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Effects of seasonal dynamics and habitat shelters on carabid beetle communities (Coleoptera: Carabidae) threatened by drought in the Gorongosa National Park (Mozambique)

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RESUMO

A nível global, devido a alterações de origem humana, os ecossistemas estão a sofrer perdas de habitats e níveis de extinção nunca antes vistos. As regiões tropicais estão particularmente vulneráveis às alterações climáticas por possuírem ecossistemas que simultaneamente têm uma biodiversidade extremamente rica e são suscetíveis a mudanças ambientais. O aumento da temperatura e a alteração dos padrões de precipitação estão a alterar profundamente estas regiões, sendo já observáveis variações no ciclo anual de estações. A estação seca está a tornar-se mais longa e intensa, o que será potencialmente devastador para uma fauna e flora ambientada a níveis de humidade estáveis.

O aumento das temperaturas e diminuição da precipitação agrava a aridificação do solo, particularmente num local como os trópicos onde o solo já é muitas vezes frágil. Este processo é um loop que se alimenta a si mesmo, ora o impacto das alterações climáticas no solo leva a uma diminuição da sua capacidade de suporte da vida vegetal, característica fundamental para limitar a erosão. Esta diminuição da cobertura vegetal, e consequente aumento da erosão, elimina as camadas superficiais de solo, ricas em matéria orgânica. Sem estas camadas, o solo perde capacidade de retenção de humidade, diminuindo ainda mais a sua capacidade de retenção de vida vegetal, o que acaba por reiniciar todo o processo de aridificação. Todo este ciclo leva a um agravamento exponencial da degradação do solo.

Um grupo de organismos particularmente afetado por este processo e pela diminuição de humidade ambiental, são os invertebrados do solo, cruciais para o ciclo de nutrientes dos ecossistemas onde ocorrem, decompondo matéria orgânica através de processos químicos e físicos. Dentro deste grupo, os carabídeos são uma família de escaravelhos de particular importância, tanto pela diversidade de papeis ecológicos que desempenham, como pelo potencial que têm como bioindicadores, podendo ser utilizados para monitorizar comunidades de invertebrados de solo. Estes escaravelhos são particularmente sensíveis às alterações climáticas e à consequente diminuição da humidade disponível, já que este fator se revela limitante para sua sobrevivência. Muitas espécies desta família são higrófilas, ou seja, necessitam de níveis elevados de humidade para sobreviver.

Apesar da sua clara importância ecológica e vulnerabilidade perante as alterações previstas, este grupo continua pouco estudado em algumas regiões geográficas, como é exemplo a região Afrotropical, onde se prevê que ocorram profundas alterações no clima ao longo deste século. Prevê-se que, nas próximas décadas, as temperaturas nesta região aumentem até 6º C, resultando em maiores taxas de evaporação e menores níveis de precipitação. Tais alterações levarão a secas mais prolongadas e intensas, além de ondas de calor mais frequentes. Manter uma monitorização atenta nos carabídeos desta região é imperativo, pois esta pode fornecer informações valiosas sobre o quão deterioradas se encontram as comunidades de artrópodes onde estão inseridos. Consequentemente, de modo a serem elaborados projetos que estudem os impactos das mudanças climáticas nas comunidades de invertebrados do solo de uma determinada área é necessário ter dados de referência sobre a diversidade de espécies de carabídeos, a sua atividade e as flutuações sazonais.

O Parque Nacional da Gorongosa é um caso de estudo particularmente interessante para este grupo, pois possui uma grande diversidade de habitats e um sistema dinâmico sazonal de inundações que poderão influenciar as comunidades de carabídeos. O parque passa anualmente por duas estações, alternando entre uma estação fria e seca, e uma estação quente e húmida, durante a qual, devido a chuvas intensas, o Lago Urema, situado no centro do parque, inunda. As inundações moldam os principais habitats do parque: pastagens, florestas de transição, florestas mistas e florestas de miombo, que apresentam um gradiente de cobertura vegetal entre eles. Estes habitats e as suas comunidades estão sob ameaça não só devido às alterações climáticas, mas também aos impactos humanos de menor escala. Os cursos de água do parque são ameaçados por possíveis construções de barragens em afluentes que alimentam os cursos do parque como pelo o aumento de campos agrícolas comerciais e aldeamentos em redor do parque que podem poluir estes cursos.

Com o intuito de obter informação sobre a distribuição, diversidade e atividade dos carabídeos do parque que auxilie futuros estudos que visem preservar este grupo, recolheram-se dados de referência de diversidade para os quatro habitats principais e ambas as estações. Adicionalmente, avaliaram-se as mudanças sazonais na comunidade de carabídeos e examinou-se o impacto da cobertura vegetal e das inundações na distribuição destes insetos. Para além disso, também se estudou o papel que habitats com grande cobertura vegetal tiveram na sobrevivência de carabídeos durante a estação seca, de modo a se compreender a possível importância que tais habitats terão durante futuras secas agravadas.

A amostragem foi feita através de *pitfalls*, nos quatro habitats principais do parque e no período de transição das duas estações. Deste modo conseguiu-se estudar as comunidades de ambas, evitando as inundações mais intensas que teriam impossibilitado o trabalho de campo. A cobertura vegetal foi registada para cada local de amostragem e a morfologia das espécies de carabídeos amostrados foi anotada, concretamente tamanho e presença ou ausência de asas, já que estas caraterísticas estão associadas, não só, à sua preferência de habitats, como, à capacidade de subsistir perante alterações no ambiente. Alguns parâmetros de diversidade foram calculados para cada local de amostragem e observou-se a sua variação entre habitats e estações, e a influência dos mesmos nestas variáveis - atividade-densidade (abundância), diversidade-Alpha, diversidade-Beta, e os valores médios de tamanho e presença de asas. Para analisar a influência que zonas florestadas têm durante períodos de seca concentrou-se a análise somente na estação seca. Para esse fim, o efeito da cobertura vegetal foi examinado nas mesmas variáveis de diversidade anteriores referentes a esta estação. Foi também estudado como o Lago Urema e as suas inundações influenciam a atividade e distribuição destes escaravelhos, observando as variações de traços morfológicos com a distância ao lago.

O parque revelou ter uma comunidade rica e diversa de carabídeos nos diferentes habitats e estações. Muitas das espécies amostradas eram raras, indicando sua vulnerabilidade a distúrbios e extinção. As florestas de transição apresentaram a maior riqueza de espécies devido à sua heterogeneidade, apresentando caraterísticas tanto dos prados como das florestas mistas, suportando tanto espécies generalistas quanto especialistas. A precipitação sazonal afetou significativamente a diversidade de escaravelhos, com períodos mais húmidos apresentando maior riqueza de espécies. Habitats florestais desempenharam um papel fundamental na manutenção da riqueza e diversidade funcional das espécies, especialmente durante os períodos secos, tendo o potencial de mitigar os impactos das mudanças climáticas. Espécies maiores e sem asas, que são mais sensíveis às mudanças ambientais, dependiam fortemente destas áreas florestais. Também se destacou o impacto significativo das inundações sazonais do Lago Urema na distribuição dos carabídeos, com maior frequência de espécies maiores a ser observada com o afastamento das planícies de aluvião.

Ao estabelecer dados de referência sobre a diversidade de carabídeos e as flutuações sazonais, o estudo contribuirá para a compreensão de como estes escaravelhos respondem às mudanças ambientais e informará futuras estratégias de conservação. Adicionalmente, estes resultados enfatizam a importância de conservar habitats florestais, já que a redução destas áreas levaria a uma maior exposição dos carabídeos a condições climáticas severas e conduziria a uma maior competição dentro dessas áreas, aumentando o stress das populações do parque. Como tal a preservação destes habitats é crucial para apoiar a diversidade de carabídeos e a resiliência dos mesmos diante das mudanças climáticas e dos impactos humanos.

PALAVRAS-CHAVE: Carabidae, períodos de seca, Moçambique, refúgios, mudanças sazonais

ABSTRACT

Some major global issues today are the loss of habitats and unprecedented extinction rates caused by human activities and climate change. Tropical regions are particularly under threat from climate change given their ecosystems' limited resilience. Drought periods are becoming longer and harsher, which severely threatens species adapted to the constant humidity levels in these areas. Soil fauna, particularly carabids, play significant ecological roles in the ecosystems where they occur. However, their sensitivity to decreased environmental and soil moisture should be a matter of concern. In some regions of the world, especially in the Afrotropics, there has been little research done on the communities of these beetles. The African continent is expected to experience significant climatic changes within the next decades. Therefore, it becomes imperative to understand the population dynamics of carabids in order to prepare measures to reduce potential impacts of climate change. Gorongosa National Park is a great case study because of its wide range of habitats and flooding system dictated by the season cycle. Research conducted on the park has revealed a rich carabid community, with several rare species. Their diversity was found to be correlated to seasonal rainfall, as greater species richness was observed during heavy rains. Carabid activity was also affected by flooding, with larger beetles avoiding the floodplains, as these species have difficulty surviving in such an unstable environment. Forested habitats were shown to be vital in maintaining high species richness, particularly during dry spells, hence they can potentially help mitigate the predicted harsher droughts. Moreover, these sites were important for larger sized wingless individuals that are more susceptible to environmental alterations. This investigation provides invaluable insights into carabid seasonal variations aiding future conservation initiatives as well as showing the necessity to preserve woodlands so as to support carabids' survival over time.

KEYWORDS: Carabidae, dry spells, Mozambique, refuges, seasonal changes

BIBLIOGRAPHIC ELEMENTS

The study detailed in this academic work allowed for the publication of the following papers:

Serrano, A., Baptista, M., Carvalho, R., Boieiro, M., Mendes, S., Bartz, M., Timóteo, S., Azevedo-Pereira, H., Aguiar, C., Alves da Silva, A., Alves, J., Briones, M., Borges, P., Sousa, J., & Martins da Silva, P. (2023). Inventory of tiger- and ground-beetles (Coleoptera, Caraboidea, Cicindelidae and Carabidae) in two sampling seasons of the Gorongosa National Park, Mozambique. *Biodiversity Data Journal, 11*. https://doi.org/10.3897/BDJ.11.e101280

Baptista, M., Carvalho, R., Boieiro, M., Bartz, M., Mendes, S., Timóteo, S., Azevedo-Pereira, H. M. V. S., Alves, J., Alves da Silva, A., Briones, M. J. I., Serrano, A. R. M., Sousa, J. P., & Martins da Silva, P. (2024). 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. *Biodiversity and Conservation*, *33*, 2345. https://doi.org/10.1007/s10531-024-02853-6

DATA AVAILABILITY

A database with the information on the environmental characteristics of the different sampling plots of the Gorongosa National Park and all the carabid beetle specimens found in each plot can be found in GBIF, with following reference:

Serrano, A. R. M., Carvalho, R., Boieiro, M., Borges, P. A. V., Martins da Silva, P., & Baptista, M. (2023). Inventory of tiger- and ground-beetles (Coleoptera Caraboidea: Cicindelidae, Carabidae) from the Gorongosa National Park (Mozambique) (Version 1.8). GBIF. Release date: 2023-6-22. http://ipt.gbif.pt/ipt/resource?r=goundbeetles_mozambique

Index

Table and Figure List

Figure 11 - Community weighted mean of body size (CWM_BS; in mm) throughout the three sampling periods (T1 - "Dry", T2 - "Intermediate", T3 - "Rainy") in each habitat type (GRA – grassland, MIO – miombo forest, MIX – mixed forest, TRA – transitional forest). Significantly different groups within each habitat, indicated by General Linear Hypotheses-tests are signaled by the letters "a" and "b ($P < 0.05$). Adapted from Martins da Silva et al., 2023b.

Figure 12 - Community weighted mean of wing typology (CWM_Wings; macropterous species – 1, apterous/brachypterous species – 0) throughout the three sampling periods (T1 - "Dry", T2 - "Intermediate", T3 - "Rainy") in each habitat type (GRA – grassland, MIO – miombo forest, MIX – mixed forest, TRA – transitional forest). Significantly different groups within each habitat, indicated by General Linear Hypotheses-tests are signaled by the letters "a" and "b ($P < 0.05$). Adapted from Martins da Silva et al., 2023b.

Figure 13 - Community weighted means: A- body size; B – wing typology; of exclusive grassland species occurring before (Dry) and after the rainfall (Grassland Exclusives), and species that only occurred in forested habitats during the dry season that were found in grasslands in the "Rainy" period (Previous Forest Exclusives); Significantly different groups indicated by General Linear Hypotheses-tests are signaled by the letters "a" and "b ($P < 0.05$). Adapted from Martins da Silva et al., 2023b.

Figure 14 - Beta diversity values between sampling periods (T1-T2 and T1-T3) in the four main habitat (GRA – grassland, TRA – transitional forest, MIX – mixed forest, MIO – miombo forest) with reference on the "Dry" sampling period (T1). Values range from 0 (the compared sites exhibit the same species at the same abundances) to 1 (the compared sites don't have any species in common). Each dot represents the dissimilarity value in each site between the "Dry" – "Intermediate" (T2) periods and "Dry" – "Rainy" (T3) periods. Asterisks denote the significance levels when comparing dissimilarity average values between T1-T2 and T1-T3 through Wilkoxon test ("*" $p < 0.05$; "**" $p < 0.01$; "***" $p < 0.001$). Adapted from Martins da Silva et al., 2023b.

Table 4 - Summary of GLM analysis of the effects ("E": positive "+" or negative "-") of each environmental variable (bare soil, herb cover, herb height, shrub cover, litter cover, canopy area) on carabid beetle diversity parameters: activity-density (N), Alpha-diversity (S) and Alpha-functional diversity (Alpha-FD) and trait values of body size and wing typology. Statistically significant results are in bold ("*" $p<0.05$; "**" $p<0.01$; "***" $p<0.001$; "a" $p = 0.084$; "b" $p = 0.052$; "c" $p = 0.093$).

Table 5 - Summary of GLMM analysis of the effects of habitat Shelter Index and distance to lake Urema on carabid beetle diversity parameters: activity-density (N), Alpha-diversity (S) and Alpha-functional diversity (Alpha-FD) and trait values of body size and wing typology. Statistically significant results are in bold (Est. – estimates, SE – standard errors). Random effects variable: habitat types.

Figure 15 - GLMM analysis effect plots of residual relationships: A - carabid body size (in mm) with Shelter Index (SI); B – body size with distance to lake Urema (in km); C - carabid wing typology (1 – macropterous species; 0 - wingless/brachypterous species; averaged per site) with habitat Shelter Index. Retrieved from Baptista et al., 2024.

Symbols and Abbreviations

BS	Bare Soil
CA	Canopy Area
ECOASSESS	ECOlogical ASSESSment
GLM	Generalized Linear Model
GLMM	Generalized Linear Mixed Model
GNP	Gorongosa National Park
GRA	Grasslands
HC	Herbaceous Cover
HH	Herbaceous Height
LC	Litter Cover
MIO	Miombo Forest
MIX	Mixed Forest
SC	Shrub Cover
SI	Shelter Index
TRA	Transitional Forest

1. Introduction

1.1 The threat of climate change to tropical ecosystems

Throughout the globe, ecosystems have been suffering from habitat loss and extinctions at unprecedented rates (Bradshaw et al., 2009; Ceballos et al., 2015). The impact of anthropogenic factors at smaller spatial scales, like changes in land-use and deforestation, have been exacerbated by climate change, leading to alarming declines in both fauna and flora. Notably, as tropical ecosystems and its species have a low resilience to slight thermal changes, they are particularly vulnerable to the rising temperatures (Perez et al., 2016; Anjos & de Toledo, 2018). Due to these pressures, it is unsurprising that the majority of the world's most threatened areas are found in the tropics (Conservation International, 1990; Miles et al., 2006; Bradshaw et al., 2009). This situation causes alarm as the rich biodiversity found in tropical regions, combined with the fragility of their ecosystems, indicates that the current loss of diversity may become catastrophic. As the effects of climate change are expected to worsen throughout the century, a special focus to mitigate these impacts needs to be put on tropical ecosystems.

