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ORIGINAL RESEARCH

The role of sheltered habitats in biodiversity conservation of species sensitive to drought: a case study using ground beetles (Coleoptera, Carabidae) in the Gorongosa National Park

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Abstract

In the aftermath of 2019' tropical cyclones Idai and Kenneth, we assessed ground beetle communities of the Gorongosa National Park (GNP) in Mozambique. The influence of habitat shelters, namely the buffering role of closed microhabitat conditions on Alpha diversity and community trait values during a long period of drought, was evaluated across the main habitat types of the park: miombo forests, mixed forests, transitional forests, and grasslands (open savannas). These habitat types comprised a distance gradient in relation to lake Urema, in the center of GNP. Miombo forests were farther from the lake while grasslands and transitional forests were in the floodplain area. Ground beetle communities were sampled using pitfall traps set up at 25 sites of each habitat type along an environmental gradient of tree canopy cover during the last twenty days of the dry season. Higher species richness of ground beetles was found in closed habitat shelters along the distance gradient to lake Urema. A higher functional diversity was also found along the canopy gradient, with larger sized and wingless species being more abundant in closed habitats than in open areas. This result highlights the crucial role of habitat closedness in the protection of sensitive ground beetles. In particular, the buffer effect of tree canopy and the protection of the understory plants and the litter layer was critical for the survival of hygrophilous species and will be key in conservation strategies to face climate aridification and habitat fragmentation.

Keywords Aridification · Body size · Caraboidea · Functional diversity · Gorongosa · Groundcovers

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Introduction

Climate change events related to El Niño/southern oscillation (ENSO) are a major driver of climatic variability in tropical biomes in Southern Africa such as the savannas in Mozambique (Kirichenko-Babko et al. 2020; Ariza et al. 2021). Particularly, the increase in long-lasting periods of drought is likely to severely affect African biodiversity due to increasing aridification (Engelbrecht et al. 2007; Massad and Castigo 2016; Mbokodo et al. 2020). Increasing drought intensity and frequency lead to tree dieback and soil desertification (Khaine and Woo 2015; Corlett 2016; Mbokodo et al. 2020), and extends beyond emblematic mammals, by impacting soil invertebrates which are pivotal for ecosystem functioning.

Among the various functional groups of soil communities, ground beetles (Coleoptera, Carabidae) serve as important ecological and biodiversity indicators of habitat quality and environmental changes (Rainio and Niemelä 2003; Koivula 2011). Specific carabid traits, namely body size and hind wing typology, reflect the species sensitivity to environmental disturbance, acting as proxies for species resilience (e.g., Ribera et al. 2001; Kotze and O'Hara 2003; Lambeets et al. 2009; Brooks et al. 2012; Nolte et al. 2017, 2019). Previous studies have found that species with smaller body size and fully developed wings can more easily escape habitat disturbance and quickly recolonize new areas (Ribera et al. 2001; Gobbi and Fontaneto 2008; Pizzolotto 2009; Gerisch 2011). In addition, while most ground beetle species are hygrophilous (Rainio 2013; Zajicek et al. 2021), some are better adapted to periodic floods (Kolesnikov et al. 2012; Kirichenko-Babko et al. 2020). Thus, the expected longer-lasting periods of drought, alternated by annual flooding, are expected to be key in determining ground beetle diversity and community changes. The outcomes will greatly depend on their dispersal ability and the availability of natural refuge habitats during desiccation and/or harsher flooding episodes.

Previous studies in Mediterranean and temperate systems have shown that ground beetle species diversity is strongly influenced by the presence of closed forest patches and shrub areas that act as shelter/refuge habitats in agroforestry landscapes (e.g., MacLeod et al. 2004; Martins da Silva et al. 2011, 2017; Zou et al. 2019). Specifically, forested shelter/refuge patches were key in supporting sensitive ground beetles, namely apterous or brachypterous species with larger body size, since they are more sensitive to changing climatic conditions and hence, require more protection (Blake et al. 1994; Brose 2003; Warnaffe and Lebrun 2004; Martins da Silva et al. 2008, 2017; Schirmel et al. 2015; Eyre et al. 2016; Wang et al. 2018). Conversely, small species with long wings are usually dominant in highly trampled open-habitat types (Blake et al. 1994; Grandchamp et al. 2000; Wang et al. 2018; Ariza et al. 2021), such as several European floodplains (e.g., Bates et al. 2006; Lambeets et al. 2009; Gerisch 2011). Yet, no study has addressed how local habitat shelters may influence ground beetle diversity and community trait patterns in dynamic tropical ecosystems, which are threatened by soil aridification due to climate change. In this context, the Gorongosa National Park (GNP) in Mozambique is an interesting case study, as comprises a dynamic ecosystem with a gradient of habitat types, from typical miombo forests to floodplain grasslands, where periodic (annual) flooding controls interannual variations in diversity, survival, and seasonal community patterns (Stalmans et al. 2019). Yet, GNP landscape configuration may change in the next decades due to deforestation and soil desertification (Herrero et al. 2020; Mbokodo et al. 2020), and for this reason, specific landscape features, such as tree canopy and soil ground cover will be key in influencing carabid survival and community patterns, particularly during the expected longer lasting periods of drought.

