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RESEARCH ARTICLE

Analysis of tropical and temperate elevational gradients in arthropod abundance

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Abstract. Arthropods are a major component of ecosystems, in terms of both their biomass and the variety of functional roles they play. Yet we lack a clear understanding of how arthropod abundance changes along environmental gradients. We compiled published literature on overall arthropod abundances (number of individuals) along elevational gradients and performed a formal meta-analysis on the role of latitude, climatic variables, and interactions with ants in shaping the pattern. Specifically, we asked if patterns of arthropod abundance along different elevational gradients are associated with gradients of seasonality and precipitation and whether ant abundance affects other arthropods. Arthropod abundance peaks at higher elevations at mid-latitudes than low latitudes; hence, the correlation between arthropod abundance and elevation shifts from negative to positive with an increase in latitude. We suggest these patterns reflect a steep elevational gradient in the length of growing season at mid-latitudes, with the short growing season at high elevations in mid-latitudes leading to synchronous emergence and reproduction of arthropods generating a sharp increase in abundance. Precipitation and ant abundance do not have a consistent effect on arthropod abundance along most elevational gradients. However, on gradients with a very dry base and sharp increase in precipitation with elevation, arthropod abundance peaks at higher elevations. Overall, our results suggest that future changes in the length of growing season will impact the elevation at which summer arthropod abundance peaks and the sharpness of the peak, likely affecting diversity and distribution of other taxa that interact with arthropods.

Keywords: altitudinal gradients, insects, meta-analysis, mountains, latitude, seasonality

Introduction

Arthropods are the most diverse phylum of animals, not just in terms of the number of species but also in their form and function, containing groups as different as butterflies, ants, spiders, springtails, millipedes, crabs, and scorpions. Despite their small size relative to vertebrates, arthropods constitute a much larger proportion of animal biomass in many terrestrial ecosystems (Fittkau and Klinge 1973). Still, we do not have a clear understanding of how arthropods are distributed across environmental gradients. Because of their enormous diversity, it is difficult to examine patterns of species richness across all arthropods, and most studies focus on one (Niemelä et al. 1992) or a few taxonomic groups (e.g., Peters et al. 2016). However, patterns in the total number of arthropod individuals are relatively easier to assess and have important ramifications for understanding ecological communities as well as predicting future change.

Arthropods play myriad roles in ecosystems as prey, predators, pollinators, parasites, and disease vectors (Miller 1993). Therefore, their numbers should have major effects on the diversity and distribution of the taxa they interact with (Bagchi et al. 2014). Indeed, reduction in arthropod abundance has been linked to declines in vertebrate populations that depend on arthropods for food (Lister and Garcia 2018) and lower, less stable crop yields for plants pollinated by insects (Aizen et al. 2009). Several studies have reported sharp declines in arthropod abundance, up to 75% over the course of 27 years (Hallmann et al. 2017, Sánchez-Bayo and Wyckhuys 2019, Lister and Garcia 2018). Although these declines might be over-estimates, it is generally accepted that arthropod abundance is declining. This is a major conservation concern because such population declines can have a large effect on ecosystem function (Ceballos et al. 2017), even if species do not go extinct. Given rapid ongoing environmental changes, establishing a baseline understanding of the effect of environmental gradients on spatial patterns of arthropod abundance becomes crucial in effective conservation planning.

Here, we address spatial patterns of arthropod abundance during the growing season (i.e., temperate summer or tropical wet season), which roughly corresponds with the breeding season of most terrestrial vertebrate and invertebrate species (Wolda 1988). We focus on elevational gradients because they encompass rapid changes in several climatic variables notably temperature but often also precipitation over a short distance (McCain and Grytnes 2010). Moreover, elevational gradients allow us to decouple effects of temperature from seasonality because tropical gradients are less seasonal at least with respect to temperature (Körner 2007). Typically, seasonality increases and minimum temperature decreases as one moves away from the equator, making it difficult to tease apart the role of seasonality and temperature. However, along tropical mountains, mean temperature drops with elevation without a corresponding decline in seasonality and hence the length of the growing season (Körner 2007).

Some previous studies have reported highest arthropod abundance at low elevations (Collins 1980), while others show highest summer arthropod abundance at mid-elevations (Ghosh-Harihar 2013). We examine three hypotheses that could explain the variation in summer arthropod abundance along elevational gradients:

i. Sharper elevational gradient in seasonality at mid-latitudes leads to summer arthropod abundance peak at higher elevations: We derive this hypothesis from patterns along latitudinal gradients. In places that experience frost in the winter, many arthropods spend the winter in a state of diapause (Denlinger 1991). Roughly synchronous emergence and reproductive activity of such arthropods in the spring or summer creates a sharp peak in abundance in temperate areas that can surpass tropical maxima (Janzen and Pond 1975, Hails 1982). For example, peak arthropod abundance as assessed using suction traps was 16x higher in Scotland (56°N) than peak arthropod abundance in Malaysia (3°N), but winter arthropod abundance in Malaysia was 22x that in Scotland (Hails 1982). Thus, greater seasonality in temperate sites can cause sharper peaks in summer arthropod abundance because of the constraints imposed by a short growing season (Lowman 1982). Note that species richness does not necessarily correlate with abundance and these sharp abundance peaks are often constituted of relatively fewer species (Lowman 1982, Janzen and Pond 1975). Elevational gradients in the temperate and sub-tropical zone might reflect this latitudinal pattern and show summer abundance maxima at higher elevations. In other words, higher elevations in seasonal (i.e., temperate) environments are expected to show a relatively short growing season, which is expected to be accompanied by synchronous emergence and reproduction of arthropods leading to a large arthropod flush. Hence, we predict that the peak in arthropod abundance should be at higher elevations and latitudes because population cycles are compressed into a shorter growing season at higher elevations compared to low elevations. This is expected to apply most strongly on gradients which include sites that frost in the winter.

ii. Summer arthropod abundance peaks at higher elevations on mountains with low precipitation at low elevations, where arthropod abundance is relatively limited: More arthropods are found in warm and wet regions than cold and dry regions (Rypstra 1986). Because temperature declines monotonically along elevational gradients, deviations from a monotonic decline in arthropod abundance with elevation might be largely set by precipitation. Such deviations are likely to be observed for mountains with dry bases but wetter mid-elevations (McCain 2007), leading to the prediction that arthropod abundance will peak at higher elevations on mountains with dry bases than on ones with wet bases.

iii. Non-ant arthropod abundance is negatively correlated with ant abundance: Apart from environmental variables, population sizes are influenced by biotic interactions. Several studies have pointed to the role of ants as important predators on other arthropods, especially in tropical lowlands (Floren et al. 2002, Sam et al. 2015). Experimental exclusion of ants from selected trees or plots has been shown to result in increased abundance of other arthropods (Schmitz et al. 2000). Patterns of ant abundance could be an important factor shaping non-ant arthropod abundance patterns at a larger spatial scale as well (Kumar et al. 2009), leading to the prediction that ant abundance across elevations should correlate negatively with abundance in other groups.

In this paper, we first describe arthropod abundance patterns along elevational gradients and then evaluate these three hypotheses.

Material and methods

Data collection: We searched for papers on arthropod abundance along elevational gradients using the Google Scholar search engine with "arthropod abundance elevation", "arthropod abundance altitude", "insect abundance elevation", and "insect abundance altitude" as keywords. We then searched bibliographies of the papers found through Google Scholar for additional relevant studies, as well as ecological databases including Dryad, knb, GBIF, DataOne, ecological data wiki, and re3data. Finally, we consulted researchers that have worked on arthropods in mountains regarding unpublished datasets or studies we may have missed. Our compilation was last updated in November 2018.

We only included studies that reported abundance (i.e., number of individuals) for all arthropods collected, sampled at a minimum of four elevations and that had equal sampling effort with identical sampling methods at each elevation. We excluded studies limited to specific taxa or microhabitats but included studies that only used one particular sampling method (e.g., pitfall traps). For example, we excluded data from Garibaldi et al. (2011) because they only sampled arthropods from a single tree species over a restricted elevational range at three elevations. Similarly, we excluded all studies that only provide information on species richness and do not report abundance (e.g., Peters et al. 2016).

Because this search yielded a small number of gradients (n = 21, see Fig.1 for locations of all the gradients) that met the criteria above, we did not filter them based on other potentially relevant criteria such as the proportion of gradient sampled and lowest elevation covered. However, all but two of the studies included in our analyses sampled at least one site within the lowest 400m of the elevational gradient for that region. The only exceptions were the elevational gradients in western Himalayas sampled by Ghosh-Harihar (2013) and northwestern Argentina sampled by González-Reyes et al. (2017), where the lowest elevations sampled were 1350m and 1586m respectively, whereas in both regions the elevational gradient extends to below 400m. Across four North American gradients, the lowest elevation sampled is over 1400m, but the lowest elevation in the region is at about 1000m. Seventeen out of the 21 studies we included in our analysis were conducted during the temperate summer or the wet season in the tropics, which corresponds with the growing season (Appendix 1). The other two studies were conducted during the dry season in the tropics, but the dry season is generally mild at these sites. One study did not specify the month of sampling and the final study sampled in all seasons but did not present the data for each season separately (Figure S1, Appendix 1).

The studies we found did not use the same methods to estimate arthropod abundance and did not sample the same substrates although there was no systematic trend in the substrates sampled or methods used for sampling (Appendix 1). We acknowledge that different sampling methods are biased in the rate at which they capture different kinds of arthropods because of differential attraction and body size limits, and these can affect the total number of arthropods caught. Therefore, we evaluate patterns within each study, and then compare these patterns (notably where the maximum abundance is reached on the gradient). Importantly, we standardized measurements of arthropod abundance across each gradient to have a mean of 0 and a standard deviation of 1 before analysis. Hence, differences in absolute abundances due to different methods and intensities of sampling and other uncontrolled differences among the gradients are not an issue. The complete data used for the analyses are given in Appendix 2.

