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The same but different : equally megadiverse but taxonomically variant spider communities along an elevational gradient

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2018-04

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Malumbres-Olarte , J , Crespo , L , Cardoso , P , Szuts , T , Fannes , W , Pape , T & Scharff , N 2018 , ' The same but different : equally megadiverse but taxonomically variant spider communities along an elevational gradient ' , Acta Oecologica , vol. 88 , pp. 19-28 . <https://doi.org/10.1016/j.actao.2018.02.012>

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<http://hdl.handle.net/10138/323344>

<https://doi.org/10.1016/j.actao.2018.02.012>

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1 **The same but different: structural changes in megadiverse spider communities along an**  
2 **elevational gradient**

3

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15

16 **Abstract**

17 Spatial variation in biodiversity is one of the key pieces of information for the delimitation and  
18 prioritisation of protected areas. This information is especially important when the protected area  
19 includes different climatic and habitat conditions, such as those along elevational gradients that are  
20 matched by differences between communities. Here we test whether the megadiverse communities  
21 of spiders along an elevational gradient change according to two diversity models – a monotonic  
22 decrease or a hump-shaped pattern in species richness, while measuring compositional variation  
23 along and within elevations, and testing the role of the habitat preference and the functional  
24 structure on the changes. We sampled multiple spider communities using standardised and  
25 optimised sampling in three forest types, each at a different elevation along a climatic gradient in  
26 the Udzungwa Mountains, Eastern Arc Mountains, Tanzania. The number of species was similar  
27 between plots and forest types, and therefore the pattern did not match either diversity model.  
28 However, species composition changed significantly with a gradual change along elevations. This  
29 elevational trend was not matched by changes in the occupancy or preference of habitat by spiders,  
30 or by any major variation in the guild structure. Interestingly, we found greater percentages of  
31 adults at higher elevations, which may be explained by the absence of strong seasonal changes and  
32 by more stable levels of humidity. The similarity in habitat conditions between elevations may  
33 explain that species richness and the functional structure of communities remain constant while  
34 composition varies between elevations. If we aim to understand and conserve some of the most  
35 diverse communities in the world, researchers and managers may need to place more attention to  
36 small scale and microhabitat characteristics upon which communities depend.

37

38 *Key words:* altitudinal/ elevational gradient, climatic stability, COBRA protocol, species richness,  
39 tropical forest.

40

41 **Introduction**

42 Whether one aims at testing the effects of environmental factors, historical events or biotic  
43 interactions on biodiversity, or at understanding the scale at which species co-exist or interact, the  
44 first step must be to quantify and characterise communities (Basset, 1996; Schaffers et al., 2008;  
45 Whittaker et al., 2001). Likewise, elucidating the trophic web dynamics that regulate nutrient and  
46 energy cycles requires knowledge of which species share a given space and time (Montoya et al.,

47 2006)□. Besides the theoretical repercussions, characterising communities by studying their  
48 composition and structure, and understanding their spatio-temporal variation is imperative to  
49 monitor and assess the effects of climatic and habitat changes on ecosystems and biodiversity  
50 (Barnosky et al., 2012; Sala, 2000), and to develop conservation priorities and policies (Pereira et  
51 al., 2013).

52 Elevational gradients have increasingly been seen as a powerful model system to disentangle the  
53 relative effects of environmental factors on biodiversity because this allows for many replicates,  
54 enables experiments and facilitates data collection, and avoids covariation between drivers (Körner,  
55 2007; Nogués-Bravo et al., 2008; Sanders and Rahbek, 2012). Gradients in temperature and  
56 humidity along elevations are usually matched by changes in species abundance and composition as  
57 well as in functional or traits community structure (Fitzpatrick et al., 2013; Graham et al., 2014;  
58 Sundqvist et al., 2013). With regard to species richness along elevational gradients, a number of  
59 diversity models have been put forward (Graham et al., 2014), those most commonly referred to  
60 being of two kinds: models that predict a monotonic decrease in the number of species with altitude,  
61 and models that expect a hump-shaped pattern with a peak in the middle of the gradient (Nogués-  
62 Bravo et al., 2008; Rahbek, 1997). Both model types can be based on the richness-productivity  
63 hypothesis (Grytnes, 2003; MacArthur .R, 1965; Rosenzweig, 1971; Wright, 1983). However, the  
64 former may also derive from hypothesised positive relationships between species richness and area  
65 or species distribution (Rapoport's rule) (Sanders, 2002; Stevens, 1992; Willig et al., 2003),  
66 whereas the latter include Mid-Domain-effect models (Colwell and Lees, 2000; Rahbek, 1997).

67 The Eastern Arc Mountains (EAM) provide an ideal system to study diversity patterns, with  
68 elevational gradients from 300 to 2400 m.a.s.l. The EAM are classified as one of the World's  
69 Biodiversity Hotspots (Myers et al., 2000) and their forests are considered some of the oldest and  
70 most stable of the African continent (Loader et al., 2014), forming an 'inland archipelago'. The  
71 limited research that has been conducted in the EAM, mainly in the Udzungwa Mountains, Uluguru  
72 Mountains, and the East and West Usambara Mountains, has revealed elevated levels of  
73 biodiversity (Nyundo, 2002; Scharff, 1992; Sørensen, 2004; Sørensen et al., 2002) and in particular  
74 a remarkable endemism compared to the surrounding savanna and lowland forest. However, no  
75 comprehensive studies of the arthropod communities have been conducted yet.

76 Spiders are one of the most diverse groups of organisms both taxonomically and ecologically. Over  
77 46,000 species and around 4000 genera have been described worldwide (Natural History Museum  
78 of Bern, 2017) and many thousands more await discovery. The myriad of habitats and feeding  
79 adaptations of spiders, and their role as one of the dominant groups of arthropod predators in  
80 terrestrial ecosystems (Marc et al., 1999), make them indicators of changes in other arthropod  
81 communities and of habitat disturbance (Cardoso et al., 2010; Malumbres-Olarte et al., 2013;  
82 Moretti et al., 2002; Romero and Harwood, 2010; Wise, 1993).

83 Here we present the first characterisation of megadiverse spider communities along elevational  
84 gradients based on optimised and standardised sampling. Our aims are: 1) to test which elevational  
85 diversity model matches best the spider species richness in the Udzungwa Mountains; 2) to measure  
86 the variation in taxonomic structure among communities within and between elevations; and 3) to  
87 test the role of functional community structure on diversity patterns along elevations.

88

## 89 **2. Material and methods**

### 90 *2.1. Study area*

91 Our study area is the Udzungwa Mountains (7.82°S, 36.70°E), Tanzania, which are recognised as a  
92 priority conservation area for mammals and birds (Dinesen et al., 2001) as well as for plants (Lovett  
93 et al., 1988; Lovett and Thomas, 1986)□. The Udzungwa Mountains are located in the southern part  
94 of the Eastern Arc Mountains and their forests are believed to have endured through millions of

95 years due to long-term climatic stability (Lovett, 1993)□. Our plots lie on the eastern slopes of the  
96 Udzungwa Mountains National Park (UMNP; 12 plots) and in the Uzungwa Scarp Forest Reserve  
97 to the south (three plots) (Fig. 1, Table 1).

