here were then either randomly sub-sampled from the total collected to equally represent samples across elevation (Formicidae, Araneae, Collembola, and Isopoda) or all collected members of the family or sub-family were analysed (Staphylinidae and Microgastrinae). All DNA sequences, trace files, collection details, and specimen images associated with the

10, 330 samples from 1243 species analysed here can be accessed on the Barcode of Life Datasystem (BOLD – [Ratnasingham and Hebert 2007]) via this DOI: https://doi.org/10.5883/DS-ASACGART.

In each of the six taxa, we used a specific molecular operational taxonomic unit (Blaxter et al. 2005) called the Barcode Index Number (or BIN) derived from the BOLD applied RESL algorithm (Ratnasingham and Hebert 2013) to estimate diversity. These BINS represent our species hypotheses. We calculated abundance and incidence matrices for each of the eight monitoring sites across Volcan Cacao. To create phylogenies for each taxon, we used a single representative high-quality sequence for each species (longest read length with the fewest ambiguities), calculated the best model for DNA substitution using MEGAX (Kumar et al. 2018), and then created a Maximum Likelihood method and General Time Reversible model (Nei and Kumar 2000). With the incidence matrix and phylogeny, we then used the picante (Kembel et al. 2010), and vegan (Oksanen et al. 2018) packages in R (Team 2021) to calculate indices of alpha diversity (phylogenetic diversity [Faith 2018], richness), betadiversity (phylobetadiversity [comdistnt]), and then to visualise community dissimilarities using Nonmetric Multidimensional Scaling (NMDS). Relationships between elevation, temperature (daily average maximum temperature [Fig. 10.2a]), and precipitation were then plotted using ggplot2 (Wickham 2016) and ggord (Beck 2017). The relationships of alpha diversity with elevation, temperature, precipitation, and area were visualised with either linear regression (lm) if the relationship was monotonic or loess (Cleveland and Loader 1996) or gam (Hastie 1992) if there were evident non-linear trends across elevation, temperature, area, or precipitation. To determine whether betadiversity exhibited spatial turnover across elevation or was nested, we used the R packages vegan and betapart (Baselga and Orme 2012).

To determine if the changes in abiotic conditions associated with elevation could influence a morphological feature (so called functional morphospace) – we estimated the length of the propodeal spines of ants in the diverse genus *Pheidole*. Here, we measured an indicator for total ant body length (Weber's length [Weber 1938]), and the length of the propodeal dorsal spine (the measurement was modified as per Sarnat et al. (2017) as beginning at the point directly dorsal to the propodeal spiracle and ending at the tip of the propodeal dorsal spine) of each specimen from images archived in BOLD using ImageJ (Schneider et al. 2012). To test whether body size and spine length were phylogenetically correlated, we calculated Blomberg's K (Blomberg et al. 2003) and Pagel's Lambda (Pagel 1999) using the R package phytools (Revell 2012). Since body size and spine length were phylogenetically correlated, we used phylogenetic independent contrasts (Felsenstein 1985) to correct for this statistical lack of independence using phytools. The highest quality sequence for each *Pheidole* BIN was then selected (as above) and then a Maximum Likelihood phylogeny was created using the General Time Reversible model (Nei and Kumar 2000). We then compared how this morphological trait varied across elevation in raw measurements and phylogenetically corrected.

10.3.2 Formicidae

Ants are the most numerous and species-rich of the social insects (Hölldobler and Wilson 1990). They have an enormous effect on the ecosystems where they live – often being called ecosystem engineers (Folgarait 1998). Their dominance extends to nearly all terrestrial environments, except Antarctica, the high latitude Arctic above the tree line, and extremely high-elevation environments such as páramo (Ward 2006). The systematics of ants, at the sub-family or generic level, is understood and well supported (Moreau et al. 2006; Borowiec et al. 2021). Within these subfamilies, there are more than 13,500 described species. However, as with most arthropod groups, there remain many species to be described. Globally, ant diversity is greatest in the tropics. For example, some have estimated that there are 900 species of ants in Costa Rica alone (a total that exceeds the United States and Canada combined [Borowiec et al. 2021]). In fact, 900 Costa Rican species is certainly an underestimate for Costa Rica, as in the ACG alone we estimate there to be at least that many species. It is well known that tropical arthropod communities change with elevation (Janzen 1973; Janzen et al. 1976; Wolda 1987; McCoy 1990; Hodkinson 2005), and ant communities conform to this trend. Ant communities become less diverse with elevation (Brühl et al. 1999; Glaser 2006; Lessard et al. 2007) or exhibit mid-elevation peaks in diversity (Andersen 1997; Samson et al. 1997; van der Hammen and Ward 2005; Longino and Branstetter 2019). These two principal patterns are not aligned with latitude (i.e. tropical and temperate elevational gradients have each been found to support each trend [Smith 2015]). One supported latitudinal comparison is that between site dissimilarity across elevation (betadiversity) changes much more rapidly in tropical rather than in temperate sites (Smith 2015).

A word about Malaise traps and ants. In the process of collecting and DNA barcoding both workers and reproductive ants collected using the standardised array of traps in ACG, we have learned much about ant species that were previously hidden. This routine explicitly includes Malaise traps, a common entomological passive intercept trap whose contents are often not used by ant biologists because it tends to catch winged males and females – the least taxonomically labile life history stages of the ant (Longino and Colwell 1997; Yoshimura and Fisher 2012). However, DNA barcodes can be used to reconcile workers and reproductive of the same species. For example, combining all trapping methods with DNA barcoding, we were able to identify males and queens of a genus of ant common in neotropical cloud forest – *Adelomyrmex* (Smith et al. 2015). Prior work had not identified these life history stages despite workers of *Adelomyrmex* being one of the more commonly encountered cloud forest ant taxa. In the dry forest, we uncovered the first known occurrence of a species from the genus *Acanthostichus* in Costa Rica (Smith et al. 2020). Before this discovery, it was a mystery as to why the distribution of species from this genus extended from Argentina to Texas without including Costa Rica, perhaps the most well-studied country in Central America for ants. *Acanthostichus* ants are subterranean termite feeders. Most survey techniques will miss them; however, reconciling queens and males via DNA barcodes of Malaise-trapped individuals

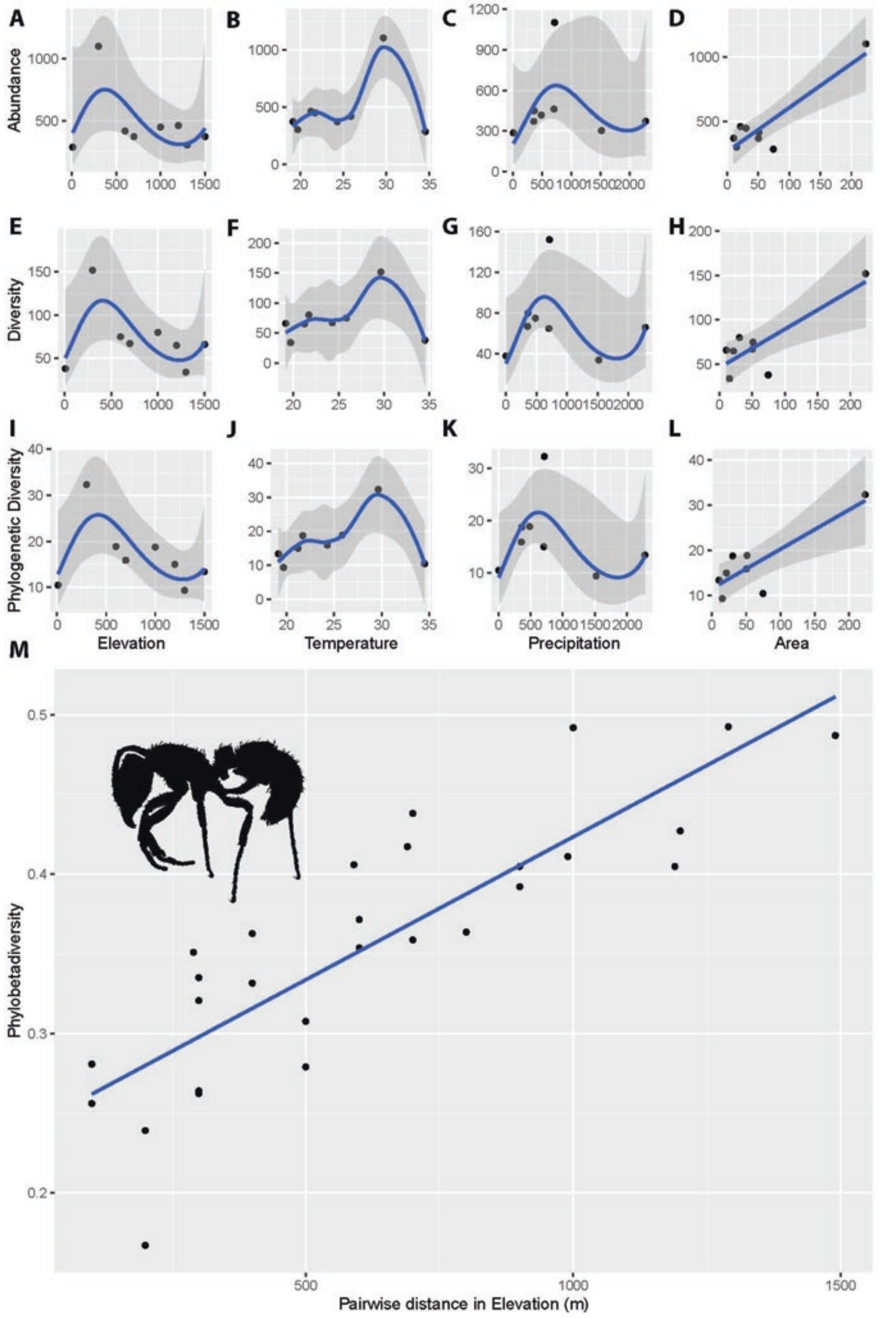

Fig. 10.5 Changes in abundance and diversity (taxonomic and phylogenetic) with elevation, temperature, and precipitation: Formicidae (ants). Ants in ACG (Smith et al. 2014) exhibit a peak in abundance and diversity at mid-elevations (**a**, **e**, **i**) or temperature (**b**, **f**, **j**). Ant diversity and

enabled the taxa to be captured in the brief window when they are above the surface for their nuptial flight. Interestingly, despite large investments in ACG into barcoding Malaise trap contents (Janzen et al. 2020), we have not seen this genus again since it's discovery. We have also documented the creep of lower elevation dry and rain forest taxa into the cloud forest in ACG by DNA barcoding older Malaise trap contents that were maintained in a freezer for a decade before our current sampling regime was initiated in 2008 (Warne et al. 2020). Barcoding Malaise trapped samples in the tropics may provide a map to reconciling parallel taxonomies that exist amongst army ant lineages (Longino 2021). Worker and male army ants are rarely found together, and parallel taxonomies have arisen as the morphologically disparate castes have been named independently. Barcoding reproductive and worker ants will help to synonymise the dual naming.