Increasing average temperatures and reduced precipitation rates are altering the yearly climatic cycle characteristic of tropical regions, in an alarming maner (Guo et al., 2022). Specifically, its wet season is becoming shorter and its dry season is getting lengthier and more severe (Fu et al., 2013; Sylla et al., 2016; Xu et al., 2022). Tropical ecosystems will be deeply affected by these longer dry periods. The species that inhabit them are dependent on stable moisture levels to survive and have little capacity to adapt to environmental changes, compared to species of higher latitudes. Additionally, the soil of tropical ecosystems, which is often already fragile, is especially prone to aridification, a process accelerated by the changing climatic conditions, that can permanently alter an area's landscape (Cardoso & Kuyper, 2006; Flores et al., 2019). The aridification affects the capacity of the soil to hold moisture, which hinders the survival of plant-life and leaves the soil bare (Rodriguéz-Lozano et al., 2023). Without protection, the soil is more susceptible to erosion, which leads to additional losses of organic matter by removing topsoil and hummus layers (Bucur et al., 2007; Balasubramanian, 2017). The removal of these layers of organic matter worsens the soil's water retention, which again hinders its capabilities of supporting plant life, creating a loop that worsens the degradation of the soil and, aggravates the deterioration of the ecosystem (Flores et al., 2019).

All these alterations have dire consequences on the fauna and flora of tropical ecosystems. Many species are forced to migrate, adapt, or risk extinction as a result of the transition in tropical ecosystems towards more arid conditions (Feeley et al., 2012; Grinder & Wiens, 2022). Highly specialized species with limited ecological niches are especially vulnerable because the unique conditions they require to survive might completely disappear (Urban, 2015). To ensure their survival and limit the deleterious effects of climate change, conservation strategies must be developed, considering the composition, distribution, and response to dry spells of these species' communities. However, in some tropical locations, such as the Afrotropics, some communities, in particular soil fauna, are severely understudied. This issue needs to be delt with to develop effective conservation measures.

1.2 Gorongosa National Park (GNP) in Mozambique

1.2.1 Description and History of the GNP

Located on the east coast of southern Africa, between 10º to 26ºS, Mozambique lies almost entirely in the tropics. With such a drastic range in latitudes, Mozambique's climate and landscapes vary considerably. The north and south of the country exhibit contrasting humidity and precipitation levels, with higher latitudes recording higher precipitation rates, creating a gradient of habitats, that range from drylands to tropical forests (Bandeira et al., 1996; Burgess et al., 2004; Toté et al., 2015). Each year, the country goes through an annual climatic cycle which shape its ecosystems. This cycle is defined by a dry season, with low temperatures and humidity, and a wet season, characterized by heavy rainfalls and warmer temperatures (Barbosa et al., 2001; Ministry for the Coordination of Environmental Affairs, 2014). The distinct environments and heterogeneous climate of Mozambique lead to a rich fauna of 726 bird species and 171 reptile species (Biofund, 2024). Its flora is incredibly diverse as well, boasting around 6000 native and naturalized plant species, 22% of which are unique to this country (Biofund, 2024).

One of the eight national parks of Mozambique, Gorongosa National Park (GNP) was established due to the region’s remarkable mammalian biodiversity and wide variety of ecosystems (Muala, 2015). Two different areas are included in the GNP, the larger area of the "Low Plateau" and Mount Gorongosa, to its northwest. The "Low Plateau" has Lake Urema in its center, which floods during the rainy season, drastically altering the surrounding landscape (Böhme, 2005; Beilfuss et al., 2007; Herrero et al, 2020). This yearly cycle is indispensable to the ecosystems of the park and influences the lifecycle of native species. The flooding not only supplies large quantities of water but replaces the nutrients in the soil, nourishing the grasslands that encircle the lake (Beilfuss et al., 2007). These grasslands serve habitat and feeding grounds for a wide array of species (Beilfuss et al., 2007).

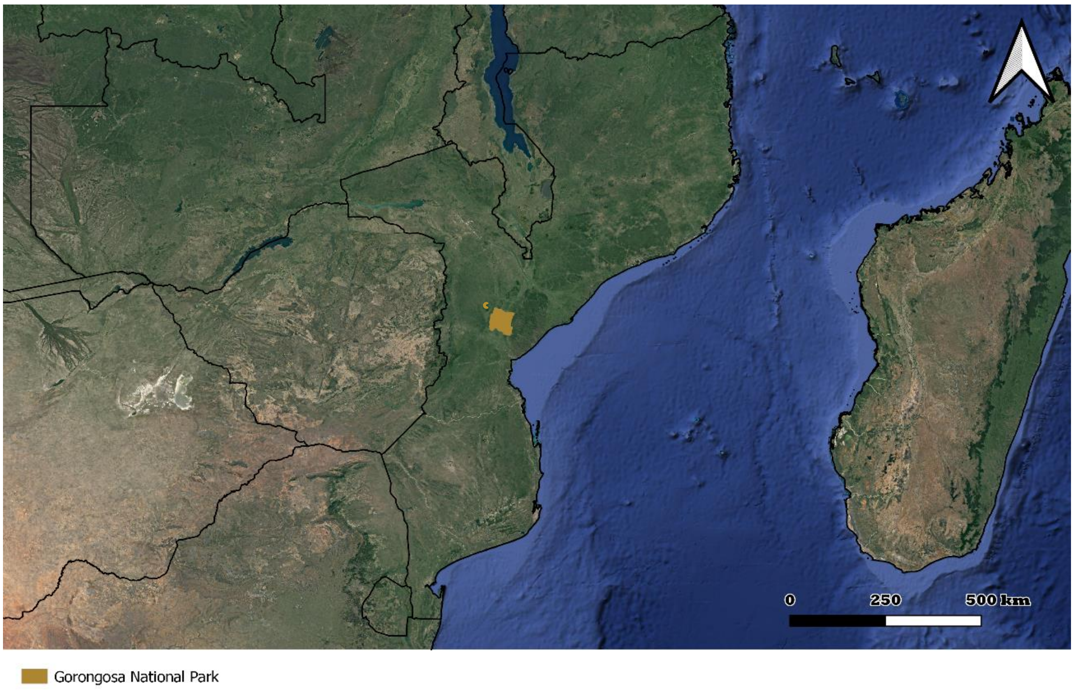

Figure 1 – Location of Gorongosa National Park within Mozambique. Retrieved from Serrano & Baptista et al., 2023.

The plateau encompasses fifteen different habitat types, with grasslands and dry sparse forests of *Acacia-Combretum* covering most of the center of the valley, while in elevated areas, to both the east and west, prevail miombo woodlands (Tinley, 1977; Stalmans & Beilfuss, 2008). The Gorongosa Mountain also exhibits a diverse landscape, with *Brachystegia* woodland at lower altitudes, a lush forest from 1,200 m to 1,500 m, and montane grassland at the highest elevations (Müller et al., 2008).

Gorongosa has characteristics not found anywhere else in sub-Saharan Africa, with its unique ecological features and high species diversity (Parque Nacional da Gorongosa, 2010). Numerous species of conservation concern, particularly mammals and birds, can be found in the GNP (WCS, Government of Mozambique & USAID, 2021). Moreover, new species have been recently recorded and described at this ecologically rich site, such as a new plant species (*Cola cheringoma*), a bat (*Rhinolophus gorongosae*), a freshwater crab (*Potamonautes gorongosa*) and a new species and genus of Katydids (Cheek et al., 2019; Naskrecki & Guta, 2019; WCS, Government of Mozambique & USAID, 2021).

Historically, the Khoisan and Bantu peoples have shaped the local ecosystems, leading a nomadic lifestyle, settling temporarily where natural resources were abundant (Muala, 2015). In the 17th century, the landscape started changing quickly when Portuguese colonists arrived in the area known today as Gorongosa, and started hunting, and deforesting (Muala, 2015; Ochs, 2021). In 1921, the Portuguese established the Gorongosa Game Hunting Reserve, which was upgraded in 1960 to Gorongosa National Park, becoming a tourist attraction, and leading to the construction of settlements for the visitants (Schuetze, 2015; Muala, 2015; Matusse, 2019).

Shortly after the independence of Mozambique in 1975, a civil war erupted, greatly affecting the park's infrastructure and wildlife (Muala, 2015; Pringle & Gonçalves, 2022). Gorongosa was one of the main stages of the war, and during the conflict, agriculture was abandoned in the region, which led both soldiers and civilians to survive on bushmeat (Muala, 2015; Schuetze, 2015). The resulting poaching, a lack of support for the park and the armed conflict itself resulted in a drop mammalian numbers, with population declines rounding the 90 to 99 percent (Stalmans et al., 2019; Herrero et al., 2020).

Even after the war ended in 1992, the park's ecosystems continued being pressured by poaching, deforestation, and arson until the early 2000s (Muala, 2015). In 2002, Greg C. Carr, an American entrepreneur and philanthropist, invested $40 million to preserve the park's biodiversity and to restore it to its old state (Pringle, 2017). A number of efforts have been conducted since then to achieve such objectives. Several mammal species have been reintroduced into the park, and native trees have been planted in key locations to reduce erosion and enhance soil water retention (Dunham, 2004; Stalmans, 2012; Bouley et al., 2018; Branco, 2018; Stalmans et al., 2019; Bouley et al., 2021). Additionally, in 2001, Mount Gorongosa was included as part of the GNP in order to protect its important habitats (Pringle & Gonçalves, 2022). As part of this current wave of restoration in the park, exhaustive studies have been made on its vertebrate populations. Nonetheless, information on invertebrate communities, namely soil fauna, is still scarce, an alarming issue that needs to be addressed due to the importance of these groups (Correia et al., 2016).

1.2.2 Threats to the GNP’s ecosystems

Despite the current efforts to protect the parks ecosystems, several factors still threaten their stability, with various human activities having the potential to prove harmful in the next decades if unregulated. The planned construction of a dam in the Pungwe River, which delimitates GNP to the south, would alter current flooding patterns, and while not impacting the whole park, would still affect its southern area (Beilfuss et al., 2007; World Bank, 2007). Commercial farming for cotton, bananas, and biodiesel has increased in the Urema catchment, and the consequent higher usage of fertilizers and pesticides will result in water contamination and eutrophication condemning downstream ecosystems (Beilfuss et al., 2007). Additionally, the construction of settlements neighboring the park could prove harmful due to the release of sewage into streams that lead into the water bodies of the GNP (Beilfuss et al., 2007).

Climate change is also a looming threat to the park. In southern Africa, temperatures are expected to rise by 2º to 6º C, in the coming decades, resulting in higher evaporation rates and lower precipitation levels (Hulme et al., 2001; Beilfuss et al., 2007; Fig. 2). These inflated temperatures will have menacing effects, dry spells will become longer and more intensive, while heat waves are expected to be more frequent and harsher (Tadross, 2009; Engelbrecht et al., 2011; Mbokodo et al., 2020; Engdaw et al., 2021). The greatest increase in temperature and one of the lowest levels of rainfall during the dry season are predicted for central Mozambique, where the park is situated (Tadross, 2009). The harsher periods of drought and increasing temperatures may also increase the wildfire frequency. Annual grass fires have occurred throughout the park since records began (Tinley, 1977). While the park's management strategy of employing patchy burns, early in the dry season, to mitigate intense fires, seems to be stabilizing their frequency in the previous decades, that could soon change (Daskin, Stalmans, & Pringle, 2016). In 2019, a severe drought, caused by an El Niño–Southern Oscillation (ENSO) enhanced by global warming, affected southern Africa and left the region more vulnerable to flooding (Alemaw, 2022). A couple of months later, central Mozambique was struck by Cyclone Idai, which then led to widespread flooding (UNICEF, 2019). The GNP was only moderately affected by this event, but this was still a warning for potential future consequences of global warming-enhanced storms.

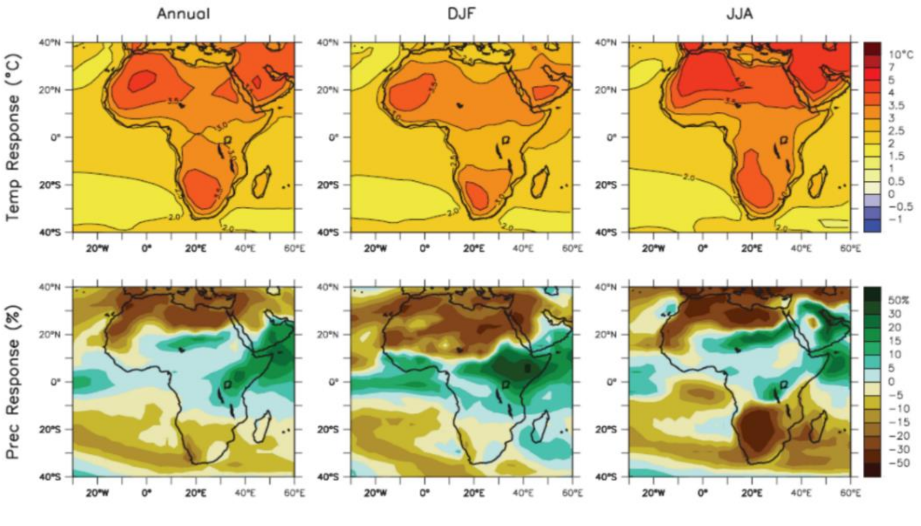

Figure 2 – Projected effects of climate change on the temperature and rainfall in Africa, from 1980 to 2099; Annual average (left), December-February (center), June-August (right). From Venables *et al.*, 2008.

All these changes threat the park's ecosystems, particularly endangering various tree species characteristic of the Sub-Saharan landscape, particularly miombo forests, which can result in a potential decline in the distribution of this habitat (Jinga & Ashley, 2019; Jinga & Palagi, 2020). Prolonged droughts consequence of climate change may even adversely impact two of the park's most abundant plant species (*Vachellia xanthophloea* and *Faidherbia albida*), given their limited resistance to drought (Massad & Castigo, 2016). These consequences are likely to have a significant impact on the park's animal communities. The fauna of the park is susceptible to the previously mentioned environmental changes, be it directly through the temperature and humidity, or the disruption of biotic interactions (Parmesan, 2006; Jaworski & Hilszczański, 2013; Janzen & Hallwachs, 2021). Despite the biodiversity conservation efforts in GNP, that have focused mostly on vertebrates, soil fauna is not the focus of any current conservation programs. Soil fauna, such as carabid beetles, play essential roles in their ecosystems and can be used to monitor biodiversity trends. Given their importance, it is imperative that the significant gaps in our understanding of this group in Gorongosa be solved quickly.

1.3 Carabidae, an integral part of the soil Fauna

1.3.1 Morphology & Ecology

Carabidae are a dominant and key group among soil arthropods as they both degrade organic matter and regulate the numbers of other soil-dwelling invertebrates via predation (Lövei & Sunderland, 1996; Diekötter et al., 2010). This cosmopolitan family encompasses beetles characterized by their long hind legs, large compound eyes, and strong mandibles making them proficient predators (Forsythe, 1981). Carabid beetles have undergone impressive diversification following their appearance in the Mesozoic, eventually colonizing almost all terrestrial habitats (Erwin, 1985; Clopton, 1991; Ober, 2003; Tian & He, 2020; Anichtchenko, 2024; Beutel et al., 2024). Their distribution seems to be the most limited in deserts where they are constrained to the periphery or areas close to rare water sources (Erbeling & Paarmann, 1985; Lövei and Sunderland, 1996). Consequently, humidity emerges as a critical limiting factor for their dispersal and diversity (Tsafack et al., 2019; Kirichenko-Babko et al., 2020). Different subfamilies and genera within Carabidae exhibit distinct habitat preferences. The selection of habitat can be further influenced by a range of seasonal factors including photoperiod, temperature, and humidity fluctuations as well as food availability (Lövei & Sunderland, 1996; Holland et al., 2005; Knap et al., 2019).

