



Insect elevational specialization in a tropical biodiversity hotspot

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

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Insect elevational specialization in a tropical biodiversity hotspot

Running title: Tropical elevational specialization

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2
3 26 **Abstract**

4
5 27 1. Tropical montane organisms are vulnerable to climate change because of elevational
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7 28 specialization, but little is known of the variability of elevational specialization across
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9 29 tropical insects.

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11 30 2. We assessed elevational specialization across several insect taxa comprising four
12
13 31 trophic groups 80-2263m up an elevational transect in Brazilian Atlantic Rainforest,
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15 32 using community-based and species-based approaches.

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17 33 3. We sampled 697 species, of which 32% were found only in the top and 45% only in
18
19 34 the bottom half of the transect. Considering only the 182 species with at least five
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21 35 individuals recorded, the percentage of species found exclusively in the top or bottom
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23 36 half drops to 16% and 24%.

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25 37 4. Across four vegetation belts (lower montane forest, montane forest, upper montane
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27 38 forest and Campos de Altitude) the Eumolpinae (herbivores) were more specialized than
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29 39 Scarabaeinae (saprotrophs), or Lampyridae (predators). This result was robust to the
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31 40 treatment of rare species, and the difference was most marked at higher elevations.
32
33 41 Lampyridae lacked upper montane forest specialists.

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35 42 5. Using all species sampled, specialization to the upper or lower half of the transect
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37 43 was greatest amongst Chrysomelidae, Curculionidae (both herbivores) and Lampyridae,
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39 44 and lowest amongst Tiphidae (parasitoids) and Coccinellidae (predators). However,
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41 45 considering only better sampled species, Lampyridae were the most specialized and
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43 46 Braconidae the least specialized. Trophic groups also varied in line with these findings.

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45 47 6. Our findings suggest high elevational specialization and concomitant extinction risk
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47 48 in Brazilian Atlantic Rainforest insects. Differences in elevational specialization
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49 49 between taxonomic groups may alter the functioning of insect communities under
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51 50 climate change.

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53 52 Key words: altitudinal ranges, climate change, elevational specialization, extinction
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55 53 risk, range shifting, tropical insects, tropical rainforest

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55 Introduction

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

65 Tropical species are generally regarded to have low thermal tolerance due to the
66 low seasonal temperature variability experienced, making them potentially vulnerable to
67 extinction from climate change (Addo-Bediako *et al.*, 2000, Deutsch *et al.*, 2008,
68 Bonebrake & Deutsch, 2012). The elevational ranges displayed by species may, at least
69 partially, indicate their thermal tolerances (McCain, 2009; Laurance *et al.*, 2011;
70 Garcia-Robledo *et al.*, 2016), and have been used to infer extinction risk from climate
71 change across taxa and geographic locations (Sekercioglu *et al.*, 2007; Colwell *et al.*,
72 2008; Feeley & Silman, 2010; La Sorte & Jetz, 2010; Mekasha *et al.*, 2013; La Sorte *et*
73 *al.*, 2014), but little is known about how elevational ranges vary in tropical insects. Here
74 we assess the variation in elevational specialization across several insect taxa **along an**
75 **elevational transect** in Brazilian Atlantic Forest, and the likely implications for
76 conservation under climate change.

77 One of the reasons for the expected high impact of global warming on tropical
78 montane organisms is their thermal specialization (e.g. Garcia-Robledo *et al.*, 2016).
79 Janzen (1967) proposed that organisms on tropical mountains (as opposed to temperate
80 mountains) experience low seasonal variation in temperature but high variation along
81 elevational gradients. He suggested that this selected organisms for narrow thermal
82 tolerance compared to those on temperate mountains, **because organisms would not**
83 **need tolerance to a broad range of thermal regimes at any altitude, and could reduce the**
84 **cost of thermal tolerance by becoming more thermally specialized.** Janzen's (1967)
85 assumptions and predictions have been tested by many authors and general support has
86 been found (e.g. Huey, 1976; Ghalambor *et al.*, 2006; McCain 2009; Bonebrake &
87 Deutsch, 2012; but see Buckley *et al.*, 2013). Spatial and temporal variation in local

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3 88 temperature also predicts thermal tolerances in insect species globally (Bonebrake &
4 89 Deutsch, 2012). However, high elevation insects are predicted to have wider elevational
5 90 ranges than low elevation species, because seasonal temperature range tends to increase
6 91 with altitude (Stevens 1992). Thus, high elevation species may require broader thermal
7 92 tolerances than lowland species, which also adapts them for wider elevational ranges
8 93 (Stevens, 1992).

94 However, the elevational ranges of tropical insects along altitudinal gradients
95 have rarely been explicitly analyzed, with most studies that contain pertinent data
96 focusing on species richness gradients or the shifting of ranges over time (see references
97 in Laurance *et al.*, 2011). Consistent with the predictions above, Gaston & Chown
98 (1999) found an increase in elevational range with altitude in 26 species of scarab dung
99 beetles across an elevational gradient of approximately 2500m in tropical Africa.
100 However, studies have also shown evidence for high-elevation endemism and narrow
101 elevational ranges in tropical montane species. Garcia-Robledo *et al.* (2016) found that
102 most of the species of rolled-leaf beetles (Chrysomelidae) occurring at mid and high
103 elevations in Central American mountains were elevational specialists. Upper thermal
104 tolerances were lower amongst high elevation species, presumably because they are less
105 exposed to high temperatures than low elevation species. In contrast, species found at
106 low altitudes had high thermal tolerances, and were often not constrained to low
107 latitudes. A similar pattern was found in schizophoran flies in the Australian wet
108 tropics, with the most restricted species at high elevations (Wilson *et al.*, 2007), which
109 was attributed to the effects of past climate change in generating a high degree of
110 endemism amongst cool-adapted species. Together these variable findings suggest that
111 there may be considerable variation in elevational specialization across taxa and
112 geographic locations.

113 Laurance *et al.* (2011) compiled data from 150 studies of species' elevational
114 specialization in the tropics, including insect and other invertebrate studies, and
115 assessed the degree of specialization to either the lower or upper half of the altitudinal
116 ranges sampled. They found that about 75% of species were elevational specialists, and
117 lower zone specialists (~50%) were more common than upper zone specialists (~20%).
118 Upper zone specialists were more common in ectothermic vertebrates and plants than
119 endothermic vertebrates, with invertebrates at intermediate values. However, the median
120 elevation considered varied markedly across studies, and there was no control for

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3 121 species' abundance across taxa, which are potential sources of bias. In addition, there
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5 122 was no explicit consideration of heterogeneity across insect taxa.
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7 123 In this paper we assess the degree of elevational specialization **along an**
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9 124 **elevational transect** in Brazilian Atlantic Rainforest. We combine the results of
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11 125 collections of several insect taxa using different sampling techniques, and ask how the
12
13 126 degree of elevational specialization varies across taxa, the functional groups to which
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15 127 they belong, and between elevation zones. We then assess the likely implications for the
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17 128 conservation of tropical insect diversity. The biodiversity hotspot known as Brazilian
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19 129 Atlantic Rainforest is distributed across a heterogenous landscape that includes
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21 130 ombrophilous forests, semi-deciduous forests, mountain cloud forests, Campos de
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23 131 Altitude (also known as Brazilian páramos), inselbergs, *restingas*, and mangroves, with
24
25 132 varying levels of endemism (Safford, 1999; Ribeiro *et al.*, 2009). Habitat heterogeneity
26
27 133 is thought to be a main driver of endemism either due to niche divergence and
28
29 134 ecological speciation (Nosil, 2012), or by niche conservatism leading to isolation in
30
31 135 refugia, areas of relative climatic stability such as tropical mountain ranges (Carnaval &
32
33 136 Moritz, 2008; Steinbauer *et al.*, 2016). Currently, less than 10% of the 150 million ha
34
35 137 originally covered by Brazilian Atlantic Rainforest is left as remnants of varied size and
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37 138 connectivity (Ab'Sáber, 2003; Morelato & Haddad, 2000; Ribeiro *et al.*, 2009).
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141 **Material and Methods**

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143 **Study area**

144 The study was conducted along an elevation transect at Serra dos Órgãos National Park
145 (22°32'S and 43°07'W), in the State of Rio de Janeiro (Brazil) (Figures 1, 2), a
146 mountainous conservation area of 20,024 ha. The Park encompasses the highest peaks
147 of the Serra do Mar, ranging from 80-2263m elevation. It was founded in 1939 and is
148 the third oldest National Park in Brazil, aiming to conserve montane biodiversity,
149 especially the Campos de Altitude (high elevation grasslands), which contain a great
150 part of the endemism in the area. The region is among the best preserved in the Atlantic
151 Forest biome (Castro, 2008), although much of the forest is secondary growth. The Park
152 encloses four different vegetation belts: lower montane forest (below ~800m), montane
153 forest (800~1500m), upper montane forest (1500~2000m) and high elevation
154 grasslands, Campos de Altitude (over ~2000m), characterized by shrubs, herbs and
155 grasses (Rizzini, 1954; Veloso *et al.*, 1991) (Figure 1).

