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Scavenging in two mountain ecosystems: Distinctive contribution of ants in grassland and non-ant invertebrates in forest

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and all packages and analyses used are cited in the main text.

1 **Abstract**

2 Scavenging is a key process for the cycling of nutrients in ecosystems, yet it is still
3 neglected in the ecological literature. Apart from the importance of specific groups of animals in
4 scavenging, there have been few ecological studies that compare them. Furthermore, the
5 ecological studies on scavenging have mainly focused on vertebrates despite the crucial
6 importance of invertebrates in this process. Here, we performed a large-scale ant suppression and
7 vertebrate exclusion experiment to quantify the relative contribution of ants, non-ant
8 invertebrates and vertebrates in scavenging nitrogen-rich (insect carcasses) and carbon-rich
9 (seeds) baits in two contrasting mountainous habitats in Brazil (grasslands and forests). Overall,
10 bait removal was 23.2% higher in forests than in grasslands. Ants were the primary scavengers in
11 grasslands, responsible for more than 57% of dead insect larvae and seed removal, while, in
12 forests, non-ant invertebrates dominated, removing nearly 65% of all baits. Vertebrates had a
13 minor role in scavenging dead insect larvae and seeds in both habitats, with < 4% of removals.
14 Furthermore, our results show that animal-based baits were more consumed in forests than seeds,
15 and both resources were equally consumed in grasslands. Therefore, we demonstrate the
16 superiority of invertebrates in this process, with a particular emphasis on the irreplaceable role of
17 ants, especially in this grassland ecosystem. As such, we further advance our knowledge of a key
18 ecosystem process, showing the relative importance of three major groups in scavenging and the
19 differences in ecosystems functioning between two contrasting tropical habitats.

20 **Keywords:** Bottom-up, Cerrado, Environmental stoichiometry, Mata Atlantica, Nutrient cycling,
21 Protein, Resource removal.

22 **Introduction**

23 Scavenging is a key process for the cycling of nutrients in ecosystems (Beasley et al.
24 2019, Eubanks et al. 2019). Scavenging occurs when animals feed on non-living animal or plant
25 matter, promoting the transport and redistribution of nutrients and accelerating the
26 decomposition process (DeVault et al. 2003). This is an essential part of the decomposition
27 process that links higher trophic level organisms, decomposers, and plants (Carter et al. 2007,
28 Barceló et al. 2022). The consumption of dead organisms by scavengers releases nutrients into
29 the trophic web, making them available to other levels of consumers (Wilson and Wolkovich
30 2011). Furthermore, the dead matter not eaten by those organisms is broken down into smaller
31 parts, which facilitates the decomposition by microorganisms (Barceló et al. 2022).

32 Vertebrates are the most studied scavenging actors, removing large portions of carrion in
33 all ecosystems. Some vertebrates, such as vultures and hyenas, have diets primarily based on
34 carrion and usually consume the majority of large carrion sources (Beasley et al. 2019).
35 Nevertheless, insects play an essential role in scavenging because they are prolific biomass
36 consumers, primary colonisers, and sometimes the only or first ones to access those resources
37 (DeVault et al. 2003, Englmeier et al. 2022). For example, blowflies (Calliphoridae) can identify
38 and dominate vertebrate carrion almost immediately, and their larvae can increase the
39 decomposition rates up to nine times (Park et al. 2021). Despite the importance of vertebrates
40 and invertebrates for scavenging and nutrient flux, few ecological studies have quantitatively
41 compared them. However, this understanding is essential in the Anthropocene when disruptions
42 to ecological communities due to climate change, overhunting, and habitat modification are
43 altering animal communities (Young et al. 2016) and, therefore, their relative role in ecosystem
44 functions, such as scavenging.

45 Scavenging ecology has mainly focused on the consumption of large carrion, especially
46 from dead vertebrates (DeVault et al. 2003, Beasley et al. 2019). Compared with dead
47 vertebrates, dead invertebrates and plants - or their parts - present higher overall biomass, are
48 individually small, widely distributed, and consistent, representing a valuable resource to
49 scavengers (Tan and Corlett 2012). Invertebrate carcasses are nitrogen (N) rich, a limiting
50 nutrient in almost all environments, and consequently are rapidly removed and consumed by
51 other animals (Kaspari and Yanoviak 2001). On the other hand, non-lignified plant parts, such as
52 seeds, are a good source of carbon (C, carbohydrate, and fat) for scavengers (Janzen 1971,
53 vander Wall et al. 2005). Although it is usually assumed that generalist scavengers consume
54 whatever they find, the Resource-ratio theory (Tilman 1982) predicts that animals achieve
55 optimal consumption of complementary nutrients by favouring the most limiting ones (Grover et
56 al. 2007). Therefore, resources rich in limited nutrients, such as N-rich ones, are likely removed
57 in greater quantities (Craine et al. 2018). However, very few studies have compared the relative
58 importance of different food sources and animal taxa for omnivorous scavengers (but see Lasmar
59 et al. 2023)

60 Ants can make a substantial contribution to scavenging in forest (Griffiths et al. 2018)
61 and savannas (Walker et al. 2024). They are the most abundant group of terrestrial ground-
62 foraging animals, and most species are omnivorous scavengers (Hölldobler and Wilson 1990).
63 They can be found in almost all terrestrial habitats and represent more than 25% of the whole
64 biomass of terrestrial animals (Schultz 2000, Tuma et al. 2020). Although the importance of ants
65 to ecosystems is mentioned in several studies (del Toro et al. 2012), few studies have measured
66 the effect of ants on scavenging. This lack of knowledge increases when we compare the amount
67 of detritus removed by ants and other animal taxa. To our knowledge, there is only one study in

68 Malaysia, Griffiths et al. (2018), showing that ants are major scavengers on the forest floor and
69 that, in their absence, no other animal group compensated for their role in this habitat (i.e. no
70 functional redundancy). Thus, there is still a lack of empirical data that quantifies the relative
71 importance of resource removal in many other ecosystems, nor do we understand how it varies
72 among habitat types.

