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Ariza, Gloria Maria

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

Short title

TDF Carabid beetle trait distribution in a harsh environment

Authors

Gloria Maria Ariza[1*], Jorge Jácome[2], D. Johan Kotze[3]

Affiliations

[1] Departamento de Biología, Unidad de Ecología y Sistemática (UNESIS), Pontificia Universidad Javeriana, Bogotá, Colombia. ORCID ID: https://orcid.org/0000-0002-6935-8022

[2] Departamento de Biología, Unidad de Ecología y Sistemática (UNESIS), Pontificia Universidad Javeriana, Bogotá, Colombia. ORCID ID: https://orcid.org/0000-0003-0972-3056

[3] Faculty of Biological and Environmental Sciences, Ecosystems and Environment Research Programme, University of Helsinki, Niemenkatu 73, 15140, Lahti, Finland. ORCID ID: https://orcid.org/0000-0003-4211-4420

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Abstract

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

Keywords

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

1. Introduction

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

The configuration of insect bodies (high surface area/volume ratio) puts an additional constraint to the persistence and success of species in this environment (Schowalter 2006). As such, an insect's survival in ENSO-affected TDF landscapes will not only depend on their behavioural adaptations, but also their morphology (Cloudsley-Thompson 1975; Crawford 1981), and the effectiveness of those adaptations will contribute to the persistence of species (Chown et al. 2011). Species traits have become an important tool to predict the presence and persistence of species in the environment (Keddy 1992; Cadotte et al. 2011; Kraft et al. 2015). Carabid beetles have a wide range of traits linked to environment conditions (Homburg et al. 2014; Fountain-Jones et al. 2015), yet knowledge regarding this group's traits are lacking in the tropics. Changes in the environment, as a result of disturbance, can play an important role in filtering traits in ground beetles (Shibuya et al. 2011; Pakeman and Stockan 2014; Piano et al. 2017; Magura and Lövei 2019; but see Kraft et al. 2015). ENSO is a recurring event in the TDF landscape (Caviedes 2001; Grove and Adamson 2018), and is likely to have had a strong filtering effect on insect communities (see Kotze and Lawes 2007; Meir and Pennington 2011). If this is the case, species in this landscape are expected to display traits that cope with harsh conditions, but abundances may fluctuate substantially between wet and dry periods, particularly so during ENSO events.

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

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

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

2. Material and Methods

2.1 Study area

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

2.2 Carabid beetle sampling

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

2.3 Trait measurements

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

2.4 Data analyses

We used the χ2 test in Past 3.x (Hammer et al. 2001) to compare the distribution of each trait among the El Niño and non-El Niño episodes.

3. Results

3.1 Carabid beetle trait characteristics in the tropical dry forest landscape

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

Twenty percent of the species had fossorial forelegs (*Aspidoglossa crenata*, *Clivina* sp. and *Camptodontus* sp.), and had a prothorax width/abdomen width and prothorax depth/abdomen depth ratio of almost 1 (Supplementary information 4). Two runner species *Athrostictus paganus* and *Enceladus gigas* had the same body configurations. In terms of the fore- and hindleg total length, differences between fossorial and runner species were also clear; these were shorter for fossorial species (Fore-LTL/BS = 0.33-0.41, Hind-LTL/BS = 0.40-0.57): except for the runner species *Stolonis interceptus,* which had shorter hindlegs and *Apenes morio* and *E. gigas,* which had shorter forelegs. Most species had a long metatrochanter (73.3%; MTL/BS = 0.09-0.13), but *M. affinis* was the only species with a long and slender metafemora, long metatibiae and small metatrochanter.

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

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

3.2.1 Distribution of species

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

The wet season during both El Niño and non-El Niño periods had the highest number of individuals (88% and 71% respectively). Only two species were collected during the dry season of the El Niño period; *Galerita* sp. and *M. affinis*. During the non-El Niño period, similar numbers of species were collected during the dry (9 species) and wet (10 species) seasons. *Aspidoglossa crenata*, *B. hoepfnery*, *E. gigas*, *M. affinis* and *Tetragonoderus* sp. were present in both seasons.