Although carabid beetles have some defining traits that are common to all species, many species differ greatly in terms of morphological characters, especially body size and the development of the hind wings, which is related to their dispersal ability (Den Boer, 1970; Kotze et al., 2011; Fig. 3). Their body size tends to increase in regions with higher precipitation and humidity and also areas where resources are readily available (Ribera et al., 2001; Homburg et al., 2012). Additionally, wingless species or species with reduced wings unable to fly (brachypterous) are more common in habitats with high humidity and also stable environments with low seasonal variability where higher dispersal power is not required (Bonn et al., 2002; Venn, 2016). These patterns show how habitat selection and distribution of carabid species can be influenced by environmental factors depending on their eco-morphological features.

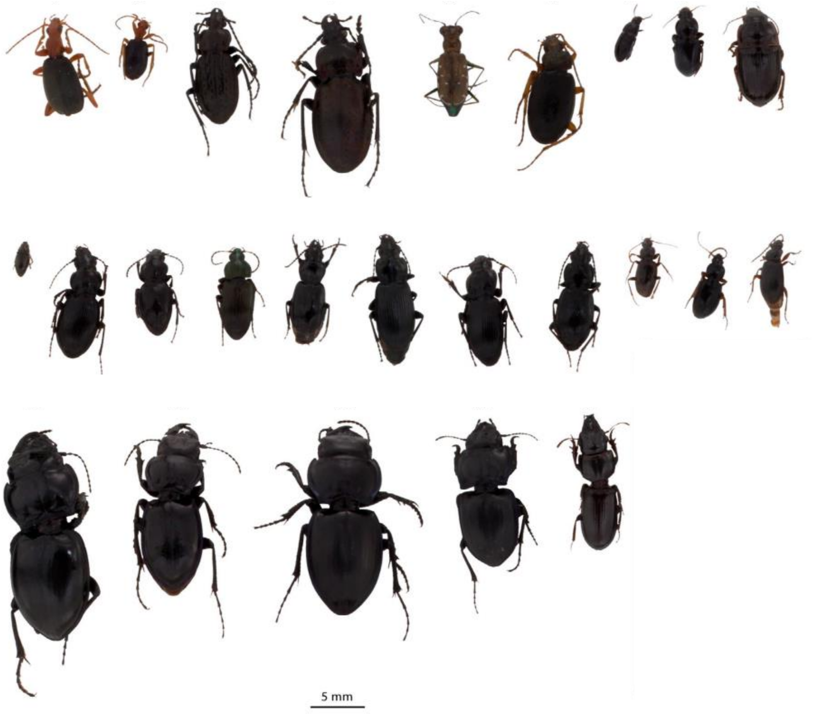

Figure 3 – Body-size diversity within Carabidae. Adapted from Blair *et al*., 2020.

This group of beetles actively engages in numerous ecosystem services. Adult carabid beetles show a wide array of feeding habits, either carnivorous, granivorous, or omnivorous (Lucas & Maisonhaute, 2015). Most species regulate ecosystems' food webs as low-tier consumers, while also being a significant food source for various vertebrates (Desender et al., 1994; Lövei & Sunderland, 1996; Orros et al., 2015; Zhang et al., 2015; Zagainova et al., 2016). As they often have predatory lifestyles, when present on agricultural fields these beetles feed on problematic invertebrates like slugs and snails, being considered as beneficial pest regulators in these systems (Niemelä, 2001; Cividanes, 2021). Furthermore, by feeding on weed seeds, granivorous species regulate the seed bank, which is also beneficial in agricultural settings, as it improves crop yields (Deroulers & Bretagnolle, 2019; Perthame et al., 2023).

Given their significant roles in ecosystems, carabid beetles' susceptibility to environmental changes and quick response time make them prime candidates for use as ecological indicators (Desender et al., 1994; Rainio & Niemelä, 2003; Avgın & Luff, 2010; Koivula, 2011; Brandmayr & Pizzolotto, 2016). Their potential as bioindicators is enhanced by their role as predators, regulating lower-tier populations in the food web, and by the standard sampling method to collect them, pitfall trapping, being cost-effective (Pearce & Vernier, 2006). It is then imperative to take into account carabid beetle communities when planning arthropod conservation efforts, as monitoring this functional group provides valuable information into the health of an ecosystem.

1.3.2 Systematics in Mozambique

While, Mozambique's carabids have been researched since mid-19th century, the majority of specimens were gathered during faunistic and entomological expeditions led by organizations or by individuals like tourists, missionaries, and naturalists, rather than as part of comprehensive studies on the country's carabid fauna. As a result, information on these beetles is dispersed and was often published as new species or records in sparse publications (e.g., Klug, 1853; Péringuey, 1896; Basilewsky, 1950; Basilewsky, 1951; Straneo, 1958; Basilewsky, 1963; Lecordier, 1978a; Lecordier, 1978b; Schüle, 2004, Schüle, 2011; Cassola & Bouyer, 2007; Kleinfeld & Puchner, 2012; Serrano, 2014). Consistent and overarching studies are needed to establish reference communities for future evaluations of biodiversity trends.

In Mozambique, the family Carabidae comprises 20 distinct subfamilies. An emblematic subfamily is Cicindelinae, also known as tiger beetles, who thrive in hot, humid tropical climates as daytime visual hunters, and whose activity is highly influenced by temperature. Although considered a distinct family by some authors, we followed here the classification by Lorenz (2021), in which the Carabidae family includes the tiger beetles. At lower taxonomic levels, 149 genera and 532 species are recorded for the country, whose ecology and community patterns remains for the most part poorly understood (Anichtchenko, 2024). This highlights the importance of ecological studies in the region to better understand its rich biodiversity.

1.3.3 Carabids and the changing environment

The distribution of carabid species is strongly correlated to both long- and short-term climatic events (Becker, 1972; Brandmayr et al., 1983; Judas et al., 2002). Historical climate shifts influence the range of numerous species, whereas others have an immediate response to quick temperature changes (Horion, 1939; Becker, 1972). The main environmental factors that influence the distribution of carabids are temperature and precipitation, which makes them particularly susceptible to the expected effects of global warming, especially in the Afrotropical region (Crist & Ahern, 1999; Müller-Kroehling et al., 2014; Liu et al., 2021; Muneret et el., 2022). As previously stated, temperatures in Southern Africa are predicted to rise throughout the century which will lead to higher evaporation rates and prolonged dry seasons (Hulme et al., 2001; Beilfuss et al., 2007; Tadross, 2009; Engelbrecht et al., 2011). European-based studies suggest that rising temperatures will have a deep impact on these beetle communities (eg. Müller-Kroehling et al., 2014; Avtaeva et al., 2021; Weiss et al., 2024). Dry-tolerant species are expected to thrive and expand their range, while hygrophilic species' ranges will decrease, with some already becoming extinct in certain areas (Staunton et al., 2014; Brandmayr & Pizzolotto, 2016; Ouisse et al., 2020). Similar patterns are expected to be found in the African continent.

Previous studies conducted in agroforestry systems of both Mediterranean and temperate regions have demonstrated that closed forest patches that serve as refuges have a significant impact on Carabid diversity (Bedford & Usher, 1994, MacLeod et al., 2004; Martins da Silva et al., 2011; Rouabah et al., 2015; Zou et al. 2019). Moreover, by mitigating the impacts of adverse environmental conditions habitat refuges influence the distribution of species based on their morphological characteristics, as the previously mentioned traits of body size and hind wing typology are directly linked to a species' sensitivity to these conditions (Venn, 2007; Brooks et al., 2012; Rouabah et al., 2015; Nolte et al., 2019). In fact, it was found that closed forested areas were essential in the survival of sensitive carabids, such as larger species not capable of flight, that require more protection and stability due to their limited dispersal ability (Blake et al., 1994; Brose, 2003; Martins da Silva et al., 2008; Martins da Silva et al., 2017; Schirmel et al., 2015; Wang et al., 2018). Conversely, smaller carabid species with fully developed wings have a higher dispersal power, and usually dominate, open and less protected habitats (Blake et al., 1994; Wang et al., 2018; Ariza et al., 2021). These species also dominate in more disturbed or dynamic areas, as is the case with environments with extreme seasonal changes, like floodplains (Bates et al., 2006; Lambeets et al., 2008; Gerisch, 2011). This information is crucial to predict how different species will respond to environmental stress and, as such, help develop conservation practices involving this group.

The significance of local habitat shelters on carabid beetle communities in tropical ecosystems, affected by soil aridification due to prolonged droughts brought on by climate change, has not yet been studied. Holarctic species have been extensively studied, over the years, concerning their ecology, distribution, and responses to climate change, contrasting to other regions like the Afrotropics, where this knowledge is severely lacking (Kotze et al., 2011; McCravy & Lundgreen, 2011; Brandmayr & Pizzolotto, 2016). To plan for future conservation efforts, these glaring knowledge gaps need to be addressed. Gorongosa having a dynamic annual system of floods that affect seasonal fluctuations in Carabidae communities, is an intriguing case study for this group (Stalmans et al., 2019). Anthropogenic factors, like deforestation and soil desertification might alter the ecosystems of the GNP throughout this century (Herrero et al., 2020; Mbokodo et al., 2020). By offering protection from desiccation during extended droughts, certain landscape features, such as tree canopy and other elements of vegetation cover, will influence carabid community patterns and be crucial for their survival in a harsher environment. In order to develop research projects targeting the impacts of climate change on soil fauna communities it is essential to have baseline data of the targeted groups. Therefore, to develop such studies on the GNP, baseline data on carabid species diversity and seasonal fluctuations is required.

1.4 Aim of this thesis

1.4.1 Survey of Carabid Beetle Diversity in GNP

In this study, we aimed to assess the diversity of Carabidae through the first standardized assessment of soil invertebrates in GNP. This research lasts from the end of the dry season to the beginning of the wet season, to capture a wide range of species from xerophilic to hydrophilic. To better understand the communities of the park, we analyzed the frequency, distribution and habitat preferences of the different carabid species, highlighting the rarer ones as they are potentially more vulnerable. By establishing a reference community for these beetles, our goal is to present baseline data for future assessments of population and diversity trends.

1.4.2 Changes in Community Composition between Seasons

As we assessed carabid beetle communities during a sampling period that spanned the transition from the dry to the wet season (marked by the first rainfalls), it became possible to study the turnover of these beetle communities across various habitats within GNP. This transition period provides a unique opportunity to observe changes in species richness and community composition as the environment shifts from dry to moist conditions.

We hypothesize that (1) species richness (Alpha-diversity) will rise after the rainfall, due to the majority of carabid beetle species being moisture dependent. Furthermore, we predict that (2) between the extreme dry and heavily rainy sampling periods carabid community turnover (Beta-diversity) will be greater due to the impact of tropical rainfall.

Moreover, as forested habitats offer more protection and retention of moisture, they may serve as shelter during dry spells for larger species with less dispersal power that are then able to colonize open areas when humidity levels rise in the wet season. We then expect that, (3) after the rainfall, the number of larger body-sized species in grasslands increases because of a rise in the frequency of carabid species previously restricted to forested habitats.

1.4.3 Habitat Shelters as Buffers Against Drought

Anticipating the threat of climate change, it is crucial to study how habitat shelters serve as a buffer and help carabids survive the current dry spells. This way we can understand how habitat elements might protect the diversity and survival of sensitive species to the predicted increase of prolonged drought periods in this region.

To achieve this goal, we focused on the carabid communities during the dry season to study the importance of microhabitat structure for these communities during severe dry spells. We hypothesize that (4) across a tree canopy cover gradient, habitat shelters will increase carabid beetle Alpha-diversity by offering more stable conditions during the dry season.

Additionally, highly dynamic and open habitats with low vegetation cover, have highly unstable conditions, and are more suitable for smaller species with higher dispersal power. In accordance, (5) we expect to find more frequently smaller-sized and winged species in grassland habitats than in forested habitats. Moreover, the flooding of Lake Urema also makes the surrounding area highly variable throughout the year. We then hypothesize that (6) the increase of the distance from the floodplain, where habitat conditions will be more stable, will lead to a higher frequency of sensitive species.

Our goal is to increase the knowledge of how carabid beetle communities in GNP are impacted by habitat structures and seasonal changes. The park's potential future conservation and management strategies will depend heavily on this data.

2. Materials and Methods

2.1 Study Area

Situated at the southern tip of the Great Rift Valley in central Mozambique, Gorongosa National Park (GNP) covers 4 000 km^2 (Pringle & Gonçalves, 2022). To further protect the reserve from external pressures, a 5 400 km^2 buffer zone was established (Fig. 4). In this zone, 200 000 inhabitants are able to explore the area's resources with restrictions on activities like mining and water diversion (Pringle & Gonçalves, 2022). This region has a tropical savanna climate, with temperatures ranging from 15° to 30ºC (Herrero et al., 2020). The park goes through an annual cycle, transitioning between a dry season and a wet season. The mean rainfall in the region is 700–900 mm, with higher precipitation levels documented on the slopes of the valley (Stalmans et al., 2019).

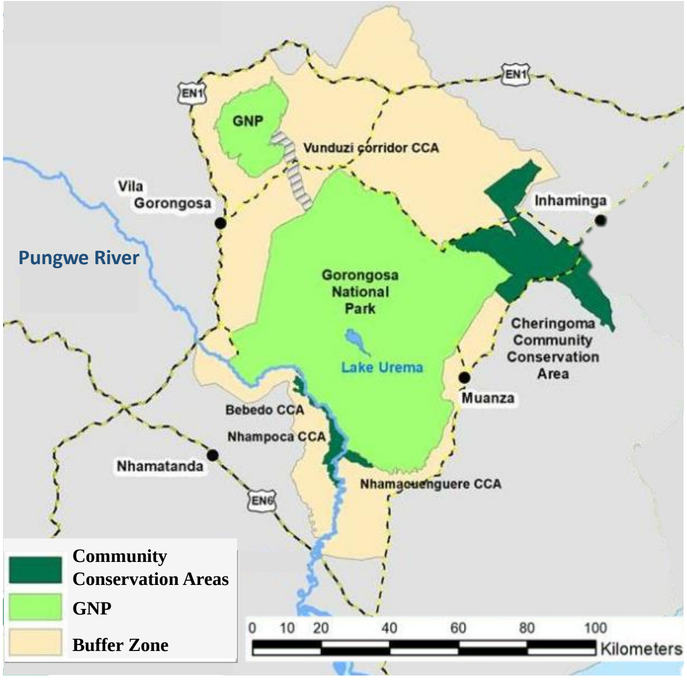

Figure 4 – Map of the Gorongosa National Park with current borders within Mozambique. Adapted from Gorongosa, 2023.

The low plateau of the GNP occupies most of the park's area and is subject both to seasonal changes and anthropologic influences. At the center of the park lies Lake Urema, a shallow and perennial natural water body. Lake Urema drains through the Urema River to the Pungwe River, which borders the low plateau area of the park to the south. The plateau is subject to seasonal flooding of the lake, during the rainy season which goes from mid-November to April (Böhme, 2005; Beilfuss et al., 2007; Herrero et al, 2020). During high flood seasons, lake Urema stretches to over 200 km^2, while it decreases to an area between 12-15 km^2 in the dry season (Beilfuss et al., 2007). While having a lesser impact on the park's ecosystems, the Pungwe River's flooding plays a crucial role in the water supply and nutrient cycle along the southern boundary of the GNP (Beilfuss et al., 2007; Desai et al., 2019).