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

163 Temperature loggers placed at 15 sampling locations, covering the same route as
164 those presented elsewhere in this paper, throughout 2015 showed that mean annual
165 temperature decreases consistently with elevation, from 22.5°C at 130m to 12.8°C at
166 2130m elevation, a 0.5°C decrease per 100m elevation. The mean monthly temperature
167 at each elevation ranges over 5.7°C ± 0.4°C. **The ratio of spatial (across sites) to**
168 **seasonal (within sites, across months) variation in temperature** ranges from 1.5 to 2,
169 which is in the higher range of values globally, typical of tropical mountains
170 (Bonebrake & Deutsch, 2012), and likely to favour elevational specialization.

171 **Insect sampling took place over a 9 year period (see below), and over this time**
172 **there is the potential for significant weather changes and potentially some biotic range**
173 **shifting. Data from an automated weather station at 991m along the sampling route**
174 **show that 2007 and 2015 (the main sampling years) had similar average temperature**

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3 175 though 2015 was drier (mean monthly temperature 2007: 18.1°C, SD 2.2 °C; 2015: 18.8
4 176 °C, SD 2.2 °C, total rainfall 2007: 2591mm; 2015: 2019mm). Between 2007 and 2015,
5 177 both the rainfall and mean monthly temperature trends were non-significant
6 178 (temperature Pearson's $R = 0.546$, $n = 9$, $P = 0.128$; rainfall $R = -0.354$, $n = 9$, $P =$
7 179 0.351), though over longer time periods significant trends are expected to emerge.
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181 **Field sampling methods**

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

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

195 Eumolpinae (Coleoptera: Chrysomelidae) and Lampyridae (Coleoptera) were
196 sampled using pairs (100m apart) of Malaise (flight interception) traps at 360 m, 550 m,
197 700 m, 880 m, 1070 m, 1250 m, 1480 m, 1680 m, 1810 m, 1940 m, 2030 m and 2170 m
198 elevation. The Lampyridae samples were considered from December 2014 to December
199 2015 and the Eumolpinae from December 2014 to February 2015.

200 Tiphiiidae (Hymenoptera) were sampled using pairs of Malaise (flight interception)
201 traps (100m apart) at each of just four different elevations, 360 m, 1250 m, 1480 m, and
202 2170 m, from December 2014 to February 2015.

203 Braconidae (Hymenoptera), Chrysomelidae (all subfamilies), Coccinellidae and
204 Curculionidae (Coleoptera) were sampled with yellow sticky traps (Bio Trap[®],
205 Biocontrole, São Paulo, Brazil). Traps consisted of a plastic yellow panel (24.5cm x
206 10cm) with adhesive on both sides. They were attached with wire to vegetation 1.5 to
207 2m above the ground. Seven panels were placed approximately 20m apart from each
208 other in the vegetation, on slopes of aspect within 45° of north, at each of just four

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3 209 different elevations: 350 m, 1280 m, 1480 m and 2100 m. Sampling was conducted
4 210 every two months from February 2007 to February 2008, resulting in seven week-long
5 211 samples. Placement of new traps, and their retrieval one week later, occurred on a single
6 212 day. Retrieved panels were placed in plastic containers and separated from each other
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9 213 by small wooden cubes, taken to the laboratory and stored in the freezer.

11 214 Trap effectiveness is an important issue in assessing species diversity (Southwood,
12 215 1978). The sampling methods used here are widely known as effective for these
13 216 respective groups. Coleoptera and Hymenoptera are widely studied using Malaise traps
14 217 (e.g. Fraser *et al.*, 2007; Ohsawa, 2010) and yellow sticky traps (e.g. Larsen *et al.*, 2014,
15 218 Thomson *et al.*, 2004). For Scarabaeinae, human faeces-baited pitfalls are one of the
16 219 most effective sampling methods (e.g. Silva *et al.*, 2012).

18 220 Where sampling took place for less than a year, the period considered was always
19 221 the warmer wetter season (December to February), during which insect species richness
20 222 and abundance are generally greatest (e.g. Flinte *et al.*, 2009). Species whose adult
21 223 phenology is restricted to other times of year will have been omitted by this sampling,
22 224 and this should be born in mind when interpreting the results. In addition, because the
23 225 sticky trap sampling (Braconidae, Chrysomelidae, Coccinellidae and Curculionidae)
24 226 occurred some eight years earlier than the other sampling, taxonomic comparisons may
25 227 be most robust within rather than between these sampling periods, since taxa in the
26 228 2014-2015 samples may have shifted range slightly during the intervening period.

29 230 **Species sorting and identification**

30 231 Sticky traps were individually submersed in paint thinner for five minutes to dissolve
31 232 the glue, and insects were carefully removed with a thin brush. This procedure was
32 233 undertaken in a fume hood with use of a gas mask. All detached material was sifted,
33 234 washed and stored in 70% ethanol. Adults of Braconidae (CVSG), Chrysomelidae (VF),
34 235 Coccinellidae (ROA) and Curculionidae (VF and COA) were identified to
35 236 morphospecies after first keying to the lowest taxonomic level possible, normally
36 237 species or genus. Eumolpinae (CC), Lampyridae (LFLS) and Tiphiidae (ES) were
37 238 removed from the Malaise traps monthly and identified to morphospecies, also after
38 239 first keying to the lowest taxonomic level possible, normally species or genus. The
39 240 Scarabaeidae were first identified by Raissa Dufrayer and then confirmed by Prof.
40 241 Fernando Zagury Vaz de Melo (Universidade Federal de Lavras), again mostly to
41 242 species and genus level and then to morphospecies. Specimens were deposited in the

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3 243 collection of the Insect Ecology Laboratory (CLEI) at the Federal University of Rio de
4 Janeiro.
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7 246 **Data analysis**

8 247 We conducted analyses on two different subsets of the data; first, we followed Laurance
9 *et al.* (2011) in maximizing inclusion of taxa by defining only two different altitudinal
10 zones (two-zone analysis) divided at the median sampling elevation. To ensure equal
11 sampling effort in the two zones, we included data from only four elevations, one each
12 approximating the four vegetation zones to minimize potential sampling bias, guided by
13 the lowest common sampling effort across taxa. This analysis allows us to compare our
14 findings directly with Laurance *et al.* (2011). The exact samples were: Eumolpinae,
15 Lampyridae and Tiphiidae: 360 m and 1250 m in the lower-zone and 1480 m and 2170 m
16 in the upper-zone; Scarabaeinae: 350 m and 1250 m in the lower-zone and 1450 m and
17 2000 m in the upper-zone; Braconidae, Chrysomelidae and Curculionidae: 350 m and
18 1280 m in the lower-zone, and 1480 m and 2100m in the upper-zone.
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28 In a different subset of the data, we doubled the number of altitudinal zones
29 sampled (four-zone analysis, approximating one of each of the four vegetation zones),
30 but this analysis could only be carried out for Eumolpinae, Lampyridae and
31 Scarabaeinae, which have the necessary finer sample distributions. Sampling effort was
32 equal across zones for Eumolpinae and Lampyridae, and the same number of elevations
33 per zone was sampled for Scarabaeinae (though the sampling method was different).
34 Finer altitudinal intervals were not considered because sample sizes became too small
35 for community analyses. In order to standardize the sampling intensity and elevations
36 across taxa and reduce potential biases, we used only the following samples from each
37 taxon: Scarabaeinae: 350 m, 500 m and 700 m approximating the lower montane forest,
38 850 m, 1050 m and 1250 m approximating the montane forest, 1450 m, 1600 m and
39 1800 m approximating the upper montane forest and 1900 m, 1950 m and 2000 m
40 approximating Campos de Altitude; Eumolpinae and Lampyridae: 360 m, 550 m and
41 700 m for lower montane forest, 880 m, 1070 m and 1250 m for montane forest, 1480
42 m, 1680 m and 1810 m for upper montane forest and 1940 m, 2030 m and 2170 m for
43 Campos de Altitude.
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54 For each of these subsets of the data we carried out three analyses. First, to
55 compare with the results of Laurance *et al.* (2011), we defined species as specialists if
56 they were restricted to a single zone. Differences in the proportion of specialists across
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3 277 zones and taxa were assessed with χ^2 tests on the species counts, and pairwise
4 278 comparisons made using the same tests but controlling for the family-wide false
5 279 discovery rate (Benjamini & Hochberg, 1995) using the fifer package in R (R core team,
6 280 2015). The above analysis was conducted with the complete dataset, which has the
7
8 281 advantage of considering all species together, but assumes that the species with low
9 282 abundance in our samples are elevational specialists. This may indeed be the case, but it
10
11 283 is possible that rare species are simply poorly sampled species (which may have large
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13 284 elevational ranges), in which case the analysis of elevational specialization needs to
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15 285 control for sampling abundance.

