

1 Carabid beetles of tropical dry forests display traits that cope with a harsh environment

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3 Short title

4 TDF Carabid beetle trait distribution in a harsh environment

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22 Abstract

23

24 The tropical dry forest (TDF) ecosystem is characterized by strong seasonality exasperated  
25 periodically by the El Niño/southern oscillation (ENSO). The environment produced by this event  
26 could constrain the survival of small organisms, such as insects. Carabid beetles were collected in a  
27 TDF in Armero, Colombia, during wet and dry seasons in both El Niño and non-El Niño periods. A  
28 series of traits linked to desiccation resistance were measured to characterize their adaptation to the  
29 TDF environment and to investigate changes experienced by carabid beetles during both episodes in  
30 quantitative (assemblage) and qualitative (traits) parameters. We found no difference in the  
31 presence of traits between El Niño and non-El Niño episodes, but carabid assemblages changed  
32 significantly in composition and assemblage structure between these episodes. During both periods,  
33 small-sized and nocturnal species dominated the assemblages, but in terms of number of  
34 individuals, medium and large-sized, and visual hunter species dominated. *Calosoma alternans* and  
35 *Megacephala affinis* were the most abundant species with high dispersal capacity. Carabid beetles  
36 exhibited morphological traits well-adapted to drought experienced in TDF, including when it is  
37 exasperated by ENSO. However, long-term studies can help to elucidate the real effects of ENSO  
38 and to confirm the adaptation of carabid beetles to cope with this extreme environment.

39

40 Keywords

41 Drought, ENSO, ground beetles, insects, Neotropical, traits

## 42 1. Introduction

43

44 The tropical dry forest (TDF) ecosystem is characterized by strong seasonal rainfall with four to six  
45 dry months (Murphy and Lugo 1986), making the availability of moisture crucial to the survival of  
46 organisms (Maass and Burgos 2011). These natural fluctuations between wet and dry periods  
47 throughout the year are exasperated by the El Niño/southern oscillation (ENSO). In South America,  
48 ENSO is characterized by high temperatures and low precipitation (Poveda et al. 2000), as has  
49 happened in 2015/2016, which was one of the strongest ENSO episodes on record of the 21<sup>th</sup>  
50 Century (Luo et al. 2018). ENSO can be critical for the maintenance of the TDF ecosystem,  
51 considering its effects on plant and animal communities (Holmgren et al. 2001) species can face  
52 local or global extinction if their populations do not have sufficient time to recover between ENSO  
53 episodes (Charrete et al. 2006). For tropical insects, ENSO has shown strong community effects.  
54 For example, Chrysomelidae beetles experienced a considerable loss of species during the event,  
55 with partial population recovery after the dry period (Kishimoto-Yamada and Itioka 2008;  
56 Kishimoto-Yamada et al. 2009). For butterflies, ENSO's effects can vary due to temporal migratory  
57 responses to drought (Srygley et al. 2010, 2014). Evidence exists that Cantharidae decrease in  
58 species richness due to this climatic event in TDF (Pérez and Zaragoza 2016). In general, it appears  
59 that the responses of insects to ENSO are related to resources, which are indirectly affected by the  
60 weather (White 2008).

61 The configuration of insect bodies (high surface area/volume ratio) puts an additional  
62 constraint to the persistence and success of species in this environment (Schowalter 2006). As such,  
63 an insect's survival in ENSO-affected TDF landscapes will not only depend on their behavioural  
64 adaptations, but also their morphology (Cloudsley-Thompson 1975; Crawford 1981), and the  
65 effectiveness of those adaptations will contribute to the persistence of species (Chown et al. 2011).  
66 Species traits have become an important tool to predict the presence and persistence of species in

67 the environment (Keddy 1992; Cadotte et al. 2011; Kraft et al. 2015). Carabid beetles have a wide  
68 range of traits linked to environment conditions (Homburg et al. 2014; Fountain-Jones et al. 2015),  
69 yet knowledge regarding this group's traits are lacking in the tropics. Changes in the environment,  
70 as a result of disturbance, can play an important role in filtering traits in ground beetles (Shibuya et  
71 al. 2011; Pakeman and Stockan 2014; Piano et al. 2017; Magura and Lövei 2019; but see Kraft et al.  
72 2015). ENSO is a recurring event in the TDF landscape (Caviedes 2001; Grove and Adamson  
73 2018), and is likely to have had a strong filtering effect on insect communities (see Kotze and  
74 Lawes 2007; Meir and Pennington 2011). If this is the case, species in this landscape are expected  
75 to display traits that cope with harsh conditions, but abundances may fluctuate substantially  
76 between wet and dry periods, particularly so during ENSO events.

77         The aims of this study were to characterize the responses of TDF carabid beetles, in terms of  
78 drought tolerance, by investigating changes in TDF carabid assemblages during a period of El Niño  
79 (2015) and non-El Niño (2016) in both (1) quantitative assemblage parameters (number of species  
80 and abundances) and (2) qualitative parameters (trait dominance). We hypothesise that carabid  
81 species that are larger in size and with functional wings are well-adapted to drought episodes in the  
82 TDF ecosystem. A larger beetle body has a lower surface area-to-volume ratio, conferring to  
83 desiccation resistance (Hood and Tschinkel 1990; Chown et al. 1995; Le Lagadec et al. 1998),  
84 while macroptery – a dominant trait in unstable habitats – facilitates an individual's escape from  
85 unfavourable conditions (Darlington 1943; Venn 2016). On the other hand, smaller bodied beetles  
86 can benefit from this environment for other reasons, including a broader selection of prey to satisfy  
87 their energetic requirements and protection against predators (Blanckenhorn 2000; Chown and Klok  
88 2003). As such, we expected small-sized carabid beetles of elongate or narrow form, fossorial legs  
89 and/or nocturnal habits to be able to escape the risk of water loss (Forsythe 1987; Erwin 1979;  
90 Bauer and Kredler 1993; Bauer et al. 1998) in the TDF landscape. These smaller species are also  
91 expected to have a long metatrochanter to aid in mobility through confined habitats (Forsythe

92 1981). In terms of flight, even though macroptery is beneficial, flight is energetically expensive,  
93 especially during periods of limited resources (Nelemans 1987). Finally, a relationship between  
94 coloration and thermoregulation in carabids have been observed in the Palearctic zone, where a dark  
95 dorsal surface is beneficial to gain heat (Schweiger and Beierkuhnlein 2016); as such, we expect  
96 that most species in this hot landscape would have lightly coloured bodies. However, colour could  
97 have a minor role in thermoregulation in TDF carabids but a prominent role in predation avoidance,  
98 due to the prominence of predator avoidance behaviour in ground beetles, although it implies some  
99 thermal cost (Schultz 1986; Hadley et al. 1988, 1992).

100         Quantitatively, we expect a decrease in carabid beetle species richness and abundance  
101 during the El Niño episode in Colombia TDF, similar to what occurred in Ecuadorian Amazonian  
102 rain forests (Lucky et al. 2002). Drought produced by ENSO may stimulate a diapause and escape  
103 response in some species to avoid desiccation and thus diminish their temporal occurrence (Dingle  
104 1972; Lövei and Sunderland 1996; Venn 2016). We presume temperature and moisture act as clues  
105 to start and end diapause during an ENSO episode (Cloudsley-Thompson 1975; Wolda and  
106 Denlinger 1984; Tauber et al. 1998; Hodek 2003, 2012). This means that species richness and  
107 abundance can decline drastically during drought events, but can also recover in relatively short  
108 time scales when precipitation returns. However, we do not suspect drastic changes in trait  
109 dominance between these two climatic states due to the strong adaptation to drought that organisms  
110 show in TDF (Dirzo et al. 2011; Pizano and García 2014; Pulla et al. 2015).

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112

## 113 2. Material and Methods

114

### 115 2.1 Study area

116

117 Ground beetles were surveyed in the dry forest biome in Armero (Tolima), Colombia (Fig. 1).  
118 Average temperatures during the surveys were 45 °C and 35 °C for the El Niño dry and wet seasons  
119 respectively, while the non-El Niño dry and wet seasons were around 30 °C. Air humidity were 36  
120 % (dry season) and 61 % (wet season) during the El Niño episode and around 70% during the non-  
121 El Niño period (see Supplementary information 1). Given the current fragmented status of tropical  
122 dry forest and that the mostly dry forest of the Valley of Magdalena River in Colombia are  
123 immersed in a mosaic of pastures and areas at different successional stages (Pizano et al. 2014,  
124 2016), we characterised the beetle assemblage and their traits in the TDF landscape by sampling  
125 three dominant habitat types: five forest patches (see F1–5 in Fig. 1b), four early successional  
126 patches (3-7 years of age, ES1–4) and three pastures (P1–3). The minimum distance between any of  
127 the 12 sites was 240 m.

128

## 129 2.2 Carabid beetle sampling

130

131 Carabid beetles were collected during an El Niño (2015) and non-El Niño (2016) event. During  
132 each period (El Niño and non- El Niño), beetles were collected in one month during the dry season  
133 (September) and one month during the wet season (October). Ten pitfall traps of 300 ml with water  
134 plus a few drops of detergent were used at each site to collect the ground beetles. The traps were  
135 installed 10 m apart along a transect of 100 m, and were operated continuously for three days per  
136 month. Each transect was at least 20 m from the edge of the site to minimize edge effects. Adult  
137 carabid beetles were identified to genus level using Martínez (2005), and to species level using  
138 Dejean (1829, 1831); Putzeys (1846, 1866); Reichardt (1967); Ball and Shpeley (2002, 2009);  
139 Vitolo (2004); Will (2005) and Bruschi (2010). However, due to the scarcity of taxonomic keys for  
140 the Neotropics, some of the identifications at species level should be confirmed. Voucher specimens  
141 are deposited in the Entomological Museum of the Universidad del Tolima, Colombia (MENT-UT).