Four main habitats are recognized for the low plateau area: miombo tropical forest, mixed dry forest, grassland, and transitional forest, which were delimited with the help of the park's staff (Stalmans & Beilfuss, 2008; Fig. 5). Grasslands are large open areas mainly composed of herbaceous plants which can have sporadic acacias and palm trees (Stalmans & Beilfuss, 2008). This biome is located near lake Urema and as such is one of the most affected by the seasonal flooding. This landscape gradually changes to a mixed dry forest, characterized by landscapes filled with species from the genus *Acacia* and *Combretum* (Stalmans & Beilfuss, 2008). Between the grasslands and mixed dry forest there are areas characterized by a blend of elements from both habitats, appropriately named transitional forest. This habitat is the most heterogenous, going from closed to open and tall to short forests possessing a variety of floral communities, of shrubs, grasses and trees (Herrero et al. 2020). The miombo forest occurs most on the edges of the plateau when elevation starts to increase (Tinley, 1977; Stalmans & Beilfuss, 2008). These are areas of wet savanna woodland with diverse tree communities usually dominated by species from the genus *Brachystegia* belonging to the legume family (Malaise, 1978; Stalmans & Beilfuss, 2008).

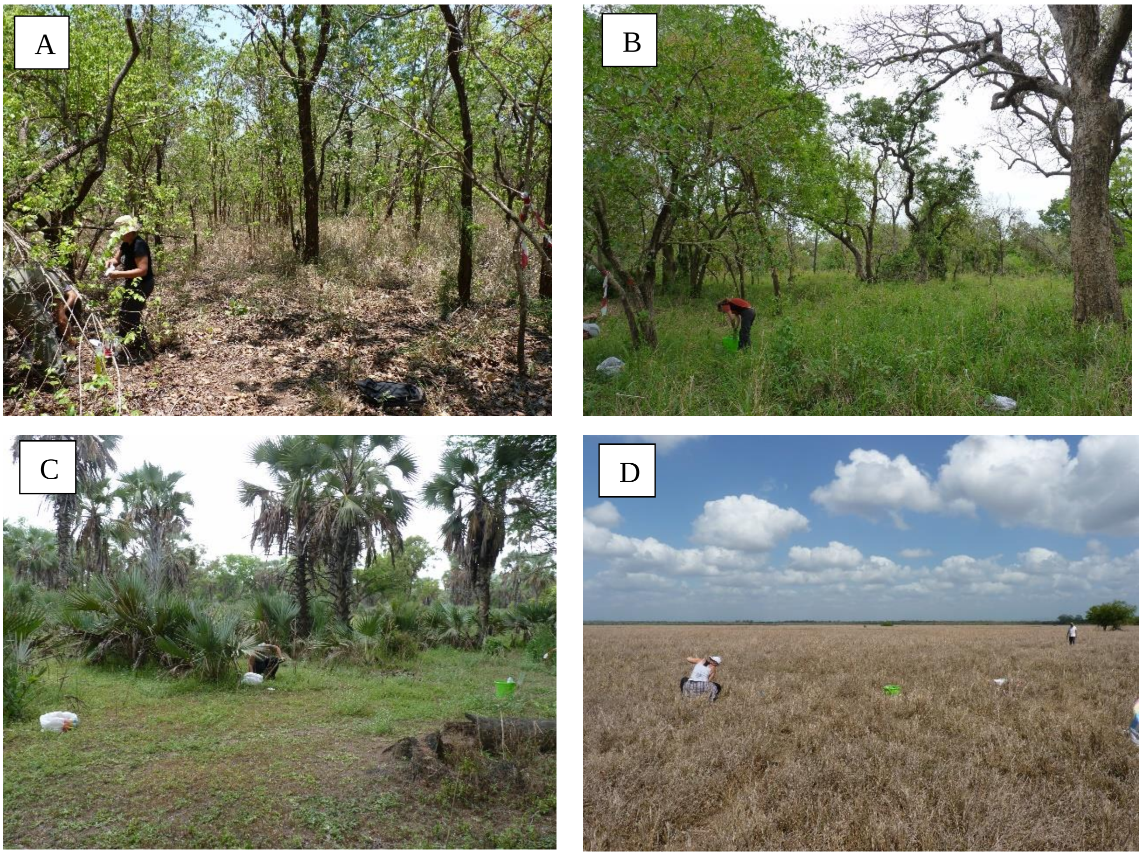

Figure 5 - Four main habitat types: A - Miombo forest; B - Mixed dry forest; C - Transitional forest; D - Grassland. Retrieved from Serrano & Baptista, 2023.

2.2 Sampling description

This research is part of the Project ECOASSESS – A biodiveristy and ECOlogical ASSESSment of soil fauna of Gorongosa National Park (Mozambique) (PTDC/BIA-CBI/29672/2017), funded by FCT / MCTES (PIDDAC)'s Programme All Scientific Domains. Field sampling for ECOASSESS was done under the guidance of Mark Stalmans, the Director of Scientific Service of the park, and Jason Denlinger, the Lab Manager, with logistical help from the Gorongosa National Park. Additionally, during the ECOASSESS team's stay at the park, there was an interaction with park researchers in experience exchanges and training activities for the local communities. The team performed dissemination activities during this period, a theorical lecture about soil fauna was presented to the park's employees and scientific team, and environmental awareness and training activities were provided to high school students of schools around the park.

With the intent to register the changeover between seasons, sampling was carried out during October and November of 2019, by a team of researchers from Portugal, of which I was not part of, and staff from the Gorongosa National Park. By only encompassing the beginning of the wet season, the sampling period avoided peak flooding, where a large percentage of the target habitats become inundated and sampling would become impossible. Traps were set during three consecutive ten-day periods. The first period, "Dry", occurred from October 25th to November 5th, preceding the first rains. The second period, "Intermediate", spanned from November 5th to the 15th, and was considered the end of the dry season as it had a climate mostly associated with this season but experienced a little rainfall, as the first rains (40 mm) started on November 14th. The last sampling period, "Rainy", lasted from November 15th to the 25th, and included the start of heavy rainfall (110-117 mm) in November 20th. Noteworthy differences in air humidity levels were detected between the "Rainy" period and the "Dry" and "Intermediate" periods, the latter two showing very little contrast. For each main habitat, grassland, mixed forest, miombo forest, and transitional forest, 25 sampling plots, with at least 1 km between each other, were selected, totaling 100 sites (4 habitats times 25 traps) (Fig. 6).

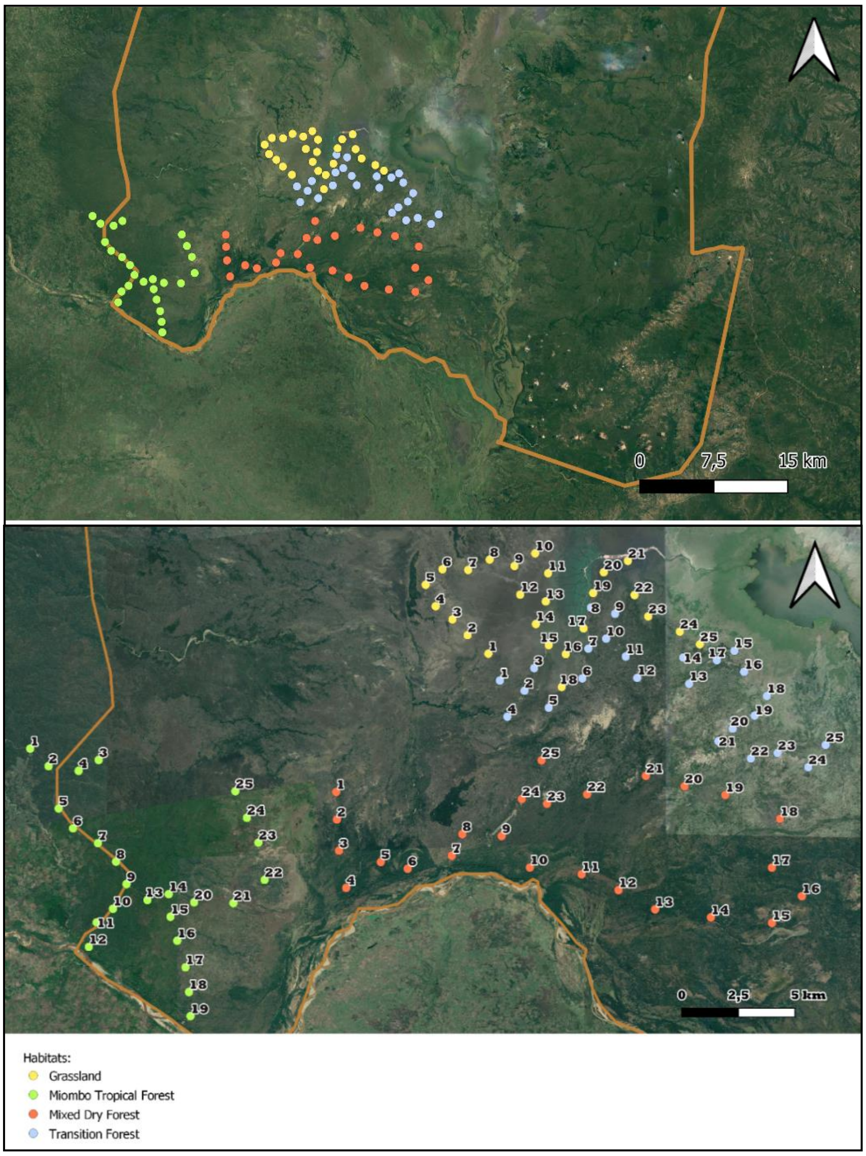

Figure 6 – Location of sampling plots of each habitat type inside the GNP at different scales. Retrieved from Serrano & Baptista et al., 2023.

Carabidae sampling was done with pitfall traps, the standardized method for sampling soil-dwelling species which make up the majority of this taxonomic group (Drift, 1951, Greenslade, 1964). Pitfall traps were made of 10 cm diameter plastic cups that were full of ethyleneglycol (5%). A plastic cover with 10 cm in diameter was mounted a few centimeters above ground to shield the traps from floods and specimen loss during heavy rain. This reduced the number of small vertebrate bycatch. At each of the 100 sampling locations three pitfall traps were used, positioned in a triangle with five meters between each trap. This process was repeated three times for each sampling period totaling 900 traps. Of these 900 pitfalls, 115 were lost, 44 either destroyed by fire or animals during the dry season, and 71 unable to be retrieved due to flooding on the rainy season. We assumed these were missing at random.

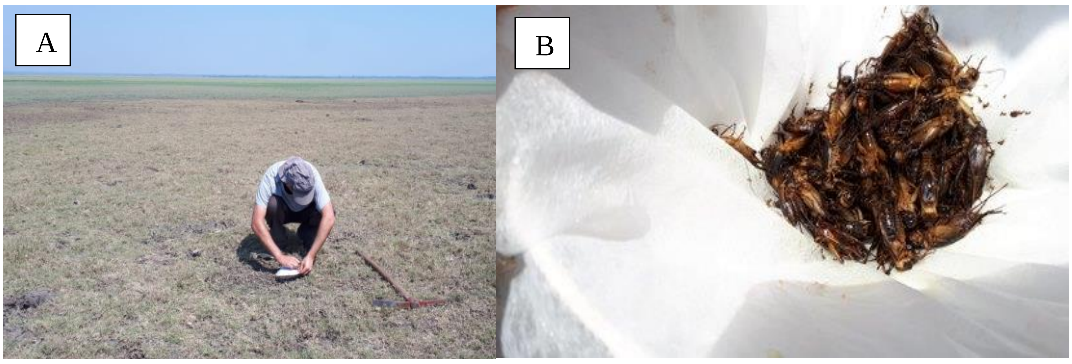

Figure 7 – A - Retrieving of a pitfall trap in the grassland habitat; B - Pitfall contents inside a fabric bag.

After the pitfall traps were collected, the contents of each pitfall were placed in a fabric bag, placed in a jerrican that was filled with 96% ethanol (Fig. 7). The specimens of Carabidae were then sorted at the laboratory of the Centre for Ecology, Evolution and Environmental Changes (University of Lisbon, Portugal). For potential future research, other arthropods were separated and preserved in 75% ethanol. A specialist in Carabidae taxonomy (Artur R.M. Serrano) identified the specimens to the species or subspecies level, when possible, if not, they were separated into morphospecies.

Several ecological studies highlighted two traits that highly impacted carabid distribution and sensitivity to disturbance, average body size (measured in cm) and flight capacity (either with functioning wings, or apterous/brachypterous species) (e.g., Ribera et al., 2001; Mullen et al., 2008; Jelaska & Durbešic, 2009; Kallio, 2014; Nolte et al. 2017). Consequently, we used both direct inspection of the collected specimens and literature to gather information about these traits (Appendix, Table S1).

2.3. Environmental variables

Apart from the habitat type, local factors that may chiefly influence carabid communities on each plot are the vegetation structure and impact from flooding (Woodcock et al., 2005; Zamora et al., 2007; Lambeets et al., 2008; Martins da Silva et al., 2011). To measure how much a site is affected by flooding, the distance of each one of them to Lake Urema was measured with the help of a GPS device. A gradient can be seen in the distances of the different habitats from the lake: miombo woodland is the furthest away, mixed dry forest is at an intermediate distance, and grasslands and transitional forest are closest to the lake (Fig. 8). Accordingly, the sites of miombo forest were found to be significantly farther away from lake Urema than the ones from transitional forests and grasslands (F= 164.2, p< 0.001, Appendix, Table S2).

Within each habitat, plots exhibited varied vegetation structures, mainly associated with the understory and canopy cover, leading to a myriad of different microhabitat conditions. This variation in habitat shelter influences the soil temperature and as a consequence dictates both the moisture levels and food resources available, affecting the carabid beetle species that are able to survive in each site (Magura and Lövei, 2019; Boutaud et al., 2022). Elements of vegetation cover that could influence carabid survival and activity were assessed at each sampling plot.

The various variables selected were bare soil (BS), herbaceous cover (HC), herbaceous height (HH), shrub cover (SC), and litter cover (LC), all of which were evaluated from 0 to 3 (0 - None; 1 - Low; 2 - Medium; 3 - High), and the percentage of canopy area (CA) (Appendix, Table S2). A proxy for the value of habitat shelter, a Shelter Index (SI) (Eq. 1), that goes from 0 to 24, was then calculated.

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

Equation 2.3.1 – Formula of Shelter Index (SI)

In equation 2.3.1, different weights were attributed to different variables based on the influence they bore on carabid presence. The Collembola communities of the park were examined as part of the project that encompasses this study, and canopy cover was found to be highly influential in boosting springtail richness and diversity (Martins da Silva et al., 2023a). Canopy is a key element for these arthropods in both woods and semi-open environments, increasing niche availability and protecting against desiccation by regulating the temperature of the soil throughout the day (Breashers et al., 1998; Liu et al., 2014; Rossetti et al., 2015; Magura & Lövei, 2019; Blaise et al., 2022; Boutaud et al., 2022). Based on this information, as carabids not only feed on these arthropods but have similar humidity needs, a higher weight of 4 was given to this variable (CA). The second most influential variable was considered to be litter cover (LC), because it not only shelters against soil desiccation, as the other variables, but also greatly promotes the abundance of microarthropods that carabids use as food, and as such, was given a weight of 2 (Martins da Silva et al., 2023a).

The segment $\frac{HC \times HH}{3}$ was developed to increase the influence of herbaceous cover in the formula while reducing the weight of herbaceous height. In contrast to the previous variables that have a positive influence on the index, the bare soil (BS) has a negative weight as it leaves carabids unprotected from predators and increases soil temperature, reducing humidity (Brose, 2003; Wang et al., 2018; Ruslan & Yusri, 2024).