98 Due to the climatic influence of the Indian Ocean, the eastern slopes of the Udzungwa Mountains  
99 experience a high average annual rainfall of 2000 mm (Mumbi et al., 2008)□, with a heavy rainy  
100 season between March–May and a lighter rainy season between November-February (Lovett,  
101 1996)□. There is a gradient in forest type from deciduous miombo woodland in the lowlands (300  
102 m a.s.l.) to evergreen montane rainforest just below the highest peaks (2400 m a.s.l.), which are  
103 covered by a mosaic of bamboo and *Hagenia abyssinica* (Bruce) J.F. Gmel. woodlands (Lovett et  
104 al., 2006; Rovero et al., 2017)□. The frequent mist in the highest parts of the mountains results in  
105 high levels of precipitation through condensation and more humid conditions during the dry season  
106 (June-October).

### 107 *Sampling*

108 We set up 15 plots, five plots at each of the three target elevations (700, 1000 and 1500 m a.s.l.)  
109 (Table 1), which correspond to three different forest types (lowland forest, submontane forest and  
110 montane forest, respectively) (Lovett, 1999, 1993)□. Horizontal distances between the first and the  
111 remaining plots of same elevation were 0.1, 1, 20 and 175 km. Each plot was a 50 m x 50 m square  
112 (0.25 hectare), within which we applied the COBRA-TF sampling protocol for spiders (Malumbres-  
113 Olarte et al., 2017)□ in October-November 2014. The COBRA protocols (Conservation Oriented  
114 Biodiversity Rapid Assessment) combine samples using different sampling methods to obtain the  
115 largest possible number of species for a given amount of effort (hence optimised) (Cardoso,  
116 2009)□. More specifically, the COBRA-TF protocol (for tropical forest spiders) includes samples  
117 from different vegetation strata/ microhabitats of a tropical forest (see Malumbres-Olarte2017 for a  
118 full description) and may provide a reliable sample of the diversity and structure of the community  
119 at a given location (Cardoso, 2009)□.

120

### 121 *2.2. Data analyses*

122 We assessed the thoroughness of our sampling by evaluating rarefied species accumulation curves  
123 visually and calculating the sampling completeness using the Chao 1 species estimator (Scharff et  
124 al., 2003)□. We analysed the species diversity in the spider communities by calculating observed  
125 and estimated numbers of species (Jackknife 1 and 2, Chao 1 and 2 and ACE estimators), the  
126 percentage of adults, and the number of individuals and species of each predatory guild (as defined  
127 in Cardoso et al., 2011)□ for each plot and elevation. We applied generalised linear models, and ran  
128 ANOVAs and linear mixed-effects analyses (with intercepts for the variable that represents the  
129 horizontal distance from the first plot as the random effect) to test the difference in these variables  
130 between elevations.

131 To examine the similarity in species composition and relative abundance between spider  
132 communities we generated a dissimilarity matrix based on the Bray-Curtis index (Legendre and  
133 Legendre, 1998)□ and created an ordination through non-metric multidimensional scaling (NMDS)  
134 (McCune and Grace, 2002)□. We tested for differences between the 15 communities using  
135 ANOSIM (Bray-Curtis index, 999 permutations) and for changes between communities (beta  
136 diversity) at the same elevation calculating the Jaccard and Bray-Curtis averaged pair-wise  
137 dissimilarity measures. Finally, we compared the species abundance distribution (SAD) curves of  
138 the communities and the alpha parameter values of the Gambin model (Matthews et al., 2014;  
139 Ugland et al., 2007)□. We based the Gambin model on species abundances rarefied (1000  
140 permutations) by the minimum number of adult individuals per plot. Before these three analyses, we  
141 applied the Hellinger transformation to equalise species weights (Legendre and Gallagher, 2001)□.

142 We handled and analysed all the data in R3.2.3. (R Development Core Team, 2017) using various  
143 packages including *vegan* (Oksanen et al., 2017) and *BAT* (Cardoso et al., 2015).

### 144 **3. Results**

145 The sampling yielded 40,613 individuals, of which 17,191 (42.3%) were adults. We observed 631  
146 species or morphospecies belonging to 54 families and estimated between 784–866 species across  
147 all the plots (Fig. 2a). The number of species per plot (alpha diversity) varied between 108–143, the  
148 total number of species at each elevation was similar as well as the beta diversity among the  
149 communities at each elevation (Jaccard and Bray-Curtis indices) (Table 2). We obtained a sampling  
150 completeness of 79% for all plots and values between 59–83% for individual plots (Table 1). The  
151 species accumulation curves changed with elevation, with lower plots providing steeper curves (Fig.  
152 2b, c). An ANOVA on the final slope of the curves showed significant differences between  
153 elevations ( $F_{2,12}=8.81$ ,  $p<0.01$ ).

154 Samples contained significantly higher percentages of adults at higher elevations (binomial [logit]  
155 distribution model,  $z_{\text{mid}}=12.65$ ,  $z_{\text{top}}=18.96$ ,  $p<0.001$ ) (Fig. 3b) but the observed (Fig. 3c) and  
156 estimated (Fig. 3d) numbers of species were similar in all the three elevations. The number of  
157 species represented by one or two specimens (here referred to as ‘rare species’) decreased with  
158 elevation (Fig. 3e).

159 The NMDS on abundance data showed a clear separation of the communities according to their  
160 elevation, with which the first axis was highly correlated (0.96). (Fig. 4). The ANOSIM confirmed  
161 significant differences between plots at the three elevations (Fig. 5). The shape of the SAD curves  
162 and the values of the alpha parameter provided by the Gambin model showed that the relative  
163 abundances of species in the low and mid elevation communities were similar (Fig. 6a, b). Some of  
164 the high elevation communities had slightly more even SAD curves and higher alpha values.

165 As for the microhabitat allocation, a greater percentage of individuals was present in the  
166 understorey vegetation at high elevations (Fig. 7a). There were more individuals and species in the  
167 understorey than on the ground and in the herbaceous vegetation at all elevations (Fig. 7b). The  
168 percentages of species belonging to the predatory guilds (Cardoso2011) were similar (Fig. 8a) with  
169 one exceptions: there were significantly more species of sheet web weavers at high elevation  
170 ( $t=4.67$ ,  $p<0.01$ ). The percentages of individuals of different guilds varied slightly between  
171 elevations (Fig. 8b). In the mid elevation plots there were proportionally more specialist spiders  
172 ( $p<0.01$ ) and fewer sheet web weavers ( $p=0.02$ ), and there were fewer sensing web weavers in the  
173 high elevation communities ( $p=0.02$ ) (Fig. 8b).