In ACG we found that ant diversity and abundance were greatest at mid-elevations, temperatures, and amounts of precipitation (Fig. 10.5; Smith et al. 2014). Diversity and abundance tended to increase with area (Fig. 10.5) and phylogenetic dissimilarity increased rapidly with increasing elevational distance between sites. Betadiversity changed rapidly with elevation (Fig. 10.12) with very little overlap between sites other than those immediately adjacent (Fig. 10.13). The community of ant species did not change via a nested process (less diverse areas being a subset of species from the more diverse areas), but rather changed via turnover where the composition of the community changed along the elevational gradient.

In the high-elevation forests of ACG, we have previously demonstrated significant phylogenetic clustering compared to lower elevation forests (Smith et al. 2014). Phylogenetic clustering is a potential signal of an "environmental filter" on the regional species pool whereby only taxa with certain morphological or physiological traits are capable of passing through the strict abiotic "filter" to be found in the "stressful" environment (cold, wet cloud forest in this case). This hypothesis of clustering and inferred abiotic filtering suggests that phylogenetic and feature diversity are coupled. Indeed, phylogenetic measures of diversity are appealing tools for the study of diverse taxa most exposed to the taxonomic impediment if they are coupled with measures of feature diversity (Owen et al. 2019). The data we have collected for the arthropod taxa of the ACG leaf-litter allow us to test this hypothesis. If phylogenetic distance and functional dissimilarity are uncoupled, as is the case when traits have evolved convergently, this would confound the phylogenetic pattern. One might predict that the localities experiencing the greatest variation in

Fig. 10.5 (continued) abundance declined with precipitation after an initial increase (**c**, **g**, **k**). Ant diversity and abundance increased with area (**d**, **h**, **l**). Community dissimilarity (here measured as phylogenetic dissimilarity) changed rapidly across elevational separation (**m**). Sites separated by more than 300 m shared few species. Temperature measured here is the daily maximum temperature recorded at each site between March 2013 and June 2022 (see Fig. 10.2). Estimates of precipitation (in mm) are a snapshot made between March and September 2013. Area is as was calculated by Dolson et al. (2021). Diversity is the number of taxa recorded at each site (richness). Phylogenetic diversity is the total branch length for the community of taxa from each site based on a maximum likelihood tree made with a GTR + G + I substitution model from the highest quality DNA barcode sequences for each species (longest read with fewest ambiguities) abiotic conditions would exhibit greater physiological tolerances (Chick et al. 2020; Mamantov et al. 2021) and/or variation in morphologies associated with survival. As an example of this extension from phylogenetic to functional patterns in diversity, we offer a case study of spine length across elevation in one diverse ant genus, *Pheidole*.

Interspecific competition among ants is so prevalent that propodeal dorsal spines have been hypothesised to serve as a protection mechanism from invertebrate attack (Dornhaus and Powell 2010). Sarnat et al. (2017) tested several mechanisms that might promote a diversity in dorsal spine length. They found evidence supporting a relationship between the length of the propodeal dorsal spine and defence against invertebrate predators (Dornhaus and Powell 2010) – those with a greater risk of predation have longer propodeal spines (Sarnat et al. 2017). They also proposed that the abiotic and biotic factors of high elevation habitats could influence the spine length of *Pheidole* but found little supporting evidence. This too is logical, since ants are ectotherms, their ability to thermoregulate is related to their microenvironment as well as their own behaviour in it (Hodkinson 2005). Ectotherms often conserve heat or prevent overheating via morphological features (Hodkinson 2005; Bishop et al. 2016) that alter the exposed surface area. Spinesence ("the elongation and proliferation of dorsal spines" [Sarnat et al. 2017]) may have evolved as a method of adjusting surface area ratios to better dissipate or absorb heat, in hot or cold environments, respectively.

We found that the relationship between *Pheidole* spine length and elevation varied among species. For example, the propodeal dorsal spine of minor *Pheidole* ants was as little as 3% and as much as 24% of the total length of the individual's mesosoma. While *Pheidole* spine length appeared to decrease with increasing elevation (Fig. 10.6a), this relationship was not significant when both the spine length and elevational range of the species were phylogenetically controlled (Fig. 10.6b). This suggests that rather than abiotic factors like temperature and precipitation that covary with elevation representing the underlying mechanism behind spine length; other factors, such as competition and predation, may affect this trait. In presenting this example, we are calling attention to the importance of testing patterns that one might consider apparent, or intuitively appealing, with data. In this case, phylogenetic corrections removed any significance to the relationship that we might have expected between a morphological trait and elevation. The capacity to conduct such phylogenetic corrections is another useful by-product of DNA barcoding a fauna since the barcodes themselves, though not accurately portraying a phylogeny; can approximate phylogenies.

10.3.3 Staphylinidae

The rove beetles (Coleoptera, Staphylinidae) are one of the largest families of insects, and eukaryotic animals worldwide (Irmler et al. 2018). They are present in an enormous range of terrestrial habitats and ecosystems (Brunke et al. 2011; Irmler et al. 2018). Staphylinid diversity is large (more than 63,000 described staphylinid

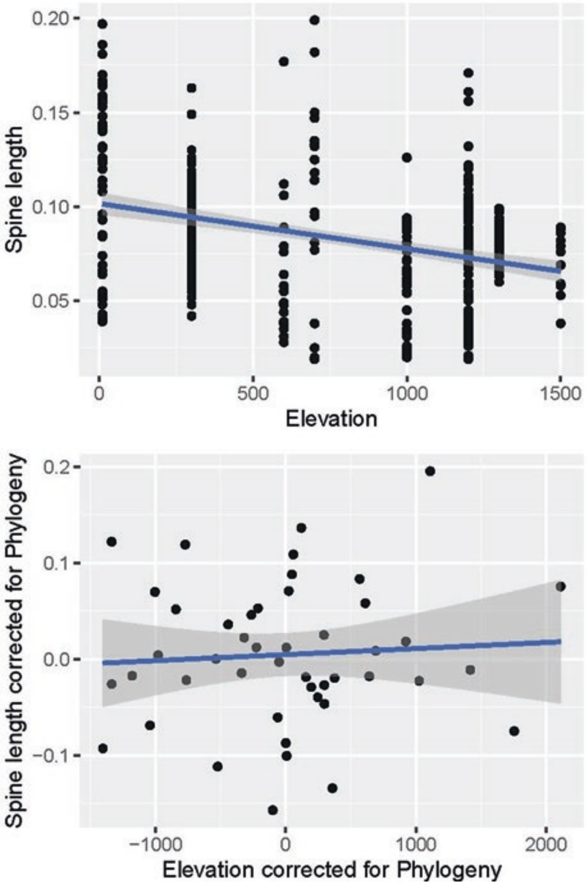

Fig. 10.6 Functional measures of diversity can change with elevation. Estimating these changes while accounting for phylogeny is important. For example, in the hyperdiverse ant genus *Pheidole*, any evident decrease in the length of propodeal spines associated with elevation (as one might expect if "spinesence" (or the elongation and proliferation of dorsal spines" [Sarnat et al. 2017]) evolved as a method of adjusting surface area ratios to better dissipate heat, in environments) (top), is removed when both spine length and elevational distribution are phylogenetically corrected (lower). In this case, removing this potential relationship (or abiotic driver) allows one to examine the likely biotic factors that could drive spinesence (such as predation)

species) and even a conservative estimate suggests there are more staphlylinid species than all vertebrate species (Irmler et al. 2018). Staphylinid species exhibit a great diversity of feeding strategies (functional groups) and occupy almost all terrestrial microhabitats (Thayer 2005). With such great diversity and so many undescribed species, much about their natural history and ecology remains unknown. Despite this, some generalisations can be made: staphylinids tend to be abundant in moist habitats (Newton and Thayer 1992; Qodri et al. 2016), their diversity is positively influenced by microhabitat diversity (Irmler and Gurlich 2007). Pohl et al.

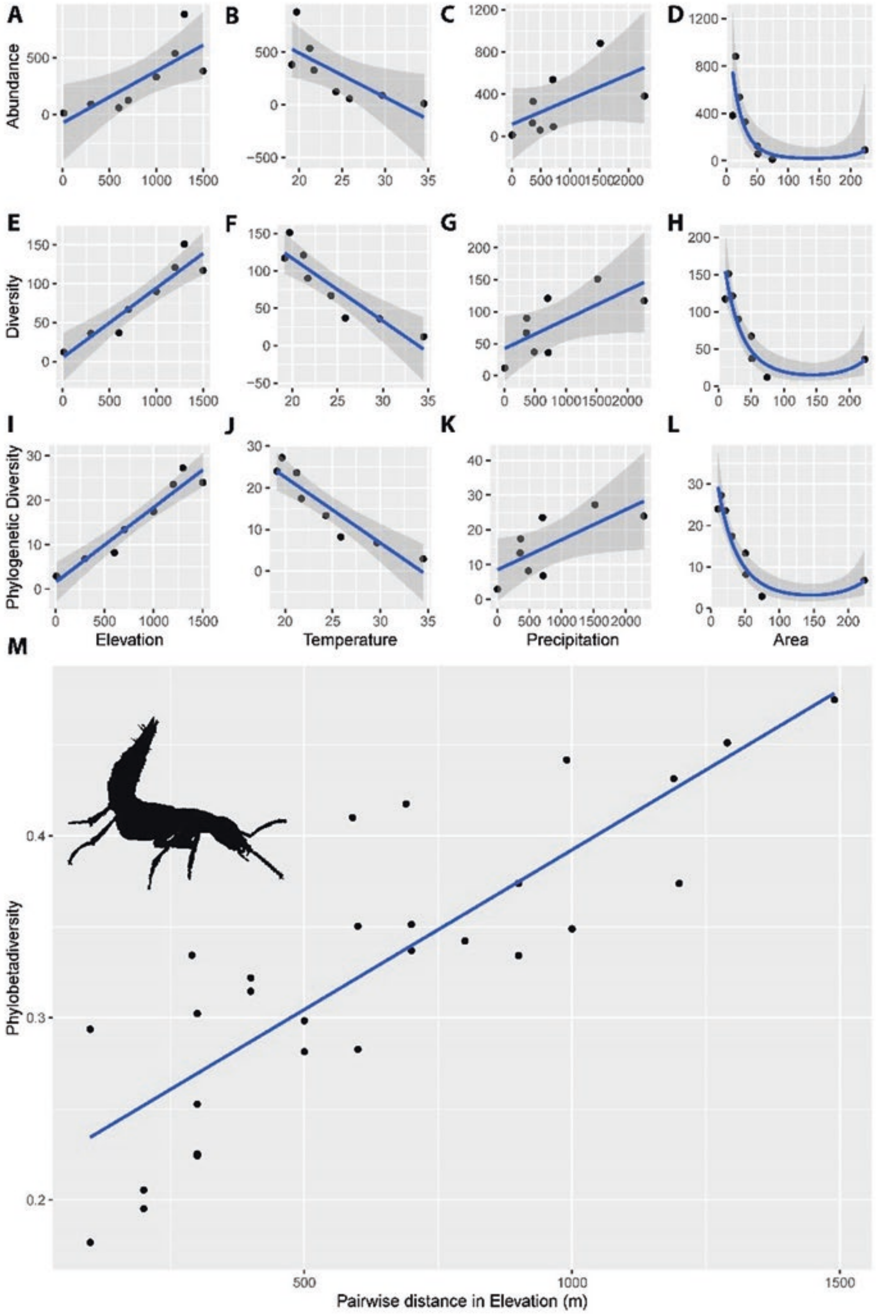

Fig. 10.7 Changes in abundance and diversity (taxonomic and phylogenetic) with elevation, temperature, and precipitation: Staphylinidae (rove beetles). Staphylinids in ACG (Dolson et al. 2021) increase in abundance and diversity with elevation (**a**, **e**, **i**), decrease with temperature (**b**, **f**, **j**) and

