

RECOVERY DYNAMICS OF CARABID BEETLES
(COLEOPTERA, CARABIDAE) IN COLOMBIAN TROPICAL
DRY FOREST



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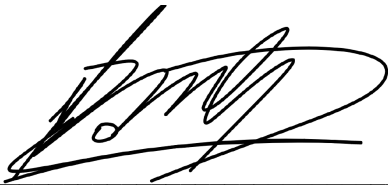
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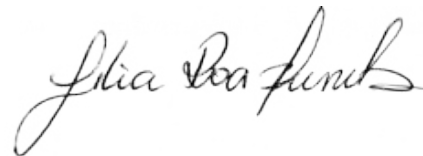
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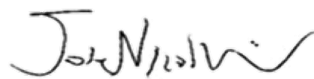
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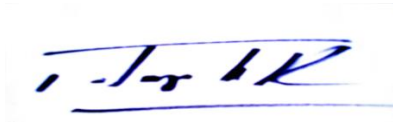


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*For all those beings
who taught me about love,
while I did science*

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"The university is not responsible for the concepts issued by its students in their thesis work. It will only ensure that nothing contrary to dogma and Catholic morality is published and because the theses do not contain personal attacks against any person, rather the desire to seek truth and justice is seen in them"

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Chapter 1

General introduction

1.1. Tropical dry forest

The tropical dry forest (TDF) ecosystem is characterized by strong seasonal rainfall with the dry season occurring during four to six months per year, with less than 100 mm of rainfall (Dirzo et al. 2011). This seasonality produces a dominance of deciduous trees as a response to a lack of water (Holbrook et al. 2009). Open tree canopies change the TDF environment and resource availability (Lebrija-Trejos et al. 2011), generating a response in many organisms to adapt to this harsh environment (e.g., Ceballos, 2009; Diaz-Pulido et al. 2014; Stoner & Timm, 2011; Urbina-Cardona et al. 2014). As such, it is not surprising that this landscape displays remarkable levels of endemism for some animals groups (Ceballos, 2009; Linares-Palomino et al. 2011) and beta diversity (Balvanera et al. 2002). This unique composition of species call for research with the aim to search for general patterns, and in this way, understand the ecological processes taking place there (Sánchez-Azofeifa et al. 2005b). Knowledge of TDF is scarce compared with other tropical forests (Sánchez-Azofeifa et al. 2005b), yet information on vegetation community dynamics is increasing in recent years. However, the same can not be said for fauna of the TDF (Ramos-Fabiel et al. 2019).

TDF is one of the most endangered tropical ecosystems (Miles et al. 2006). Anthropogenic activities produce landscape transformation (Sánchez-Azofeifa et al. 2005a), generating a matrix of forest, pasture, and crops as happens in Colombia in general (García et al. 2014; Portillo-Quintero & Sánchez-Azofeifa, 2010). These activities have resulted in a highly fragmented landscape of small forest patches (Pizano et al. 2016), calling for urgent restoration activities (Vargas & Ramírez, 2014). Threats to the preservation of TDF is exasperated by climate change (Miles et al. 2006). Drought events are expected to increase and made worse by more intense El Niño/Southern Oscillation episodes. However, given the adaptation of species to water limitation, it is possible that this ecosystem is more resilient to drought than to extreme precipitation (Stan & Sánchez-Azofeifa, 2019).

The El Niño/Southern Oscillation (ENSO) climatic phenomenon is an inter-annual cycle produced by an unusual warming of the surface temperature in the Pacific Ocean. This event affects many tropical countries like Colombia, where El Niño has a warm phase (Poveda & Mesa, 1996; Timmermann et al. 1999) characterized by high temperatures and low precipitation (Poveda et al. 2000). This was the case in 2015/2016, which is considered one of the stronger ENSO episodes reported since the end of the twentieth century (Luo et al. 2018; Panisset et al. 2017). In Colombia, the episode started in March 2015 and lasted until July 2016 (UNGRD, 2016).

1.2. TDF insects: Dynamics and succession

Seasonality in TDF affects insect dynamics considerably (see Wolda, 1988). Insects in TDF show seasonal peaks in richness and abundance during the wet season. This is true for groups like Cantharidae (Pérez & Zaragoza, 2016), Buprestidae (Corona-López et al. 2017), Cerambycidae (Noguera-Martínez et al. 2007; Noguera et al. 2018; Noguera et al. 2002; Toledo et al. 2002), Scarabaeidae (Liberal et al. 2011; Novais et al. 2016; Rangel-Acosta & Martínez-Hernández, 2017) and Staphylinidae (Jiménez-Sánchez et al. 2009), but not for dung beetle richness in Brazil (Medina & Lopes, 2014), since differences between the wet and dry season are small. Insect seasonal patterns are affected by the relationship among community variables and rainfall (Jiménez-Sánchez et al. 2009; Liberal et al. 2011; Pérez & Zaragoza, 2016) or air humidity (García et al. 2001; Rangel-Acosta & Martínez-Hernández, 2017), demonstrating the important role of water for these organisms.

Regarding TDF succession, little is known about the responses of insects to vegetation development during this process (Neves et al. 2014; Neves et al. 2010a; Neves et al. 2010b). For arboreal ants, successional changes were registered in species composition but not in richness, and it is estimated that it will take 25 years of forest regeneration for the community to recover completely (Neves et al. 2010b). Similar results were found in Brazilian

ants by Marques et al. (2017), where arboreal and epigaeic ant communities showed compositional changes with succession but not species richness, yet hypogaeic ants changed in both richness and composition. No consistent seasonal pattern was exhibited by this group; richness was high in the dry season without compositional changes among seasons. Similarly, Neves et al. (2010b) found seasonal differences in ant species composition but not in richness.

On the contrary, dung beetle richness and species composition did change with succession and season (Neves et al. 2010a). Even though knowledge of successional dynamics of insects in TDF is lacking, the different responses of groups can be related to the environment and resource requirements (Neves et al. 2014). Nevertheless, richness does not appear to reflect recovery well (Jaunatre et al. 2013; Noss, 1990; Ottonetti et al. 2006), while species composition does (e.g., Déri et al. 2011). A more mechanistic approach, such as trait diversity, can potentially better explain the link between insect community responses and succession in this harsh landscape (Audino et al. 2014; Derhé et al. 2016). For instance, bee succession evaluated along a 2-67 year chronosequence using a trait-based approach (Ramos-Fabiel et al. 2019), showed relations among functional response traits and vegetation structure.

1.3. Insects in ecosystems that experience drought

The adaptation of insects to arid environments is well-documented (Cloudsley-Thompson, 1975; Crawford, 1981). Two principal characteristics of such insects make them vulnerable to the environment experienced in arid ecosystems: (1) ectothermic body regulation, and (2) high area-volume ratio (Schowalter, 2006). Insects resolve challenges to live in extreme temperatures, low humidity, and water shortages through morphological, behavioral and physiological adaptations (Cloudsley-Thompson, 2001). Physiological adaptations to conserve water is well-known (Zachariassen, 1996), and will not be investigated in this thesis. I will mainly focus on adaptive responses that deal with morphology and behaviour. The most

common morphological adaptations of insects in arid environments is an increased body size, which is considered an effective adaptation to resist desiccation risk (Chown et al. 1995; Le Lagadec et al. 1998), and nocturnal activity (Cloudsley-Thompson, 2001). However, Buxton (1923) document that some Tenebrionidae species can change their activity period depending on the season, so that in summer they can adopt a crepuscular activity and in spring a daily activity. Another behavioural adaptation is burrowing, which allows the individual to escape bad conditions during the day (Cloudsley-Thompson, 1975). Seasonal activity linked to life cycles of species is another adaptation to escape bad conditions, which includes diapause as a strategy to synchronise the life cycle with suitable environmental conditions (see Hodek, 2012; Masaki, 1980; Wilches et al. 2016).

In quantitative terms, although droughts can substantially reduce numbers of species and individuals, there is no general pattern in tropical insects, and their response (besides environmental factors) can be influenced by food requirements of each species (White, 2008). For instance, it is known that drought can produce an outbreak in plant-eating insects (Mattson & Haack, 1987). In Bornean leaf beetles, species were severally affected by a drought event, however, after the event the recovery of insects was not uniform. While some species' abundances increased, others decreased, and some species experienced local extinctions (Kishimoto-Yamada et al. 2009; Kishimoto-Yamada & Itioka, 2008), similar to bees (Harrison, 2001). For Cantharidae beetles, they showed a substantial decrease in richness in TDF as a result of drought (Pérez & Zaragoza, 2016).

Knowledge about adaptive traits in the tropics is scarce. A study in Panamanian ants evaluated desiccation resistance in different forest strata (Bujan et al. 2016). Canopy ants showed considerable desiccation resistance (measured as the number of hours individuals survive desiccation stress), similar to ants with greater mass. Other herbivores in TDF displayed high diversity during the dry season because of two strategies: (1) escape in space, using evergreen species as hosts, and (2) escape in time, changing their behaviour towards a nocturnal activity (Silva et al. 2017). Finally, in a Colombian coffee agroforestry landscape,

generalist ants were favoured by an ENSO drought event (Arenas-Clavijo & Armbrrecht, 2019).

1.4. Carabid beetles

Carabidae is a large beetle family (ca. 37 404 described species) (Lorenz, 2019), widely used as bioindicators in temperate regions, partly because of the long history in studying this group and, consequently, the vast amount of information available on their taxonomy and biology (Kotze et al. 2011). In the Neotropics, little is known about this group, including whether carabid beetles are suitable for bioindication (Martínez, 2005; Rainio & Niemelä, 2003). The principal reason of this lack of information is its high diversity in the tropics and hence the difficulty in classifying and identifying carabid species (Erwin et al. 2015; Lucky et al. 2002; Maveety et al. 2011). This results in scarce taxonomic keys to species level for carabid beetles in the tropics.

The response of carabid beetles to the environment is well-known (Thiele, 1977), including to disturbance and landscape management (Lövei & Sunderland, 1996; Rainio & Niemelä, 2003). Environmental variables such as soil humidity (Fidan & Sirin, 2016; Kaizuka & Iwasa, 2015; Niemelä et al. 1992), litter (Antvogel & Bonn, 2001; Koivula et al. 1999) and vegetation structure (Molnár et al. 2001) influence their presence and distribution. Thiele (1977) attributes the influence of vegetation structure to microclimatic changes that vegetation cover produces. Similarly, litter provides food and shelter from predation and adverse environmental conditions (Antvogel & Bonn, 2001) – for instance the amount of prey correlates with litter depth, and in this way affects carabid assemblages (Koivula et al. 1999). Soil humidity is considered an important factor due to the desiccation risk that carabids experience during their immature stages (Lövei & Sunderland, 1996).

1.5. General aims of this thesis

The overall aim of this thesis was to characterize the successional and seasonal dynamics of carabid beetles in tropical dry forest in Colombia, using assemblage variables, including the number of species and individuals, and functional response traits. Similarly, with the goal of finding a mechanistic understanding of the responses of carabid beetles to this harsh environment, I related the responses of the assemblage, individual species and traits to environmental variables. The specific objectives developed included:

1. To characterize the responses of TDF carabid beetles - focusing on drought tolerance - by investigating changes in TDF carabid assemblages during an El Niño (2015) and non-El Niño (2016) event in both (1) quantitative assemblage parameters and (2) qualitative parameters.
2. To evaluate carabid beetle assemblage changes during succession in tropical dry forest in Colombia, and their response to environmental variables along this successional process and season (wet and dry periods).
3. To identify ecological groups of carabid beetles at different successional stages and the environmental variables that filter their traits in this harsh environment.
4. To present a list of species collected from TDF in the Valley of Magdalena River and to link ecological information with its taxonomic identity.

1.6. Thesis outline

In this work, I characterized the dynamics of carabid beetles along an environmental gradient formed by successional processes and a marked dry season in three different habitat types (pasture as initial point, early successional stage, and forest as intermediate successional stage) in a Colombian tropical dry forest landscape. In the first chapter, background context is provided and the scope of the thesis is established. In chapter 2, I analyzed the suitability of morphological traits to infer not only functional response traits but also the adaptability of carabid beetles to the harsh TDF environment exasperated by the El Niño/Southern Oscillation (ENSO). I also compared qualitative and quantitative variables among the El Niño and non-El Niño events to observe possible carabid beetle changes as a result of environmental variability. In chapter 3, I evaluated the response of carabid beetles (both at the assemblage and individual species levels) along TDF succession and dry and wet periods, which was exasperated by the El Niño/Southern Oscillation (ENSO). To better understand these responses, I related environmental variables (soil and air humidity and temperature, leaf litter depth and canopy cover) to the beetle assemblage to identify drivers of successional dynamics. Similarly, and with the goal to have a better understanding of the successional dynamics of these organisms, I explored in chapter 4 the functional response of carabid beetles to succession. I identified ecological groups present in different successional habitat types in TDF, and environmental variables related to each trait. In chapter 5, I present a list of TDF carabid species collected from the Valley of Magdalena River (Colombia), and ecological information associated with these species inferred from morphological traits, in an attempt to offer a starting point for future studies on this taxonomic group. Finally, in chapter 6, I provide a general overview of my thesis to synthesize the findings and propose general patterns of the dynamics of carabid beetles in the TDF successional environment.

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Chapter 2

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

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Abstract

The tropical dry forest (TDF) ecosystem is characterised 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 characterise 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

2.1. Introduction

The tropical dry forest (TDF) ecosystem is characterised by strong seasonal rainfall with four to six dry months (Murphy & Lugo, 1986), making the availability of moisture crucial to the

survival of organisms (Maass & 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 characterised 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 & 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 (Hernández & Caballero, 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 (Cadotte et al. 2011; Keddy, 1992; Kraft et al. 2015). Carabid beetles have a wide range of traits linked to environment conditions (Fountain-Jones et al. 2015; Homburg et al. 2014), 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 (Magura & Lövei, 2019; Pakeman

& Stockan, 2014; Piano et al. 2017; Shibuya et al. 2011; but see Kraft et al. 2015). ENSO is a recurring event in the TDF landscape (Caviedes, 2001; Grove & Adamson, 2018), and is likely to have had a strong filtering effect on insect communities (see Kotze & Lawes, 2007; Meir & 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 characterise 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 (Chown et al. 1995; Hood & Tschinkel, 1990; 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 requiring fewer resources to satisfy their energetic requirements and protection against predators (Blanckenhorn, 2000; Chown & Gaston, 2010). 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 (Bauer et al. 1998; Bauer & Kredler, 1993; Erwin, 1979; Forsythe, 1987) 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 & 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 (Hadley et al. 1992, 1988; Schultz, 1986).

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 & Sunderland, 1996; Venn, 2016). We presume temperature and moisture act as clues to start and end diapause during an ENSO episode (Cloudsley-Thompson, 1975; Hodek, 2003, 2012; Tauber et al. 1998; Wolda & Denlinger, 1984). 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 & García, 2014; Pulla et al. 2015).

2.2. Material and methods

2.2.1. Study area

Ground beetles were surveyed in the dry forest biome in Armero (Tolima), Colombia (Fig. 2.1). 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 2.1). 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.

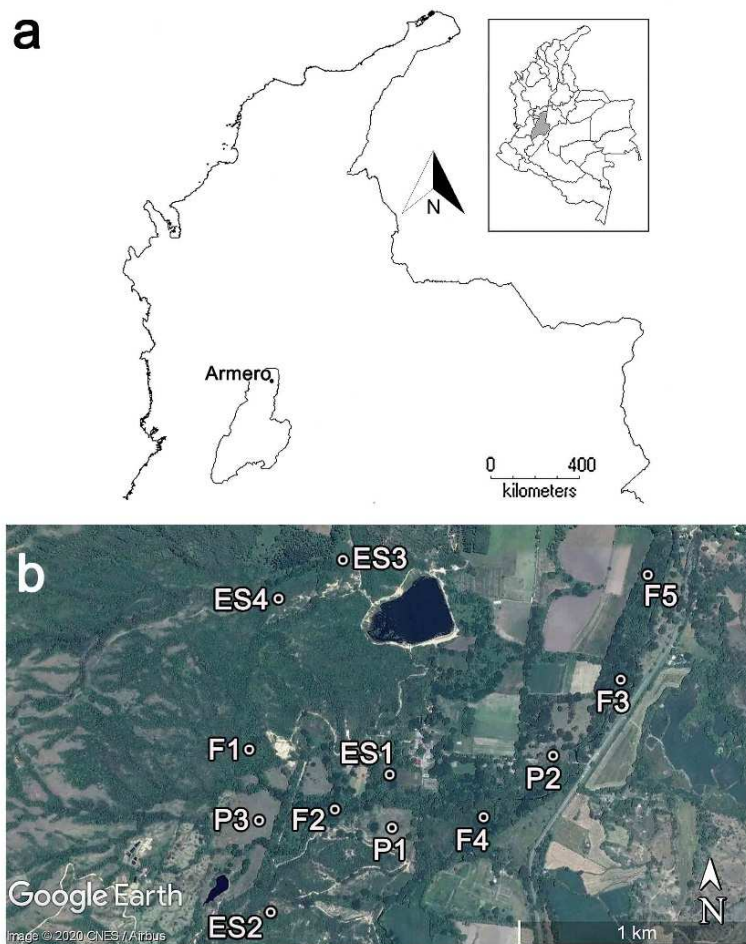


Figure 2.1 Geographic locations of study sites in Armero: (a) the location of Armero in Colombia, (b) Armero. Abbreviations: F = forest; ES = early succession; P = pasture. Maps courtesy of DIVA-GIS 7.5 and Google Earth Image © 2020.

2.2.2. 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 Ball & Shpeley (2002, 2009), Bruschi (2010), Dejean (1829, 1831); Putzeys (1846, 1866); Reichardt (1967); Vitolo (2004) and Will (2005). 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).

2.2.3. Trait measurements

Based on a literature review, a series of traits related to the adaptation to desiccation were measured (Supplementary information 2.2). Information about the ecology and dispersal power (at genus level) were obtained from Larochelle & Larivière (2003), Martínez (2005), Vitolo (2004) 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 2.1). 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 1.52 k

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 2.3). 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 characterise certain attributes were from Bauer & Kredler (1993) and Forsythe (1981, 1987). Flight muscle development was determined by comparing the flight muscles of specimens to the flight muscle figures in Desender (2000).

2.2.4. Data analyses

We used the χ^2 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.

2.3. Results

2.3.1. Carabid beetle trait characteristics in the tropical dry forest landscape

The traits of 15 species were measured (Supplementary information 2.3); *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 2.2). 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 2.4). 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 2.4). 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=0.36–0.42, Hind-LTL/BS=0.40–0.57): except for the runner species *Apenes morio* (both fore- and hindlegs shorter), *Stolonis interceptus*, which had shorter hindlegs and, *A. paganus* 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.

Table 2.1 Range of values of functional response traits measured on the carabid beetle species collected. See Supplementary information 2.2 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	0.36-0.42
		Long	lg	0.45-0.59
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	0.62-1

Table 2.2 Trait characterisation of carabid beetles collected in Armero, Colombia during El Niño and non-El Niño periods. Abbreviations are explained in detail in Supplementary information 2.2.