174

### 175 **4. Discussion**

176 This study is the largest study of spider communities so far, in terms of observed species richness,  
177 habitat coverage and number of communities. Our species richness values surpass those of previous  
178 studies in other tropical areas (Baldissera et al., 2012; Coddington et al., 2009; Floren and  
179 Deeleman-Reinhold, 2005; Pinkus-Rendon et al., 2006; Pinto-Leite and Rocha, 2012), with the only  
180 exception of the survey conducted in Peru, where 1140 morphospecies were observed (Silva-Davila  
181 and Coddington, 1996). There are likely to be other spider communities that are even more species-  
182 rich, perhaps in the forests of the neotropics, and the sampling design and methodology used in this  
183 study can certainly help discover, survey and analyse these. The relatively high sampling  
184 completeness for all plots at all three elevations testify to the thoroughness of our sampling, and  
185 therefore the adequate characterisation of the spider communities (Table 2).

#### 186 *4.1. Elevational diversity model*

187 Contrary to our expectations of elevational changes in diversity, the observed and estimated  
188 numbers of species in each plot were very similar at the three elevations (Fig. 3a, b, Table 2), and

189 therefore the diversity patterns did not match any of the elevational models. Indeed, communities  
190 have been found to track gradients along elevations (Graham et al., 2009; Machac et al., 2011;  
191 Peters et al., 2016), and several possible explanations have been put forward for changes in the  
192 number of species, including range size (Stevens, 1992), productivity (Hutchinson, 1959),  
193 environmental filtering (Graham et al., 2009; Maglianesi et al., 2015), geographic constraints  
194 (Colwell and Lees, 2000) and competition (Graham et al., 2009)□. More specifically, in the  
195 Udzungwa Mountains the number of species of plants, rodents and molluscs have been found to  
196 increase with elevation in a manner that fits with the mid-domain effect (Lovett et al., 2006; Stanley  
197 and Hutterer, 2007; Tattersfield et al., 2006). However, our data did not show such patterns and the  
198 differences among communities resided in their species composition (Figs. 4 and 5) and, to a certain  
199 point, relative species abundances (Fig. 6a,b).

200 The simplest explanation for the similarity in the number of species may be that the differences in  
201 climatic and habitat conditions along the modest elevation range (700-1500 m) are too small to  
202 result in significant differences in the number of spider species collected with the applied sampling  
203 protocol. However, we found differences of up to 5° C and 10% of humidity between the low and  
204 high elevation plots, and we propose another possible explanation based on habitat availability  
205 (Greenstone, 1984; Malumbres-Olarte et al., 2013; Riechert and Gillespie, 1986)□ and  
206 environmental filtering (Chatzaki et al., 2005; Foord and Dippenaar-Schoeman, 2016). The habitat  
207 in the forests of the Udzungwa Mountains has been considered to be homogeneous between 300-  
208 1850 m (Romdal and Rahbek, 2009)□, and yet, different studies have found elevational changes in  
209 species composition (Poynton et al., 2007; Romdal and Rahbek, 2009). If the number and structure  
210 of available habitats for spiders are also similar at different elevations, the number of species and  
211 the functional types that each elevation can contain may be similar. However, due to differences in  
212 climatic adaptations between species (environmental filtering), distinct spider communities may be  
213 found at different elevations. Considering the importance of three-dimensional habitat structure for  
214 spiders, testing our hypotheses may require studies that incorporate detailed data on space, habitat  
215 structure and climatic conditions.

216 We found that the percentage of adult spiders was greater at higher elevations, which may be the  
217 result of sampling at the end of the dry season, when forests at low elevations are considerably  
218 drier. Adults are individuals that have reached the reproductive stage and may require more prey  
219 (especially females) for themselves and their growing gonads. Therefore, the percentage of adults of  
220 most species may be higher when climatic conditions are most favourable and more prey is  
221 available (Cardoso et al., 2007; Gasnier et al., 2002). This ‘favourable’ time-window is often when  
222 the most limiting resource is most abundant. For instance, late spring-early summer may be the time  
223 with the highest percentages of adults in Mediterranean ecosystems (Cardoso et al., 2007) because  
224 combination of temperature and rain/humidity conditions is optimal for producing offspring,  
225 whereas it may be in late summer in subalpine areas where water is never scarce and when the  
226 average daily temperature is the highest (Malumbres-Olarte, 2011)□. However, in the absence of  
227 strong seasonal changes there may not be any ‘favourable time-windows’, and the percentage of  
228 adults may be stable throughout the year. This may be the case for the higher elevation plots, where  
229 levels of humidity are higher (pers. obs.) and may be less influenced by dry and wet seasonal  
230 cycles. To test whether this hypothesis is true, future observational studies should look for  
231 associations or correlations between seasonal variability in climatic conditions, breeding seasonality  
232 and variability in percentage of adults. It is also possible that the greater number of adults may be  
233 the result of more intense and efficient sampling at high elevations, which would also explain the  
234 lower number of rare species collected in high plots (Coddington et al., 2009)□.

#### 235 *4.2. Variation in taxonomic and functional structures*

236 Although the alpha and beta diversity, and the species richness at each elevation remain the same at  
237 all three elevations, the species composition does change. The latter could be accredited to the

238 changes in habitat composition and structure, and the associated adaptations and functional roles of  
239 the species. However, we did not detect any obvious trends in habitat preference or guild structure  
240 (Figs. 6, 7). It is possible that the (homogeneity of) local-scale characteristics, such as habitat  
241 structure or microclimatic conditions, explain the similarities in functional structure in all the  
242 studied communities. In connection with what we pointed out above, more data on forest  
243 microhabitats and the morphological, physiological or behavioural adaptations of the species  
244 associated with them might serve to explain our findings.

#### 245 *4.3. Repercussions for conservation*

246 Our findings support the notion that safeguarding the biotic communities of the Udzungwa  
247 Mountains, and probably of other parts of the Eastern Arc Mountains, requires protecting areas with  
248 different ecosystems and habitats. This is of utmost importance in the Udzungwa Mountains given  
249 the current pace of vegetation degradation and fragmentation (Barelli et al., 2015)□ in unprotected  
250 or semi-protected areas outside the National Park, such as the Kilombero Nature Reserve and  
251 Uzungwa Scarp Forest Reserve (Hegerl et al., 2017; Rovero et al., 2015)□. Unlike the areas within  
252 the National Park, the natural vegetation of the surrounding lands have become severely degraded  
253 in recent decades (Brink et al., 2016)□, so legal protection may be necessary to conserve native  
254 vegetation, and thereby native arthropod communities associated with it. The negative effects of  
255 human disturbance on mammals have been used to point out the urgent need for better protection of  
256 the EAM forests (Rovero et al., 2017)□ Here we make the point that the spatial distribution of  
257 biodiversity of less iconic but more diverse taxa should also be taken into consideration, so that  
258 protected areas includes a variety of climatic conditions and habitat types that allow their continued  
259 survival.