(2008) and Bohac (1999) showed that staphylinid diversity is also influenced by disturbance. Because staphylinids are present in most terrestrial ecosystems, some have proposed that they would be a useful indicator taxon when developing conservation priorities (Bohac 1999; Anderson and Ashe 2000; Cajaiba et al. 2017). While hyperdiverse and omnipresent, relatively few studies have examined how they relate to elevation. This is likely due to the enormous diversity of staphylinids that remain to be described (Gutiérrez-Chacon et al. 2009; Irmler et al. 2018). In particular, much remains to be known regarding how staphylinid communities change with elevation in the tropics (Irmler and Lipkow 2018).

In ACG, we found the surprising pattern that staphylinid diversity (taxonomic and phylogenetic) and abundance increased with elevation and precipitation while decreasing with increasingly hot air temperatures (Dolson et al. 2021) (Fig. 10.7). Betadiversity changed rapidly with elevation (Fig. 10.12) with very little overlap between sites outside of those immediately adjacent (Fig. 10.13). The community of staphylinid species changed between sites via turnover more than a nested process (in which less diverse areas were not a subset of species from the more diverse areas).

10.3.4 Araneae

Spiders are a dominant predator in terrestrial ecosystems (Symondson et al. 2001). Across elevational gradients, spider species and communities have exhibited both direct and indirect sensitivity to the associated changing abiotic conditions. However, spider diversity does not change uniformly across elevation. Spiders have been observed to decline (Greenstone 1984; Yanoviak et al. 2003; Binkenstein et al. 2017; González-Reyes et al. 2017; Müller et al. 2022), increase (Uetz 1976; Nogueira et al. 2021), peak at mid-elevations (McCoy 1990; Chatzaki et al. 2005; Jimenez-Valverde and Lobo 2007; Peters et al. 2016), or exhibit no change at all (Reta-Heredia et al. 2018) with elevational change.

In ACG, we examined the diversity of leaf-litter spiders across elevation and found high turnover across the entire gradient (Dolson et al. 2020). While phylogenetic- or richness-based indices weakly appeared to decline after reaching a moderate mid-elevation peak, neither the diversity nor the abundance of spiders was significantly correlated with precipitation or area (Fig. 10.8).

Fig. 10.7 (continued) increase with precipitation (**c**, **g**, **k**). Diversity and abundance declined rapidly with area (**d**, **h**, **l**). Community dissimilarity (measured as phylogenetic dissimilarity) changed rapidly across elevational separation (**m**). Sites separated by more than 300 m shared few species. Temperature measured here is the daily maximum temperature recorded at each site between March 2013 and June 2022 (see Fig. 10.2). Estimates of precipitation (in mm) are based on a snapshot made between March and September 2013. Area is as was calculated by Dolson et al. (2021). Diversity is the number of taxa recorded at each site (richness). Phylogenetic diversity is the total branch length for the community of taxa from each site based on a maximum likelihood tree made with a GTR + G + I substitution model from the highest quality DNA barcode sequences for each species (longest read with fewest ambiguities)

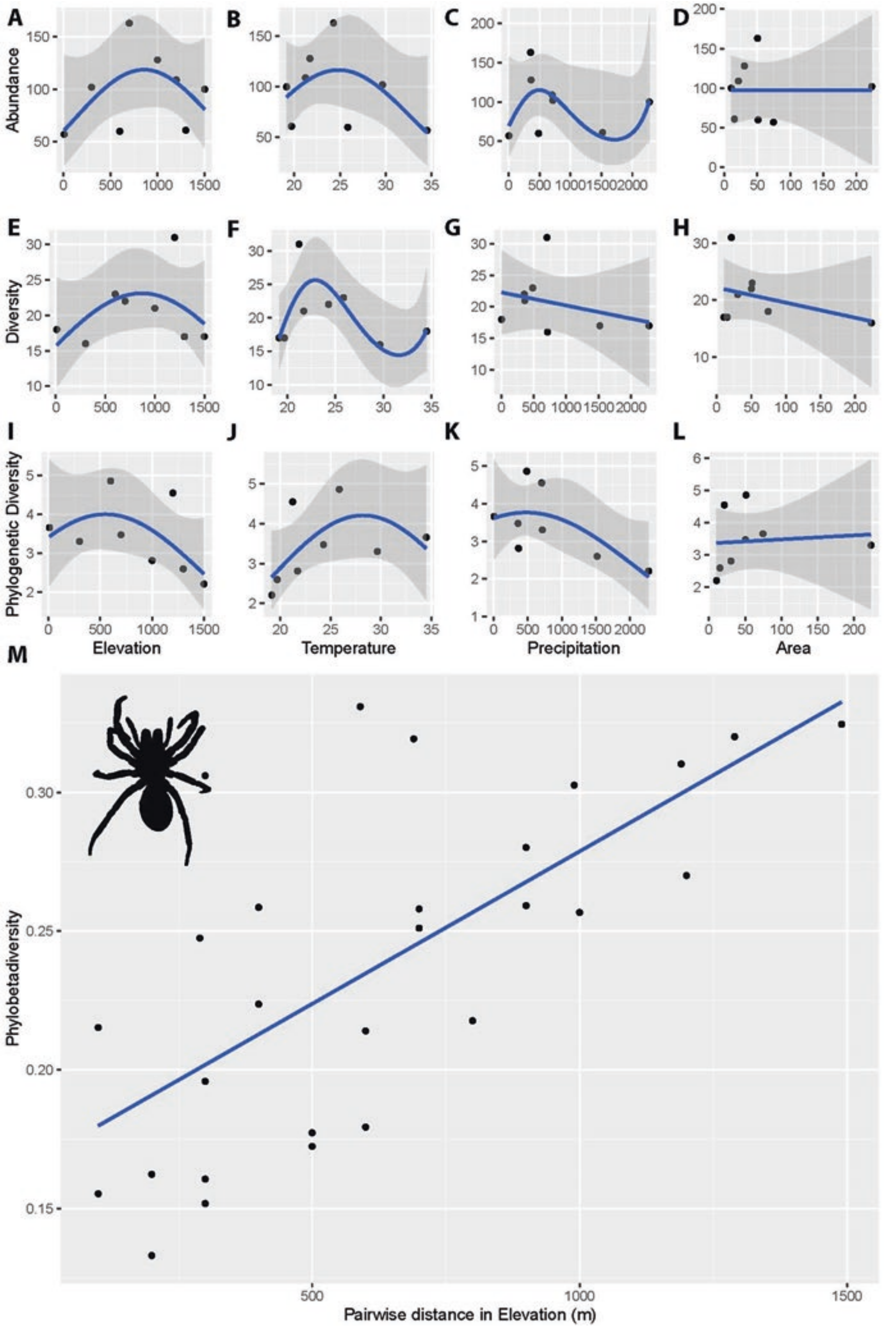

Fig. 10.8 Changes in abundance and diversity (taxonomic and phylogenetic) with elevation, temperature, and precipitation: Araneae (spiders). Spiders in ACG (Dolson et al. 2020) display a slight intermediate peak in abundance and diversity with elevation (**a**, **e**, **i**), and temperature (**b**, **f**, **j**) and

Spiders are the dominant predators in many terrestrial environments (Turnbull 1973) and have been used by others as an indicator taxon (Marc et al. 1999). However, on Cacao, we found no prominent change with elevation for indices of alpha diversity. Malumbres-Olarte et al. (2018) also found no relationship between spider diversity and elevation in Tanzania. They proposed that if niche availability was equivalent at different elevations then richness ought not to vary across the apparent gradient.

10.3.5 Collembola

Collembola (springtails) are a class of small, wingless hexapods that live within the top 10–15 cm of soil (Whalen and Sampedro 2010), in leaf litter, and on vegetation (Illig et al. 2010). Here, they are one of the most abundant taxa (Potapov et al. 2020); they are often found in large densities in most terrestrial ecosystems and on every continent, including Antarctica, (Plowman 1979; Rusek 1998; Whalen and Sampedro 2010; Fiera and Ulrich 2012). Due to their high abundance, Collembola can influence ecological processes such as the mechanical breakdown of organic matter, soil aggregation, plant establishment, and plant diversity (Rusek 1998; Siddiky et al. 2012; Caravaca and Ruess 2014). Furthermore, Collembola grazing can change the soil microbial community by spreading fungal spores (Poole 1959; Parkinson et al. 1979; Hanlon 1981; Newell 1984).

Collembola species show preference in their habitat selection; and distinct forest types differ in their species diversity and composition (Bolger et al. 2013). The majority of species within Collembola communities are only represented by a few individuals, while the majority of individuals in the community belong to just a few species (Bolger et al. 2013). Collembola are sensitive to conditions that change with elevation, especially desiccation (Pflug and Wolters 2001). Drought can cause some species to stop molting and reproducing and can reduce Collembola diversity and species richness (Waagner et al. 2011; Xu et al. 2012). Despite their abundance, they are a morphologically cryptic group (Cicconardi et al. 2013) and, particularly in the tropics, are exposed to a taxonomic impediment (Smith 2012; Potapov et al. 2020) that leaves them frequently understudied.