Therefore, in this study, we assessed ground beetle communities at the main GNP habitat types, covering a wide range of environmental conditions, from the typical miombo forests to transitional and grassland habitats in the floodplains. We focused on the role of microhabitat structure as shelters for ground beetles during intense drought periods. We hypothesized that, by providing more stable microhabitat conditions during the dry season, habitat shelters will promote higher ground beetle Alpha-diversity across a tree canopy cover gradient (H1). Accordingly, larger-sized apterous/brachypyterous species will be more sensitive to drought as they are more dependent on habitat shelters than the smaller species with higher dispersal abilities. In addition, we hypothesized that the number of sensitive carabid species will increase with the increasing distance of miombo habitats to the floodplain (H2), reflecting community patterns primarily shaped by the flooding gradient.

Materials and methods

Study site

Gorongosa National Park (GNP) occupies approximately 4000 km^2 in the Sofala Province, central Mozambique, at the southernmost end of Africa's Great Rift Valley (18°58′04.84″ S, 34°21′41.64″ E) (Stalmans et al. 2019). The wet season in Mozambique normally lasts from November to April and mean annual rainfall within the Rift is 700–900 mm (Stalmans et al. 2019). Average annual temperatures range between 15 ºC in the dry season and 30 ºC in the wet season (Herrero et al. 2020).

GNP encompasses a vast ecosystem diversity, including Afromontane rainforest and riverine forest at Mount Gorongosa (> 700 m elevation), as well as wooded savannas and open floodplain at lower elevations (Massad and Castigo 2016). The plateaus encircling the park's central area are covered with a closed-canopy savanna named "miombo" due to the dominant tree, a member of the genus *Brachystegia.* In the central part of the park ("lower Gorongosa") savannas range from "open" savanna (floodplain grassland) to "mixed" savanna (grass-shrub-open tree: transitional forest), as well as "closed" savannas dominated by different tree species, i.e. mixed forests and miombo forests (Herrero et al. 2020). Hence, GNP low plateau comprises four main habitat types, from the woodland patches of miombo or mixed forests to the more open savannas, namely transitional forests, and floodplains near lake Urema (Stalmans et al. 2019).

Sampling design, carabid sample processing and record of species traits

Field work was carried out during October-November of 2019, following Cyclone Idai which occurred in March of the same year. In 2019 the dry season lasted till mid-November. The first mild rainfall started on November 14th (40 mm) and heavy rain only fell after November 20th (110–117 mm) (Martins da Silva et al. 2023a). Therefore, from October 25th to November 15th, pitfall traps were set to sample ground beetles, with beetle collections conducted each ten-day period.

We selected 100 sampling sites, 25 per each main habitat type (miombo forest, mixed forest, transitional forest, and open savanna) with a minimum distance between any two sites greater than 1 km (detailed sampling design in Serrano et al. 2023). This selection allowed us to analyze an environmental gradient, in terms of tree canopy cover, along with geographical distance to the lake Urema, located at the center of the park (Martins da Silva et al. 2023a, b; Serrano et al. 2023). Sampling sites within each of these habitat types also varied in terms of microhabitat conditions due to differences in tree canopy cover and local vegetation structure (Sect. 2.3 below).

At each sampling site, sampling was carried out using three pitfall traps (sub-samples) arranged in a triangle, with 5 m between pitfalls, summing a total of 600 pitfalls, although part of them (44) were destroyed by animals or fire during the dry season.

Pitfall traps consisted of plastic vials of 10 cm diameter filled with 5% ethylene glycol. The traps were covered with a plastic lid (10 cm diameter) fixed a few centimeters aboveground to minimize bycatches of small vertebrates.