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18 286 We therefore carried out two analyses that controlled for sampling abundance. In
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20 287 a similar community-level analysis, we carried out the same analyses above but only
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22 288 considering species with at least five individuals **sampled (e.g. following the approach**
23
24 289 **of Wilson *et al.* (2007)).** Some of the finer scale tests were omitted because sample size
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26 290 was smaller in this dataset due to the omission of many rare species. **To visually assess**
27
28 291 **the effect of this cutoff on inclusion across taxonomic groups, rank-abundance plots**
29
30 292 **were constructed for the different taxa and sample designs.**

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32 293 We also used a species-focused rather than community-focused approach. For
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34 294 each species we counted the number of elevational zones in-and-between the highest
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36 295 and lowest zones in which it was found. This number of zones (out of the total of four
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38 296 for the four-zone analysis, or simply presence in two zones or not in the two-zone
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40 297 analysis) was then subjected to a **generalized** linear model with a binomial error
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42 298 structure using the glm function in R (R core team, 2015). The explanatory variable was
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44 299 the interaction between \log_{10} abundance and taxon. This effectively asks if the slope of
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46 300 the relationship between \log_{10} abundance and observed elevational range is different for
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48 301 different taxa; taxa with high slopes tend to have wide elevational ranges at high
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50 302 abundances, and taxa with low slopes have narrower elevational ranges at high
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52 303 abundance (all species have narrow elevational ranges at low abundance). Differences
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54 304 between taxa were tested by merging the factor levels designating taxon identity and
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56 305 observing the significance of the change in model deviance with a χ^2 test. Checks for
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58 306 overdispersion were made by dividing the residual deviance of models by the residual
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60 307 degrees of freedom, but none of the models indicated overdispersion as this ratio was
308 always < 1 .

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310 **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

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3 311 plotted associated species accumulation curves. Because of the diversity of sampling
4 312 approaches used, accumulation approaches based on individuals rather than samples are
5 313 most applicable, straightforward and comparable: in the vegan package in R rarefaction
6 314 curves were constructed on the species abundance data using the 'rarefy' function, and
7 315 Chao1 (Chao, 1984) and the Abundance-based Coverage Estimator (ACE, Chao 2005)
8 316 measures of asymptotic richness made using the 'estimateR' function.
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320 **Results**

321 **Sampling completeness and rank abundance**

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

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

341 **Specialization to upper and lower zones**

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

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3 351 Coccinellidae (Figure 5a). Taxonomic differences in specialization were generally
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5 352 similar in the upper and lower zones. Pooling species from the same functional groups,
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7 353 unsurprisingly, trophic groups differed significantly ($\chi^2_3 = 24.76$, $P < 0.0001$). There
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9 354 were more herbivore specialists than predators ($P_{adj} = 0.0098$) and parasitoids ($P_{adj} =$
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11 355 0.0001), although no other trophic groups differed significantly ($P_{adj} = 1.00$).

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13 356 In the analysis including only the 182 species with at least five sampled individuals, 73
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15 357 species (40.1%) were elevational specialists, comprising 28.8% of species in the lower
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17 358 zone and 21.0% of species in the upper zone, (a non-significant difference, Figure 4b),
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19 359 so as in the all-species analysis, the level of specialization was not much higher in the
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21 360 lower zone (Figure 4a,b). For individual taxa, the only group to show a difference in
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23 361 specialization in the two zones was Tiphidae, which was more specialized in the lower
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25 362 than upper zone (Figure 4b). Differences across taxa were again found in the degree of
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27 363 specialization, but they were different to those found when all species were analyzed
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29 364 (Figure 5b). Now, Lampyridae contained the highest proportion of specialists, and
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31 365 Braconidae the lowest. Chrysomelidae, Scarabaeinae and Curculionidae had reasonably
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33 366 high proportions of specialists, and Tiphidae and Coccinellidae quite low proportions.
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35 367 Functional groups again differed in their specialization ($\chi^2_3 = 18.64$, $P = 0.0002$). Across
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37 368 functional groups, herbivores, predators and saprotrophs now had similar levels of
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39 369 specialization ($P_{adj} = 0.99$), with parasitoids having lower levels than all three others
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41 370 ($P_{adj} < 0.05$).

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43 371 In the species-focused analysis, the taxon with the highest slope of the relationship
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45 372 between logit probability of occupying two zones and log abundance (hence the
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47 373 broadest elevational ranges for abundant species) was Braconidae ($b = 7.422$, $SE =$
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49 374 0.818 , $P < 0.001$), followed by Coccinellidae ($b = 5.019$, $SE = 0.953$, $P < 0.001$),
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51 375 Curculionidae ($b = 3.652$, $SE = 0.532$, $P < 0.001$), Tiphidae ($b = 3.231$, $SE = 0.523$, P
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53 376 < 0.001), Chrysomelidae ($b = 2.593$, $SE = 0.322$, $P < 0.001$), Scarabaeinae ($b = 2.304$,
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55 377 $SE = 0.508$, $P < 0.001$), and Lampyridae ($b = 1.737$, $SE = 0.424$, $P < 0.001$) (Figure 6a).
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57 378 This is a different rank order of elevational specialization than found in the community-
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59 379 focused analysis with all species, but, unsurprisingly, similar to the results of the
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380 community analysis restricted to species with > 4 individuals, as both effectively ignore
381 rare species. Across trophic groups, results were similar. The group with the highest
382 slope of the relationship between logit probability of occupying two zones and log
383 abundance was the parasitoids ($b = 5.353$, $SE = 0.559$, $P < 0.001$), followed by

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3 384 herbivores ($b = 2.586$, $SE = 0.259$, $P < 0.001$), predators ($b = 2.317$, $SE = 0.334$, $P <$
4 385 0.001), and saprotrophs ($b = 2.116$, $SE = 0.489$, $P < 0.001$) (Figure 6b). The predators,
5 386 herbivores and saprotrophs did not have significantly different slopes ($\chi^2_2 = 1.06$, $P =$
6 387 0.588), but the parasitoids had significantly higher slopes than the other species
7 388 combined ($\chi^2_1 = 44.19$, $P < 0.001$). Again, this is a different rank order of elevational
8 389 specialization than found in the community analysis with all species, but similar to the
9 390 results of the community analysis restricted to species with > 4 individuals.
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18 392 **Specialization across four vegetation zones.**

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20 393 A total of 3874 individuals belonging to 156 species of Eumolpinae, Lampyridae and
21 394 Scarabaeinae were collected using the four-zone analysis. Overall, 53.8% of species
22 395 were found in one zone only. For the lower montane forest 33.3% were specialized, for
23 396 the montane forest 32.6%, upper montane forest 31.9%, and Campos de Altitude 41.2%.
24 397 Considering all the insect species together there was no significant difference in the
25 398 relative frequencies of specialists in each zone (Figure 7a). The only significant
26 399 difference in elevational specialization detected across zones was the low level of
27 400 specialization in the upper montane forest in the lampyrids (Figure 7a). The total
28 401 proportion of elevational specialists among the Eumolpinae was significantly higher
29 402 than those among the Lampyridae and the Scarabaeinae (Figure 8a).
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38 403 When only species with > 4 individuals sampled were included, results again differed
39 404 from when all sampled species were included. Now only 37.6% of species were
40 405 specialists on one of the four zones, including 14.7% of species in lower montane forest,
41 406 22.0% in montane forest, 12.8% in upper montane forest, and 37.5% of species in
42 407 Campos de Altitude (Figure 7b). There were also differences across taxa, with
43 408 Eumolpinae having a higher proportion of specialists than the other two taxa (Figure
44 409 8b). Specialization was generally low in Scarabaeinae, and non-existent in Campos de
45 410 Altitude.
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52 411 The species-focused approach largely confirmed the differences in specialization
53 412 across taxa in the above analysis. The slope of the relationship between logit number of
54 413 zones and log abundance was not significant for Eumolpinae ($b = 0.316$, $SE = 0.180$, P
55 414 $= 0.0789$) indicating that elevational range does not increase with abundance, but was
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3 415 significant for Lampyridae ($b = 0.540$, $SE = 0.150$, $P < 0.001$), and Scarabaeinae ($b =$
4 416 0.713 , $SE = 1.680$, $P < 0.001$) (Figure 6c), and the difference between the slopes was
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6 417 different for Eumolpinae and Scarabaeinae ($\chi^2_1 = 3.872$, $P = 0.0491$), but not for
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8 418 Eumolpinae and Lampyridae ($\chi^2_1 = 1.479$, $P = 0.224$) or Lampyridae and Scarabaeinae
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10 419 ($\chi^2_1 = 0.926$, $P = 0.336$). This suggests that the differences in elevational specialization
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12 420 in the full dataset are not simply due to differences in the proportion of rare species, but
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14 421 also reflect the elevational ranges of abundant species, which are wider in Scarabaeinae
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16 422 than Eumolpinae.