260

#### 261 **Contribution of the authors**

262 JMO, NS, TP and PC conceived and designed the study and the sampling. JMO, LC, PC and TS  
263 collected the samples, JMO, LC and WF generated the data from the samples, and JMO analysed  
264 the data. NS and TP provided the logistical and financial support from grants (see  
265 acknowledgements). JMO, NS, PC and TP wrote the paper and all authors approved it.

266

#### 267 **Compliance with ethical standards**

268 This study does not infringe any bio-ethical principles.

269

#### 270 **Conflict of interest**

271 The authors had no conflict of interest.

272

#### 273 **Acknowledgements**

274 NS and JM- O acknowledge the Danish National Research Foundation for the funding (grant no.  
275 DNRF96) provided to the Center for Macroecology, Evolution and Climate. NS and TP also  
276 acknowledge the support by the Carlsberg Foundation (project 2012\_01\_0504). We thank Tanzania  
277 National Parks (TANAPA), the Tanzania Commission for Science and Technology (COSTECH)  
278 and the Tanzania Wildlife Research Institute (TAWIRI) for providing permits to do research in the  
279 Udzungwa Mountains National Park. Richard M. L. Laizzer and Aloyce Mwakisoma provided  
280 invaluable assistance in the field, and the Udzungwa Ecological Monitoring Centre (UEMC) and its  
281 staff provided logistical support. We also thank Bjørn Hermansen, Natural History Museum of  
282 Denmark, for his help with GIS data.

283

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529 **Tables**

530

Plot	Latitude	Longitude	Altitude	Elevation	Sampling completeness	Observed species richness	Estimated species richness (Chao 1)
1	-7.687091	36.94129	650.212	Low	71%	115	162.6
2	-7.687496	36.94022	649.972	Low	68%	136	201.0
3	-7.684011	36.93038	1004.936	Mid	63%	119	189.3
4	-7.684797	36.93014	993.160	Mid	68%	135	199.8
5	-7.679317	36.91859	1447.860	High	72%	134	185.8
6	-7.678377	36.91857	1481.747	High	72%	124	171.6
7	-7.689854	36.93354	707.651	Low	74%	143	193.5
8	-7.686934	36.92758	977.779	Mid	59%	126	214.5
9	-7.685076	36.91458	1526.688	High	72%	135	188.5
10	-7.841573	36.86703	674.245	Low	66%	125	188.1
11	-7.840599	36.85917	1006.378	Mid	68%	110	162.2
12	-7.827731	36.84056	1551.922	High	79%	126	159.4
13	-8.503722	35.91915	659.345	Low	75%	108	143.2
14	-8.499499	35.91654	908.324	Mid	80%	116	144.7
15	-8.488775	35.90760	1531.494	High	83%	127	152.2

531 Table 1. Location and climatic features, sampling efficiency and observed number of species of sampling plots.

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Elevation	Observed species richness	Estimated species richness ( $\pm$ s.e.m.)	Sampling completeness	Beta Jaccard (95% CI)	Beta Bray-Curtis (95% CI)
Low (~700 m.a.s.l.)	305	398.52 $\pm$ 11.80	77%	0.68 (0.68, 0.71)	0.67 (0.67, 0.68)
Mid (~1000 m.a.s.l.)	307	418.05 $\pm$ 10.23	73%	0.70 (0.72, 0.76)	0.70 (0.69, 0.72)
High (~1500 m.a.s.l.)	311	386.77 $\pm$ 13.92	80%	0.68 (0.69, 0.73)	0.64 (0.65, 0.67)

534 Table 2. Total observed and estimated number of species (Chao 1), sampling completeness and beta diversity for each  
535 of the three elevations. Confidence intervals were calculated from rarefied communities.

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**Figure legends**

Fig. 1. Study area and plots. Close-ups show the plots in the Udzungwa Mountains National Park (A and B) and in the Uzungwa Scarp Forest Reserve (C). Plots are coloured according to whether they were at low (red), mid (purple) and high (blue) elevations.

Fig. 2. Number of species in the study plots over the number of collected spider individuals. a) Observed and estimated number of species in all plots. b) Rarefied accumulated number of species at each elevation. c) Rarefied accumulated number of species in each plot.

Fig. 3. Diversity values for the sampling plots according to elevation. a) Number of spider individuals per plot. b) Percentage of adults per plot. c) Observed number of species per plot. d) Estimated number of species (Chao 1 and Abundance Coverage Estimator) per plot. e) Number of rare species (species represented by one or two specimens in the entire dataset) at each elevation.

551 Fig. 4. Abundance-based species similarity among the studied communities. The ordination is a  
552 Non-Metric Multidimensional Scaling based on the Bray-Curtis similarity index values. Colours  
553 represent plots at low (red), mid (purple) and high (blue) elevations.

554

555 Fig. 5. Dissimilarity values among the spider communities obtained from an ANOSIM based on  
556 Bray-Curtis dissimilarity index.

557

558 Fig. 6. Species abundance distributions using the Gambin model. Curves (a) and alpha values (b)  
559 for each of the 15 spider communities at the three elevations.

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561 Fig. 7. Diversity values in each stratum of the vegetation at the three elevations. a) Percentage of  
562 spider individuals on the ground (black), in herbaceous vegetation (grey) and in the understorey or  
563 lower canopy (white). b) Number of species in ground (G), herbaceous (H) and understorey (U)  
564 vegetations in low (red), mid (purple) and high (blue) elevation plots.