Sampled beetles were preserved in absolute ethanol and transported to the entomological laboratory at the Centre for Ecology, Evolution and Environmental Changes, at the University of Lisbon (Portugal), for taxonomic identification of all specimens. A total of 62 species belonging to 32 genera and 17 tribes were taxonomically identified, resulting in a ground beetle dataset provided by Serrano et al. (2023). For pragmatic reasons we followed here the recent classification by Lorenz (2021), which includes tiger beetles and ground beetles in the Carabidae family. Information on species traits was collected from literature and by direct morphological measurement of the specimens.

We selected two species traits, average body size, i.e. species length (measured in mm) and wing typology, i.e., whether they are macropterous (fully developed hind wings) or brachypterous/apterous species, since the use of these traits proved to be informative for ecological studies (e.g., Ribera et al. 2001; Nolte et al. 2017). All data on species taxonomy and traits are provided in Martins da Silva et al. (2023a).

Environmental variables

Martins da Silva et al. (2023b) noted substantial variability in prey availability (e.g. Collembola) and abiotic conditions within each GNP habitat type, mainly associated with the understory structure (amount of herbaceous plants, shrubs and litter) and canopy cover. This intra-habitat variation can potentially influence ground beetle populations, namely due to differences in moisture conditions (Martins da Silva et al. 2023a), and niche availability or food resource (Magura and Lövei 2019; Boutaud et al. 2022) which are dependent on the buffer role of habitat shelters (e.g. Marañón et al. 2009; Rossetti et al. 2015; Widenfalk et al. 2015). As a proxy of habitat shelter, different local environmental variables related to the vegetation cover were selected at each sampling site, namely canopy area (CA - calculated as a percentage), as well as the levels of bare soil (BS), herbaceous cover (HC), herbaceous height (HH), shrub cover (SC), and litter (L), which were assessed on a scale from 0 to 3 (Appendix Table S1).

We then calculated the Shelter Index (SI) by attributing a weight to each of these variables:

$$SI = 4 \times \frac{3 \times CA}{100} + \frac{HC \times HH}{3} + 2 \times L + HC + SC - BS$$

where $\frac{HC \times HH}{3}$ corresponds to the formula for Herbaceous Protection, calculated to minimize the impact of herbaceous height while emphasizing the influence of herbaceous cover. Based on the previous Collembola diversity information (Martins da Silva et al. 2023b) higher weight (4) was attributed to canopy area (CA) since it provides shadow and leaf litter material, and hence is a major driver of habitat protection against desiccation and of niche availability in woodlands and semi-open habitats (Rossetti et al. 2015; Magura and Lövei 2019; Boutaud et al. 2022; Martins da Silva et al. 2023b). Litter cover (L) was the second most relevant parameter, with twice the weight of herbaceous (HC) and shrub covers (SC), since its contribution is twofold, by directly protecting against soil desiccation but also supporting more food resources through a positive impact on microarthropods (Martins da Silva et al. 2023b). In contrast, the bare soil (BS) has a negative impact on the index as it reduces habitat capacity to retain moisture and refuge against predators (Brose 2003; Wang et al. 2018).

Another potentially important factor influencing ground beetle population survival and community patterns is the distance from lake Urema (distance gradient), which was determined using a GPS device. The two main environmental factors, i.e., habitat Shelter Index and geographical distance to lake Urema, were not correlated (Pearson: $r = 0.103$, $p = 0.382$; Fig. 1). Miombo forest sampling sites were significantly more distant from lake Urema than transitional forests and grasslands ($F = 164.2$, $p < 0.001$; Fig. 1, Table S1).

Data analyses

Pitfall sub-samples from each sampling point were pooled before data analysis. Alpha-diversity (abundance) was calculated using R BAT package, version 2.9.5 (Cardoso et al. 2015), implemented in the statistical software R version 4.1.3 (R Core Team 2022).