As a result of their tight association with water/humidity, one might expect that there would be evident associations between abundance and diversity across

◄

Fig. 10.8 (continued) appear to decrease slightly with precipitation (**c**, **g**, **k**). Diversity and abundance have no apparent change with area (**d**, **h**, **l**). Community dissimilarity (measured as phylogenetic dissimilarity) changed rapidly across elevational separation (**m**). Sites separated by more than 300 m shared few species. Temperature measured here is the daily maximum temperature recorded at each site between March 2013 and June 2022 (see Fig. 10.2). Estimates of precipitation (in mm) are a snapshot made between March and September 2013. Area is as was calculated by Dolson et al. (2021). Diversity is the number of taxa recorded at each site (richness). Phylogenetic diversity is the total branch length for the community of taxa from each site based on a maximum likelihood tree made with a GTR + G + I substitution model from the highest quality DNA barcode sequences for each species (longest read with fewest ambiguities)

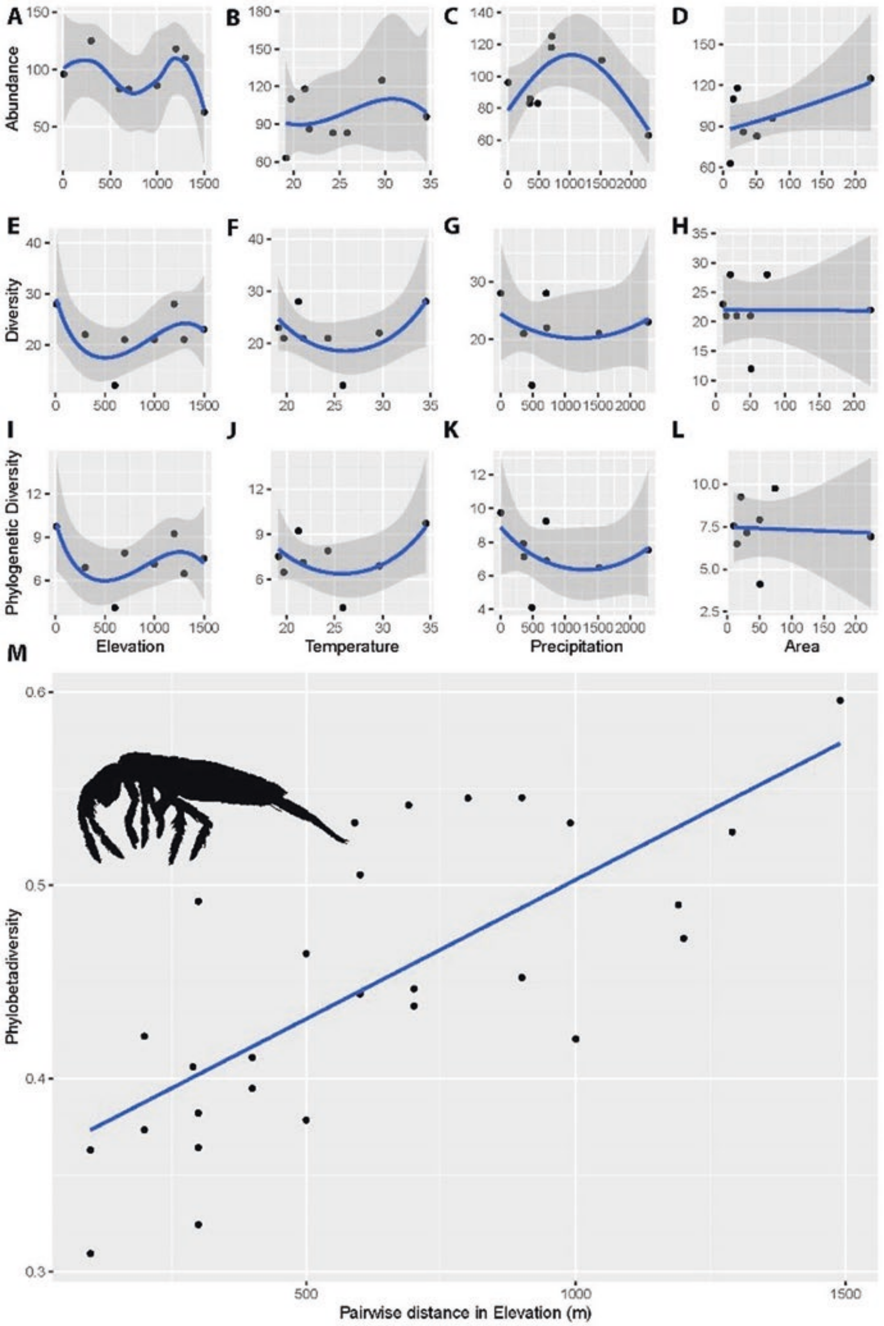

Fig. 10.9 Changes in abundance and diversity (taxonomic and phylogenetic) with elevation, temperature, and precipitation: Collembola (springtails). As a Class, the ACG springtails display no

neotropical elevation. Indeed, in some localities, their diversity (often estimated as morphospecies) declined with elevation (Cutz-Pool et al. 2010; Sun et al. 2020); however, mid-elevation peaks in diversity have also been observed (García-Gómez et al. 2009; Greenslade and Kitching 2011; Xie et al. 2022). The relationship between Collembola abundance and elevation is also variable among mountains. Abundance has been shown both to increase (Sadaka and Ponge 2003) and decrease (Jing et al. 2005; Sun et al. 2020) with elevation.

In ACG, we found that abundance displayed two apparent peaks with elevation, no clear trend with temperature, a mid-value peak with precipitation, and an increase with area (Fig. 10.9a–d). Collembola richness and phylogenetic diversity displayed a mid-elevation trough with elevation and temperature, and no clear relationship to precipitation or temperature (Fig. 10.9e–l). Collembolan patterns of betadiversity across elevation were steep (communities changed rapidly [Fig. 10.12]), had little overlap other than among adjacent sites, and patterns were principally based on turnover and not nesting (Fig. 10.13).

Interestingly, there was some indication of competing elevational patterns of diversity amongst the orders within the taxon as a whole – a mid-elevation peak in Poduromorpha, an elevational trough in Symphypleona, and a negative relationship between diversity and elevation for the Entomobryomorpha (Pare 2015). Similar patterns of taxonomic discontinuity across elevation have been uncovered in other taxa. For example, Fiedler et al. (2008) found multiple elevation/diversity patterns within multiple moth families across an Ecuadorian elevation gradient. We found two peaks in collembola abundance across the ACG elevational gradient. Xie et al. (2022) also found a secondary peak in abundance at a higher elevation site than the peak that corresponded with their mid-elevation diversity peak. They associated their second peak with the large number of individuals associated with taxa adapted to the harsh and cold conditions. Further sampling and sequencing of these abundant and charismatic groups will be needed to elucidate these relationships in ACG.

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Fig. 10.9 (continued) clear relationship between diversity or abundance with elevation, temperature, or precipitation. Abundance is only idiosyncratically related to elevation and temperature (**a**, **b**), displays a mid-value peak with elevation (**c**), and is positively related to area (**d**). Diversity appears to show a mid-elevation trough (**e**, **f**, **i**, **j**) and no apparent trend with precipitation or area (**g**, **h**, **k**, **l**). While ambiguous as a class, there are apparently conflicting patterns within the class at the Ordinal level (Pare 2015). Community dissimilarity (measured as phylogenetic dissimilarity) changed rapidly across elevational separation. Sites separated by more than 300 m shared few species (**m**). Temperature measured here is the daily maximum temperature recorded at each site between March 2013 and June 2022 (see Fig. 10.2). Estimates of precipitation (in mm) are a snapshot made between March and September 2013. Area is as was calculated by Dolson et al. (2021). Diversity is the number of taxa recorded at each site (richness). Phylogenetic diversity is the total branch length for the community of taxa from each site based on a maximum likelihood tree made with a GTR + G + I substitution model from the highest quality DNA barcode sequences for each species (longest read with fewest ambiguities)

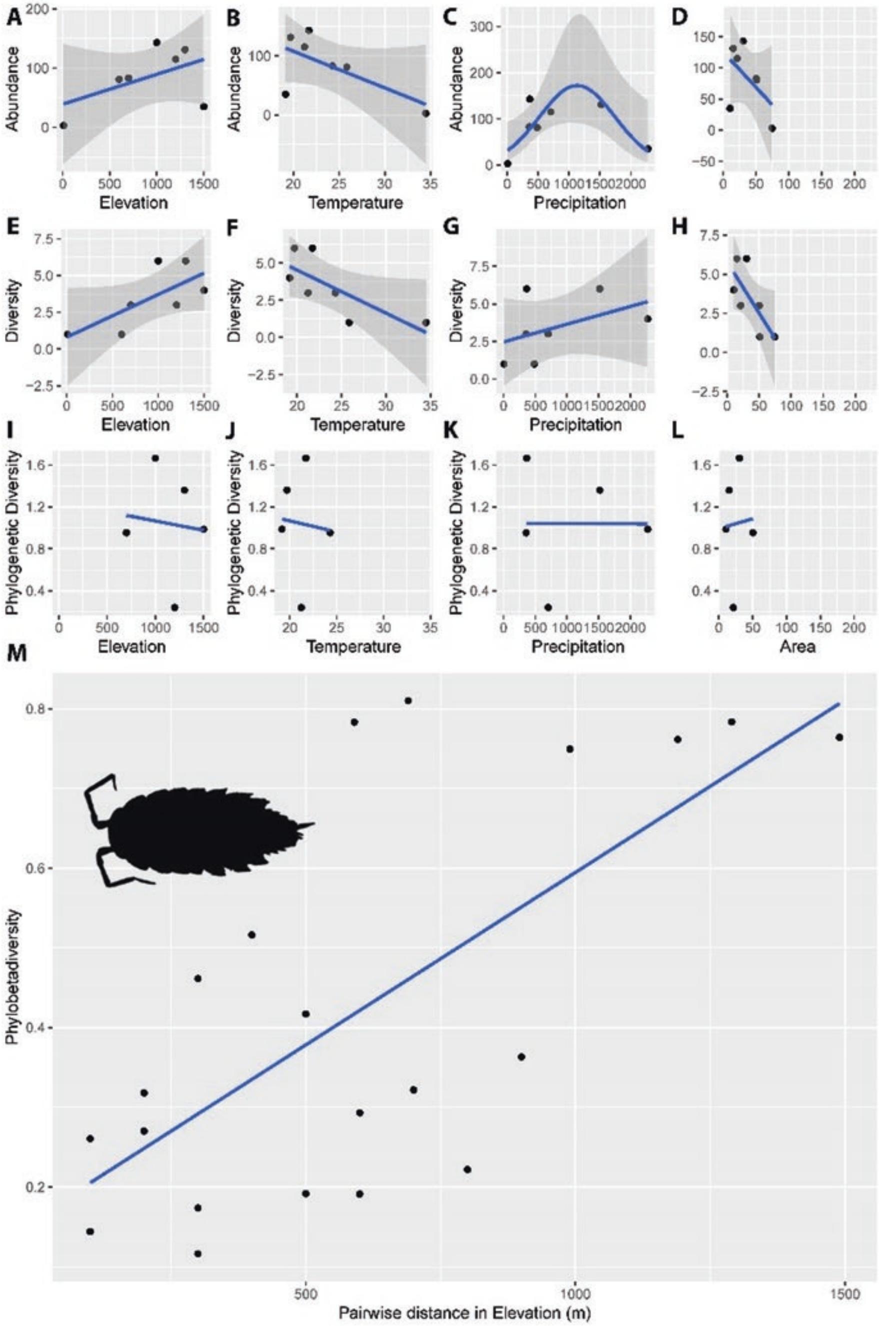

Fig. 10.10 Changes in abundance and diversity (taxonomic and phylogenetic) with elevation, temperature, and precipitation: Isopoda (pill bugs). ACG isopods increased in abundance and

10.3.6 Isopoda

Terrestrial isopod crustaceans are omnivorous detritivores that can be omnipresent in and on leaf-litter. As their cuticle is relatively thin (compared to other arthropods in the leaf-litter), they tend to exhibit a marked dependence on high temperature and humidity (Sfenthourakis 1992; Sfenthourakis and Hornung 2018). However, despite these tight associations, isopod abundance and diversity does not change uniformly with elevation (Sfenthourakis 1992; Sfenthourakis et al. 2005; Khila et al. 2018). For example, in Greece, Sfenthourakis (1992) found that diversity decreased with elevation, while in Tunisia, (Khila et al. 2018) reported that isopod diversity peaked at mid-elevations. Although there are taxonomic and phylogenetic descriptions of terrestrial isopods in Costa Rica (e.g. Leistikow 2000), much remains to be learned regarding the distribution and diversity of terrestrial isopods – in Costa Rica and in the tropics in general (Sfenthourakis and Hornung 2018) (Fig. 10.10).