3.2.2 Distribution of functional response traits

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

4. Discussion

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

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

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

Quantitatively, TDF carabid beetles were affected by El Niño (ENSO), as has happened with other tropical beetle groups (Lucky et al. 2002; Kishimoto-Yamada and Itioka 2008; Kishimoto-Yamada et al. 2009; Pérez and Zaragoza 2016). The number of species and individuals decreased more than two fold during the El Niño period. However, carabids showed differential responses to drought, similarly to the Chrysomelidae in Borneo during the 1998 ENSO event (Kishimoto-Yamada et al. 2009). In Colombian TDF, 62% of the collected species were not present during the El Niño period, *C. alternans* was the only species showing a substantial decrease during the non-El Niño period, its numerical decrease could be related to its life span (see Burgess 1911): its larvae were seen in high numbers in pastures in October and November (Ariza 2016, pers. obs.), however long-term studies can help to elucidate the life cycle of this species. On the contrary, *M. affinis* benefited considerably from an improved environment during non-El Niño periods. This fast running and flight capable species may be particularly vulnerable to desiccation during dry ENSO periods (Pearson and Vogler 2001). In general, the carabid beetle assemblage recovered quickly (within three months after El Niño ended), which may be due to diapause as an adaptive mechanism to survive harsh conditions (see Burgess 1911; Jeffords and Case 1987; Jacobs et al. 2011).

4.2 Carabid beetle trait distribution in the tropical dry forest landscape

Even though the carabid beetle assemblage in TDF was dominated by small species, more individuals of medium and large sized species were collected; the two most abundant species *C. alternans* (large) and *M. affinis* (medium) possibly benefitting from their lower volume-to-surface area ratio, thus resisting desiccation during dry conditions (Hood and Tschinkel 1990; Chown et al. 1995; Le Lagadec et al. 1998). These species were observed walking during the day (Ariza 2016, pers. obs.), but are considered to be active both during the day and night (intermediate activity) (Larochelle and Larivière 2003; Vitolo 2004). Another medium-size species, *Galerita* sp. is consider nocturnal (Larochelle and Larivière 2003), and is the only nocturnal species of TDF that meets all the characteristic traits described as typical of this life-style: long antennae, small eyes and a narrow head (Bauer and Kredler 1993). The rest of the nocturnal species (which are also small) have short antennae, or at least shorter than *Galerita* sp. and *M. affinis*. However, antennal length and head width differences between nocturnal and intermediate species groups were small, making it difficult to characterize daily activity using these traits. Carabid beetles use three methods to detect prey: visual, tactile and olfactory, or a combination of these; species that do not hunt visually, use their antennae and palps (Wheater 1989). Antennae are an important sensory structure (Chapman 1998; Ploomi et al. 2003), but it is unclear how prominent its role is in prey detection. On the contrary, eye surface area has distinct differences between nocturnal and diurnal active species. Studies have shown that eyes are a better trait to reflect activity period (Bauer 1985; Talarico et al. 2007, 2011, 2018). For instance, *C. alternans* and *M. affinis* have large eyes, and although they can hunt both during the day and night, they are probably better visual hunters.

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

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

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

5. Conclusions

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

Supplementary information

Additional information can be found online in the Supporting Information section

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

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

Supplementary information 3 Means (SD) of the functional response traits measured for carabid beetle species collected in Armero, Colombia 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 be measured. Abbreviations are explained in Supplementary information 2.

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

Declarations

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Conflict of interest: The authors declare that there are no conflicts of interest in conducting the research

Ethics approval: Not applicable

Consent to participate: Not applicable

Consent for publication: The first author declares that the two co-authors of this contribution are aware of the fact and have agreed to being so named