We extracted data on five climatic variables (mean annual temperature, annual precipitation, minimum temperature, temperature seasonality, and precipitation seasonality) from the Worldclim 2 database (Fick and Hijmans 2017) using spatial coordinates for sampled sites based on the original papers. Because precipitation data from Chelsa climatological data is more accurate (Karger et al. 2017a), we repeated our analyses using annual precipitation as a variable with data from Chelsa (Karger et al. 2017b). Seven of the papers did not include latitude and longitude information for every site, and in such cases, we either contacted the authors or inferred co-ordinates from other sources.

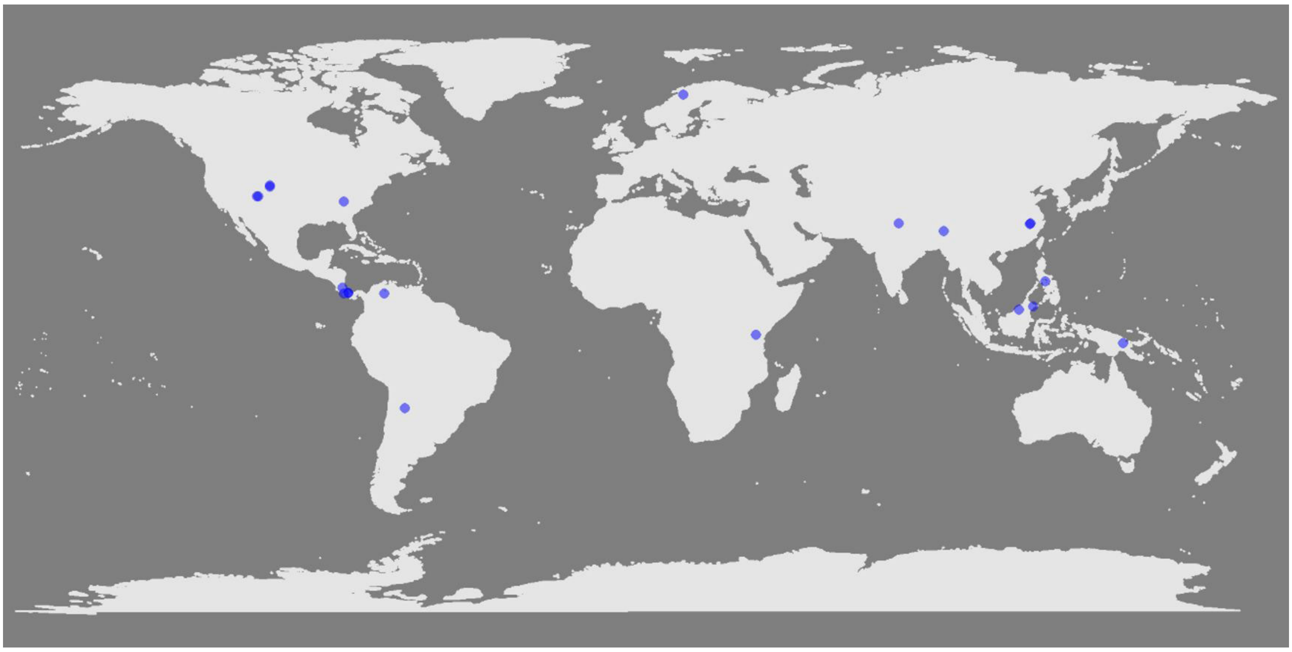

Figure 1. Locations of the surveys of arthropod abundance along elevational gradients included in this study. Darker points indicate places where two surveys were conducted and both were included in our study.

For example, Collins (1980) sampled along a regular hiking route to the summit of Gunung Mulu, so we obtained GPS co-ordinates from a hiking website and corroborated some of the points from a study of birds along the same elevational gradient (Burner et al. 2016). For three studies, we estimated the latitude and longitude of the sampling sites using Google Earth based on the study site description provided in the paper. For Janzen (1976), we could not estimate the location co-ordinates and used the precipitation and minimum temperature data as provided in the paper (hence, we could not use this data set for all the analyses). We could not estimate locations for Leakey and Proctor (1987) and had to exclude this study from several analyses.

In addition to temperature and precipitation variables, we included Actual evapotranspiration (AET) as a climatic variable in our analyses because it might reflect water availability better than precipitation alone. We used annual temperature and precipitation data extracted from Worldclim to calculate Actual Evapotranspiration using Turc's formula: $AET= P/[0.9 + (P/L)^2]^{1/2}$,where $L= 300 + 25T + 0.05T^3$ and T stands for mean annual temperature and P is annual precipitation (Turc 1954, Yu et al. 2013). Finally, we gathered data on ant abundance from the same studies where available. All compiled data are available on Dryad and as a supplement to this paper.