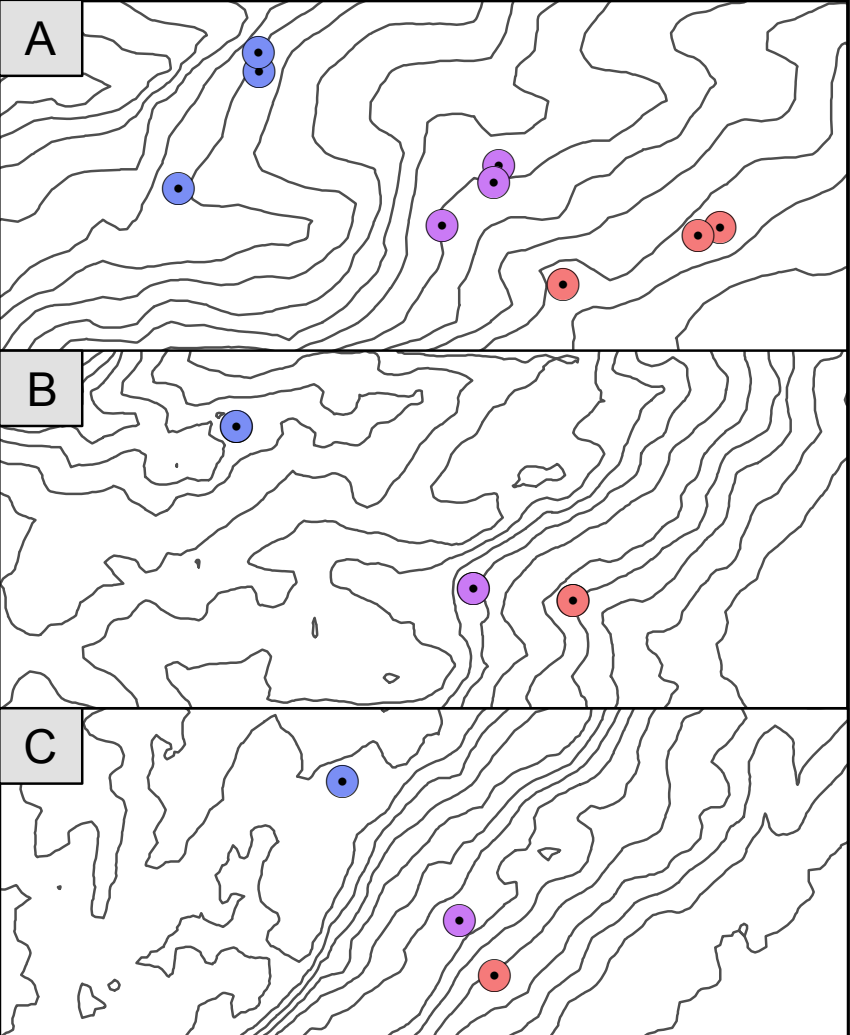
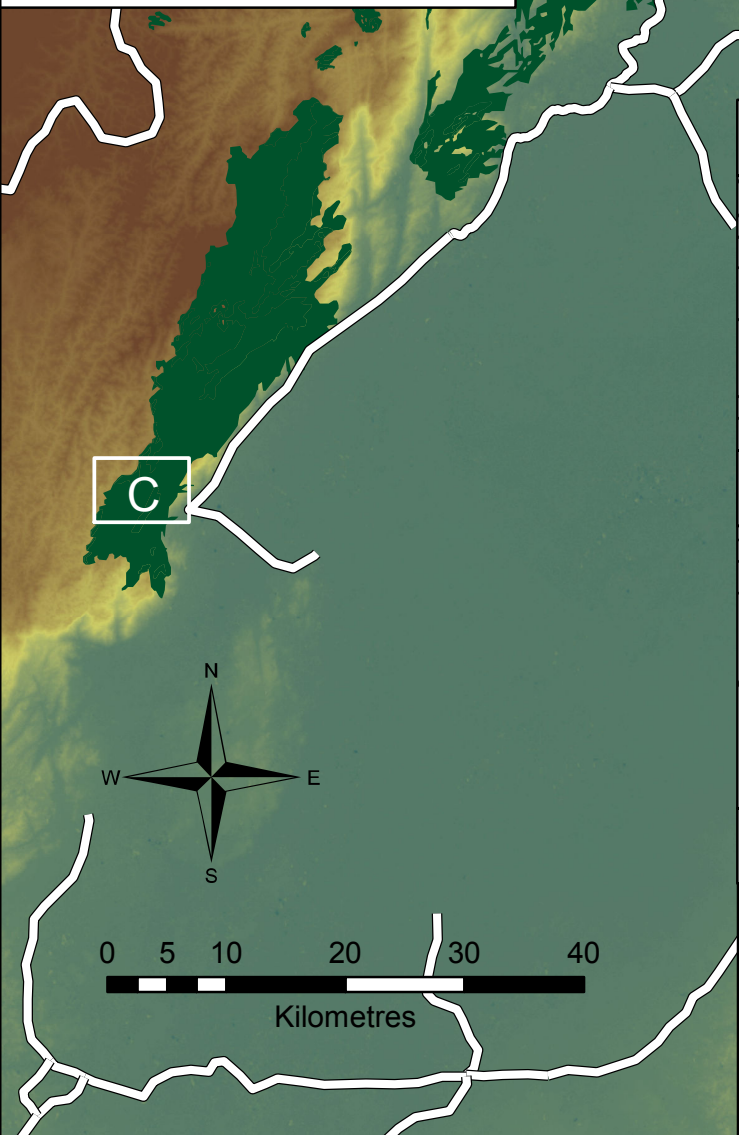
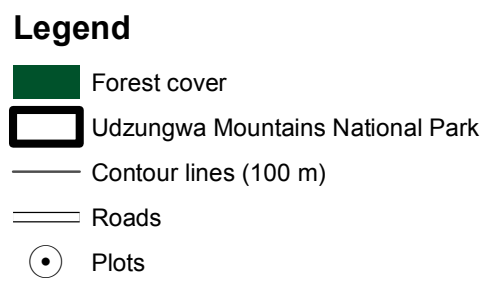
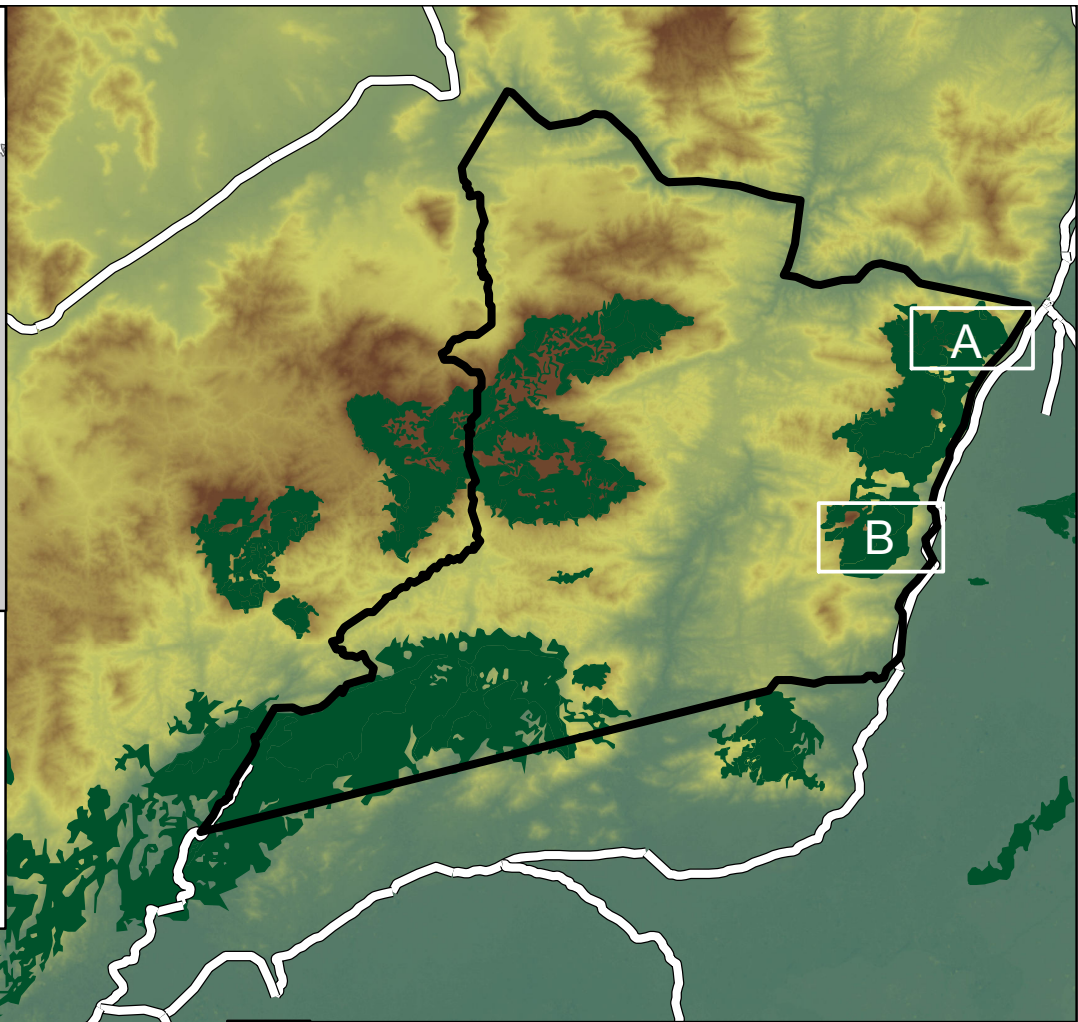
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566 Fig. 8. Percentages of spiders of different predatory guilds in the 15 communities. a) Percentage of  
567 species per plot. b) Percentage of individuals per plot.