73 Ants are very sensitive to habitat openness and vegetation structure, which can also affect
74 their role in the ecosystem (Andersen 2019, Castro et al. 2020, Fontenele and Schmidt 2021).
75 Compared with forests, open environments such as savanna and grassland, usually support a
76 higher biomass of dominant epigeic ant species that can control and remove resources faster than
77 subordinates (Andersen 2019). As ants are thermophilic organisms, greater solar radiation in
78 open areas increases ground temperature and, consequently, ant activity (Bucy and Breed 2006,
79 Parr and Bishop 2022). Therefore, we could expect that habitat openness increases the
80 scavenging activity provided by ants when compared with forests. Indeed, Salas-López et al.
81 (2022) demonstrated that ants occurred at a greater number of baits in cropland compared with
82 forests in six out of the seven different bait types offered. Unfortunately, we have no information
83 on how habitat openness could differentially affect the relative role of ants in scavenging
84 compared with vertebrate and non-ant scavengers.

85 We therefore asked the following questions: (1) Do scavenging rates vary with habitat?
86 (2) What is the contribution of vertebrates, non-ant invertebrates, and ants to scavenging in each
87 habitat? (3) Is there evidence of functional redundancy among taxa? (4) How does removal of
88 different resources vary according to habitat type? To answer those questions, we established a
89 large-scale manipulative field experiment (80 x 80 m plots) where we suppressed ants in two
90 contrasting natural habitats that occur together as a mosaic in the Brazilian mountain: grasslands

91 (*campo rupestre*) and forest (montane rainforest). We predicted that (1) baits are more likely to
92 be removed from the forest floor than grassland due to higher plant biomass in forest than in
93 savannas (Miranda et al. 2014), which could indicate a higher animal biomass in the forest.
94 However, (2) ants would have higher relative importance in scavenging in open habitats
95 (grasslands) than in closed (forests) because in open habitats, ants have higher activity (Bucy and
96 Breed 2006), richness (Castro et al. 2020), and there are more dominant species (Andersen
97 2019). (3) The role of ants in scavenging is not compensated for by other taxa when ants are
98 absent. Finally, (4) the removal rates of animal-based baits on the ground are higher than seed
99 baits in both environments, since animal resources are more limiting than plant resources in most
100 habitats (Kaspari and Yanoviak 2001, Bar-On et al. 2018).

101

102 Methods

103 *Study area*

104 We undertook this study at the Serra do Cipó National Park, located in the southern
105 portion of the Espinhaço Range Biosphere Reserve (19°14'19"S, 43°31'35"W), in the central
106 region of Minas Gerais state, Brazil. It is a mountainous area with elevations ranging from 1300
107 m to 1350 m and two marked seasons, wet (October to March) and dry (April to September). The
108 average annual temperature in this area is 20.7°C, and the average rainfall is 1500 mm
109 (Fernandes and Madeira 1999). Two distinct and contrasting habitats occur together in this area:
110 *campo rupestre* (grasslands) and semi-deciduous forest islands, allowing us to test our
111 hypotheses within the same broad climatic conditions (Figure 1). The *campo rupestre*, which
112 dominates the landscape, is an ancient ecosystem, climatically buffered and, an infertile
113 landscape (OCBIL; Hopper et al. 2021; Figure 1A). It is characterised by the dominance of herbs

114 and shrubs covering nutrient-poor quartzitic soil (Fernandes 2016). Within the *campo rupestre*
115 matrix are natural islands of montane rainforest (locally called *Capões de Mata*), with floristic
116 composition resembling the semi-deciduous Atlantic Forests (Coelho et al. 2018). Those two
117 habitats have a very diverse and well-study ant community, with approximately 195
118 species/morphospecies (50 genera) sampled together (Castro et al. 2020, Nunes et al. 2020, Brant
119 et al. 2021)

120 *Experimental design*

121 We set a factorial experimental design with 14 plots divided into i) four forest control; ii)
122 four forest ant-suppression; iii) three grassland control; iv) three grassland ant-suppression
123 treatments. Each plot consisted of an experimental area of 50 x 50 meters and a buffer area of 15
124 meters on each side (80 x 80 m total plot size). Control and ant suppression plots were paired
125 with each control plot located 100 m from its respective suppression plot. Each pair of plots was
126 at least 1 km apart, and in the case of forest plots, each pair was placed on a different forest
127 island (map in Appendix S1). We used this experimental design to: i) reduce variation between
128 control and suppression plots, ii) capture habitat special heterogeneity, and iii) take independent
129 samples.

130 To suppress ants, we used two poison bait types: homemade imidacloprid ant bait (100
131 ppm w/v); and ATTA MEX-S® (Sulfonamide 300 ppm m/m). We prepared the homemade ant
132 bait following Griffiths *et al.* (2018) and Parr *et al.* (2016) by soaking 1 kg of Whiskas® cat
133 food (mostly grain-based carbohydrates and protein) in a solution of 40 g of jelly (gelatin and
134 sugar), 1 litre of distilled water, and 0.0285 g of Evidence 700 WG from Bayer AG
135 (imidacloprid 70 % m/m). In December 2019 (wet season), we started the ant suppression by
136 spreading 10 kg of homemade and 5 kg of commercial ant baits across each suppression plot,

137 including the buffer area. The ant suppression was monitored and maintained for 90 days. The
138 method described here has already been tested in the studies by Parr et al. (2016) in African
139 savannas, and Griffiths et al. (2018) carried out in Bornean forests and has no detrimental effect
140 on animal groups other than ants. In addition, we took measures to minimise or remove any
141 possible effect on other non-target organisms and the environment (please see Appendix S2 for
142 details). To minimise the use of chemical baits, we monitored ant abundance monthly, and
143 reapplied the baits when ant activity in suppression plots was 20% of the control plots (Appendix
144 S2: Figure S1).

145 *Monitoring ant abundance*

146 To monitor ant activity, we used two methods: i) baiting and ii) pitfall trap approaches.
147 The baiting method gave us rapid estimates of ant activity and allowed us to compare the effect
148 of ant suppression between each pair of control and ant suppression plots monthly. We used the
149 baiting method exclusively to know when to repeat the application of ant suppression baits (ant
150 activity in suppression plots was 20% of the control plots). However, to quantify the effects of
151 the ant suppression treatment more accurately on ant numerical abundance between habitats and
152 treatments, we used the pitfall trap method. The pitfall method is more accurate because it stays
153 longer in the field (48 h), can capture a larger spectrum of ant foraging behaviours and provides a
154 more robust measure of ant abundance.