Data analysis: Our dataset included one study in Sweden at 67°N (Fig.1, Franzén and Dieker 2014), while all the other studies fell between 0-40°. We excluded the Sweden outlier from all analyses. To visualize patterns, we first fit a loess smoother to each gradient using the R package ggplot2 (Wickham 2011). Next, following Werenkraut & Ruggiero (2014), we evaluated the pattern of abundance along individual elevational gradients by comparing the regression coefficients and P-values for (1) a null model ($y = a$), (2) a linear model of abundance with elevation ($y = a + bx$), (3) a quadratic model with high arthropod abundance from low to mid-elevations followed by a gradual decline (i.e., low plateau [$y = a + cx^2$]), and (4) a full quadratic model with mid-elevational peak in abundance ($y = a +bx + cx^2$;note that a negative value for b indicates a decrease in abundance with elevation and vice versa, and a negative value for c indicates a hump-shaped pattern, while a positive value for c indicates a U-Shaped pattern). Note that a single study could potentially fit all three models (i.e., models 2, 3, and 4). We estimated spatial autocorrelation for each of the gradients as Moran's I using the R package Ape (Paradis et al. 2004, R Core Team 2014). For gradients with statistically significant spatial autocorrelation, we assessed the fit of models 1, 2, 3, and 4 accounting for spatial autocorrelation by incorporating spatial correlation structures using corSpher, corExp, and corGaus in linear mixed effects models using the R package nlme (Pinheiro et al. 2014). If incorporating spatial correlation structures led to a better-fit model assessed conservatively using AICc values, we used the spatial models to identify the pattern of arthropod abundance with elevation.

Next, we conducted a formal meta-analysis (Koricheva et al. 2013) to examine the effect of latitude and climatic variables related to temperature and precipitation on arthropod abundance along elevational gradients. We also analyzed the effect of standardized ant abundance on abundance of other arthropods, after standardizing non-ant arthropod abundance data. We calculated linear correlations between arthropod abundance, all six climatic variables, and ant abundance for all the gradients for which we had these data. We converted these correlations to effect sizes using Fisher's z transformation with the function escalc in the R package metafor (Viechtbauer 2010). Effect sizes are correlations between variables normalized and corrected for sample size to enable comparisons across studies. Because spatial autocorrelation was low for most of the studies included in our analyses, we did not account for it in calculations of the effect sizes.

We asked if the effect size of any of these variables on arthropod abundance was significantly different from zero using a meta-analytic random-effects model. Next, we used these effect sizes and conducted a meta-regression with latitude as a modifier to ask if the relationship between arthropod abundance and climatic variables is associated with latitude. For all of these analyses, we had to drop three studies that sampled only 4 locations, leaving 17 studies (the variance of the effect size for these studies is $1/(n – 3) = 1$, which prevents the estimation of sampling variance across studies; Field 2005). In our analyses of climatic variables, we had to further exclude one study, that is, Leakey & Proctor (1987) because the relevant data was lacking. For analyses of the effect of ant abundance, we had to drop 10 more studies because they did not report ant abundances.

Finally, to ask if seasonality or precipitation best predicts the elevation of maximum non-ant arthropod abundance in the datasets, we used a general linear model (GLM) approach. Specifically, we used the following independent variables in our full models: (1) precipitation at lowest elevation, (2) "freezing fraction", that is, fraction of sampled gradient that freezes over, calculated as (maximum elevation sampled – lowest freezing elevation)/elevational range sampled, (3) latitude. Because freezing fraction and latitude are highly correlated ($r= 0.91$, $P< 0.0001$, $N=19$), we did not include a model with both as independent variables. We fit all possible subsets of our full models including an intercept-only null model and compared them using AICc values (Burnham and Anderson 2002). All analyses were done in the R programming environment (R Core Team 2014) using the packages raster (Hijmans et al. 2017), rgdal (Bivand et al. 2015), plyr (Wickham 2016), Rmisc (Hope 2013), metafor (Viechtbauer 2010), nlme (Pinheiro et al. 2014), ape (Paradis et al. 2004), MuMIn (Bartoń 2016), and ggplot2 (Wickham 2011).

Results

Patterns of abundance: We found 21 studies that reported data on overall arthropod abundance along elevational gradients at a total of 206 sites (Appendix 1). The lowest elevation sampled by these studies ranged from 20m to 1811m, and the highest elevation sampled ranged from 869m to 4550m (Fig. S2). The elevational range covered by the studies varied from 590m to 3690m. All but two of these studies focused on only one substrate for arthropod collection (i.e., ground, air, or leaves). Patterns of arthropod abundance varied greatly. They included a monotonic decline in abundance with elevation, a mid-elevation peak, a monotonic increase in abundance, a U-shaped pattern with greater abundance at low and high elevations and no obvious pattern (Fig. 2 & Figs. S2 & S3, Appendix 1). We found significant support for a linear model of declining abundance in only two studies (Appendix 1). Four studies showed significant support for mid-elevational peak and low-plateau models for arthropod abundance, one of which showed significant support for both (Appendix 1). Moran's I was positive and significant for 6 of the 19 gradients. However, the values were low (Appendix 1) and a model with spatial correlation structure performed better than a non-spatial model for only one study (i.e., Binkenstein et al. 2017).