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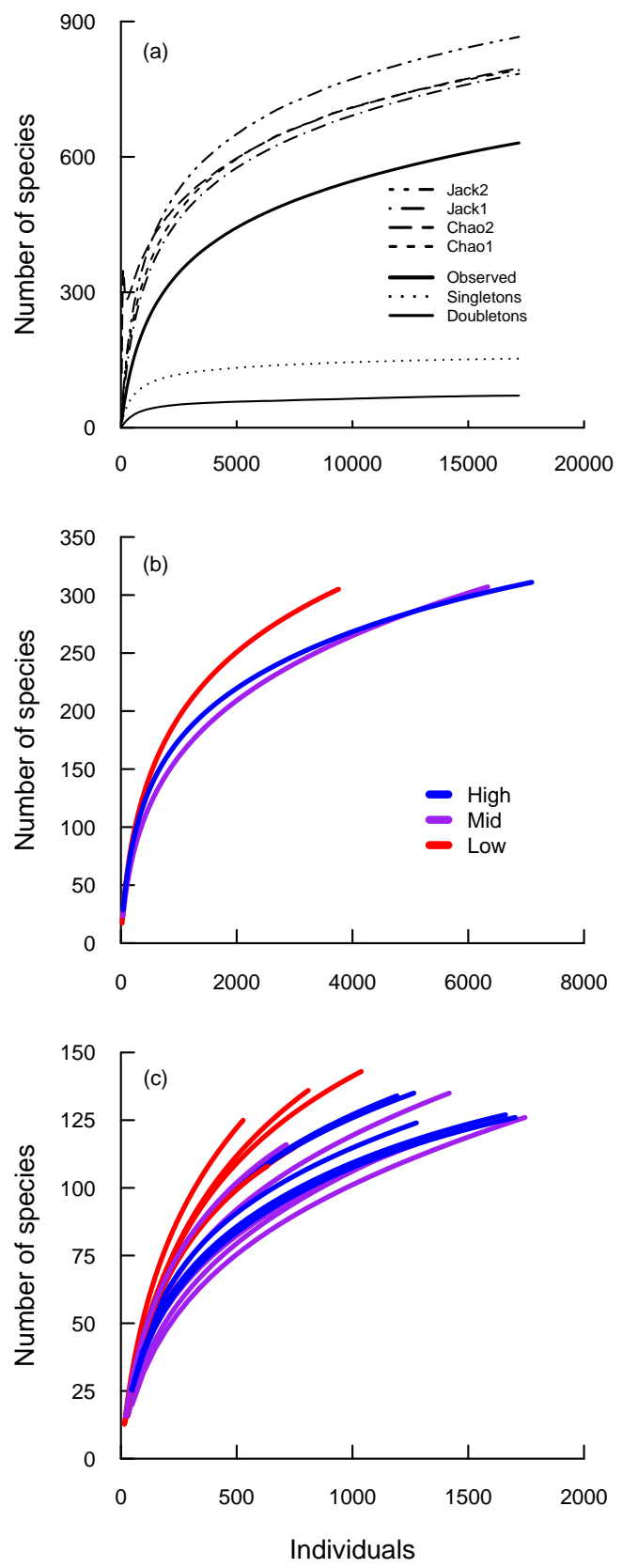