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	sh	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. 1	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	sh	lg	lg	sl	lg	lg	low	dk	pl
<i>Barysomus boeppferi</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

*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.

2.3.2. Assemblage changes between El Niño and non-El Niño episodes

2.3.2.1. 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 2.3). 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. hoepfneri*, *E. gigas*, *M. affinis* and *Tetragonoderus* sp. were present in both seasons.

2.3.2.2. 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. 2.2. 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 individuals collected, was dominant during both periods.

Table 2.3 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
<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			1	d
<i>Aspidoglossa crenata</i>			3	dW
<i>Athrostictus 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
Total number of individuals	17		53	
Total number of species	6		14	

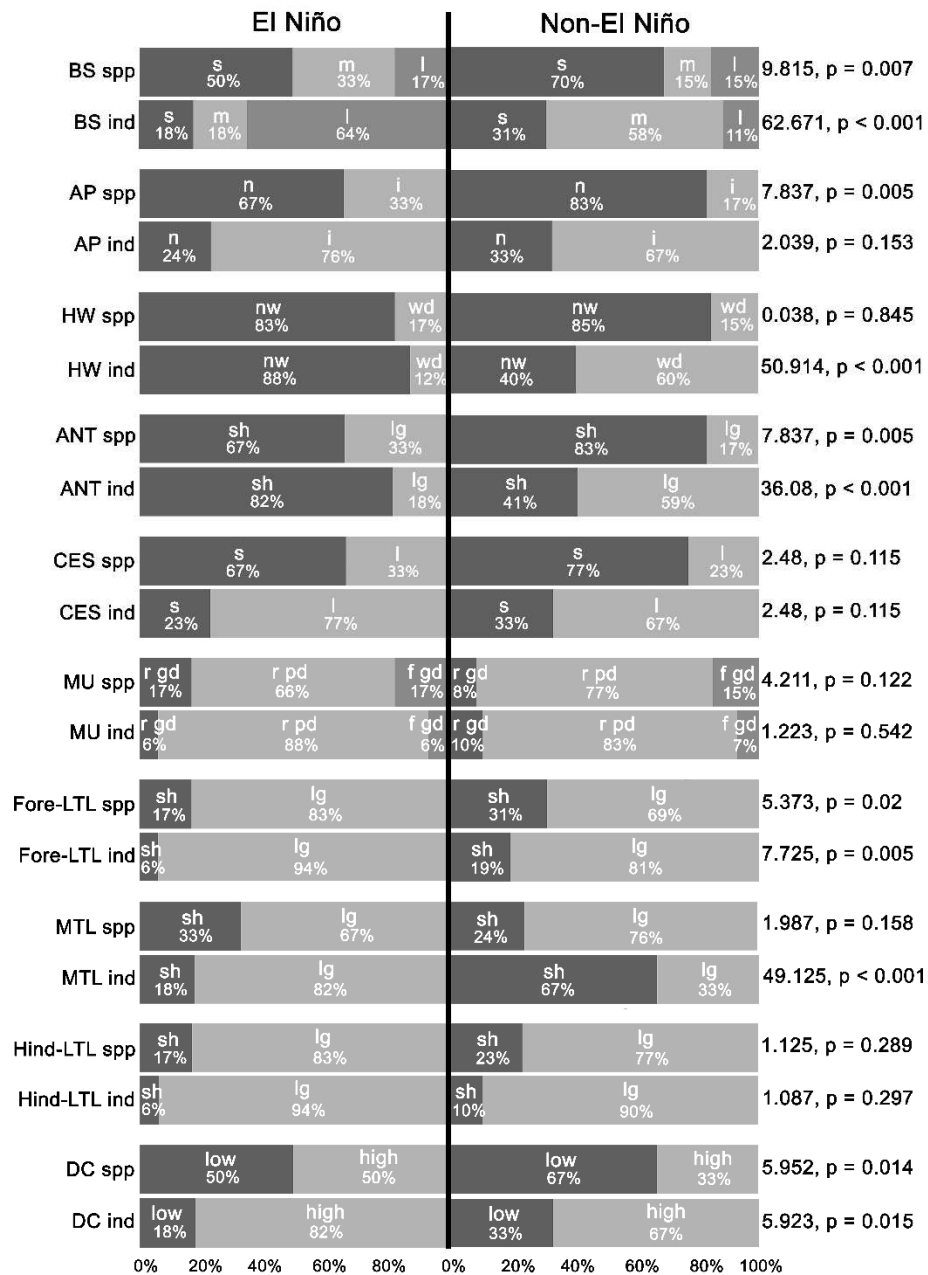


Figure 2.2 Distribution of carabid beetle functional response traits among El Niño and non-El Niño periods in Armero, Colombia. Abbreviations are explained in Supplementary information 2.2. χ^2 and p values are presented that test for differences in the distribution of attributes within each trait between the two climatic periods. spp = species, ind = individuals.

2.4. 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.

2.4.1. 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 (Hernández & Caballero, 2016; Kishimoto-Yamada & Itioka, 2008; Kishimoto-Yamada et al. 2009; Lucky et al. 2002). 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 & 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; Jacobs et al. 2011; Jeffords & Case, 1987).

2.4.2. 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 (Chown et al. 1995; Hood & Tschinkel, 1990; 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 & Larivière, 2003; Vitolo, 2004). Another medium-size species, *Galerita* sp. is considered nocturnal (Larochelle & 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 & 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. 2011, 2018, 2007). 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 & 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 & 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 2.2). *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 & 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).

2.5. 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 (Matsuo, 2006; Nelemans et al. 1989). Long term studies on the effects of ENSO linked with other anthropogenic pressures can clarify the real risks to carabid beetle communities during ENSO, especially given additional threats, such as climate change.

Supplementary information

Supplementary information 2.1 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	Air	Air	Air	Air	Air	Air	Air
	humidity	temperature	humidity	temperature	humidity	temperature	humidity	temperature
	(%)	(°C)	(%)	(°C)	(%)	(°C)	(%)	(°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 2.2 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 s = small (4-12 mm) m = medium (15-16 mm) l = large (23-50 mm)	Desiccation resistance	Schoener & Janzen, 1968 Le Lagadec et al. 1998 Chown & Klok, 2003
Daily activity period	AP	d = diurnal n = nocturnal i = intermediate (both d and n)	Activity time	Bauer & 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 & 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 & 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		

(Supplementary information 2.2, continue)

Trait	Abbreviation	Criteria to measure	Trait linked to	Author
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. 1992, 1988 Schweiger & Beierkuhnlein, 2016
Leg colour	LC	pl = Pale dk = Dark	Thermoregulation	Schultz, 1986 Hadley et al. 1992, 1988 Schweiger & Beierkuhnlein, 2016

Supplementary information 2.3 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 2.2.

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	3.63	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)	5.11 (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. 1	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)	4.51 (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)	6.74 (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)	3.13 (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)	19.16 (1.16)	3.86 (0.2)	9.72 (0.39)	2.92 (0.21)	10.31 (0.6)	9.81 (0.33)	29.85 (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)	9.10 (0.8)	1.55 (0.07)	5.52 (0.26)	0.81 (0.07)	5.06 (0.28)	4.37 (0.24)	14.95 (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)	8.85 (0.43)	1.32 (0.15)	5.05 (0.31)	0.84 (0.08)	5.21 (0.29)	5.64 (0.46)	15.91 (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)	3.25 (0.19)

Supplementary information 2.4 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 2.2.

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	0.41	0.09 (0.01)	0.23 (0.01)	0.06 (0.01)	0.21 (0.03)	0.16 (0.01)	0.57 (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. 1	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)	0.49 (0.12)	0.11 (0.01)	0.26 (0.01)	0.07 (0.01)	0.24 (0.02)	0.24 (0)	0.74 (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)	0.56 (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)	0.66 (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)	0.56 (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)	0.36 (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)	0.40 (0.03)	0.08 (0.01)	0.2 (0.01)	0.06 (0)	0.21 (0.02)	0.2 (0.02)	0.62 (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)	0.59 (0.06)	0.1 (0.01)	0.36 (0.02)	0.05 (0)	0.33 (0.02)	0.29 (0.02)	0.97 (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)	0.56 (0.05)	0.08 (0.01)	0.32 (0.03)	0.05 (0)	0.33 (0.02)	0.36 (0.03)	1 (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)	0.47 (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)

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Chapter 3

Early successional dynamics of ground beetles (Coleoptera, Carabidae) in the tropical dry forest ecosystem in Colombia

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Abstract

Little is known about the successional dynamics of insects in the highly threatened tropical dry forest (TDF) ecosystem. For the first time, we studied the response of carabid beetles to vegetal succession and seasonality in this ecosystem in Colombia. Carabid beetles were collected from three TDF habitat types in two regions in Colombia: initial successional state (pasture), early succession, and intermediate succession (forest). The surveys were performed monthly for 13 months in one of the regions (Armero) and during two months, one in the dry and one in the wet season, in the other region (Cambao). A set of environmental variables were recorded per month at each site. Twenty-four carabid beetle species were collected during the study. *Calosoma alternans* and *Megacephala affinis* were the most abundant species, while most species were of low abundance. Forest and pasture beetle assemblages were distinct, while the early succession assemblage overlapped with these assemblages. Canopy cover, litter depth, and soil and air temperatures were important in structuring the assemblages. Even though seasonality did not affect the carabid beetle assemblage, individual species responded positively to the wet season. It is shown that early successional areas in TDF could potentially act as habitat corridors for species to recolonize forest areas, since these successional areas host a number of species that inhabit forests and pastures. Climatic variation, like the El Niño episode during this study, appears to affect the carabid beetle assemblage negatively, exasperating concerns of this already threatened tropical ecosystem.

Keywords

Climatic variation, ENSO, environmental variables, natural recovery, seasonality

3.1. Introduction

Tropical dry forest (TDF) is considered the most threatened tropical ecosystem in South America and Africa (Janzen, 1988; Miles et al. 2006) and is simultaneously one of the lesser-known ecologically (Sánchez-Azofeifa et al. 2005). Recent studies have shown that TDF has high levels of beta diversity and endemism, which could be lost if inappropriate conservation strategies are applied (Banda-R et al. 2016). In the Americas, Colombia hosts extensive dry forest areas (Miles et al. 2006). However, with high anthropogenic pressure, these forests are historically characterized by high levels of fragmentation (Etter et al. 2008), which in turn results in a reduction in habitat connectivity (Balzotti et al. 2020), ecosystem functions and services (Balvanera et al. 2011). Today, only 8% of the original TDF in Colombia remains (Pizano et al. 2016). An example is TDF in the Valley of the Magdalena River in Colombia, which has experienced intensive agriculture resulting in a heterogeneous landscape (Fernández-Méndez et al. 2014), with most forest patches reduced to less than 30 ha in size (Pizano et al. 2016). This landscape mosaic is characterized by areas at various stages of succession, similar to other countries (Quesada et al. 2009), which generate potential sources for spontaneous succession (Prach, 2003). Spontaneous succession is considered a cheap and rapid recovery tool (Prach & Pyšek, 2001), which in the case of TDF could improve connectivity, at least for poorly dispersing insects species (Aparicio et al. 2018). As such, the application of conservation strategies and ecological restoration is of paramount importance (Vargas & Ramírez, 2014), especially since TDF succession is slow compared to wet tropical forest (Murphy & Lugo, 1986), because water is a limiting factor when it comes to recovery (Fajardo et al. 2013).

Knowledge on succession, defined as species turnover with time (Walker & del Moral, 2003), is necessary to understand changes experienced by communities due to anthropogenic disturbances as well as the activities necessary for their recovery (Prach, 2003; Prach & Walker, 2011). Since insects are a major component of terrestrial ecosystems

(Samways, 1994; Schowalter, 2006; Scudder, 2009), knowledge on how they respond to succession is paramount. Yet, tropical insects do not show consistent patterns during succession and appear to be highly dynamic; their response to succession depends on the community variable evaluated (species richness, diversity or abundance), the region, and type of disturbance (e.g., Hernández et al. 2014; Hilt et al. 2006; Neves et al. 2010a; Nyafwono et al. 2014). For TDF insects, successional pathways are also difficult to predict, since changes are related to seasonal variability (Neves et al. 2010a). Seasonal fluctuations in insects in TDF are well document (e.g., Corona-López et al. 2017; Noguera-Martínez et al. 2007; Noguera et al. 2018; Pérez & Zaragoza, 2016), however, peaks in species richness are not clear when successional stages are included (e.g., Neves et al. 2010b). Additionally, taxa occupying different forest strata respond differently to succession; e.g., dung beetles and hypogaeic ant richness change with succession (Marques et al. 2017; Neves et al. 2010a), while arboreal and epigaeic ant do not (Marques et al. 2017; Neves et al. 2010b). The mechanisms of these differences are not completely understood, but may be related to specific resource use and abiotic requirements (Neves et al. 2014).

Carabidae is a large coleopteran family (ca. 34,000 species) (Bousquet, 2010), extensively distributed and with high abundance (Larochelle & Larivière, 2003), making them a prevalent model organism, especially in the temperate region (Koivula, 2011). The well-documented information about its taxonomy and biology, and its response to environmental change helped in its wide used as bioindicators (Koivula, 2011; Kotze et al. 2011). However, in the Neotropics, little is known about this group (Lucky et al. 2002; Martínez, 2005; Maveety et al. 2011; Rainio & Niemelä, 2003). One considerable hurdle is taxonomy with few identification keys and a great number of undescribed species (Erwin et al. 2015; Lucky et al. 2002; Maveety et al. 2011). Knowledge on carabid beetles in TDF is scarce, with most studies dealing with assemblage characterization (Arenas et al. 2013; Arenas & Ulloa-Chacón, 2016; Uribe & Vallejo, 2013). Baseline information on how carabid beetle assemblages respond to succession, and their seasonal dynamics in TDF, is urgently

needed both from an ecological and conservation perspective. The present study is the first to investigate these issues in this highly threatened ecosystem.

The overall aims of our study were to investigate carabid beetle assemblage changes during early succession in TDF in Colombia, and their response to environmental variables along this successional process. Furthermore, given the strong seasonality experienced in this ecosystem, and that the data were collected during an El Niño event (Varotsos et al. 2016; Whitfield et al. 2019), we evaluate the response of this group to wet and dry periods. The El Niño/Southern Oscillation (ENSO) is a periodic climatic event that affects inter-annual rainfall regimes. In Colombia, it consists of a dry episode with a precipitation deficit and raising air temperatures (Poveda et al. 2000). It can produce severe droughts as has happened in Colombian TDF during the study period (Montealegre, 2014).

We hypothesize that the carabid beetle assemblage in early successional TDF is speciose with high abundance compared to forest (e.g., Barber et al. 2017; Magura et al. 2015), due to the arrival of open-habitat and habitat generalist species (similar to temperate ground beetles) (e.g., Nagy et al. 2016). If the majority of carabid species of the TDF matrix are polyphagous predators (Lövei & Sunderland, 1996) and habitat generalists (Rainio & Niemelä, 2003) (as in other ecosystems), they will benefit from exploiting resources in the initial stages of TDF recovery, where resources are heterogeneous (Lebrija-Trejos et al. 2009). We also expect carabid beetles to respond to architectural attributes of the habitat, like vegetation cover and leaf litter (e.g., Molnár et al. 2001), since cover and litter influence environmental conditions (Facelli & Pickett, 1991; Lebrija-Trejos et al. 2011), and are considered important in structuring carabid assemblages (Antvogel & Bonn, 2001; Koivula et al. 1999). However, we expect that soil humidity will be a major factor that affects ground beetles in this ecosystem, because (1) it has been showed to influence carabid assemblages (Fidan & Sirin, 2016; Kaizuka & Iwasa, 2015; Niemelä et al. 1992), (2) water is a structuring and limiting factor of dry forest (Maass & Burgos, 2011), and (3) dry habitat carabid beetles synchronize their life cycle to optimal soil humidity conditions (Paarmann, 1979; Paarmann

et al. 1986). Other insects in TDF have shown to be influenced by soil/litter humidity, which are linked to precipitation (García et al. 2001; Rangel-Acosta & Martínez-Hernández, 2017).

3.2. Materials and methods

3.2.1. Study areas

The study was performed in the tropical dry forest biome in the Valley of the Magdalena River region (Colombia), in the municipalities of Armero-Tolima (305 m a.s.l.) and Cambao-Cundinamarca (294 m a.s.l.), both of which consist of a matrix of forest, pasture, and crops (Fig. 3.1). The average annual temperature is 27.4 °C in Armero and 28.5 °C in Cambao. Annual precipitation is 746.7 mm and 744.8 mm, respectively. This biome is characterized by two periods of marked drought in December–March and July–September.

The disturbance history of dry forest in this region is highly variable, due to agriculture and cattle ranching (clear-cutting), the use of timber trees (selective cutting) and a volcanic eruption in 1985 (Esquivel et al. 2016; Fernández-Méndez et al. 2014). In Armero the forest patches are of two types: forests that have never been clear-cut but experience selective cutting (see F1–2 in Fig. 3.1b), and forests with 32 years of primary succession (F3–5 in Fig. 3.1b). In Cambao (Fig. 3.1c), forests are areas with 15 years of secondary succession. Using a floristic characterization (Supplementary information 3.1), these forest areas were classified as being at an intermediate stage of succession, defined as arbustive areas with between 10 and 50 years of succession (Nassar et al. 2008).

We collected carabid beetles in three successional stages in Armero and Cambao: pasture as an initial point, early succession (3–7 years of succession), and forest (intermediate successional stage). Each habitat type was replicated three times per area except for the forest

and early successional sites in Armero, which had five and four replicates, respectively. This resulted in 12 sites at Armero and 9 sites at Cambao (Fig. 3.1). The minimum distance between sites within a study area was 240 m and the maximum distance was 2.2 km, while Armero and Cambao are 25 km apart.