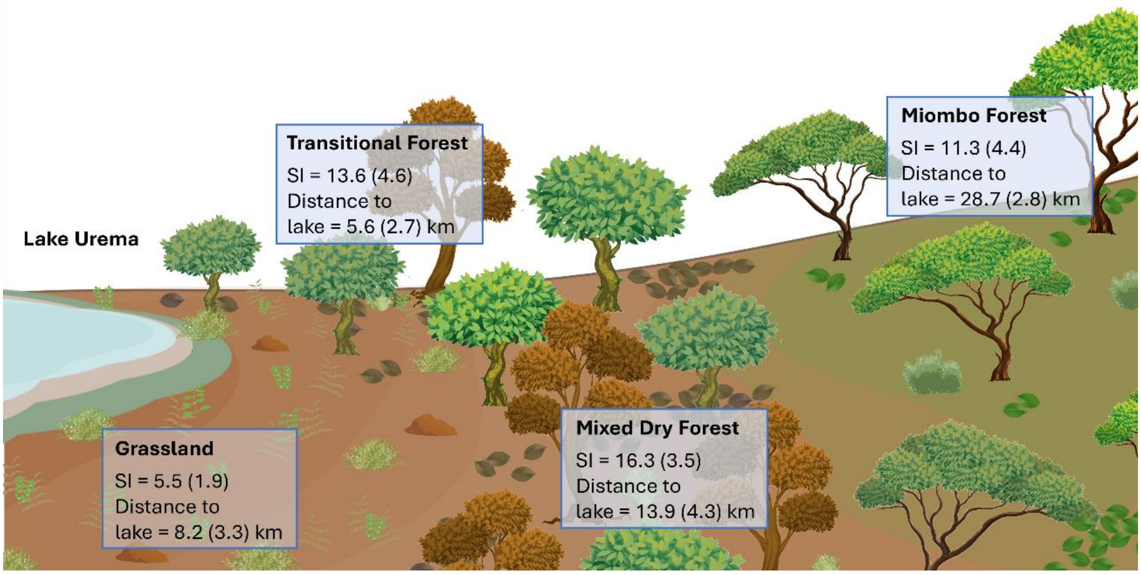

Figure 8 – Gradients of habitat Shelter Index (SI) and habitat distance to Lake Urema (Mean ± SD) across the four main habitat types. Retrieved from Baptista et al., 2024.

2.4 Data Analysis

2.4.1 Analysis of Seasonal Species Turnover

Data from the three pitfall subsamples within each site was pooled, in each of the three sampling periods. Plots were only considered if out of the 9 possible pitfalls, at least 6 were retrieved and no sampling season was completely missing. Utilizing the software R version 4.1.3 (R Core Team, 2022), specifically the package "BAT", version 2.9.5 (Cardoso et al., 2015), activity-density (N) and Alpha-diversity (S) were calculated. Activity-density is a metric often used in Carabidae studies and represents the abundance of a community (e.g., Hummel et al., 2012; Pozsgai et al., 2022).

Beta-diversity was also calculated using the "BAT" package, to characterize the turnover of species from the dry season to the wet season. Within each sampling plot the "Dry" period was compared to both "Intermediate" and "Rainy" periods. Beta-diversity ranges from 0 to 1, where a score of 0 indicates that in the two communities evaluated all species present are the same and have the same abundance. Maximum dissimilarity between the communities is indicated by a value of 1, meaning that there is no species shared by the communities under comparison. As such, a value closer to 0 denotes lower species turnover while a value closer to 1 suggests a high variation in the composition of communities.

Applying the "glm" function from R's native package "Stats", we used GLM to examine the effect of sampling period within each habitat type in order to assess the habitat's influence on activity-density, Alpha- and Beta-diversity across seasons. Then, to examine how those diversity variables varied across sampling periods, we used mixed-models (GLMM), with the habitat as the random factor. The "lme4" R package, version 1.1-33 (Bates et al., 2015) was used to carry out these analyses, and to subsequently get R2 values and assess for collinearity between fixed variables the "performance" package (Lüdecke et al., 2021) was employed. In both GLM and GLMM analysis, for activity-density and Alpha-diversity, we employed the Poisson (link = log) distribution family, and for beta diversity, we used the binomial (link = logit) family. We also ran Wilcoxon tests using the package "Stats" from R core to assess compare the different Beta results (Dry-Intermediate and Dry-Rainy).

Community Weighted Means ("CWM") represent the average value of a specific trait within a community, where the influence of a specific trait is adjusted according to its relative abundance (Garnier et al., 2004). Using the "FD" package (Laliberté et al., 2014), "CWM" values of species body size (in cm) and wing typology ("1" corresponds to macropterous species, with functional wings, and "0" to apterous or brachypterous species, unable to fly) were computed and compared across habitat types and sampling intervals. This was accomplished through GLM analysis with Gaussian family (link = identity), with the "CWM" as the response variable and the effects of habitat, sampling period, and interactions habitat-season were employed as fixed variables.

Seasonal variations were observed in the "CWM" of body size and wing typology in the grasslands. Such a drastic change in functional diversity between seasons could be explained by species that were only previously found in forested habitats migrating to the grasslands when humidity levels rise with rainfall. GLM analyses were then employed to compare three different categories of grassland communities in each plot: the dry season communities, rainy season communities with exclusively grassland species, and the rainy communities with only species found in forested areas during the dry season.

GLMs were also used to test these associations to specific sampling periods and habitat types of the most common carabids (minimum of 15 specimens).

Analysis of deviance was used to determine the impact of the fixed effects on the response variables in all the GLM analyses. To identify significant differences between habitat types and between sampling periods, we conducted pairwise comparisons using post-hoc General Linear Hypotheses tests. These tests were performed with the "multcomp" R package, version 1.4-20 (Hothorn et al., 2017).

2.4.2 Analysis of the Influence of Shelter during dry spells

To analyze the influence of the shelter provided by the various elements of vegetation during periods of drought, the focus was made on the first two periods of sampling (within dry season). The information from these two periods was combined as the "Intermediate" period had minimal rain that only started in the penultimate day, and as such, we do still consider it as part of the dry season in terms of communities assessed. Once more, Alpha-diversity (S) and activity-density (N) were calculated using the "BAT" package.

Again, "CWM" of species body size (cm) and dispersal ability, were calculated using "FD" package, version 1.0-12.3, but this time utilizing only data from the first two sampling periods. Using the same package, Alpha-functional diversity (Alpha_FD) for average beetle body size (Alpha-FD_Body_size) and wing typology (Alpha-FD_Wings) were also computed, to further explore how habitat influences these traits.

To understand how the habitat shelter affects carabid beetle communities, the isolated impact of each component of vegetation cover (bare soil (BS), herbaceous cover (HC), herbaceous height (HH), shrub cover (SC), litter cover (LC), canopy area (CA)) was first assessed. Generalized linear models (GLMs) were employed for this end with the following response variables: activity-density (N), Alpha-diversity (S), Alpha-functional diversity of body size (Alpha-FD_Body_size), Alpha-functional diversity of wing typology (Alpha-FD_Wings), and trait values of body size (Trait-values_Body_size) and wing typology (Trait-values_Wings). Different error distribution families were utilized for each response variable: Negative Binomial (link = log) for N, Poisson (link = log) for S, Inverse-Gamma (link = inverse) for Alpha-FD_Body_size, Alpha-FD_Wings and Trait-values_Body_size, and Binomial (link = logit) for Trait-values_Wings. Then, in order to investigate the combined effects of the Shelter Index and distance to Lake Urema on those same response variables, GLMMs were used with habitat type as a random factor, maintaining the corresponding error distribution families. These analyses were again performed using the "lme4" package in R.

Additionally, distance from Lake Urema and Shelter Index were tested for correlation, through Pearson correlation test.

3. Results

3.1 GNP’s Carabid Beetle Assemblage Composition

A total of 1777 specimens of carabid beetles representing 98 distinct species and morphospecies were collected (Table 1). *Microlestes zambezianus* (Mateu, 1960) and *Pheropsophus mashunus* (Péringuey, 1896) were the most common species among them, whereas the only species found in all habitat types were *Chlaenius conformis* (Dejean, 1831), *Phesopsorus insignis insignis* (Boheman, 1848) and *Graphipterus tristis* (Klug, 1853) (Table 1). Moreover, there were 49 genera and 17 subfamilies among the 98 species.

In terms of each habitat’s community composition, the transitional forest showed a rich community of carabid beetles dominated by *P. insignis insignis*, *P. mashunus*, *Distichus picicornis* (Dejean, 1831), *Tetragonoderus immaculatus* LaFerté-Sénectère, 1853, *Microlestes flavipes micromys* Alluaud, 1918 and *M. zambezianus* (Table 1). Similarly, *D. picicornis*, *M. zambezianus, Abacetus perturbator* Péringuey, 1899 and *Chlaenius discopictus nuncius* Péringuey, 1908 were the most abundant species found in grasslands (Table 1). Miombo forest habitats were dominated by *Crepidogaster langenhani* Liebke, 1927 as well as *P. mashunus* (Table 1). In the mixed forest, species like *Crepidogaster langenhani*, *Scarites tenebricosus molossus* Klug, 1853, *Abacetus percoide*s Fairmaire, 1868 and *Orthotrichus insolitum* (Péringuey 1896) were the most frequent (Table 1).

Table 1 - Abundance of Carabidae species and subspecies throughout the four main habitat types, during the three sampling periods (T1: “Dry” - 25 October to 5 November; T2: “Intermediate” – 5 to 15 November; T3: “Rainy” – 15 to 25 November 2019). “*” – new species records for Mozambique; “**” – new subgenera records for Mozambique; “***” – new genera records for Mozambique. Singletons are marked in bold and doubletons are underlined.

	Miombo			Mixed			Transitional			Grassland			Total
	T1	T2	T3	T1	T2	T3	T1	T2	T3	T1	T2	T3	
Anthiinae													
***Triaenogenius carinulatus carinulatus* (Fairmaire, 1887)**	0	0	0	0	0	1	0	0	0	0	0	0	1
Cypholoba alveolata ranzanii (Bertoloni, 1849)	2	3	0	0	0	0	0	0	0	0	0	0	5
Cypholoba graphipteroides bilunata (Boheman, 1860)	0	0	7	1	1	3	4	0	7	0	0	0	23
Cypholoba rutata (Péringuey, 1892)	2	0	5	5	2	2	0	0	0	0	0	0	16
***Cypholoba semisuturata vassei* (Sternberg, 1907)**	0	0	1	0	0	0	0	0	0	0	0	0	1
Eccoptoptera mutilloides mutilloides (Bertoloni, 1857)	1	1	0	0	0	1	0	0	0	0	0	0	3
Anthia (Termophilum) alternata Bates, 1878	2	0	2	8	4	3	2	0	0	0	0	3	24
Anthia (Termophilum) burchelli petersi Klug, 1853	0	0	0	0	0	1	2	1	1	0	0	0	5
Anthia (Termophilum) omoplata Lequien, 1832	1	3	1	0	0	0	0	0	0	0	0	0	5
Anthia (Termophilum) fornasinii fornasinii Bertoloni, 1845	3	0	1	0	0	0	1	0	0	0	0	0	5
Anthia (s. str.) circumscripta circumscripta Klug, 1853	0	0	2	0	1	0	4	2	0	0	0	0	9

Apotominae													
***Apotomus annulaticornis* Péringuey, 1896 ***	0	0	0	0	0	0	0	0	1	0	0	0	1
Apotomus sp.	0	0	0	0	0	0	0	0	0	0	0	1	1
Brachininae													
Crepidogaster (s. str.) langenhani (Liebke, 1927) *****	0	0	18	4	5	17	2	0	0	0	0	0	46
Crepidogaster (s. str.) protuberata Basilewsky, 1959	1	1	3	0	0	0	0	0	0	0	0	0	5
Crepidogaster (Tyronia) longelineata (Basilewsky, 1988) ******	0	1	3	1	0	4	0	0	0	0	0	0	9
Crepidogastrillus curtulus* Basilewsky, 1959 **	0	0	0	0	1	0	0	0	0	0	0	0	1
Pheropsophus (Stenaptinus) dregei Chaudoir, 1876	0	0	0	0	0	0	0	0	4	4	0	6	14
Pheropsophus (Stenaptinus) insignis insignis (Boheman, 1848)	0	0	1	0	0	14	23	21	56	2	4	3	124
Pheropsophus (Stenaptinus) mashunus Péringuey, 1896	6	15	14	0	0	11	160	114	46	0	0	0	366
Pheropsophus (Stenaptinus) stenopterus Chaudoir, 1878	0	0	0	0	0	0	0	0	3	2	0	0	5
Styphlomerus (s. str.) neavei neavei Liebke, 1934 *****	2	1	0	4	2	3	1	1	1	0	0	0	15
Brachinus (subg. incertae) distans Lorenz, 1998	0	0	0	0	0	0	0	0	0	1	0	4	5
Brachinus (subg. incertae) laetus Dejean, 1831 *****	0	0	0	0	0	0	0	0	0	1	0	1	2
***Brachinus (subg. incertae) leprieuri* Gory, 1833 ***	0	0	0	0	0	0	0	0	0	0	0	1	1
Carabinae													
***Calosoma (Ctenosta) planicolle* Chaudoir, 1869**	0	0	0	0	0	1	0	0	0	0	0	0	1
Cicindelinae													
Manticora scabra Klug, 1849	0	0	7	0	0	0	0	0	0	0	0	0	7
Megacephala asperata (Waterhouse, 1877)	0	0	11	0	2	10	0	0	0	0	0	0	23
Dromica dolosa latepolita Schüle, 2011	0	0	0	0	0	4	0	0	0	0	0	0	4
Prothymidia angusticollis (Boheman, 1848)	0	0	0	0	0	4	0	0	0	0	0	0	4
***Elliptica compressicornis compressicornis* (Boheman, 1861)**	0	0	1	0	0	0	0	0	0	0	0	0	1
Dryptinae													
***Planetes (s. str.) quadricollis* Chaudoir, 1878**	0	0	0	0	0	1	0	0	0	0	0	0	1
Galerita angustipennis Gerstaecker, 1867	0	0	0	0	0	2	0	0	0	0	0	0	2
Harpalinae													
Notiobia (Diatypus) sp.	0	0	0	1	0	0	0	0	0	0	0	0	1
***Omostropus mandibularis* (Roth, 1851)**	0	0	0	0	0	1	0	0	0	0	0	0	1
***Parophonus (Hyparpalus) tomentosus* (Dejean, 1829)**	0	0	0	1	0	0	0	0	0	0	0	0	1
***Siopelus (Haplocoleus) lucens* Putzeys in Chaudoir, 1878**	0	0	0	0	0	0	0	0	1	0	0	0	1
Siopelus (Aulacoryssus) sp.	0	0	0	0	0	1	0	0	0	0	0	0	1
Lebiinae													
Perigona (Trechicus) schmitzi* (Basilewsky, 1989) *	0	0	0	0	1	0	0	0	0	0	0	0	1
Graphipterus lineelus Péringuey, 1896	0	0	8	0	1	4	0	0	0	0	0	0	13
***Graphipterus horni staudingeri* Burgeon, 1928 ***	0	0	1	0	0	0	0	0	0	0	0	0	1
Graphipterus tristis Klug, 1853	2	1	1	14	2	0	4	1	0	1	0	0	26
Anaulacus (Aephnidius) madagascariensis (Chaudoir, 1850)	0	0	0	1	0	0	7	1	1	0	0	0	10