142

### 143 2.3 Trait measurements

144

145 Based on a literature review, a series of traits related to the adaptation to desiccation were measured  
146 (Supplementary information 2). Information about the ecology and dispersal power (at genus level)  
147 were obtained from Laroche and Larivière (2003), Vitolo (2004), Martínez (2005) and Will  
148 (2005). However, in an attempt to develop ecological information at species level, a set of traits  
149 were measured from the specimens collected to deduce habit and microhabitat use: desiccation  
150 resistance, daily activity time (nocturnal, diurnal), microhabitat use (burrowing habit and capacity  
151 to shelter in confined habitats, fast runner, slow runner), and dispersal capacity (high, low) (Table  
152 1). The specimens collected were mounted on an entomological pin, and photographed with a  
153 Canon camera (PowerShot SX200 IS) through a stereomicroscope (Motic SMZ-168).  
154 Measurements were taken with ImageJ 1.52k software (Schneider et al. 2012). Ten individuals per  
155 species were used for measurements (means were used), unless fewer than 10 individuals were  
156 collected, in which case all of the individuals were measured (see Supplementary information 3).  
157 The ratio between traits that involves size and body length was used to compare between species.  
158 For the capacity to shelter in confined spaces (microhabitat use), the ratio between prothorax width-  
159 depth and abdomen width-depth was used. The range of measures to classify and characterize  
160 certain attributes were from Forsythe (1981, 1987) and Bauer and Kredler (1993). Flight muscle  
161 development was determined by comparing the flight muscles of specimens to the flight muscle  
162 figures in Desender (2000).

163

### 164 2.4 Data analyses

165

166 We used the  $\chi^2$  test in Past 3.x (Hammer et al. 2001) to compare the distribution of each trait among  
167 the El Niño and non-El Niño episodes.

168

169

### 170 3. Results

171

#### 172 3.1 Carabid beetle trait characteristics in the tropical dry forest landscape

173

174 The traits of 15 species were measured (Supplementary information 3); *Meotachys* sp. was excluded  
175 due to its small body size (2.2 mm). 73.3% of the species collected were classified as small (4-12  
176 mm), and 26.6% as either medium or large (Table 2). The literature (see Trait measurements section  
177 above) classified 80% of the collected species as nocturnal, 13.3% intermediate (both diurnal and  
178 nocturnal activity) and for one species, daily activity period is unknown. However, the most  
179 abundant species, *Calosoma alternans* and *Megacephala affinis*, were intermediate. All nocturnal  
180 species had short antennae (ANT/BS = 0.28-0.47) except *Galerita* sp., whose antennae were longer  
181 (ANT/BS = 0.62) (Supplementary information 4). Head width also did not show clear differences  
182 between nocturnal and intermediate species, only two species had wide heads; *Barysomus hoepfneri*  
183 (nocturnal, HW/BS = 0.29) and *M. affinis* (intermediate HW/BS = 0.27). On the contrary, eye  
184 surface area reflected behaviour presented in the literature, i.e., nocturnal species had small eyes  
185 (CES/BS = 0.01-0.05) and intermediate species had large eyes (CES/BS = 0.08-0.13).

186 Twenty percent of the species had fossorial forelegs (*Aspidoglossa crenata*, *Clivina* sp. and  
187 *Camptodontus* sp.), and had a prothorax width/abdomen width and prothorax depth/abdomen depth  
188 ratio of almost 1 (Supplementary information 4). Two runner species *Athrostictus paganus* and  
189 *Enceladus gigas* had the same body configurations. In terms of the fore- and hindleg total length,  
190 differences between fossorial and runner species were also clear; these were shorter for fossorial



191 species (Fore-LTL/BS = 0.33-0.41, Hind-LTL/BS = 0.40-0.57): except for the runner species  
192 *Stolonis interceptus*, which had shorter hindlegs and *Apenes morio* and *E. gigas*, which had shorter  
193 forelegs. Most species had a long metatrochanter (73.3%; MTL/BS = 0.09-0.13), but *M. affinis* was  
194 the only species with a long and slender metafemora, long metatibiae and small metatrochanter.

195 Most species were macropterous (80%), however only 41% of these had developed flight  
196 muscles. *Apenes prasinus* was brachypterous and *E. gigas* was apterous. None of the species  
197 collected showed hindwing polymorphism. Also, 80% of the species were dark in body colour and  
198 53% had dark legs. *Apenes coriacea* was unique with a lightly coloured body.

199

## 200 3.2 Assemblage changes between El Niño and non-El Niño episodes

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### 202 3.2.1 Distribution of species

203

204 Sixteen carabid beetle species (70 individuals) were collected; six species (17 individuals) during  
205 the El Niño period, and 14 species (53 individuals) during the non-El Niño period (Table 3). During  
206 the El Niño episode, the most abundantly collected species was *C. alternans*, but during the non-El  
207 Niño episode, only one individual of this species was collected. During the non-El Niño period, the  
208 most abundantly collected species was *M. affinis*, followed by *E. gigas* and *Tetragonoderus* sp.;  
209 these two last mentioned species were not collected during the El Niño event. Despite the low  
210 abundance of carabids, a marked change in assemblage composition and structure was observed.  
211 There is a clear substitution in dominance and the disappearance of many species during the El  
212 Niño period.

213 The wet season during both El Niño and non-El Niño periods had the highest number of  
214 individuals (88% and 71% respectively). Only two species were collected during the dry season of  
215 the El Niño period; *Galerita* sp. and *M. affinis*. During the non-El Niño period, similar numbers of

216 species were collected during the dry (9 species) and wet (10 species) seasons. *Aspidoglossa*  
217 *crenata*, *B. hoepfneri*, *E. gigas*, *M. affinis* and *Tetragonoderus* sp. were present in both seasons.

218

### 219 3.2.2 Distribution of functional response traits

220

221 All measured traits and attributes were present in both episodes, except for light coloured bodies,  
222 which was not present during the El Niño event. The ratios of attributes within each trait during  
223 these two periods, and their significant differences are presented in Fig. 2. During both El Niño and  
224 non-El Niño periods, small-sized species dominated the assemblages, but in terms of individuals,  
225 medium and large-size dominated. In terms of daily activity period, most species collected were  
226 nocturnal (which was also reflected in the traits associated with daily activity period; head width,  
227 antennal length and compound eye surface area), while most individuals were intermediate  
228 (reflected only in compound eye surface area). This applied to both El Niño and non-El Niño  
229 periods. The runner/poor digger trait was dominant during both periods, with long fore- and hind  
230 legs. Short metatrochanter was abundant in the non-El Niño period, so too were metallic body  
231 colour and pale legs. High dispersal capacity, in terms of the proportion of individual collected, was  
232 dominant during both periods.

233

234

## 235 4. Discussion

236

237 Despite the fact that ecological information on tropical carabid beetles is sparse, studies have shown  
238 that there are direct relationships between traits and habits/lifestyles (Forsythe 1983, 1987, 1991;  
239 Talarico et al. 2007). This was also confirmed in our study, which showed that the traits displayed  
240 by carabids are reflective of this group being well-adapted to environmental change experienced in

241 TDF, including when it is exasperated by the El Niño/southern oscillation (ENSO). As predicted,  
242 changes in the assemblage between El Niño and non-El Niño were more quantitative than  
243 qualitative. All traits and attributes (except light body colour) were present during both climatic  
244 episodes and marked changes were perceived in the number of species and individuals, which  
245 recovered relatively fast after the climatic anomaly ended. Most of the carabid species collected  
246 were small and nocturnal, although in terms of numbers of individuals collected, medium and large  
247 sizes and intermediate activity trait attributes were most dominant, contrary to our expectation. It  
248 appears that resource availability is a limiting factor for large-sized species during droughts, while  
249 small-sized species persist in a low-resource environment and benefit from being nocturnal, thus  
250 avoiding desiccation. Similarly, runner species was a dominant trait, but with a long metatrochanter  
251 that reduces the ability to run, yet aids in the species' ability to move through confined spaces or  
252 litter. A long metatrochanter was also present in medium-sized and large species. Almost all species  
253 were macropterous (80%), although only five species showed developed flight muscles, perhaps as  
254 a consequence of limited resources (Nelemans 1987; Nelemans et al. 1989). *Calosoma alternans*  
255 and *M. affinis* were the most abundant species with high dispersal capacity.

256

#### 257 4.1 Quantitative carabid beetle changes between El Niño and non-El Niño periods

258

259 Quantitatively, TDF carabid beetles were affected by El Niño (ENSO), as has happened with other  
260 tropical beetle groups (Lucky et al. 2002; Kishimoto-Yamada and Itioka 2008; Kishimoto-Yamada  
261 et al. 2009; Pérez and Zaragoza 2016). The number of species and individuals decreased more than  
262 two fold during the El Niño period. However, carabids showed differential responses to drought,  
263 similarly to the Chrysomelidae in Borneo during the 1998 ENSO event (Kishimoto-Yamada et al.  
264 2009). In Colombian TDF, 62% of the collected species were not present during the El Niño period,  
265 *C. alternans* was the only species showing a substantial decrease during the non-El Niño period, its

266 numerical decrease could be related to its life span (see Burgess 1911): its larvae were seen in high  
267 numbers in pastures in October and November (Ariza 2016, pers. obs.), however long-term studies  
268 can help to elucidate the life cycle of this species. On the contrary, *M. affinis* benefited considerably  
269 from an improved environment during non-El Niño periods. This fast running and flight capable  
270 species may be particularly vulnerable to desiccation during dry ENSO periods (Pearson and Vogler  
271 2001). In general, the carabid beetle assemblage recovered quickly (within three months after El  
272 Niño ended), which may be due to diapause as an adaptive mechanism to survive harsh conditions  
273 (see Burgess 1911; Jeffords and Case 1987; Jacobs et al. 2011).

#### 274 275 4.2 Carabid beetle trait distribution in the tropical dry forest landscape

276  
277 Even though the carabid beetle assemblage in TDF was dominated by small species, more  
278 individuals of medium and large sized species were collected; the two most abundant species *C.*  
279 *alternans* (large) and *M. affinis* (medium) possibly benefitting from their lower volume-to-surface  
280 area ratio, thus resisting desiccation during dry conditions (Hood and Tschinkel 1990; Chown et al.  
281 1995; Le Lagadec et al. 1998). These species were observed walking during the day (Ariza 2016,  
282 pers. obs.), but are considered to be active both during the day and night (intermediate activity)  
283 (Larochelle and Larivière 2003; Vitolo 2004). Another medium-size species, *Galerita* sp. is  
284 consider nocturnal (Larochelle and Larivière 2003), and is the only nocturnal species of TDF that  
285 meets all the characteristic traits described as typical of this life-style: long antennae, small eyes and  
286 a narrow head (Bauer and Kredler 1993). The rest of the nocturnal species (which are also small)  
287 have short antennae, or at least shorter than *Galerita* sp. and *M. affinis*. However, antennal length  
288 and head width differences between nocturnal and intermediate species groups were small, making  
289 it difficult to characterize daily activity using these traits. Carabid beetles use three methods to  
290 detect prey: visual, tactile and olfactory, or a combination of these; species that do not hunt visually,

291 use their antennae and palps (Wheater 1989). Antennae are an important sensory structure  
292 (Chapman 1998; Ploomi et al. 2003), but it is unclear how prominent its role is in prey detection.  
293 On the contrary, eye surface area has distinct differences between nocturnal and diurnal active  
294 species. Studies have shown that eyes are a better trait to reflect activity period (Bauer 1985;  
295 Talarico et al. 2007, 2011, 2018). For instance, *C. alternans* and *M. affinis* have large eyes, and  
296 although they can hunt both during the day and night, they are probably better visual hunters.