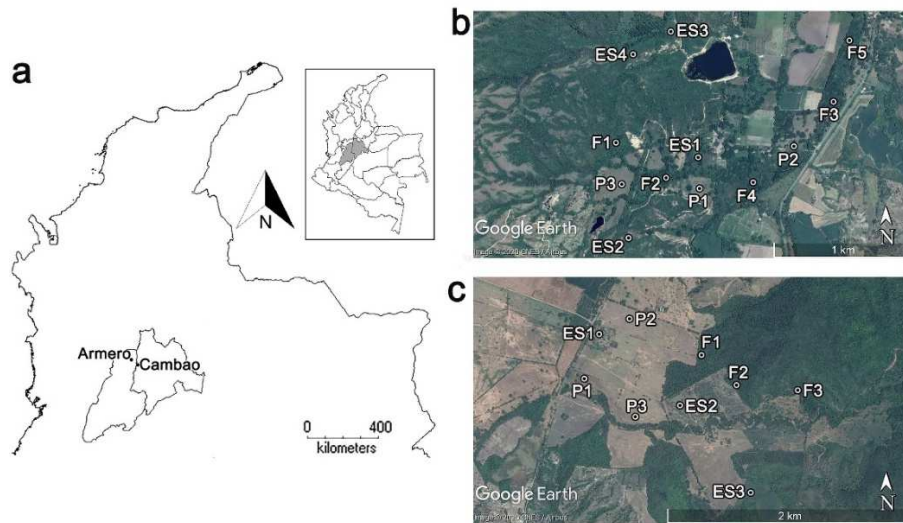


Figure 3.1 Geographic location of the study sites: (a) the location of Armero and Cambao in Colombia, (b) Armero, (c) Cambao. Abbreviations: F = forest, ES = early succession, P = pasture. Maps courtesy of DIVA-GIS 7.5 and Google Earth Image 2020. For more details, see the online map at <https://www.google.com/maps/d/u/3/edit?mid=1le-kOOQFh8RumUibWP3D8ghtxVvGM-eF&usp=sharing>

3.2.2. Carabid beetle sampling

Epigeic ground beetles were collected using 300 ml transparent pitfall traps (7 cm Ø), which were filled three-quarters of the way with a solution of water and a few drops of detergent. The surveys were performed on a monthly basis (the traps were active for three days per month) for 13 months from June 2015 to June 2016 in Armero. Due to financial constraints, surveys in Cambao were only performed during two months, one in the dry season (December 2015) and one in the wet season (May 2016).

Ten traps were installed at each site along a transect of 100 m, with traps 10 m apart. Each transect was at least 20 m from the edge of the site to minimize edge effects, however, average distance from the edge was 140 m. The catch of the ten traps per site was pooled per visit. A trap was considered “lost” if it disappeared, was flooded, or dried in its entirety: 10.4% of the traps were lost in Armero and 5% in Cambao. Losses were considered in the statistical analyses (see below). Adult carabid beetles (including the subfamily Cicindelinae, see Bousquet, 2012) were identified to genus level using taxonomic keys of the region from Martínez (2005) and to species level using taxonomic keys and/or original descriptions from Ball & Shpeley (2002, 2009), Ball et al. (1991), Bruschi (2010), Dejean (1829, 1831), Putzeys (1846, 1866), Reichardt (1967), Vitolo (2004), and Will (2005). However, given the scarcity of taxonomic keys for the Neotropics, some of the identifications should be confirmed. Voucher specimens are deposited in the Entomological Museum of the Universidad del Tolima, Colombia (MENT-UT).

3.2.3. Environmental variables

A set of environmental variables, including soil and air humidity and temperature, leaf litter depth and canopy cover were recorded per month at each site. Soil measurements (humidity and temperature) were taken using an Em50 Decagon digital data logger, which was installed in the vicinity of each transect and programmed to take measurements at 30 min intervals during three hours at midday (between 11:00 and 14:00) and then averaged. Air moisture and temperature were measured 2 cm above ground in the middle of the transect, using an Extech Thermohygrometer. Both soil and air variables were registered once per month in each site during the survey event.

Canopy cover (as a percentage) was calculated with a spherical crown densitometer at each pitfall trap (Lemmon, 1956); the 10 measures per transect were averaged. The same was done with leaf litter depth, which was determined using the Kostel-Hughes et al. (1998)

method. This method consists of inserting a wooden stick (3 mm in diameter) into the litter until it touched the humus layer. Four litter depth measures were taken per pitfall trap, two at 25 cm distance from the trap and two at 50 cm from the trap (Supplementary information 3.2).

3.2.4. Statistical analyses

Data were analyzed at the individual species and assemblage levels to determine how ground beetles respond to habitat type (forest, early succession, and pasture), environmental variables and seasonality. Analyses were performed on two datasets; Armero (13 months of data), and Armero and Cambao combined (two months of data collected per locality, December 2015 and May 2016).

For both datasets, species richness of each habitat type was calculated using sample-size-based and coverage-based rarefaction/extrapolation curves with Hill numbers ($q = 0$) (Chao et al. 2014), using the iNEXT package (Hsieh et al. 2016) in R (R Core Team, 2020). This approach estimates richness for standardized samples (number of individuals) using a common sample size (114 individuals for Armero and 321 for Armero and Cambao combined) and sample completeness (0.97 for Armero and 0.99 for Armero and Cambao combined). The 95% confidence intervals were calculated using bootstrapping (200 bootstrapped samples).

Non-metric multidimensional scaling (NMDS) was used to display the response of the carabid beetle assemblage at Armero to habitat type, seasonality, and the measured environmental variables. The analysis was run with the vegan package (Oksanen, 2015) in R, using the Horn measure as similarity index (Jost et al. 2011). The envfit function in vegan was used to evaluate the significance of seasonality and environmental variables in explaining the structure of the beetle assemblage. A permutational multivariate analysis of variance (PERMANOVA) test was performed, using the adonis2 function and the Horn similarity

measure in vegan, to evaluate whether the carabid beetle assemblages were significantly different between the three habitat types. The beetle catch was standardized to 60 traps per season (wet or dry) per site to take into account lost traps.

Generalized linear models (GLMs) were run in R to relate habitat type (as a factor), environmental variables and seasonality to abundantly collected species in Armero (13 months of data). The most abundant species were analyzed individually (with more than 100 individuals collected), while species of lower abundances were grouped together; models with species of fewer than 100 individuals collected were unstable with unrealistic coefficients and standard errors. Species collected in Armero were analyzed using the glm function in the lme4 package, with the response variable (active density, hereafter referred to as abundance) modelled following a quasi-Poisson distribution (see Ver Hoef & Boveng, 2007). The following variables were included in the models: (1) logged trap number as an offset term to account for trap losses (Kotze et al. 2012), (2) habitat type as a factor, (3) season as a two-level factor (dry and wet), and (4) environmental variables (soil and air humidity and temperature, leaf litter depth and canopy cover). To minimize collinearity between environmental variables, a correlation was run using the corrplot package in R. Canopy cover and air humidity and temperature were removed because they correlated strongly with soil temperature ($r = -0.72$, $p < 0.001$; $r = -0.62$, $p = 0.004$; $r = 0.83$, $p < 0.001$, respectively). Then a VIF (variance inflation factor) was run using the car package in R (Fox et al. 2016) to test collinearity of the environmental variables in the final models. Litter depth was removed from the *C. alternans* model (VIF = 10.94), and soil humidity was removed from the “rest of the species” model (VIF = 5.82).

Generalized linear mixed models (GLMMs) were run in R to relate habitat type (as a factor), environmental variables and seasonality to abundantly collected carabid beetle species for Armero and Cambao combined (two months of data per locality). The most abundant species were analyzed individually (with more than 39 individuals collected), while species of lower abundances were grouped together. The glmer function in the lme4 package

(Bates et al. 2015) was used to analyze the Armero and Cambao combined dataset. Abundance data (per species) were modelled following a Poisson distribution (see O'Hara & Kotze, 2010) and an observation-level random effect was added to deal with possible overdispersion (Harrison, 2014). The following fixed effects were included in the GLMM models: (1) logged trap number as an offset term to account for trap losses, (2) habitat type as a factor, (3) season as a two-level factor (dry and wet), and (4) environmental variables (soil and air humidity and temperature, leaf litter depth and canopy cover). Study area (Armero and Cambao) was added as a random term to account for locality effects. Air ($r = -0.6$, $p = 0.001$) and soil humidity ($r = -0.57$, $p = 0.002$) and air temperature ($r = 0.51$, $p = 0.009$) were removed because they correlated with soil temperature. For *C. alternans* and the “rest of the species” models, canopy cover was removed from the final models (VIF = 5.26, 7.72, respectively). We performed model selection on both GLMs and GLMMs by removing nonsignificant environmental variable terms one at a time, but habitat type was retained even if statistically insignificant since it was part of the main design. Model validation was performed using the k-fold cross-validation procedure in the R library caret (Kassambara, 2018). The predict function was used to predict the number of individuals from the final models. Finally, using the package multcomp and the function glht in R, a Tukey's HSD post-hoc test was performed to identify significant differences between habitat type categories.

3.3. Results

3.3.1. Distribution of species among habitat types

Eighteen carabid beetle species (182 individuals) were collected in Armero and ten species (355 individuals) in Cambao (Table 3.1). In Armero, seven species were collected from forest,

with *Anaulacus piceolus* exclusively from this habitat type. In pasture, nine species were collected, with *Apenes* sp. 1, *Barysomus hoepfneri*, and *Selenophorus parvus* occurring only in this habitat type. Most species were collected from the early succession habitat type (13 species), also with four exclusive species (*Apenes* sp. 2, *Peleciium laevigatum*, *Stolonis notula*, and *Stolonis parvulus*). However, most exclusive species in these habitat types are singletons, and their habitat preference should be considered with caution. *Calosoma alternans* and *Megacephala affinis* were the most abundantly collected species (113 and 21 individuals respectively), *C. alternans* occurring in all habitat types while *M. affinis* was not present in forest.

In Cambao, four species were collected from forest, with *Apenes morio* exclusively so. Early succession and pasture had similar numbers of species (six and seven). *Stenomorphus angustatus* was collected exclusively from the early succession habitat type, while pasture had three exclusive species *Apenes* sp. 3, *Selenophorus clypealis*, and *Tetragonoderus* sp. *Calosoma alternans* and *M. affinis* were the most abundantly collected species (299 and 20 individuals respectively), both occurring in all habitat types and in both localities (Armero and Cambao). *Megacephala affinis* was collected abundantly in pasture in Armero, but in the early succession habitat in Cambao. Differences in the assumed preferences of species between Armero and Cambao should be treated with caution given the vastly different sampling intensities between these two regions. *Megacephala cribrata* was also reasonably abundant (16 individuals). *Calosoma alternans* contributed 62% of the total catch in Armero and 84% in Cambao. It dominated pastures in both localities.

Table 3.1 Number of individuals of all carabid beetle species collected in each habitat type at Armero and Cambao, Colombia. The season column represents the season during which the species was collected; w = wet, d = dry; capital letter represents the season with the most abundant catch. Abbreviations: F = forest, ES = early succession, P = pasture.

Species	Habitat type						Total	Season
	F		ES		P			
	w	d	w	d	w	d		
Armero								
<i>Anaulacus piceolus</i> (Chaudoir, 1876)		1					1	d
<i>Apenes prasinus</i> Ball & Shpeley, 1992	2	1	1	1			5	dW
<i>Apenes</i> sp.1					1		1	w
<i>Apenes</i> sp.2				1			1	d
<i>Athrostictus chlaenioides</i> Dejean, 1829	1				2		3	w
<i>Athrostictus paganus</i> (Dejean, 1831)				1	1		2	dw
<i>Barysomus hoepfneri</i> Dejean, 1829					1	2	3	Dw
<i>Calosoma alternans</i> (Fabricius, 1792)	8	5	17	3	75	5	113	dW
<i>Clivina</i> sp.	1			2			3	Dw
<i>Enceladus gigas</i> Bonelli, 1813	2		2	4			8	dw
<i>Galerita</i> sp.	4	1		1			6	dW
<i>Megacephala affinis</i> Dejean, 1825			3	1	14	3	21	dW
<i>Meotachys</i> sp.				1		1	2	d
<i>Peleciium laevigatum</i> Guérin-Ménéville, 1843			1				1	w
<i>Selenophorus parvus</i> Darlington, 1934					2	2	4	dw
<i>Stolonis notula</i> Motschulsky, 1866			1				1	w
<i>Stolonis parvulus</i> (Straneo, 1951)				1			1	d
<i>Tetragonoderus</i> sp.			1		2	3	6	dw
Total number of individuals	18	8	26	16	98	16	182	
Total number of species	7		13		9		18	
Cambao								
<i>Apenes</i> sp.3						3	3	d
<i>Apenes morio</i> (Dejean, 1825)		1					1	d
<i>Calosoma alternans</i> (Fabricius, 1792)	1		15	4	273	6	299	dW
<i>Megacephala affinis</i> Dejean, 1825	1	1	7	8	1	2	20	Dw
<i>Megacephala cribrata</i> Steinheil, 1875			10	1	3	2	16	dW
<i>Selenophorus parvus</i> Darlington, 1934	1		1				2	w
<i>Selenophorus woodruffi</i> Ball & Shpeley, 1992			1	1	4	3	9	dW
<i>Selenophorus clypealis</i> Ball & Shpeley, 1992					2		2	w
<i>Stenomorphus angustatus</i> Dejean, 1831				2			2	d
<i>Tetragonoderus</i> sp.						1	1	d
Total number of individuals	3	2	34	16	283	17	355	
Total number of species	4		6		7		10	

3.3.2. Carabid beetle assemblage structures

Sample size-based rarefaction/extrapolation curves showed no significant differences in species richness between habitat types in either datasets, as reflected by overlapping confidence intervals (Fig. 3.2). In Armero (13 months of data), early succession habitat appears to host more species than pasture and forest (Fig. 3.2a, c). Sample completeness (Fig. 3.2b) for all habitat types ranged between 81% and 97%, and estimated carabid species richness (Hill number $q = 0$) at 91% sample coverage were 9, 22, and 6 for forest, early succession, and pasture, respectively (Fig. 3.2c). Rarefaction/extrapolation curves for Armero and Cambao combined showed a different tendency, but with no significant difference between habitat types: forest had the highest number of species (Fig. 3.2d, f), but also had the lowest sample completeness (28%) (Fig. 3.2e), with an estimated richness of 22 (at 99% sample coverage), while early succession and pasture had 13 and 12 species, respectively (Fig. 3.2f).

The NMDS ordination for Armero showed that forest and pasture have characteristic and distinct species assemblages, while the early succession habitat type overlapped in assemblage structure with these other habitat types (Fig. 3.3). The assemblage in forest and pasture were most homogenous, while the early succession habitat was heterogeneous. Habitat type did not affect the carabid beetle assemblage significantly (PERMANOVA $F = 1.281$, $p = 0.253$), but the architectural variables like canopy cover ($r^2 = 0.342$, $p = 0.037$) and leaf litter depth ($r^2 = 0.330$, $p = 0.041$) did (Table 3.2). Although soil and air humidity did not influence the carabid beetle assemblage distribution significantly ($r^2 = 0.044$, $p = 0.694$; $r^2 = 0.114$, $p = 0.380$), soil and air temperature did ($r^2 = 0.452$, $p = 0.008$; $r^2 = 0.321$, $p = 0.046$), which related positively with the pasture beetle assemblage.

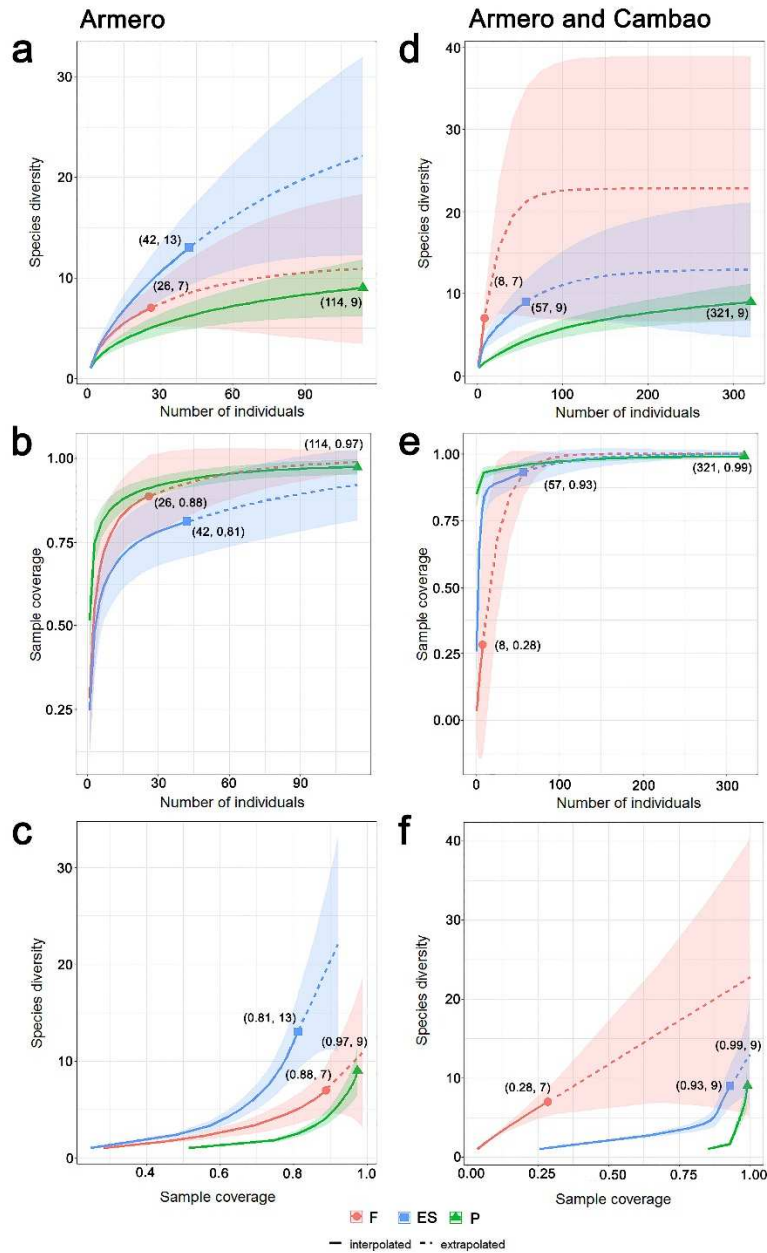


Figure 3.2 Rarefaction and extrapolation richness curves for carabid beetles from Armero (a–c), and Armero and Cambao combined (d–f): (a, d) comparison of richness between habitats using sample-size-based curves, (b, e) sample completeness curves, (c, f) comparison of richness using coverage-based curves. Abbreviations: F = forest, ES = early succession, P = pasture. Numbers in parentheses denote sample sizes and the observed Hill number ($q = 0$) (a, d), sample size and the estimated sample coverage (b, e), and the estimated sample coverage and the observed Hill number ($q = 0$) (c, f), respectively.