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425 Discussion

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

434 To compare our findings with the broad meta-analysis of Laurance *et al.* (2011) we
435 conducted an analysis using maximal taxonomic inclusion and contrasting only two
436 broad elevational zones (lower and upper halves). Our overall findings bear some
437 similarity to theirs. The high percentage of species that are specialists (77%) is typical
438 of tropical studies at this scale, especially on continents and in the neotropics, as ours is.
439 The high proportion of species that were specialized to lower zones was also typical, but
440 we found a high proportion of specialization in the upper elevational zone that has not
441 generally been found in other datasets analyzed in this way. In our dataset this finding is
442 largely driven by the high proportion of upper zone specialists in Chrysomelidae,
443 Curculionidae and Braconidae, which include many species with few individuals
444 sampled, which naturally tends to make them appear in one zone. This feature of the
445 data makes the exact percentage potentially suspect, since although the rarely collected
446 species may genuinely be specialized (e.g., species might have small populations
447 because they are specialized), they may also simply be poorly sampled, and would
448 prove to have wider ranges if sampled better (Wilson *et al.*, 2007). Nonetheless, the
449 high value compared to previous datasets is in line with the known high levels of
450 endemism found in other mountaintop taxa in Brazilian Atlantic Rainforest (Safford,
451 1999; Morellato & Haddad, 2000; Myers *et al.*, 2000), a likely result of the historical
452 interactions between climate and topography (Carmaval & Moritz, 2008; Steinbauer *et al.*, 2016).

454 Our data also confirm another general finding of Laurance *et al.* (2011): that of
455 differences in specialization across taxa. In their meta-analysis, differences were
456 confined to the upper zone, but they did not explicitly consider variation across insect

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3 457 groups. Studies focused on insects, such as ours, are needed to help “defy the curse of
4 458 ignorance” about the macroecology of this large component of biodiversity (Diniz-Filho
5 459 *et al.*, 2010). In our equivalent analyses we found strong differences across taxa in both
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8 460 the upper zones and lower zones that were generally consistent except in Scarabaeinae,
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10 461 which were one of the least specialized groups in the upper zone, but most specialized
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12 462 in the lower zone. Our study therefore highlights that taxonomic differences might also
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14 463 exist at lower elevational zones, with potential implications for community structure
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16 464 and function under environmental change.

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18 465 In order to investigate the robustness of our findings to assumptions about rarely
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20 466 sampled species, we conducted two analyses that effectively ignored them: a
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22 467 community-focused and a species-focused analysis. These produced findings in
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24 468 accordance with each other, but which diverged from the analyses of all species above.
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26 469 In particular, when sufficient data were available to more accurately judge elevational
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28 470 specialization, levels of specialization decreased markedly, although the level of
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30 471 specialization was still similar in the upper and lower zones. **This reduction was likely**
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32 472 **because rarely captured species had fewer opportunities to appear in two or more zones,**
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34 473 **and were excluded in this analysis.** However, different taxa now appeared the most and
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36 474 least specialized, with Lampyridae the highest and Braconidae the lowest. This indicates
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38 475 that the high level of specialization shown by Chrysomelidae and Curculionidae is not
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40 476 retained at this scale when only quite abundant species are considered. **For the**
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42 477 **Curculionidae this is surprising as the most abundant species are never extremely**
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44 478 **abundant (see Figure S2), and high elevational specialization might be expected to**
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46 479 **remain, suggesting that a larger fraction of species in this group cross the boundary**
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48 480 **between upper and lower halves of the transect.** Abundant braconids are also nearly
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50 481 always elevationally widespread, whilst, in contrast, abundant lampyrids are often very
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52 482 elevationally specialized.

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54 483 **The reduced level of specialization in Chrysomelidae and Curculionidae in the more**
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56 484 **restricted dataset does not necessarily mean that the higher levels in the full dataset were**
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58 485 **an artefact;** it just means that the true elevational ranges of the rarely-collected species
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60 486 need further study (Wilson *et al.*, 2007). This alternative view of the different taxa also
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488 487 has consequences for the way functional groups are viewed: the herbivores we studied
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490 488 are the most specialized trophic group if all species are included, but if rarely-collected
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492 489 species are ignored, herbivores do not differ from predators and saprotrophs, and

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3 490 parasitoids are the most generalist in elevation. Overall then these new analyses suggest
4 491 that the findings of studies that include all taxa collected may not hold if rare species'
5 492 elevational ranges are underestimated by the data.
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9 493 Since we had comparable data at finer elevational scales for three taxa, we could also
10 494 investigate the effect of increasing the number of elevational zones. Overall there was a
11 495 lower proportion of specialists when elevation zones are more finely divided. This is
12 496 unsurprising, as species ranging over two of the four zones would never appear as
13 497 specialists in the four-zone analysis, but could do in the two-zone analysis if those zones
14 498 were restricted to the top or bottom halves of the mountain. Between the four zones
15 499 there was also not much difference in specialization overall. There were consistent
16 500 differences across taxa, with Eumolpinae showing higher levels of specialization than
17 501 the other two taxa, and importantly this difference was retained when rarely-collected
18 502 species were ignored. The difference was most marked amongst the higher elevational
19 503 zones. At this spatial scale, the Lampyridae were not the most elevationally specialized
20 504 when rarely-collected species were ignored, but elevational range still only rises quite
21 505 slowly with abundance for both them and Scarabaeinae (Figure 6c), indicating that there
22 506 are still many range restricted species at this scale. The chief difference between the
23 507 two-zone and four-zone analysis in these taxa is that specialization differs between
24 508 zones for Scarabaeinae in the two-zone analysis (Figure 4), but never in the four zone
25 509 analysis (Figure 7). This implies that the degree of specialization at low elevations is not
26 510 very high in this group, thus being lost when finer scales are examined.
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39 511 Several factors are likely to contribute to different taxa displaying different levels of
40 512 elevational specialization. Dispersal tendency, habitat specialization, the tendency and
41 513 speed of ecological speciation, and the tolerance of environmental gradients are all
42 514 likely candidates (Magurran & May, 1999; Schluter, 2000; Coyne and Orr, 2004; Nosil,
43 515 2012), but these are very difficult to quantify for a single taxon, less alone several. The
44 516 Chrysomelidae contains subfamilies with different feeding habits and host plant
45 517 specificity, but the Galerucinae and Eumolpinae comprise around 95% of the
46 518 individuals on one tropical mountain (Bouzan *et al.*, 2015). These subfamilies have
47 519 root-feeding larvae and the adults feed on foliage (Jolivet & Hawkeswood, 1995).
48 520 Curculionidae adults are typically found on foliage or flowers, and most larvae are
49 521 subterranean or internal feeders (Daly *et al.*, 1998). Although these feeding habits are
50 522 considered among those with low host specificity amongst herbivores (Novotny &
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3 523 Basset, 2005), herbivorous insects on mountains may have characteristics that can
4 524 restrict their elevational-range both in evolutionary and ecological time, such as limited
5 525 dispersal (e.g. Rank, 1992) and tight dependence upon host phenology and distribution,
6 526 which can greatly vary along elevational gradients (e.g. Merrill *et al.*, 2008).

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10 527 Lampyridae have soft carapaces compared to other Coleoptera, and are often associated
11 528 with moist environments (Branham, 2010), so they may require particular adaptations to
12 529 different physical conditions, which could also encourage elevational specialization.
13 530 They also commonly show intensive sexual selection (Lewis & Cratsley, 1988; South *et*
14 531 *al.*, 2011) and many have poorly dispersive females (Cicero, 1988; Bocak *et al.*, 2008;
15 532 South *et al.*, 2011; Silveira *et al.*, 2016), which might encourage ecological speciation
16 533 and subdivision of the ecological niche by elevation. Some of the common braconids
17 534 might be ecological- or host-generalists, encouraging broader ecological tolerances and
18 535 elevational ranges. The two species which ranged all the way from the lowest to the
19 536 highest sampling sites belong to genera known for their generalist habits: *Bracon* (Shaw
20 537 & Huddleston, 1991) and *Ascogaster* (e.g. Stiling, 2004). The most species rich genus
21 538 was the generalist *Heterospilus* (Cirelli & Pentead-Dias, 2003), and all species with >
22 539 4 individuals occurred in both the upper and lower elevational zones.