297         Small-sized species in dry ecosystems risk desiccation (Schoener and Janzen 1968), yet  
298 most species in TDF are small but at low abundance (27% of the total number of individuals).  
299 Although a large size has physiological advantages, it also has disadvantages in terms of food  
300 resources (high energetic requirements), and are more visible to predators (Blanckenhorn 2000).  
301 Small insects resolve the challenge to conserve moisture through, amongst others, behavioural  
302 adaptations, for instance by minimizing their exposure to harsh conditions (Chown and Klok 2003).  
303 In TDF, those adaptations include nocturnal activity and a digger habit (Hadley 1974; Remmert  
304 1981); all small carabid species captured are nocturnal, and although only three species are  
305 burrowing specialists, all non-fossorial species have a long metatrochanter, which is related to the  
306 ability to push the body into confined habitats and leaf litter, both to hunt and for shelter (Forsythe  
307 1981, 1987). Burrowing species are characterized by fossorial legs and short fore- and hindlegs,  
308 which help with entering the ground (Forsythe 1981). Additional to these morphological  
309 adaptations, burrowing species like *A. crenata*, *Clivina* sp. and *Camptodontus* sp., and runner  
310 species like *A. paganus* have similar proportions of the prothorax and hind body (width and depth)  
311 that permit them to move in fissures and avoid friction and obstruction (Forsythe 1987).

312         Based on the traits measured, we can infer that all small species have low desiccation  
313 resistance, are olfactory/tactile hunters and good diggers or with good abilities to move in restricted  
314 spaces, while medium and large sized species have higher desiccation resistance (Table 2). *Galerita*  
315 sp. is the only species from this last group with an olfactory/tactile hunter strategy. This species and

316 *C. alternans* have long metatrochanter, probably as a mechanisms to hunt in the litter layer or  
317 shelter from predation (Forsythe 1991; Larochele and Larivière 2003). *Enceladus gigas* was the  
318 biggest and only apterous species, and although its metatrochanter does not aid in its ability to push  
319 into narrow spaces, its pedunculate body facilitate movement through them (Forsythe 1987).  
320 Finally, *M. affinis* could be consider a fast visual hunter, with large and slender legs, and a short  
321 metatrochanter (Forsythe 1981). Both *C. alternans* and *M. affinis* are macropterous with flight  
322 muscles developed, allowing these open-habitat species to escape predation (Forsythe 1987).  
323 Additionally, the iridescent body colour of *M. affinis* and iridescent shades of *C. alternans* provides  
324 additional protection against predators, which may get disorientated when these carabids fly  
325 between sunny and shady areas (Seago et al. 2009).

326

327

## 328 5. Conclusions

329

330 We showed that the ratios of attributes in carabid beetle response traits between the El Niño and  
331 non-El Niño periods differed in the tropical dry forest ecosystem, yet trait occurrence was similar  
332 between the two periods. Species were generally small in size, with nocturnal activities, while in  
333 terms of abundance, medium and large sized beetles with intermediate daily activity dominated. It  
334 appears that in this dry ecosystem, resource limitation is a greater challenge to the presence of  
335 carabid beetles than desiccation risk. Carabid beetles possess a set of traits that show adaptation to  
336 harsh conditions experience during El Niño in the TDF. Diapause could have a prominent role in  
337 species present in the TDF. Yet, despite the importance of diapause to survive bad conditions,  
338 insects experience mortality and other costs during diapause (Nelemans et al. 1989; Matsuo 2006).  
339 Long term studies on the effects of ENSO linked with other anthropologic pressures can clarify the

340 real risks to carabid beetle communities during ENSO, especially given additional threats, such as  
341 climate change.

342

343 Supplementary information

344

345 Additional information can be found online in the Supporting Information section

346 **Supplementary information 1** Air humidity and temperature measured in Armero, Colombia  
347 during the dry and wet seasons of the non-El Niño and El Niño periods.

348 **Supplementary information 2** Functional response traits to desiccation resistance (and their  
349 definitions) measured on carabid beetle species collected in Armero, Colombia, during El Niño and  
350 non-El Niño periods.

351 **Supplementary information 3** Means (SD) of the functional response traits measured for carabid  
352 beetle species collected in Armero, Colombia during El Niño and non-El Niño periods. All  
353 measures are in mm. n = number of individuals measured. unk = unknown, i.e., the trait could not  
354 be measured. Abbreviations are explained in Supplementary information 2.

355 **Supplementary information 4** Mean (SD) functional response trait ratios for carabid beetle species  
356 collected in Armero, Colombia during El Niño and non-El Niño periods. All measures are in mm. n  
357 = number of individuals measured. unk = unknown, which means that the trait could not be  
358 measured. Abbreviations are explained in Supplementary information 2.

359

360 Declarations

361

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364 research

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368 aware of the fact and have agreed to being so named

369 Availability of data or material: The authors confirm that the data supporting the findings of this  
370 study are available within the article (and/or) its supplementary materials

371 Code availability: Not applicable

372 Authors' contributions: GMA collected the data and performed laboratory activities. GMA and DJK  
373 performed the analyses. All authors participated in the writing of the manuscript

374

375 References

376

377 Ball GE, Shpeley D (2002) The Neotropical subgenera and species of the pantropical genus  
378 *Anaulacus* MacLeay (sensu novo) (Coleoptera: Carabidae: Masoreini): a taxonomic revision, with  
379 notes about way of life, evolution, and geographical history. T Am Entomol Soc 128:265–343.  
380 <https://www.jstor.org/stable/25078782>

381

382 Ball GE, Shpeley D (2009) A taxonomic review of the genus *Apenes* Leconte (Coleoptera:  
383 Carabidae: Lebiini) in the West Indies, with descriptions of new species and notes about  
384 classification and biogeography. Ann Carnegie Mus 78:79–191.  
385 <https://doi.org/10.2992/007.078.0201>

386



387 Bauer T (1985) Different adaptation to visual hunting in three ground beetle species of the same  
388 genus. *J Insect Physiol* 31:593–601. [https://doi.org/10.1016/0022-1910\(85\)90057-5](https://doi.org/10.1016/0022-1910(85)90057-5)

389

390 Bauer T, Desender K, Morwinsky T, Betz O (1998) Eye morphology reflects habitat demands in  
391 three closely related ground beetle species (Coleoptera: Carabidae). *J Zool* 245:467–472.  
392 <https://doi.org/10.1111/j.1469-7998.1998.tb00121.x>

393

394 Bauer T, Kredler M (1993) Morphology of the compound eyes as an indicator of life-style in  
395 carabid beetles. *Can J Zool* 71:799–810. <https://doi.org/10.1139/z93-105>

396

397 Bernays EA, Minkenberg OPJM (1997) Insect herbivores: different reasons for being a generalist.  
398 *Ecology* 78:1157–1169. <https://doi.org/10.2307/2265866>

399

400 Blanckenhorn WU (2000) The evolution of body size: what keeps organisms small? *Q Rev Biol*  
401 75:385–407. <https://doi.org/10.1086/393620>

402

403 Bruschi S (2010) Key to the species of subgenus *Castrida* Motschulsky.

404 [http://www.calosomas.com/Castrida/Castrida\\_keys.html](http://www.calosomas.com/Castrida/Castrida_keys.html). Accessed 17 September 2018

405

406 Büchi L, Vuilleumier S (2014) Coexistence of specialist and generalist species is shaped by  
407 dispersal and environmental factors. *Amer Naturalist* 183:612–624. <https://doi.org/10.1086/675756>

408

409 Burgess AF (1911) *Calosoma sycophanta*: its life history, behaviour, and successful colonization in  
410 New England. US Dept. of Agriculture, Bureau of Entomology, Washington.  
411 <https://doi.org/10.5962/bhl.title.65273>  
412

413 Cadotte MW, Carscadden K, Mirotchnick N (2011) Beyond species: functional diversity and the  
414 maintenance of ecological processes and services. *J Appl Ecol* 48:1079–1087.  
415 <https://doi.org/10.1111/j.1365-2664.2011.02048.x>  
416

417 Caviedes CN (2001) *El Niño in history storming through the ages*. University Press of Florida,  
418 Florida  
419

420 Chapman RF (1998) *The insects structure and function*. Cambridge University Press, New York  
421

422 Charrete NA, Cleary DFR, Mooers AØ (2006) Range-restricted, specialist bornean butterflies are  
423 less likely to recover from ENSO-induced disturbance. *Ecology* 87:2330–2337.  
424 <https://www.jstor.org/stable/20069234>  
425

426 Chown SL, Klok CJ (2003) Water-balance characteristics respond to changes in body size in  
427 subantarctic Weevils. *Physiol Biochem Zool* 76:634–643. <https://doi.org/10.1086/376919>  
428

429 Chown SL, Scholtz CH, Klok CJ, Joubert FJ, Coles KS (1995) Ecophysiology, range contraction  
430 and survival of a geographically restricted African Dung beetle (Coleoptera: Scarabaeidae). *Funct*  
431 *Ecol* 9:30–39. <https://doi.org/10.2307/2390087>

432

433 Chown SL, Sørensen JG, Terblanche JS (2011) Water loss in insects: an environmental change  
434 perspective. *J Insect Physiol* 57:1070–1084. <https://doi.org/10.1016/j.jinsphys.2011.05.004>

435

436 Cloudsley-Thompson JL (1975) Adaptations of Arthropoda to arid environments. *Annu Rev*  
437 *Entomol* 20:261–283. <https://doi.org/10.1146/annurev.en.20.010175.001401>

438

439 Crawford CS (1981) *Biology of desert invertebrates*. Springer-Verlag, Berlin

440

441 Darlington PJ (1943) Carabidae of mountains and islands: data on the evolution of isolated faunas,  
442 and on atrophy of wings. *Ecol Monogr* 13:37–61. <https://doi.org/10.2307/1943589>