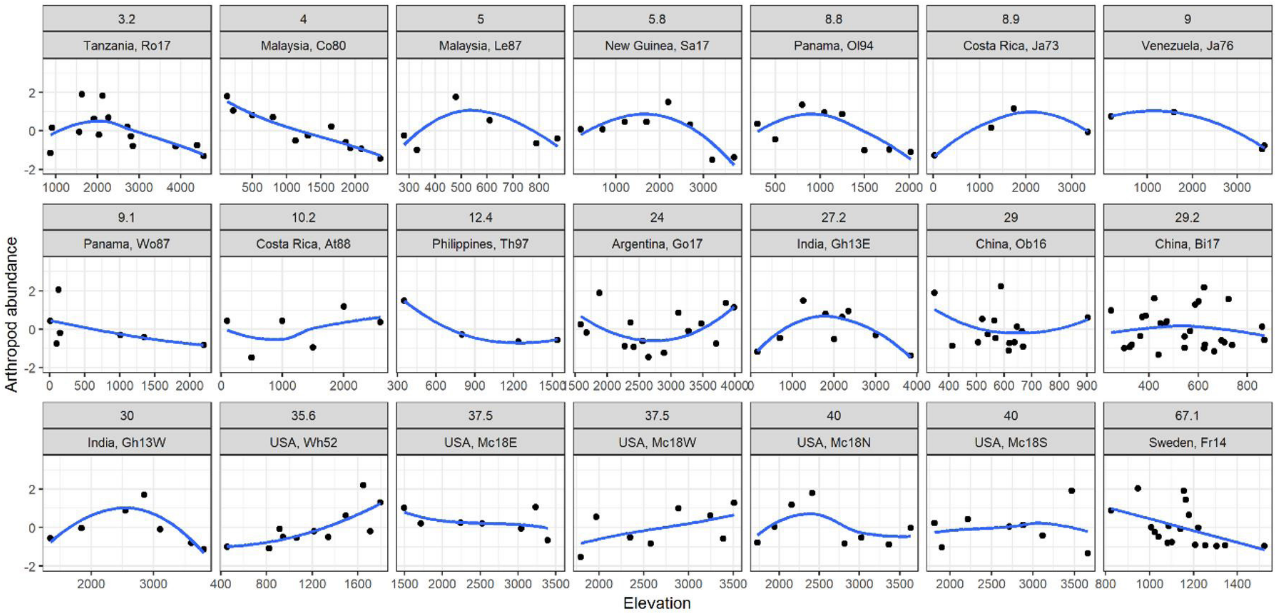

Figure 2. Patterns of arthropod abundance along elevational gradients. Latitude, location, and Study ID (see Appendix 1) are indicated on top of each panel, arranged from lowest to highest latitude. Elevation in meters is indicated on the bottom of each panel. The curves show loess smooth fits to the data. Abundance data were standardized to have a mean of zero and standard deviation of one before plotting. See Figure S2 for a version of this figure where all plots cover the same elevational range on the x-axis.

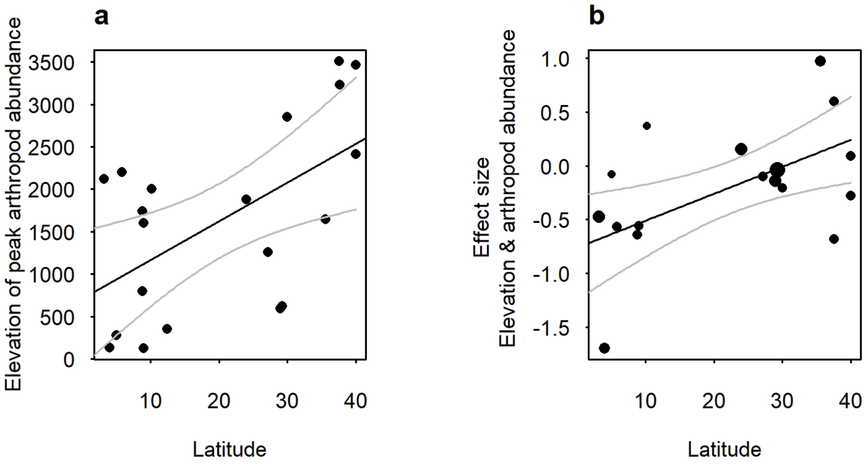

Figure 3. a Relationship between elevation of peak arthropod abundance and latitude; **b** Relationship between effect size of the correlation between arthropod abundance and elevation and latitude. Size of each point indicates sample size of the gradient. Grey lines in both plots indicate 95% confidence interval.

