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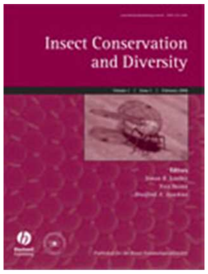

Insect elevational specialization in a tropical biodiversity hotspot

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Insect elevational specialization in a tropical biodiversity hotspot

Running title: Tropical elevational specialization

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Abstract

1. Tropical montane organisms are vulnerable to climate change because of elevational specialization, but little is known of the variability of elevational specialization across tropical insects.

2. We assessed elevational specialization across several insect taxa comprising four trophic groups 80-2263m up an elevational transect in Brazilian Atlantic Rainforest, using community-based and species-based approaches.

3. We sampled 697 species, of which 32% were found only in the top and 45% only in the bottom half of the transect. Considering only the 182 species with at least five individuals recorded, the percentage of species found exclusively in the top or bottom half drops to 16% and 24%.

4. Across four vegetation belts (lower montane forest, montane forest, upper montane forest and Campos de Altitude) the Eumolpinae (herbivores) were more specialized than Scarabaeinae (saprotrophs), or Lampyridae (predators). This result was robust to the treatment of rare species, and the difference was most marked at higher elevations. Lampyridae lacked upper montane forest specialists.

5. Using all species sampled, specialization to the upper or lower half of the transect was greatest amongst Chrysomelidae, Curculionidae (both herbivores) and Lampyridae, and lowest amongst Tiphiidae (parasitoids) and Coccinellidae (predators). However, considering only better sampled species, Lampyridae were the most specialized and Braconidae the least specialized. Trophic groups also varied in line with these findings.

6. Our findings suggest high elevational specialization and concomitant extinction risk in Brazilian Atlantic Rainforest insects. Differences in elevational specialization between taxonomic groups may alter the functioning of insect communities under climate change.

Key words: altitudinal ranges, climate change, elevational specialization, extinction risk, range shifting, tropical insects, tropical rainforest

Introduction

Climate change is now widely recognized to be a major cause of extinction risk globally (Thomas *et al*., 2004; Parmesan, 2006; Brierley & Kingsford, 2009; Hannah, 2012; Urban, 2015). One of the mechanisms by which changing climates might cause extinction is when rising temperatures exceed critical physiological thresholds, forcing species to shift their ranges to suitable habitats or leading them to extinction (Parmesan & Yohe, 2003; Thomas *et al*., 2004; Urban, 2015). The ability of a species to persist in a wide range of thermal conditions is therefore likely to make it more resistant to climate change, whilst species that can only persist in a narrow range of thermal conditions will be more vulnerable (Deutsch *et al*., 2008; Huey *et al*., 2012).

Tropical species are generally regarded to have low thermal tolerance due to the low seasonal temperature variability experienced, making them potentially vulnerable to extinction from climate change (Addo-Bediako *et al*., 2000, Deutsch *et al*., 2008, Bonebrake & Deutsch, 2012). The elevational ranges displayed by species may, at least partially, indicate their thermal tolerances (McCain, 2009; Laurance *et al*., 2011; Garcia-Robledo *et al*., 2016), and have been used to infer extinction risk from climate change across taxa and geographic locations (Sekercioglu *et al*., 2007; Colwell *et al*., 2008; Feeley & Silman, 2010; La Sorte & Jetz, 2010; Mekasha *et al*., 2013; La Sorte *et al*., 2014), but little is known about how elevational ranges vary in tropical insects. Here we assess the variation in elevational specialization across several insect taxa along an elevational transect in Brazilian Atlantic Forest, and the likely implications for conservation under climate change.

One of the reasons for the expected high impact of global warming on tropical montane organisms is their thermal specialization (e.g. Garcia-Robledo *et al*., 2016). Janzen (1967) proposed that organisms on tropical mountains (as opposed to temperate mountains) experience low seasonal variation in temperature but high variation along elevational gradients. He suggested that this selected organisms for narrow thermal tolerance compared to those on temperate mountains, because organisms would not need tolerance to a broad range of thermal regimes at any altitude, and could reduce the cost of thermal tolerance by becoming more thermally specialized. Janzen's (1967) assumptions and predictions have been tested by many authors and general support has been found (e.g. Huey, 1976; Ghalambor *et al*., 2006; McCain 2009; Bonebrake & Deutsch, 2012; but see Buckley *et al*., 2013). Spatial and temporal variation in local temperature also predicts thermal tolerances in insect species globally (Bonebrake & Deutsch, 2012). However, high elevation insects are predicted to have wider elevational ranges than low elevation species, because seasonal temperature range tends to increase with altitude (Stevens 1992). Thus, high elevation species may require broader thermal tolerances than lowland species, which also adapts them for wider elevational ranges (Stevens, 1992).

However, the elevational ranges of tropical insects along altitudinal gradients have rarely been explicitly analyzed, with most studies that contain pertinent data focusing on species richness gradients or the shifting of ranges over time (see references in Laurance *et al*., 2011). Consistent with the predictions above, Gaston & Chown (1999) found an increase in elevational range with altitude in 26 species of scarab dung beetles across an elevational gradient of approximately 2500m in tropical Africa. However, studies have also shown evidence for high-elevation endemism and narrow elevational ranges in tropical montane species. Garcia-Robledo *et al*. (2016) found that most of the species of rolled-leaf beetles (Chrysomelidae) occurring at mid and high elevations in Central American mountains were elevational specialists. Upper thermal tolerances were lower amongst high elevation species, presumably because they are less exposed to high temperatures than low elevation species. In contrast, species found at low altitudes had high thermal tolerances, and were often not constrained to low latitudes. A similar pattern was found in schizophoran flies in the Australian wet tropics, with the most restricted species at high elevations (Wilson *et al*., 2007), which was attributed to the effects of past climate change in generating a high degree of endemism amongst cool-adapted species. Together these variable findings suggest that there may be considerable variation in elevational specialization across taxa and geographic locations.

Laurance *et al*. (2011) compiled data from 150 studies of species' elevational specialization in the tropics, including insect and other invertebrate studies, and assessed the degree of specialization to either the lower or upper half of the altitudinal ranges sampled. They found that about 75% of species were elevational specialists, and lower zone specialists (~50%) were more common than upper zone specialists (~20%). Upper zone specialists were more common in ectothermic vertebrates and plants than endothermic vertebrates, with invertebrates at intermediate values. However, the median elevation considered varied markedly across studies, and there was no control for species' abundance across taxa, which are potential sources of bias. In addition, there was no explicit consideration of heterogeneity across insect taxa.

In this paper we assess the degree of elevational specialization along an elevational transect in Brazilian Atlantic Rainforest. We combine the results of collections of several insect taxa using different sampling techniques, and ask how the degree of elevational specialization varies across taxa, the functional groups to which they belong, and between elevation zones. We then assess the likely implications for the conservation of tropical insect diversity. The biodiversity hotspot known as Brazilian Atlantic Rainforest is distributed across a heterogenous landscape that includes ombrophilous forests, semi-deciduous forests, mountain cloud forests, Campos de Altitude (also known as Brazilian páramos), inselbergs, *restingas*, and mangroves, with varying levels of endemicity (Safford, 1999; Ribeiro *et al.*, 2009). Habitat heterogeneity is thought to be a main driver of endemism either due to niche divergence and ecological speciation (Nosil, 2012), or by niche conservatism leading to isolation in refugia, areas of relative climatic stability such as tropical mountain ranges (Carnaval & Moritz, 2008; Steinbauer *et al.*, 2016). Currently, less than 10% of the 150 million ha originally covered by Brazilian Atlantic Rainforest is left as remnants of varied size and connectivity (Ab'Sáber, 2003; Morelatto & Haddad, 2000; Ribeiro *et al.*, 2009).

Material and Methods

Study area

The study was conducted along an elevation transect at Serra dos Órgãos National Park (22°32´S and 43°07´W), in the State of Rio de Janeiro (Brazil) (Figures 1, 2), a mountainous conservation area of 20,024 ha. The Park encompasses the highest peaks of the Serra do Mar, ranging from 80-2263m elevation. It was founded in 1939 and is the third oldest National Park in Brazil, aiming to conserve montane biodiversity, especially the Campos de Altitude (high elevation grasslands), which contain a great part of the endemism in the area. The region is among the best preserved in the Atlantic Forest biome (Castro, 2008), although much of the forest is secondary growth. The Park encloses four different vegetation belts: lower montane forest (below ~800m), montane forest (800~1500m), upper montane forest (1500~2000m) and high elevation grasslands, Campos de Altitude (over ~2000m), characterized by shrubs, herbs and grasses (Rizzini, 1954; Veloso *et al.*, 1991) (Figure 1).