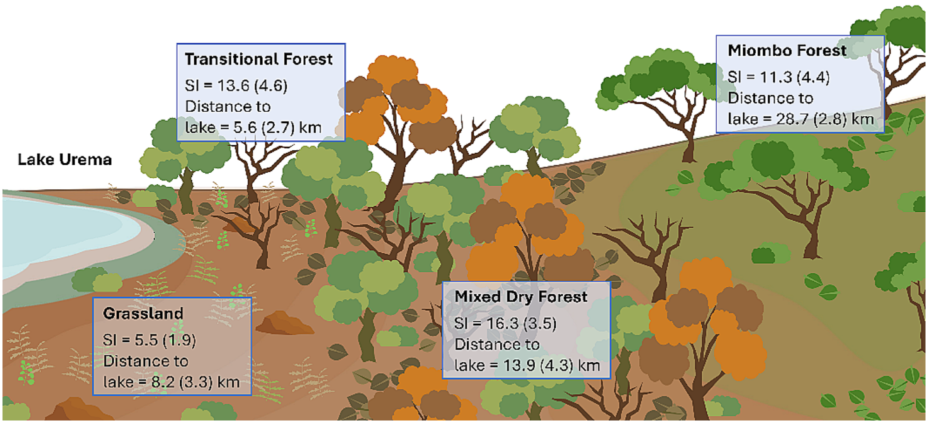

Fig. 1 Environmental gradients of habitat Shelter Index (SI) and habitat distance to lake Urema (Mean ± SD) along the GNP landscape comprising four main habitat types: Miombo forests, Mixed forests, Transitional forests, and Grasslands

Alpha-functional diversity (Alpha_FD) for average beetle body size (Alpha-FD_Body_size) and wing typology (Alpha-FD_Wings) was calculated using FD package, version 1.0-12.3 (Laliberté et al. 2014).

Before testing the influence of habitat shelter through the composite Shelter Index, the single role of each environmental predictor on ground beetle activity-density (N), Alpha-diversity (S) and Alpha-functional diversity (Alpha-FD) of carabid body size (Alpha-FD_Body_size) and wing typology (Alpha FD_Wings), as well as the responses of trait values of beetle body size (Trait-values_Body_size) and wing typology (Trait-values_Wings), was checked with generalized linear models (GLM). For each response variable (N, S, Alpha-FD_Body_size, Alpha-FD_Wings, Trait-values_Body_size, Trait-values_Wings), GLMs were fitted with different error distribution families (N – "GLM: Negative Binomial", S – "GLM: Poisson", FD Alpha_body_size – "GLM: Inverse-Gamma", FD-Alpha_wing_typology – "GLM: Inverse-Gamma", Trait-values_Body_size – "GLM: Inverse Gamma", Trait-values_ Wings – "GLM: Binomial").

Subsequently, we used generalized linear mixed-models (GLMM), fitted by maximum likelihood (Laplace approximation), with habitat type (i.e., grasslands, transitional forests, mixed forests, miombo forests) as a random factor, to test the effects of Shelter Index (SI) and the distance to lake Urema (floodplain center) on the variation of ground beetle N, S, Alpha-FD_Body_size, Alpha FD_Wings, Trait-values_Body_size and Trait-values_Wings. In line with the GLM models, each GLMM response variable was fitted with the correspondent error distribution family (N – "GLMM: Negative Binomial", S – "GLMM: Poisson", FD Alpha_body_size – "GLMM: Inverse-Gamma", FD-Alpha_wing_typology – "GLMM: Inverse-Gamma", Trait-values_Body_size – "GLMM: Inverse Gamma", Trait-values_ Wings – "GLMM: Binomial"). GLMM analyses were performed using the "lme4" R package, version 1.1–33 (Bates et al. 2015).

Results

Individual GLM models showed a significantly positive canopy effect (through the variables canopy area and litter cover) on ground beetle activity-density (N), Alpha-diversity (S), Alpha-FD of carabid body size and wing typology (Table 1). The amount of shrub cover was also related to higher N values, in contrast to the herb cover and herb height, which were negatively related to N and S parameters (Table 1). Moreover, larger ground beetles and a higher number of brachypterous/apterous species were associated to forested sites (higher canopy area and litter cover), while macropterous beetles were positively associated to sites with higher amount of herb cover (Table 1).

With the GLMM models comparing the effects of habitat shelter vs. site distance to lake Urema, we observed that higher N values of ground beetles were significantly explained by the distance gradient, while the shelter gradient was not important across the GNP landscape (Table 2). As for the ground beetle S values, both factors were significant, although the Shelter Index effect was only borderline significant, with a positive effect on S while the distance factor showed a strong negative effect (Table 2).