Predictors of abundance: Consistent with the expectations from our seasonality hypothesis, the peak in arthropod abundance is at higher elevations at higher latitudes (Fig. 3a). Correspondingly, the correlation between elevation and arthropod abundance shows a linear increase with latitude, that is, abundance decreases with elevation in the tropics but increases with elevation at mid-latitudes (Fig. 3b, meta-regression,

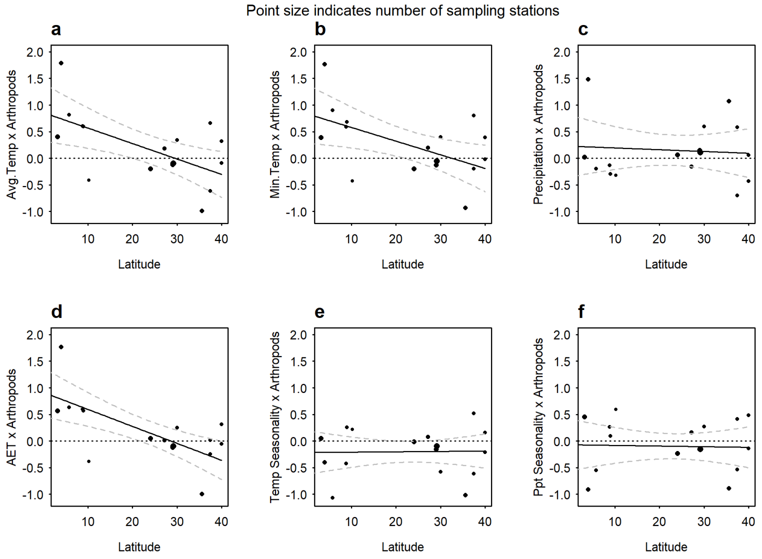

Figure 4. Relationship between latitude and effect size of the correlation between arthropod abundance and various climatic variables. Size of each point indicates number of sampling stations along the gradient. **a** (mean temperature x arthropod abundance) ~ latitude: slope ± SE = -0.029 ± 0.01, P = 0.005; **b** (minimum temperature x arthropod abundance) ~ latitude: slope ± SE = -0.026 ± 0.011, P = 0.014; **c** (annual precipitation x arthropod abundance) ~ latitude: slope ± SE = -0.003 ± 0.011, P = 0.76; **d** (actual evapotranspiration x arthropod abundance) ~ latitude: slope ± SE = -0.032 ± 0.009, P = 0.0002; **e** (temperature seasonality x arthropod abundance) ~ latitude: slope ± SE = -0.007 ± 0.008, P = 0.93; **f (**precipitation seasonality x arthropod abundance) ~ latitude: slope ± SE = -0.0012 ± 0.009, P = 0.89. Dashed grey lines indicate 95% confidence interval. Dotted black line indicates zero effect size.

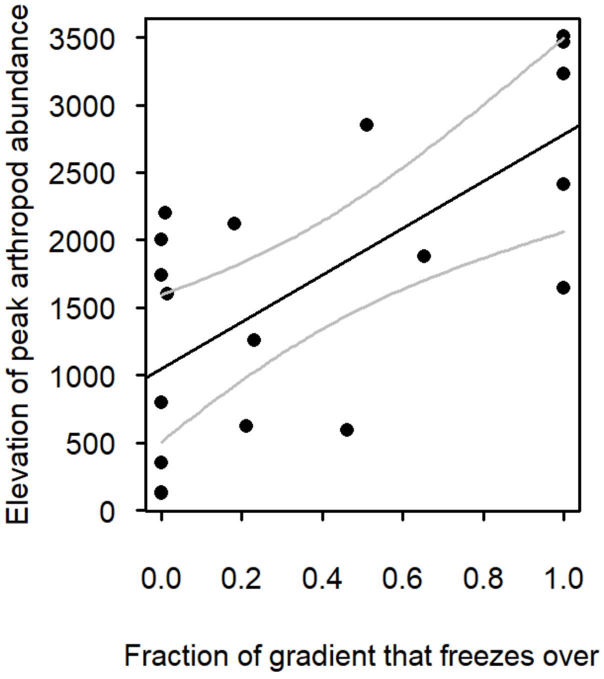

Figure 5. Correlation between elevation of peak arthropod abundance and fraction of the sampled gradient that experiences freezing temperatures. Grey lines indicate 95% confidence interval.

correlation of elevation and arthropod abundance, N= 17, R^2 = 53%, slope (latitude) = 0.025 ± 0.009 SE, z = 2.69, P = 0.007). Associated with this trend, mean annual temperature, minimum temperature, and actual evapotranspiration are positively correlated with arthropod abundance along gradients in the tropics, decreasing to a weak or negative correlation at higher latitudes (Fig. 4, all $P < 0.01$). Correlations between arthropod abundance and annual precipitation, precipitation seasonality, and temperature seasonality are not related to latitude (Fig. 4, all $P > 0.7$; Fig. S3). Finally, the correlation between ant abundance and non-ant arthropod abundance was not significantly different from zero across all studies (Fig. S4, average ES = -0.018 ± 0.11, P = 0.87) and was also not significantly affected by latitude (meta-regression, ant abundance x arthropod abundance: slope = -0.014 ± 0.009 SE, N= 10, P = 0.15).

The finding that temperature correlates of abundance vary with latitude but precipitation correlates do not suggests that some feature of absolute temperature is affecting the position of peak abundance. Indeed, the most plausible model for position of peak abundance supports a positive relationship between arthropod abundance and the fraction of the gradient that freezes over (AICc weight= 0.57, Table 1, Fig. 5). This model has even stronger support (AICc weight= 0.72) when we used the Chelsa precipitation data in the analysis (Table S1). The model with precipitation at the lowest elevation as a predictor was a close second when we used the Worldclim data (AICc weight= 0.20, ΔAICc = 2.15), lending some support to the idea that dry mountain bases do tend to have peak abundances at higher elevations than those with wetter bases (Fig. S5).