Fig. 2

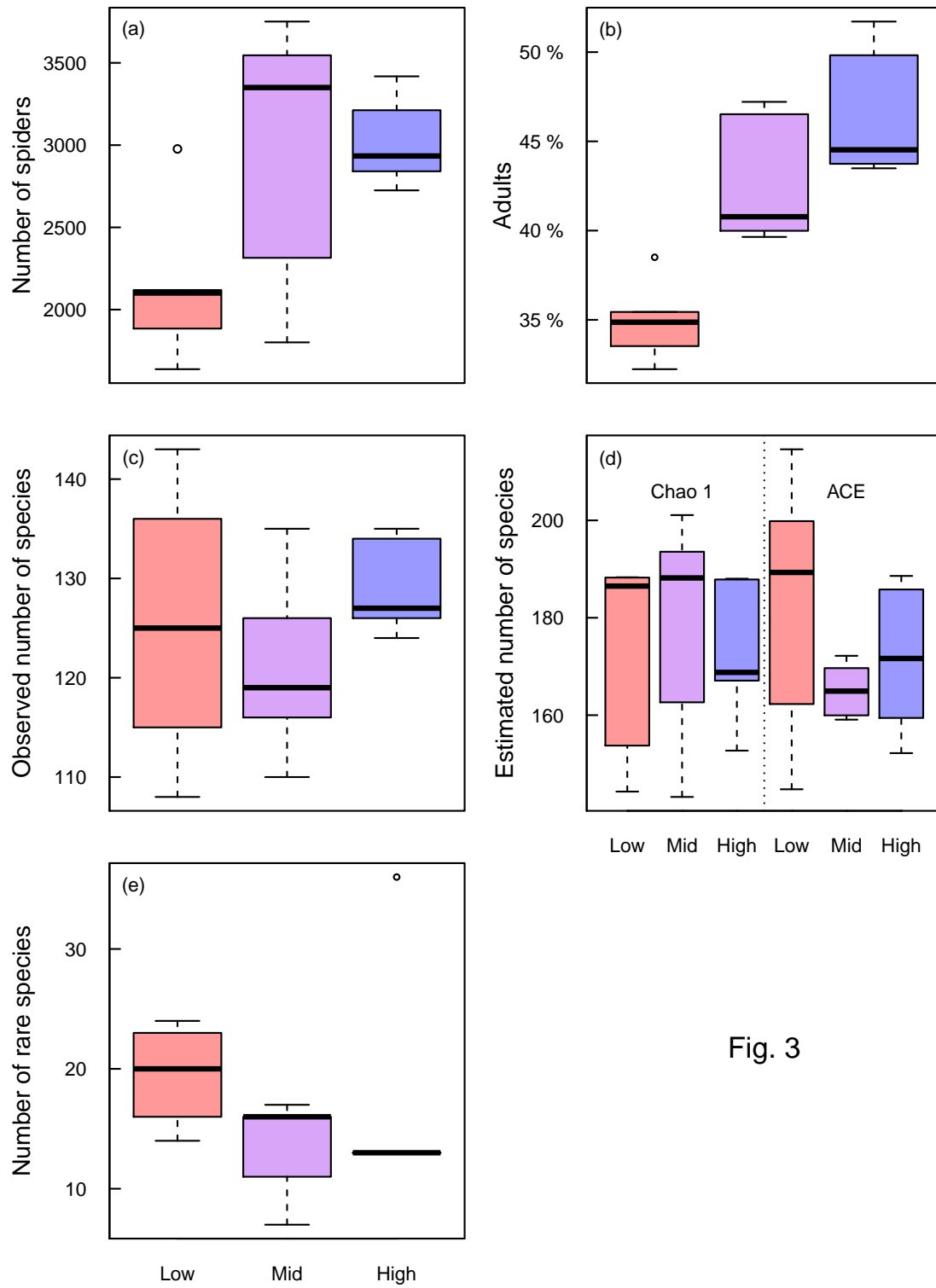


Fig. 3

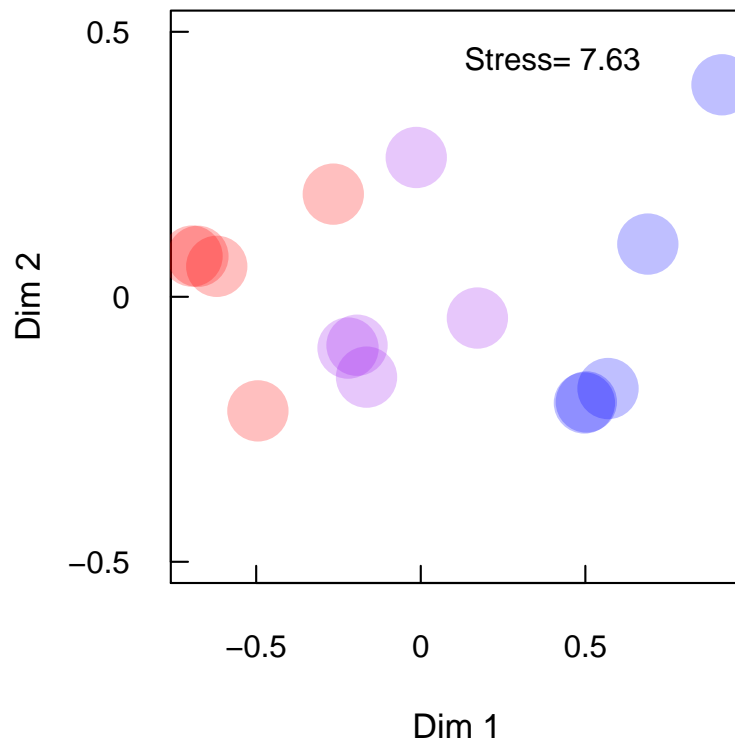


Fig. 4  
Steinhaus (abundance)  
Distance in taxonomic structure  
between communities (NMDS)

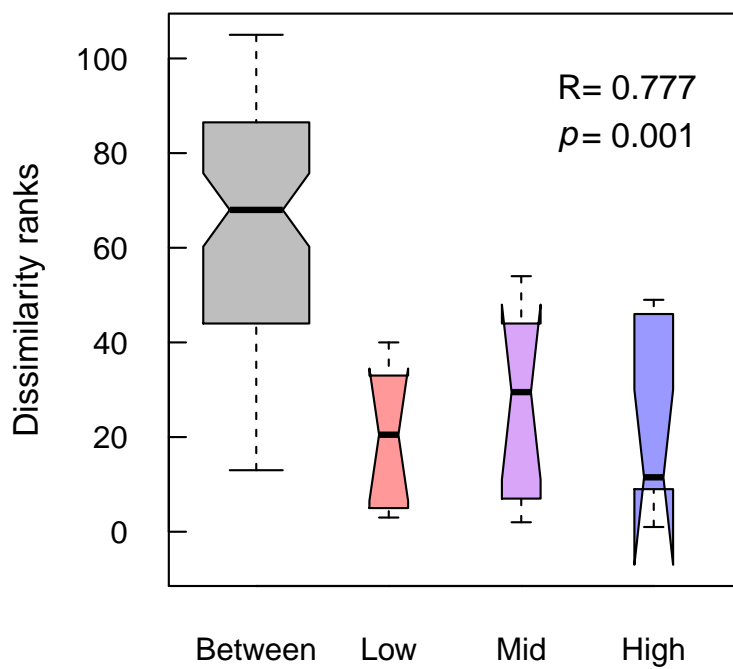


Fig. 5

ANOSIM – Plots – Bray–Curtis

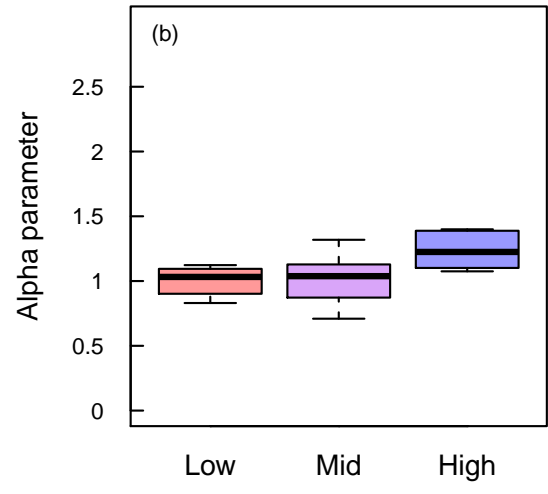
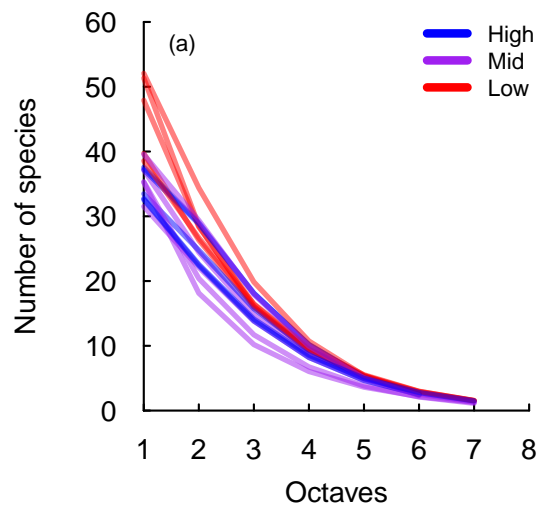