The climate is marked by a drier cool season, a hot season of high precipitation, and temperature reduction with elevation (Viveiros de Castro, 2008). Superhumid conditions prevail for most of the year, marked by intense rainfall from November to March (460mm mean monthly rainfall), while the drier season (though still humid) extends from June to August (49mm mean monthly rainfall). The coolest months are between May and August (mean 16.4°C), and the hottest from December to March (mean 21.1°C) (Flinte *et al.*, 2009).

Temperature loggers placed at 15 sampling locations, covering the same route as those presented elsewhere in this paper, throughout 2015 showed that mean annual temperature decreases consistently with elevation, from 22.5ºC at 130m to 12.8ºC at 2130m elevation, a 0.5ºC decrease per 100m elevation. The mean monthly temperature at each elevation ranges over 5.7ºC ± 0.4ºC. The ratio of spatial (across sites) to seasonal (within sites, across months) variation in temperature ranges from 1.5 to 2, which is in the higher range of values globally, typical of tropical mountains (Bonebrake & Deutsch, 2012), and likely to favour elevational specialization.

Insect sampling took place over a 9 year period (see below), and over this time there is the potential for significant weather changes and potentially some biotic range shifting. Data from an automated weather station at 991m along the sampling route show that 2007 and 2015 (the main sampling years) had similar average temperature though 2015 was drier (mean monthly temperature 2007: 18.1°C, SD 2.2 °C; 2015: 18.8 °C, SD 2.2 °C, total rainfall 2007: 2591mm; 2015: 2019mm). Between 2007 and 2015, both the rainfall and mean monthly temperature trends were non-significant (temperature Pearson's $R = 0.546$, $n = 9$, $P = 0.128$; rainfall $R = -0.354$, $n = 9$, $P = 0.351$), though over longer time periods significant trends are expected to emerge.

Field sampling methods

To maximize taxonomic comparisons, we compiled data from several separate samples aimed at different taxa using different methods. Sampling locations followed the path of the road from Guapimirim up to Teresópolis (land inside the park boundary), and then from the Park entrance at Teresópolis up the Pedra do Sino trail (Figure 2, for exact sampling locations see Supporting Information).

Scarabaeinae (Coleoptera: Scarabaeidae) were sampled in January 2014, at 50 m intervals from 100 to 2000 m elevation. At each site, the beetles were sampled using three pitfall traps (14cm diameter) containing a solution of water, detergent and salt. They were baited with human faeces, suspended in a small plastic cup (4.5cm diameter) at ground level over the pitfall trap with wire. A plastic rain-lid was placed 15cm over the top of the trap supported by wooden skewers placed in the ground. Traps at the same elevation were 50m apart. The traps were left for 48 hours and the beetles captured were taken to the laboratory and preserved in 98% ethanol.

Eumolpinae (Coleoptera: Chrysomelidae) and Lampyridae (Coleoptera) were sampled using pairs (100m apart) of Malaise (flight interception) traps at 360 m, 550 m, 700 m, 880 m, 1070 m, 1250 m, 1480 m, 1680 m, 1810 m, 1940 m, 2030 m and 2170 m elevation. The Lampyridae samples were considered from December 2014 to December 2015 and the Eumolpinae from December 2014 to February 2015.

Tiphiidae (Hymenoptera) were sampled using pairs of Malaise (flight interception) traps (100m apart) at each of just four different elevations, 360 m, 1250 m, 1480 m, and 2170 m, from December 2014 to February 2015.

Braconidae (Hymenoptera), Chrysomelidae (all subfamilies), Coccinellidae and Curculionidae (Coleoptera) were sampled with yellow sticky traps (Bio Trap®, Biocontrole, São Paulo, Brazil). Traps consisted of a plastic yellow panel (24.5cm x 10cm) with adhesive on both sides. They were attached with wire to vegetation 1.5 to 2m above the ground. Seven panels were placed approximately 20m apart from each other in the vegetation, on slopes of aspect within 45° of north, at each of just four different elevations: 350 m, 1280 m, 1480 m and 2100 m. Sampling was conducted every two months from February 2007 to February 2008, resulting in seven week-long samples. Placement of new traps, and their retrieval one week later, occurred on a single day. Retrieved panels were placed in plastic containers and separated from each other by small wooden cubes, taken to the laboratory and stored in the freezer.

Trap effectiveness is an important issue in assessing species diversity (Southwood, 1978). The sampling methods used here are widely known as effective for these respective groups. Coleoptera and Hymenoptera are widely studied using Malaise traps (e.g. Fraser *et al.,* 2007; Ohsawa, 2010) and yellow sticky traps (e.g. Larsen *et al.,* 2014, Thomson *et al.,* 2004). For Scarabaeinae, human faeces-baited pitfalls are one of the most effective sampling methods (e.g. Silva *et al.*, 2012).

Where sampling took place for less than a year, the period considered was always the warmer wetter season (December to February), during which insect species richness and abundance are generally greatest (e.g. Flinte *et al.*, 2009). Species whose adult phenology is restricted to other times of year will have been omitted by this sampling, and this should be born in mind when interpreting the results. In addition, because the sticky trap sampling (Braconidae, Chrysomelidae, Coccinellidae and Curculionidae) occurred some eight years earlier than the other sampling, taxonomic comparisons may be most robust within rather than between these sampling periods, since taxa in the 2014-2015 samples may have shifted range slightly during the intervening period.

Species sorting and identification

Sticky traps were individually submersed in paint thinner for five minutes to dissolve the glue, and insects were carefully removed with a thin brush. This procedure was undertaken in a fume hood with use of a gas mask. All detached material was sifted, washed and stored in 70% ethanol. Adults of Braconidae (CVSG), Chrysomelidae (VF), Coccinellidae (ROA) and Curculionidae (VF and COA) were identified to morphospecies after first keying to the lowest taxonomic level possible, normally species or genus. Eumolpinae (CC), Lampyridae (LFLS) and Tiphiidae (ES) were removed from the Malaise traps monthly and identified to morphospecies, also after first keying to the lowest taxonomic level possible, normally species or genus. The Scarabaeidae were first identified by Raissa Dufrayer and then confirmed by Prof. Fernando Zagury Vaz de Melo (Universidade Federal de Lavras), again mostly to species and genus level and then to morphospecies. Specimens were deposited in the collection of the Insect Ecology Laboratory (CLEI) at the Federal University of Rio de Janeiro.

Data analysis

We conducted analyses on two different subsets of the data; first, we followed Laurance *et al*. (2011) in maximizing inclusion of taxa by defining only two different altitudinal zones (two-zone analysis) divided at the median sampling elevation. To ensure equal sampling effort in the two zones, we included data from only four elevations, one each approximating the four vegetation zones to minimize potential sampling bias, guided by the lowest common sampling effort across taxa. This analysis allows us to compare our findings directly with Laurance *et al*. (2011). The exact samples were: Eumolpinae, Lampyridae and Tiphiide: 360 m and 1250 m in the lower-zone and 1480 m and 2170 m in the upper-zone; Scarabaeinae: 350 m and 1250 m in the lower-zone and 1450 m and 2000 m in the upper-zone; Braconidae, Chrysomelidae and Curculionidae: 350 m and 1280 m in the lower-zone, and 1480 m and 2100m in the upper-zone.

In a different subset of the data, we doubled the number of altitudinal zones sampled (four-zone analysis, approximating one of each of the four vegetation zones), but this analysis could only be carried out for Eumolpinae, Lampyridae and Scarabaeinae, which have the necessary finer sample distributions. Sampling effort was equal across zones for Eumolpinae and Lampyridae, and the same number of elevations per zone was sampled for Scarabaeinae (though the sampling method was different). Finer altitudinal intervals were not considered because sample sizes became too small for community analyses. In order to standardize the sampling intensity and elevations across taxa and reduce potential biases, we used only the following samples from each taxon: Scarbaeinae: 350 m, 500 m and 700 m approximating the lower montane forest, 850 m, 1050 m and 1250 m approximating the montane forest, 1450 m, 1600 m and 1800 m approximating the upper montane forest and 1900 m, 1950 m and 2000 m approximating Campos de Altitude; Eumolpinae and Lampyridae: 360 m, 550 m and 700 m for lower montane forest, 880 m, 1070 m and 1250 m for montane forest, 1480 m, 1680 m and 1810 m for upper montane forest and 1940 m, 2030 m and 2170 m for Campos de Altitude.

For each of these subsets of the data we carried out three analyses. First, to compare with the results of Laurance *et al.* (2011), we defined species as specialists if they were restricted to a single zone. Differences in the proportion of specialists across zones and taxa were assessed with χ^2 tests on the species counts, and pairwise comparisons made using the same tests but controlling for the family-wide false discovery rate (Benjamini & Hochberg, 1995) using the fifer package in R (R core team, 2015). The above analysis was conducted with the complete dataset, which has the advantage of considering all species together, but assumes that the species with low abundance in our samples are elevational specialists. This may indeed be the case, but it is possible that rare species are simply poorly sampled species (which may have large elevational ranges), in which case the analysis of elevational specialization needs to control for sampling abundance.