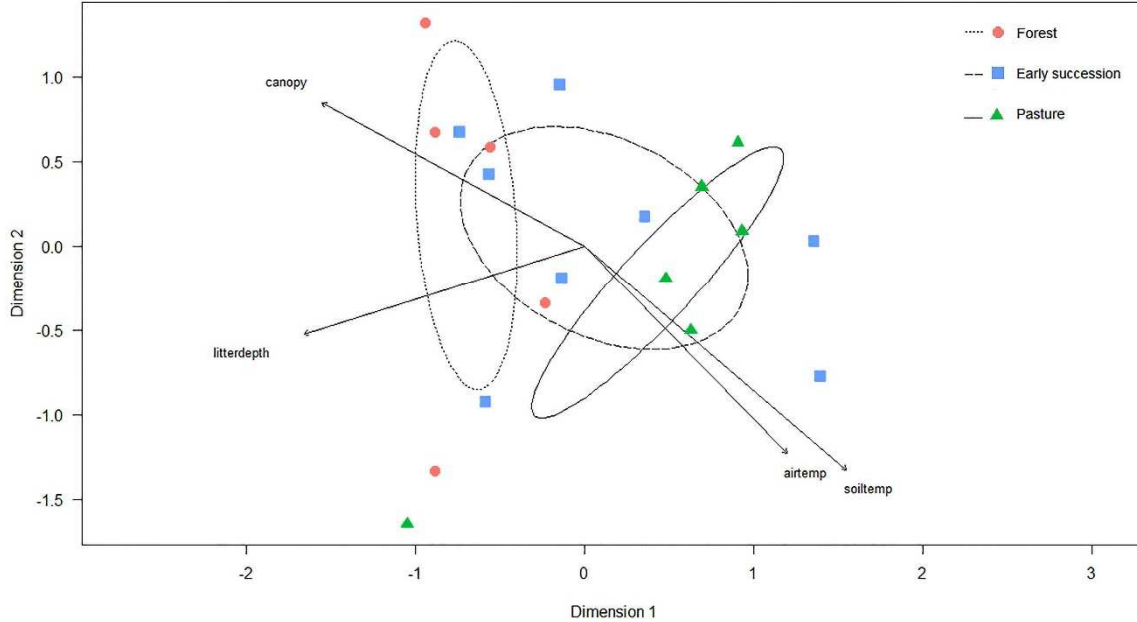


Figure 3.3 Non-metric multidimensional scaling ordination of carabid beetle assemblages at Armero (Colombia). Wet and dry season catches were analyzed and plotted separately. The catch in five of the ten forest samples returned zero individuals, and were removed from the analysis. The ellipses indicate 1 SD of the weighted average of site scores of forest (dotted line), early succession (long dashed line), and pasture (solid line). Abbreviations of the significant environmental vectors: soiltemp = soil temperature, airtemp = air temperature, litterdepth = leaf litter depth (cm), canopy = percentage canopy cover. Stress value 0.06.

Table 3.2 Correlations (r^2 and p-values) of vectors in the non-metric multidimensional scaling ordination of carabid beetle assemblages at Armero (Colombia).

	r^2	p-value
Air humidity	0.114	0.380
Air temperature	0.321	0.046
Soil humidity	0.044	0.694
Soil temperature	0.452	0.008
Canopy cover	0.342	0.037
Leaf litter depth	0.330	0.041
Season	0.061	0.356

3.3.3. Responses of individual species

Calosoma alternans was most abundantly collected from pasture in both datasets (Table 3.3, Figs 3.4, 3.5): this habitat showed significant differences with both forest and early succession habitat types (Table 3.4). The same tendency was observed for the “rest of the species” group analyzed in Armero and Armero and Cambao combined, although without significant differences between habitat types. The combined Armero and Cambao dataset showed that the genus *Megacephala* (*M. affinis* and *M. cribrata*) was slightly most abundantly collected from early succession, with statistical differences between this habitat type and pasture (Table 3.4). None of the environmental variables were retained in the models (Table 3.3), except for litter depth ($p = 0.001$), which had a negative effect on *Megacephala* in the Armero and Cambao dataset.

3.3.4. Seasonality

Seasonality did not affect the carabid beetle assemblage in Armero significantly ($r^2 = 0.061$, $p = 0.356$) (Table 3.2), but did so for individual responses of *C. alternans* in both datasets ($p = 0.006$ in Armero, $p < 0.001$ in Armero and Cambao), and for the “rest of species” group ($p = 0.037$) in Armero (Table 3.3). Observed species richness was the same between the wet and dry season (14 species each season) in Armero, while Cambao had small differences (6 wet, 8 dry) (Table 3.1). However, abundances were higher during the wet season for both localities (78% for Armero and 90% for Cambao). These differences were mainly due to *C. alternans* being significantly more abundant during the wet season (Table 3.3). When *C. alternans* is removed, differences between seasons were smaller (66% of the catch during the wet season in Armero, and 62% in Cambao).

Table 3.3 Generalized Linear Model and Generalized Linear Mixed Model results for carabid beetle species and species group (data of less abundant species pooled: Rest of the species) collected at Armero, and Armero and Cambao combined. Coefficients, standard errors (SE), and p-values are shown for intercepts, habitat type, season (wet and dry), and litter depth. Forest habitat type and dry season are in the intercept. Additionally, adjusted R² and Mean Absolute Error (MAE) values from the k-fold cross-validation model performance procedure are shown.

		Intercept	Early succession	Pasture	Season	Litter depth	R ²	MAE
Armero								
<i>Calosoma alternans</i>	Coefficient	-4.911	0.164	1.778	2.411		0.936	5.252
	(SE)	(0.984)	(0.887)	(0.744)	(0.761)			
	p-value	< 0.001	0.855	0.03	0.006			
Rest of species	Coefficient	-3.511	0.130	0.830 (0.41)	0.711		0.608	2.159
	(SE)	(0.408)	(0.441)		(0.311)			
	p-value	< 0.001	0.771	0.061	0.037			
Armero and Cambao								
<i>Calosoma alternans</i>	Coefficient	-6.440	3.031	4.860	2.438		0.561	13.26
	(SE)	(1.396)	(1.323)	(1.293)	(0.577)			
	p-value	< 0.001	0.022	< 0.001	< 0.001			
<i>Megacephala</i> species grouped (<i>M.affinis</i> and <i>M. cribrata</i>)	Coefficient	-3.169	1.218 (0.84)	-0.276		-1.688	0.737	1.174
	(SE)	(0.805)		(0.899)		(0.541)		
	p-value	< 0.001	0.147	0.758		0.001		
Rest of species	Coefficient	-2.424	-0.172	0.371			0.197	1.077
	(SE)	(0.538)	(0.665)	(0.629)				
	p-value	< 0.001	0.796	0.555				

3.4. Discussion

This study was performed during an El Niño event (2015/16), which means that the TDF ecosystem experienced harsh conditions, reflected by a considerable decrease in rainfall and an increase in air and soil temperatures (Montealegre, 2014). We showed that the carabid beetle catches in both Armero and Cambao did not reach species saturation. Rarefaction/extrapolation curves approached an asymptote in pasture only, and pasture also

showed a homogenous assemblage structure, distinct from forest. Early succession assemblage structure was highly heterogeneous, encompassing both forest and pasture, sharing 28% of species with both habitat types. Canopy cover, litter depth and soil and air temperatures were influential variables in structuring the carabid assemblage. Surprisingly, neither soil humidity nor seasonality affected assemblage structure significantly. Finally, *C. alternans* dominated pasture in both Armero and Cambao, while species of the genus *Megacephala* (*M. affinis* and *M. cribrata*) were more abundant in the early succession habitat type. None of the other species was collected abundantly enough to be analyzed individually.

Table 3.4 Tukey's HSD post-hoc test results, comparing differences in the number of individuals of the carabid beetle species and species group collected in the three habitat types (forest, early succession, and pasture).

		Pasture - Forest	Early succession - Forest	Early succession - Pasture
Armero				
<i>Calosoma alternans</i>	Coefficient (SE)	1.778 (0.745)	0.164 (0.887)	-1.614 (0.622)
	p-value	0.043	0.981	0.025
Rest of species	Coefficient (SE)	0.83 (0.41)	0.13 (0.441)	-0.7 (0.344)
	p-value	0.105	0.952	0.103
Armero and Cambao				
<i>Calosoma alternans</i>	Coefficient (SE)	4.86 (1.293)	3.031 (1.323)	-1.829 (0.587)
	p-value	< 0.001	0.052	0.004
<i>Megacephala</i> species grouped (<i>M. affinis</i> and <i>M. cribrata</i>)	Coefficient (SE)	-0.276 (0.898)	1.218 (0.84)	1.494 (0.476)
	p-value	0.947	0.303	0.004
Rest of species	Coefficient (SE)	0.371 (0.629)	-0.172 (0.665)	-0.542 (0.53)
	p-value	0.825	0.964	0.56

The epigeaic carabid assemblage in tropical dry forest was species poor but with high dominance, like in other tropical carabid communities (Paarmann et al. 2002; Rosero, 2010; Vieira et al. 2008). Only 12% of the species collected had more than 10 individuals, while 46% were singletons or doubletons. This low abundance was reflected in the rarefaction/extrapolation curves, which did not reach an asymptote, suggesting that epigeaic

carabid beetle diversity in the TDF is certainly higher than presented here. Although rarity may be common in tropical ecosystems, the pattern we observed could appear as a consequence of an inappropriate sampling method and/or intensity (Magurran & Henderson, 2011). Vennila & Rajagopal (1999) recommended more than 35 pitfall traps per site for quantitative studies in tropical agroforests, and Boetzl et al. (2018) showed that the use of guidance barriers could improve the efficiency of the catch. Furthermore, Liu et al. (2007) indicated that pitfall traps do not permit a complete inventory and recommended using light traps as a compliment. Many tropical carabid species live in the canopy (Erwin, 1979), and will not be collected using pitfall trapping (see Boetzl et al. 2018; Kotze et al. 2011). To collect TDF carabid beetles more efficiently, we recommend increasing the number of traps and the length of the survey (one complete year of continuous trapping at minimum), use guidance barriers if possible, and include other methods to sample arboreal species. Additionally, high soil and air temperatures during the dry season (see Supplementary information 3.2) result in the rapid evaporation of pitfall trap collecting fluid (Ariza, 2016; pers. obs.), and we recommend using deeper pitfall traps with more collecting fluid. Apart from the method used here, the El Niño event, which coincided with our sampling, could be an important component to the depauperate carabid community in TDF. During a previous El Niño event (1996) in the Amazonian rainforest, carabid beetle richness decreased drastically compared with other periods (Lucky et al. 2002). In Mexican TDF, a decrease in Cantharidae beetle richness was also observed during the 1997/8 El Niño event (Pérez & Zaragoza, 2016). Finally, the historic use of forest fragments and agricultural practices in pastures may explain the poor carabid community in this landscape. Harvey et al. (2008) indicated that beside severe fragmentation experienced in the TDF, contamination by agro-chemicals and illegal logging could be additional drivers of biodiversity loss. The degree to which these aspects affect carabid beetles in the region remains to be investigated.

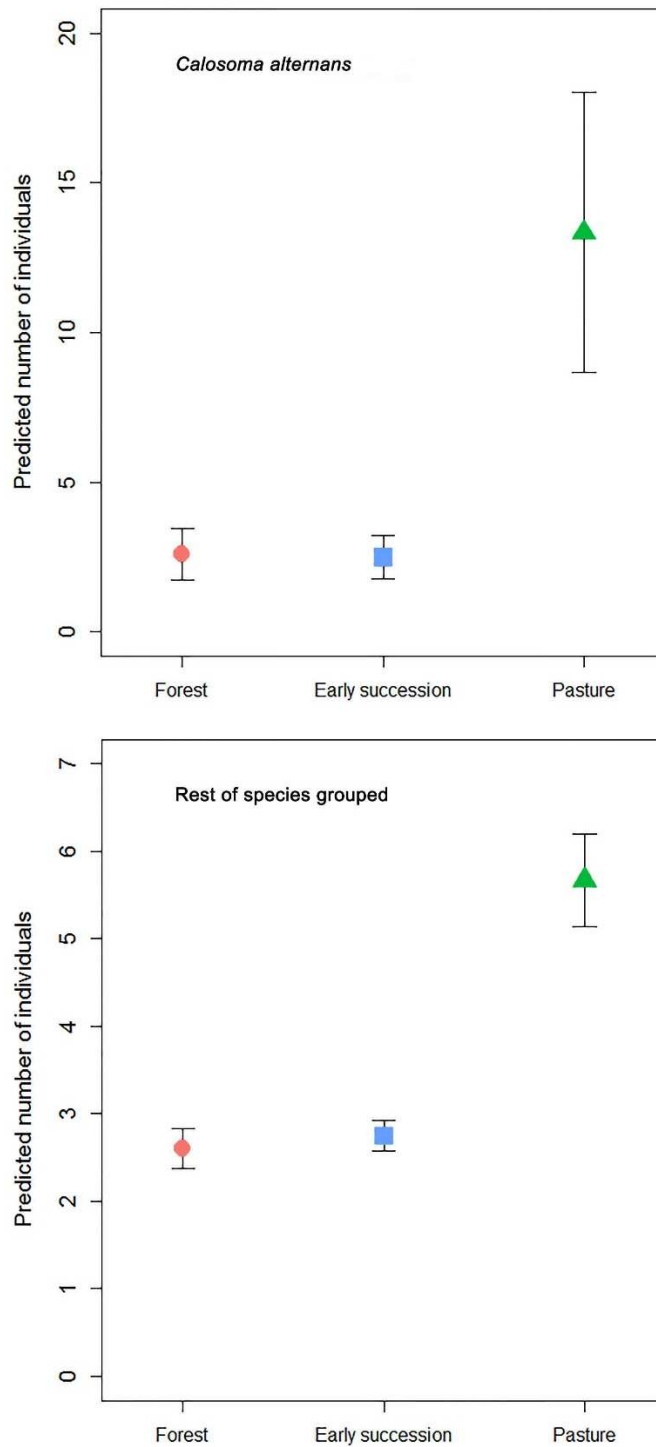


Figure 3.4 Generalized Linear Model predicted (mean \pm SE) number of individuals of *Calosoma alternans* and the remaining carabid beetle species collected from Armero across the three habitat types (forest, early succession, and pasture). Note different y-axis scales.

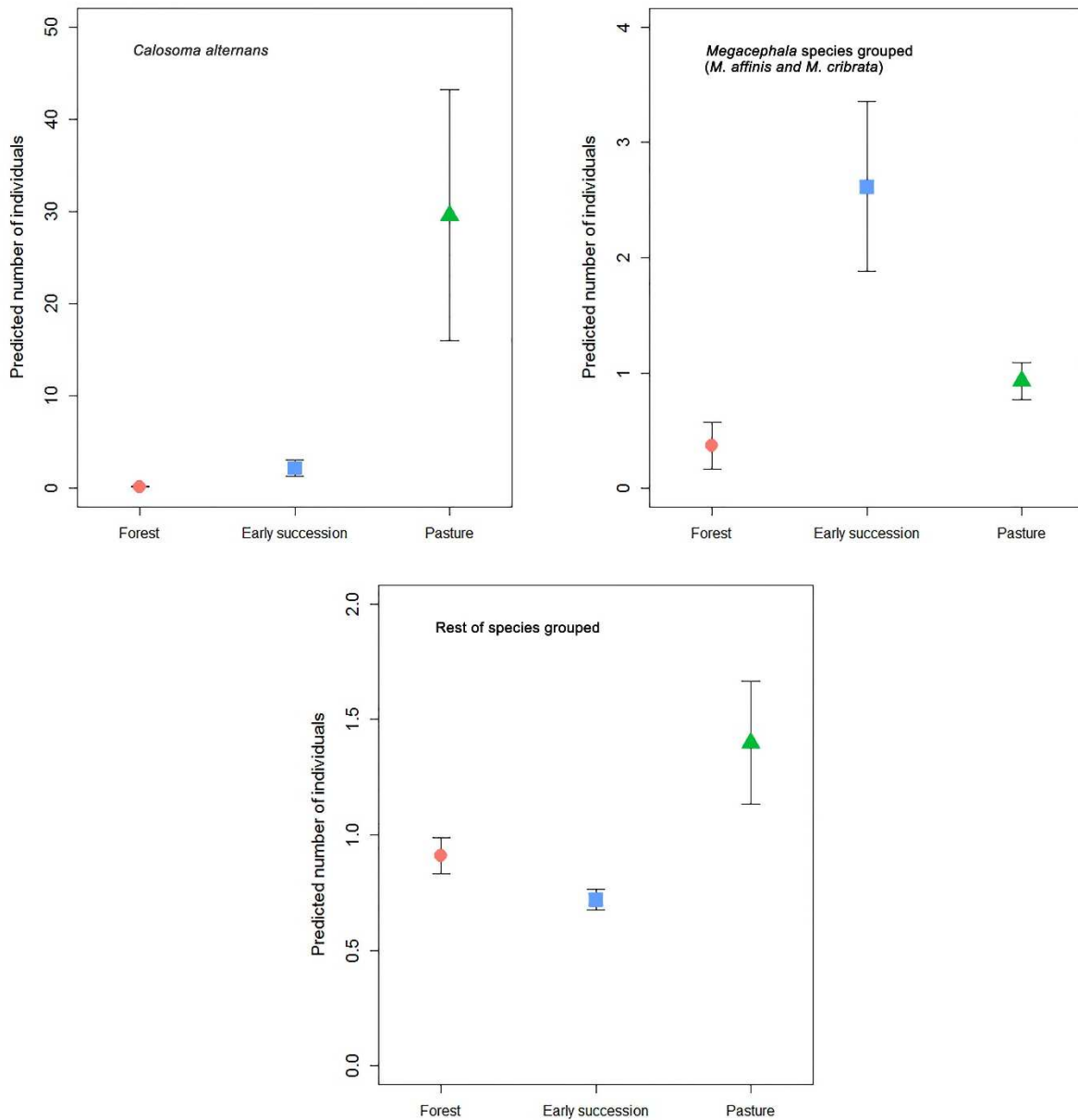


Figure 3.5 Generalized Linear Mixed Model predicted (mean \pm SE) number of individuals of *Calosoma alternans*, genus *Megacephala* and the remaining carabid beetle species collected from Armero and Cambao combined across the three habitat types (forest, early succession, and pasture). Note different y-axis scales.

The carabid beetle assemblage in the early succession habitat overlapped with assemblages in pasture and forest habitat types, a pattern not observed for dung beetles (Neves et al. 2010a) or arboreal ants (Neves et al. 2010b) in Brazilian TDF, where communities were more distinct between early succession and forest habitat types. Reasons for this discrepancy may be related to habitat complexity and the biology of these groups (Neves et al. 2010a, b). Dung beetles depend on ephemeral resources produced by larger animals that may be more sensitive to changes in the landscape (Hanski, 1991), while ground-nesting ants in early successional TDF forage in trees, but do not do so in late successional stages (Neves et al. 2010b). For carabid beetles, early successional TDF sites may provide a mixed environment with elements from both pasture and forest, thus providing a heterogeneity of resources (Lebrija-Trejos et al. 2009) to be exploited by a subset of carabid beetle species. The lack of knowledge of the natural history of tropical species prevents us from identifying the habitat preferences of species found in the TDF early succession habitat type. Despite this, the little knowledge that do exist is reflected in the heterogeneous resource used by the carabid species collected from forest and early successional sites in Armero; *Apenes prasinus*, *Clivina* sp., and *Galerita* sp. are related to leaf-litter (Erwin, 1991; Laroche & Larivière, 2003; Martínez, 2005), while species shared between early succession and pasture (*Athrostictus paganus*, *M. affinis* and *Tetragonoderus* sp.) prefer open areas and/or pasture (Laroche & Larivière, 2003; Shpeley et al. 2017; Vitolo, 2004). *Calosoma alternans* (in Armero and Cambao) and *M. affinis* (Cambao) were present in all habitat types, suggesting that these species are habitat generalists. Indeed, *C. alternans* can be found in a wide variety of habitats and ecosystems (Gidaspow, 1963), but also seems to prefer pastures (Bruschi, 2010) as confirmed by our results. Nevertheless, it is difficult to attribute a particular habitat preference to species occurring in the early succession habitat type, partly because ground beetles readily disperse at the local level, even to suboptimal habitat (e.g., Boetzl et al. 2016; Knapp et al. 2019; Niemelä & Halme, 1992; Schneider et al. 2016). Resources are heterogeneous and patchy, both at the fine and coarse scale (Pickett & Rogers, 1997; Wiens, 1976), thus carabid species

of different preferences could occasionally occur in early successional stages, even if such habitat is suboptimal to them.