443

444 Dejean PFMA (1829) *Spécies général des Coléoptères, de la collection de M. le Comte Dejean*.  
445 Crevot, Paris

446

447 Dejean PFMA (1831) *Spécies général des Coléoptères, de la collection de M. le Comte Dejean*.  
448 Crevot, Paris

449

450 Desender K (2000) Flight muscle development and dispersal in the life cycle of carabid beetles:  
451 patterns and process. *Bull Inst Roy Sci Nat Belgique* 70:13–31

452  
453 Dingle H (1972) Migration strategies of insects. *Science* 175:1327–1335.  
454 <https://doi.org/10.1126/science.175.4028.1327>

455  
456 Dirzo R, Young HS, Mooney HA, Ceballos G (2011) Seasonally dry tropical forests: ecology and  
457 conservation. Island Press, Washington

458  
459 Erwin TL (1979) Thoughts on the evolutionary history of ground beetles: hypotheses generated  
460 from comparative faunal analyses of lowland forest sites in temperate and tropical regions. In:  
461 Erwin TL, Ball GE, Whitehead DR, Halpern AL (eds) *Carabid beetles their evolution, natural*  
462 *History, and classification*. Springer Netherlands, Dordrecht, pp 539–592

463  
464 Forsythe TG (1981) Running and pushing in relationship to hind leg structure in some Carabidae  
465 (Coleoptera). *Coleopt Bull* 35:353–378. <https://www.jstor.org/stable/4007954>

466  
467 Forsythe TG (1983) Locomotion in ground beetles (Coleoptera carabidae): an interpretation of leg  
468 structure in functional terms. *J Zool* 200:493–507. [https://doi.org/10.1111/j.1469-](https://doi.org/10.1111/j.1469-7998.1983.tb02811.x)  
469 [7998.1983.tb02811.x](https://doi.org/10.1111/j.1469-7998.1983.tb02811.x)

470

471 Forsythe TG (1987) The relationship between body form and habit in some Carabidae (Coleoptera).  
472 J Zool 211:643–666. <https://doi.org/10.1111/j.1469-7998.1987.tb04477.x>

473

474 Forsythe TG (1991) Feeding and locomotory functions in relation to body form in five species of  
475 ground beetle (Coleoptera: Carabidae). J Zool 223:233–263. [https://doi.org/10.1111/j.1469-](https://doi.org/10.1111/j.1469-7998.1991.tb04763.x)  
476 [7998.1991.tb04763.x](https://doi.org/10.1111/j.1469-7998.1991.tb04763.x)

477

478 Fountain-Jones NM, Baker SC, Jordan GJ (2015) Moving beyond the guild concept: developing a  
479 practical functional trait framework for terrestrial beetles. Ecol Entomol 40:1–13.  
480 <https://doi.org/10.1111/een.12158>

481

482 Grove R, Adamson G (2018) El Niño in World history. Palgrave Macmillan UK, London

483 Hadley NF (1974) Adaptational biology of desert Scorpions. J Arachnol 2:11–23

484

485 Hadley NF, Savill A, Schultz TD (1992) Coloration and its thermal consequences in the New  
486 Zealand tiger beetle *Neocicindela perhispidata*. J Therm Biol 17:55–61. [https://doi.org/10.1016/0306-](https://doi.org/10.1016/0306-4565(92)90020-G)  
487 [4565\(92\)90020-G](https://doi.org/10.1016/0306-4565(92)90020-G)

488

489 Hadley NF, Schultz TD, Savill A (1988) Spectral reflectances of three tiger beetle subspecies  
490 (*Neocicindela perhispidata*): correlations with their habitat substrate. New Zeal J Zool 15:343–346.  
491 <https://doi.org/10.1080/03014223.1988.10422624>

492

493 Hammer Ø, Harper DAT, Ryan PD (2001) PAST: paleontological statistics software package for  
494 education and data analysis. *Palaeontol Electron* 4:1–9

495

496 Hodek I (2003) Role of water and moisture in diapause development (A review). *Eur J Entomol*  
497 100:223–232. <https://doi.org/10.14411/eje.2003.037>

498

499 Hodek I (2012) Adult diapause in coleoptera. *Psyche* 249081:1–10.  
500 <https://doi.org/10.1155/2012/249081>

501

502 Holmgren M, Scheffer M, Ezcurra E, Gutiérrez JR, Mohren GMJ (2001) El Niño effects on the  
503 dynamics of terrestrial ecosystems. *Trends Ecol Evol* 16:89–94. [https://doi.org/10.1016/S0169-](https://doi.org/10.1016/S0169-5347(00)02052-8)  
504 [5347\(00\)02052-8](https://doi.org/10.1016/S0169-5347(00)02052-8)

505

506 Homburg K, Homburg N, Schäfer F, Schuldt A, Assmann T (2014). *Carabids.org* - a dynamic  
507 online database of ground beetle species traits (Coleoptera, Carabidae). *Insect Conserv Divers*  
508 7:195–205. <https://doi.org/10.1111/icad.12045>

509

510 Hood WG, Tschinkel WR (1990) Desiccation resistance in arboreal and terrestrial ants. *Physiol*  
511 *Entomol* 15:23–35. <https://doi.org/10.1111/j.1365-3032.1990.tb00489.x>

512

513 Jacobs JM, Colin Bergeron JA, Work TT, Spence JR (2011) Low intensity surface fire instigates  
514 movement by adults of *Calosoma frigidum* (Coleoptera, Carabidae). ZooKeys 147:641–649.  
515 <https://doi.org/10.3897/zookeys.147.2084>

516

517 Jeffords M, Case L (1987) Effect of prey density on diurnal activity and ovarian development in  
518 *Calosoma calidum* (Coleoptera: Carabidae): implications for biological control of the Gypsy moth,  
519 *Lymantria dispar* (Lepidoptera: Lymantriidae) in the Midwest. Great Lakes Entomol 20:9

520

521 Keddy PA (1992) Assembly and response rules: two goals for predictive community ecology. J Veg  
522 Sci 3:157–164. <https://doi.org/10.2307/3235676>

523

524 Kishimoto-Yamada K, Itioka T (2008) Consequences of a severe drought associated with an El  
525 Niño-Southern Oscillation on a light-attracted leaf-beetle (Coleoptera, Chrysomelidae) assemblage  
526 in Borneo. J Trop Ecol 24:229–233. <https://doi.org/10.1017/S0266467408004811>

527

528 Kishimoto-Yamada K, Itioka T, Sakai S, Momose K, Nagamitsu T, Kaliang H, Meleng P, Chong L,  
529 Karim AAH, Yamane S, Kato M, Reid CA, Nakashizuka T, Inoue T (2009) Population fluctuations  
530 of light-attracted chrysomelid beetles in relation to supra-annual environmental changes in a  
531 Bornean rainforest. Bull Entomol Res 99:217–227. <https://doi.org/10.1017/S000748530800624X>

532

533 Koivula M, Punntila P, Haila Y, Niemelä J (1999) Leaf litter and the small-scale distribution of  
534 carabid beetles (Coleoptera , Carabidae ) in the boreal forest. *Ecography* 22:424–435.  
535 <https://doi.org/10.1111/j.1600-0587.1999.tb00579.x>  
536  
537 Kotze DJ, Lawes MJ (2007) Viability of ecological processes in small Afromontane forest patches  
538 in South Africa. *Austral Ecol* 32:294–304. <https://doi.org/10.1111/j.1442-9993.2007.01694.x>  
539  
540 Kraft NJB, Adler PB, Godoy O, James EC, Fuller S, Levine JM (2015) Community assembly,  
541 coexistence and the environmental filtering metaphor. *Funct Ecol* 29:592–599.  
542 <https://doi.org/10.1111/1365-2435.12345>  
543  
544 Le Lagadec MD, Chown SL, Scholtz CH (1998) Desiccation resistance and water balance in  
545 southern African keratin beetles (Coleoptera, Trogidae): the influence of body size and habitat. *J*  
546 *Comp Physiol B* 168:112–122. <https://doi.org/10.1007/s003600050127>  
547  
548 Laroche A, Larivière MC (2003) A natural history of the ground-beetles (Coleoptera: Carabidae)  
549 of America north of Mexico. Pensoft Publishers, Bulgaria  
550  
551 Lövei GL, Sunderland KD (1996) Ecology and behavior of ground beetles (Coleoptera: Carabidae).  
552 *Annu Rev Entomol* 41:231–256. <https://doi.org/10.1146/annurev.en.41.010196.001311>  
553



554 Lucky A, Erwin TL, Witman JD (2002) Temporal and spatial diversity and distribution of arboreal  
555 Carabidae (Coleoptera) in a Western Amazonian rain forest. *Biotropica* 34:376–386.  
556 <https://doi.org/10.1111/j.1744-7429.2002.tb00551.x>  
557  
558 Luo X, Keenan TF, Fisher JB, Jiménez-Muñoz JC, Chen JM, Jiang C, Ju W, Perakalapudi NV, Ryu  
559 Y, Tadić JM (2018) The impact of the 2015/2016 El Niño on global photosynthesis using satellite  
560 remote sensing. *Philos Trans R Soc B* 373:20170409. <https://doi.org/10.1098/rstb.2017.0409>  
561  
562 Maass M, Burgos A (2011) Water dynamics at the ecosystem level in Seasonally dry tropical  
563 forests. In: Dirzo R, Young HS, Mooney HA, Ceballos G (eds) *Seasonally dry tropical forests:*  
564 *ecology and conservation*. Island Press, Washington, pp 141–156  
565  
566 Magura T, Lövei GL (2019) Environmental filtering is the main assembly rule of ground beetles in  
567 the forest and its edge but not in the adjacent grassland. *Insect Sci* 26:154–163.  
568 <https://doi.org/10.1111/1744-7917.12504>  
569  
570 Martínez C (2005) *Introducción a los escarabajos Carabidae*. Instituto de Investigación de Recursos  
571 *Biológicos Alexander von Humboldt*, Bogotá  
572  
573 Matsuo Y (2006) Cost of prolonged diapause and its relationship to body size in a seed predator.  
574 *Funct Ecol* 20:300–306. <https://doi.org/10.1111/j.1365-2435.2006.01097.x>  
575