155 We monitored ant activity using the baiting methods every month for four months in each
156 experimental area by setting three linear 50-m transects apart 25 m from each other. Each
157 transect had three sampling stations, where we placed 0.3 g of the homemade bait (catfood
158 without Imidacloprid) onto three white laminated cards (10 × 10 cm), each separated by 25 m.
159 After one hour, we inspected and counted the number of ants on the card. Following the ant

160 count, we promptly removed the cards and baits to eliminate/minimise any potential interference
161 of ant monitoring with other experiments. To estimate the ant suppression, we monitored the ant
162 activity simultaneously on an ant suppression and its respective control plot.

163 We sampled ants with pitfall traps in March 2020, 91 days after initiating ant
164 suppression, immediately following the completion of the resource removal experiment
165 (described below). We used nine pitfall traps per plot arranged in three linear equidistant
166 transects. Each pitfall trap consisted of 350 ml containers (8 cm diameter) buried flush with the
167 ground level and 1/3 filled with a solution of water and detergent. Pitfall traps remained in the
168 field for 48 h, then we filtered their solution placed the collected invertebrates in a 70% alcohol
169 solution. In the lab, we counted and identified the ants to species/morphospecies and other
170 invertebrates to order level.

171 *Resource removal*

172 To perform the resource removal trials, we followed the experimental design used by
173 Griffiths *et al.* (2018). We set 40 stations per plot equally divided into: 20 stations with 2 g of
174 dried *Tenebrio molitor* larvae (hereafter: animal bait) and 20 with 3 g of crushed sunflower
175 seeds (*Helianthus annuus*; hereafter: seed bait). The baits were used to mimic natural resources
176 used by scavengers. Moreover, baits used also differ in their origin, animal and plant, and
177 nutritional composition (Appendix S3: Table S1), with insect larvae being N-rich (53% protein,
178 30.8% fat and ~0% carbohydrates) and seed bait C-rich (18.7% protein, 44% fat and 6.11%
179 carbohydrates). We oven-dried all baits at 50°C for 48h and weighed all resources before placing
180 them in the field (Initial dried weight). Reducing animal bait weight was necessary because,
181 unlike seeds, this bait has a lower density, resulting in a larger volume.

182 We also covered half of the stations with metal cages (cage dimension= 20 diameter × 20
183 height, mesh = 1 × 1 cm) to prevent vertebrates from accessing the resources. Each station
184 consisted of an open petri dish (6 cm width; 0.5 cm depth) where we randomly placed one of the
185 two food sources and covered it with metal mesh cages (caged stations) or not (open stations).
186 With this design in combination with our ant suppression plots, we could separately estimate the
187 resources removed by: *Non-ant invertebrates* = bait mass removed in caged stations in ant-
188 suppression plots; *Vertebrates* = the difference between bait mass removed by the whole
189 community (open stations in control plots) and bait mass removed by invertebrates (caged
190 stations in control plot) and *Ants* = the difference between bait mass removed by invertebrates
191 (caged stations in control plots) and bait mass removed by non-ant invertebrates. Moreover, we
192 checked the functional redundancy of vertebrates, ants, and non-ant invertebrates in scavenging,
193 by comparing the relative (rather than absolute) contribution of each animal group in removing
194 C-rich and N-rich baits in forests and grassland. To calculate the relative contribution of each
195 group, we used the same estimation method presented above regarding the total amount each bait
196 removed. It is important to note that because we were unable to eliminate all ants from our ant
197 suppression plots, our estimation of the role of ants in this process is conservative, and their
198 actual contribution is likely to be greater than that demonstrated here.

199 The stations were placed on the floor 5 m apart from each other in six equidistant transects
200 within the 50 x 50 experimental plots. All stations were protected from the rain by a plastic cover
201 and left in the field for 24 hours. After, we took the bait to the lab oven-dried them at 50°C for
202 48h and weighed them to access the final dried weight. To calculate the mass of the resource
203 removed, we subtract the final dried weight of each bait from its initial dried weight. The
204 scavenging experiment took place in March 2020, 90 days after we began the ant suppression.

205 *Statistical analyses*

206 We evaluated the success of ant suppression in each habitat (grassland/forest) using a
207 Generalized Linear Mixed Models (GLMM) with a negative binomial error distribution. Ant
208 suppression treatment (control/suppression) and habitat were set as explanatory variables, the
209 number of ants collected in pitfall traps was selected as the response variable, and the plot
210 identity as a random effect. We used the negative binomial error distribution to correct for the
211 overdispersion presented by the Poisson error distribution.

212 To test whether the habitat type (grassland/forest), ant suppression treatments
213 (control/suppression), cages (open/caged), bait type (dead insect larvae/seeds) and their potential
214 interactions on resource removal, we used a Generalized Linear Mixed Model (GLMM) with
215 Binomial distribution. To account for initial mass differences between bait types, we used the
216 proportion of bait removed as our response variable and included the initial dry mass of each bait
217 as weight in our model. We included ant suppression, habitat, cages, and bait type as explanatory
218 variables and plot identity as a random effect.

219 We conducted all analyses in R v 4.1.2 (Crawley 2013, R Core Team 2021). We
220 graphically examined the residuals for model assumptions, including normality of errors and
221 homogeneity of variances, to assess model suitability in all models using the package DHARMA.
222 We used the lme4 package v 1.1-12 to build GLMM. We computed the significance of each
223 model using type II Wald chi-square tests, “*mixlm*” package v 1.2.3 (Liland 2018). We used a
224 backward model selection approach based on likelihood ratio test to determine the simplest fitted
225 models.