Soil and air temperatures were the only microclimatic variables that influenced the structuring of the carabid assemblage in our study. Carabid beetles, similar to other insects, are poikilothermic and sensitive to temperature (Beck, 1983; Bowler & Terblanche, 2008; Neven, 2000), mainly during egg and larvae stages (Lövei & Sunderland, 1996; Potter et al. 2009). Surprisingly, soil humidity did not affect the beetle assemblage, even though moisture is considered important in these dry forests (Balvanera & Aguirre, 2006; Espinosa et al. 2011). During 2015/6, one of the strongest El Niño episodes occurred in Colombia (UNGRD, 2016), producing a severe rainfall deficit that affected soil humidity negatively. This was reflected in our measurement of soil humidity, where differences between habitat and season were minimal. It is expected that in normal years, seasonality will result in more contrasting differences in soil humidity between open and forest habitats (Ceccon et al. 2006; Zhang et al. 2010). This could explain why variation in soil humidity did not affect carabid beetles significantly. Canopy cover and litter depth significantly influenced carabid assemblage structure in our study (see also Antvogel & Bonn, 2001; Koivula et al. 1999; Ogai & Kenta, 2016; Taboada et al. 2008; Yu et al. 2008). These structural variables can reflect and influence microclimatic conditions (Gardner, 1991; Sanderson et al. 1995). In TDF, structural and environmental variables are related to succession but also depend on season, thus strong environmental gradients are not observed during the dry season (Lebrija-Trejos et al. 2009). For instance, TDF forests consists of deciduous trees that shed their leaves during the dry season, creating an open canopy (Holbrook et al. 2009; Murphy & Lugo, 1986) thus minimizing differences between habitat types in terms of climatic gradients. On top of that, due to an extremely dry period because of the El Niño phenomenon (even during the wet season), microclimatic conditions (apart from soil and air temperature, see above) likely varied little between habitat types. Alternatively, conserving water is a challenger for small organisms in these harsh environments (Chown & Klok, 2003), and as such, litter

depth become an important environmental variable to these beetles in providing shelter (Koivula et al. 1999; Magura et al. 2005). Hopp et al. (2010) found that litter quantity was a better predictor of beetle assemblage recovery than soil humidity. Litter improve the environment in the soil (Facelli & Pickett, 1991; Magura et al. 2004), offer habitat structure for organisms (Kalinkat et al. 2013; Magura et al. 2000) and supplies prey for carnivorous species (Guillemain et al. 1997).

Seasonality did not significantly influence the carabid beetle assemblage, even though numerous studies have shown seasonality to be important in dry forest beetles (e.g., Noguera et al. 2018; Novais et al. 2016; Pérez & Zaragoza, 2016; Rangel-Acosta & Martínez-Hernández, 2017). However, there are exceptions; for example dung beetle richness differences between wet and dry seasons in the Caatinga forest in Brazil were small (Medina & Lopes, 2014). A reason for the lack of a seasonality signal in our data may, again, be due to a deficit in precipitation during the 2015/6 El Niño southern oscillation. Many carabid species diapause as an adaptation to harsh environmental conditions (Lövei & Sunderland, 1996). Some observational studies have suggested that moisture could be a trigger for diapause development (Hodek, 2003; Tauber et al. 1998). Either because of low humidity or environmental signals generated by the El Niño phenomenon, carabids species could display a lengthened diapause (during a drought event), thus resulting in the absence of seasonal peaks in their numbers (see Hanski, 1987; Matsuo, 2006). At the species level, *C. alternans* and the “rest of species” group did respond to the wet season. Some *Calosoma* species are associated with open habitats and dry soils (Larochelle & Larivière, 2003), so a slight improvement of environmental conditions in the wet season during El Niño could be sufficient for this species to express seasonal peaks (e.g., Jacobs et al. 2011).

3.5. Conclusions

Our study showed that early successional areas in TDF have a prominent role in the conservation of carabid beetles since it can act as a temporal habitat for a number of species that occur in forest and pasture. The loss of connectivity between dry forest patches limits the dispersal of species (Balzotti et al. 2020; Kindlmann & Burel, 2008). Early successional stages could act as habitat corridors for carabid beetles, including some stenotopic species (e.g., Eggers et al. 2010; Noordijk et al. 2009, 2011, 2008), and promote the recolonization of forest patches. Land-use intensification homogenizes carabid assemblages (Meng et al. 2012), which is also the case for pasture in our study. In Armero and Cambao, pasture was dominated by *C. alternans*, which seems well-adapted to dry soils. We showed the importance of restoration to the recovery of this ecosystem. We demonstrated that climatic variation, like the El Niño episode, impacts the abundances and species richness of TDF carabid beetles markedly, necessitating the call for long-term studies to evaluate recovery in this landscape.

Supplementary information

Supplementary information 3.1 List of plant species of each habitat type at Armero and Cambao. Abbreviations: F = forest, ES = early succession, P = pasture.

Species	Habitat type					
	Armero			Cambao		
	F	ES	P	F	ES	P
Arboreal stratum						
<i>Anacardium excelsum</i> Skeels	x	x				
<i>Aspidosperma polyneuron</i> Müll.Arg.				x		
<i>Astronium graveolens</i> Jacq.				x		
<i>Attalea butyracea</i> (Mutis ex L.f.) J.G.W.Boer	x	x		x		
<i>Azadirachta indica</i> A.Juss.	x					
<i>Bulnesia arborea</i> Engl.				x		
<i>Casearia nitida</i> Jacq.	x					

(Supplementary information 3.1, continue)

Species	Habitat type					
	Armero			Cambao		
	F	ES	P	F	ES	P
<i>Cecropia angustifolia</i> Trécul	x	x		x		
<i>Ceiba pentandra</i> (L.) Gaertn.	x	x		x		
<i>Crescentia cujete</i> L.				x		
<i>Croton</i> sp.	x					
<i>Croton leptostachyus</i> Kunth		x	x	x		
<i>Cupania cinerea</i> Poepp. & Endl	x			x		
<i>Eugenia</i> sp.				x		
<i>Ficus insipida</i> Willd.	x					
<i>Gliricidia sepium</i> (Jacq.) Kunth		x		x		
<i>Gmelina arborea</i> Roxb. ex Sm.	x					
<i>Guarea guidonia</i> (L.) Sleumer	x					
<i>Guazuma ulmifolia</i> Lam.	x	x		x		
<i>Handroanthus ochraceus</i> (Cham.) Mattos				x		
<i>Juglans regia</i> L.	x					
<i>Leucaena leucocephala</i> (Lam.) de Wit				x	x	
<i>Machaerium capote</i> Triana ex Dugand	x			x		
<i>Machaerium microphyllum</i> Standl.		x				
<i>Maclura tinctoria</i> (L.) D.Don ex Steud.	x	x		x		
<i>Melicoccus bijugatus</i> Jacq.	x			x		
<i>Nectandra</i> sp	x					
<i>Ocotea</i> sp.	x			x		
<i>Piper</i> sp.1	x					
<i>Pouteria</i> sp.				x		
<i>Pseudosamanea guachapele</i> (Kunth) Harms	x			x		
<i>Psidium guineense</i> Sw.		x				
<i>Rollinia</i> sp.	x					
<i>Samanea saman</i> (Jacq.) Merr.	x	x		x		
<i>Senna spectabilis</i> (DC.) H.S.Irwin & Barneby	x					
<i>Senegalia affinis</i> Britton & Killip		x				
<i>Stemmadenia grandiflora</i> (Jacq.) Miers	x	x		x		
<i>Trichilia</i> sp.	x					
<i>Trichilia carinata</i> M.E.Morales				x		
<i>Trichilia oligofoliolata</i> M.E.Morales-Puentes				x		
<i>Triplaris americana</i> (L.) Pav. ex Meisn.	x			x		
<i>Urera caracasana</i> Griseb.	x					
Shrub stratum						
<i>Acacia farnesiana</i> (L.) Willd				x	x	
<i>Amyris balsamifera</i> L.				x		
<i>Ardisia foetida</i> Willd. ex Roem. & Schult.	x					
<i>Bactris</i> sp.	x					

(Supplementary information 3.1, continue)

Species	Habitat type					
	Armero			Cambao		
	F	ES	P	F	ES	P
<i>Capparis odoratissima</i> Jacq				x		
<i>Coccoloba obovata</i> Kunth	x			x		
<i>Cordia</i> sp.				x		
<i>Erythroxylum</i> sp.	x	x				
<i>Euphorbia cotinifolia</i> L.				x		
<i>Jatropha gossypifolia</i> L.					x	x
<i>Mimosa pigra</i> Willd.			x			x
<i>Piper crassinervium</i> Kunth	x					
<i>Randia armata</i> (Sw.) DC.				x		
<i>Solanum cornifolium</i> Humb. & Bonpl.			x			
<i>Waltheria indica</i> L.			x			x
Liana stratum						
<i>Serjania</i> sp.	x					
<i>Serjania clematidea</i> Triana & Planch.	x					
Herbaceous stratum						
<i>Alysicarpus vaginalis</i> (L.) A.DC.			x			
<i>Bothriochloa pertusa</i> (L.) Maire			x			
<i>Bouchea prismatica</i> (L.) Kuntze						x
<i>Bouteloua repens</i> (Kunth) Scribn. & Merr.		x	x			
<i>Carludovica palmata</i> Ruiz & Pav.	x			x		
<i>Chamaesyce hirta</i> (L.) Millsp.			x			
<i>Cleome viscosa</i> L.						x
<i>Cnidioscolus urens</i> Arthur			x			x
<i>Cordia polycephala</i> (Lam.) I.M.Johnst.						x
<i>Croton hirtus</i> L'Hér.			x			
<i>Cynodon dactylon</i> (L.) Pers.			x			x
<i>Desmodium triflorum</i> Schumach. & Thonn.			x			x
<i>Digitaria violascens</i> Link			x			x
<i>Eclipta alba</i> Hassk.			x			
<i>Fleischmannia granatensis</i> R.M.King & H.Rob.			x			
<i>Heliconia marginata</i> Pittier	x					
<i>Mimosa quadrivalvis</i> L.		x	x			x
<i>Pavonia sidaefolia</i> Kunth					x	
<i>Piper</i> sp.2	x					
<i>Piper umbellatum</i> Sieber ex Kunth		x				
<i>Senna tora</i> (L.) Roxb.		x			x	x
<i>Sida rhombifolia</i> L.		x			x	x
<i>Talinum fruticosum</i> (L.) Juss.					x	
<i>Tridax procumbens</i> L.			x			x
<i>Urtica</i> sp.		x		x		

Supplementary information 3.2 Means (SD) of the environmental variables measured in Armero, Colombia during 13 months. The dry season period includes months 1-4, 7-9 and 13; wet season 5-6 and 10-12. For Cambao, data were collected one month during the dry and one month during the wet season.

Habitat type	Season	Environmental Variables					
		Soil humidity (VWC)	Soil temperature (°C)	Air humidity (%)	Air temperature (°C)	Leaf litter depth (cm)	Canopy cover (%)
Armero							
Forest 1	Dry	0.07 (0.035)	31.35 (2.5)	40.05 (20.41)	37.45 (5.48)	3.78 (1.78)	87.66 (12)
	Wet	0.06 (0.05)	28.26 (0.55)	68 (18.56)	31.28 (4.89)	3.26 (0.59)	99.10 (0.47)
Forest 2	Dry	0.10 (0.04)	31.04 (2.46)	42.96 (11.03)	34.58 (2.29)	3.05 (1.04)	91.46 (8.01)
	Wet	0.15 (0.12)	27.1 (1.27)	62.26 (17.37)	31.88 (2.9)	3.22 (0.58)	98.16 (0.97)
Forest 3	Dry	0.06 (0.03)	33.19 (5.91)	45.24 (18.18)	36.55 (6.85)	4.31 (1.3)	89.21 (10.84)
	Wet	0.11 (0.07)	30 (3.93)	66.78 (13.14)	32.04 (4.48)	4.03 (0.73)	98.29 (0.49)
Forest 4	Dry	0.06 (0.03)	32.67 (3.16)	44.7 (12.22)	35.75 (3.38)	3.21 (0.70)	87.78 (8.13)
	Wet	0.16 (0.08)	28.42 (1.72)	59.5 (15.6)	34.06 (5.16)	3.90 (1.17)	98.42 (0.83)
Forest 5	Dry	0.07 (0.04)	35.1 (6.59)	42.36 (3.59)	35.21 (3.56)	2.95 (1.01)	89.38 (10.38)
	Wet	0.11 (0.03)	32.34 (5.11)	69.62 (14.27)	31.06 (3.77)	4.16 (0.97)	99.12 (0.49)
Early succession 1	Dry	0.06 (0.04)	33.09 (4.23)	47.94 (13.88)	35.13 (3.86)	1.61 (0.60)	85.06 (13.07)
	Wet	0.17 (0.09)	29.18 (3.21)	58.04 (4.67)	34.86 (1.52)	1.89 (0.73)	97.32 (1.08)
Early succession 2	Dry	0.07 (0.04)	42.07 (5.17)	38.63 (9.4)	40.02 (4.03)	2.96 (1.8)	47.4 (26.92)
	Wet	0.13 (0.08)	34.06 (4.37)	50.98 (6.43)	36.4 (1.71)	2.24 (0.8)	65.88 (3.87)
Early succession 3	Dry	0.09 (0.03)	37 (7.07)	42.17 (13.37)	39.2 (5.06)	3.92 (1.44)	33.68 (17.08)
	Wet	0.18 (0.09)	31.32 (1.97)	61.32 (10.01)	36.36 (2.87)	3.16 (0.14)	33.77 (9.46)
Early succession 4	Dry	0.06 (0.04)	35.34 (4.34)	41.13 (15.09)	37.4 (4.32)	2.93 (0.58)	67.54 (21.82)
	Wet	0.2 (0.18)	31.3 (0.6)	59.52 (9.02)	35.96 (3.15)	2.41 (0.25)	76.88 (3.1)
Pasture 1	Dry	0.07 (0.03)	39.96 (6.36)	40.86 (11.37)	41.66 (4)	1.28 (0.44)	0
	Wet	0.13 (0.08)	35.64 (7.44)	53.92 (10.61)	37.76 (2.38)	1.15 (0.60)	0

(Supplementary information 3.2, continue)

Habitat type	Season	Environmental Variables					
		Soil humidity (VWC)	Soil temperature (°C)	Air humidity (%)	Air temperature (°C)	Leaf litter depth (cm)	Canopy cover (%)
Pasture 2	Dry	0.09 (0.08)	39.63 (9.74)	46.83 (15.54)	38.95 (6.93)	0.75 (0.21)	0
	Wet	0.14 (0.08)	34.38 (5.67)	62.22 (13.48)	35.72 (2.77)	0.61 (0.28)	0
Pasture 3	Dry	0.12 (0.1)	39.21 (4.69)	44.53 (11.42)	40.06 (3.97)	2.82 (1.98)	0
	Wet	0.17 (0.11)	37.44 (4.58)	58.46 (9.23)	38.7 (3.34)	2.15 (1.01)	0
Cambao							
Forest 1	Dry	0.10	35.60	36	39	2.33	99.01
	Wet	0.29	28.30	70	31	1.65	88.89
Forest 2	Dry	-0.02	29.20	31	37	2.23	97.32
	Wet	0.15	30.60	68	31	1.16	85.96
Forest 3	Dry	0.12	36.60	25	39	0.76	94.25
	Wet	0.22	29.20	77	31	1.26	89.73
Early succesion 1	Dry	0.13	37.10	42	34	0.88	45.29
	Wet	0.26	26.00	89	30	0.58	60.81
Early succesion 2	Dry	0.04	38.80	41	36	0.78	25.48
	Wet	0.13	31.90	87	32	0.61	10.50
Early succesion 3	Dry	0.07	39.20	20	40	0.69	85.51
	Wet	0.25	25.80	66	30	0.50	89.62
Pasture 1	Dry	0.12	46.60	35	37	0.85	0
	Wet	0.28	27.50	53	34	0.09	0
Pasture 2	Dry	0.06	43.60	41	34	0.71	0
	Wet	0.29	26.40	66	33	0.13	0
Pasture 3	Dry	0.08	51.10	40	34	0.86	0
	Wet	0.25	27.30	47	32	0.21	0

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Chapter 4

Canopy cover and temperature filter carabid beetle
(Coleoptera, Carabidae) traits during tropical dry
forest succession

Abstract

Environmental changes experienced during succession are expected to filter insect communities. Strong seasonal drought experienced in the tropical dry forest ecosystem together with the open canopy of deciduous trees can influence the habits and preferences of species occupying this harsh environment. Carabid beetles were collected in Armero (Colombia) in three habitat types (open habitat as an initial point, early successional stages and intermediate successional forest), during 13 months. A cluster analysis was performed to identify ecological groups; additionally, a RLQ combined with fourth corner analysis were used to test the relationship between functional response traits and environmental variables (soil and air humidity and temperature, canopy cover and litter depth). We identified two main ecological groups produced by traits related to desiccation resistance (body size and daily activity): mostly small-nocturnal species (G1) and mostly large-diurnal species (G2). G1 was associated with intermediate successional forest and G2 with initial habitat types, while the early successional habitat type was characterised by traits from both ecological groups. Air and soil temperature correlated negatively, and canopy cover positively with small and nocturnal species. Our results showed that the preservation of water is a limiting factor for carabid beetles in the TDF, similar to other arid ecosystems, influencing the habits of this insect group.

Keywords

Colombia, deciduous vegetation, environmental variables, ecological groups, ENSO, insects, Neotropics

4.1. Introduction

Although information on tropical dry forest (TDF) succession is accumulating (e.g., Griscom & Ashton, 2011; Lebrija-Trejos et al. 2010a; Lévesque et al. 2011; Maza-Villalobos et al. 2011), little is known about insect successional dynamics in the region (Neves et al. 2014; Neves et al. 2010a; Neves et al. 2010b), especially regarding mechanism driving this process (see Marques et al. 2017). During TDF succession, the environment changes gradually: air and soil temperature decrease while relative humidity increases (Lebrija-Trejos et al. 2011). These changes can act as environmental filters for the establishment and survival of insect species (Jaworski & Hilszczański, 2013; Schowalter, 2006), thus community assembly is expected to change with succession (Fattorini & Halle, 2004). In general, the response of insects to forest ecosystem recovery is expected to progress from open-environment species towards forest generalist and specialist species (e.g., Alanen et al. 2011; Davis et al. 2013; Magura et al. 2015; Ottonetti et al. 2006).