We therefore carried out two analyses that controlled for sampling abundance. In a similar community-level analysis, we carried out the same analyses above but only considering species with at least five individuals sampled (e.g. following the approach of Wilson *et al*. (2007). Some of the finer scale tests were omitted because sample size was smaller in this dataset due to the omission of many rare species. To visually assess the effect of this cutoff on inclusion across taxonomic groups, rank-abundance plots were constructed for the different taxa and sample designs.

We also used a species-focused rather than community-focused approach. For each species we counted the number of elevational zones in-and-between the highest and lowest zones in which it was found. This number of zones (out of the total of four for the four-zone analysis, or simply presence in two zones or not in the two-zone analysis) was then subjected to a generalized linear model with a binomial error structure using the glm function in R (R core team, 2015). The explanatory variable was the interaction between $\log_{10}$ abundance and taxon. This effectively asks if the slope of the relationship between $\log_{10}$ abundance and observed elevational range is different for different taxa; taxa with high slopes tend to have wide elevational ranges at high abundances, and taxa with low slopes have narrower elevational ranges at high abundance (all species have narrow elevational ranges at low abundance). Differences between taxa were tested by merging the factor levels designating taxon identity and observing the significance of the change in model deviance with a χ^2 test. Checks for overdispersion were made by dividing the residual deviance of models by the residual degrees of freedom, but none of the models indicated overdispersion as this ratio was always < 1.

In order to assess the completeness of our sampling, we compared observed richness for each sample design and taxon with estimates of asymptotic richness, and plotted associated species accumulation curves. Because of the diversity of sampling approaches used, accumulation approaches based on individuals rather than samples are most applicable, straightforward and comparable: in the vegan package in R rarefaction curves were constructed on the species abundance data using the ‘rarefy’ function, and Chao1 (Chao, 1984) and the Abundance-based Coverage Estimator (ACE, Chao 2005) measures of asymptotic richness made using the ‘estimateR’ function.

Results

Sampling completeness and rank abundance

Over the whole of the two-zone dataset, species continued to accumulate as more individuals were added (Figure 3a), and the Chao1 and ACE estimators are nearly double that of observed richness (Table 1). Examination of individual taxa (Table 1, Figure S1) shows that this undersampling was mostly due to the three richest taxa (Braconidae, Chrysomelidae and Curculionidae); in contrast the other taxa (Coccinellidae, Lampyridae, Tiphiidae and Scarabaeinae) were relatively completely sampled. In the four-zone analysis by contrast, species richness had nearly asymptoted (Figure 3b), and the Chao1 and ACE estimators were only slightly higher than observed richness (Table 1). This is true of all three taxa (Figure S1), none of which are very rich (Table 1), but all of which are better sampled in terms of numbers of individuals than in the two-zones analysis.

In the four-zone sample design, rank abundance plots are fairly similar in the three taxa considered (Figure S2), with fewest rare species in the Scarabaeinae, most in the Eumolpinae, with Lampyridae in between. In the two zone analysis, rank abundance plots differ more markedly across taxa, with Braconidae and Curculionidae having shallow curves with many rare species, Chrysomelidae a concave curve with many rare species and several abundant species, and Tiphiidae, Coccinellidae and Scarabaeinae having steep curves with few rare species and a few abundant species (Figure S2). Lampyridae has a curve of intermediate steepness.

Specialization to upper and lower zones

In the two-zone samples there were 6577 individuals in 697 species of the seven insect taxa sampled (Braconidae, Chrysomelidae, Coccinellidae, Curculionidae, Lampyridae, Scarabaeinae and Tiphiidae; exact counts of each species per zone are given in the Supporting Information). Across all species sampled, 77.2% were found in only one of the two zones. In the lower zone, 66.5% of species were specialized, and 58.3% in the upper zone, a small but significant difference (Figure 4a). Differences across zones were, however, not generally significant for individual taxa, except for Scarabaeinae. The proportion of elevation specialists differed across taxa and was highest in Chrysomelidae, Curculionidae, and Lampyridae and lowest in Tiphiidae and

Coccinellidae (Figure 5a). Taxonomic differences in specialization were generally similar in the upper and lower zones. Pooling species from the same functional groups, unsurprisingly, trophic groups differed significantly ($\chi^2_3 = 24.76$, $P < 0.0001$). There were more herbivore specialists than predators ($P_{adj} = 0.0098$) and parasitoids ($P_{adj} = 0.0001$), although no other trophic groups differed significantly ($P_{adj} = 1.00$).

In the analysis including only the 182 species with at least five sampled individuals, 73 species (40.1%) were elevational specialists, comprising 28.8% of species in the lower zone and 21.0% of species in the upper zone, (a non-significant difference, Figure 4b), so as in the all-species analysis, the level of specialization was not much higher in the lower zone (Figure 4a,b). For individual taxa, the only group to show a difference in specialization in the two zones was Tiphiidae, which was more specialized in the lower than upper zone (Figure 4b). Differences across taxa were again found in the degree of specialization, but they were different to those found when all species were analyzed (Figure 5b). Now, Lampyridae contained the highest proportion of specialists, and Braconidae the lowest. Chrysomelidae, Scarabaeinae and Curculionidae had reasonably high proportions of specialists, and Tiphiidae and Coccinellidae quite low proportions. Functional groups again differed in their specialization ($\chi^2_3 = 18.64$, $P = 0.0002$). Across functional groups, herbivores, predators and saprotrophs now had similar levels of specialization ($P_{adj} = 0.99$), with parasitoids having lower levels than all three others ($P_{adj} < 0.05$).

In the species-focused analysis, the taxon with the highest slope of the relationship between logit probability of occupying two zones and log abundance (hence the broadest elevational ranges for abundant species) was Braconidae ($b = 7.422$, SE = 0.818, $P < 0.001$), followed by Coccinellidae ($b = 5.019$, SE = 0.953, $P < 0.001$), Curculionidae ($b = 3.652$, SE = 0.532, $P < 0.001$), Tiphiidae ($b = 3.231$, SE = 0.523, $P < 0.001$), Chrysomelidae ($b = 2.593$, SE = 0.322, $P < 0.001$), Scarabaeinae ($b = 2.304$, SE = 0.508, $P < 0.001$), and Lampyridae ($b = 1.737$, SE = 0.424, $P < 0.001$) (Figure 6a). This is a different rank order of elevational specialization than found in the community-focused analysis with all species, but, unsurprisingly, similar to the results of the community analysis restricted to species with > 4 individuals, as both effectively ignore rare species. Across trophic groups, results were similar. The group with the highest slope of the relationship between logit probability of occupying two zones and log abundance was the parasitoids ($b = 5.353$, SE = 0.559, $P < 0.001$), followed by herbivores (*b* = 2.586, SE = 0.259, $P < 0.001$), predators (*b* = 2.317, SE = 0.334, $P < 0.001$), and saprotrophs (*b* = 2.116, SE = 0.489, $P < 0.001$) (Figure 6b). The predators, herbivores and saprotrophs did not have significantly different slopes ($\chi^2_2 = 1.06$, $P = 0.588$), but the parasitoids had significantly higher slopes than the other species combined ($\chi^2_1 = 44.19$, $P < 0.001$). Again, this is a different rank order of elevational specialization than found in the community analysis with all species, but similar to the results of the community analysis restricted to species with > 4 individuals.

Specialization across four vegetation zones.

A total of 3874 individuals belonging to 156 species of Eumolpinae, Lampyridae and Scarabaeinae were collected using the four-zone analysis. Overall, 53.8% of species were found in one zone only. For the lower montane forest 33.3% were specialized, for the montane forest 32.6%, upper montane forest 31.9%, and Campos de Altitude 41.2%. Considering all the insect species together there was no significant difference in the relative frequencies of specialists in each zone (Figure 7a). The only significant difference in elevational specialization detected across zones was the low level of specialization in the upper montane forest in the lampyrids (Figure 7a). The total proportion of elevational specialists among the Eumolpinae was significantly higher than those among the Lampyridae and the Scarabaeinae (Figure 8a).

When only species with > 4 individuals sampled were included, results again differed from when all sampled species were included. Now only 37.6% of species were specialists on one of the four zones, including 14.7% of species in lower montane forest, 22.0% in montane forest, 12.8% in upper montane forest, and 37.5% of species in Campos de Altitude (Figure 7b). There were also differences across taxa, with Eumolpinae having a higher proportion of specialists than the other two taxa (Figure 8b). Specialization was generally low in Scarabaeinae, and non-existent in Campos de Altitude.