226 Results

227 We collected 1464 ants (Forest = 900; Grassland= 564) from 49 morphospecies (22
228 genera) from the pitfall trapping: 33 morphospecies in the grassland and 31 in the forest with
229 distinct species compositions (Appendix S4). We suppressed a similar proportion of ants in both
230 habitats: ant suppression plots had 73% and 70% fewer ants than control plots in the forest and
231 grassland, respectively (forest control= 14 ± 12.46 mean \pm SD ants/pitfall, forest suppression =
232 3.9 ± 2.9 ants/pitfall; Grassland control= 26.8 ± 16.7 ants/pitfall, Grassland suppression = 8 ± 5.25
233 ants/pitfall; Chi= 72.7; $P < 0.01$). The average number of ants per pitfall in control and
234 suppression plots combined was twice as high in the grassland than in the forest (grassland=
235 17.3 ± 15.39 ants/pitfall; forest = 7.94 ± 7.02 ants/pitfall; Chi= 22.25, $P < 0.01$; Figure 2). Finally,
236 numerically dominant genera (e.g. *Linepithema*, *Pheidole* and *Ectatomma*) were more affected
237 by suppression (Appendix S2: Figure S2-S3).

238 All variables influenced the proportion of bait removed. Habitat type (forest/grassland;
239 Chi = 18.54, $P < 0.01$), ant suppression treatment (ant suppression/control; Chi = 16.61, $P < 0.01$),
240 bait type (dead insect larvae/seeds ; Chi = 33.52, $P < 0.01$), and cage treatment (caged/open; Chi
241 = 7.9, $P = 0.004$). In 24 hours, 23.2% more bait mass was removed in forests than in grasslands;
242 24% more baits were removed in control plots than in ant suppression plots, and 18.9% more
243 dead insect larvae were removed than seeds (Figure 3, figure 4A, Appendix S3). The effect of
244 ant suppression on scavenging activity was consistent between habitats (Chi = 1.07, $P = 0.29$),
245 resulting in 27.02% and 23.36 % more removal in control than ant suppression plots in forest and
246 grassland, respectively. We found a statistical interaction between habitat and bait type (Chi=
247 52.12, $P < 0.01$), showing that removal of dead insect larvae baits was higher in forests than in
248 grassland, while removal of seeds in forests and grassland did not differ (figure 4A). The

249 interaction between ant suppression treatment and bait type ($\text{Chi} = 7.58, P = 0.005$), indicates that
250 the effect of ant suppression on bait removal was greater for dead insect larvae than for seeds
251 (figure 4A, Appendix S3).

252 The difference between bait mass removed in closed stations in control plots (resources
253 available to all invertebrates only) and open stations in control plots (full community access)
254 suggests that vertebrates play a minor role in resource removal in both habitats, being
255 responsible for $\sim 4\%$ and 3% of removals in forest and grassland respectively (Figure 4A). On the
256 other hand, non-ant invertebrates removed 65% and 40% of baits in the forest and grassland,
257 respectively (caged stations in suppression plots). Finally, to estimate the contribution of ants to
258 scavenging activities, we subtracted the resources removed at caged stations in suppression plots
259 (mostly non-ant invertebrates) from the scavenging activity observed at caged stations in control
260 plots (where resources are accessible to all invertebrates). Using this estimation, we found that
261 ants removed at least 31% of baits in forest and 57% in grassland. However, our figures on bait
262 mass removal are likely to be underestimated for ants and overestimated for non-ant
263 invertebrates as we could not remove the whole ant community from suppression plots (the
264 average ant suppression was 70% , Figure 2).

265 For the relative contribution of each animal group to bait removal in each habitat, we
266 found that in forests, the removal of dead insect larvae was led by non-ant invertebrates (69.2%),
267 followed by ants (27.1%) and vertebrates (2%). While in grassland, ants were responsible for
268 57.7% of the removal of dead insect larvae, followed by non-ant invertebrates (37.6%) and
269 vertebrates (4.7% , Figure 4b). Nearly half of the seeds were removed in both habitats, and the
270 contribution of each animal group was similar to the removal of dead insect larvae, with non-ant
271 invertebrates (61.3%) leading the removal of seeds in the forest, followed by ants (35.7%) and

272 vertebrates (5.6%). Whereas, in grassland, ants were the main removers of seeds (57.3%),
273 followed by non-ant invertebrates (40.8%) and vertebrates (1.9%, Figure 4b). Although overall
274 small, the contribution of vertebrates to the removal of seeds was three times higher in forest
275 (5.6%) than in grassland (1.9%).

276 **Discussion**

277 Here, we experimentally quantified simultaneously the relative contribution of ants, non-
278 ant invertebrates and vertebrates in scavenging insect carcasses and seeds in two adjacent and
279 contrasting natural habitats (grassland and forests). Considering the entire scavenging community,
280 we found less bait removal in the grassland than in the forest. Ants were the primary scavengers
281 of invertebrate carcasses and seeds in grassland, non-ant invertebrates were the main ones in
282 forests, while vertebrates had a minor role in both habitats. Although the relative contribution of
283 ants varied between habitats, their role in scavenging was not replaced by any other group when
284 ants were absent (i.e. seldom functional redundancy). This finding highlights the importance of
285 ants in this crucial ecosystem process and indicates that ant prevalence can indirectly affect
286 community dynamics and ecosystem structure (Parr et al. 2016, Griffiths et al. 2018). Finally, we
287 showed that the scavenging on animal baits in forests was twice as high as seeds (plant-based
288 baits), while there was no difference in removal between bait types in grassland. As such, we bring
289 new insights into the role of three animal groups in maintaining key ecosystem processes and
290 further our understanding of differences in ecosystems functioning among habitats.

291 Our finding that 50% and 73% of the baits were removed in 24h in grassland and forest,
292 respectively, illustrates how fast and efficient the scavenging process can be. Scavenging small
293 detritus (e.g. dead invertebrates and seeds) may play a significant role in ecosystem nutrient flux
294 because at least half of the resources were rapidly taken by scavengers and not directly

295 decomposed. Moreover, the impact of scavengers on nutrient removal was stronger in forests
296 than in grasslands (as overall more baits were removed), likely leading to a faster nutrient cycle
297 in forest. While most scavenging studies focus on vertebrate carcasses (DeVault et al. 2003), we
298 show that dead invertebrates and seeds are also essential resources for scavengers. However, the
299 broader implications of our findings should be interpreted with caution because the amount and
300 type of resources that naturally occur in each habitat may also differ.