Discussion

Three possible explanations were explored here for why arthropod abundance along elevational gradients should vary geographically: seasonality, precipitation, and interactions with ants. Across 20 studies of arthropod abundance along elevational gradients spanning 0-40° latitude, we found that correlation of elevation and arthropod abundance increases with latitude (Fig. 3). Moreover, we found that arthropod abundance peaks at higher elevations on gradients where freezing temperatures are recorded over a greater fraction of the gradient (Table 1, Fig. 5). We suggest that this is driven by variation in seasonality along elevational gradients with high variation in the length of growing season along gradients at mid-latitudes but little variation along gradients in the tropics. A relatively short growing season at high elevations and latitudes leads to synchronous emergence and reproduction of arthropods causing a sharp peak, often referred to as a large arthropod flush. We also found some support for the precipitation hypothesis as peak arthropod abundance is higher on gradients with an arid base (Table 1, Fig. S5). However, precipitation did not emerge as an important factor across all gradients, which might be explained by low variation in precipitation on most individual gradients (Appendix 2). Lastly, we found no evidence that ants influence abundance of other arthropods. However, ant abundance data was not available for seven of the 20 gradients, reducing our ability to evaluate this hypothesis.

We suggest that the abundance peaks at higher elevations at higher latitudes are caused largely by synchronous emergence and reproduction due to the constraints on the growing season. These abundance

Table 1. General linear models for elevation of peak arthropod abundance (meters above sea level). Slope and standard errors obtained using scaled predictors are in parentheses. Model 1 is the most plausible model based on AICc values.

Model ID	Independent variables	Slope ± S. E.	p	AICc	AICc weight
Model 1	Freezing fraction	1728.8 ± 457.6 (734.3 ± 194.4)	0.002	314.58	0.57
Model 2	Precipitation at lowest elevation	-0.59 ± 0.18 (-679.9 ± 205.7)	0.004	316.73	0.20
Model 3	Latitude	42.45 ± 16.34 (579.6 ± 223)	0.019	319.8	0.04
Full model 1	Precipitation at lowest elevation	-0.17 ± 0.32 (-201.4 ± 376.4)	0.6	317.49	0.13
	Freezing fraction	1326.1 ± 886.2 (563.3 ± 376.4)	0.15		
Full model 2	Precipitation at lowest elevation	-0.48 ± 0.27 (-552.8 ± 310.4)	0.09	319.62	0.05
	Latitude	12.64 ± 22.74 (172.5 ± 310.4)	0.59		
Null model	Intercept-only			323.31	0.01

peaks may be constituted by large numbers of individuals belonging to a few species and not necessarily correlate with species richness peaks. Discordant patterns of abundance and species richness along elevational gradients have been widely reported. At temperate latitudes, maximum insect species richness along elevational gradients is often at low elevations (McCoy 1990), whereas abundance peaks at intermediate elevations (Figs. 2 and 3). For example, in the Smoky mountains, Whittaker (1952) found that insect species diversity is highest at about 945m elevation while total abundance peaks at about 1645m. Similarly in New South Wales, Australia (≈30°S), Lowman (1982) sampled three sites at 760, 900 and 1200m elevation and found a sharp spring arthropod abundance peak at 1200m elevation which was seemingly constituted of fewer species. Similar findings have been reported for specific arthropod groups. Brehm et al. (2007) found a near monotonic increase in moth abundance along an elevational gradient from 40m to 2730m in Costa Rica but recorded highest species richness at mid-elevations. Kumar et al. (2009) found almost twice as many paper wasp species at 500m compared to 1100m elevation in Costa Rica despite finding more than 5x as many individuals at 1100m elevation compared to 500m elevation in their malaise and flight-intercept traps.

Together, these findings suggest that the summer abundance peak at higher elevations in mid-latitudes is constituted of larger populations of relatively few species, akin to the latitudinal pattern of more arthropod individuals but fewer species in the temperate versus the tropics (Janzen and Pond 1975). This is consistent with expectations that seasonality, that is, a short growing season and synchronous emergence are responsible for greater arthropod abundance at mid- or high elevations at mid-latitudes. This effect may diminish towards polar latitudes where growing seasons at different elevations might not vary much. Indeed, the only study in our dataset in the frigid zone (Franzén and Dieker 2014), which we omitted from all analyses, showed a strong negative correlation between elevation and arthropod abundance (r = -0.49). Note that our study only examines summer arthropod abundance, and patterns of arthropod abundance in other seasons are expected to be different and likely shaped by other factors.