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

Code availability: Not applicable

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

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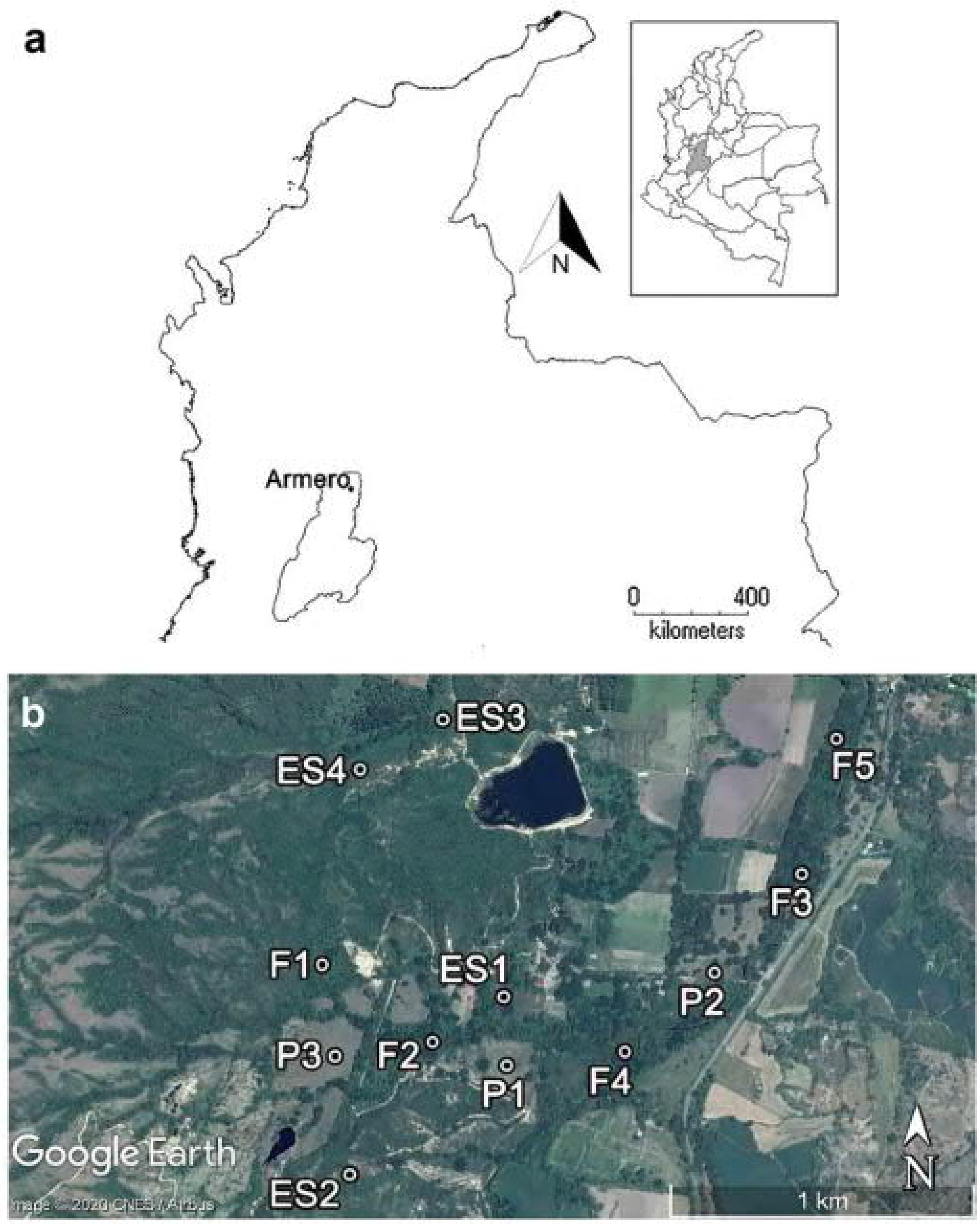

Fig. 1 Geographic locations of study sites in Armero. a: The location of Armero in Colombia. b: Armero. Abbreviations: F = forest; ES = early succession; P = pasture. Maps courtesy of DIVA-GIS 7.5 and Google Earth Image © 2020.