301 Invertebrates were responsible for virtually all scavenging of small resources (e.g.
302 invertebrate carcasses and seeds) in both forest and grassland, while vertebrates have a minor
303 contribution to this process. Among invertebrates, ants had a higher relative importance in
304 scavenging in grassland and non-ant invertebrates in the forest. Thus, we support our prediction
305 that ants are more critical for scavenging in grassland than in forest habitats. Following previous
306 studies (e.g., Bucy and Breed 2006, Andersen 2019), we suggest that the difference in ant
307 scavenging between habitats is related to high ant abundance and ground activity in open habitats
308 (grassland) compared with close habitats (forests; Figure 2). The habitat openness also enhances
309 ants' role in other ecosystem processes. For example, Jones *et al.* (2017) showed that ant
310 protection against plant herbivory is higher in patches with greater insolation.

311 Ants are social insects, mostly living in fixed colonies, usually with hundreds of
312 individuals (Beckers et al. 1989). When foraging, ants typically take the food source to their
313 colony before consuming it (Hölldobler and Wilson 1990). This characteristic behaviour
314 contributes to the redistribution and concentration of nutrients in ecosystems, increasing the
315 nutrients in the nest area (e.g., N, P, organic matter; Farji-Brener and Werenkraut 2017).
316 Consequently, the concentration of nutrients on ant nests can increase environmental
317 heterogeneity and impact soil biota and plant communities (Farji-Brener and Werenkraut 2017,

318 Swanson et al. 2019, Lash et al. 2020). Conversely, non-ant invertebrate scavengers, such as
319 beetles and cockroaches observed in the monitoring baits and in the pitfall traps (Appendix S5),
320 are solitary foragers that could either consume it on the site or remove small portions of the
321 source (Durier and Rivault 2001, Ilardi et al. 2021). Therefore, ant and non-ant invertebrates may
322 have different outcomes for ecosystem scavenging dynamics and nutrient cycling, with ants
323 promoting greater heterogeneity of nutrients. We might therefore expect soil nutrients to be
324 patchier in grassland, where ants are the main scavengers, than in forests where non-ant
325 invertebrates are the main ones. The nutrient patches created by ants could ultimately influence
326 the plant community dynamic by increasing plant performance and survival (Farji-Brener and
327 Werenkraut 2017). The effect of nutrient patches could be especially pronounced in *campo*
328 *rupestre* because soils in this habitat are particularly nutrient-poor (Silveira et al. 2016).

329 Scavenging of dead insects and seeds in both habitats studied was lower on ant
330 suppression plots. According to the redundancy hypothesis, species loss should not affect
331 ecosystem processes if there are functionally similar taxa capable of replacing them in
332 performing those processes (Grime 1997, Yachi and Loreau 1999). We experimentally
333 demonstrated a low functional redundancy regarding the importance of ants in the scavenging
334 process in the mountain habitats studied here (Figure 3 and also supported by Griffiths et al. 2018
335 and Walker et al. 2024 in other tropical environments). In the absence of ants, no other taxa
336 could compensate for the reduction in ants. Because of their great diversity and abundance, ants
337 are key actors in many ecosystem processes (del Toro et al. 2012). Therefore, the lack of
338 functional redundancy of ants as scavengers may also extend to other ecosystem processes
339 dominated by ants.

340 By consuming resources, vertebrates usually transport and deposit nutrients and seeds
341 over much longer distances than invertebrates (Beasley et al. 2019, Potapov et al. 2022).
342 Consequently, they spread nutrients at the landscape level and connect ecosystems through the
343 nutrient flux (DeVault et al. 2003, Almeida-neto et al. 2008). However, the limited role of
344 vertebrates in scavenging the small baits we used in our experiment (<4% of removal) could
345 mean there is low nutrient transport across large distances or even among ecosystems. In contrast,
346 Griffiths et al. (2018), using a similar experimental design, found that the role of vertebrates in
347 scavenging in a Bornean rainforest is five times higher than we found here (25%). This disparity
348 may also be attributed to a relatively low vertebrate relative abundance within the confines of our
349 experimental sites, which are situated at high elevations in tropical mountainous regions, and the
350 forest patches tend to be small (average of 77141 m², Brant et al. 2021). Consequently, the lack
351 of vertebrates can limit the import and export of nutrients in those ecosystems and affect other
352 ecosystem processes and services related to this group (e.g. seed dispersal and biological
353 control).

354 Considering the entire scavenger community, our study suggests that nitrogen may be
355 more limited in forests than carbon, whereas both nutrients appear to be equally limited in
356 grasslands. Most terrestrial organisms are assumed to be limited by nitrogen availability (White
357 1978). According to the Resource-ratio theory (Tilman 1982), consumers achieve optimal ratios
358 of complementary nutrients (Grover et al. 2007, Ribeiro et al. 2019). Here, we showed that there
359 was no difference in the N-rich and C-rich baits removal proportion in grassland, indicating that
360 both nutrients might equally limit those communities. The *campo rupestre* is a nutrient-poor and
361 moisture-limited environment, so plant development is mostly slow (Silveira et al. 2016), thus
362 the production of reliable C sources available to animals (fruit, nectar, seeds) tends to be small

363 and/or sporadic (Silveira et al. 2016, Hopper et al. 2021). Conversely, scavengers removed
364 animal-based baits rich in nitrogen (N) almost twice as often as they removed plant-based C-rich
365 baits, which suggests the possibility of N-limitation in this forest habitat. However it is important
366 to acknowledge that grasslands generally host a higher density of granivores compared to forests,
367 which results in seeds being more prone to scavenging in grasslands than in forests, this dynamic
368 may also contribute to the removal rate of seed removal observed in our study.