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33 540 Our study has implications for the conservation of tropical insects under climate change.
34 541 It is widely recognized that species' ranges may be moving uphill in response to
35 542 warming climates, both in temperate zones and in the tropics (Konvicka *et al.*, 2003;
36 543 Pounds *et al.*, 2006; Chen *et al.*, 2009; Forero-Medina *et al.*, 2011; Telwala *et al.*, 2013).
37 544 Species confined to high elevational zones are likely to be most at risk because tracking
38 545 suitable climates will require dispersing across warmer areas of lower and less suitable
39 546 elevation. Our finding that a higher proportion of species is confined to high elevational
40 547 zones in this study from Brazilian Atlantic Rainforest (up to 58% as opposed to the
41 548 ~20% found generally in invertebrates) suggests that previous general figures may
42 549 underestimate the risk to many tropical insects, especially those in rich zones of
43 550 endemism. The Brazilian Atlantic Rainforest is known to contain many endemic species
44 551 that account for a high proportion of richness (Safford, 1999; Ribeiro *et al.*, 2009),
45 552 including many in the Campos de Altitude (Macedo *et al.*, 2016). It is important
46 553 therefore to establish if this is also true of insects in other tropical zones of endemism.
47 554 **In addition, it is crucial to establish to what extent vegetation changes can be expected,**
48 555 **particularly in the high altitude zones (Safford, 1999). Naively, one might expect the**

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3 556 tree line to shift uphill under warming, leading to the loss of the Campos de Altitude
4 557 and its endemic species. However, the tree line in Brazilian Atlantic Forest may not be
5 558 determined solely by temperature, but also by edaphic factors, as well as disturbance
6 559 such as fire (Safford, 1999). Under such a scenario the habitat might remain in a
7 560 modified state, although insects with low upper thermal tolerance might nonetheless go
8 561 extinct.

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14 562 The level of specialization to the lower of two zones that we found is also high, but
15 563 more in accord with previous work (Laurance *et al.*, 2011). It is uncertain whether low
16 564 elevation tropical species are more or less at risk from climate change. Low elevation
17 565 tropical species might be adapted to a narrower range of conditions than high elevation
18 566 tropical species, which might make them more susceptible to climate change if they
19 567 cannot move uphill due to lack of contiguous higher elevation sites (Bonebrake &
20 568 Deutsch, 2012). On the other hand, if such sites are available, low elevation species
21 569 might better resist climate change, but even so low elevation sites might become
22 570 impoverished as species move uphill (Colwell *et al.*, 2008).

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30 571 Our finding that different insect taxa have different degrees of elevational
31 572 specialization, and to different zones, may mean that the taxonomic composition of
32 573 insect communities will shift under climate change (e.g. Zografou *et al.*, 2014; Nieto-
33 574 Sánchez *et al.*, 2015) especially if some are more vulnerable to extinction. Our work
34 575 highlights the likely local loss of many Chrysomelidae (especially Eumolpinae),
35 576 possibly Curculionidae and also Lampyridae, all of which show high degrees of
36 577 elevational specialization, but it is possible that many abundant Braconidae and
37 578 Scarabaeinae will be less affected. The former are especially worrisome because of their
38 579 very high species richness. Although strong conclusions cannot be made about
39 580 functional groups given the small number of taxonomic groups contributing to each, and
40 581 especially since we have ignored here the effects of biotic interactions with other
41 582 species under climate change, our data suggest the hypothesis that the more abundant
42 583 tropical parasitoids will be fairly immune from the effects of climate change whilst
43 584 herbivores may be more at risk. This is potentially at odds with some previous work that
44 585 suggests that higher trophic levels may be more at risk under climate change for other
45 586 reasons (Voigt *et al.*, 2003; Zarnetske *et al.*, 2012). More data from other groups is
46 587 needed to test this more rigorously.

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3 588 Our conclusions come with several caveats. Sampling periods and methods varied
4 589 across taxa and sampling efficacy too, caveats which are, however, even more
5 590 applicable to a previous meta-analytical study (Laurance *et al.*, 2011), but naturally less
6 591 so to other studies that have considered fewer taxa (e.g. Wilson *et al.*, 2007). Even so,
7 592 some of our major conclusions are likely robust to these problems because they consider
8 593 identical sampling periods and methods: for example, the differences between
9 594 Braconidae, Curculionidae, Chrysomelidae and Coccinellidae in the two-zone analyses.
10 595 Although several of our (less species rich) taxa appear to have been fairly completely
11 596 sampled within the confines of the altitudes and months considered, our analyses show
12 597 that for three taxa (Braconidae, Chrysomelidae and Curculionidae) many more species
13 598 would be found through further sampling. Thus, the high level of specialization found in
14 599 Curculionidae and Chrysomelidae in the two-zones analysis which included rare species
15 600 would likely be even more extreme than that found, had more sampling been done. This
16 601 again, however, suggests that some differences between taxa are also quite robust to
17 602 undersampling since further sampling would only exacerbate a trend already present in
18 603 the data.

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30 604 In summary, we have provided data that show a high level of high elevational
31 605 specialization of insects in a tropical biodiversity hotspot, implying a higher level of
32 606 climate-induced extinction risk than might previously have been assumed. The data also
33 607 imply differences in elevational specialization amongst taxonomic and trophic groups
34 608 that hold the potential for changes in community structure and function under climate
35 609 change. We have also shown that the treatment of rarely-observed species can matter
36 610 when assessing the elevational specialization of communities, as well as the way in
37 611 which elevational zones are treated. These findings should help future researchers to
38 612 better understand how tropical insect communities are distributed across elevations, and
39 613 the consequences for conservation under climate change.

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833 Table 1. Observed and asymptotic estimates of species richness (\pm SE) for the different
834 taxa and sampling designs.

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

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3 838 Figure 1. Study location a) with the Serra dos Órgãos National Park (shaded area) and
4 839 views of the four vegetation zones studied. b) Lower Montane Forest c) Montane Forest
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6 840 d) Upper Montane Forest e) Campos de Altitude.
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9 841 **Figure 2. Location of the sampling transect route showing the different elevation zones:**
10 842 **for the two-zones analysis, A-D = lower-zone; E-H = upper zone. For the four-zones**
11 843 **analysis, A-B = lower montane; C-D = montane; E-F = upper montane; G-H = Campos**
12 844 **de Altitude.**
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16 845 **Figure 3. Rarefaction curves (mean \pm 95% CI) for all taxa in (a) the two-zones dataset**
17 846 **and (b) the four-zones dataset.**
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20 847 **Figure 4. Specialization to upper and lower elevational zones. a) across all species**
21 848 **collected in the different taxonomic groups and b) only including species in which >4**
22 849 **individuals were collected. The lower zone was 350m to 1280m and upper-zone 1450m**
23 850 **to 2170 m. Asterisk above bar indicates significant difference using Pearson's χ^2 test (P**
24 851 **< 0.05). Specialists are species which are only found in one of the zones.**
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29 852 **Figure 5. Taxonomic differences in specialization to upper or lower elevation zones. a)**
30 853 **across all species collected in the different taxonomic groups and b) only including**
31 854 **species in which >4 individuals were collected. The lower zone was 350m to 1280m**
32 855 **and upper-zone 1450m to 2170 m. Different letters above bars indicate significant**
33 856 **differences among groups using Pearson's χ^2 test (FDR correction χ^2 , P < 0.05).**
34 857 **Specialists are species which are only found in one of the zones.**
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40 858 **Figure 6. Elevational range against log abundance across species. Data are jittered**
41 859 **slightly vertically to aid visibility although species are all either found in one zone or**
42 860 **two in the two-zones analysis (a, b) or 1-4 in the four-zones analysis (c). Predicted**
43 861 **values from logistic regressions show different taxa (a & c) or trophic groups (b). Brac**
44 862 **= Braconidae Chry = Chrysomelidae, Cocc = Coccinellidae, Curc = Curculionidae;;**
45 863 **Eumol = Eumolpinae, Lamp = Lampyridae, Scara = Scarabaeinae, Tiph = Tiphidae,**
46 864 **Herb = Herbivores, Para = Parasitoids, Pred = Predators, Sapro = Saprotraphs.**
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53 865 **Figure 7. Specialization across four vegetational zones. a) across all species collected in**
54 866 **the different taxonomic groups and b) only including species in which >4 individuals**
55 867 **were collected. Different letters above bars indicate significant differences among**
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3 868 groups using Pearson's χ^2 test (FDR correction χ^2 , $P < 0.05$). Specialists are species
4 869 which are only found in one of the zones.