Isopod abundance may already have changed from a historical norm. DHJ and WH remember sampling in the cloud forest of Volcan Cacao in the mid-1980s, where all exposed surfaces were covered with active isopods. This is not the case today when Smith samples in the same forests. We found that isopod abundance in the ACG peaked at mid-elevations and was not highest in the wettest environments at the highest elevations. Though isopod betadiversity shows a pattern of spatial turnover with elevation, it also showed the strongest component of nestedness of all the taxa we observed. In addition, the relationship between dissimilarity and elevational separation is the steepest compared to the other taxa. While this may suggest that the isopods are more isolated between elevational bands (as their dependence on moist and humid conditions and lack of areal dispersal might suggest), these results may be impacted by the comparatively sparse specimen sampling and barcoding. More work on these crustaceans is required to determine whether the relationship between their betadiversity and elevational separation are in fact different from the other taxa we have examined here.

Fig. 10.10 (continued) diversity with elevation (**a**, **d**) and decreased with temperature (**b**, **e**). Diversity increased with precipitation (**g**), while abundance showed a mid-value peak (**c**). Both diversity and abundance declined with area (**d**, **h**). Because of the presence of only one taxon in the lowest elevation forests recovered to date, phylogenetic patterns of diversity are available across only the mid-high elevation part of the volcano and patterns are ambiguous (**i**, **j**, **k**, **l**). Community dissimilarity (measured as phylogenetic dissimilarity) changed rapidly across elevational separation (**m**). Sites separated by more than 1–200 m shared few species. Temperature measured here is the daily maximum temperature recorded at each site between March 2013 and June 2022 (see Fig. 10.2). Estimates of precipitation (in mm) are a snapshot made between March and September 2013. Area is as was calculated by Dolson et al. (2021). Diversity is the number of taxa recorded at each site (richness). Phylogenetic diversity is the total branch length for the community of taxa from each site based on a maximum likelihood tree made with a GTR + G + I substitution model from the highest quality DNA barcode sequences for each species (longest read with fewest ambiguities)

10.3.7 Microgastrinae Parasitoid Wasps

Parasitoid insects (those whose larvae develop by feeding on a single arthropod host, killing it in the process [Godfray 1994]) may be the most species-rich group of insects in the world (Forbes et al. 2018). With extreme taxonomic and functional diversity, perhaps it is not surprising that there is no uniform elevational pattern exhibited by parasitoid insects. One family of parasitoid fly (Tachinidae) was shown to have a negative relationship between diversity and elevation, and a positive relationship with temperature (Corcos et al. 2018). Ichneumonidae in Honduras, Guatemala, and Nicaragua were found to peak in diversity at mid-elevations (Veijalainen et al. 2014). Another family of Hymenopteran parasitoids (Encyrtidae) exhibited a positive relationship between diversity and elevation (Veijalainen et al. 2014). Gauld (1988) reported that diversity declined between the lowland dry forest and higher cloud forest in northwestern Costa Rica for the Ophioninae (a subfamily of Ichneumonidae), while for another subfamily (the Pimplinae) diversity increased (Gaston and Gauld 1993) as collected by Malaise traps – which catch enormous numbers of species, but conspicuously catch a very small proportion of other parasitoid species and higher taxa, known to be in the same forest by rearing them. Also working in Costa Rica, Aguirre et al. (2018) found that one subfamily of Braconidae exhibited a negative relationship between diversity and elevation, while another displayed two peaks of diversity before declining at high elevations. McCoy found that parasitoid abundance increased with elevation (1990). Janzen found that parasitoid abundance exhibited a mid-elevation plateau and then declined in high elevations in the Venezuelan Andes (Janzen et al. 1976). While there may be a diversity of relationships to elevation within the hyperdiverse parasitoid insects, one common deterministic driver is likely to be the diversity of actual or potential hosts that these predators can consume.

The Microgastrinae are a subfamily of braconid (Hymenoptera) parasitoid wasp. They are globally hyperdiverse, ubiquitous obligate endoparasitoids of larval Lepidoptera (butterflies and moths) (Rodriguez et al. 2013; Whitfield et al. 2018; Fernandez-Triana et al. 2020). Global diversity of the group may be as high as 40–50,000 species (Rodriguez et al. 2013; Whitfield et al. 2018; Fernandez-Triana et al. 2020). Within the ACG, our understanding of this group has been dramatically altered by DNA barcoding of parasitoids derived from the rearing of caterpillar hosts and the Malaise trapping of adult wasps in the same forests (Smith et al. 2008). In many cases, what were previously thought to be host generalists were better understood as complexes of morphologically cryptic complexes of host specialists. Indeed, in one case, a specimen initially identified by specialists on the family Braconidae as belonging to a single previously described species, *Apanteles leucostigmus,* was eventually formally split into 39 different species based on host taxon, genetic differences, and morphological discontinuities (Fernandez-Triana et al. 2014b). Many, many more new species of microgastrine wasp remain to be described in ACG.

We used microgastrine wasps Malaise-trapped between 300 and 1500 m on Volcan Cacao that had been DNA barcoded (including some that have been used in the description of new species (e.g. Fernandez-Triana et al. 2014a; Carolina Arias-Penna et al. 2019) to determine whether the diversity and abundance of these important predators changed with elevation. These sites represent a subset (four sites between 300 and 1500 m) of the total elevational gradient considered for the other taxa described here (eight sites between 10 and 1500 m); however, this comparison includes all three forest types and is not a subset of the animals trapped (i.e. all microgastrine wasps collected in the traps–1565 specimens from 165 species) that were DNA barcoded (Rodriguez 2009).

In ACG, we found that the relationship between the diversity and abundance of micrograstrines exhibited an apparent trough with elevation and diversity was higher in dry forest and cloud forest than in rain forest (Fig. 10.11). This relationship was more strongly associated with area and temperature than precipitation (Fig. 10.11). Microgastrine patterns of betadiversity across elevation were steep (communities changed rapidly Fig. 10.12), with little overlap outside of adjacent sites and patterns were principally based on turnover and not nesting (Fig. 10.13). Interestingly, the trough revealed here with Malaise-trapped microgastrines is very similar to what Malaise traps at nearly the same locations captured for another subfamily of parasitoids (Pimplinae, Ichneumonidae) in terms of diversity and abundance (Gaston and Gauld 1993). The similar pattern suggests perhaps a common mechanism underlying the pattern, but current ongoing sampling from rearing and Malaise trapping are showing that all of these Microgastrinae data are far too preliminary to be used for generalisations at this time. There is as little as 15–20% overlap between the species reared in these forests and the species Malaise trapped in them.

Does the trough of microgastrine diversity track diversity and/or abundance of host taxa? Host use by a parasitoid species is intimate and important information. However, since a large proportion of described taxa are from intercept traps like the Malaise, host-use is unknown for more than half the described species of Micrograstrinae (Fernandez-Triana et al. 2020). For those species for which it is known, they come predominantly from ten families of Lepidoptera (Noctuidae, Tortricidae, Pyralidae, Crambidae, Geometridae, Gracillariidae, Depressariidae, Hesperiidae, Gelechiidae, and Nymphalidae [Fernandez-Triana et al. 2020]). Is there a trend of similar host use with the parasitoid groups where Gauld may also have found rain forest diversity to be lower than dry or cloud forests? The Pimplinae are also predominantly parasitoids of Lepidoptera larvae and pupae (although some are parasitoids of spiders [Gauld and Dubois 2006]). Based on the Pimplinae reared from the Janzen-Hallwachs caterpillar rearing program in ACG that have been DNA barcoded – the top four Lepidopteran host familes represented are Saturniidae, Sphingidae, Hesperiidae, and the Erebidae. Between the two parasitoid taxa, we see limited taxonomic overlap with one of the two taxa (the Pimplinae) tending towards larger host species. If there is a common mechanism underlying these patterns that is related to host use, it is not discernable at a coarse taxonomic level. More study is required to unravel the potential relationship between parasitoid diversity and host