369 Here, we experimentally support E.O. Wilson's statement (1987): "the little things that
370 run the world" by showing that invertebrates rule the scavenging of small resource patches in
371 two contrasting tropical mountainous habitats (grassland and forests). Invertebrates are an
372 overlooked scavenging group, but we showed that they remove more than half of all baits offered
373 in forests and grasslands within 24 hrs. Our results suggest that most non-living insects or seeds
374 may be consumed by invertebrate scavengers rather than decomposed. In such a way, nutrients
375 are rapidly recycled and inserted back into the trophic chain. We also show a minor contribution
376 of vertebrates in this process, which could limit the long-distance import and export of nutrients
377 in these mountainous ecosystems. Furthermore, a single animal group, the ants, was responsible
378 for most of the scavenging of small-sized resources in mountainous grassland but not in forests,
379 suggesting the possible dominance of this group in governing processes in this open montane
380 habitat. Knowing that ants can be especially important in open habitats, human activities that
381 affect the ant community (e.g. change in land use and climate change), especially their
382 abundance, would greatly affect non-forest ecosystems. However, further studies across other
383 habitats, including in different forests and grasslands, are needed to assess if the key importance
384 of ants in scavenging is also applied to lowland environments. Finally, we further advance our

385 knowledge on the relative importance of three major groups in scavenging and the differences in
386 ecosystems functioning between two contrasting tropical habitats.

387

388

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403

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563

564

565 **Figure captions**

566 **Figure 1.** Study sites at Serra do Cipó National Park, Minas Gerais state, Brazil. A) *campo*
567 *rupestre* (rocky grassland) and B) tropical montane forests islands surrounded by *campo rupestre*
568 matrix. Photos by Ricardo Solar

569 **Figure 2.** Number of ants per pitfall trap in ant suppression plots (suppression) and control plots
570 set in two mountainous habitats in southeast Brazil, forest (montane rainforest) and Grassland
571 (*campo rupestre*). Pitfall traps were set 90 days after the beginning of ant suppression. Statistical
572 differences are represented by different letters. Black points represent average and lines standard
573 errors of groups.

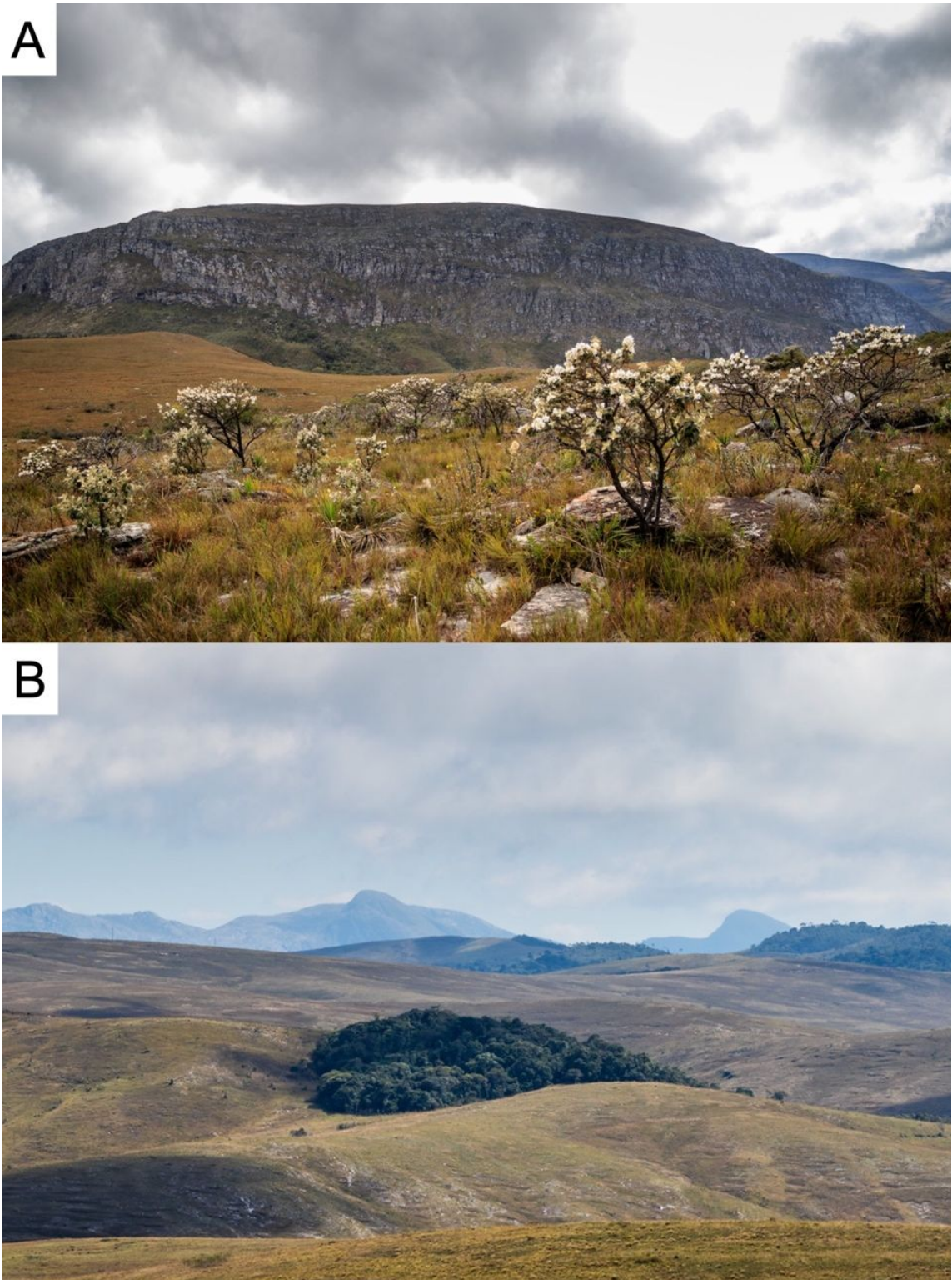
574 **Figure 3.** Proportion of **A)** Larvae (2 g of *Tenebrio molitor* larvae) and **B)** Seeds (3g of
575 sunflower seeds) removed per station according to ant suppression (suppression/control) and
576 caged treatments (caged/open) in two mountainous habitats in southeast Brazil montane
577 rainforest forest and Grassland (*campo rupestre*). Horizontal lines represent average, and boxes
578 show standard errors. Statistical differences are represented by different letters.