576 Meir P, Pennington RT (2011) Climatic change and seasonally dry tropical forests. In: Dirzo R,  
577 Young HS, Mooney HA (eds) Seasonally dry tropical forests: ecology and conservation. Island  
578 Press, Washington, pp 279–299

579

580 Murphy PG, Lugo AE (1986) Ecology of Tropical dry forest. *Annu Rev Ecol Evol Syst* 17:67–88.  
581 <https://doi.org/10.1146/annurev.es.17.110186.000435>

582

583 Nelemans MNE (1987) Possibilities for flight in the carabid beetle *Nebria brevicollis* (F.). The  
584 importance of food during larval growth. *Oecologia* 72:502–509.  
585 <https://doi.org/10.1007/BF00378974>

586

587 Nelemans MNE, Den Boer PJ, Spee A (1989) Recruitment and summer diapause in the dynamics of  
588 a population of *Nebria brevicollis* (Coleoptera: Carabidae). *Oikos* 56:157–169.  
589 <https://doi.org/10.2307/3565331>

590

591 Pakeman RJ, Stockan JA (2014) Drivers of carabid functional diversity: abiotic environment, plant  
592 functional traits, or plant functional diversity? *Ecology* 95:1213–1224. [https://doi.org/10.1890/13-](https://doi.org/10.1890/13-1059.1)  
593 [1059.1](https://doi.org/10.1890/13-1059.1)

594

595 Pearson DL, Vogler AP (2001) Tiger Beetles: the evolution, ecology, and diversity of the  
596 cicindelids. Cornell University Press, United States of America

597

598 Pérez Hernández XC, Zaragoza Caballero S (2016) Temporal variation in the diversity of  
599 Cantharidae (Coleoptera), in seven assemblages in Tropical dry forest in Mexico. *Trop Conserv Sci*  
600 9:439–464. <https://doi.org/10.1177/194008291600900124>  
601

602 Piano E, De Wolf K, Bona F, Bonte D, Bowler DE, Isaia M, Lens L, Merckx T, Mertens D, Van  
603 Kerckvoorde M, De Meester L, Hendrickx F (2017) Urbanization drives community shifts towards  
604 thermophilic and dispersive species at local and landscape scales. *Glob Change Biol* 23:2554–2564.  
605 <https://doi.org/10.1111/gcb.13606>  
606

607 Pizano C, García H (2014) El Bosque seco tropical en Colombia. Instituto de Investigación de  
608 Recursos Biológicos Alexander von Humboldt (IAvH), Bogotá  
609

610 Pizano C, González-M R, González MF, Castro-Lima F, López R, Rodríguez N, Idárraga-Piedrahíta  
611 Á, Vargas W, Vergara-Varela H, Castaño-Naranjo A, Devia W, Rojas A, Cuadros H, Toro JL  
612 (2014) Las plantas de los bosques secos de Colombia. In: Pizano C, García H. (eds) *El Bosque seco*  
613 *tropical en Colombia*. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt,  
614 Bogotá, pp. 48–93  
615

616 Pizano C, González-M R, López R, Jurado RD, Cuadros H, Castaño-Naranjo A, Rojas A, Pérez K,  
617 Vergara-Varela H, Idárraga Á, Isaacs P, García H (2016) El Bosque seco tropical en Colombia:  
618 distribución y estado de conservación. In: Gómez MF, Moreno LA, Andrade GI, Rueda C (eds)  
619 *Biodiversidad 2015: estado y tendencias de la biodiversidad continental de Colombia*. Instituto  
620 Alexander von Humboldt, Bogotá, pp ficha 202.

621

622 Ploomi A, Merivee E, Rahi M, Bresciani J, Ravn HP, Luik A, Sammelseg V (2003) Antennal  
623 sensilla in ground beetles (Coleoptera, Carabidae). *Agron Res* 1:221–228.

624

625 Poveda G, Graham NE, Epstein PR, Rojas W, Quiñones ML, Vélez ID, Martens WJM (2000)  
626 Climate and ENSO variability associated with vector-borne diseases in Colombia. In: Diaz HF,  
627 Markgraf V (eds) *El Niño and the Southern oscillation: multiscale variability and global and*  
628 *regional impacts*. Cambridge University Press, Cambridge, pp 183–204

629

630 Pulla S, Ramaswami G, Mondal N, Chitra-Tarak R, Suresh HS, Dattaraja HS, Vivek P,  
631 Parthasarathy N, Ramesh BR, Sukumar R (2015) Assessing the resilience of global Seasonally dry  
632 tropical forests. *Int For Rev* 17:91–113. <https://doi.org/10.1505/146554815815834796>

633

634 Putzeys J (1846) Monographie des *Clivina* et genres voisins, précédée d'un tableau synoptique des  
635 genres de la tribu des Scaritides. *Mémoires de la Société R. des Sciences de Liege* 2:521–663

636

637 Putzeys J (1866) Révision générale des Clivinides. *Annales de la Société Entomologique de*  
638 *Belgique* 10:1–242

639

640 Reichardt H (1967) A monographic revision of the american Galeritini (Coleoptera:Carabidae). *Arq*  
641 *Zool* 15:1–176. <https://doi.org/10.11606/issn.2176-7793.v15i1-2p1-176>

642

643 Remmert H (1981) Body size of terrestrial Arthropods and biomass of their populations in relation  
644 to the abiotic parameters of their milieu. *Oecologia* 50:12–13. <https://doi.org/10.1007/BF00378789>  
645

646 Schneider CA, Rasband WS, Eliceiri KW (2012) NIH Image to ImageJ: 25 years of Image  
647 Analysis. *Nat Methods* 9:671–675. <https://doi.org/10.1038/nmeth.2089>  
648

649 Schoener TW, Janzen DH (1968) Notes on environmental determinants of Tropical versus  
650 Temperate insect size patterns. *Am Nat* 102:207–224. <https://doi.org/10.1086/282538>  
651

652 Schowalter TD (2006) *Insect ecology - An ecosystem approach*. Academic Press, San Diego  
653

654 Schultz TD (1986) Role of structural colors in predator avoidance by tiger beetles of the genus  
655 *Cicindela* (Coleoptera: Cicindelidae). *Bull Entomol Soc Am* 32:142–146.  
656 <https://doi.org/10.1093/besa/32.3.142>  
657

658 Schweiger AH, Beierkuhnlein C (2016) Size dependency in colour patterns of Western Palearctic  
659 carabids. *Ecography* 39:846–857. <https://doi.org/10.1111/ecog.01570>  
660

661 Seago AE, Brady P, Vigneron JP, Schultz TD (2009) Gold bugs and beyond: a review of  
662 iridescence and structural colour mechanisms in beetles (Coleoptera). *J R Soc Interface* 6:165–184.  
663 <https://doi.org/10.1098/rsif.2008.0354.focus>  
664

665 Shibuya S, Kubota K, Ohsawa M, Kikvidze Z (2011) Assembly rules for ground beetle  
666 communities: what determines community structure, environmental factors or competition? Eur J  
667 Entomol 108:453–459. <https://doi.org/10.14411/eje.2011.058>  
668

669 Srygley RB, Dudley R, Oliveira EG, Aizprúas R, Pelaez NZ, Riveros AJ (2010) El Niño and dry  
670 season rainfall influence hostplant phenology and an annual butterfly migration from Neotropical  
671 wet to dry forests. Glob Change Biol 1:936–945. <https://doi.org/10.1111/j.1365-2486.2009.01986.x>  
672

673 Srygley RB, Dudley R, Oliveira EG, Riveros AJ (2014) El Niño, host plant growth, and migratory  
674 butterfly abundance in a changing climate. Biotropica 46:90–97. <https://doi.org/10.1111/btp.12081>  
675

676 Talarico F, Brandmayr P, Giglio A, Massolo A, Brandmayr TZ (2011) Morphometry of eyes,  
677 antennae and wings in three species of *Siagona* (Coleoptera, Carabidae). ZooKeys 100:203–214.  
678 <https://doi.org/10.3897/zookeys.100.1528>  
679

680 Talarico F, Cavaliere F, Mazzei A, Brandmayr P (2018) Morphometry and eye morphology of three  
681 scaritine ground beetles relate to habitat demands and behavioural traits (Coleoptera, Carabidae,  
682 Scaritinae). Zool Anz 277:190–196. <https://doi.org/10.1016/j.jcz.2018.10.002>  
683

684 Talarico F, Romeo M, Massolo A, Brandmayr P, Zetto T (2007) Morphometry and eye morphology  
685 in three species of *Carabus* (Coleoptera: Carabidae) in relation to habitat demands. J Zool Syst Evol  
686 Res 45:33–38. <https://doi.org/10.1111/j.1439-0469.2006.00394.x>

687

688 Tauber MJ, Tauber CA, Nyrop JP, Villani MG (1998) Moisture, a vital but neglected factor in the  
689 seasonal ecology of insects: hypotheses and tests of mechanisms. *Environ Entomol* 27:523–530.  
690 <https://doi.org/10.1093/ee/27.3.523>

691

692 Venn S (2016) To fly or not to fly: Factors influencing the flight capacity of carabid beetles  
693 (Coleoptera: Carabidae). *Eur J Entomol* 113:587–600. <https://doi.org/10.14411/eje.2016.079>

694

695 Vitolo AL (2004) Guía para la identificación de los escarabajos tigre. Instituto de la Investigación  
696 de Recursos Biológicos Alexander von Humboldt, Bogotá

697

698 Wheeler C (1989) Prey detection by some predatory Coleoptera (Carabidae and Staphylinidae). *J*  
699 *Zool* 218:171–185. <https://doi.org/10.1111/j.1469-7998.1989.tb02531.x>

700

701 White TCR (2008) The role of food, weather and climate in limiting the abundance of animals. *Biol*  
702 *Rev* 83:227–248. <https://doi.org/10.1111/j.1469-185X.2008.00041.x>