The species-focused approach largely confirmed the differences in specialization across taxa in the above analysis. The slope of the relationship between logit number of zones and log abundance was not significant for Eumolpinae (*b* = 0.316, SE = 0.180, $P = 0.0789$) indicating that elevational range does not increase with abundance, but was significant for Lampyridae ($b = 0.540$, SE = 0.150, $P < 0.001$), and Scarabaeinae ($b = 0.713$, SE = 1.680, $P < 0.001$) (Figure 6c), and the difference between the slopes was different for Eumolpinae and Scarabaeinae ($\chi^2_1 = 3.872$, $P = 0.0491$), but not for Eumolpinae and Lampyridae ($\chi^2_1 = 1.479$, $P = 0.224$) or Lampyridae and Scarabaeinae ($\chi^2_1 = 0.926$, $P = 0.336$). This suggests that the differences in elevational specialization in the full dataset are not simply due to differences in the proportion of rare species, but also reflect the elevational ranges of abundant species, which are wider in Scarabaeinae than Eumolpinae.

Discussion

In this paper we investigated levels of elevational specialization across several insect taxa along an elevational transect in Brazilian Atlantic Rainforest. We found strong evidence for taxonomic differences in elevational specialization, and therefore potentially across the functional groups which they represent. We also found differences in the degree of specialization to different elevational belts. Importantly, findings could differ in detail when examined at different spatial scales. Below we consider these findings in a broader context and their implications for the conservation of tropical insects under climate change.

To compare our findings with the broad meta-analysis of Laurance *et al*. (2011) we conducted an analysis using maximal taxonomic inclusion and contrasting only two broad elevational zones (lower and upper halves). Our overall findings bear some similarity to theirs. The high percentage of species that are specialists (77%) is typical of tropical studies at this scale, especially on continents and in the neotropics, as ours is. The high proportion of species that were specialized to lower zones was also typical, but we found a high proportion of specialization in the upper elevational zone that has not generally been found in other datasets analyzed in this way. In our dataset this finding is largely driven by the high proportion of upper zone specialists in Chrysomelidae, Curculionidae and Braconidae, which include many species with few individuals sampled, which naturally tends to make them appear in one zone. This feature of the data makes the exact percentage potentially suspect, since although the rarely collected species may genuinely be specialized (e.g., species might have small populations because they are specialized), they may also simply be poorly sampled, and would prove to have wider ranges if sampled better (Wilson *et al*., 2007). Nonetheless, the high value compared to previous datasets is in line with the known high levels of endemism found in other mountaintop taxa in Brazilian Atlantic Rainforest (Safford, 1999; Morellato & Haddad, 2000; Myers *et al*., 2000), a likely result of the historical interactions between climate and topography (Carmaval & Moritz, 2008; Steinbauer *et al*., 2016).

Our data also confirm another general finding of Laurance *et al*. (2011): that of differences in specialization across taxa. In their meta-analysis, differences were confined to the upper zone, but they did not explicitly consider variation across insect groups. Studies focused on insects, such as ours, are needed to help "defy the curse of ignorance" about the macroecology of this large component of biodiversity (Diniz-Filho *et al*., 2010). In our equivalent analyses we found strong differences across taxa in both the upper zones and lower zones that were generally consistent except in Scarabaeinae, which were one of the least specialized groups in the upper zone, but most specialized in the lower zone. Our study therefore highlights that taxonomic differences might also exist at lower elevational zones, with potential implications for community structure and function under environmental change.

In order to investigate the robustness of our findings to assumptions about rarely sampled species, we conducted two analyses that effectively ignored them: a community-focused and a species-focused analysis. These produced findings in accordance with each other, but which diverged from the analyses of all species above. In particular, when sufficient data were available to more accurately judge elevational specialization, levels of specialization decreased markedly, although the level of specialization was still similar in the upper and lower zones. This reduction was likely because rarely captured species had fewer opportunities to appear in two or more zones, and were excluded in this analysis. However, different taxa now appeared the most and least specialized, with Lampyridae the highest and Braconidae the lowest. This indicates that the high level of specialization shown by Chrysomelidae and Curculionidae is not retained at this scale when only quite abundant species are considered. For the Curculionidae this is surprising as the most abundant species are never extremely abundant (see Figure S2), and high elevational specialization might be expected to remain, suggesting that a larger fraction of species in this group cross the boundary between upper and lower halves of the transect. Abundant braconids are also nearly always elevationally widespread, whilst, in contrast, abundant lampyrids are often very elevationally specialized.

The reduced level of specialization in Chrysomelidae and Curculionidae in the more restricted dataset does not necessarily mean that the higher levels in the full dataset were an artefact; it just means that the true elevational ranges of the rarely-collected species need further study (Wilson *et al*., 2007). This alternative view of the different taxa also has consequences for the way functional groups are viewed: the herbivores we studied are the most specialized trophic group if all species are included, but if rarely-collected species are ignored, herbivores do not differ from predators and saprotrophs, and parasitoids are the most generalist in elevation. Overall then these new analyses suggest that the findings of studies that include all taxa collected may not hold if rare species' elevational ranges are underestimated by the data.

Since we had comparable data at finer elevational scales for three taxa, we could also investigate the effect of increasing the number of elevational zones. Overall there was a lower proportion of specialists when elevation zones are more finely divided. This is unsurprising, as species ranging over two of the four zones would never appear as specialists in the four-zone analysis, but could do in the two-zone analysis if those zones were restricted to the top or bottom halves of the mountain. Between the four zones there was also not much difference in specialization overall. There were consistent differences across taxa, with Eumolpinae showing higher levels of specialization than the other two taxa, and importantly this difference was retained when rarely-collected species were ignored. The difference was most marked amongst the higher elevational zones. At this spatial scale, the Lampyridae were not the most elevationally specialized when rarely-collected species were ignored, but elevational range still only rises quite slowly with abundance for both them and Scarabaeinae (Figure 6c), indicating that there are still many range restricted species at this scale. The chief difference between the two-zone and four-zone analysis in these taxa is that specialization differs between zones for Scarabaeinae in the two-zone analysis (Figure 4), but never in the four zone analysis (Figure 7). This implies that the degree of specialization at low elevations is not very high in this group, thus being lost when finer scales are examined.

Several factors are likely to contribute to different taxa displaying different levels of elevational specialization. Dispersal tendency, habitat specialization, the tendency and speed of ecological speciation, and the tolerance of environmental gradients are all likely candidates (Magurran & May, 1999; Schluter, 2000; Coyne and Orr, 2004; Nosil, 2012), but these are very difficult to quantify for a single taxon, less alone several. The Chrysomelidae contains subfamilies with different feeding habits and host plant specificity, but the Galerucinae and Eumolpinae comprise around 95% of the individuals on one tropical mountain (Bouzan *et al.*, 2015). These subfamilies have root-feeding larvae and the adults feed on foliage (Jolivet & Hawkeswood, 1995). Curculionidae adults are typically found on foliage or flowers, and most larvae are subterranean or internal feeders (Daly *et al.*, 1998). Although these feeding habits are considered among those with low host specificity amongst herbivores (Novotny &

Basset, 2005), herbivorous insects on mountains may have characteristics that can restrict their elevational-range both in evolutionary and ecological time, such as limited dispersal (e.g. Rank, 1992) and tight dependence upon host phenology and distribution, which can greatly vary along elevational gradients (e.g. Merrill *et al*., 2008).

Lampyridae have soft carapaces compared to other Coleoptera, and are often associated with moist environments (Branham, 2010), so they may require particular adaptations to different physical conditions, which could also encourage elevational specialization. They also commonly show intensive sexual selection (Lewis & Cratsley, 1988; South *et al*., 2011) and many have poorly dispersive females (Cicero, 1988; Bocak *et al*., 2008; South *et al*., 2011; Silveira *et al*., 2016), which might encourage ecological speciation and subdivision of the ecological niche by elevation. Some of the common braconids might be ecological- or host-generalists, encouraging broader ecological tolerances and elevational ranges. The two species which ranged all the way from the lowest to the highest sampling sites belong to genera known for their generalist habits: *Bracon* (Shaw & Huddleston, 1991) and *Ascogaster* (e.g. Stiling, 2004). The most species rich genus was the generalist *Heterospilus* (Cirelli & Penteado-Dias, 2003), and all species with > 4 individuals occurred in both the upper and lower elevational zones.