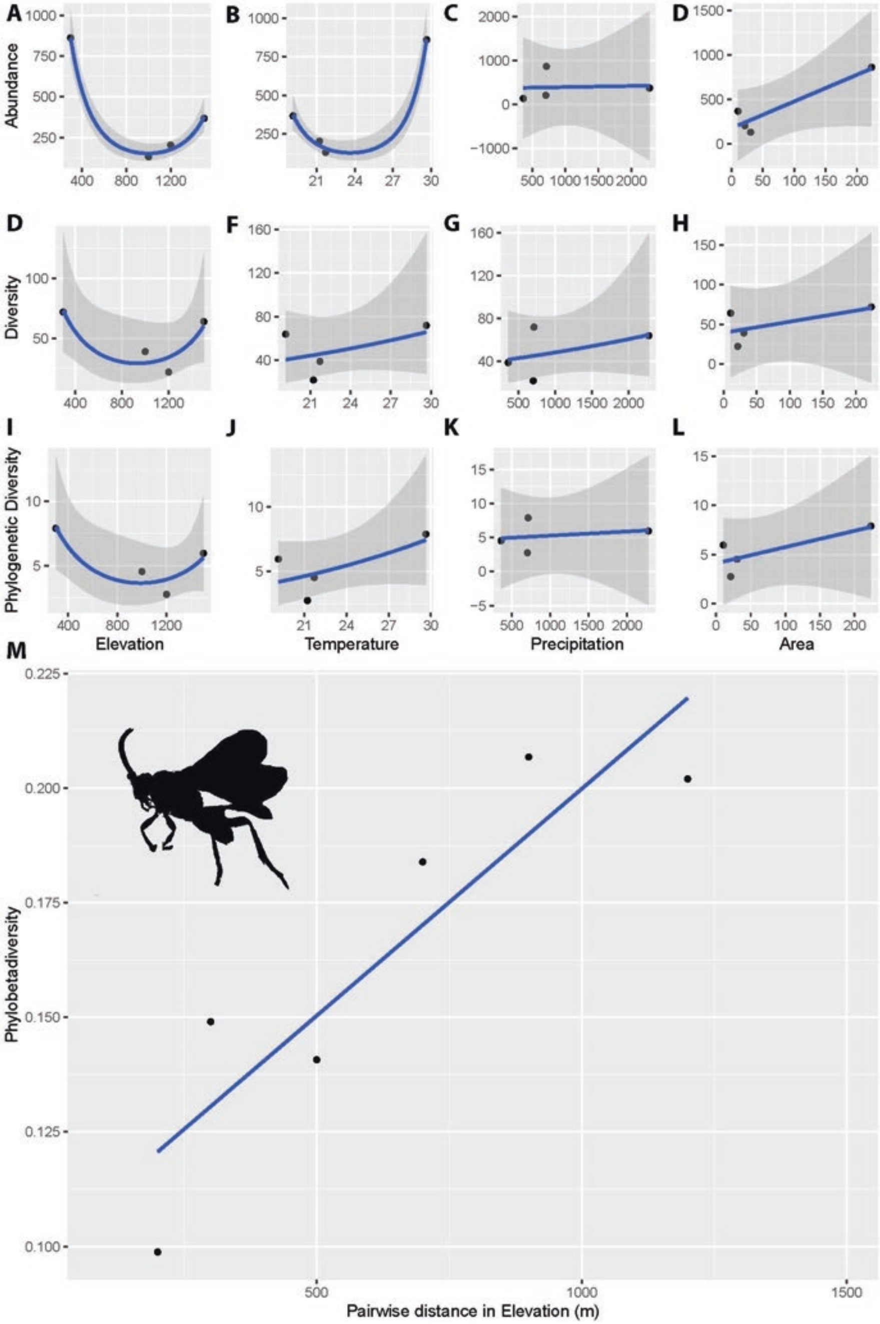

Fig. 10.11 Changes in abundance and diversity (taxonomic and phylogenetic) with elevation, temperature, precipitation, and area: Microgastrinae (parasitoid wasps). ACG microgastrine (Rodriguez 2009) decline with elevation, exhibiting a mid-elevation trough in abundance and

diversity across elevation in ACG other than there are obviously many fewer species at higher elevations than lower elevations, and that with only Malaise trapping, it cannot be known which species are seasonal migrants passing the lowland dry season refuging in moist cool cloud forest, before returning to the lowlands when the rains begin (Hunt et al. 1999).

10.4 Conclusions and Next Steps

Stable bands of temperature along this small volcano in northwestern Costa Rica present a significant boundary to some of the most abundant and diverse taxa of leaf-litter invertebrates across elevation. Although separated by only hundreds of meters, community change across this elevational gradient occurs with dramatic speed (Fig. 10.14). The cold, historically invariant cloud forests are rapidly heating and drying. Declines in cloud immersion frequency may remove up to 80% or more of Neotropical cloud forests (Helmer et al. 2019). Species will track this phenomenon and move upslope (Feeley et al. 2013; Pecl Gretta et al. 2017; Warne et al. 2020), but there is no more "top." Most species of cloud forest trees are unable to invade higher or lower elevations (Rehm and Feeley 2015), and it will be the same for their resident arthropod communities. It is very likely that many downslope taxa will establish successfully upon arrival; and many endemics to these cold wet places will soon become locally extinct. For some taxa that can get there, the wet Caribbean slopes to the east of our study transect may be accessible as a refuge from the dry warmth of the lower elevation Pacific slope marching into what used to be cloud forest. For the others (for the majority?), to whom such a distance or habitat represents an impossible dispersal, there will be local extirpations and even extinctions. It has become increasingly clear that many of the unnamed insect taxa in these tropical mountains are smaller, more regionally restricted, and/or more host-specific than had been imagined (Bickford et al. 2007; Scheffers et al. 2012; Hood et al. 2015), and many of the taxa in these sky islands are likely endemic (Myers et al. 2000; Dirnböck et al. 2011; Rahbek et al. 2019a), so in many of these cases, an

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Fig. 10.11 (continued) diversity between dry forest and rain forest and then increase towards the cloud forest (**a**, **d**, **i**). Microgastrine diversity and abundance increased with temperature (**b**, **f**, **j**), showed no apparent relationship with precipitation (**c**, **j**, **k**) and increased with area (**d**, **h**, **l**). Community dissimilarity (measured as phylogenetic dissimilarity) changed rapidly across elevational separation (**m**). Sites separated by more than 1–200 m shared few species. Collection of microgastrine wasps differed from the other invertebrates analysed here. Parasitoids were captured exclusively using Malaise traps (Townes 1962) maintained at four elevation sites between 1998–2000, 2008, and 2012/2013. Temperature presented here is the daily maximum temperature recorded at each site between March 2013 and June 2022 (see Fig. 10.2). Estimates of precipitation (in mm) are a snapshot made between March and September 2013. Area is as was calculated by Dolson et al. (2021). Diversity is the number of taxa recorded at each site (richness). Phylogenetic diversity is the total branch length for the community of taxa from each site based on a maximum likelihood tree made with a GTR + G + I substitution model from the highest quality DNA barcode sequences for each species (longest read with fewest ambiguities)

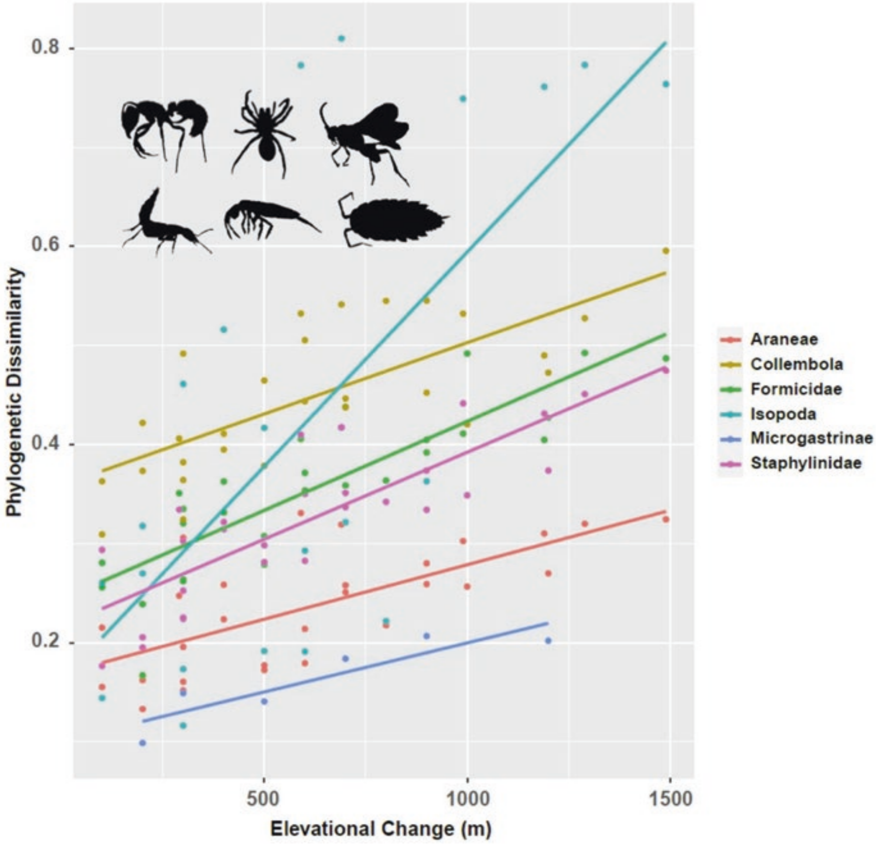

Fig. 10.12 Changes in community dissimilarity (betadiversity) across the ACG elevational gradient. Betadiversity (measured here as phylogenetic dissimilarity) changes rapidly for all taxa examined here. What does this rapid change look like on the ground? Of the nearly 1300 species examined here, sites that are 3–400 m apart share less than 0.5% species. Outside of the taxa with the least intense sampling (Isopoda), the slopes of the relationships are nearly identical, differing only in intercept

extirpation is an extinction and represents a global loss. These, “escalators to extinction” (Marris 2007; Urban Mark 2018), are occurring on elevational gradients around the world, but due to the greater diversity and ecophysiologically sensitive lifestyles on tropical mountains, the climate-driven population extinctions have been higher in tropical than on temperate mountains (Parmesan et al. 2022). Thus, while the largest amplitude changes in temperature are occurring in high-latitude locales – the most rapidly changing environments are tropical high-elevation communities. Here, long-term temperature stability has resulted in both high diversity and small species ranges – each highly vulnerable to changes in temperature and precipitation.

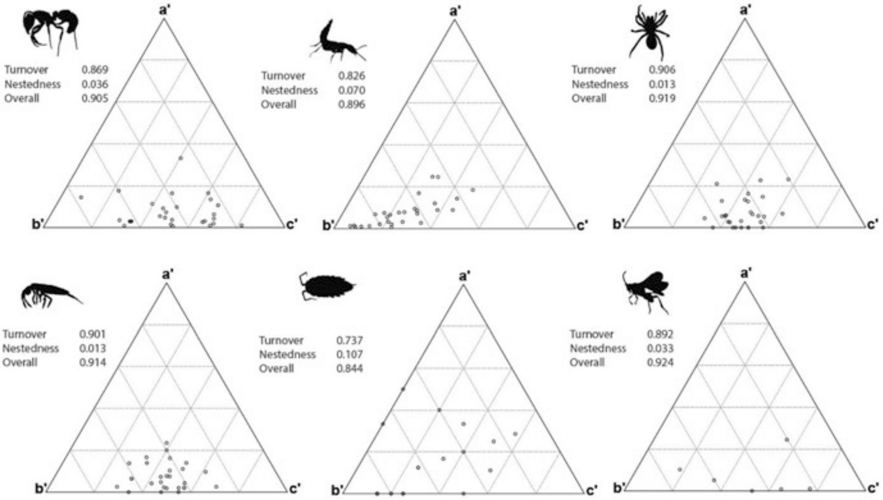

Fig. 10.13 Triangular ternary plots where points of the triangle represent (a′) the % of species shared, (b′) the % of species present exclusively in the neighbouring site, and (c′) the % species present only in the focal site (Koleff et al. 2003). Statistics describing betadiversity partitioning derived from betapart (Baselga and Orme 2012) where turnover (or spp. replacement) is beta.SIM, nestedness (spp. loss) is beta.SNE and overall betadiversity is beta.SOR. While elevational patterns in alpha diversity change in taxon-specific manners, patterns in betadiversity are markedly similar (Fig. 10.12). Change between sites separated by elevation is based on turnover (i.e. species are replaced) and not nested (where species present at the least diverse site are a subset of a larger pool present at other elevations). All taxa exhibit very few shared taxa where, if shared with other sites, they tend to be adjacent, or not at all