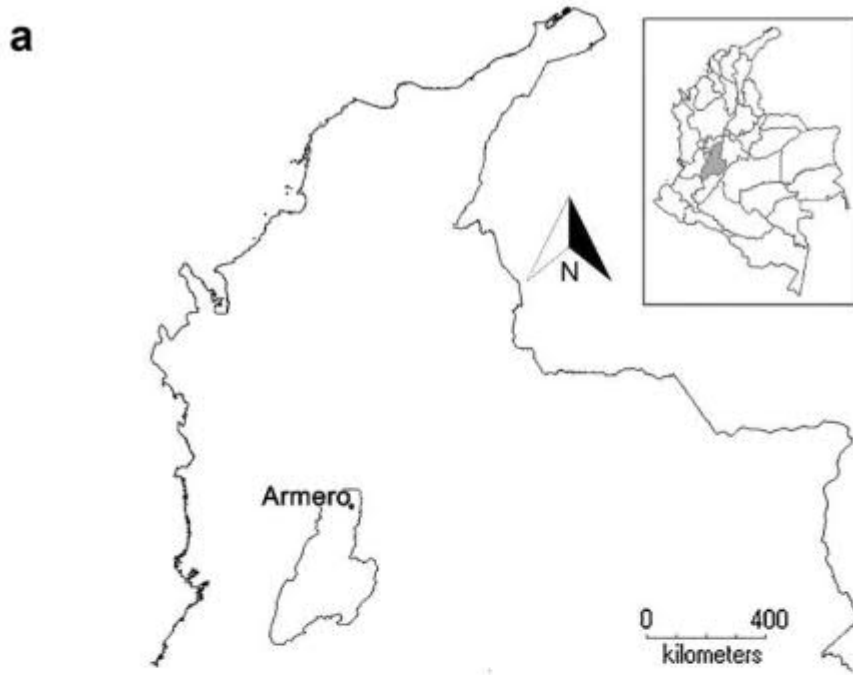
703

704 Will K W (2005) The Neotropical genera *Oxycrepis* Reiche and *Stolonis* Motschulsky: a taxonomic  
705 review, key to the described species and description of new *Stolonis* species from Ecuador  
706 (Coleoptera: Carabidae: Loxandrinini). *Zootaxa* 17:1–17. <https://doi.org/10.11646/zootaxa.1049.1.1>

707

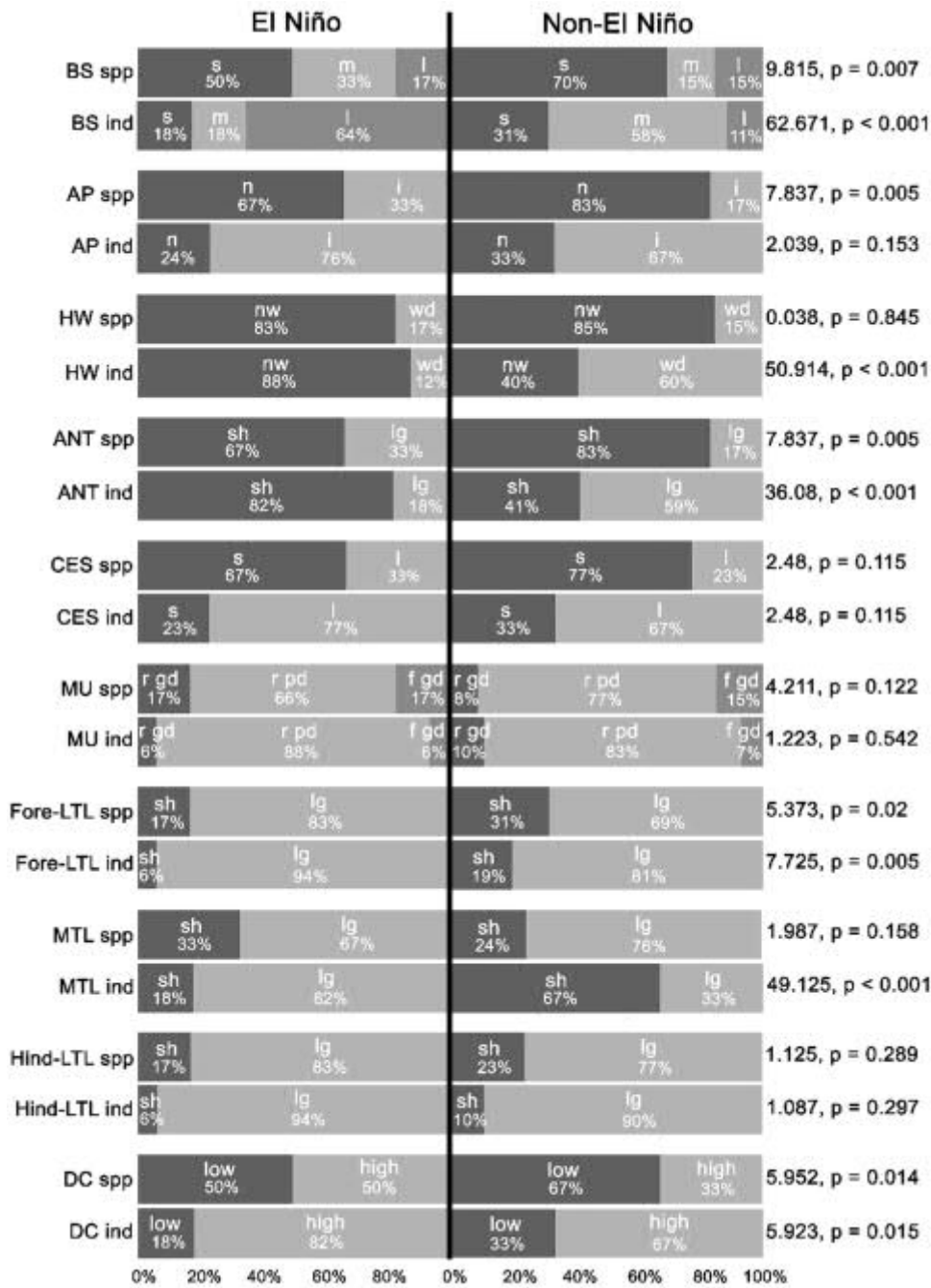
708 Wolda H, Denlinger DL (1984) Diapause in a large aggregation of a tropical beetle. *Ecol Entomol*  
709 9:217–230. <https://doi.org/10.1111/j.1365-2311.1984.tb00717.x>





710

711 **Fig. 1** Geographic locations of study sites in Armero. a: The location of Armero in Colombia. b:  
 712 Armero. Abbreviations: F = forest; ES = early succession; P = pasture. Maps courtesy of DIVA-GIS  
 713 7.5 and Google Earth Image © 2020.



714

715 **Fig. 2** Distribution of carabid beetle functional response traits among El Niño and non-El Niño  
 716 periods in Armero, Colombia. Abbreviations are explained in Supplementary information 2.  $\chi^2$  and  
 717 p values are presented that test for differences in the distribution of attributes within each trait  
 718 between the two climatic periods. spp = species, ind = individuals.

719 **Table 1** Range of values of functional response traits measured on the carabid beetle species collected. See Supplementary information 2 for  
 720 more details.

Trait	Trait linked to	Classification	Abbreviation	Range
Body size	Desiccation resistance	Small	s	4-12 mm
		Medium	m	15-16 mm
		Large	l	23-50 mm
Head width/Body size	Daily activity time (nocturnal, diurnal)	Narrow	nw	0.15-0.22
		Wide	wd	0.27-0.29
Antenna length/Body size	Daily activity time (nocturnal, diurnal)	Short	sh	0.28-0.47
		Long	lg	0.58-0.65
Compound eye surface area/Body size	Daily activity time (nocturnal, diurnal)	Small	s	0.01-0.05
		Large	l	0.08-0.13
Prothorax width/Abdomen width	Microhabitat use (burrowing habit and capacity to shelter in confined habitats)	Poor digger	pd	0.64-0.80
		Good digger	gd	0.87-1.20
Prothorax depth/Abdomen depth		Poor digger	pd	0.78-0.94
		Good digger	gd	0.97-1.32
Profemur length/Body size	Microhabitat use (fast runner, slow runner, fossorial)	Short	sh	0.14-0.17
		Long	lg	0.18-0.23
Protibia Length/Body size		Short	sh	0.12-0.15
		Long	lg	0.16-0.20
Foreleg total length/Body size		Short	sh	0.33-0.41
		Long	lg	0.42-0.57
Metatrochanter length/Body size	Microhabitat use (burrowing habit and capacity to shelter in confined habitats)	Short	sh	0.06-0.08
		Long	lg	0.09-0.13
Metafemur length/Body size	Microhabitat use (fast runner, slow runner, fossorial)	Short	sh	0.14-0.22
		Long	lg	0.23-0.36
Metafemur width/Body size		Slender	sl	0.04-0.06
		Wide	wd	0.07-0.08
Metatibia/Body size		Short	sh	0.14-0.21

Hind leg total length/Body size	Long	lg	0.22-0.33
	Short	sh	0.40-0.57
	Long	lg	0.59-1.02

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722 **Table 2** Trait characterization of carabid beetles collected in Armero, Colombia during El Niño and non-El Niño periods. Abbreviations are  
 723 explained in detail in Supplementary information 2.

Species	BS	AP	HW	ANT	CES	MU	Pro-FL	Pro-TL	Fore-LTL	MTL	Meta-FL	Meta-FW	Meta-TL	Hind-LTL	DC	BC	LC
<i>Apenes coriacea</i> (Chevrolat, 1863)	s	n	nw	unk	s	r pd	sh	sh	lg	lg	lg	sl	sh	lg	low	lh	pl
<i>Apenes morio</i> (Dejean, 1825)	s	n	nw	sh	s	r pd	sh	sh	sh	lg	lg	sl	sh	lg	high	dk	pl
<i>Apenes prasinus</i> Ball & Shpeley, 1992	s	n	nw	sh	s	r pd	lg	lg	lg	lg	lg	wd	lg	lg	low	mt	dk
<i>Apenes</i> sp.	s	n	nw	sh	s	r pd	lg	lg	lg	lg	lg	wd	lg	lg	low	dk	pl
<i>Aspidoglossa crenata</i> (Dejean, 1825)	s	n	nw	sh	s	f gd	sh	sh	sh	lg	sh	sl	sh	sh	high	dk	dk
<i>Athrostictus paganus</i> (Dejean, 1831)	s	n	nw	sh	s	r gd	sh	sh	lg	lg	lg	sl	lg	lg	low	dk	pl
<i>Barysomus hoepfneri</i> Dejean, 1829	s	n	wd	sh	s	r pd	lg	sh	lg	lg	sh	wd	lg	lg	low	dk	pl
<i>Calosoma alternans</i> (Fabricius, 1792)	l	i	nw	sh	l	r pd	lg	lg	lg	lg	lg	wd	lg	lg	high	dk	dk
<i>Camptodontus</i> sp.	s	n	nw	sh	s	f gd	sh	sh	sh	sh	sh	sl	sh	sh	unk	dk	dk
<i>Clivina</i> sp.	s	n	nw	sh	s	f gd	sh	sh	sh	sh	sh	sl	sh	sh	high	dk	dk
<i>Enceladus gigas</i> Bonelli, 1813	l	unk	nw	sh	l	r gd	sh	sh	sh	sh	sh	sl	sh	lg	low	dk	dk
<i>Galerita</i> sp.	m	n	nw	lg	s	r pd	lg	lg	lg	lg	lg	sl	lg	lg	low	dk	dk
<i>Megacephala affinis</i> Dejean, 1825	m	i	wd	lg	l	r pd	lg	lg	lg	sh	lg	sl	lg	lg	high	mt	pl
<i>Stolonis interceptus</i> Chaudoir, 1873	s	n	nw	sh	s	r pd	lg	lg	lg	lg	lg	sl	sh	sh	low	dk	pl
<i>Tetragonoderus</i> sp.	s	n	nw	sh	s	r pd	lg	lg	lg	lg	lg	wd	lg	lg	low	dk	dk