Our findings come with caveats. First, the studies included in our analyses sampled different substrates and used different methods. Thus, the component of arthropod fauna measured could be quite different from each other, and we have assumed that the estimates obtained correlate generally with arthropod abundance. However, previously published work in the Andes (Guevara and Avilés 2007) and our own unpublished studies from the eastern Himalayas show that arthropod abundances do vary similarly across methods (M. Schumm, A. White, K. Supriya and T.D. Price, unpublished). Moreover, because we standardized arthropod abundance before analyses, the difference in capture rates of different field methods does not influence our results. A second caveat is that we did not account for the effect of human disturbance on arthropod abundance in our analyses. This could have a particularly large impact at low elevations, which tend to have larger human settlements (Lee et al. 2004). As the studies included in our analyses spanned a long timescale (1952 - 2017), it was difficult to include a meaningful measure of human disturbance for all the gradients at the time that they were sampled. However, the correlates we uncovered with latitude seem most likely to be driven by climatic factors.

Our study also demonstrates the limited number of published datasets on arthropod abundance patterns. Given the importance of arthropods and the reported declines in arthropod population in some places (Hallmann et al. 2017, Sánchez-Bayo and Wyckhuys 2019, Lister and Garcia 2018), more studies of arthropod abundance along environmental gradients would be valuable, using similar sampling methods across different gradients. Data on arthropod abundance across all seasons at different sites are also needed. Some studies show sharper peaks of arthropod abundance in temperate regions compared to the tropics (Janzen and Pond 1975, Hails 1982). However, Lowman (1982) is the only study we could find that compares seasonal patterns of arthropod abundance across different substrates at different elevations.

In conclusion, we find that arthropod abundance in the growing season peaks at higher elevations on elevational gradients at higher latitudes (Fig. 3). We suggest that this is because short growing seasons at these higher elevations lead to a sharp increase in summer arthropod abundance, that is, the length of growing season is negatively correlated with arthropod abundance maxima. Length of growing season has been increasing in many places over the past few years (Walther et al. 2002). Our interpretation suggests that this may reduce maxima in arthropod abundance with potentially cascading effects, including effects on the populations of insectivorous vertebrate species and transmission of diseases with insect vectors. Hodkinson (2005) came to a similar conclusion in his review of single species abundance patterns along elevational gradients. Global changes in precipitation patterns might also affect the shape of elevational patterns of arthropod abundance, with hump-shaped patterns becoming more common in regions where the low elevations become drier over time.

Global climate change is likely to have an enormous impact on species distributions, abundances, and interactions in mountains (Pounds et al. 1999). Moreover, stable or positive abundance trends of species over time appear to be necessary to allow species range expansion in response to climate change (Mair et al. 2014). Only with increased documentation of arthropod abundance patterns along elevational gradients and across different seasons will we be able to predict the changes in arthropod abundance patterns and their consequences.

Data accessibility

All the data included in this paper are included as part of the online supplementary materials.

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Author contributions

K. Supriya collected the data, conducted the analyses, and wrote the manuscript. Katerina Sam contributed the Papua New Guinea dataset; CSM and TDP gave input on the data analyses. All authors contributed to the final version of the manuscript.

Supplementary Materials

The following materials are available as part of the online article from https://escholarship.org/uc/fb

Table S1 General linear models for elevation of peak arthropod abundance (meters above sea level). Model 1 is the most plausible model based on AICc values. Precipitation at lowest elevation was taken from the Chelsa dataset for these sets of models instead of the Worldclim dataset, which was used for a similar table in the main manuscript.

Figure S1 **a** Minimum and maximum elevations sampled in the 21 gradients we found in our literature search; **b** Months of sampling for each study that were included in the analyses. Study ID (see Table S1) indicated on the Y-axis.

Figure S2 Pattern of non-ant arthropod abundance along elevational gradients. Latitude, location and Study ID (see Table S1) are indicated on top of each panel. Elevation in meters is indicated on the bottom of each panel and ranges from 0-4000m for all the plots. The curves show loess smooth fits to the data. Abundance data were standardized to have a mean of zero and standard deviation of one before plotting.

Figure S3 Relationship between latitude and effect size of the correlation between arthropod abundance and precipitation using precipitation data from Worldclim and Chelsa datasets. Size of each point indicates number of sampling stations along the gradient. **a** (annual precipitation from Worldclim x arthropod abundance) ~ latitude: slope ± SE = -0.003 ± 0.011, P = 0.76; **b** (annual precipitation from Chelsa x arthropod abundance) ~ latitude: slope ± SE = 0.012 ± 0.011, P = 0.26

Figure S4 Pattern of non-ant arthropod abundance (black filled circles) and ant abundance (red filled circles) along elevational gradients. Latitude, location, and Study ID are indicated on top of each panel. Elevation in meters is indicated on the bottom of each panel. The curves show loess smooth fits to the non-ant arthropod abundance data. Abundance data were standardized to have a mean of zero and standard deviation of one before plotting.

Figure S5 Elevation of peak arthropod abundance is negatively correlated to the amount of precipitation at the lowest sampled site. Grey lines indicate 95% confidence interval.

Appendix 1 Summary of data for each of the gradients included in our analyses, correlations between various environmental variables and non-ant arthropod abundance, Moran's I and the observed patterns of arthropod abundance for each gradient.

Appendix 2 Detailed data on arthropod abundance and climatic variables from all gradients at all sampling locations.

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