Tetragonoderus (s. str.) immaculatus La Ferté-Sénectère, 1853 *****	0	0	0	7	5	0	22	0	0	0	0	0	34
***Cymindoidea regularis* Basilewsky, 1961 ***	0	0	0	0	1	0	0	0	0	0	0	0	1
Platytarus tessellatus* (Dejean, 1831) **	0	0	0	1	0	0	0	0	0	0	0	0	1
Apristus latipennis latipennis* Chaudoir, 1878 **	0	0	0	0	1	0	0	0	0	0	0	0	1
Microlestes flavipes micromys Alluaud, 1918	0	0	0	0	0	0	26	3	2	1	0	3	35
Microlestes zambezianus Mateu, 1960	0	0	0	0	0	0	41	7	11	225	34	52	370
Mesolestes (s. str.) machadoi Mateu, 1965 *****	0	0	0	0	0	0	6	0	0	0	0	0	6
Mesolestes (s. str.) nigrocephalus Mateu, 1962 *****	0	0	5	0	0	1	10	2	0	0	0	0	18
Mesolestes sp.	1	0	0	0	0	0	0	0	0	0	0	0	1
***Singilis (s. str.) africaorientalis kenyacus* Anichtchenko, 2016 ***	0	0	0	0	0	0	1	0	0	0	0	0	1
Licininae													
Systolocranius goryi (Goryi, 1833)	0	0	7	0	1	10	0	0	1	0	0	0	19
***Melanchiton lucidulus* (Boheman, 1848)**	0	0	0	0	0	0	0	0	0	0	0	1	1
Chlaenius (Pachydinodes) conformis Dejean, 1831	1	2	0	1	0	0	0	0	1	1	0	2	8
Chlaenius (Prochlaeniellus) peringueyi Kuntzen, 1919 *****	0	0	0	0	0	0	1	0	5	0	0	6	12
***Chlaenius (Pseudochlaeniellus) paenulatus* Erichson, 1843**	0	0	0	0	0	0	0	0	0	0	0	1	1
Chlaenius (Chlaenionus) zanzibaricus giganteus (Péringuey, 1885)	0	0	0	0	0	0	1	0	1	0	0	1	3
Chlaenius (Chlaeniostenus) cylindricollis Dejean, 1831	0	0	0	0	0	0	9	5	11	3	1	6	35
Chlaenius (Amblygenius) sp.	0	0	0	0	0	0	0	0	1	0	0	0	1
Chlaenius (Chlaenius) cosciniophorus Chaudoir, 1876 *****	0	0	0	0	0	0	0	2	0	0	0	1	3
Chlaenius (Chlaenius) discopictus nuncius Péringuey, 1908 *****	0	0	0	0	0	0	0	2	10	0	0	69	81
***Chlaenius (Chlaenius) dusaultii diagraphus* Alluaud, 1922**	0	0	0	0	0	0	0	0	1	0	0	0	1
Chlaenius (Chlaenius) notabilis La Ferté-Sénectère, 1851	0	0	0	0	0	0	2	1	14	0	0	9	26
Chlaenius (Macrochlaenites) lugens Chaudoir, 1876	0	0	0	0	0	0	1	0	1	0	0	4	6
Chlaenius (Paracallistoides) fulvicollis Chaudoir, 1876	0	0	0	0	0	0	1	0	0	1	0	9	10
Chlaenius (Paracallistoides) kirki kirki Chaudoir, 1876	0	0	0	0	0	3	0	0	0	0	0	0	3
Melaeninae													
Melaenus elegans Dejean, 1831	0	0	0	0	0	0	0	0	2	0	0	1	3
***Cymbionotum (s. str.) schueppelii* (Dejean, 1825)**	0	0	0	0	0	0	0	0	0	0	0	1	1
Panagaeinae													
Disphericus sp.	0	0	0	0	0	1	0	0	0	0	0	0	1
Tefflus carinatus carinatus Klug, 1853	0	0	8	0	1	4	0	0	2	0	0	0	15
Microschemus sp.	1	0	0	0	0	0	0	0	0	0	0	0	1
Paussinae													
***Pentaplatarthrus gestroi* Kolbe, 1896**	0	0	1	0	0	0	0	0	0	0	0	0	1
Paussus (Bathypaussus) cultratus* Westwood, 1850 *	0	0	1	0	0	0	0	0	0	0	0	0	1
***Paussus (Klugipaussus) pseudoklugi* Luna de Carvalho, 1963**	0	0	0	0	0	0	0	1	0	0	0	0	1
Platyninae													
Orthotrichus insolitum (Péringuey, 1904) *****	0	0	0	0	2	47	0	0	0	0	0	0	49

Pterostichinae													
Abacetus (Distrigus) denticollis Chaudoir, 1878	0	0	3	0	0	0	0	0	0	0	0	0	3
Abacetus (Distrigus) nigrinus (Boheman, 1848) *****	0	0	0	0	0	0	0	0	3	0	0	1	4
Abacetus (Abacetus) percoides Fairmaire, 1868	1	1	8	1	3	55	0	0	0	0	0	0	69
***Abacetus (Abacetus) pseudomashunus* Straneo, 1950 ***	0	0	0	0	0	0	0	0	1	0	0	0	1
Abacetus (Abacetus) sp.	0	0	0	0	0	0	0	0	1	0	0	0	1
Abacetus (Abacetillus) discolor (Roth, 1851) *****	0	0	0	1	0	11	0	0	0	0	0	0	12
Abacetus (Distrigodes) perturbator Péringuey, 1899 *****	0	0	0	0	0	0	0	0	1	2	0	34	37
Abacetus (Astigis) cursor Péringuey, 1898 *****	0	0	0	0	0	0	0	0	0	0	0	2	2
Scaritinae													
Distichus (s. str.) bisquadripunctatus (Klug, 1862)	0	0	0	0	0	0	1	0	1	0	0	1	3
Distichus (s. str.) picicornis (Dejean, 1831)	0	0	0	0	0	0	12	5	3	1	3	18	42
Scarites aestuans Klug, 1853	0	0	0	0	0	0	0	0	0	1	2	8	11
Scarites (s. str.) tenebricosus molossus Klug, 1853	0	0	7	1	1	18	0	0	2	0	0	0	29
Siagoninae													
Siagona caffra Boheman, 1848	0	0	0	0	0	0	0	0	1	0	1	0	2
***Siagona levasseuri* Lecordier, 1970**	0	0	0	0	0	0	0	0	1	0	0	0	1
***Siagona partita* Lecordier, 1979**	0	0	0	0	0	0	0	0	1	0	0	0	1
Trechinae													
Elaphropus (s. str.) aethiopicus Chaudoir, 1876	2	2	6	0	1	4	0	0	0	0	1	0	16
Elaphropus (s. str.) sp.	0	0	0	1	0	0	0	0	0	0	0	0	1
Elaphropus (Sphaeorotachys) haemorrhoidalis (Ponza, 1805) *****	0	0	0	0	2	0	0	0	0	0	0	0	2
***Tachys (Paratachys) iridipennis* Chaudoir, 1876 ***	0	0	0	0	0	0	0	0	1	0	0	0	1
*Tachys (Paratachys) sp.*1	0	0	0	0	0	0	0	0	0	0	1	1	2
***Tachys (Paratachys) sp.*2**	0	0	0	0	0	0	0	0	1	0	0	0	1

Most of the sampled species are new records for the GNP, as previously only a small number of species from the southeast area of the park was known (e.g. Alves, 1974, Schüle, 2011). Moreover, significant additions were made to Mozambique’s species list, as 28 species/subspecies, three subgenera and three genera were newly recorded for this country, according to the most recent checklist (Lorenz, 2019; Table 1).

Almost half of the recorded carabid beetles were rare species, since 39.8% were found only once and 6.1% were recorded twice (Table 1). Singletons and doubletons were observed in all habitats, but the highest frequency was recorded in the transitional and mixed forests (Table 1). Additionally, we found that almost all of the 20 most common species exhibited a strong correlation to certain habitat types and sampling periods (Table 2). Most of these species were restricted either to forest or open habitats, with the transitional forest harboring species from both types of habitats, as it comprises an ecotone zone, exhibiting both open and closed habitat areas (Table 2).

Table 2 - Percentage distribution (%) of the 20 most common species (ones that constitute more than 80% of the total specimens captured) for each habitat (MIO – miombo forests, MIX – mixed forests, TRA – transitional forests, GRA – grasslands) and each sampling period (T1 – "Dry", T2 – "Intermediate", T3 – "Rainy"). Analysis of Deviance: F-values (nDF, dDf) show how strongly each species is associated with each habitat and sampling period. Statistically significant results are in bold.

	Total Habitats						Total Seasons				
	MIO	MIX	TRA	GRA	$F_{(3,288)}$	*p*	T1	T2	T3	$F_{(2,288)}$	*p*
Anthiinae											
Anthia alternata	16.7	62.5	8.33	12.5	3.48	**0.02**	50	17	33.3	1.56	0.21
Cypholoba graphipteroides	30.4	21.7	47.83		2.23	0.08	22	4.4	73.9	5.75	**< 0.01**
Brachininae											
Pheropsophus mashunus	9.56	3.01	87.43		41.2	**< 0.01**	45	35	19.4	0.14	0.87
Pheropsophus insignis	0.81	11.3	80.65	7.26	28.2	**< 0.01**	20	20	59.7	1.91	0.15
Crepidogaster langenhani	39.1	56.5	4.35		10.6	**< 0.01**	13	11	76.1	12.9	**< 0.01**
Cicindelinae											
Megacephala asperata	47.8	52.2			5.48	**< 0.01**		8.7	91.3	12.7	**< 0.01**
Lebiinae											
Microlestes flavipes			88.57	11.43	16.1	**< 0.01**	77	8.6	14.3	11.1	**< 0.01**
Microlestes zambezianus			15.95	84.05	24	**< 0.01**	72	11	17	7.02	**< 0.01**
Tetragonoderus immaculatus		35.3	64.71		3.98	**< 0.01**	85	15		6.26	**< 0.01**
Graphipterus notabilis	15.4	61.5	19.23	3.85	0.8	0.49	81	15	3.85	2.78	0.06
Mesolestes nigrocephalus	27.8	5.56	66.67		2.82	**0.04**	56	11	33.3	0.77	0.46
Licininae											
Chlaenius cylindricollis			71.43	28.57	8.28	**< 0.01**	34	17	48.6	1.45	0.24
Chlaenius discopictus			14.81	85.19	2.51	0.06		2.5	97.5	4.64	**0.01**
Chlaenius notabilis			65.38	34.62	5.35	**< 0.01**	7.7	3.9	88.5	7.56	**< 0.01**
Systolocranius goryi	36.8	57.9	5.26		3.74	**0.01**		5.3	94.7	10.6	**< 0.01**
Platyninae											
Orthothricus insolitum		100			8.94	**< 0.01**		4.1	95.9	6.95	**< 0.01**
Pterostichinae											
Abacetus percoides	14.5	85.5			9.67	**< 0.01**	2.9	5.8	91.3	11.1	**< 0.01**
Abacetus pertubator			2.7	97.3	5.59	**< 0.01**	5.4		94.6	4.35	**0.01**
Scaritinae											
Distichus picicornis			47.62	52.38	6.54	**< 0.01**	31	19	50	0.42	0.66
Scarites tenebricosus	24.1	69	6.9		5.71	**< 0.01**	3.5	3.5	93.1	11.8	**< 0.01**

3.2 Temporal and Spatial Variations in Carabidae Diversity and Morphology

Comparing the different sampling periods, the “Rainy” period exhibited higher activity-density values overall while the “Intermediate” period recorded the lowest values (Fig. 9). Although forested habitats consistently recorded fewer individuals, activity-density values were more evenly distributed throughout the different habitat types during the “Rainy” sampling period (Fig. 9). Focusing on individual habitats, while the miombo and mixed forest habitats showed similarly low values of activity-density in the “Dry” and “Intermediate” periods (which highly increased in the “Rainy” period) the same pattern was not seen in the other two habitats both with higher carabid activity-density during the “Dry” sampling period (Fig. 9, Table 3). In the transitional forest, while the “Dry” period recorded a higher number of specimens, the variation in activity-density was not significantly different among sampling periods (Fig. 9, Table 3).

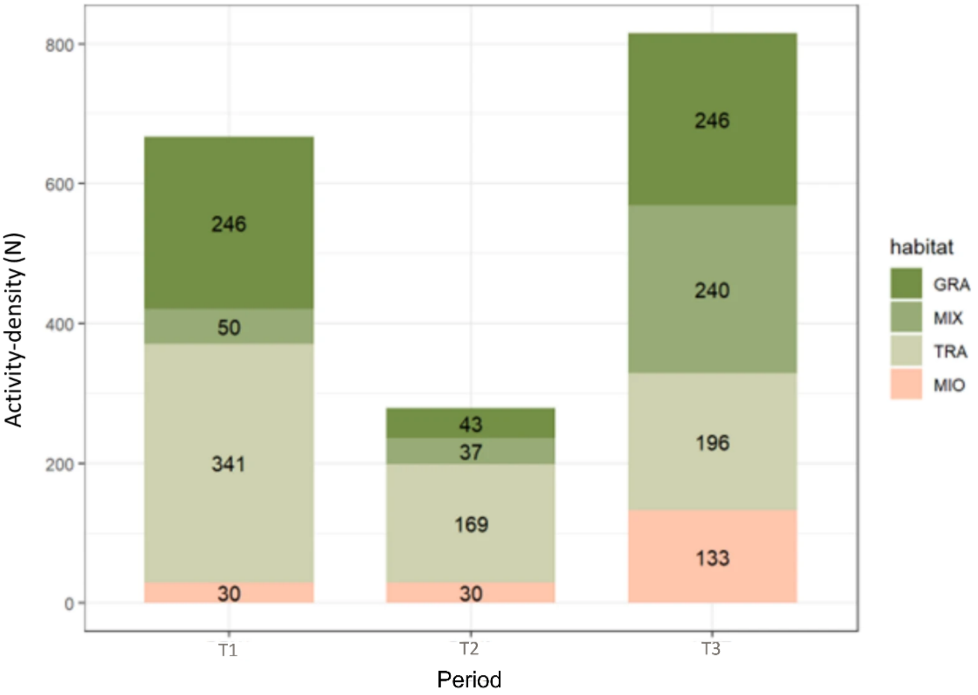

Figure 9 - Activity-density of carabids in the four habitats (GRA – grassland, MIX – mixed forest, TRA – transitional forest, MIO – miombo forest) throughout the three sampling periods (T1 – “Dry”, T2 – “Intermediate”, T3 – “Rainy”). Adapted from Martins da Silva et al., 2023b.

Table 3 - GLMM analysis' coefficients and R2 of the influence of the sampling period, on the activity-density and Alpha-diversity of carabid beetle communities, using the "Dry" period as reference. Random effects variable: Habitat. Statistically significant results are in bold.

	Activity-density			Alpha-diversity		
	E	*p*	R2	E	*p*	R2
Dry-Intermidiate						
Grassland	0.041	0.874	0.601	-0.572	0.097	0.502
Transitional Forest	0.353	0.104	0.782	0.689	0.009	0.526
Mixed Forest	-0.661	< **0.001**	0.456	-0.643	< **0.001**	0.228
Miombo Forest	-1.702	< **0.001**	0.909	-0.525	0.083	0.601
All Habitats	-0.742	< **0.001**	0.336	-0.346	0.04	0.316
Dry-Rainy						
Grassland	1.489	< **0.001**	0.601	1.679	< **0.001**	0.502
Transitional Forest	1.696	< **0.001**	0.782	1.139	< **0.001**	0.526
Mixed Forest	-0.513	< **0.001**	0.456	1.36	0.379	0.228
Miombo Forest	0.847	< **0.001**	0.909	-0.128	< **0.001**	0.601
All Habitats	0.482	< **0.001**	0.336	0.766	< **0.001**	0.316

Alpha-diversity in grasslands, miombo and mixed forests did not significantly change between the "Dry" and "Intermediate" periods, whereas their highest values of Alpha-diversity were observed in the "Rainy" period (Table 3). The highest increment was recorded in the grasslands, with a high increase in the number of species in the "Rainy" period in relation to the "Dry" and "Intermediate" periods (Fig. 10). Transitional forest showed an opposite pattern as there was a significant variation between the "Dry" and "Intermediate" periods, and no significant differences between "Dry" and "Rainy" sampling periods were found (Table 3).