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7 870 **Figure 8.** Taxonomic differences in specialization across four vegetational zones. a)
8 871 across all species collected in the different taxonomic groups and b) only including
9 872 species in which >4 individuals were collected. Different letters above bars indicate
10 873 significant differences among groups using Pearson's χ^2 test (FDR correction χ^2 , $P <$
11 874 0.05). Specialists are species which are only found in one of the zones.
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For Review Only

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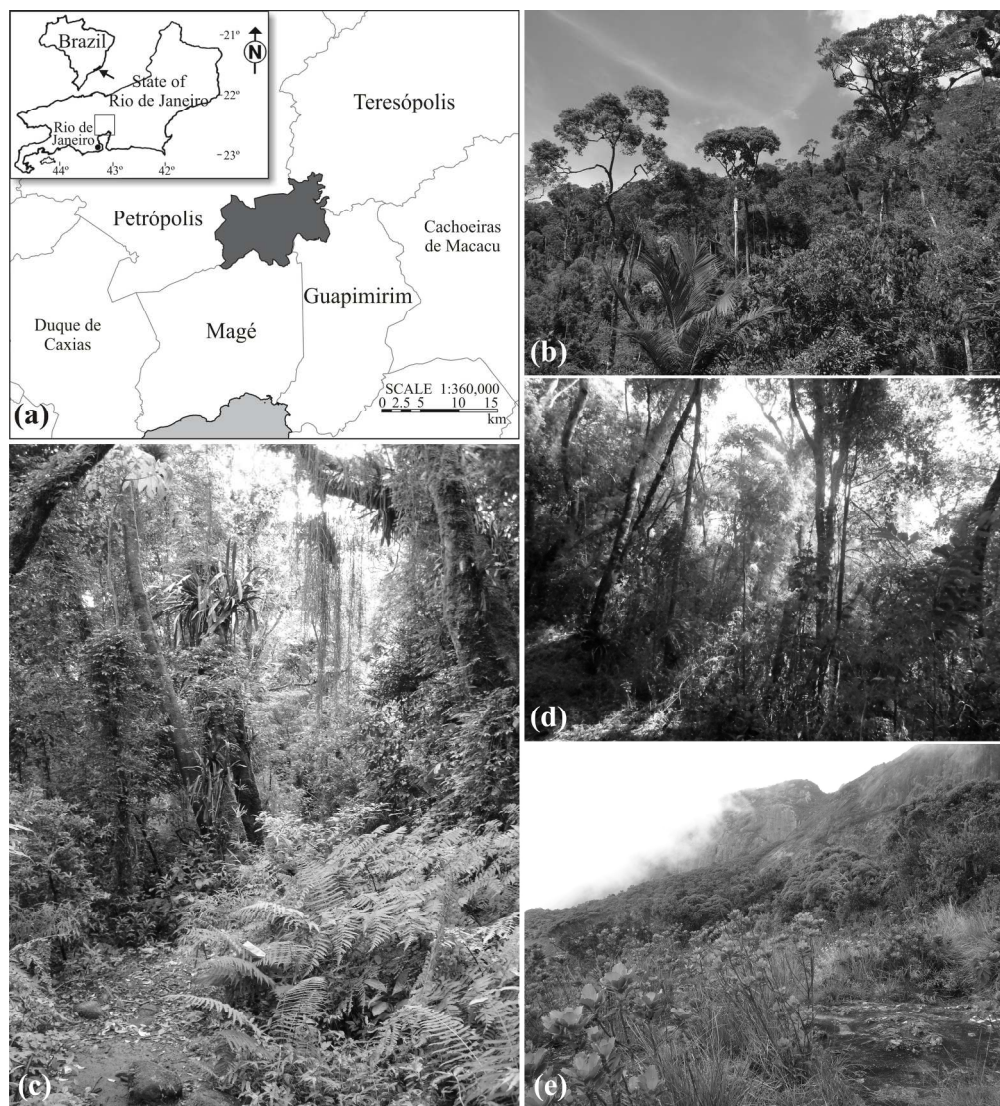


Figure 1. Study location a) with the Serra dos Órgãos National Park (shaded area) and views of the four vegetation zones studied. b) Lower Montane Forest c) Montane Forest d) Upper Montane Forest e) Campos de Altitude.

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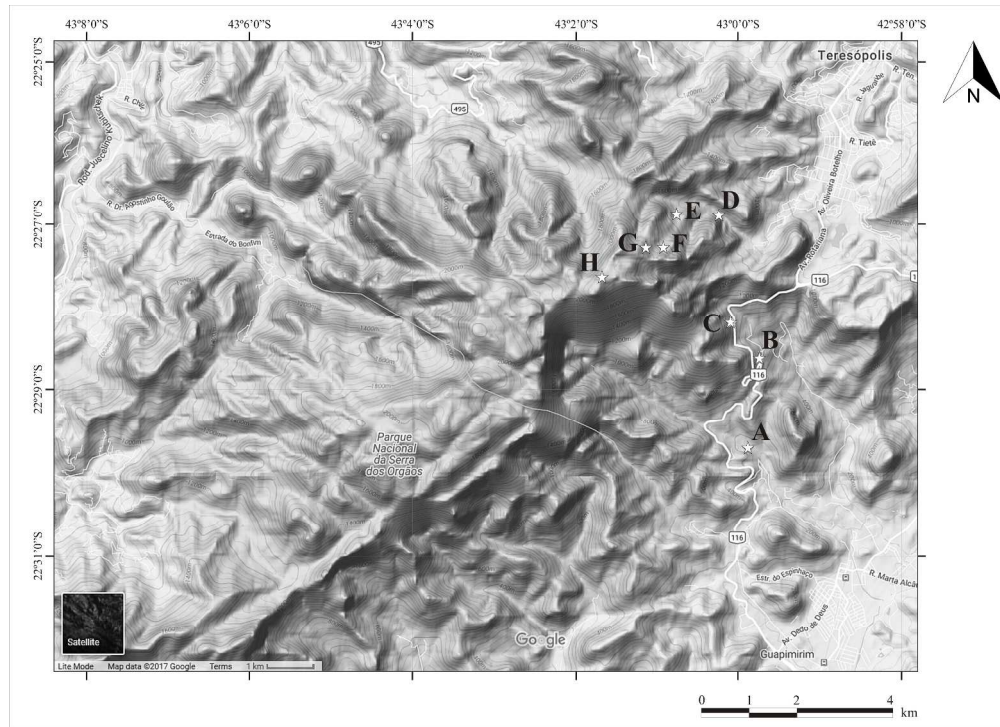


Figure 2. Location of the sampling transect route showing the different elevation zones: for the two-zones analysis, A-D = lower-zone; E-H = upper zone. For the four-zones analysis, A-B = lower montane; C-D = montane; E-F = upper montane; G-H = Campos de Altitude.

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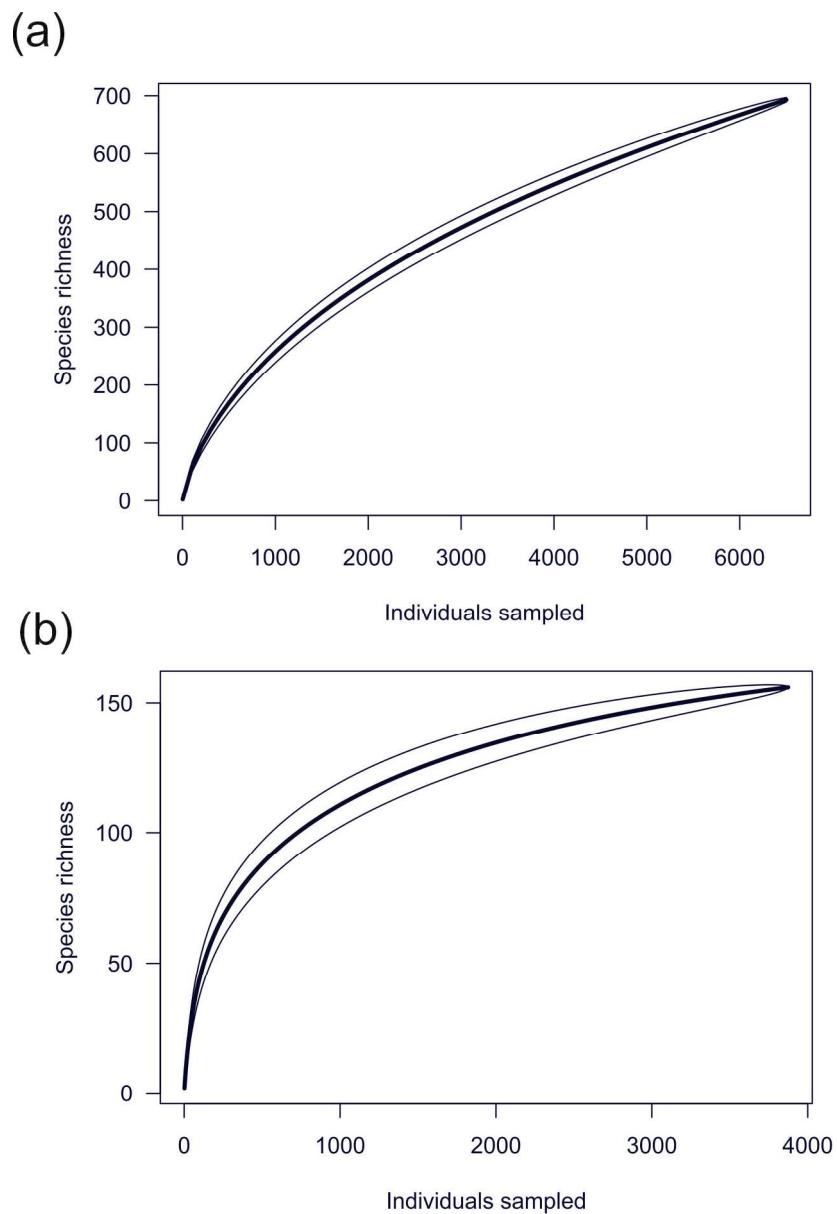


Figure 3. Rarefaction curves (mean \pm 95% CI) for all taxa in (a) the two-zones dataset and (b) the four-zones dataset.