724 \***BS** = body size, **AP** = daily activity period, **HW** = head width, **ANT** = antenna length, **CES** = compound eye surface area, **MU** = microhabitat use, **Pro-FL** = pro-femur length, **Pro-TL** = pro-  
 725 tibia length, **Fore-LTL** = foreleg total length, **MTL** = metatrochanter length, **Meta-FL** = meta-femur length, **Meta-FW** = meta-femur width, **Meta-TL** = meta-tibia length, **Hind-LTL** =  
 726 hindleg total length, **DC** = dispersal capacity, **BC** = body colour, **LC** = leg colour.

727 **Table 3** Number of individuals of all carabid beetle species collected in Armero, Colombia, during El Niño and non-El Niño periods. The season  
 728 column represents the season during which a species was collected; w = wet, d = dry; capital letters represent the season with the most abundant  
 729 catch.

Species	El Niño		Non-El Niño	
	Total	Season	Total	Season
<i>Apenes coriacea</i>			1	w
<i>Apenes morio</i>			1	w
<i>Apenes prasinus</i>	1	w	1	d
<i>Apenes</i> sp.			1	d
<i>Aspidoglossa crenata</i>			3	dW
<i>Athrostiticus paganus</i>	1	w		
<i>Barysomus hoepfneri</i>			2	dw
<i>Calosoma alternans</i>	11	w	1	w
<i>Camptodontus</i> sp.			1	w
<i>Clivina</i> sp.	1	w		
<i>Enceladus gigas</i>			5	dW
<i>Galerita</i> sp.	1	d	1	w
<i>Megacephala affinis</i>	2	dw	29	dW
<i>Meotachys</i> sp.			1	d
<i>Stolonis interceptus</i>			1	d
<i>Tetragonoderus</i> sp.			5	Dw
<b>Total number of individuals</b>	<b>17</b>		<b>53</b>	
<b>Total number of species</b>	<b>6</b>		<b>14</b>	

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731 **Supplementary information 1** Air humidity and temperature measured in Armero, Colombia during the dry and wet seasons of the non-El Niño  
 732 and El Niño periods.

Habitat type	Non-El Niño				El Niño			
	Dry season		Wet season		Dry season		Wet season	
	Air humidity (%)	Air temperature (°C)	Air humidity (%)	Air temperature (°C)	Air humidity (%)	Air temperature (°C)	Air humidity (%)	Air temperature (°C)
Forest 1	65	28.4	52	30.6	35	48.2	91	28.2
Forest 2	77	27.3	72	25.5	46	38.6	91	27.9
Forest 3	57	30.8	69	28.6	33	49.5	68	33.2
Forest 4	78	27.4	79	25.7	42	43.2	51	38.5
Forest 5	69	28.7	70	28.1	29	40.6	61	34.8
Early succession 1	77	27.8	79	26.1	43	41.3	58	35.8
Early succession 2	63	30.7	62	31.9	37	45.7	52	37.9
Early succession 3	84	31.7	63	31.9	29	46.7	45	40.2
Early succession 4	79	27.3	63	32.4	33	43.3	47	39.3
Pasture 1	72	31.1	83	27.2	39	42.8	44	41.6
Pasture 2	62	36.5	72	33.3	29	53.5	62	35.2
Pasture 3	71	30.6	61	39.4	40	45.5	69	33.7
<b>Mean</b>	<b>71.17</b>	<b>29.86</b>	<b>68.75</b>	<b>30.06</b>	<b>36.25</b>	<b>44.91</b>	<b>61.58</b>	<b>35.53</b>

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734 **Supplementary information 2** Functional response traits to desiccation resistance (and their definitions) measured on carabid beetle species  
 735 collected in Armero, Colombia, during El Niño and non-El Niño periods.

Trait	Abbreviation	Criteria to measure	Trait linked to	Author
Body size	BS	From the base of the mandibles to the tip of the abdomen s = small (4-12 mm) m = medium (15-16 mm) l = large (23-50 mm)	Desiccation resistance	Schoener and Janzen 1968 Le Lagadec et al. 1998 Chown and Klok 2003
Daily activity period	AP	d = diurnal n = nocturnal i = intermediate (both d and n)	Activity time	Bauer and Kredler 1993
Head width	HW	Maximum width, including compound eyes nw = narrow (HW/BS: 0.15-0.22) wd = wide (HW/BS: 0.27-0.29)	Activity time	Bauer and Kredler 1993
Antenna length	ANT	From the base of the first antennomere until the apex sh = short (ANT/BS: 0.28-0.47) lg = long (ANT/BS: 0.58-0.65)	Activity time	Bauer and Kredler 1993
Compound eye surface area	CES	Longest axis (long, width): $A = \pi LW/4$ s = small (CES/BS: 0.01-0.05) l = large (CES/BS: 0.08-0.13)	Activity time	Bauer et al. 1998 Talarico et al. 2018
Microhabitat use	MU	r = runner f = fossorial	Microhabitat use	Forsythe 1981, 1987
Prothorax width	PW	Maximum width between each lateral margin	Microhabitat use	Forsythe 1987
Prothorax depth	PD	Maximum depth between upper and lower margin		
Abdomen width	ABW	Maximum width between each lateral margin	Microhabitat use	Forsythe 1987
Abdomen depth	ABD	Maximum depth between upper and lower margin		
Femur length (pro-meta)	FL	Length from the base to the apex	Microhabitat use	Forsythe 1981, 1987
Femur width (pro-meta)	FW	Maximum width between each lateral margin		
Tibia length (pro-meta)	TL	Length from apex margin of femur to base of tarsus		



Tarsus length (pro-meta)	TSL	Length from apex margin of tibiae to claw		
Metatrochanter length	MTL	Length from base to apex		
Fore leg total length	Fore-LTL	Sum of each part of the fore leg		
Hind leg total length	Hind-LTL	Sum of each part of the hind leg		
Functional hind wings	FHW	m = Macropterous: hind wings always fully developed, longer than elytra b = Brachypterous: hind wings always shorter than elytra a = Apterous: without hind wings	Potential ability to escape bad conditions	Venn 2016
Flight muscles	FM	1 = Developed 0 = Not developed	Potential ability to escape bad conditions	Desender 2000
Dispersal capacity	DC	high = Functional hind wing and flight muscles developed low = Functional hind wing or not and flight muscles not developed	Potential ability to escape bad conditions	Desender 2000 Venn 2016
Body colour	BC	lh = mostly light dk = mostly dark mt = mostly metallic	Thermoregulation	Schultz 1986 Hadley et al. 1988, 1992 Schweiger and Beierkuhnlein 2016
Leg colour	LC	pl = Pale dk = Dark	Thermoregulation	Schultz 1986 Hadley et al. 1988, 1992 Schweiger and Beierkuhnlein 2016

737 **Supplementary information 3** Means (SD) of the functional response traits measured for carabid beetle species collected in Armero, Colombia  
738 during El Niño and non-El Niño periods. All measures are in mm. n = number of individuals measured. unk = unknown, i.e., the trait could not  
739 be measured. Abbreviations are explained in Supplementary information 2.