579 **Figure 4.** Estimations of *Tenebrio molitor* larvae (N-rich) and sunflower seeds (C-rich) removal
580 by ants, non-ant invertebrates and vertebrates in forest and grassland **A)** Proportion of mass
581 removed from the total offered (Larvae 2g, Seeds 3g) **B)** Relative contribution of each animal
582 group to mass removal, based on the total removal for each bait type in each habitat. By:
583 VERTEBRATES= the difference between bait mass removed in open stations in control plots
584 and bait mass removed in caged stations in control plot; ANTS = the difference between the bait
585 mass removed in caged stations in control plots and bait mass removed in closed stations in ant-
586 suppression plots; NON-ANT INVERTEBRATES = bait mass removed in caged stations in ant-

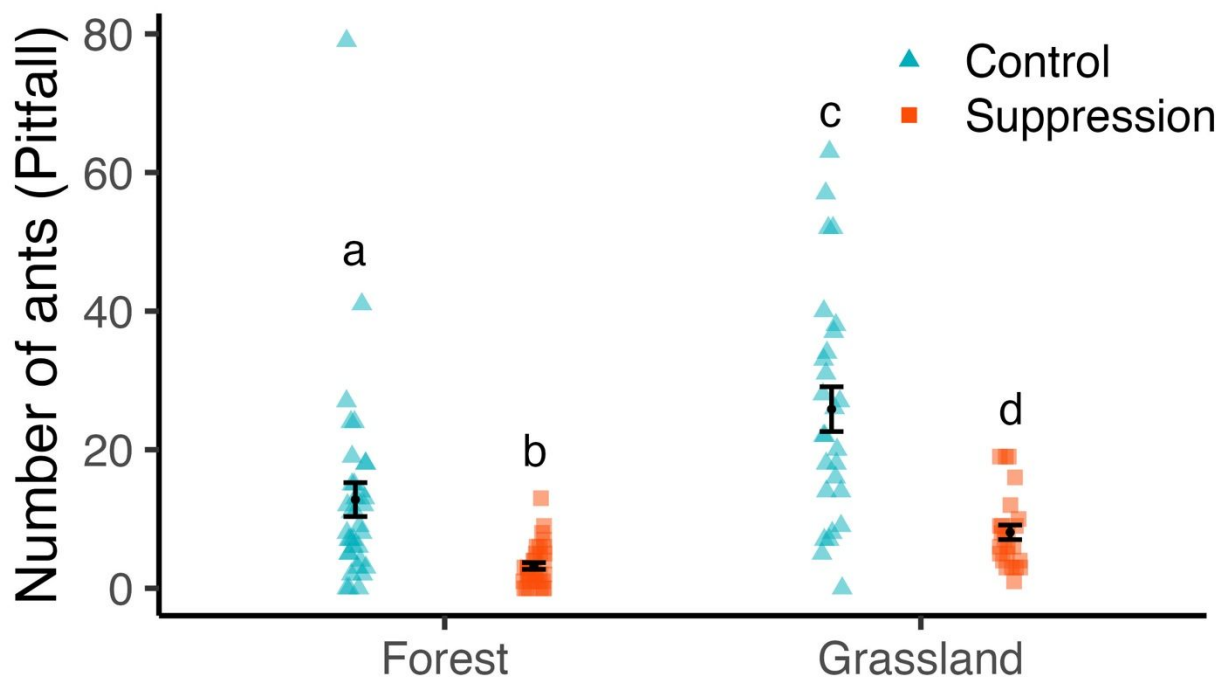
587 suppression plots. Icons were designed by Flaticon and are used with permission from
588 www.flaticon.com.