151x222mm (300 x 300 DPI)

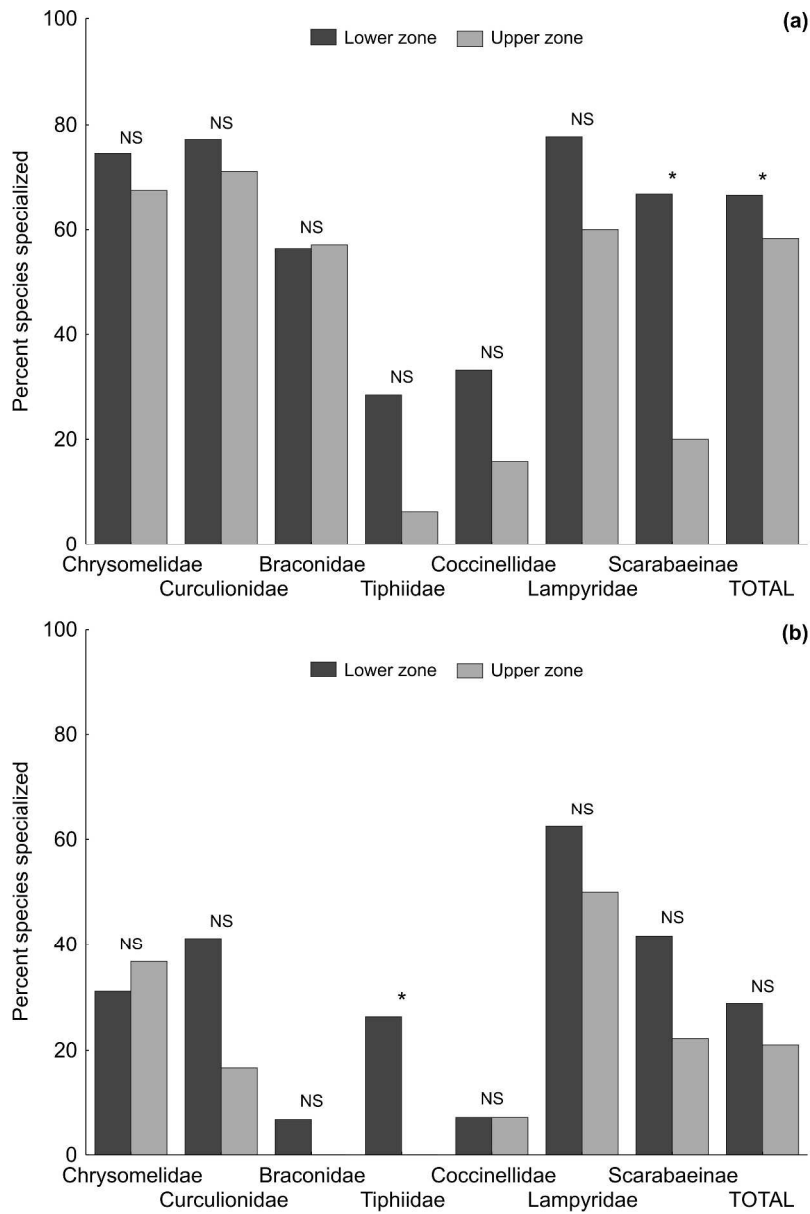


Figure 4. Specialization to upper and lower elevational zones. a) across all species collected in the different taxonomic groups and b) only including species in which >4 individuals were collected. The lower zone was 350m to 1280m and upper-zone 1450m to 2170 m. Asterisk above bar indicates significant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

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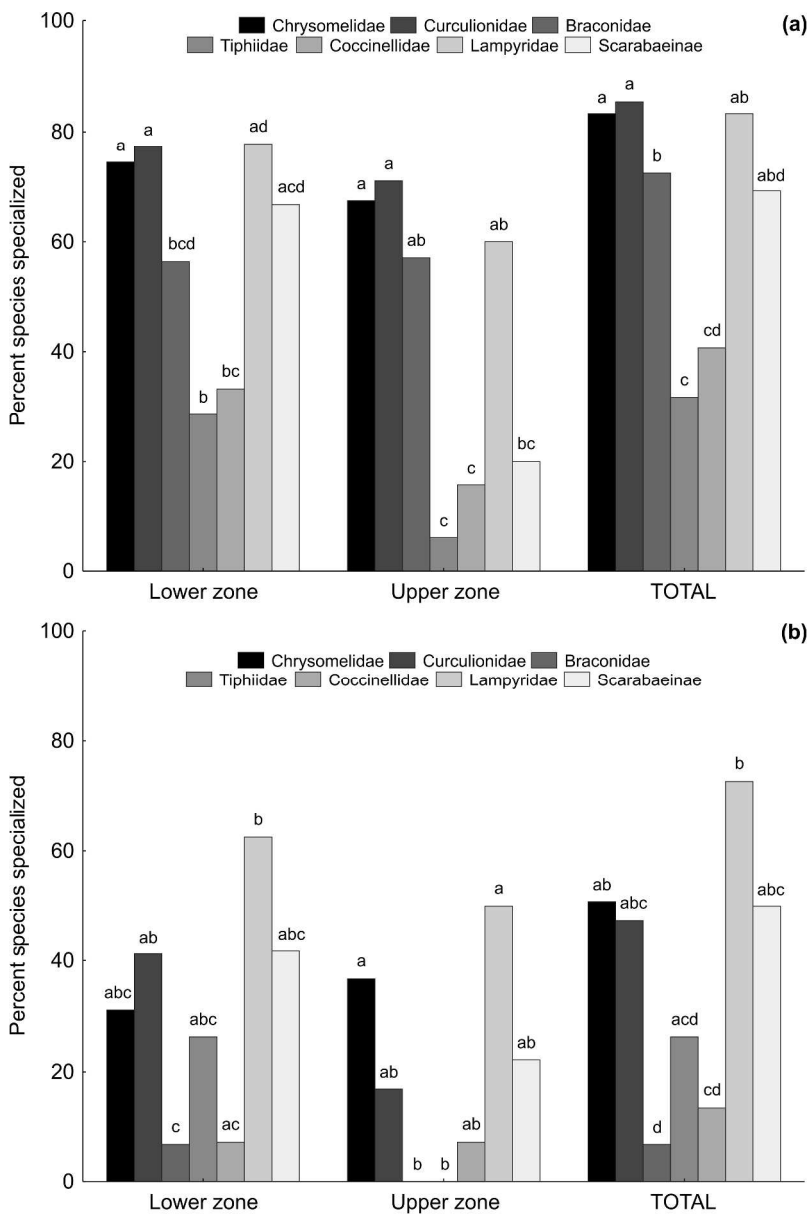


Figure 5. Taxonomic differences in specialization to upper or lower elevation zones. a) across all species collected in the different taxonomic groups and b) only including species in which >4 individuals were collected. The lower zone was 350m to 1280m and upper-zone 1450m to 2170 m. Different letters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

283x425mm (300 x 300 DPI)