Our study has implications for the conservation of tropical insects under climate change. It is widely recognized that species' ranges may be moving uphill in response to warming climates, both in temperate zones and in the tropics (Konvicka *et al*., 2003; Pounds *et al*., 2006; Chen *et al*., 2009; Forero-Medina *et al*., 2011; Telwala *et al*., 2013). Species confined to high elevational zones are likely to be most at risk because tracking suitable climates will require dispersing across warmer areas of lower and less suitable elevation. Our finding that a higher proportion of species is confined to high elevational zones in this study from Brazilian Atlantic Rainforest (up to 58% as opposed to the ~20% found generally in invertebrates) suggests that previous general figures may underestimate the risk to many tropical insects, especially those in rich zones of endemism. The Brazilian Atlantic Rainforest is known to contain many endemic species that account for a high proportion of richness (Safford, 1999; Ribeiro *et al.,* 2009), including many in the Campos de Altitude (Macedo *et al*., 2016). It is important therefore to establish if this is also true of insects in other tropical zones of endemism. In addition, it is crucial to establish to what extent vegetation changes can be expected, particularly in the high altitude zones (Safford, 1999). Naively, one might expect the tree line to shift uphill under warming, leading to the loss of the Campos de Altitude and its endemic species. However, the tree line in Brazilian Atlantic Forest may not be determined solely by temperature, but also by edaphic factors, as well as disturbance such as fire (Safford, 1999). Under such a scenario the habitat might remain in a modified state, although insects with low upper thermal tolerance might nonetheless go extinct.

The level of specialization to the lower of two zones that we found is also high, but more in accord with previous work (Laurance *et al*., 2011). It is uncertain whether low elevation tropical species are more or less at risk from climate change. Low elevation tropical species might be adapted to a narrower range of conditions than high elevation tropical species, which might make them more susceptible to climate change if they cannot move uphill due to lack of contiguous higher elevation sites (Bonebrake & Deutsch, 2012). On the other hand, if such sites are available, low elevation species might better resist climate change, but even so low elevation sites might become impoverished as species move uphill (Colwell *et al*., 2008).

Our finding that different insect taxa have different degrees of elevational specialization, and to different zones, may mean that the taxonomic composition of insect communities will shift under climate change (e.g. Zografou *et al*., 2014; Nieto-Sánchez *et al*., 2015) especially if some are more vulnerable to extinction. Our work highlights the likely local loss of many Chrysomelidae (especially Eumolpinae), possibly Curculionidae and also Lampyridae, all of which show high degrees of elevational specialization, but it is possible that many abundant Braconidae and Scarabaeinae will be less affected. The former are especially worrisome because of their very high species richness. Although strong conclusions cannot be made about functional groups given the small number of taxonomic groups contributing to each, and especially since we have ignored here the effects of biotic interactions with other species under climate change, our data suggest the hypothesis that the more abundant tropical parasitoids will be fairly immune from the effects of climate change whilst herbivores may be more at risk. This is potentially at odds with some previous work that suggests that higher trophic levels may be more at risk under climate change for other reasons (Voigt *et al*., 2003; Zarnetske *et al*., 2012). More data from other groups is needed to test this more rigorously.

Our conclusions come with several caveats. Sampling periods and methods varied across taxa and sampling efficacy too, caveats which are, however, even more applicable to a previous meta-analytical study (Laurance *et al*., 2011), but naturally less so to other studies that have considered fewer taxa (e.g. Wilson *et al*., 2007). Even so, some of our major conclusions are likely robust to these problems because they consider identical sampling periods and methods: for example, the differences between Braconidae, Curculionidae, Chrysomelidae and Coccinellidae in the two-zone analyses. Although several of our (less species rich) taxa appear to have been fairly completely sampled within the confines of the altitudes and months considered, our analyses show that for three taxa (Braconidae, Chrysomelidae and Curculionidae) many more species would be found through further sampling. Thus, the high level of specialization found in Curculionidae and Chrysomelidae in the two-zones analysis which included rare species would likely be even more extreme than that found, had more sampling been done. This again, however, suggests that some differences between taxa are also quite robust to undersampling since further sampling would only exacerbate a trend already present in the data.

In summary, we have provided data that show a high level of high elevational specialization of insects in a tropical biodiversity hotspot, implying a higher level of climate-induced extinction risk than might previously have been assumed. The data also imply differences in elevational specialization amongst taxonomic and trophic groups that hold the potential for changes in community structure and function under climate change. We have also shown that the treatment of rarely-observed species can matter when assessing the elevational specialization of communities, as well as the way in which elevational zones are treated. These findings should help future researchers to better understand how tropical insect communities are distributed across elevations, and the consequences for conservation under climate change.

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Table 1. Observed and asymptotic estimates of species richness (±SE) for the different taxa and sampling designs.

Taxon	Sample design	Observed richness	Chao 1 richness	ACE richness
All	two-zone	697	1193.50 ± 75.53	1227.61 ± 20.52
All	four-zone	156	174.45 ± 9.05	179.00 ± 6.67
Braconidae	two-zone	174	303.33 ± 35.75	355.23 ± 11.64
Chrysomelidae	two-zone	263	452.02 ± 46.82	452.85 ± 12.58
Coccinellidae	two-zone	27	28.00 ± 1.58	29.40 ± 2.56
Curculionidae	two-zone	137	284.27 ± 46.61	309.78 ± 11.47
Lampyridae	two-zone	48	61.13 ± 9.01	64.43 ± 4.03
Scarabaeinae	two-zone	26	36.50 ± 10.52	31.30 ± 2.72
Tiphiidae	two-zone	22	23.00 ± 2.31	22.76 ± 2.29
Eumolpinae	four-zone	56	65.55 ± 6.56	70.33 ± 4.45
Lampyridae	four-zone	65	67.80 ± 2.83	69.92 ± 4.12
Scarabaeinae	four-zone	35	40.00 ± 5.52	39.22 ± 3.11

Figure 1. Study location a) with the Serra dos Órgãos National Park (shaded area) and views of the four vegetation zones studied. b) Lower Montane Forest c) Montane Forest d) Upper Montane Forest e) Campos de Altitude.

Figure 2. Location of the sampling transect route showing the different elevation zones: for the two-zones analysis, A-D = lower-zone; E-H = upper zone. For the four-zones analysis, A-B = lower montane; C-D = montane; E-F = upper montane; G-H = Campos de Altitude.

Figure 3. Rarefaction curves (mean ± 95% CI) for all taxa in (a) the two-zones dataset and (b) the four-zones dataset.

Figure 4. Specialization to upper and lower elevational zones. a) across all species collected in the different taxonomic groups and b) only including species in which >4 individuals were collected. The lower zone was 350m to 1280m and upper-zone 1450m to 2170 m. Asterisk above bar indicates significant difference using Pearson's χ^2 test ($P < 0.05$). Specialists are species which are only found in one of the zones.

Figure 5. Taxonomic differences in specialization to upper or lower elevation zones. a) across all species collected in the different taxonomic groups and b) only including species in which >4 individuals were collected. The lower zone was 350m to 1280m and upper-zone 1450m to 2170 m. Different letters above bars indicate significant differences among groups using Pearson's χ^2 test (FDR correction χ^2, $P < 0.05$). Specialists are species which are only found in one of the zones.

Figure 6. Elevational range against log abundance across species. Data are jittered slightly vertically to aid visibility although species are all either found in one zone or two in the two-zones analysis (a, b) or 1-4 in the four-zones analysis (c). Predicted values from logistic regressions show different taxa (a & c) or trophic groups (b). Brac = Braconidae Chry = Chrysomelidae, Cocc = Coccinellidae, Curc = Curculionidae;; Eumol = Eumolpinae, Lamp = Lampyridae, Scara = Scarabaeinae, Tiph = Tiphiidae, Herb = Herbivores, Para = Parasitoids, Pred = Predators, Sapro = Saprotrophs.

Figure 7. Specialization across four vegetational zones. a) across all species collected in the different taxonomic groups and b) only including species in which >4 individuals were collected. Different letters above bars indicate significant differences among

groups using Pearson's χ^2 test (FDR correction χ^2, $P < 0.05$). Specialists are species which are only found in one of the zones.

Figure 8. Taxonomic differences in specialization across four vegetational zones. a) across all species collected in the different taxonomic groups and b) only including species in which >4 individuals were collected. Different letters above bars indicate significant differences among groups using Pearson's χ^2 test (FDR correction χ^2, $P < 0.05$). Specialists are species which are only found in one of the zones.