Ground beetle functional diversity (Alpha-FD), in terms of species' average body size only responded to the shelter gradient across the GNP habitat types, while Alpha-

Table 1 Single effects ("E": positive "+" or negative "-") of each environmental variable (bare soil, herb cover, herb height, shrub cover, litter cover, canopy area) on ground beetle diversity parameters: activity-density (N), Alpha-diversity (S), and Alpha- functional diversity (Alpha-FD) and trait values of carabid body size and wing typology. Statistically significant results of GLM Z-values are in bold ("*" $p<0.05$; "**" $p<0.01$; "***" $p<0.001$)

		Bare soil		Herb cover		Herb height		Shrub cover		Litter		Canopy	
		E	Z-value	E	Z-value	E	Z-value	E	Z-value	E	Z-value	E	Z-value
N		+	1.60	-	**14.8*** **	-	**4.53*** **	+	**4.96*** **	+	**6.92*** **	+	**4.65*** **
S		-	0.58	-	**4.55*** **	-	1.68[c]	+	1.69[c]	+	**3.82*** **	+	**3.67*** **
Alpha-FD	B_Size	-	1.34	-	1.28	-	0.81	+	0.73	+	**2.80** **	+	**2.75** **
	Wings	-	0.26	-	1.98[b]	+	0.05	+	1.13	+	**2.65** **	+	**3.07** **
Trait values	B_Size	-	1.75[a]	-	0.51	+	0.93	+	1.05	+	**2.32***	+	**2.00***
	Wings	+	0.24	+	**2.52***	+	0.97	-	1.19	-	**2.50***	-	**3.05** **

"a" $p=0.084$; "b" $p=0.052$; "c" $p=0.093$

FD of wing typology was not significantly explained by the Shelter Index, and neither by the distance to lake Urema (Table 2).

Community trait values of carabid body size were influenced by both environmental gradients, as significantly bigger-sized species occurred in more closed habitat shelters (Table 2; Fig. 2a), as well as in habitats farther from the floodplains (Fig. 2b).

Higher habitats shelter also harbored a significantly higher number of apterous/brachypterous species compared to the open habitats, which were richer in beetles with higher dispersal power, i.e., macropterous species (Table 2; Fig. 3). This same pattern was observed for the distance gradient, but it was not significant (Table 2).

Discussion

Ground beetle richness along the tree canopy gradient

Climate change is expected to drive changes to future ground beetle diversity patterns in tropical ecosystems, mainly due to the longer periods of drought and severe flooding events related to the El Niño/southern oscillation (e.g., Ariza et al. 2021; Peterson et al. 2021). In this study, our main hypothesis was that habitat closedness was a major factor governing ground beetle diversity by protecting more sensitive species, namely bigger sized species with lower dispersal ability. Supporting this hypothesis, higher species richness of ground beetles was associated to habitat shelters along the distance gradient from miombo forest to the floodplains. This result highlights the important role of habitat closedness, namely the buffer effect of tree canopy and understory structure (e.g. litter layers). This is highly important for the protection of sensitive taxa such as those hygrophilous species (e.g. *Abacetus percoides* Fairmaire, 1868; *Metagonum insolitum* Péringuey. 1904) that need habitat shelters to withstand climatic extremes (Rainio 2013; Zajicek et al. 2021). In fact, most ground beetles benefit from moist environments promoted by canopy shading and thicker litter layers, enabling a higher number of species to co-exist (Niemelä 1993; Magura and Lövei 2019; Marrec et al. 2021; Zajicek et al. 2021). Contrarily, in more exposed habitat areas, ground beetle communities tend to be dominated by those few species (e.g. *Microlestes zambezianus* Mateu. 1960) that are more tolerant to drought (e.g., Brandmayr et al. 1983; Tsafack et al. 2020). This result is in line with earlier studies on Mediterranean and temperate ecosystems, which emphasized the importance of forested habitats as important refuges in grassland-forest mosaics to ensure biodiversity conservation of ground beetles (Romero-Alcaraz and Ávila 2000; Woodcock et al. 2005; Zamora et al. 2007; Martins da Silva et al. 2011).