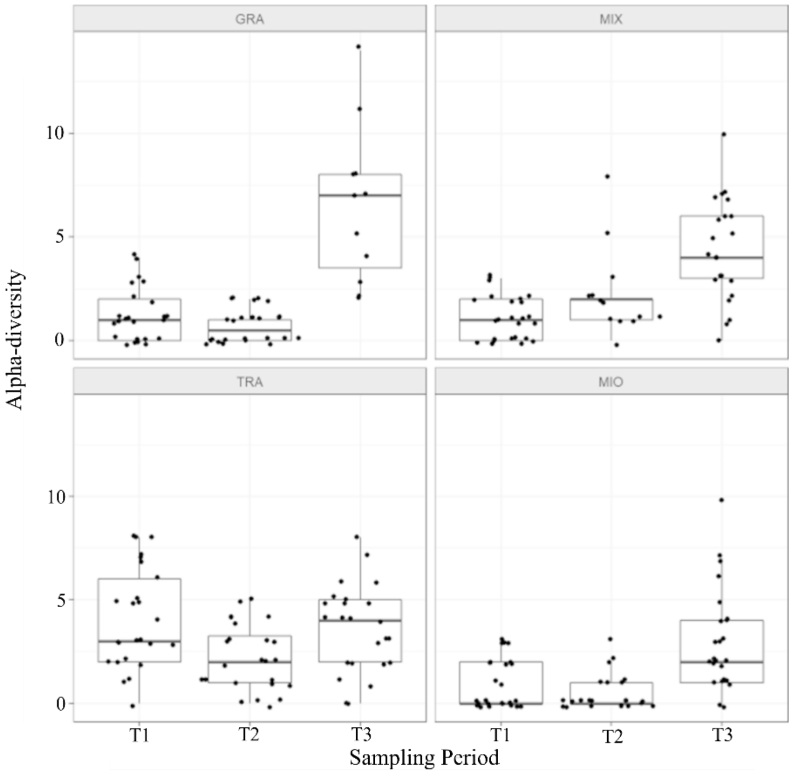

Figure 10 - Mean Alpha-diversity values in the four main habitats (GRA – grassland, MIX – mixed forest, TRA – transitional forest, MIO – miombo forest) throughout the three sampling periods (T1 – “Dry” period, T2 – “Intermediate”, T3 – “Rainy”). Each dot represents a sampling site. Adapted from Martins da Silva et al., 2023b.

Lower values of CWM of body size were found in grasslands, compared to the miombo and mixed forests but not to the transitional forest ($F_{(3,190)} = 14.71$, $P < 0.001$; Fig. 11). The contrary was found in the CWM of wing typology, where the grasslands showed the highest values (Fig. 12, $F = 20.24$, $P < 0.001$). These two traits were found to be inversely related, meaning larger species were found to be frequently flightless ($F_{(1,188)} = 105.9$, $P < 0.001$; Appendix, Table S3). The increase in species average body size was significant in the open habitat of the grasslands, as opposed to the forested ones where no significant variations were observed (Fig. 11). This increase between periods was due to the emergence of exclusive species to this habitat in the “Rainy” period, but also by the occurrence of species previously confined to forested habitats (Fig. 13A). Opposed to body size, the average wing typology values showed no differences between periods across the different habitat types (Fig. 12).

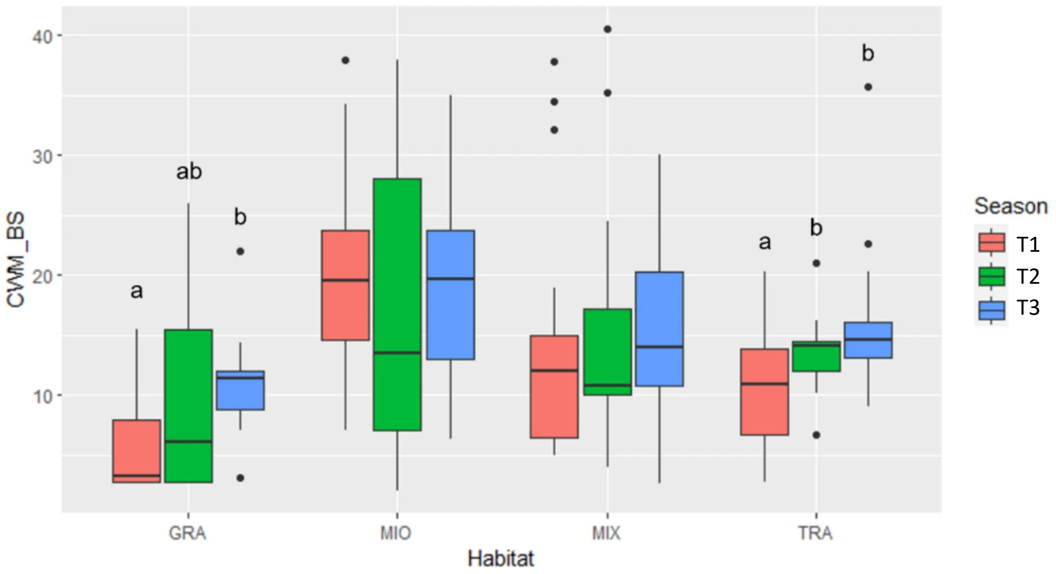

Figure 11 - Community weighted mean of body size (CWM_BS; in mm) throughout the three sampling periods (T1 - "Dry", T2 - "Intermediate", T3 - "Rainy") in each habitat type (GRA – grassland, MIO – miombo forest, MIX – mixed forest, TRA – transitional forest). Significantly different groups within each habitat, indicated by General Linear Hypotheses-tests are signaled by the letters "a" and "b ($P < 0.05$). Adapted from Martins da Silva et al., 2023b.

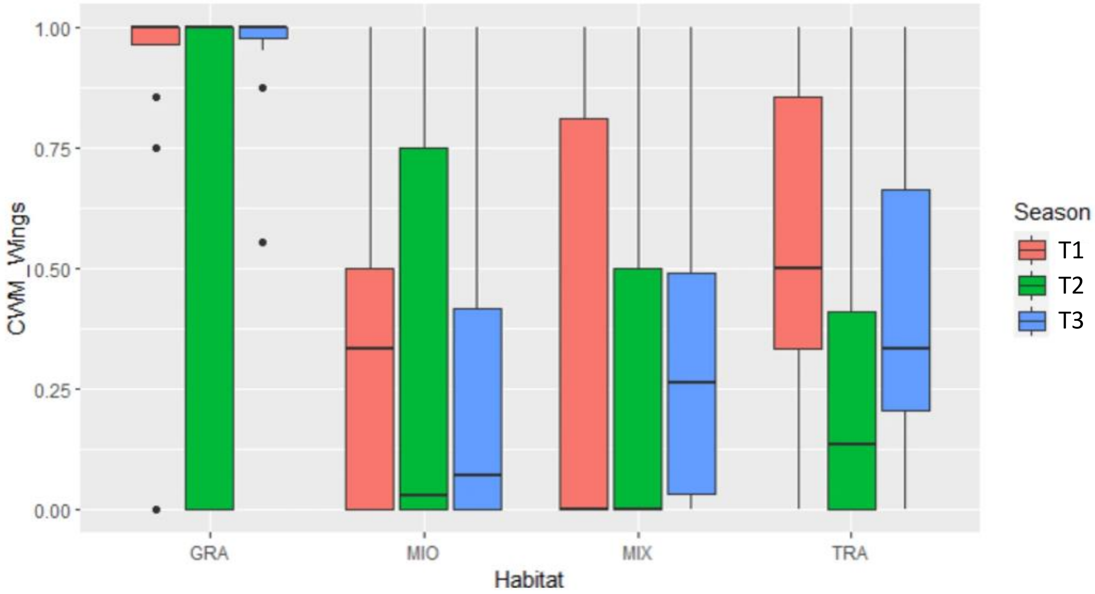

Figure 12 - Community weighted mean of wing typology (CWM_Wings; macropterous species – 1, apterous/brachypterous species – 0) throughout the three sampling periods (T1 - "Dry", T2 - "Intermediate", T3 - "Rainy") in each habitat type (GRA – grassland, MIO – miombo forest, MIX – mixed forest, TRA – transitional forest). Significantly different groups within each habitat, indicated by General Linear Hypotheses-tests are signaled by the letters "a" and "b ($P < 0.05$). Adapted from Martins da Silva et al., 2023b.

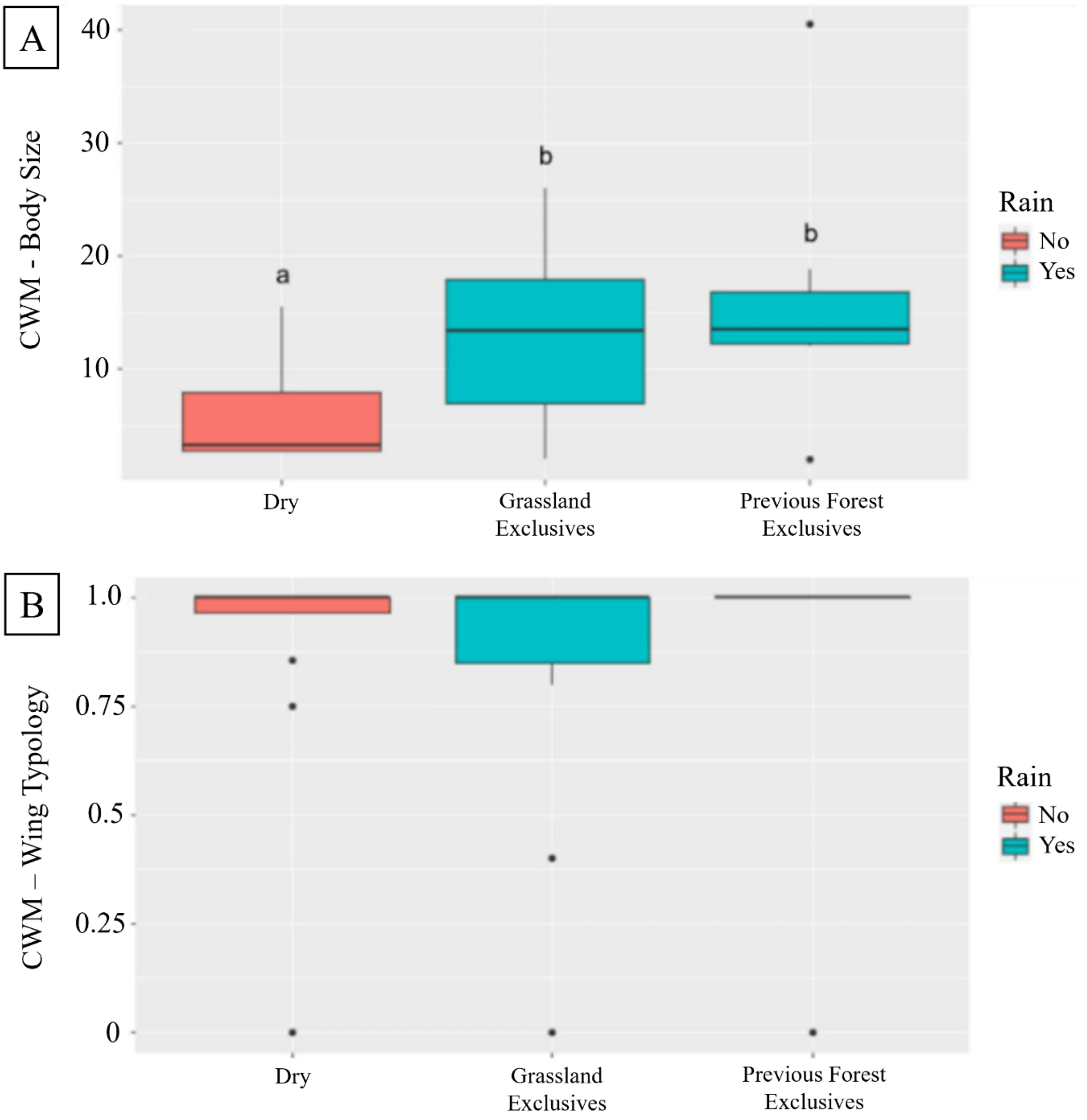

Figure 13 - Community weighted means: A- body size; B – wing typology; of exclusive grassland species occurring before (Dry) and after the rainfall (Grassland Exclusives), and species that only occurred in forested habitats during the dry season that were found in grasslands in the “Rainy” period (Previous Forest Exclusives); Significantly different groups indicated by General Linear Hypothesis-tests are signaled by the letters “a” and “b ($P < 0.05$). Adapted from Martins da Silva et al., 2023b.

In terms of beta diversity, a higher difference was observed between the communities of “Dry” and “Rainy” periods than between the “Dry” and “Intermediate” ones, for all habitats except transitional forest (Fig. 14).

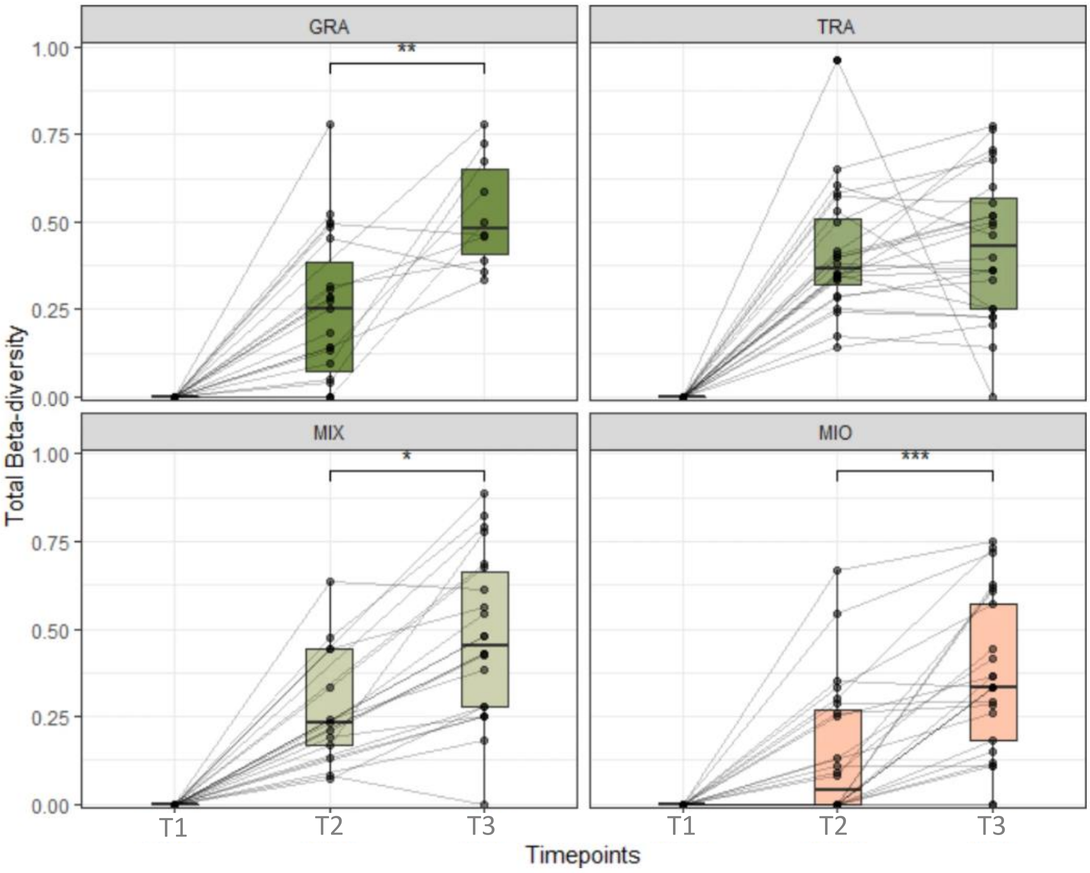

Figure 14 - Beta diversity values between sampling periods (T1-T2 and T1-T3) in the four main habitat (GRA – grassland, TRA – transitional forest, MIX – mixed forest, MIO – miombo forest) with reference on the "Dry" sampling period (T1). Values range from 0 (the compared sites exhibit the same species at the same abundances) to 1 (the compared sites don't have any species in common). Each dot represents the dissimilarity value in each site between the "Dry" – "Intermediate" (T2) periods and "Dry" – "Rainy" (T3) periods. Asterisks denote the significance levels when comparing dissimilarity average values between T1-T2 and T1-T3 through Wilkoxon test ("*" $p < 0.05$; "**" $p < 0.01$; "***" $p < 0.001$). Adapted from Martins da Silva et al., 2023b.