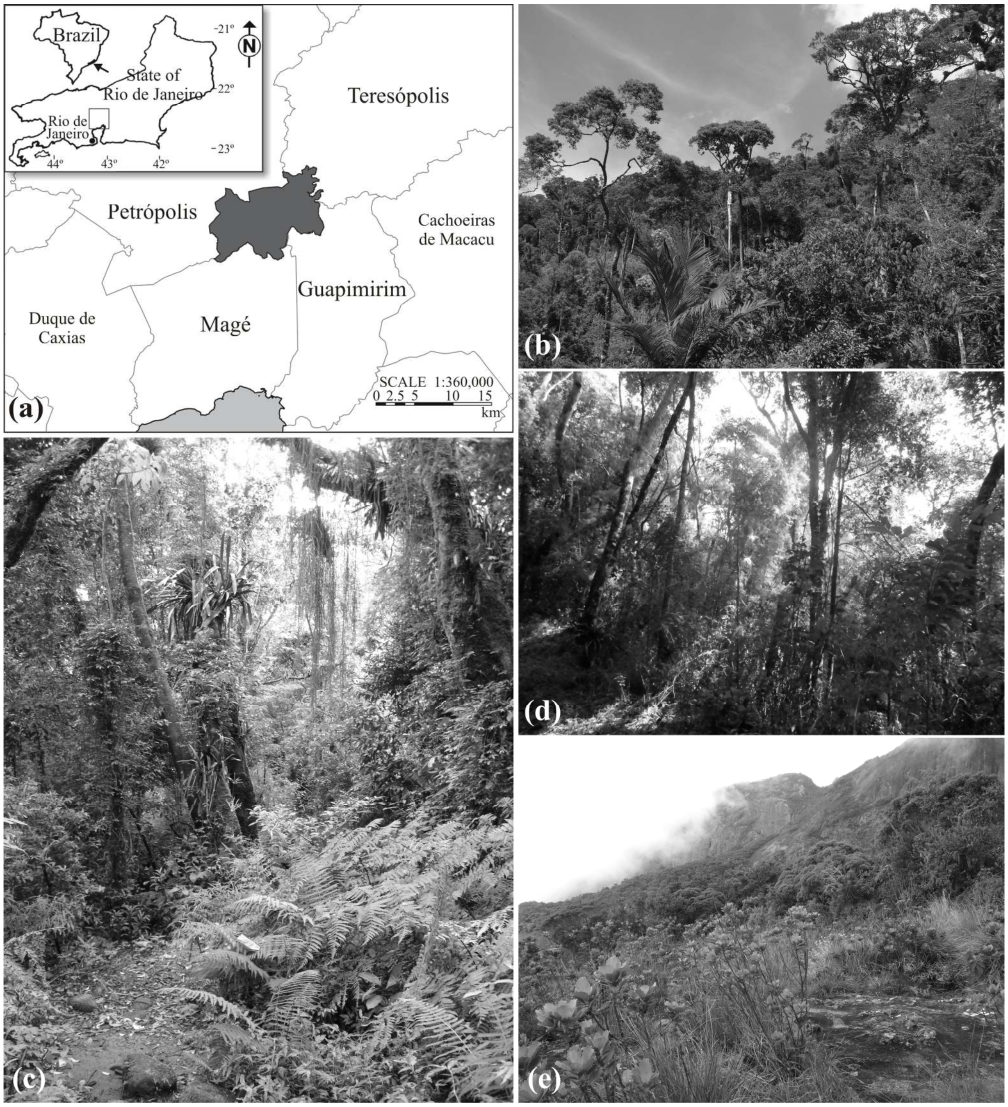

Figure 1. Study location a) with the Serra dos Órgãos National Park (shaded area) and views of the four vegetation zones studied. b) Lower Montane Forest c) Montane Forest d) Upper Montane Forest e) Campos de Altitude.

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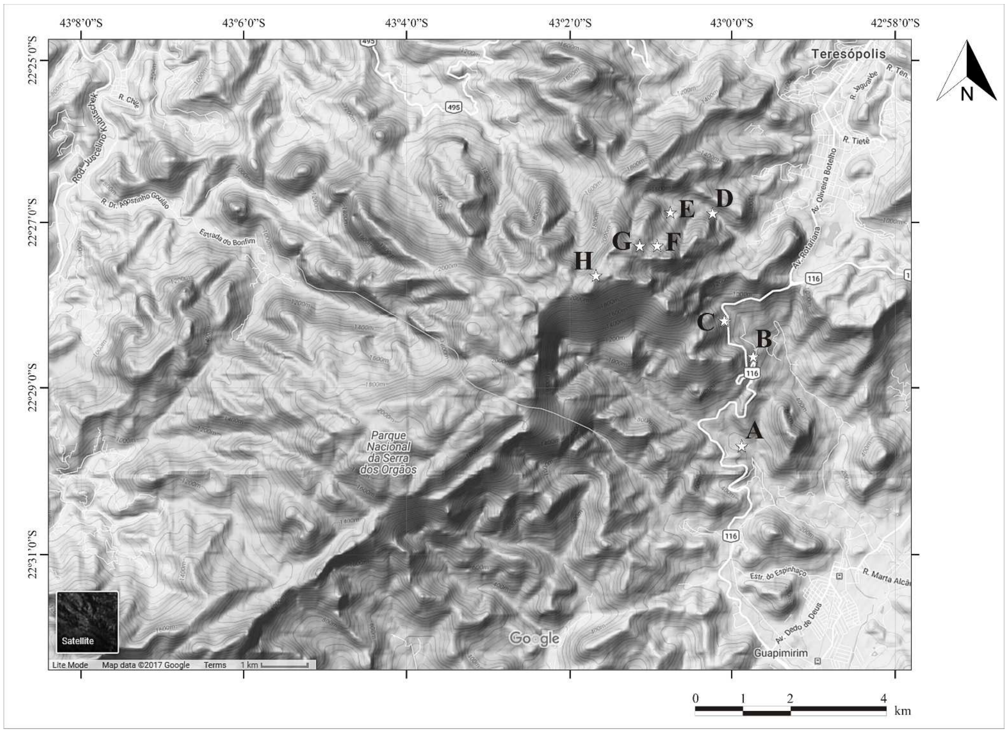

Figure 2. Location of the sampling transect route showing the different elevation zones: for the two-zones analysis, A-D = lower-zone; E-H = upper zone. For the four-zones analysis, A-B = lower montane; C-D = montane; E-F = upper montane; G-H = Campos de Altitude.

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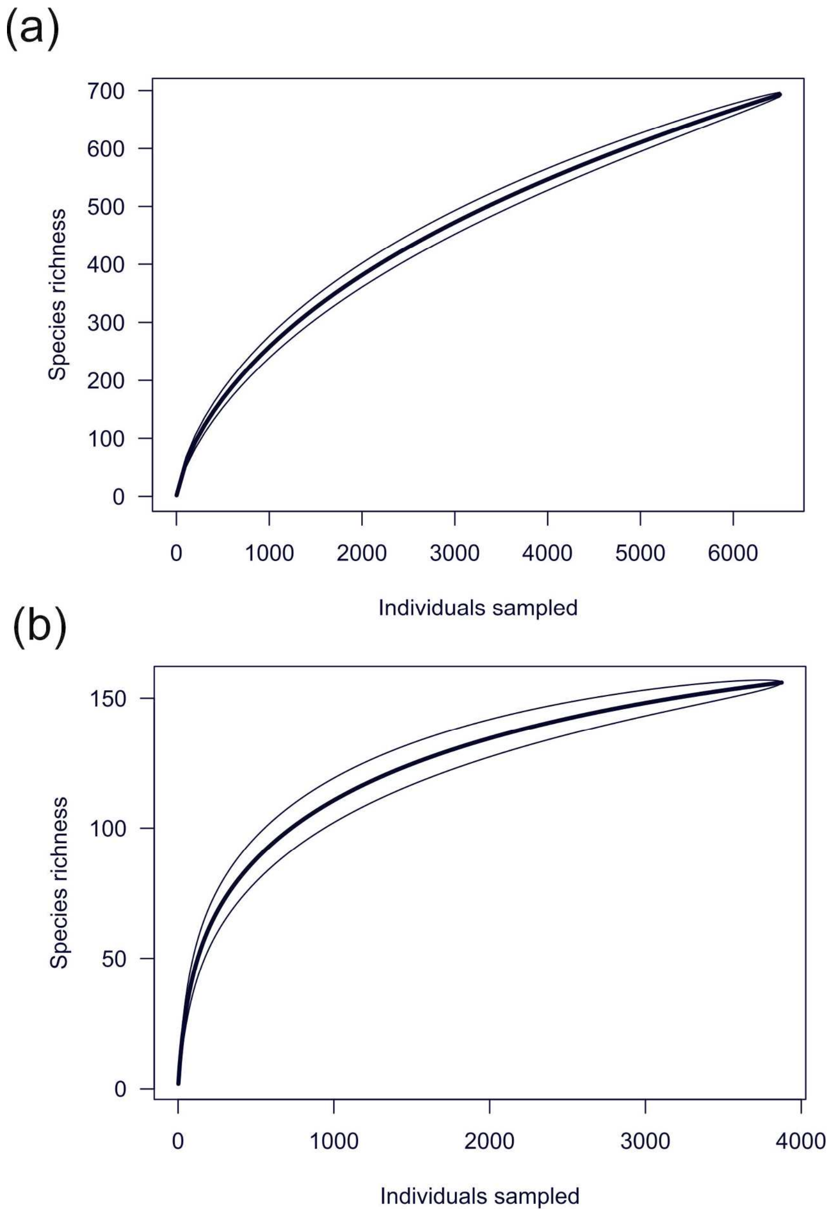

Figure 3. Rarefaction curves (mean ± 95% CI) for all taxa in (a) the two-zones dataset and (b) the four-zones dataset.