Higher richness and activity-density were found in miombo habitats farther from lake Urema, i.e., more distant from the floodplain area. Previous authors have shown that ground-beetles' activity and dynamics are driven by temporal flooding (Lambeets et al. 2008; Kirichenko-Babko et al. 2020). Carabid communities inhabiting floodplains are adapted to survive the periodic flooding episodes, although only a small number of species can survive in the inundated habitat (Tamm 1984, 1986; Zerm and Adis 2001; Kolesnikov et al. 2012). Except for a few tolerant species (e.g., Adis 1982; Amorim et al. 1997), most ground beetles avoid flooding by dispersing to adjacent, non-inundated habitats (Zerm and Adis 2001; Andersen 2005; Kolesnikov et al. 2012), i.e., the

Table 2 Summary of the effects of habitat Shelter Index and distance to lake Urema on ground beetle diversity parameters: activity-density (N), Alpha-diversity (S), and Alpha- functional diversity (Alpha-FD) and trait values of carabid body size and wing typology. Statistically significant results of GLMM Z-values are in bold (Est. – estimates, SE – standard errors). Random effects variable: habitat types

		Fixed effects	Est.	SE	Z-value	*p* value
N		Shelter index	0.042	0.176	0.237	0.813
		Habitat distance	-0.628	0.197	-3.197	**0.001**
S		Shelter index	0.177	0.090	1.974	**0.048**
		Habitat distance	-0.243	0.107	-2.271	**0.023**
Alpha-FD	Body size	Shelter index	0.110	0.037	-2.807	**0.005**
		Habitat distance	-0.054	0.036	1.483	0.138
	Wings	Shelter index	-0.064	0.034	-1.857	0.063
		Habitat distance	0.008	0.042	0.201	0.841
Trait values	Body size	Shelter index	0.189	0.067	-2.594	**0.009**
		Habitat distance	0.189	0.063	-3.049	**0.002**
	Wings	Shelter index	-0.565	0.256	-2.208	**0.027**
		Habitat distance	-0.501	0.272	-1.842	0.066

miombo forest in the case of the GNP. In contrast to the eurytopic species, and those with higher dispersal ability, the dynamics of stenotopic species may be confined to sheltered habitats located farther from the disturbance source, i.e., those associated with the miombo forested habitats that are significantly less affected by annual inundation (Kirichenko-Babko et al. 2020). Hence, the alternative hypothesis that ground beetle communities could be also shaped by the event of seasonal flooding is also supported by the results of this study.

Response of carabid functional diversity and community traits

According to our results, higher levels of species richness in habitat shelters were reflected in higher functional diversity in terms of species body size and wing morphology, with bigger sized and brachypterous/apterous species being mostly found in closed habitats in relation to open areas. Previous studies showed that wingless species with a larger body size are typically more sensitive to disturbance (Halme and Niemela 1993; Koivula 2002; Jelaska and Durbešic 2009; Wamser et al. 2011; Brandmayr and Pizzolotto 2016; Wang et al. 2018). Body size and dispersal ability respond to local habitat configuration, particularly vegetation structure and canopy cover, and are the main factors explaining community patterns in European agricultural and forested ecosystems (e.g., Brose 2003; Woodcock et al. 2005; Vandewalle et al. 2010; Spake et al. 2016; Martins da Silva et al. 2017). In this study, habitat shelters promoted by forest patches supported larger species with poorer dispersal abilities, as they require more stable habitat conditions (Warnaffe and Lebrun 2004; Martins da Silva da Silva et al. 2008, 2017; Schirmel et al. 2015; Eyre et al. 2016) and protection against natural predators (Blake et al. 1994; Brose 2003; Wang et al. 2018). Supporting these findings, and in line with our predictions, larger ground beetles and species with less dispersal potential have likely found refuge in closed habitats with denser vegetation cover that provided more suitable microclimate conditions, namely moisture, across the GNP landscape. Conversely, small species with long wings are usually dominant in disturbed and exposed open habi-