Species	n	BS	HW	ANT	CES	PW	PD	ABW	ABD	Pro-FL	Pro-FW	Pro-TL	Pro-TSL	Fore-LTL	MTL	Meta-FL	Meta-FW	Meta-TL	Meta-TSL	Hind-LTL
<i>Apenes coriacea</i>	1	11.69	2.01	unk	0.45	2.56	1.54	3.56	1.38	1.91	0.63	1.78	1.68	5.36	1.16	2.67	0.69	2.29	2.34	7.29
<i>Apenes morio</i>	2	8.85	1.67 (0.17)	2.73	0.27 (0.04)	2.04 (0.16)	1.21 (0.11)	3.14 (0.43)	1.07 (0.05)	1.61 (0.07)	0.47 (0.05)	1.2 (0.13)	0.83	3.34	0.82 (0.04)	1.99 (0.05)	0.55 (0.05)	1.71 (0.26)	1.37 (0.09)	5.07 (0.22)
<i>Apenes prasinus</i>	6	10.94 (0.52)	2.20 (0.12)	4.05 (0.11)	0.39 (0.04)	3.08 (0.15)	1.51 (0.06)	4 (0.22)	1.27 (0.13)	2.04 (0.13)	0.7 (0.04)	1.76 (0.13)	1.31 (0.07)	5.12 (0.3)	1.32 (0.11)	2.96 (0.08)	0.74 (0.03)	2.5 (0.12)	2.33 (0.13)	7.78 (0.18)
<i>Apenes</i> sp.	2	9.21 (1.34)	1.75 (0.3)	3.93 (0.43)	0.28 (0.07)	2.08 (0.39)	1.12 (0.01)	2.93 (0.35)	1.21 (0.13)	1.65 (0.35)	0.58 (0.08)	1.6 (0.34)	1.26 (0.23)	3.96 (1.69)	1.05 (0.21)	2.37 (0.39)	0.61 (0.13)	2.22 (0.52)	2.2 (0.34)	6.78 (1.24)
<i>Aspidoglossa crenata</i>	3	7.12 (0.36)	1.29 (0.05)	2.41 (0.02)	0.18 (0)	1.9 (0.07)	1.15 (0.13)	2.19 (0.09)	0.87 (0.03)	1.21 (0.05)	0.55 (0.04)	1.07 (0.05)	0.67 (0.08)	2.94 (0.16)	0.71 (0.02)	1.53 (0.03)	0.28 (0.02)	1.32 (0.05)	1.17 (0.06)	4.01 (0.07)
<i>Athrostictus paganus</i>	1	9.08	1.88	2.93	0.30	2.81	0.94	2.91	0.98	1.53	0.54	1.22	1.04	3.79	1.19	2.09	0.57	2.02	1.92	6.02
<i>Barysomus hoepfneri</i>	5	10.21 (0.68)	2.95 (0.08)	3.26 (0.2)	0.48 (0.03)	4.16	1.43 (0.42)	3.48 (0.16)	1.67 (0.27)	1.81 (0.09)	0.68 (0.02)	1.51 (0.06)	1.24 (0.06)	4.57 (0.19)	1.22 (0.08)	2.21 (0.14)	0.74 (0.02)	2.67 (0.98)	1.86 (0.1)	6.38 (0.07)
<i>Calosoma alternans</i>	10	23.65 (1.37)	4.61 (0.25)	11.17 (1.09)	1.86 (0.22)	6.94 (0.52)	5.02 (0.81)	9.07 (0.57)	4.08 (0.65)	4.88 (0.45)	1.62 (0.24)	4.52 (0.39)	3.95 (0.31)	13.35 (0.95)	2.31 (0.37)	6.15 (0.38)	1.63 (0.17)	7.08 (0.51)	5.83 (0.71)	19.06 (1.44)
<i>Camptodontus</i> sp.	1	10.13	2.06	2.82	0.25	2.69	1.41	2.67	1.29	1.41	0.71	1.44	1.12	3.97	0.61	1.59	0.49	1.62	1.39	4.60
<i>Clivina</i> sp.	3	8.57 (0.05)	1.45 (0.06)	2.39 (0.03)	0.11 (0.01)	2.07 (0.18)	1.28 (0.06)	1.96 (0.06)	1.05 (0.02)	1.22 (0.11)	0.61 (0.06)	1.05 (0.03)	0.85 (0.11)	2.82 (0.43)	0.54 (0.04)	1.24 (0.11)	0.39 (0.03)	1.23 (0.1)	0.94 (0.07)	3.4 (0.27)
<i>Enceladus gigas</i>	9	48.48 (4.35)	10.15 (0.49)	18.62 (1.69)	4.47 (0.26)	12.16 (0.73)	5.77 (0.56)	11.62 (0.81)	5.08 (0.52)	6.37 (0.38)	2.49 (0.15)	6.45 (0.29)	6.34 (0.86)	15.28 (1.16)	3.86 (0.2)	9.72 (0.39)	2.92 (0.21)	10.31 (0.6)	9.81 (0.33)	29.99 (1.02)

<i>Galerita</i> sp.	7	15.38 (0.22)	2.38 (0.03)	9.66 (0.5)	0.68 (0.05)	2.69 (0.06)	2.38 (0.2)	4.19 (0.31)	2.3 (0.19)	3.56 (0.13)	0.95 (0.06)	3.05 (0.16)	2.48 (0.17)	8.73 (0.8)	1.55 (0.07)	5.52 (0.26)	0.81 (0.07)	5.06 (0.28)	4.37 (0.24)	14.97 (0.47)
<i>Megacephala affinis</i>	10	15.91 (1.59)	4.27 (0.28)	10.19 (0.83)	2.05 (0.34)	3.94 (0.28)	1.89 (0.27)	4.4 (0.33)	2.46 (0.37)	3.25 (0.18)	0.97 (0.06)	2.67 (0.17)	2.93 (0.37)	9.04 (0.43)	1.32 (0.15)	5.05 (0.31)	0.84 (0.08)	5.21 (0.29)	5.64 (0.46)	15.9 (0.96)
<i>Stolonis interceptus</i>	1	6.79	1.21	3.08	0.15	1.69	0.79	2.13	0.93	1.32	0.42	1.13	0.70	3.16	0.74	1.63	0.44	1.18	1.07	3.88
<i>Tetragonoderus</i> sp.	6	4.22 (0.18)	0.87 (0.04)	1.6 (0.3)	0.09 (0)	1.17 (0.04)	0.68 (0.06)	1.49 (0.06)	0.67 (0.08)	0.78 (0.06)	0.26 (0.03)	0.67 (0.08)	0.52 (0.07)	1.97 (0.12)	0.56 (0.03)	1.11 (0.06)	0.32 (0.01)	1.04 (0.05)	1.1 (0.08)	3.23 (0.19)

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741 **Supplementary information 4** Mean (SD) functional response trait ratios for carabid beetle species collected in Armero, Colombia during El  
742 Niño and non-El Niño periods. All measures are in mm. n = number of individuals measured. unk = unknown, which means that the trait could  
743 not be measured. Abbreviations are explained in Supplementary information 2.

Species	n	HW/BS	ANT/ BS	CES/BS	PW/ ABW	PD/ ABD	Pro- FL/BS	Pro- FW/BS	Pro- TL/BS	Pro- TSL/BS	Fore- LTL/BS	MTL/ BS	Meta- FL/BS	Meta- FW/BS	Meta- TL/BS	Meta- TSL/BS	Hind- LTL/BS
<i>Apenes coriacea</i>	1	0.17	unk	0.04	0.72	1.11	0.16	0.05	0.15	0.14	0.46	0.10	0.23	0.06	0.20	0.20	0.62
<i>Apenes morio</i>	2	0.19 (0.02)	0.31	0.03 (0)	0.65 (0.04)	1.13 (0.05)	0.16 (0.01)	0.05 (0.01)	0.14 (0.01)	0.09	0.38	0.09 (0.01)	0.23 (0.01)	0.06 (0.01)	0.21 (0.03)	0.16 (0.01)	0.59 (0.02)
<i>Apenes prasinus</i>	6	0.20 (0.01)	0.36 (0.02)	0.04 (0)	0.78 (0.03)	1.22 (0.15)	0.19 (0.01)	0.06 (0)	0.16 (0.01)	0.12 (0)	0.47 (0.02)	0.12 (0.01)	0.27 (0.01)	0.07 (0)	0.23 (0.01)	0.21 (0.02)	0.71 (0.04)
<i>Apenes</i> sp.	2	0.19 (0.01)	0.43 (0.02)	0.03 (0)	0.71 (0.05)	0.94 (0.11)	0.18 (0.01)	0.06 (0)	0.17 (0.01)	0.14 (0)	0.42 (0.12)	0.11 (0.01)	0.26 (0.01)	0.07 (0.01)	0.24 (0.02)	0.24 (0)	0.73 (0.03)
<i>Aspidoglossa crenata</i>	3	0.18 (0)	0.34 (0.02)	0.02 (0)	0.87 (0.07)	1.32 (0.10)	0.17 (0.01)	0.08 (0)	0.15 (0.01)	0.09 (0.01)	0.41 (0.03)	0.1 (0)	0.22 (0.01)	0.04 (0)	0.19 (0)	0.16 (0.02)	0.57 (0.02)
<i>Athrostictus paganus</i>	1	0.21	0.32	0.03	0.96	0.97	0.17	0.06	0.13	0.11	0.42	0.13	0.23	0.06	0.22	0.21	0.66
<i>Barysomus hoepfneri</i>	5	0.29 (0.02)	0.31 (0.03)	0.05 (0)	1.2 (0.09)	0.84 (0.16)	0.18 (0.01)	0.07 (0)	0.15 (0.01)	0.12 (0.01)	0.45 (0.03)	0.12 (0.01)	0.22 (0.02)	0.07 (0)	0.26 (0.09)	0.18 (0.02)	0.63 (0.05)
<i>Calosoma alternans</i>	10	0.2 (0.01)	0.47 (0.03)	0.08 (0.01)	0.77 (0.06)	1.26 (0.10)	0.21 (0.02)	0.07 (0.01)	0.19 (0.01)	0.17 (0.01)	0.57 (0.03)	0.1 (0.01)	0.26 (0.01)	0.07 (0)	0.3 (0.01)	0.25 (0.02)	0.81 (0.03)
<i>Camptodontus</i> sp.	1	0.20	0.28	0.02	1.01	1.09	0.14	0.07	0.14	0.11	0.39	0.06	0.16	0.05	0.16	0.14	0.45
<i>Clivina</i> sp.	3	0.17 (0.01)	0.28 (0)	0.01 (0)	1.11 (0.04)	1.24 (0.10)	0.14 (0.01)	0.07 (0.01)	0.12 (0)	0.1 (0.01)	0.33 (0.05)	0.06 (0)	0.14 (0.01)	0.05 (0)	0.14 (0.01)	0.36 (0.43)	0.4 (0.03)
<i>Enceladus gigas</i>	9	0.21 (0.02)	0.38 (0.03)	0.09 (0.01)	1.04 (0.05)	1.12 (0.08)	0.13 (0.01)	0.05 (0)	0.13 (0.01)	0.13 (0.02)	0.32 (0.03)	0.08 (0.01)	0.2 (0.01)	0.06 (0)	0.21 (0.02)	0.2 (0.02)	0.61 (0.05)
<i>Galerita</i> sp.	7	0.15 (0)	0.62 (0.02)	0.04 (0)	0.64 (0.06)	1.01 (0.06)	0.23 (0.01)	0.06 (0)	0.2 (0.01)	0.16 (0.01)	0.57 (0.06)	0.1 (0.01)	0.36 (0.02)	0.05 (0)	0.33 (0.02)	0.29 (0.02)	0.98 (0.03)
<i>Megacephala affinis</i>	10	0.27 (0.02)	0.65 (0.08)	0.13 (0.01)	0.9 (0.04)	0.78 (0.11)	0.2 (0.02)	0.06 (0)	0.17 (0.01)	0.18 (0.02)	0.55 (0.05)	0.08 (0.01)	0.32 (0.03)	0.05 (0)	0.33 (0.02)	0.36 (0.03)	1.02 (0.07)
<i>Stolonis interceptus</i>	1	0.18	0.45	0.02	0.79	0.85	0.19	0.06	0.17	0.10	0.47	0.11	0.24	0.06	0.17	0.16	0.57
<i>Tetragonoderus</i> sp.	6	0.22 (0.01)	0.38 (0.06)	0.02 (0)	0.80 (0.05)	1.06 (0.13)	0.19 (0.02)	0.06 (0.01)	0.16 (0.02)	0.12 (0.02)	0.46 (0.03)	0.13 (0.01)	0.27 (0.01)	0.08 (0)	0.25 (0.26)	0.26 (0.02)	0.77 (0.05)