In temperate regions, forest ground beetle species are characteristically brachypterous, large in size and predacious, while open-land species are generally macropterous, smaller in size and more phytophagous or omnivorous (Barber et al. 2017; Gobbi & Fontaneto, 2008). However, desiccation risk should be a challenge for insect inhabiting the TDF ecosystem, similar to insects from xeric ecosystems, where a larger size is an advantage to cope with this environment (Chown et al. 1995). Laboratory studies have demonstrated that large size and dry habitat carabid species are more resistant to desiccation than small size and wet habitat species (Baranovská et al. 2019). Other studies during a drought event have shown a shift in butterflies from monophagous species towards generalist species (De Palma et al. 2017), or drought tolerant species in the case of ground beetles (Morecroft et al. 2002). In areas with periodic droughts, r-strategist species are more frequent since they are able to colonize new areas quickly (Holeski, 1984).

Carabid beetles have been used to evaluate the effects of forest recovery (e.g., Günther & Assmann, 2005; Kędzior, 2018; Liu et al. 2012; Poole et al. 2003; Skłodowski, 2014), and are considered an indicator group in temperate ecosystems (Kotze et al. 2011). Yet, their suitability as study subject and an indicator group in tropical ecosystems are uncertain due to many taxonomic and ecological gaps (Martínez, 2005; Rainio & Niemelä, 2003). However, morphology can be used to infer some ecological information because of the correlation of some body forms with carabid habits (Bauer & Kredler, 1993; Forsythe, 1981, 1987). The use of morpho-ecological traits is recommended to clarify mechanisms driving the response of ground beetles to environmental change (as individual species and at the assemblage level) (Barber et al. 2017; Cole et al. 2002; Evans et al. 2019; Gobbi & Fontaneto, 2008), including changes that occur during ecosystem recovery.

The aims of this study were to identify ecological groups of carabid beetles along a successional gradient in TDF and the environmental variables related to their response, using data collected in Colombian TDF (see also Ariza et al. 2021a, accepted, 2021b). The successional gradient is characterised as open-habitat as an initial point, early succession, and forest as an intermediate successional stage. In Ariza et al. (2021a) we showed that the carabid assemblage is different between initial and intermediate successional stages, however in the early successional stage, the assemblage is a mix of species from both initial and intermediate stages. This distribution is driven by temperature and architectural variables of the habitat. In Ariza et al. (2021b) we showed that during the harsh environment produced by the El Niño/Southern oscillation (ENSO), traits including body size, daily activity and pusher habit have a prominent role in the survival of these insects, but it is unknown whether these traits are grouped in an ecologically meaningful way in this harsh environment. In the current paper, we focus more on the successional changes of carabids in terms of traits, which remains unexplored in this harsh ecosystem.

Given the strong seasonality characteristic of TDF (Murphy & Lugo, 1986) and that the survey was performed during ENSO (Varotsos et al. 2016), we hypothesise that carabid

beetles are principally divided by characteristics related to desiccation resistance in TDF: (1) small and nocturnal beetles associate with forests, and (2) large and diurnal activity associate with open habitats. Early successional stages will constitute a mix of open and forest species. Larger carabid beetles appear to be well-adapted to harsh conditions of TDF, hunting even during the day, while small species are vulnerable to desiccation, using nocturnal activity as an adaptation to escape unfavourable conditions (Ariza et al. 2021b). On the other hand, early successional areas are characterized by patchy vegetation growth, thus a discontinuity of vegetation cover (Lebrija-Trejos et al. 2009), permitting the co-occurrence of open and forest species (Ariza et al. 2021a, accepted). Finally, we expect that canopy cover and litter depth affect carabid trait changes in TDF during succession. In TDF, succession results in the progression of cover structure from sunny, hot and dry to a shady, cool and moist environment (Lebrija-Trejos et al. 2011). Litter depth influences the microenvironment of the soil (Facelli & Pickett, 1991), and offers both shelter from harsh daily conditions and food (Kalinkat et al. 2013; Koivula et al. 1999). A developed canopy and litter layer are expected to benefit smaller species, due to the higher surface area to volume ratio making them more vulnerable to desiccation (Bujan et al. 2016). Furthermore, species with pusher ability are expected to benefit from a well-developed litter layer since these species are adapted to shelter and hunt in confined spaces offered by litter (Forsythe, 1981).

4.2. Material and methods

4.2.1. Study areas

Carabid beetles were collected from Armero (Tolima), Colombia (5° 0' 7.27" N 74° 54' 27.26" W); located in the dry forest biome. We collected carabid beetles from three successional stages (Ariza et al. 2021a, accepted): pasture as an initial point, early succession

(3–7 years of succession), and forest as intermediate successional stage (arbustive areas with between 10 and 50 years of succession; Nassar et al. 2008). Ground beetles were collected using 10 pitfall traps that were installed at each site along a transect of 100 m, with traps 10 m apart. The surveys were performed on a monthly basis (the traps were open for 72 h) for 13 months (June 2015– June 2016). Additionally, a set of environmental variables, including soil and air humidity and temperature, leaf litter depth and canopy cover were recorded per month at each site. For more study area, environmental measurements and taxonomic identifications details, see Ariza et al. (2021a, accepted).

4.2.2. Trait measurements

A series of carabid beetle traits related to resource use were measured or registered (Table 4.1) and converted to categorical variables, except for body size (see Supplementary information 4.1). Due to ecological knowledge gaps of tropical carabid species, measurements were directly taken from the specimens collected to deduce the follow ecological responses: desiccation resistance using body size (Chown & Klok, 2003; Schoener & Janzen, 1968), daily activity using compound eye surface area (Bauer et al. 1998; Talarico et al. 2018), microhabitat use using type of fore-leg and metatrochanter length (Forsythe, 1981, 1987) and dispersal capacity by taking into account the type of hind wing and flight muscle development (Desender, 2000; Venn, 2016). These measurements were tested previously to establish the link between morphological structure and ecological responses (Ariza et al. 2021b). All measures were standardized to body size (the ratio between traits that involves size and body length) to compare between species. Information about diet (at genus level) were obtain from Ball & Shpeley (2009), Erwin (1991), Larochelle & Larivière (2003), Martínez (2005), Straneo & Ball (1989) and Vitolo (2004). The specimens collected were mounted 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; the lowest number being one individual.

4.2.3. Statistical analyses

To test our hypothesis that ecological groups of carabid beetles collected are divided principle by body size and daily activity period, we performed average linkage clustering that preserve the original dissimilarity structure (see data used in Supplementary information 4.1), and Gower dissimilarity used for mixed data types (Pla et al. 2012). This combination showed the best clustering solution (cophenetic correlation = 0.945). The analysis was carried out in R (R Core Team, 2020) using the cluster, Factoextra and FactoMineR packages. With the aim to find a mechanistic understanding of distinct ecological groups in the habitat types sampled, we used RLQ combined with fourth corner methods (Dray et al. 2014) to test the relationship between ground beetle traits and the TDF environment, including soil and air humidity and temperature, canopy cover and litter depth. This analysis combines information on species abundances, their traits and the environment to uncover how the environment filters certain species traits, using three tables: R, which includes environmental characteristics of the TDF successional gradient; L, the species collected (and their abundances) in each successional stage, and Q, a set of traits of each species collected (Dray et al. 2014). RLQ explores the structure of each table and their association, while fourth corner analysis establishes the relationship between each trait and each environmental variable (bivariate associations). RLQ and fourth corner analyses were performed in R using the ade4 package (Dray, 2013). A Global Monte-Carlo test was performing using 99999 random permutations to evaluate the overall significance of the associations between each RLQ table.

Table 4.1 Functional response traits (and their definitions) measured on carabid beetle species collected in Armero, Colombia.

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 & Janzen, 1968 Le Lagadec et al. 1998 Chown & Klok, 2003
Daily activity period, using compound eye surface area (CES)	AP	Longest axis (long, width): $A = \pi LW/4$ n = nocturnal: small eyes (CES/BS: < 0.06) d = mostly diurnal: large eyes (CES/BS: > 0.08)	Daily activity	Bauer et al. 1998 Talarico et al. 2018
Microhabitat use, using type of leg and metatrochanter length (MET)	MU	r = runner: runner leg but without long metatrochanter (MET/BS < 0.08) f = fossorial leg p = pusher: runner leg with long metatrochanter (MET/BS > 0.1)	Microhabitat use	Forsythe, 1981, 1987
Diet	D	z = zoophagous o = omnivorous	Resource use	Moretti et al. 2017 Fountain-Jones et al. 2015
Dispersal capacity	DC	h = high: functional hind wing and flight muscles developed l = low: functional hind wing or not and flight muscles not developed	Potential ability to escape bad conditions	Desender, 2000 Venn, 2016

4.3. Results

4.3.1. Ecological groups

The cluster analyses showed two main ecological groups based principally on body size and daily activity traits (Fig. 4.1): small (< 12 mm) and medium-sized (> 15 mm) species that are exclusively nocturnal (G1) and medium and large-sized species (> 20 mm) with diurnal activity (G2). The first group was diverse, consisting of 12 species. This group was further divided into two subgroups, based on diet and dispersal capacity traits. The first subgroup (G1a, Fig. 4.1) consisted of two species (*Clivina* sp. and *Selenophorus parvus*), which besides being small and nocturnal, have high dispersal capacity and are omnivorous (Supplementary information 4.1). The remaining species belong to subgroup 2 (G1b, Fig. 4.1) and are primarily zoophagous with low dispersal capacity; except *Galerita* sp. (omnivorous) and *Stolonis notula* (high dispersal capacity). The second group (G2) consisted of one medium-sized species (*Megacephala affinis*) and two large species (*Calosoma alternans* and *Enceladus gigas*) with the following traits; two runner and two highly dispersive species.

4.3.2. Trait-environment relation

RLQ analyses showed a similar tendency to the cluster analyses (Fig. 4.2, Table 4.2): here the species were also divided into small and medium-sized and nocturnal (G1) and medium and large-sized and diurnal traits (G2). *Calosoma alternans* and *M. affinis* (species in G2) were associated with pasture (except *E. gigas*) and species in G1 occurred in forest, while species from both groups occurred in early successional areas (Fig. 4.2a, b). Diurnal and high dispersive species were associated with hot sites, species with a low dispersal capacity and omnivorous diet were associated to high canopy cover and nocturnal activity species were associated both with high canopy cover and high air humidity (Fig. 4.2c, d). The Global test

was significantly for Model 2 (Model 2 $p = 0.028$; Model 4 $p = 0.221$), indicating that the environment influence the distribution of ecological groups. Finally, the fourth corner analysis showed a significant correlation between environmental variables and traits on the first axis ($p < 0.05$); of the six environmental variables tested, air and soil temperature had a significantly negative relationship with axis 1, while canopy cover showed a significantly positive relationship with the same axis (Fig. 4.3, Tables 4.3). None of the five traits tested had a relationship with this axis.

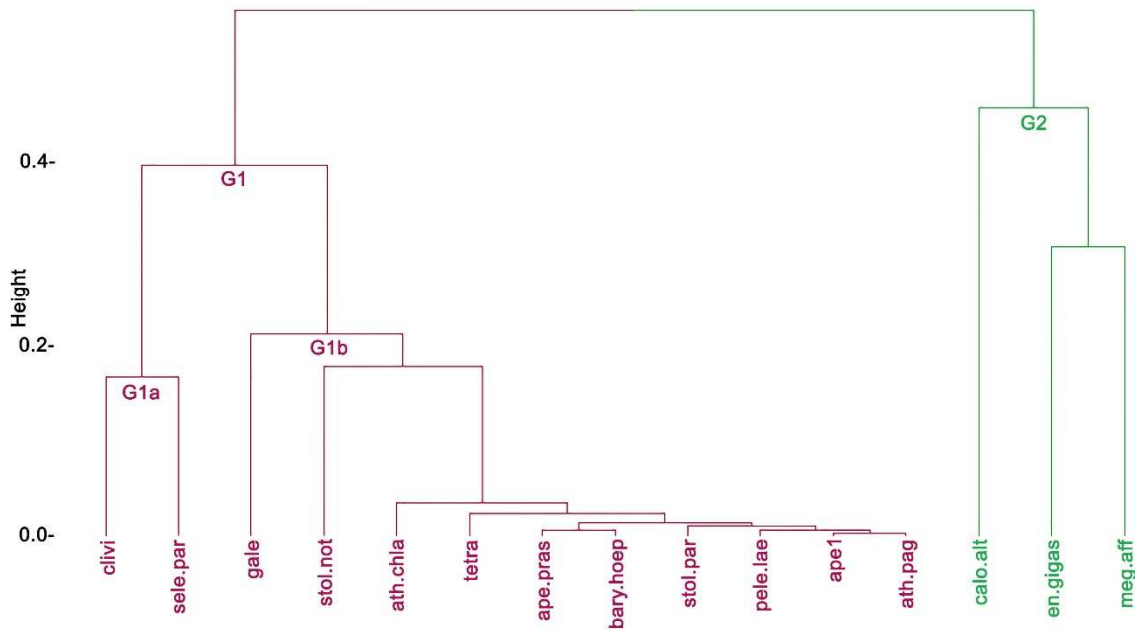


Figure 4.1 Ground beetle ecological groups based on functional response traits. Two principal groups were defined using average linkage clustering and Gower dissimilarity. G1 = group 1 (red colour), G2 = group 2 (green colour). Species name abbreviations are explained in Supplementary information 4.1.

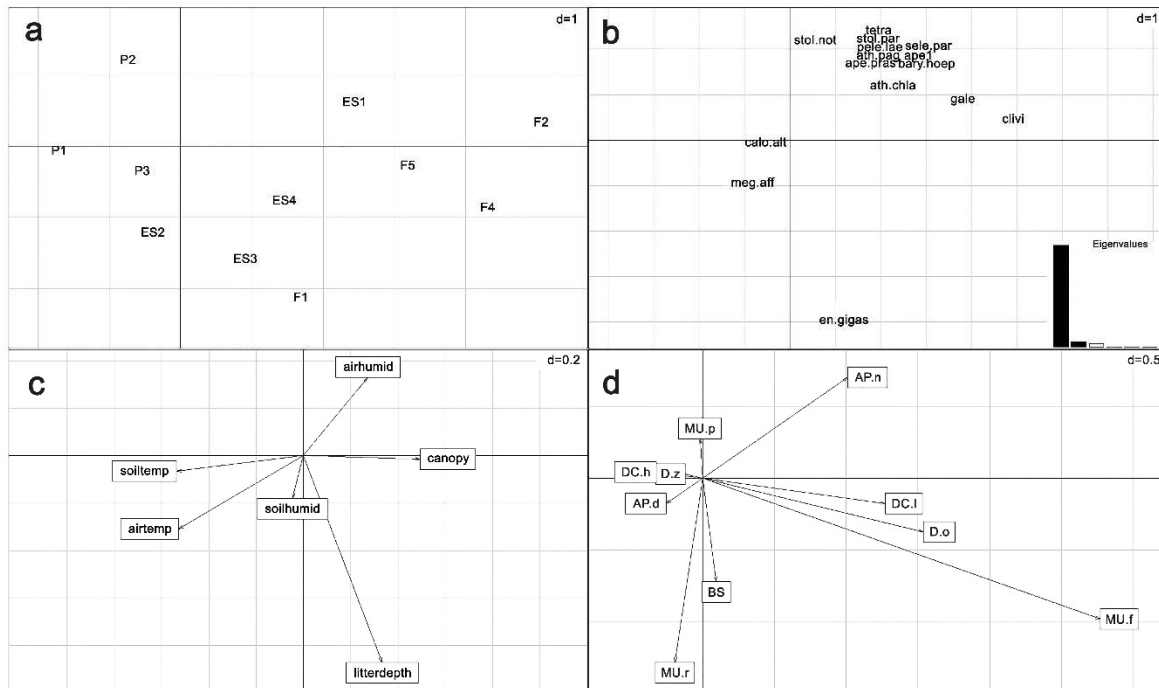


Figure 4.2 First two axis of the RLQ analysis: (a) sites scores, (b) species scores (the insert shows eigenvalues of the first two axes in black), (c) environmental variables, (d) response traits. Species name abbreviations are explained in Supplementary information 4.1. Other abbreviations: P = pasture, ES = early successional stage, F = forest, airhumid = air humidity, airtemp = air temperature, soilhumid = soil humidity, soiltemp = soil temperature, litterdepth = leaf litter depth (cm), canopy = percentage canopy cover, BS = body size, AP.d = diurnal activity period, AP.n = nocturnal activity period, MU.f = fossorial microhabitat use, MU.p = pusher microhabitat use, MU.r = runner microhabitat use, D.o = omnivorous diet, D.z = zoophagous diet, DC.h = high dispersal capacity, DC.l = low dispersal capacity.

4.4. Discussion

Successional habitats in the Colombian tropical dry forest landscape filter carabid species traits differently than temperate regions. Here, traits related to desiccation resistance (body size) and adaptations related to escaping harsh environmental conditions during the day (daily activity), divided the beetles into distinct groups, as hypothesised. Ecological group 1

(G1) was present in forest, the majority species from group 2 (G2) were associated with open pastures, whereas that early successional stages showed a confluence of species with morphological characteristics to survive in both forest and pasture. Species of low dispersal capacity and nocturnal activity are associated with denser canopies (Fig. 4.2): this environmental variable had a significantly positive correlation with RLQ axis 1, while soil and air temperature showed a strongly negative correlation with this RLQ axis. Despite our expectations, neither litter depth nor humidity had a significant correlation with any of the beetle traits analysed.

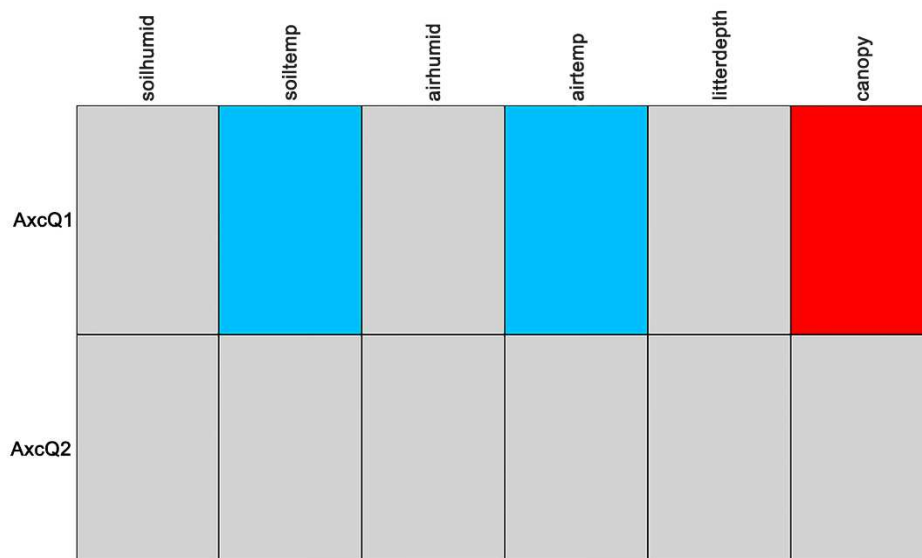


Figure 4.3 Combination of RLQ and fourth-corner results. Fourth-corner tests between the first two RLQ axes for functional response traits (AxcQ1 and AxcQ2) and environmental variables. Significantly associations are represented by blue (negative) and red (positive) cell.