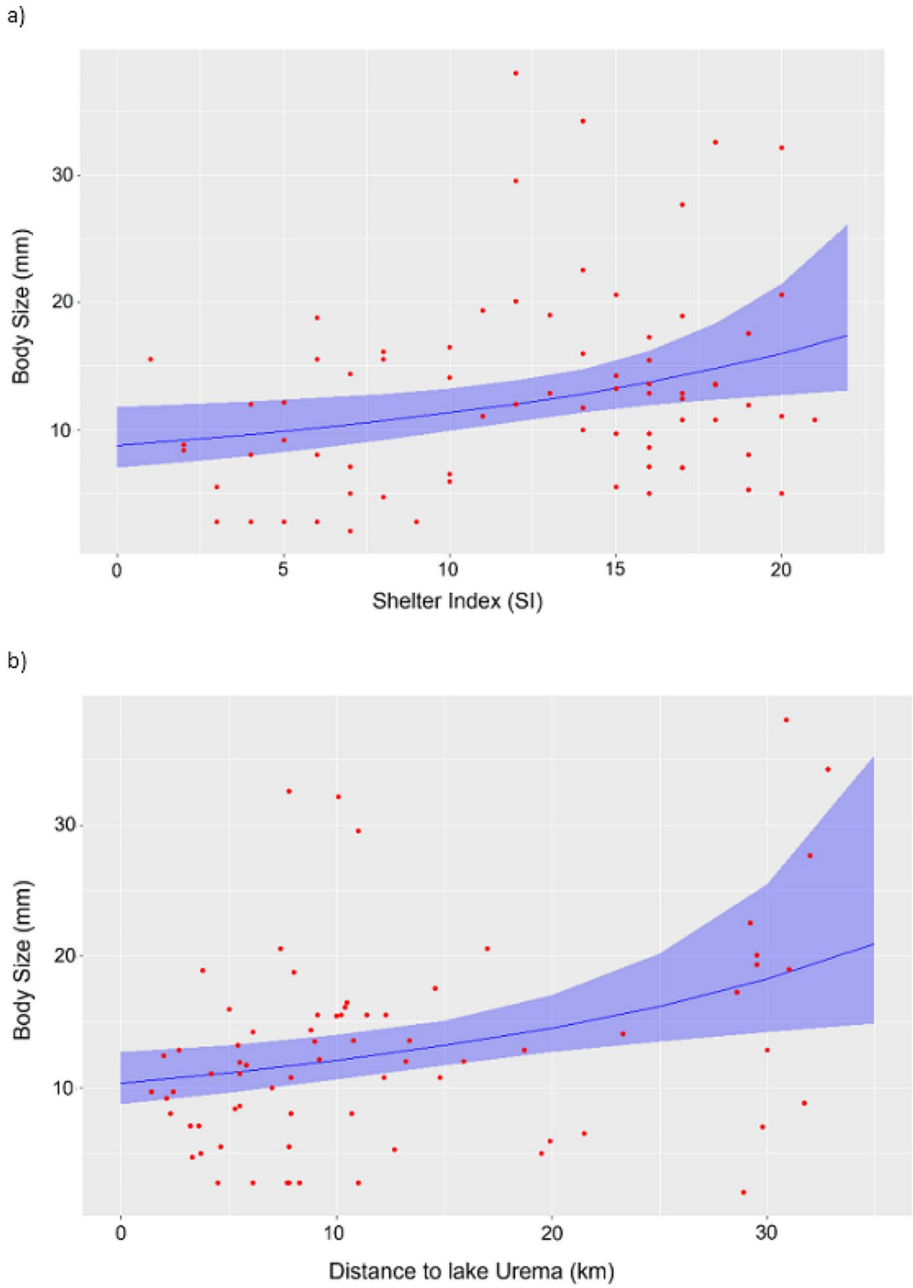

Fig. 2 GLMM effect plot showing residual relationships of carabid body size (mm) with (a) habitat Shelter Index (SI) and (b) distance to lake Urema (km)

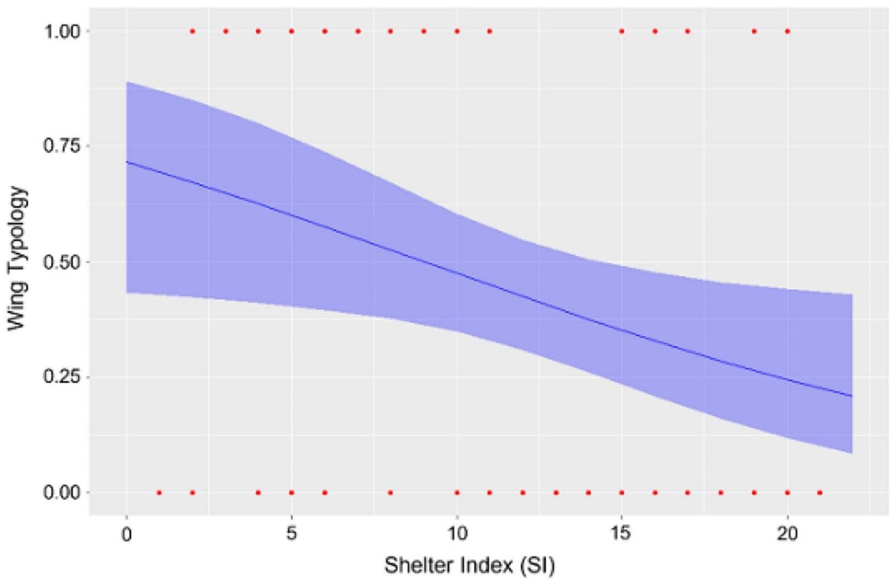

Fig. 3 GLMM effect plot showing residual relationships of carabid wing typology (winged species – "1", wingless species – "0", averaged per site) with habitat Shelter Index (SI)