10.4.1 Insect Decline

Discussions about the global loss of insect diversity and abundance (a so-called insect apocalypse [Jarvis 2018]) have exploded into the scientific literature (Hallmann et al. 2017; Leather 2018; Lister and Garcia 2018; Forister et al. 2019; Goulson 2019; Sánchez-Bayo and Wyckhuys 2019; Wagner 2020; Kehoe et al. 2021; Uhler et al. 2021; Wagner David et al. 2021; Wilson and Fox 2021; Milman 2022; New 2022; Outhwaite et al. 2022). However, the unambiguous loss of insect species and abundance in both low- and high-elevation forest of ACG has been apparent for years (Janzen and Hallwachs 2019, 2021). In most of the world, the likely traditional explanations are habitat destruction and degradation (Sánchez-Bayo and Wyckhuys 2019). In ACG, habitat destruction occurred in the 400 years following European colonisation (Janzen and Hallwachs 2016). While the focus of these efforts was principally on the easier to access low-elevation dry forest areas of Guanacaste that were deforested and converted to agriculture or ranching – the efforts were opportunistic and nearly comprehensive (Janzen and Hallwachs 2016). Higher elevation forests (rain and cloud forests), which could have been cut for

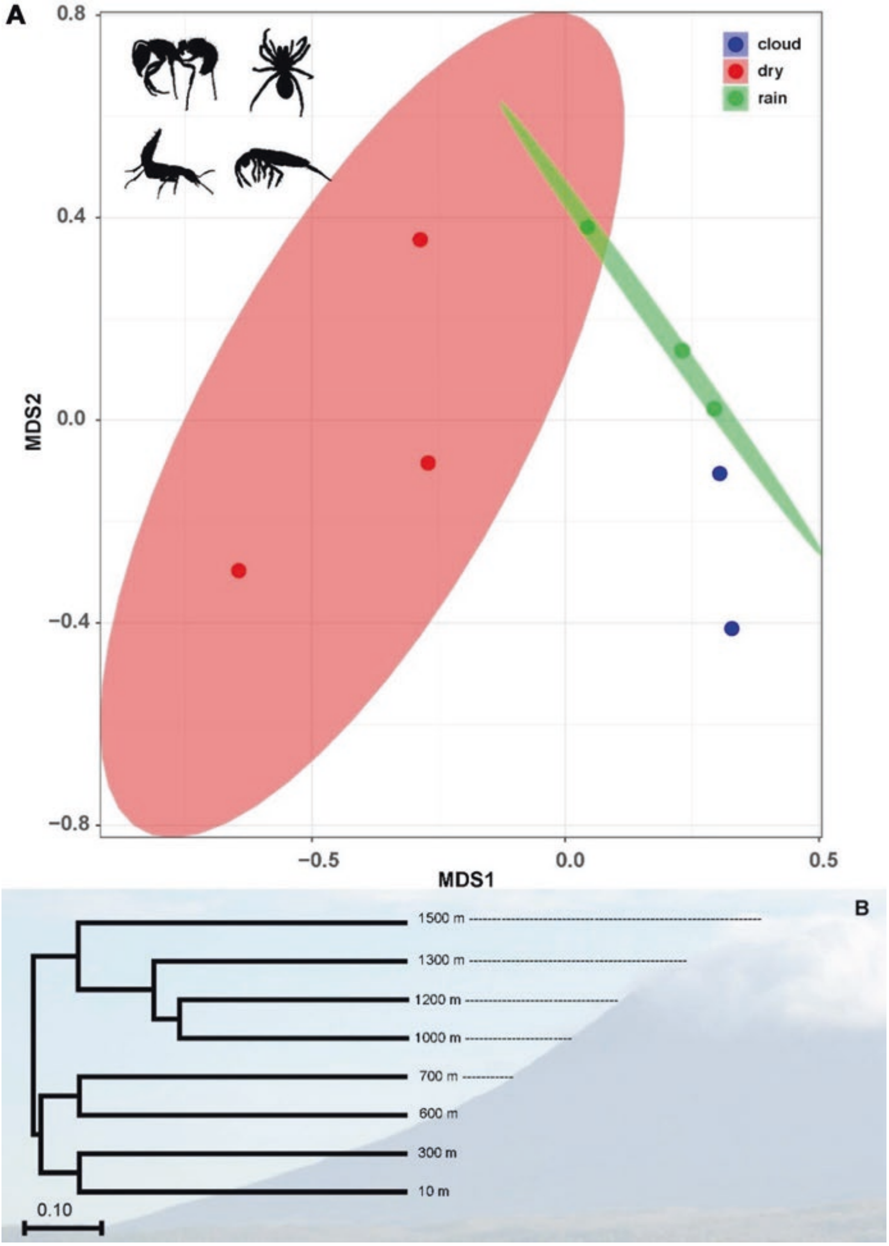

Fig. 10.14 Visualising community structure across forest types associated with elevation on Volcan Cacao (ACG) using non-metric multi-dimensional scaling (NMDS) based on the 1078 species from four leaf-litter taxa (Staphylinidae, Formicidae, Araneae, and Collembola) sampled at all eight locations. (**a**) The first NMDS dimension is largely an expression of temperature, while the second is of precipitation and elevation. The communities in the three forest types are significantly different (ANOSIM statistic $R = 0.537$, $p = 0.027$). (**b**) the Bray-Curtis dissimilarity index between communities clustered using UPGMA projected on the elevational gradient of Cacao's northern neighbour volcano – Volcan Orosi. Communities in similar forest types are more similar. As these forests change with elevation, this can result in nearby communities exhibiting markedly different communities (e.g. 600–700 m) or extreme similarity (1000–1200 m)

coffee plantations, avoided deforestation largely due to the inconvenient distance from Guanacaste to the Central Valley (Janzen and Hallwachs 2016). While there has always been some small-scale agriculture on the mid-elevation slopes of Guanacaste, the cloud forest peaks were likely too inhospitable and difficult to access to be thoroughly deforested. In recent times, the creation of the ACG from Santa Rosa National Park has seen the amount of total habitat protected increase from 9900 ha in 1971 to 169,000 ha in 2022 (Pringle 2017). So, in ACG, where the most dramatic deforestation events are decades (several or many) in the past – what is driving insect decline? The answer appears to be anthropogenic climate change and the associated changes in temperature and precipitation (Janzen and Hallwachs 2021). Warm temperatures are moving upslope, variation in temperatures exceeding levels experienced historically, precipitation levels and predictability are changing. These mechanisms have effects across the ACG elevational gradient – but likely manifest differently at different elevations. While the cloud forest peaks on the ACG stratovolcanoes avoided historic deforestations – they are not avoiding the changes in amount, variation, and predictability of temperature and precipitation. Thus, species here that may be specialised to an existence in such a refrigerator-like environment (Smith et al. 2014) will be at a disadvantage in the warmer and drier future. There is nowhere colder, wetter, and higher up to migrate to – and thus they are likely to go locally extinct. Dry forest species live in the warm lowland forests with the highest variance in temperature and precipitation – and so one might expect them to have the greatest resilience to a changing climate. However, they are likely already living at their environmental thermal optima (Deutsch et al. 2008), and so increases in the temperature extremes and averages that the dry forests experience will also result in species loss here. Colwell et al. (2008) referred to these respectively as high-elevation extinction and low elevation attrition – but we prefer to think of them each as thermal tolerance extinctions.

10.4.2 Thermal Tolerance

How insects regulate their temperature intimately affects their local and global distributions (Parmesan 2006; Sinclair et al. 2016; González-Tokman et al. 2020). Tropical insects already live close to their thermal optima and so are most likely to be negatively affected by the climate crisis (Deutsch et al. 2008; Duffy et al. 2015), both by absolute values and by the obvious asynchronies among seasonal and biological cues brought on by the changes. Indeed, despite the comparatively smaller changes in temperature forecast for the tropics (compared to the polar regions), there is likely to be a disproportionately large effect of climate change on tropical ectotherms (Dillon et al. 2010). While such a disproportionately large effect is likely – we also predict it from a profoundly uninformed position. Uninformed simply due to the scale of the problem(s) of social disinterest, the taxonomic impediment, and competition with other human agendas. There are many species of arthropods – and for most of these we know nothing about their existence, let alone their thermal tolerance (and of course knowing it will not change the impact of climate change). In the tropics is where this trend of "unknown" is felt most keenly. For example, while there have been nearly 50 years of studies examining the thermal tolerance for the soil hexapod taxon, the collembola, there are nearly no tolerance estimates of for tropical species (Escribano-Álvarez et al. 2022). Moreover, given that staphylinids are the most diverse beetle family, with over 60,000 described species (Betz et al. 2018), there is surprisingly little known regarding their thermal tolerance – in fact, to date, only one record of staphylinid thermal tolerance exists in the literature (Slabber and Chown 2005). The thermal breadth of ants has been better studied than many other insects (see Roeder et al. 2021; Nascimento et al. 2022), however, even in what may be the best studied insect taxon (for thermal limits) there are a conspicuous lack of tropical studies (Nascimento et al. 2022). In one recent example, a small period of experimental warming (2 years) resulted in changes in community composition that resulted in more ant taxa with moderate thermal tolerance and invasive qualities moving into the newly warmed environments (Bujan et al. 2022). While there is variation, across elevations of different absolute intensity, in the abiotic values changing with elevation (like temperature, clouds humidity, solar radiation, etc.), in general, it appears that species in lower elevations have higher thermal tolerances than do mountaintop species (García-Robledo et al. 2016). These low-elevation species with higher thermal tolerances are moving upslope and replacing species with lower thermal tolerance (Warren et al. 2016). More generally, a recent review found that species living across gradients of anthropogenic change were exposed to a wider thermal envelope in more disturbed areas (Williams et al. 2020). However, estimating the thermal envelope in the tropics for most taxa remains elusive as estimates of cold tolerance (chill coma recovery time or critical minimum temperature [CT_{min}]) are infrequently studied in tropical insects (Roeder et al. 2021). The relationship between an individual's fitness and temperature represents a multidimensional envelope of history (how many exposures to extreme high or low values), life history (variation between life-history stages), taxon and additive effects, including biotic ones (Sinclair et al. 2016). The response of any one taxon may be idiosyncratic, making predictions complicated (Sinclair et al. 2016). To begin to better understand how these knowledge gaps (taxonomic, high tolerance, and low tolerance) affect the species of ACG, we have initiated experiments to estimate ACG leaf-litter arthropod thermal tolerance (higher and lower). Preliminary results suggest that high temperature thermal tolerance does change across the ACG elevation gradient.