The TDF landscape produced two distinct ecological groups in the ground beetle assemblage, the first group considered to include species more vulnerable to desiccation, and the second group with desiccation resistant species. Such trait divisions were also found in a plant community in Mexican TDF (Lebrija-Trejos et al. 2010b). The first group (G1) was characterized mostly by smaller-sized and nocturnally activity species. Nocturnal activity is a

well-known strategy to cope with harsh environments in arid ecosystems, where diurnal activity is considered an unusual habit (Cloudsley-Thompson, 2001). All species in this group are pushers and could be considered litter exploiters, likewise most species are poor dispersers and were associated with forest and early successional stages. This ecological group was diverse and consisted of twelve species, and was probably a consequence of the lack of ecological knowledge of tropical carabid species and the difficulty in associating functional response traits to each species. The addition of more traits, and their refinement, could result in more consistent groupings.

Table 4.2 Eigenvalues, percentage and cumulative percentage of variance (Cum %) explained by the first five axes of the RLQ analysis.

Axis	Eigenvalue	%	Cum.%
1	0.993	92.278	92.28
2	0.049	4.601	96.88
3	0.031	2.93	99.81
4	0.001	0.158	99.97
5	< 0.001	0.03	100

The second group (G2) was characterized by medium and large-size and diurnally active species, which exploited pasture (except *E. gigas*). The large sizes of these species protect them against desiccation (Baranovská et al. 2019) in this dry and open landscape (Maza-Villalobos et al. 2011). *Calosoma alternans*, an abundant member of this group, seems to be well adapted to open habitats, here pastures, with a long metatrochanter that permits it to shelter in shady places during sunny hours or to hide in narrow spaces to escape predators. The larger size and stronger legs of species in this genus permit individuals to

move easily between different types of habitats (Forsythe, 1987); indeed *C. alternans* was found in all habitat types in TDF. High dispersal capacity appears important to the survival of species in open habitats, for instance, although *E. gigas* is the biggest species inhabiting TDF (48.5 mm), it was absent from pasture, yet was collected in forests and particularly in early successional habitats. This could be because it is apterous, which is a disadvantage in terms of escaping predators, and thus it prefers habitats that are more structurally complex (Brose, 2003).

Finally, soil humidity is a limiting factor for carabids, given the risk of desiccation, especially during the early developmental stages of these beetles (Lövei & Sunderland, 1996). Despite this, only air and soil temperature (negatively) and canopy cover (positively) correlated with RQL axis 1 of the fourth-corner analysis. In TDF, canopy development results in a decrease in air and soil temperature, a pattern not observed for soil humidity, which shows a non-linear increase with canopy development (see Lebrija-Trejos et al. 2009, 2011). Carabid beetles as heterothermic organisms, depend on temperature for physiological processes (Schowalter, 2006). Temperature affects the geographical distribution of carabids (Thiele, 1977), their activity patterns (Neve, 1994) and seed consumption (Saska et al. 2010), among others. It appears that in the TDF, air and soil temperatures modulated by canopy development, filter carabid traits associated with desiccation resistance. Indeed, air temperature was a predictor of community assembly in TDF vegetal succession (Lebrija-Trejos et al. 2010b), and also showed to be important in structuring the carabid assemblage together with soil temperature and canopy cover (Ariza et al. 2021a, accepted).

To conclude, we showed that temperature is an important factor for the survival of carabid beetles in this harsh environment, similarly to other arthropods in arid ecosystems (Cloudsley-Thompson, 1975). We identified two main ecological groups, which were primarily separated by two traits linked to hot conditions in this system: body size and daily activity period. The distribution of ecological groups associated with TDF successional

stages mirrored our previous findings with respect to assemblage response to succession (Ariza et al. 2021a, accepted).

Table 4.3 The percentage contribution to total inertia of RLQ and Pearson correlations (r) of environmental variables and functional response traits with axes 1 and 2 of RLQ according to the Fourth-corner statistic. For AP, MU, D and DC traits the analyses were F tests.

Variables	Contribution %	Axis 1	Axis 2
Environmental			
Soil humidity	2.557	-0.033	-0.034
Soil temperature	27.168	-0.387*	-0.012
Air humidity	7.582	0.196	0.062
Air temperature	26.249	-0.379*	-0.058
Leaf litter depth	13.738	0.239	-0.165
Canopy cover	22.703	0.356*	-0.002
Traits/Attributes			
BS	3.31	0.05	-0.207
AP		13.898	1.856
AP.d	4.955		
AP.n	19.547		
MU		3.493	2.603
MU.f	13.682		
MU.p	0.438		
MU.r	1.98		
D		9.815	0.162
D.o	16.782		
D.z	1.322		
DC		23.141	0.116
DC.h	7.681		
DC.l	30.298		

Supplementary information

Supplementary information 4.1 Categorical and continuous trait properties of carabid beetle species collected in Armero, Colombia. Traits are explained in detail in Table 4.1. n = number of individuals measured; body size in mm.

Species	Abbreviation	n	Abundance	Body size	Activity period	Microhabitat use	Diet	Dispersal capacity
<i>Apenes prasinus</i> Ball & Shpeley, 1992	ape.pras	6	5	10.94	nocturnal	pusher	zoophagous	low
<i>Apenes</i> sp.	ape	2	1	9.20	nocturnal	pusher	zoophagous	low
<i>Athrodictus chlaenioides</i> Dejean, 1829	ath.chla	3	3	16.64	nocturnal	pusher	zoophagous	low
<i>Athrodictus paganus</i> (Dejean, 1831)	ath.pag	1	2	9.08	nocturnal	pusher	zoophagous	low
<i>Barysomus hoepfneri</i> Dejean, 1829	bary.hoep	5	3	10.21	nocturnal	pusher	zoophagous	low
<i>Calosoma alternans</i> (Fabricius, 1792)	calo.alt	10	113	23.65	diurnal	pusher	zoophagous	high
<i>Clivina</i> sp.	clivi	3	3	8.57	nocturnal	fossorial	omnivorous	high
<i>Enceladus gigas</i> Bonelli, 1813	en.gigas	9	8	48.47	diurnal	runner	zoophagous	low
<i>Galerita</i> sp.	gale	7	6	15.37	nocturnal	pusher	omnivorous	low
<i>Megacephala affinis</i> Dejean, 1825	meg.aff	10	21	15.91	diurnal	runner	zoophagous	high
<i>Pelecium laevigatum</i> Guérin-Ménéville, 1843	pele.lae	1	1	7.90	nocturnal	pusher	zoophagous	low
<i>Selenophorus parvus</i> Darlington, 1934	sele.par	4	4	8.44	nocturnal	pusher	omnivorous	high
<i>Stolonis notula</i> Motschulsky, 1866	stol.not	1	1	7.58	nocturnal	pusher	zoophagous	high
<i>Stolonis parvulus</i> (Straneo, 1951)	stol.par	1	1	6.20	nocturnal	pusher	zoophagous	low
<i>Tetragonoderus</i> sp.	tetra	6	6	4.22	nocturnal	pusher	zoophagous	low

The number of individual measured (n) represent all individuals collected from the study area between June 2015 and October 2016. Abundances represent the number of individuals collected between June 2015 and June 2016.

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Chapter 5

Summary

Checklist and ecological notes of ground beetles
(Coleoptera, Carabidae) collected from tropical dry
forests in the Valley of the Magdalena River,
Colombia

Abstract

Carabid beetles are a well-known insect group in temperate regions, but is less-known in the tropics where a lack of taxonomic keys makes it difficult to use them in ecological studies. However, this lack of knowledge can be partially resolved through ecological information deduced from morphological traits. Carabid beetles were collected from the dry forest ecosystem in Armero (Tolima) and Cambao (Cundinamarca) in three habitat types: forest, early successional stage and pasture. The beetles were collected from June 2015 to October 2016 at Armero, and in Cambao once in December 2015 (dry season) and once in May 2016 (wet season). Adult carabid beetles were identified to species level, and ecological information including daily activity, microhabitat use and dispersal power were inferred from morphological traits. Twenty-eight species were collected; *Calosoma alternans*, *Megacephala affinis* and *Selenophorus parvus* were the only species found in all habitat types, and 54% of the species were collected from only one habitat type. Most of the collected species were small, nocturnal, pushers and macropterous. The small size trait in this dry ecosystem is surprising since studies on insects in xeric environments have shown that large body size is a trait related to desiccation resistance. Small-sized carabid beetles, together with nocturnal and pusher behaviours, are likely better at escaping unfavourable conditions in this harsh landscape. In Colombian TDF, knowledge of ground beetles is incipient, and the list presented here corresponds to only 3.5% of the carabid species reported for the country. Long-term studies involving both assemblage and trait-based approaches are required to better understand the dynamics of these insects in this harsh environment.

Keywords

Trait, carabid, insect, daily activity, body size

5.1. Introduction

Carabid beetles are a well-known Coleoptera family in temperate regions, with ca. 37 404 described species around the world (Lorenz, 2019) and ca. 8 537 species in the Neotropical region (including Cicindelinae; Bousquet, 2012) (Cassola & Pearson, 2001; Martínez, 2005). The group is divided into twenty-two subfamilies (Bouchard et al. 2011), fifteen of them with a Neotropical distribution (Martínez, 2005; Reichardt, 1977). In Colombia, ca 800 carabid species have been registered (Martínez, 2005; Vitolo, 2004), six of which have distribution in tropical dry forest (Arenas & Ulloa-Chacón, 2016). In this ecosystem, most identifications have been made at the morphospecies level (Arenas & Ulloa-Chacón, 2016; Uribe & Vallejo, 2013), making it difficult to link ecological information to particular species.

Tropical insects are declining (Janzen & Hallwachs, 2019), and together with the fact that the TDF landscape is highly transformed by anthropogenic activities (Sánchez-Azofeifa et al. 2005a; Sánchez-Azofeifa et al. 2005b), prioritizes the study of insects in Colombian TDF. Conservation actions for this ecosystem require substantial knowledge of the biology and distribution of species (Pennington, 2014), yet little is known about insects in this landscape, including their taxonomy (e.g., Medina & González, 2014). Dry forest insect studies in Colombia focus mainly on ants, butterflies and dung beetles (e.g., Achury et al. 2012; Armbrecht et al. 2001; Barraza et al. 2010; Casas-Pinilla et al. 2017; Delgado-Gómez et al. 2012; Peña & Flórez, 2016), and is scarce for ground beetles (see Arenas & Ulloa-Chacón, 2016; Uribe & Vallejo, 2013).

The amount of information that exists in terms of the taxonomy and ecology of carabid beetles have permitted its use as bioindicator and biological models (Koivula, 2011; Kotze et al. 2011). This is not the same for the tropics where the lack of taxonomic keys, makes it difficult not only to identify the species, but also to develop ecological knowledge at the species-level (Martínez, 2005; Maveety et al. 2011; Rainio & Niemelä, 2003). Currently,

it is widely accepted that species traits can be used to evaluate the responses of insect to environmental change (Evans et al. 2019), but the lack of such trait information in the tropics limits their use. Despite this lack, European studies have shown that some ecological information can be inferred using morphology (Bauer & Kredler, 1993; Desender, 2000; Forsythe, 1981). Using both taxonomic identification and morpho-traits of the species, we present a preliminary checklist of tropical dry forests species of the Valley of Magdalena River, Colombia, with ecological notes and habits as a starting point for future research with this insect group.

5.2. Material and methods

Carabid beetles collected from the dry forest ecosystem in Armero (Tolima) and Cambao (Cundinamarca) from previous studies were register (see Ariza et al. 2021a, accepted, 2021b). The ecological information of the species from Cambao were inferred from morphological traits using the methodology of Ariza et al. (2021b).

For daily activity, compound eye surface area was used, following the affirmation that nocturnal species have small eyes and visual hunters (mostly diurnal) large (Bauer & Kredler, 1993; Talarico et al. 2018). For the microhabitat use classification, type of fore-legs and length of the metatrochanter were used. Beetles with fossorial legs were classified as fossorial, runner species with a long metatrochanter as pusher species, and runner species with a short metatrochanter as runner species. Finally, dispersal power was classified as low if the beetles were apterous, brachypterous or macropterous and do not possess developed flight muscles. Dispersal capacity was high if they were macropterous and with flight muscles developed (Desender, 2000; Venn, 2016). Body size was measure from the base of the mandibles to the tip of the abdomen (Moretti et al. 2017).

To establish the ecological groups divided by the morpho-traits listed here, we performed a cluster analysis with the average linkage method and Gower as a distance measure (Pla et al. 2012) (cophenetic correlation = 0.904). The analyses were performed using the cluster, Factoextra and FactoMineR packages in R (R Core Team, 2020). Three species from the list were excluded, due to their unknown morpho-traits.

5.3. Results

Twenty eight species were register in the Valley of the Magdalena River dry forest (Table 5.1). *Calosoma alternans*, *Megacephala affinis* and *Selenophorus parvus* were found in all habitat types, 36% of the species were found in two habitat types and 54% only in one habitat. The species found in only one season (dry or wet) were 46%.

In terms of the ratio of species per trait, most were small (75%), nocturnal (75%), pusher (61%) and macropterous (71%) (Fig. 5.1). The ratio of species with high and low dispersal power was slightly different (36% and 46% respectively). The cluster analyses grouped the species by traits principally into four groups: two groups with medium and large-size species and with diurnal activity (G1-G2) and two groups with medium and small-size species and nocturnal activity (G3-G4) (Fig. 5.2).

Table 5.1 List of species in the tropical dry forest in Armero (arm) and Cambao (cam) with ecological information. Abbreviations: F = forest, ES = early successional stage, P = pasture, d = dry, w = wet, n = nocturnal, d = diurnal, f = fossorial, p = pusher, r = runner, a = apterous, b = brachypterous, m = macropterous, unk = unknown, N/A = species excluded from the cluster analyses. The capital letter in season box means that the species was mainly collected in that season.

Species	Abbreviation	Locality	Habitat type	Season	Body size (mm)	Daily activity	Microhabitat use	Type of hind wing	Dispersal power
<i>Anaulacus piccolus</i> (Chaudoir, 1876)	N/A	arm	F	d	3.7	unk	unk	unk	unk
<i>Apenes</i> cf. <i>coriacea</i> (Chevrolat, 1863)	ape.cor	arm	P	w	11.69	n	p	m	low
<i>Apenes</i> cf. <i>morio</i> (Dejean, 1825)	ape.mor	arm cam	F	dw	8.85	n	p	m	high
<i>Apenes</i> cf. <i>prasinus</i> Ball & Shpeley, 1992	ape.pras	arm	F ES	dw	10.94	n	p	b	low
<i>Apenes</i> sp. 1	ape1	arm	P	dw	9.21	n	p	m	low
<i>Apenes</i> sp. 2	N/A	arm	ES	d	unk	unk	unk	unk	unk
<i>Apenes</i> sp. 3	ape3	cam	P	d	9.84	n	r	m	high
<i>Aspidoglossa crenata</i> (Dejean, 1825)	aspi.cre	arm	P	dW	7.12	n	f	m	high
<i>Athrostictus chlaenioides</i> Dejean, 1829	ath.chla	arm	F P	w	16.64	n	p	m	low
<i>Athrostictus paganus</i> (Dejean, 1831)	ath.pag	arm	ES P	dw	9.08	n	p	m	low
<i>Barysomus hoepfneri</i> Dejean, 1829	bary.hoep	arm	P	Dw	10.21	n	p	m	low
<i>Calosoma alternans</i> (Fabricius, 1792)	calo.alt	arm cam	F ES P	dW	23.65	d	p	m	high
<i>Camptodontus</i> sp.	camp	arm	F	w	10.13	n	f	unk	unk
<i>Clivina</i> sp.	clivi	arm	F ES	Dw	8.57	n	f	m	high
<i>Enceladus gigas</i> Bonelli, 1813	en.gigas	arm	F ES	dW	48.48	d	r	a	low
<i>Galerita</i> sp.	gale	arm	F ES	dW	15.38	n	p	m	low
<i>Megacephala affinis</i> Dejean, 1825	meg.aff	arm cam	F ES P	dW	15.91	d	r	m	high
<i>Megacephala cribrata</i> Steinheil, 1875	meg.cri	cam	ES P	dW	17.15	d	r	m	high

(Table 5.1, continue)

Species	Abbreviation	Locality	Habitat type	Season	Body size (mm)	Daily activity	Microhabitat use	Type of hind wing	Dispersal power
<i>Meotachys</i> sp.	N/A	arm	ES P	d	2.22	unk	unk	unk	unk
<i>Pelecium laevigatum</i> Guérin-Méneville, 1843	pele.lae	arm	ES	w	7.9	n	p	a	low
<i>Selenophorus parvus</i> Darlington, 1934	sele.par	arm cam	F ES P	dW	8.44	n	p	m	high
<i>Selenophorus</i> cf. <i>clypealis</i> Ball & Shpeley, 1992	sele.cly	cam	P	w	8.51	n	p	m	low
<i>Selenophorus woodruffi</i> Ball & Shpeley, 1992	sele.wood	cam	ES P	dW	8.86	n	p	m	low
<i>Stenomorphus angustatus</i> Dejean, 1831	sten.angus	cam	ES	d	13.02	n	p	m	high
<i>Stolonis</i> cf. <i>notula</i> Motschulsky, 1866	stol.not	arm	ES	w	7.58	n	p	m	high
<i>Stolonis interceptus</i> Chaudoir, 1873	stol.inter	arm	ES	d	6.79	n	p	m	low
<i>Stolonis parvulus</i> (Straneo, 1951)	stol.par	arm	ES	d	6.2	n	p	m	low
<i>Tetragonoderus</i> sp.	tetra	arm cam	ES P	Dw	4.22	n	p	m	low

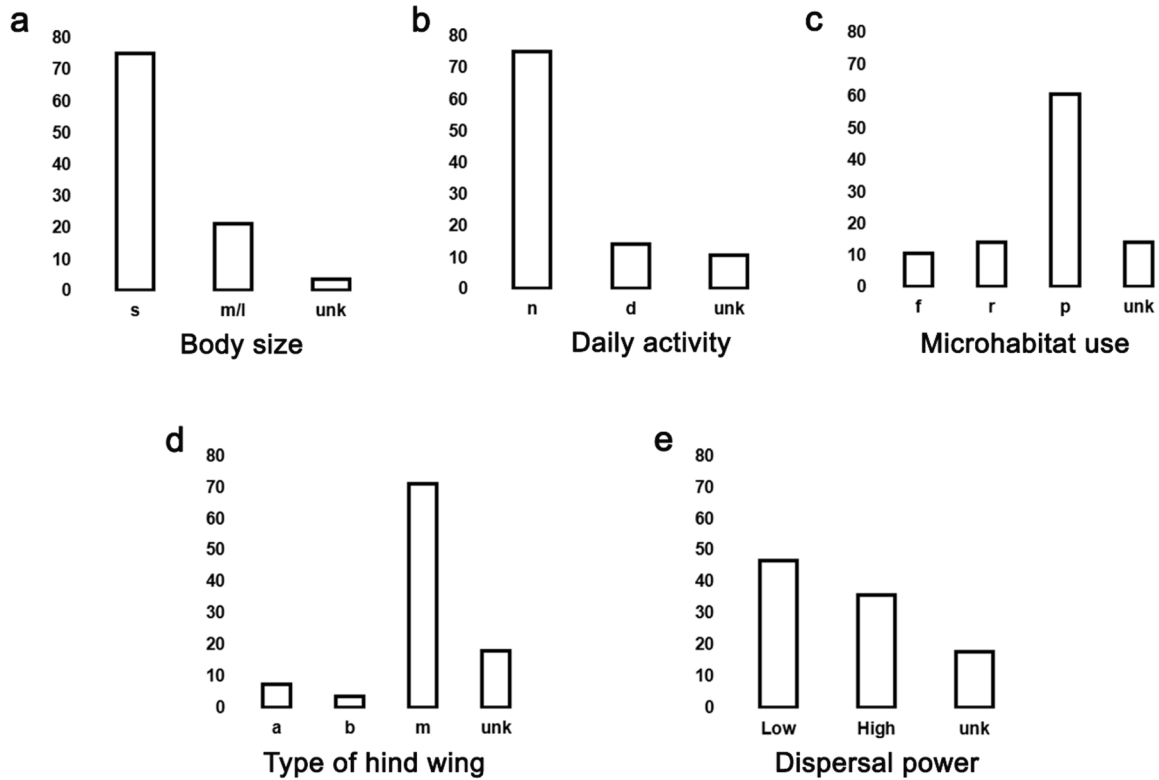


Figure 5.1 Percentage of species presenting attributes of a trait: (a) body size, (b) daily activity, (c) microhabitat use, (d) type of hind wing, (e) dispersal power. Abbreviations: s = small, m/l = medium or large, n = nocturnal, d = diurnal, f = fossorial, r = runner, p = pusher, a = apterous, b = brachypterous, m = macropterous, unk = unknown.