tats (Blake et al. 1994; Grandchamp et al. 2000; Wang et al. 2018; Ariza et al. 2021). Previous studies have shown that smaller species with fully developed wings, i.e., with greater dispersal capabilities, are better adapted to disturbances and/or more able to escape and colonize new areas (Blake et al. 1994; Grandchamp et al. 2005; Wang et al. 2018). During periods of drought, these species not only benefit from closed habitats as shelter areas interspersed in the landscape due to their better dispersal abilities (Jelaska and Durbešic 2009; Eyre et al. 2016; Martins da Silva et al. 2017); they also benefit from finding refuges in ground slits, shrubs, and small tussocks in grasslands (MacLeod et al. 2004; Schirmel et al. 2015; Ariza et al. 2021).

In a previous study, Martins da Silva et al. (2023a) compared ground beetle communities in dry and wet seasons, and concluded that wet conditions, provided by rainfall after a long period of drought, were crucial to support species richness, particularly for larger species with poorer dispersal ability. In this study, we can conclude that during the drought period beetle survival and activity strongly depends on the provision of habitat shelters. This finding is relevant considering the anticipated increase in extreme climatic events in the next decades, namely hurricanes/flooding (e.g., Lambeets et al. 2008; Lafage and Pétillon 2016; Litavský et al. 2021) and longer-lasting periods of drought (e.g., Šustek et al. 2017; Šiška et al. 2020; Ariza et al. 2021) with consequent landscape changes in tropical ecosystems. These disruptive events are likely to affect ground beetle species, particularly those more moisture dependent, and favor more eurytopic species with smaller size and higher dispersal ability (Ariza et al. 2021; Zajicek et al. 2021). In contrast, larger-sized and wingless species will probably be more vulnerable to extinction in response to future climate aridification and landscape homogenization and habitat changes (Kirichenko-Babko et al. 2020; Ariza et al. 2021). Habitat shelters providing microhabitat conditions to buffer arid conditions during drought will be essential for ground beetle diversity conservation and should be integrated in future conservation activities.

Recommendations for land management

Our results highlighted the importance of habitat shelters for ground beetle diversity in the Gorongosa National Park, namely by supporting larger-sized sensitive species during a long-lasting drought season. Thus, conservation initiatives and management planning need to take into consideration the key role of closed habitat patches, provided by trees and shrubs, as essential buffers for ground beetle protection against environmental disturbance and climatic extremes. Land management towards the maintenance of woodland patches is critical considering the degradation of Gorongosa miombo expected in the long term, due to human activities (e.g. agriculture, fires) but also to the predicted longer lasting periods of drought (Massad and Castigo 2016; Herrero et al. 2020). Besides the heuristic importance of ground beetle diversity conservation, they play a key role in tropical food webs (Kotze et al. 2011), for instance as prey for several birds, reptiles, and mammals (Brose 2003). Hence, biodiversity protection of ground beetles, and especially the larger-sized species, will also contribute to higher habitat quality and life support of emblematic fauna of the GNP, also threatened by increasing environmental instability and climate extremes that are predicted to increase in Mozambique in the next decades.

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Author contributions PMS and MB(Baptista) wrote the first draft of the manuscript. MB(Baptista) and RC analized the data. MB(Boieiro), ST, JA, AAdS, MJIB, ARMS and JPS reviewed previous versions of the ms. MB(Bartz), ARMS, SM, ST, MB(Boieiro), HMVSAP, MJIB, JPS and PMS collected the data. PMS and JPS coordinated the data management and field sampling. ARMS performed taxonomic identification of all Caraboidea specimens. PMS concieved the conceptual framework of the study.

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Data availability Dataset that supported the findings of this study is provided in a reference within the manuscript.

Declarations

Competing interests The authors declare no competing interests.

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