Fig. 6

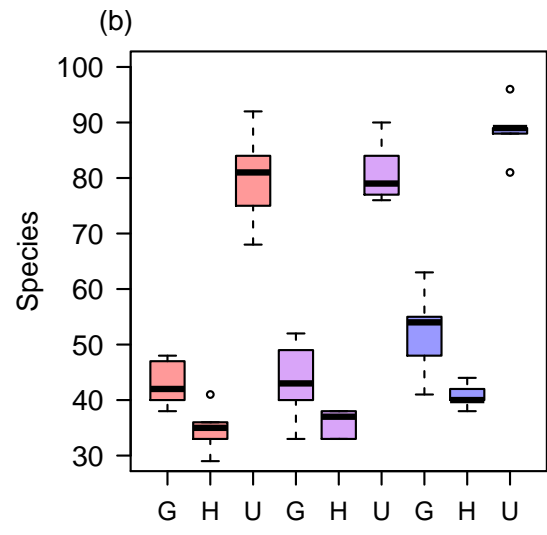
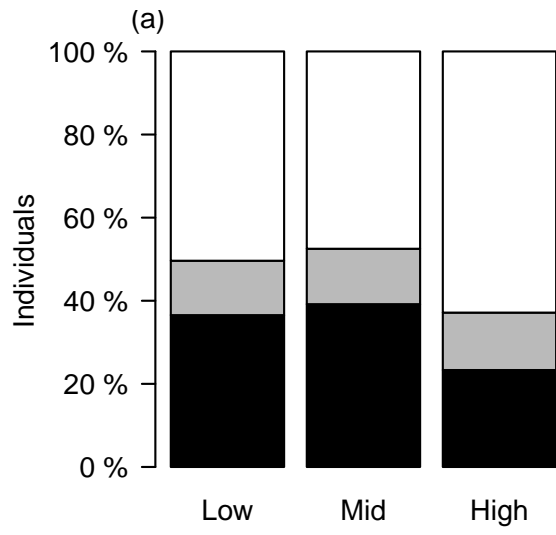


Fig. 7

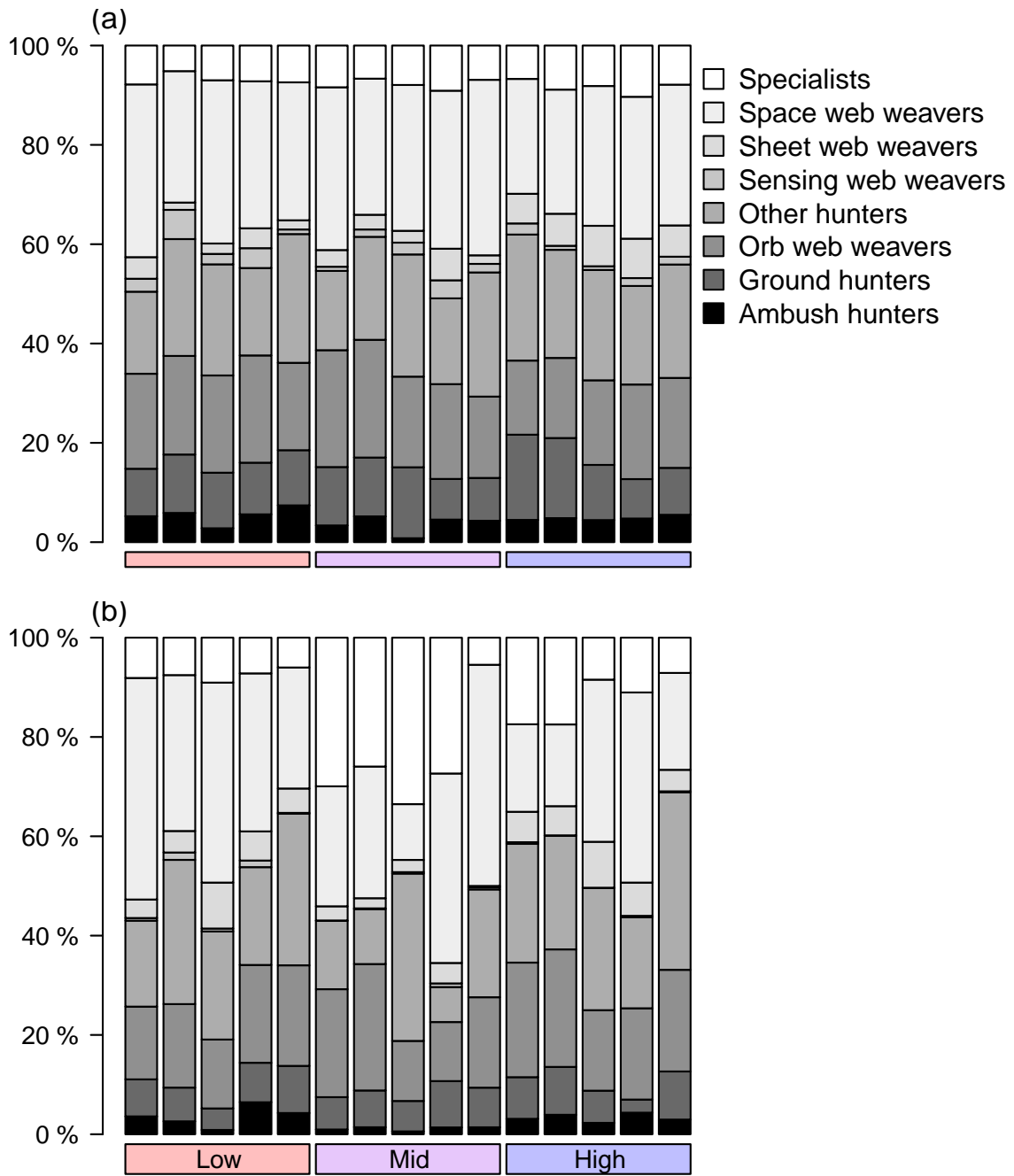


Fig. 8