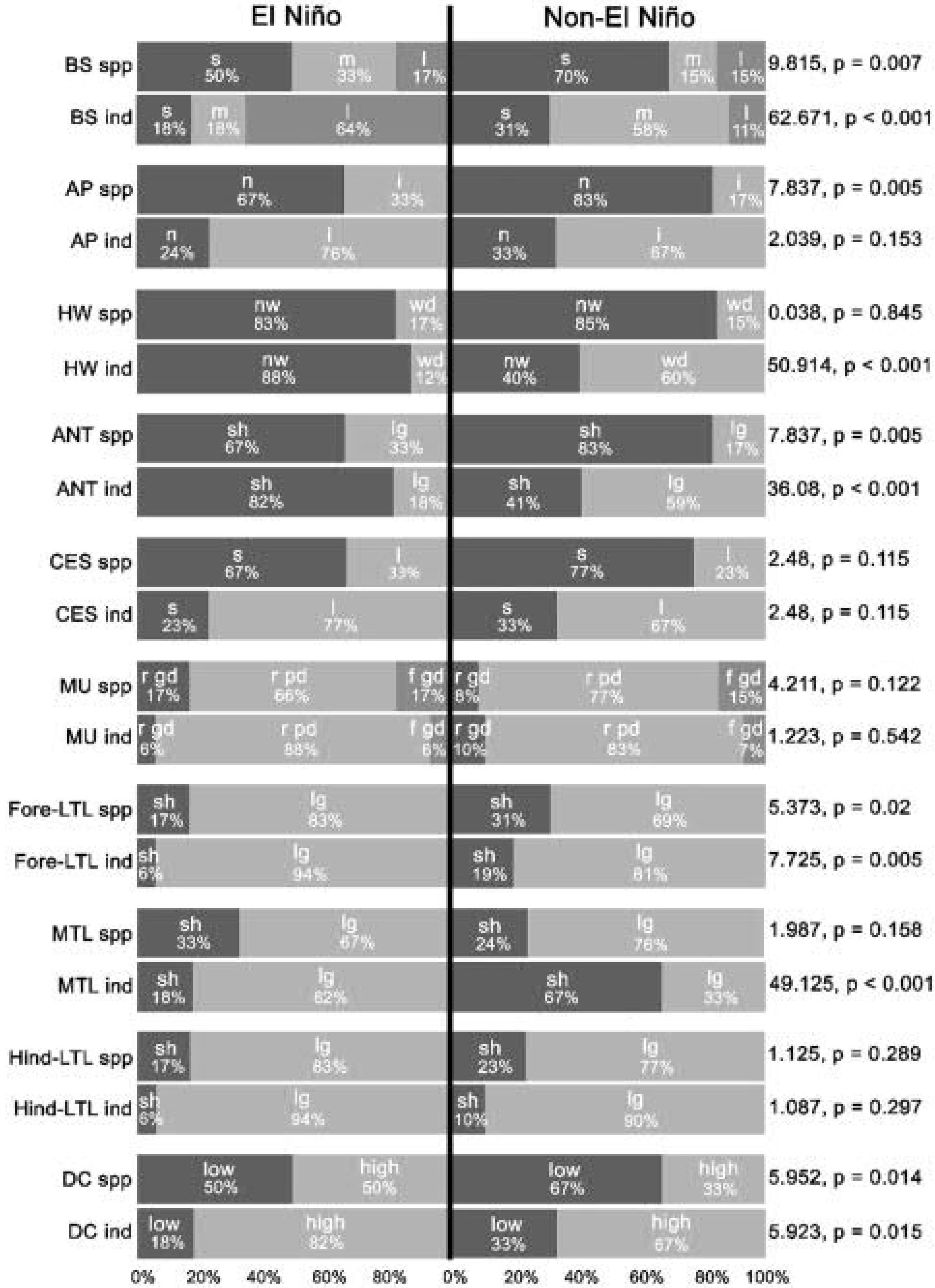

Fig. 2 Distribution of carabid beetle functional response traits among El Niño and non-El Niño periods in Armero, Colombia. Abbreviations are explained in Supplementary information 2. χ^2 and p values are presented that test for differences in the distribution of attributes within each trait between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