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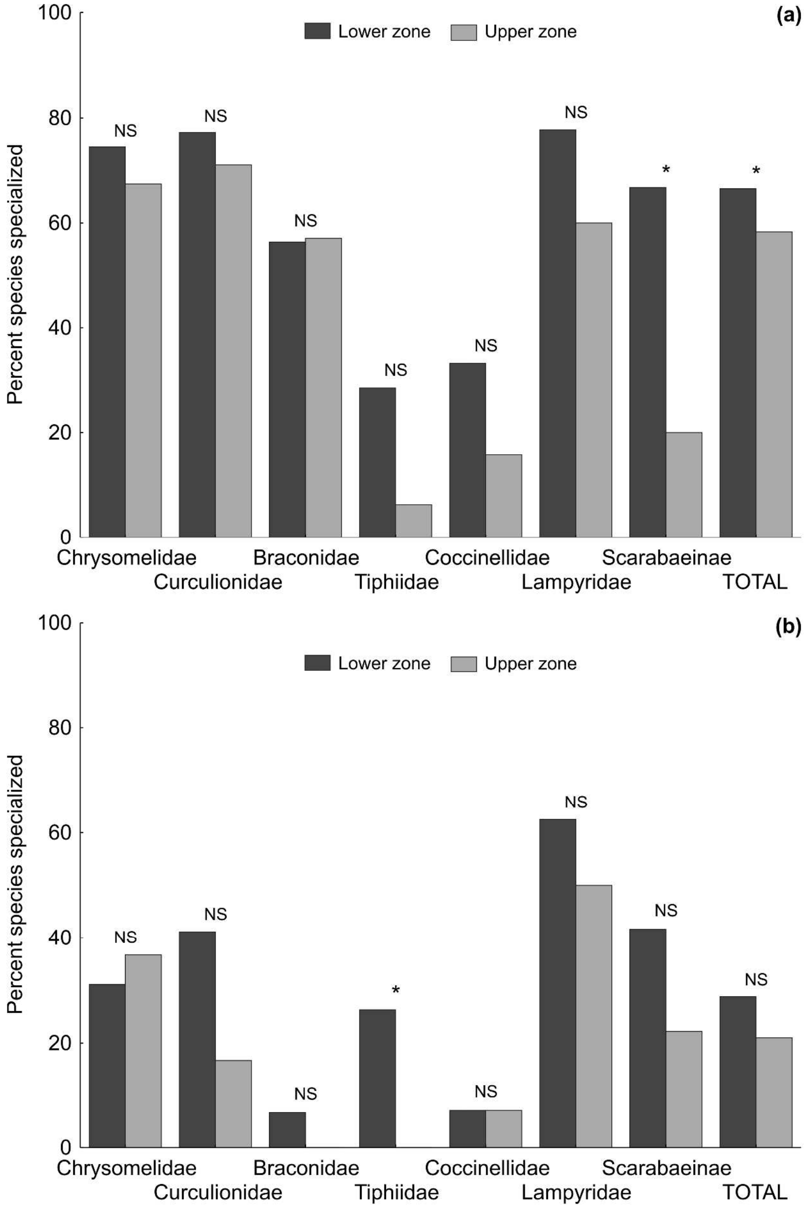

Figure 4. Specialization to upper and lower elevational zones. a) across all species collected in the different taxonomic groups and b) only including species in which >4 individuals were collected. The lower zone was 350m to 1280m and upper-zone 1450m to 2170 m. Asterisk above bar indicates significant difference using Pearson's χ2 test ($P < 0.05$). Specialists are species which are only found in one of the zones.

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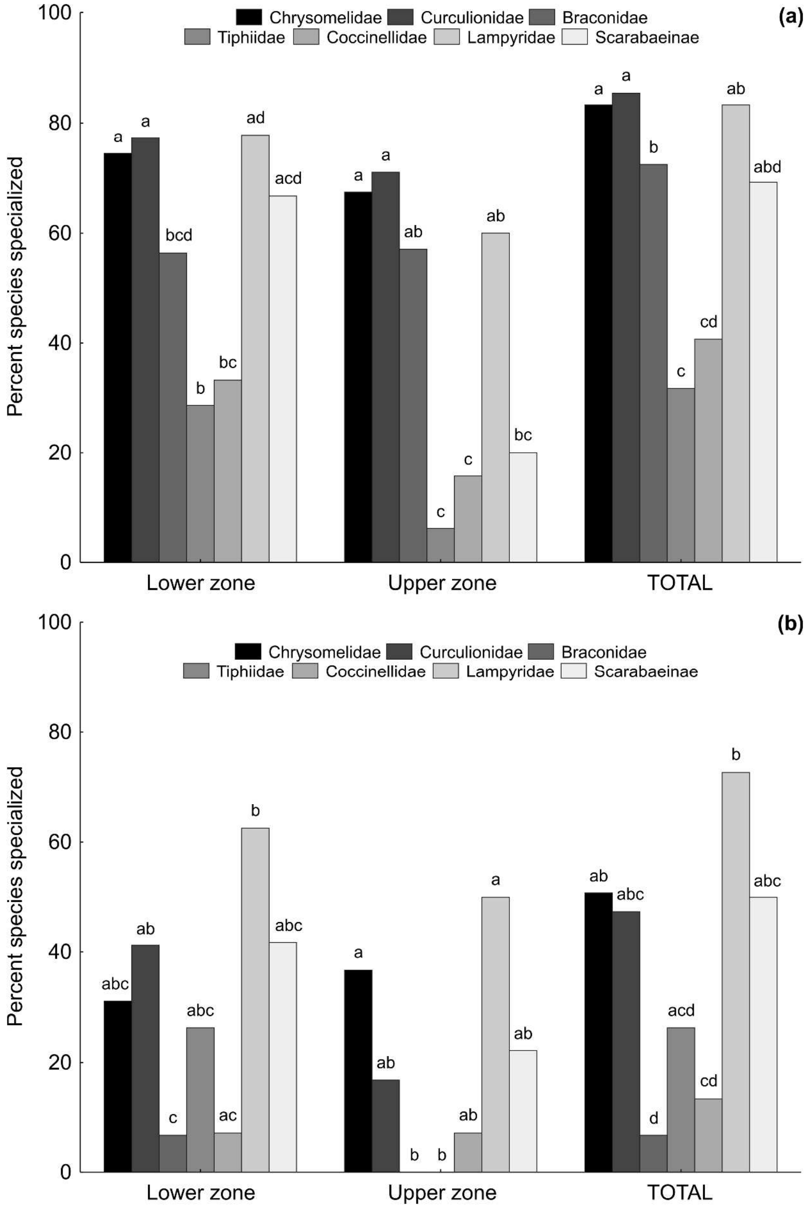

Figure 5. Taxonomic differences in specialization to upper or lower elevation zones. a) across all species collected in the different taxonomic groups and b) only including species in which >4 individuals were collected. The lower zone was 350m to 1280m and upper-zone 1450m to 2170 m. Different letters above bars indicate significant differences among groups using Pearson's χ2 test (FDR correction χ2, P < 0.05). Specialists are species which are only found in one of the zones.

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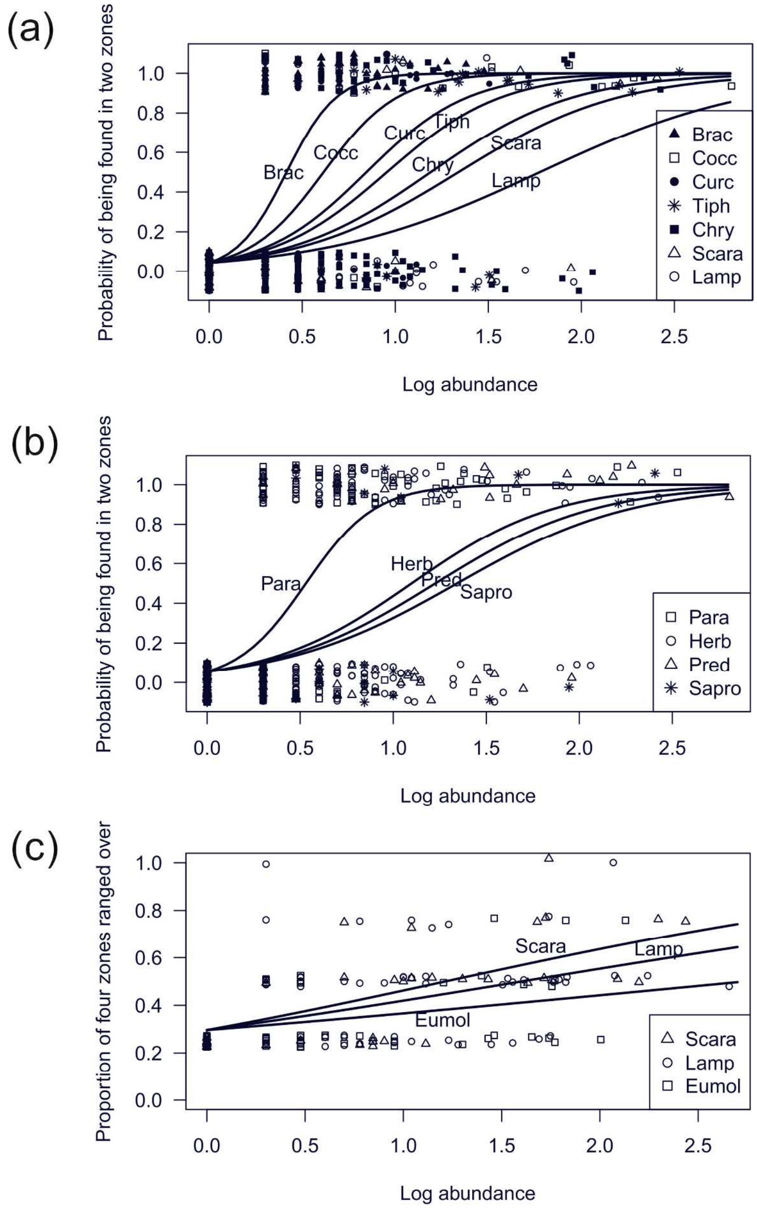