10.4.3 Upslope Migration

High elevation insect taxa may be pushed out of their habitat and driven locally extinct as the arriving higher temperatures exceed their thermal tolerances (Shah et al. 2020). These species may endure an increase in temperatures (Muhlfeld et al. 2020) or they may experience the re-wiring of seasonal events such that formerly predictable elements of their phenology (such as the return of the rains in the lower elevations) is no longer a dependable signal. For example, there are many species of insect characteristic of drier, low elevation ACG forests which seasonally migrate upslope in ACG to escape the heat, dryness, and lack of prey of the dry season (Janzen 1993, 2004; Hunt et al. 1999; John and Post 2021). As higher temperatures move upslope and precipitation is reduced and less predictable, these seasonal migrants will be without a reprieve from the violent dry-season furnace below (Janzen and Hallwachs 2021). Some taxa may escape the direct effects of the new normal hot temperatures by altering their activity patterns into the night. While this strategy will not be available to all, the trends in temperature we see within years and across elevation (Fig. 10.2) are indeed more amplified for daily maximums achieved during the daytime and more muted overnight (when the daily minimum temperatures are typically achieved). Some terrestrial taxa will have, at least a temporary, opportunity for small scale spatial retreats into more amenable micro-habitats (Duffy et al. 2015). While habitat heterogeneity (and associated micro-climates) is likely to be important for insects impacted by climate change-caused temperature extremes (Harvey et al. 2020; McCain and Garfinkel 2021), they will not provide sanctuary for the long term (or through extreme events).

10.4.4 Idiosyncratic Changes in Alpha Diversity – Consistent Changes in Betadiversity

One clear message from examining the species richness (alpha diversity) of the ACG leaf-litter fauna across elevation is the absence of any one single pattern that captures all taxa. The taxonomically idiosyncratic relationship between richness and elevational variables reinforces what others have found across elevation with different taxonomic combinations (Fiedler et al. 2008; Peters et al. 2016; Corcos et al. 2018). Fiedler et al. (2008) found that examining the relationship between diversity and elevation at high taxonomic levels for Ecuadorian moths concealed differences evident at smaller systematic scales. Working with 25 plant and animal taxa on Mt. Kilimanjaro, Peters et al. (2016) found that approximately half the taxa displayed declines in richness with elevation, while the other half displayed more complex (hump shaped or multiple peaks) relationships. In the European Alps, Corcos et al. (2018) reported variable trends across elevation for the diversity parasitoid and predatory insects. Our work in ACG and the observations of others suggests that the desire to extrapolate from one taxa to others as indicator (Kremen 1992) or umbrella strategies (Noss 1990), will not work (Prendergast et al. 1993; Prendergast and Eversham 1997). However, while we have documented extremely variable influences of elevation on alpha diversity in taxa of the ACG leaf litter – there is one strikingly uniform response that was not dependent on the taxon – all communities were increasingly dissimilar with increasing elevational separation. While elevationally adjacent sites may share a small subset of species, most species were found in only one or two elevational sites. Betadiversity changes across elevation were never nested – but instead, exhibited turnover as one travelled up- or downslope. The homogeneity of the relationship between betadiversity and elevational separation exhibited here suggests a similar mechanism may be behind the pattern – and we feel that it is likely the bands of stable temperature that stack upslope across these volcanos. While the absolute distance between locations is small, the stable differences in temperature have selected for taxa that do not move easily across these bands (Janzen 1967). In examining multiple lepidopteran taxa in Ecuador, Fiedler et al. (2008) found support for the same pattern of increasing dissimilarity with increasing elevational separation. They concluded that this concordance supported the dominant role for temperature in determining community composition. When considering a surrogate in questions of montane diversity, our results suggest that approaches based on alpha diversity are to be avoided. They do, however, suggest that analyses of betadiversity may itself provide a measure of surrogacy, suggesting the degree of connection/isolation between various elevational bands and how those change into the future. A recent, non-terrestrial example found that the betadiversity patterns of one taxon of benthic coral reef denizens was a significant predictor for other taxa (McDevitt-Irwin et al. 2021). While suggestive for gradients of elevation, betadiversity surrogacy across taxa will not provide a total panacea. For example, in examining how alpha and betadiversity changed across a gradient of land use intensity in Colombia, Cabra-García et al. (2012) found little congruence between patterns of betadiversity and more congruence in patterns of alpha diversity. In the end, the use of a subset of taxa as surrogates for others will be fraught with problems (Westgate et al. 2014) and likely the best strategy is the most work – a range of taxa rather than a subset. In this regard, our work suggests that phylogenetically expressed patterns of diversity (alpha and beta), rather than taxon-specific strategies, may be a surrogacy measure that frees resources. Phylogenetic measures of alpha (PD) and beta (comdistnt) diversity, in particular those derived from a standardised gene region like a DNA barcode, permit one to examine patterns of community similarity across a gradient without necessarily being exposed to the taxonomic impediment particularly prevalent among small tropical invertebrates (Smith et al. 2009, 2014; Swenson 2012, 2019; Brehm et al. 2016; García-Robledo et al. 2016; Dolson et al. 2020, 2021).

10.4.5 Beyond Abiotic Factors

We have measured abiotic factors here that change with elevation (temperature, precipitation, and area). We could certainly improve the scale at which we measure these factors (e.g. microclimatic conditions vary dramatically from the measures we have captured as coarse descriptions of these locations [Duffy et al. 2015]). As well as the traits of the organisms – pill bugs are not rove beetles.

One potential mechanism that might help explain some of the alpha diversity idiosyncrasy is habitat complexity. For several of the taxa we examined here, others have documented that habitat complexity was positively correlated with richness. In the Collembola, Loranger et al. (2001) found that any effect of elevation on diversity was coincident with changes in soil chemistry, nutrient availability, and soil food webs. Staphylinids are known to live in numerous microhabitats (Thayer 2005) – and thus a reasonable supposition would be that sites with a greater diversity of microhabitats would host a greater diversity of staphylinids. Finally, for spiders, others have shown that the number of available microhabitats and three-dimensional structure both positively influence spider diversity as much or more than those abiotic factors associated with elevation alone (Jimenez-Valverde and Lobo 2007; Malumbres-Olarte et al. 2018). In ACG, we envision utilising the high-resolution panoramic photographs we have collected through time and across elevation to provide a gross estimate of forest complexity. When used in temperate forests, we found that this technique was an efficient predictor of spider diversity (Ho and Smith 2015; Ho 2019).

In addition, another potentially important driver untouched in our investigation is the role that biotic effects (competition, predation, parasitism, etc.) may play in community assembly across this gradient. Quite frankly, the intimate, species-specific knowledge that is required to estimate biotic factors remains qualitatively or quantitatively out of reach for most taxa in the neotropical leaf-litter (90% of which perhaps remains undescribed). However, as we uncover the taxa and their distribution across this ACG gradient, what roles might we expect biotic interactions to play? Hargreaves et al. (2014) found that the low elevation ranges of a species' distribution were better described by biotic than abiotic effects. In a recent meta-analysis, Paquette and Hargreaves (2021) supported this observation and suggested that biotic interactions are more important at "warm" range edges than "cold" range edges. Their analysis predicts that as climate change alters the forests across neotropical elevational gradients, the changes in the hot low-elevation dry forests will be associated with competition and parasitism as opposed to the cloud forests where exceeded thermal tolerances may best predict the coming losses. What kinds of significant biotic changes might the high-elevation cloud forest expect? Consider the role that predators such as army ants may have in the cloud forests. *Eciton* species are now found across the elevation gradient on Volcan Cacao, in a frequency with which they were not in the late twentieth century (Janzen and Hallwachs 2016). Interestingly, *Eciton* themselves are a key architect of neotropical biodiversity – upon whom numerous other taxa depend and live symbiotically, including entire systematic radiations of staphylinid beetles that live cryptically inside *Eciton* colonies (Parker and Kronauer 2021) as well as having lineage-specific prey concentrations (Hoenle et al. 2019). These kinds of far-reaching relationships have led some to propose that army ant taxa can serve as an umbrella for neotropical conservation (Pérez-Espona 2021). Army ants are voracious, carnivorous predators – and their move upslope may perhaps provide a contrast to the patterns shown by Hargreaves et al. (2019) that showed seed predation decreases with elevation. What is clear, is that as the abiotic factors continue to change and challenge the tight belts of environmental conformity across elevation, biotic factors will play a role in determining which species can survive. These effects may be most visible at warm range edges.

However, as these warm edges move upslope, what we eventually observe may include both the loss of specialised endemic high-elevation taxa to increased and efficient predation via army ants and then the eventual loss of taxa specialised to live within/depend upon those army ant species as conditions eventually become so eroded that their resilience is broken. Tracking the interaction diversity (Gaüzère et al. 2022) through time and across elevation would be a useful way to track these changes as we better understand the "players in the play" of this ecological and evolutionary drama.

10.4.6 Going Forward

Stroud and Feeley wrote that "neglect of the tropics is widespread in ecology and evolution" (2017). To us, it seems that the neglect is much more widespread and extends to conservation biology and management; particularly to the knowledge, understanding, and protection of the most diverse of terrestrial taxa; the invertebrates. If we wish to better understand the causes and consequences of diversity and elevation patterns in the neotropics (and to protect what we understand), then we need to lift the veil on cryptic tropical arthropod species biology. What species live where? What is the thermal tolerance of these species (García-Robledo et al. 2016)? How do the species deal with the heat and dryness of low elevation dry forest and the cold and wet of high elevation cloud forest? How is this changing through time? Who cares about these questions and how to make more people care more? And many other things as well. Which are more important? Is it the ones we are equipped already to deal with or the ones that matter to the audience with their jillions of competing agendas? Unpacking these questions will result in better delineation of elevational ranges for tropical arthropod species resulting in a more thorough understanding of evolution and ecology for ectotherms, a baseline toolkit of predictions regarding which species will be most affected by hot temperatures on their relentless march upslope and, finally, a description of many tropical species which frees them into the scientific literature for future work. Ultimately, however, further study of these questions will not provide solutions to the underlying problem. While the climate and biodiversity crises are linked, and while tropical forests themselves are considered a "natural climate solution" (Malhi et al. 2020), what is needed are two local strategies and one global. Locally, when possible, increase the size of the protected area in order to permit more chances for climate refugees to attempt their range-shifting (Thomas Chris et al. 2012; Bates et al. 2014; Lehikoinen et al. 2021), and maintain/expand long-term monitoring and expertise, such as the experienced biodiversity managers of the ACG already do. Long-term trends and baseline data will be critical to understanding the continuing biological context of the climate crisis as well as helping us in the future to evaluate the efficacy of specific management decisions (Malhi et al. 2020). This baseline is particularly important if we find evidence of decline within protected areas (Pollock et al. 2022) as already documented and encountered all over the tropics. Globally, and most importantly, is to accelerate and entrench strategies to reduce greenhouse gas emissions as rapidly as possible and transition the global economy to a sustainable, low-carbon future (Pettorelli et al. 2021). If this does not happen, the long-term narrative for the species across elevational gradients of the ACG, as with the majority of the tropics, will be of the loss of diversity and the degradation of its forests.

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