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

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

Table 2 Trait characterization of carabid beetles collected in Armero, Colombia during El Niño and non-El Niño periods. Abbreviations are 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
Apenes coriacea (Chevrolat, 1863)	s	n	nw	unk	s	r pd	sh	sh	lg	lg	lg	sl	sh	lg	low	lh	pl
Apenes morio (Dejean, 1825)	s	n	nw	sh	s	r pd	sh	sh	sh	lg	lg	sl	sh	lg	high	dk	pl
Apenes prasinus Ball & Shpeley, 1992	s	n	nw	sh	s	r pd	lg	lg	lg	lg	lg	wd	lg	lg	low	mt	dk
Apenes sp.	s	n	nw	sh	s	r pd	lg	lg	lg	lg	lg	wd	lg	lg	low	dk	pl
Aspidoglossa crenata (Dejean, 1825)	s	n	nw	sh	s	f gd	sh	sh	sh	lg	sh	sl	sh	sh	high	dk	dk
Athrostictus paganus (Dejean, 1831)	s	n	nw	sh	s	r gd	sh	sh	lg	lg	lg	sl	lg	lg	low	dk	pl
Barysomus hoepfneri Dejean, 1829	s	n	wd	sh	s	r pd	lg	sh	lg	lg	sh	wd	lg	lg	low	dk	pl
Calosoma alternans (Fabricius, 1792)	l	i	nw	sh	l	r pd	lg	lg	lg	lg	lg	wd	lg	lg	high	dk	dk
Camptodontus sp.	s	n	nw	sh	s	f gd	sh	sh	sh	sh	sh	sl	sh	sh	unk	dk	dk
Clivina sp.	s	n	nw	sh	s	f gd	sh	sh	sh	sh	sh	sl	sh	sh	high	dk	dk
Enceladus gigas Bonelli, 1813	l	unk	nw	sh	l	r gd	sh	sh	sh	sh	sh	sl	sh	lg	low	dk	dk
Galerita sp.	m	n	nw	lg	s	r pd	lg	lg	lg	lg	lg	sl	lg	lg	low	dk	dk
Megacephala affinis Dejean, 1825	m	i	wd	lg	l	r pd	lg	lg	lg	sh	lg	sl	lg	lg	high	mt	pl
Stolonis interceptus Chaudoir, 1873	s	n	nw	sh	s	r pd	lg	lg	lg	lg	lg	sl	sh	sh	low	dk	pl
Tetragonoderus sp.	s	n	nw	sh	s	r pd	lg	lg	lg	lg	lg	wd	lg	lg	low	dk	dk

***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-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** = hindleg total length, **DC** = dispersal capacity, **BC** = body colour, **LC** = leg colour.

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

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

Supplementary information 1 Air humidity and temperature measured in Armero, Colombia during the dry and wet seasons of the non-El Niño 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
Mean	**71.17**	**29.86**	**68.75**	**30.06**	**36.25**	**44.91**	**61.58**	**35.53**

Supplementary information 2 Functional response traits to desiccation resistance (and their definitions) measured on carabid beetle species 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	Desiccation resistance	Schoener and Janzen 1968
		s = small (4-12 mm)		Le Lagadec et al. 1998
		m = medium (15-16 mm)		Chown and Klok 2003
		l = large (23-50 mm)		
Daily activity period	AP	d = diurnal	Activity time	Bauer and Kredler 1993
		n = nocturnal		
		i = intermediate (both d and n)		
Head width	HW	Maximum width, including compound eyes	Activity time	Bauer and Kredler 1993
		nw = narrow (HW/BS: 0.15-0.22)		
		wd = wide (HW/BS: 0.27-0.29)		
Antenna length	ANT	From the base of the first antennomere until the apex	Activity time	Bauer and Kredler 1993
		sh = short (ANT/BS: 0.28-0.47)		
		lg = long (ANT/BS: 0.58-0.65)		
Compound eye surface area	CES	Longest axis (long, width): $A = \pi LW/4$	Activity time	Bauer et al. 1998
		s = small (CES/BS: 0.01-0.05)		Talarico et al. 2018
		l = large (CES/BS: 0.08-0.13)		
Microhabitat use	MU	r = runner	Microhabitat use	Forsythe 1981, 1987
		f = fossorial		
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

Supplementary information 3 Means (SD) of the functional response traits measured for carabid beetle species collected in Armero, Colombia 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 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**
Apenes coriacea	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
Apenes morio	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)
Apenes prasinus	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)
Apenes 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)
Aspidoglossa crenata	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)
Athrostictus paganus	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
Barysomus hoepfneri	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)
Calosoma alternans	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)
Camptodontus 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
Clivina 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)
Enceladus gigas	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)

Galerita 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)
Megacephala affinis	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)
Stolonis interceptus	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
Tetragonoderus 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)

Supplementary information 4 Mean (SD) functional response trait ratios for carabid beetle species collected in Armero, Colombia during El Niño and non-El Niño periods. All measures are in mm. n = number of individuals measured. unk = unknown, which means that the trait could 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
Apenes coriacea	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
Apenes morio	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)
Apenes prasinus	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)
Apenes 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)
Aspidoglossa crenata	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)
Athrostictus paganus	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
Barysomus hoepfneri	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)
Calosoma alternans	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)
Camptodontus 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
Clivina 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)
Enceladus gigas	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)
Galerita 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)
Megacephala affinis	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)
Stolonis interceptus	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
Tetragonoderus 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)