Figure 6. Elevational range against log abundance across species. Data are jittered slightly vertically to aid visibility although species are all either found in one zone or two in the two-zones analysis (a, b) or 1-4 in the four-zones analysis (c). Predicted values from logistic regressions show different taxa (a & c) or trophic groups (b). Brac = Braconidae Chry = Chrysomelidae, Cocc = Coccinellidae, Curc = Curculionidae;; Eumol = Eumolpinae, Lamp = Lampyridae, Scara = Scarabaeinae, Tiph = Tiphiidae, Herb = Herbivores, Para = Parasitoids, Pred = Predators, Sapro = Saprotrophs.

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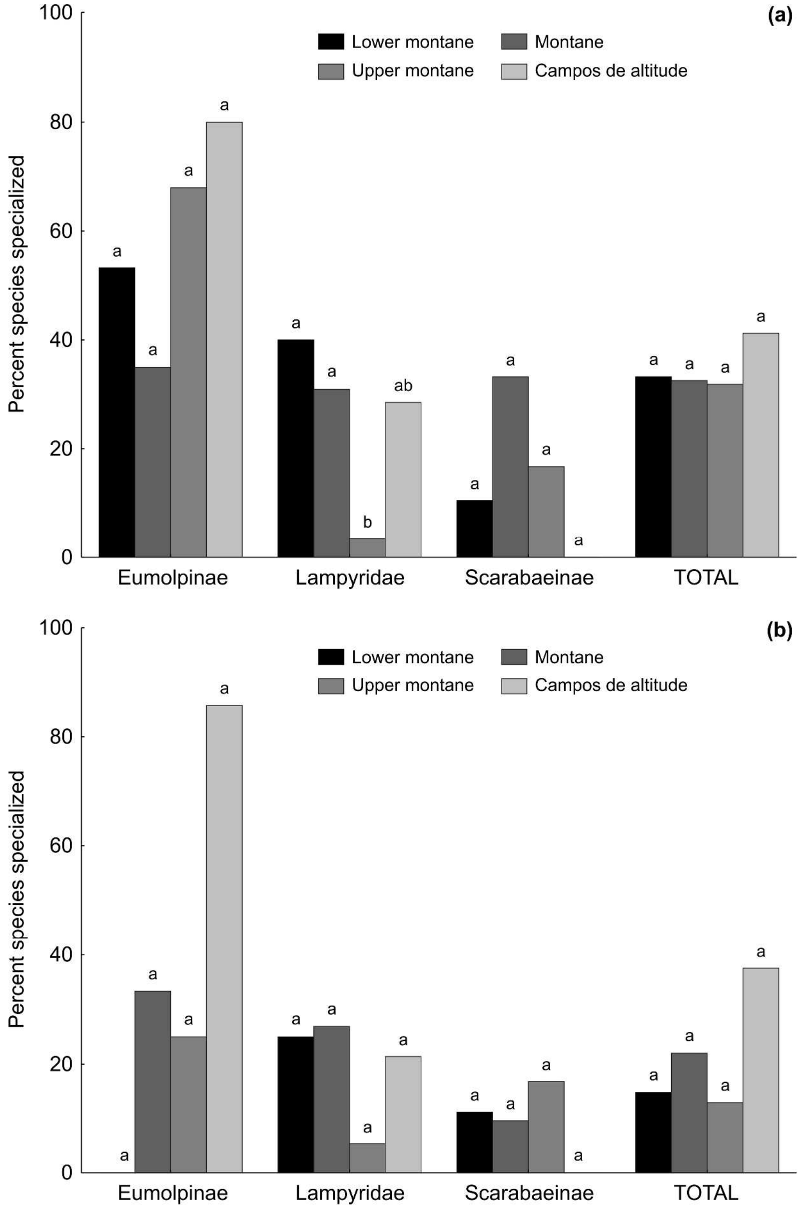

Figure 7. Specialization across four vegetational zones. a) across all species collected in the different taxonomic groups and b) only including species in which >4 individuals were collected. Different letters above bars indicate significant differences among groups using Pearson's χ2 test (FDR correction χ2, $P < 0.05$). Specialists are species which are only found in one of the zones.

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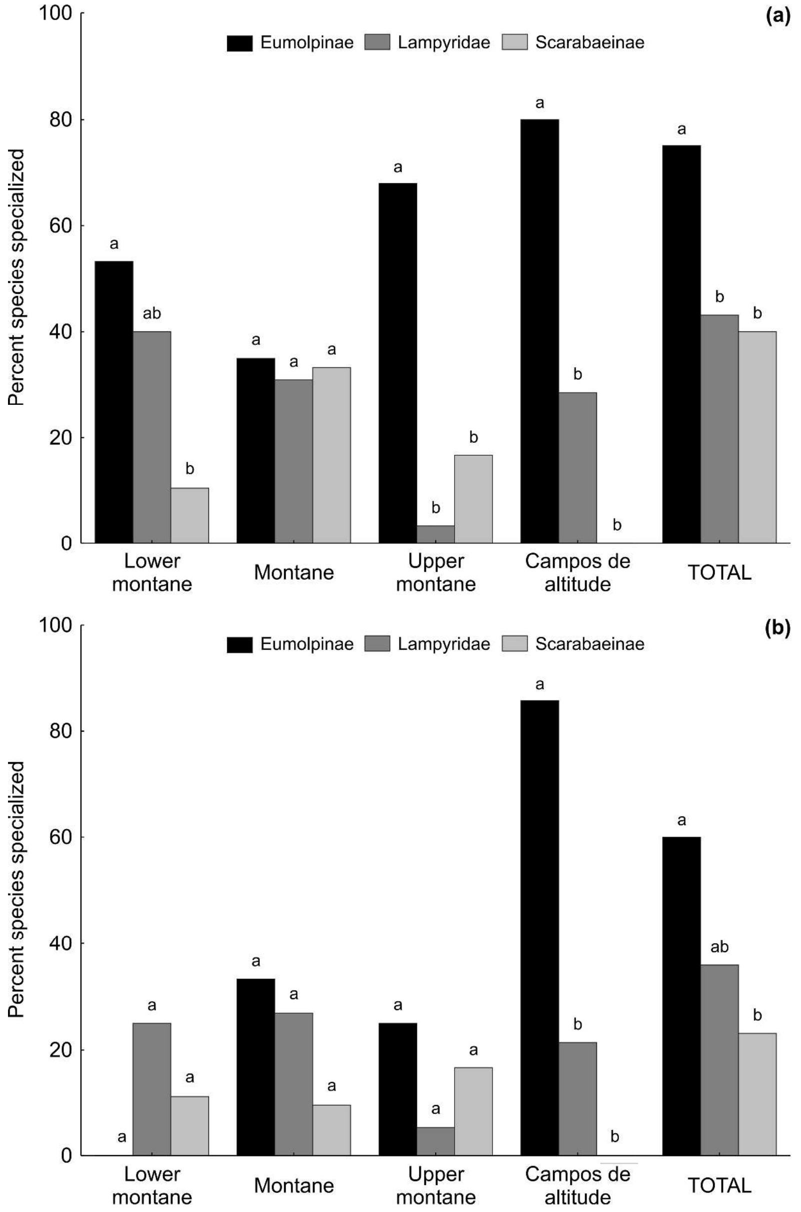

Figure 8. Taxonomic differences in specialization across four vegetational zones. a) across all species collected in the different taxonomic groups and b) only including species in which >4 individuals were collected. Different letters above bars indicate significant differences among groups using Pearson's χ2 test (FDR correction χ2, $P < 0.05$). Specialists are species which are only found in one of the zones.

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