The first group consisted of the largest and apterous species found in this dry ecosystem (*Enceladus gigas*). The second group (G2) consisted of three high dispersive species: *C. alternans* (large-size and pusher species) and two species belonging to the genus *Megacephala* (medium-size and runner species). All species from group 3 (G3) were characterized to be small, nocturnal and with high dispersal capacity, this group was subdivided into three subgroups: four pusher species, one runner species and three fossorial species. Finally, group 4 (G4) consisted of small and medium-size, nocturnal, pusher and low dispersive species.

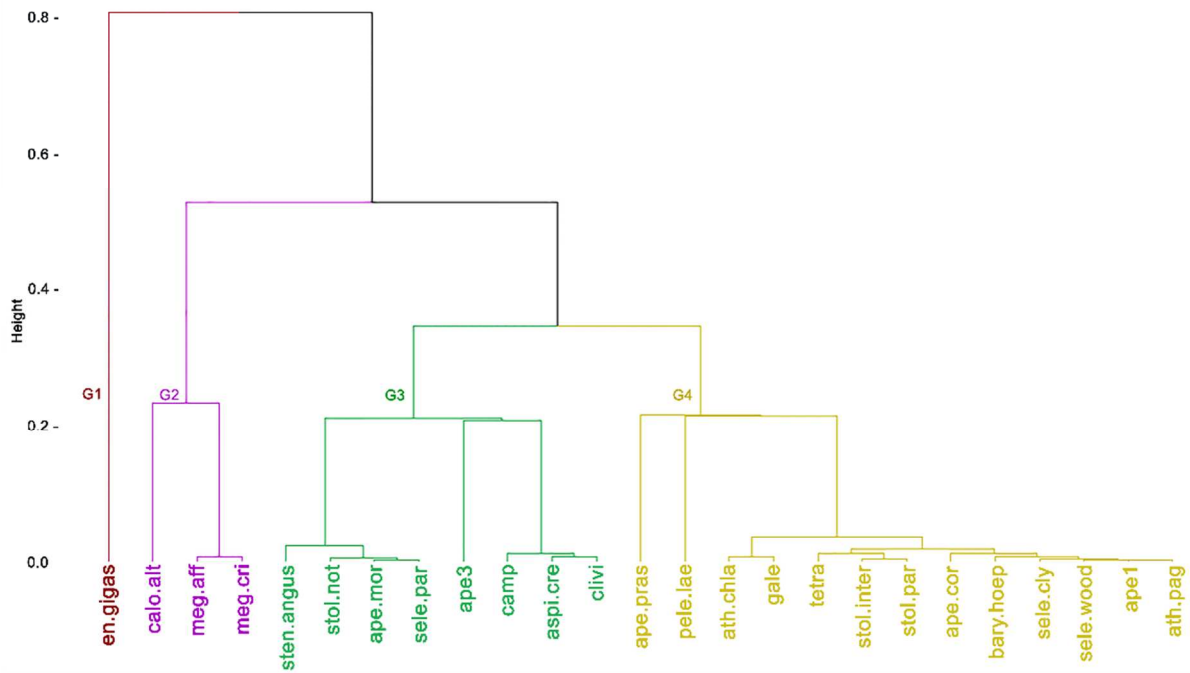


Figure 5.2 Ecological groups of carabids divided by morpho-traits presented in Table 5.1. Abbreviations: G1 = group 1 (red colour), G2 = groups 2 (purple colour), G3 = group 3 (green colour), G4 = group 4 (yellow colour). Species abbreviation are explained in Table 5.1.

5.4. Discussion

In Colombian TDF, knowledge of ground beetles is incipient. The list of species presented here corresponds to only 3.5% of the species reported for Colombia. Additionally, thirteen genera registered for the Valley of the Magdalena River TDF (Martínez, 2005) were not collected in this study. Comparing our list with the two studies performed in this ecosystem (in the Valley of the Cauca River and in the Middle Magdalena) (Arenas & Ulloa-Chacón, 2016; Uribe & Vallejo, 2013), showed that seven genera were shared between them (five and three respectively). It was not possible to compare species between these studies since these studies did not identify most of their catch to species level. However, and interestingly, *C.*

alternans, *M. affinis* and *Megacephala cribrata* (the most abundant species in the Valley of the Magdalena River) were not collected from TDF in the Valley of Cauca River – but it hosted *Megacephala sobrina*. The absence of *C. alternans* was surprising given that it was abundant in the region in the past. The authors speculated that this species may have gone locally extinct as a consequence of agronomic management (Arenas & Ulloa-Chacón, 2016). *Enceladus gigas* was also not found in these localities, and seems to be restricted to TDF of the Valley of the Magdalena River (Estrada & Salazar, 2004).

The high beta diversity of TDF (Banda-R et al. 2016) makes it difficult to generalize ecological patterns using species composition, but species traits are a useful tool to elucidate ecological mechanisms (Poorter et al. 2019). First, however, it is necessary to collect basic information on species in this tropical landscape. For carabid beetles, European studies have shown a relation between morphology and species habit (Bauer et al. 1998; Forsythe, 1981, 1991; Talarico et al. 2018). We used the same reasoning to infer some habits of the carabid beetles collected in TDF. In this dry forest ecosystem, species were primarily small (Fig. 5.1a), even though studies of desert arthropods have shown that size is a restrictive trait to survive harsh conditions produced by high temperatures and low humidity (Cloudsley-Thompson, 2001) as is true for TDF (Lebrija-Trejos et al. 2011). To escape desiccation, these small-sized carabids were also nocturnal and pushers (Fig. 5.1b-c, Table 5.1; see Ariza et al. 2021b, 2021c, in preparation). Pusher is a trait that involves a morphological adaptation of the metatrochanter (larger) to push through litter or into narrow spaces (Forsythe, 1981) – litter plays an important role in ground beetle distribution patterns (Antvogel & Bonn, 2001).

On the contrary, large and some medium-sized species were diurnal, possibly because of their resistance to desiccation (Baranovská et al. 2019). There were no large differences between low and high dispersal power, probably because, (1) to escape from bad conditions is a critical trait in unstable habitats (Darlington, 1943), but (2) is also energetically expensive (Nelemans, 1987). The three species found in all habitat types – *C. alternans*, *M. affinis* and

S. parvus - had high dispersal powers. It is known that many species express the development of flight muscles in accordance of environmental factors; favourable conditions encourage their development (Nelemans, 1987).

On the other hand, TDF carabid species showed four ecological groups divided principally by body size, daily activity and dispersal capacity (Fig. 5.2; see Ariza et al. 2021c, in preparation). As mentioned above, in hot ecosystems, body size has a prominent role to avoid desiccation (Chown et al. 1995; Le Lagadec et al. 1998) similar to daily activity as has been shown for canopy insects in TDF (Silva et al. 2017). However, the addition of feeding guild information could affect the ecological group structure presented here. This trait is considered a surrogate of trophic level (Moretti et al. 2017), and although most carabid species are predators (Lövei & Sunderland, 1996), studies are needed to confirm this for tropical species. At the moment, morphology has not shown consistent patterns to provide information on feeding preferences (Ingerson-Mahar, 2014), although this would help to establish a general pattern with respect to resource use.

It is clear that more studies following the trait-based approach are needed to better understand the dynamics of these insects in the harsh TDF environment. The purpose of this study was to provide trait information as a starting point to do just that.

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Chapter 6

General discussion

6.1. Adaptations of carabid beetles to the harsh tropical dry forest landscape

The marked seasonality experienced in tropical dry forest (Murphy & Lugo, 1986) produces characteristic dynamics in insects inhabiting this zone. Desiccation risk is an important limiting factor for survival in the dry season, when water is scarce (Maass & Burgos, 2011) and air temperature high (Lebrija-Trejos et al. 2011). TDF carabid beetles display morpho-traits to help them survive seasonal droughts, even when it is exasperated by the El Niño phenomenon. In general, there were no differences in the occurrence of trait attributes between the El Niño and non-El Niño episode (Ariza et al. 2021b, see Chapter 2); changes were reflected in the proportions of trait attributes (Fig. 2.2). This means that carabid beetles have experienced severe and recurring drought episodes produced by ENSO for a long period of time (Caviedes, 2001; Grove & Adamson, 2018), which has already filtered traits that permit these insects to survive in this landscape (see Kotze & Lawes, 2007; Meir & Pennington, 2011). Yet, it is necessary to perform long-term studies to confirm these findings. With the evidence presented here, carabid beetles seem well-adapted to seasonal drought experienced in TDF, even when exasperated by ENSO episodes.

For insects, large body size is a morpho-trait usually linked to survival in dry environments (Baranovská et al. 2019; Bujan et al. 2016; Chown et al. 1995), due to (among others) the low surface area-to-volume ratio (Hood & Tschinkel, 1990) and a higher water content in the body (Le Lagadec et al. 1998). However, contrary to expectations, the harsh TDF environment filtered small-bodied species (<15 mm), which represents 75% of the species collected in this study (see Chapter 5, Fig. 5.1a). All smaller species were also nocturnal and pushers or fossorials (except *Apenes* sp. 3, which was a runner), which means they need to escape from these environmental conditions to avoid desiccation. Pusher is a morphological adaptation that involves a long metatrochanter that helps to push the individuals through confined spaces, such as litter (Forsythe, 1981), which they exploit (see Chapter 3).

Only 21% of species were medium and large sized (Fig. 5.1a), and most of them were collected in open habitats (four of six species, Table 5.1). Three of these species (*Calosoma alternans*, *Megacephala affinis* and *Megacephala cribrata*) had diurnal activity, supporting the notion that larger species are more resistant to dry conditions, such as TDF pastures (Baranovská et al. 2019). Nevertheless, although water is considered a limiting factor for species in TDF (Maass & Burgos, 2011), the high number of small species could be interpreted such that food resources and predation risk are also important limiting factors in this landscape. In fact, large-sized individuals need more energy to carry out crucial processes for their life-history, including larval development, maturity, fecundity, etc. Activities associated with resource acquisition of larger species also make them more visible to predators (Blanckenhorn, 2000).

Within the diurnal and medium-large-size species, *C. alternans*, *M. affinis* and *M. cribrata* were also flight capable, but not *Enceladus gigas*, which despite its large size (48 mm), was associated with forest and early successional habitats, probable supporting the enemy-free space hypothesis (Brose, 2003). This hypothesis considers larger-size species vulnerable to predation and for that reason avoid open spaces. In the case of *E. gigas*, given that it is flightless and thus cannot escape quickly from predators, it prefers a habitat with dense vegetation. Despite the advantages of flight, there were few differences among the proportions of low and high dispersal capacity in TDF (46% and 36% respectively, Fig. 5.1e). Flight capacity is a trait associated with unstable environments (Darlington, 1943; Venn, 2016), but is also energetically expensive (Nelemans, 1987), which may be the reason for the slight differences observed between flight capabilities of ground beetles in TDF. No polymorphism was found in the dispersal power trait for any TDF species, although it is considered an adaptative trait dependent on favourable environmental conditions and the availability of resources (Venn, 2016). Long-term population studies would help to understand the factors that influence the expression of this functional response trait.

6.2. Quantitative effects of seasonal environmental gradients

The 13 month study performed here, influenced by the El Niño/ENSO episode, showed that even though ENSO diminishes rainfall considerably, it did not suppress TDF seasonality (UNGRD, 2016). During this time, seasonality did not significantly affect carabid beetle assemblage structure in Armero (Ariza et al. 2021a, accepted; Chapter 3), but ground beetle numbers did peak during the wet season. However, the comparison among El Niño and non-El Niño episodes showed that the ground beetle assemblage exhibited strong differences; the number of species and individuals decreased more than two-fold during the El Niño period, but in both episodes, abundance peaked during the wet season (Ariza et al. 2021b; Chapter 2).

The lack of a seasonality effect during the 13 months of the El Niño episode could be explained by the open canopy of deciduous trees in these forests as a response to severe drought (Holbrook et al. 2009; Murphy & Lugo, 1986). Even during the wet season, rainfall was insufficient to establish favourable conditions, expressed in no assemblage effects. However, three months after the episode ended, the beetle assemblage showed fast recovery, probably due to the termination of diapause in many species (Lövei & Sunderland, 1996) using moisture as a signal of a favourable environment (Hodek, 2003; Tauber et al. 1998). Abundance peaks observed in the wet season during ENSO was primarily caused by *C. alternans*, a dry habitat species (Larochelle & Larivière, 2003). When this species was removed from the dataset, wet season abundance peaks disappeared (Ariza et al. 2021a, accepted; Chapter 3).

6.3. Carabid beetle succession in the tropical dry forest landscape

Evaluation of the carabid beetle assemblage and ecological group distribution during TDF succession showed that early successional stages have a prominent role as habitat corridors

for species. Environmental heterogeneity of this landscape (Lebrija-Trejos et al. 2011) results from the overlap of species and ecological groups from both forest and pasture (Ariza et al. 2021a, accepted, Chapter 3-4). As canopy cover progresses, the environment changes from hot-dry to warm-moist (Lebrija-Trejos et al. 2009). This progression was reflected in the carabid beetle ecological groups, which were divided into desiccation resistant species (mostly large-size and diurnal, G2) present in pastures and desiccation vulnerable species (mostly small-size and nocturnal, G1) in the forest (Fig. 4.1). Species vulnerable to desiccation (primarily in group G1) had a pusher habit to permit them exploiting narrow spaces in the litter (Forsythe, 1981). However, this trait was not exclusive to this group; *C. alternans* a species in the desiccation resistant ecological group is also a pusher. Although this species was most abundant in pastures, it was found in all habitat types, so this adaptation can help to protect it in dry and hot pastures, and hunt through the litter.

In terms of environmental drivers, canopy cover and soil and air temperature affected both the ground beetle assemblage and their functional response traits in the TDF landscape (Figs. 3.3, 4.3). Although soil humidity is considered a major factor influencing carabid beetles (Fidan & Sirin, 2016; Kaizuka & Iwasa, 2015; Niemelä et al. 1992), this environmental variable did not have the same influence on TDF carabids. These results could be attributed partially to the ENSO event, which produced a considerable reduction in precipitation (UNGRD, 2016), followed by the response of deciduous trees to produce an open canopy. An open canopy homogenize environmental conditions in all habitat types (Lebrija-Trejos et al. 2011), and as has been observed in other studies, an open canopy favours generalist species that can survive in this harsh environment (Arenas-Clavijo & Armbrrecht, 2019; Neves et al. 2010). On the other hand, another reason why soil humidity does not appear to be significant in this landscape is because this environmental variable does not have a linear progression with TDF canopy development (Lebrija-Trejos et al. 2009). Both approaches (assemblage and traits) showed the importance of temperature - modulated by canopy progression - to structure carabid beetle species and ecological groups.

6.4. Survey effort and methods used to collect carabid beetles in TDF

Carabid beetle trait distribution during TDF succession showed the occurrence of two principal ecological groups defined by body size and daily activity patterns. These groups formed using the traits of fifteen species during 13 months of survey in Armero (Chapter 4). When the pool of species increased to 28 species (the carabid beetles collection during 15 months at two localities: Armero and Cambao; Chapter 5), the cluster analyses showed four ecological groups, also divided by dispersal capacity (Fig. 5.2).

The 28 species collected in this study represent only 3.5% of the species register for Colombia (from the species list presented by Martínez, 2005 and Vitolo, 2004). Here, the catches were made using ten pitfall traps per site, and active for three days. Pitfall traps are considered a suitable method for the collection of ground-dwelling carabid species (e.g., Boetzi et al. 2018; Digweed et al. 1995; Moret, 2001), but canopy species are not included in the catches. A complete survey of TDF carabid beetles will provide a better understanding of the ecology of this group and will improve the possibilities of their use as bioindicators in the TDF. In this thesis, rarefaction/extrapolation curves did not reach saturation of species (Ariza et al., 2021a, accepted; Fig. 3.2). To reach acceptable completeness, I recommend increasing the number of pitfall traps per site (Vennila & Rajagopal, 1999), open the traps continuously at least for one year, and add methods of collection to catch arboreal species (Rainio, 2012). However, it seems that most tropical carabid beetle species are low in number (Paarmann et al., 2002; Rosero, 2010; Vieira et al., 2008).

Besides limitations in carabid catches, I recommend taking environmental variables measures *in situ* continuously during all the surveys to understand the link between carabid beetle distribution patterns and habitat conditions. For example, soil humidity has a prominent role in larval development (Lövei & Sunderland, 1996), but did not show a significant relationship with TDF carabid response. Insects are sensitive to environmental changes, however they respond to all complexities of habitat attributes, which include

environmental variables fluctuations in time and space. Some authors (e.g., Antvogel & Bonn, 2001; Mitchell, 2005), however, have discussed the limited utility of taking environmental measurements at the moment of the survey, due to the possibility that environmental fluctuations in time are ignored, and that the response of insects to the environment is not immediate.

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