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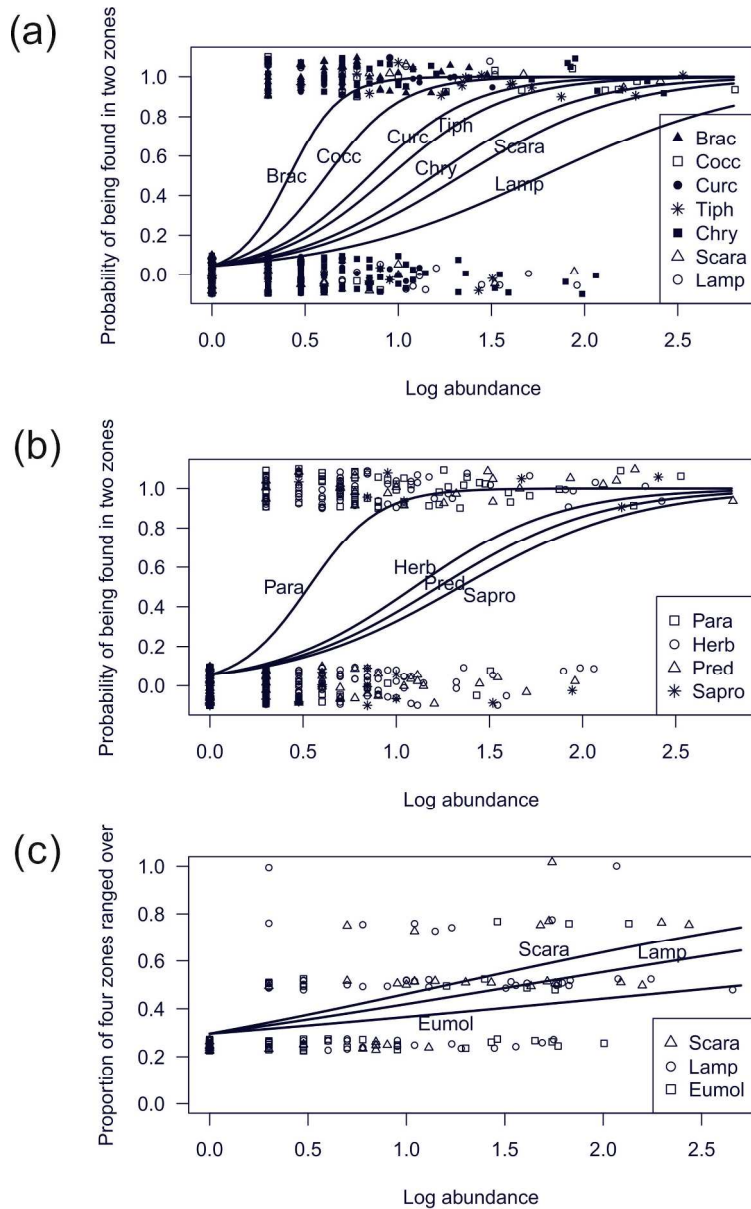


Figure 6. Elevational range against log abundance across species. Data are jittered slightly vertically to aid visibility although species are all either found in one zone or two in the two-zones analysis (a, b) or 1-4 in the four-zones analysis (c). Predicted values from logistic regressions show different 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.

159x256mm (300 x 300 DPI)

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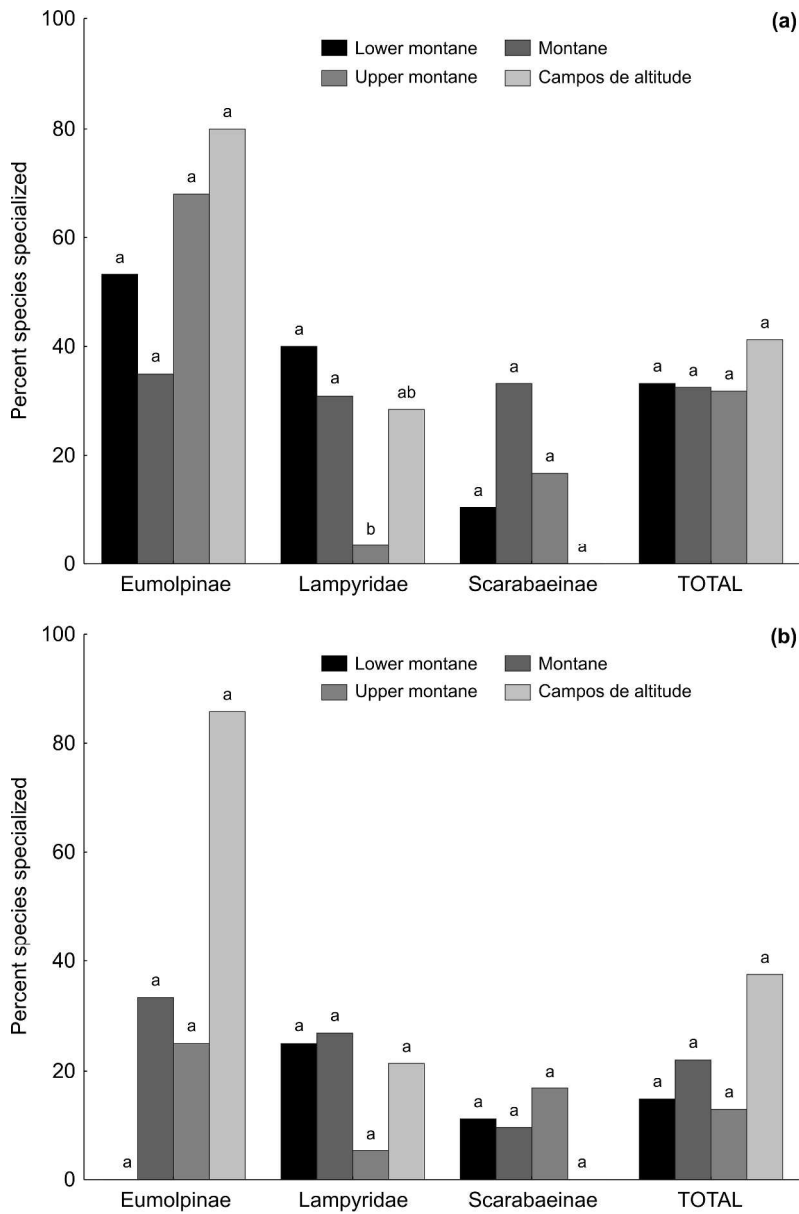


Figure 7. Specialization across four vegetational zones. a) across all species collected in the different taxonomic groups and b) only including species in which >4 individuals were collected. Different letters above bars indicate significant differences among groups using Pearson's χ^2 test (FDR correction χ^2 , $P < 0.05$). Specialists are species which are only found in one of the zones.

285x434mm (300 x 300 DPI)

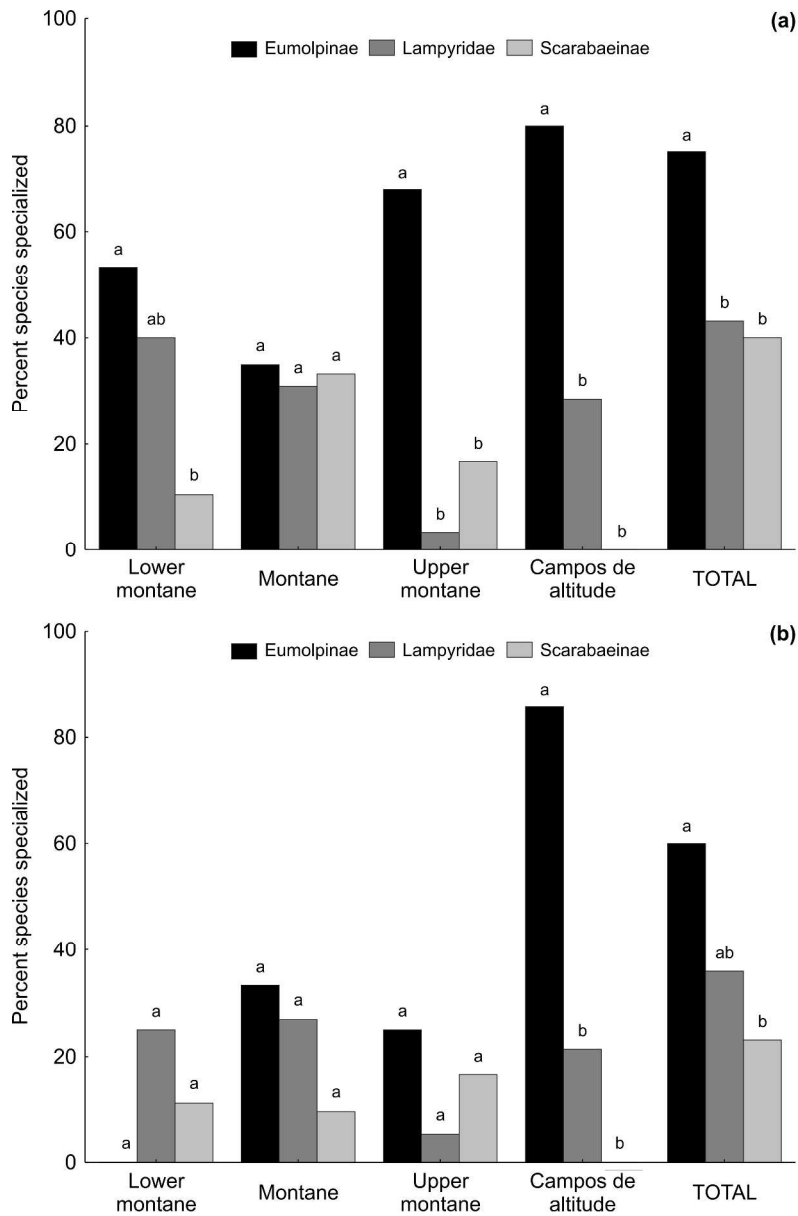


Figure 8. Taxonomic differences in specialization across four vegetational zones. a) across all species collected in the different taxonomic groups and b) only including species in which >4 individuals were collected. Different letters above bars indicate significant differences among groups using Pearson's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

286x438mm (300 x 300 DPI)