589 **Figures**

590 **Figure 1:**



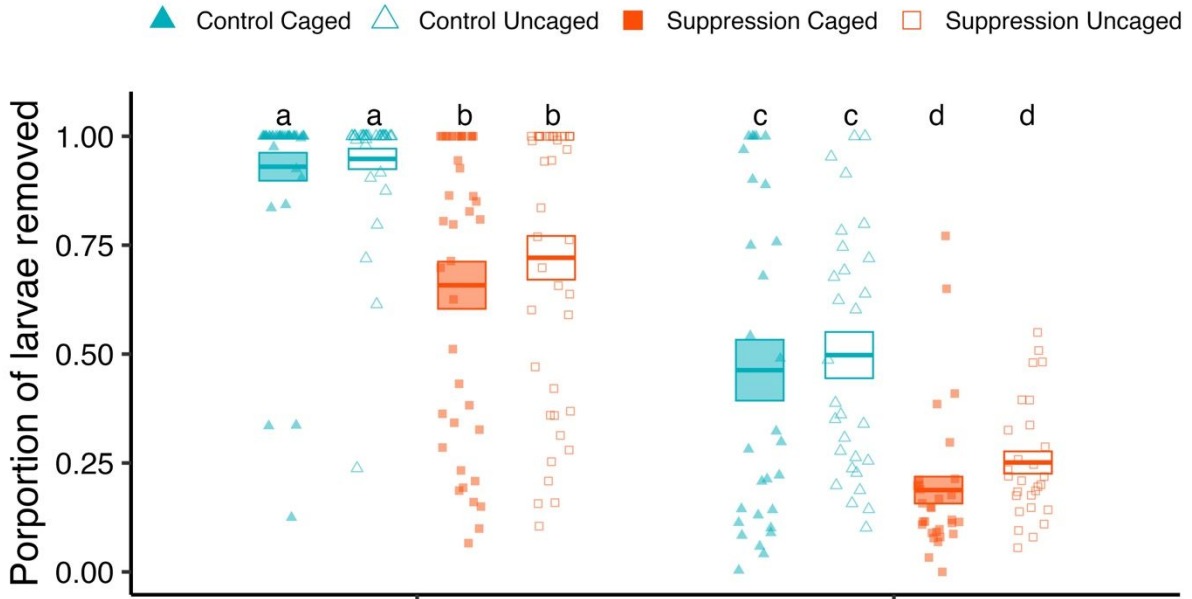
592 **Figure 2**



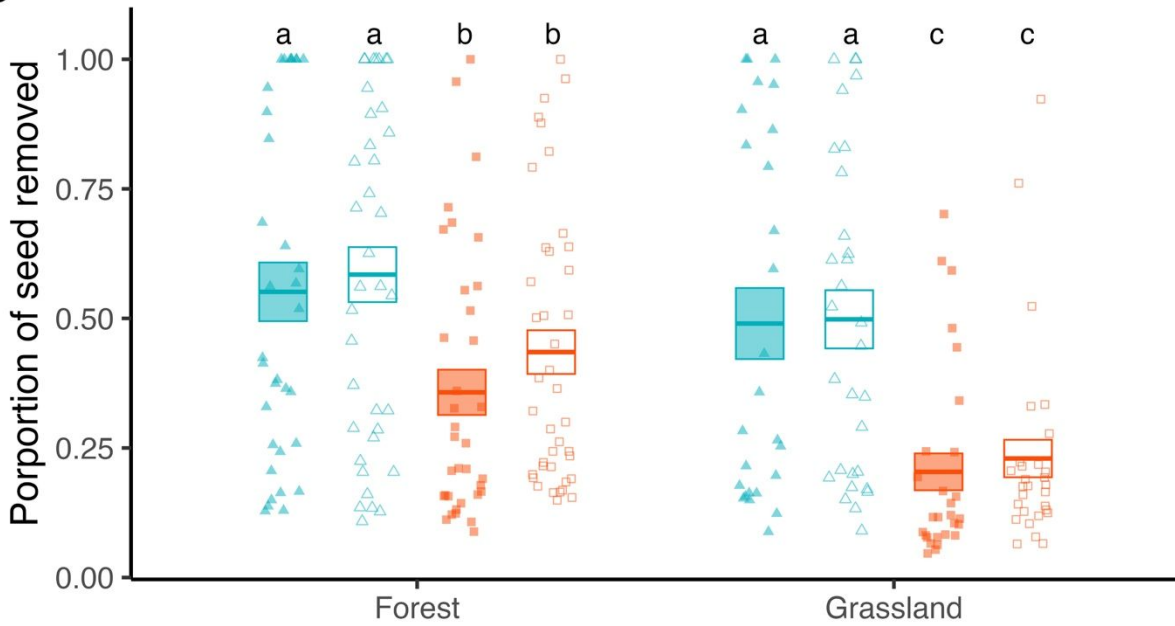
593

594 **Figure 3:**

A

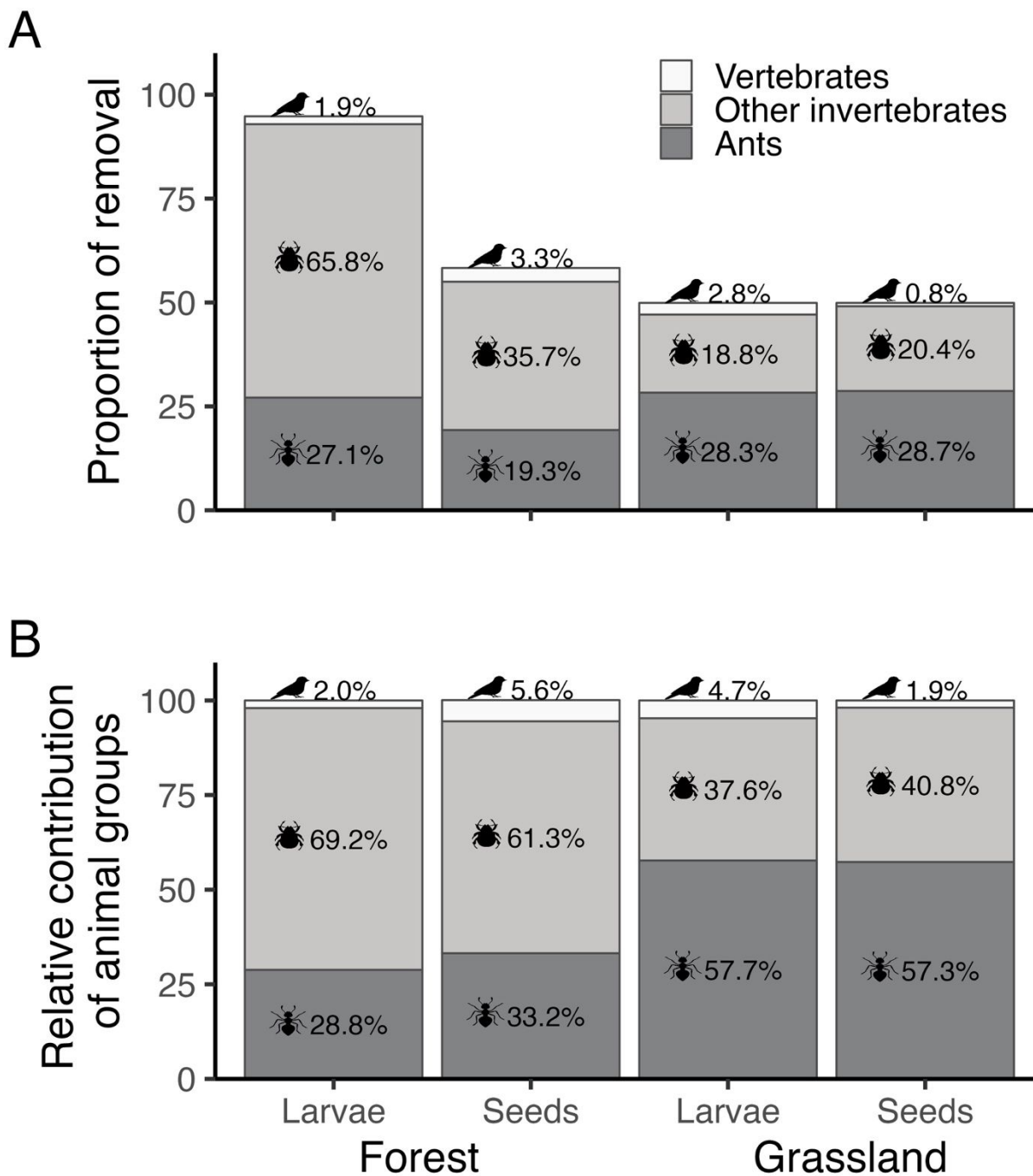


B



595

596 **Figure 4:**



597