3.3 Effects of Vegetation Elements and Lake Urema on Carabid Diversity and Morphology

During the dry season ("Dry" and "Intermediate" periods), the GLM analysis examining the effects of local vegetation features revealed the significant influence of litter and canopy cover on all measured variables (Table 4). Both factors positively affected activity-density (N), Alpha-diversity (S), Alpha-functional diversity (Alpha-FD) concerning both body size and wing typology, and the trait of body size itself (Table 4). Contrarily, wing typology was found to be negatively correlated to canopy cover and litter (Table 4). Additionally, shrub cover positively impacted activity-density, whereas, the herbaceous variables, more associated with open environments, exhibited mixed effects. Herbaceous cover positively affected wing typology but had a negative influence in species richness and activity-density while the height of herbaceous plants also negatively impacted activity-density (Table 4). Bare soil showed no significant influence on any of the variables (Table 4).

Table 4 – Summary of GLM analysis of the effects (“E”: positive “+” or negative “-”) of each environmental variable (bare soil, herb cover, herb height, shrub cover, litter cover, canopy area) on carabid beetle diversity parameters: activity-density (N), Alpha-diversity (S) and Alpha-functional diversity (Alpha-FD) and trait values of body size and wing typology. Statistically significant results are in bold (“*” p<0.05; “**” p<0.01; “***” p<0.001).

		E	Z-value	E	Z-value	E	Z-value
		Canopy Cover		Shrub Cover		Herbaceous Height	
N		+	**4.65*** **	+	**4.96*** **	-	0.176
S		+	**3.67*** **	+	1.68	-	0.090
Trait Values	Body Size	+	**2.00***	+	0.93	+	0.067
	Wings	-	**3.05*** *	-	0.97	+	0.256
Alpha-FD	Body Size	+	**2.75*** *	+	0.81	-	0.037
	Wings	+	**3.07*** *	+	0.05	+	0.034

		E	Z-value	E	Z-value	E	Z-value
		Litter Cover		Herbaceous Cover		Bare Soil	
N		+	**6.93*** **	-	**14.8*** **	+	1.60
S		+	**3.82*** **	-	**4.55*** **	-	0.58
Trait Values	Body Size	+	**2.32***	-	0.51	-	1.75
	Wings	-	**2.50***	+	**2.52***	+	0.24
Alpha-FD	Body Size	+	**2.80*** *	-	1.28	-	1.34
	Wings	+	**2.65*** *	-	1.98	-	0.26

According to the GLMMs assessing the influence of habitat shelter (local vegetation structure) and distance to Lake Urema on the diversity variables, the habitat shelter had no impact on the variation of activity-density across GNP landscape (Table 5). Additionally, the influence of the habitat shelter on the Alpha-diversity was found to be only marginally significant (Table 5). The only functional diversity parameter affected by the shelter index was carabid species' body size, while wing typology did not appear to be affected (Table 5). Furthermore, both community trait values of carabid body size and wing typology were influenced by habitat shelter (Table 5). Concretely, bigger species occurred in more closed sites, while these sites presented lower numbers of winged carabids, i.e. less species with higher dispersal power (Fig. 15A; Fig. 15B).

Table 5 - Summary of GLMM analysis of the effects of habitat Shelter Index and distance to lake Urema on carabid beetle diversity parameters: activity-density (N), Alpha-diversity (S) and trait values and Alpha-functional diversity (Alpha-FD) of body size and wing typology. Statistically significant results are in bold (Est. – estimates, SE – standard errors). Random effects variable: habitat types.

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

On the other hand, the GLMM analysis showed that the proximity to Lake Urema affected both activity-density and species richness (Table 5). Nevertheless, this factor presented no effect on either of the Alpha-functional diversity variables (Table 5). The body size trait was affected by distance gradient, as larger sized species were more abundant in sites farther from the floodplains (Table 5; Fig. 15C). Although there was a negative correlation between the lake and wing typologies, it was not statistically significant (Table 5).

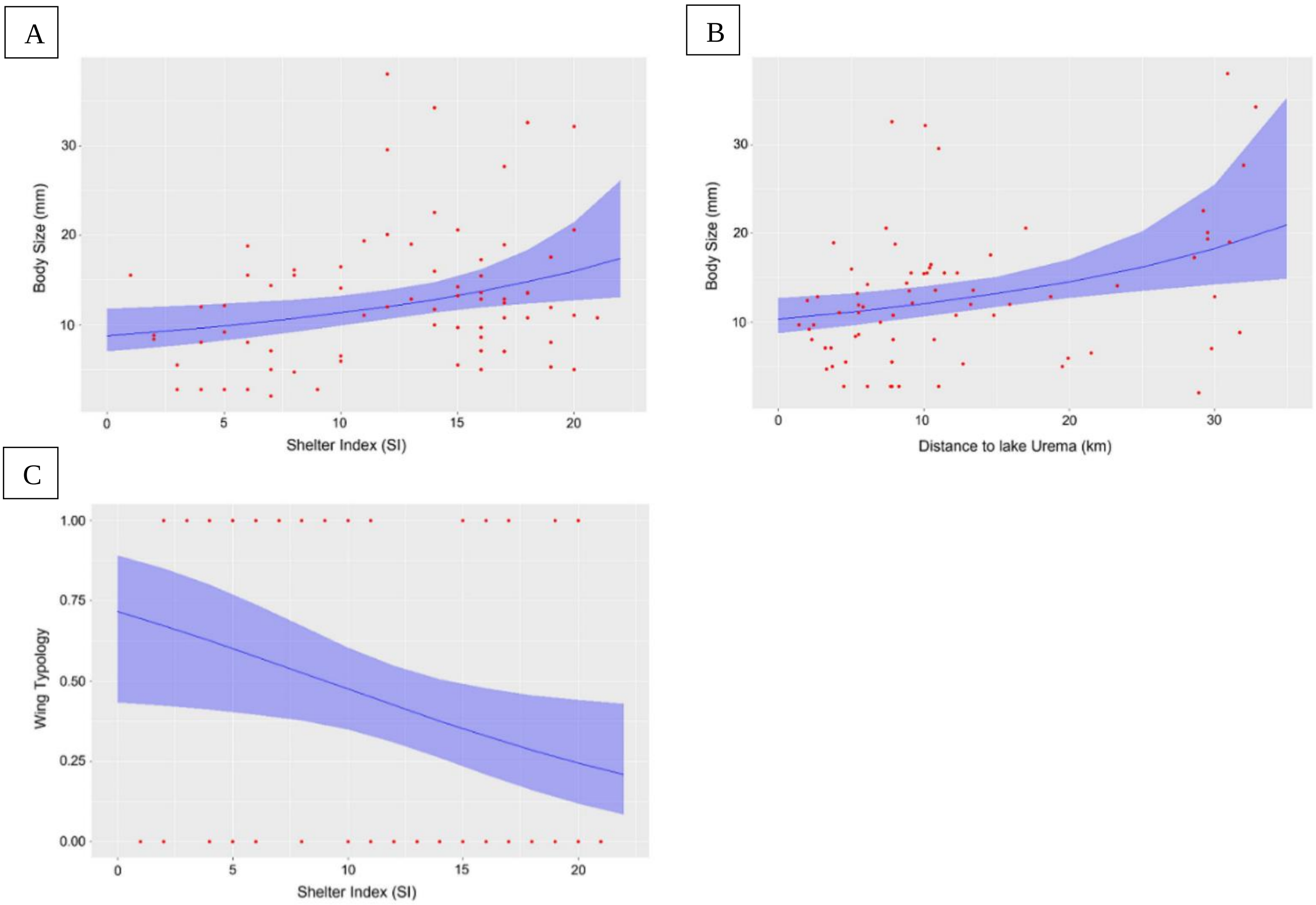

Figure 15 - GLMM analysis effect plots of residual relationships: A - carabid body size (in mm) with Shelter Index (SI); B – body size with distance to lake Urema (in km); C - carabid wing typology (1 – macropterous species; 0 - wingless/brachypterous species; averaged per site) with habitat Shelter Index. Retrieved from Baptista et al., 2024.

No correlation was found between the Shelter Index and the distance to Lake Urema (Pearson: r= 0.103, p= 0.382).

4. Discussion:

4.1 Carabid Community Structure in the GNP

An important checklist for the park was elaborated, as the GNP revealed a rich community of carabid beetles across its different habitats and seasons. Furthermore, a high percentage of the sampled species were rare, as they were only recorded one or two times. As rarer species are more vulnerable to disturbance and extinction usually having narrower niches, it is crucial to develop further studies focusing on these species' population trends in the near future (Harnik et al., 2012; Chichorro et al., 2019). Moreover, almost all most common species occurred only in forested or open habitats, with the transitional forest harboring species with both habitat preferences. In fact, the transitional forest presented the highest species richness and number of carabid beetles recorded, which could be explained by the heterogeneity of this habitat type, in the ecotone between forest and grassland areas across the GNP landscape. Previous studies have highlighted the importance of these ecotone zones for beetle diversity (Molnár et al., 2001; Yu et al., 2007; Tóthmérész et al., 2014). By having elements from both open and forest environments the transitional forests likely present conditions to harbor not only generalists but also specialist species from both woodland and grassland habitats.

4.2. Rain effects on carabid diversity

Humidity is one of the major drivers of activity and population dynamics of carabid beetles (Lövei & Sunderland, 1996). In fact, soil humidity has a significant impact on carabid beetle survival, with egg development and larval stage being the most humidity dependent (Holland et al., 2007). Because of their dependence on soil moisture throughout their life cycle, ground-beetle populations experience changes in their activity, composition and diversity due to the seasonal variations in precipitation and environmental humidity (Thiele, 1977; Chen & Willson, 1996; Koivula, 2011; McCravy & Willand, 2020; Tsafack et al. 2020; Liu et al. 2022). Notably, in tropical settings, peak diversity is usually found during periods of higher humidity (eg. Rainio, 2013; Sahito et al., 2020; Mwambala & Nyundo, 2024). This impact is not always easily observed, as some studies have not found a significant increase in species richness corresponding to the seasonal rise in humidity (Schirmel et al., 2014; Kirichenko-Babko et al., 2020; Peterson et al., 2021). This may be due to ecosystems hosting a rich community of xerophilous species, which are better adapted to drier conditions, and with the onset of heavy rainfall, their numbers tend to drop, potentially balancing out the increase in hygrophilous species (Martins da Silva et al., 2011; Sun et al., 2020; Scarbek et al., 2021; Zajicek et al., 2021). However, few studies have focused on the Afrotropical region, which has highly contrasting seasons, and so, may have drastic differences in carabid activity throughout the year.

Our results supported our first hypothesis that the increase in precipitation in the "Rainy" period would lead to an increase in the number of carabid species when compared with drier periods. A rise in Alpha-diversity following the start of heavy rains, was observed across various GNP habitats, with the grasslands showing the most drastic rise from the "Dry" period. However, the "Intermediate" period had the lowest Alpha-diversity values, not the "Dry" period, which may be due to the transitional nature of the former period, characterized by mixed conditions. As humidity rises, xerophilous species may no longer be able to survive, while the humidity may still be insufficient for the emergence of hygrophilous species.

The transitional forest was the only habitat where carabid diversity did not increase significantly between seasons, which might be explained by its ecotone nature, functioning as a gradient between forested and grassland ecosystems. Some species like *Microlestes flavipes*, *M. zambezianus* and *Tetragonoderus immaculatus* that were found to be xerophilous due to their increased activity and dominance in the "Dry" period, were abundant in grasslands and in the transitional forest. These xerophilous species, which can use the grassland habitat for feeding during the "Dry" period, may find refuge in the adjacent transitional forest during peak heat spells (Petit & Usher, 1998; Macleod et al., 2004; Ariza et al., 2021).

Seasonal changes promote a turnover in carabid beetle communities. The increase in rainfall promotes a change in species composition with hygrophilous species replacing the dominance of xerophilous ones. (Schirmel et al., 2014). Consequently, in our study, Beta diversity values were observed to be significantly higher between the "Dry and "Rainy" sampling periods, which have very distinct abiotic conditions, than between the "Dry" and "Intermediate" periods across various habitats, supporting our second hypothesis. Carabid beetle communities of arid habitats often have a low number of species compared to more temperate ones, being dominated by few xerophilous species that are resistant to drought, having adapted to these harsh environments (e.g., Brandmayr et al., 1983; Tsafack et al., 2019; Tsafack et al., 2020). This may explain why species richness is lower during the "Dry" period, in various GNP ecosystems, emphasizing the difficult conditions that species encounter during drought, and revealing that fewer xerophylous species are present in the GNP main habitats. The transitional forest showed a low turnover in community composition after the heavy rainfall, represented by low Beta-diversity values, which might be a consequence of the role of this forested habitat as a refuge for certain species. During dry spells, the shelter offered by suitable habitat conditions of forested habitats, like canopy and litter cover, may benefit the survival of numerous species, shielding them from environmental pressures across seasons (Heliölä et al., 2001; Yu et al., 2007; Marrec et al., 2021; Zajicek et al., 2021; Boutaud et al., 2022).

4.3. Response of community traits to habitat characteristics

Shelter provided by vegetation elements of local habitats affect not only carabid survival but also influence the eco-morphology of species that inhabit them, influencing traits like body size and wing typology (e.g., Venn, 2007; Rouabah et al., 2015). Research conducted in Europe found that vegetation cover was a main influence of carabid beetle community patterns (e.g., Brose, 2003; Woodcock et al., 2005; Vandewalle et al., 2010; Martins da Silva et al., 2017). During the dry season (the period before heavy rainfall, i.e. "Dry" plus "Intermediate" period), the local vegetation structure within different GNP habitats types presented a significant impact on species distribution based on their morphology. This is evident by the different traits found in species from open and forested habitats. While wingless species, having lower dispersal capacity, were restricted to closed forest habitats during this season, a higher activity-density of macropterous species was observed in both transitional forest and grassland.

Additionally, both smaller species and species with higher dispersal power were more common in grasslands than in forests, supporting our hypothesis that such characteristics would be more frequently in open habitats. The transitional forest also supports communities with numerous winged species, probably due to its open patches. Smaller species with developed wings are not only more suited to open areas but are also more adapted to survive during dry spells (Blake et al., 1994; Jelaska & Durbešic, 2009; Ariza et al., 2021; Zajicek et al., 2021). Because of their greater dispersal capabilities, these species can use scattered shelter elements throughout open areas as refuge (Jelaska & Durbešic, 2009; Kallio, 2014; Eyre et al., 2016; Martins da Silva et al., 2017).

On the other hand, wingless and larger species are usually more sensitive to unstable environments, needing the habitat shelters provided by vegetation cover (Halme & Niemelä, 1993; Jelaska & Durbešić, 2009; Brandmayr & Pizzolotto, 2016; Wang et al., 2018). During the dry season, species with these characteristics were therefore more frequently found in the forested habitats of the GNP, with their enclosed areas offering good moisture retention and other beneficial microclimate conditions. Larger species with lesser dispersion capacities are dependent on the more stable habitat conditions and defense from predators that forest patches provide (Blake et al., 1994; Brose, 2003; Martins da Silva et al., 2008; Eyre et al., 2016; Martins da Silva et al., 2017; Wang et al., 2018).

4.4. Response of carabid diversity to flooding

Floodplain dynamic environments determine the activity and survival of carabid beetles, especially the sensitive species. Notably, seasonal flooding is an additional factor that highly impacts carabid populations and community dynamics (Den Boer et al., 1986; Lambeets et al., 2008; Lessel et al., 2011; Sienkiewicz & Żmihorski, 2012; Kirichenko-Babko et al., 2020). Only a relatively small number of species living in floodplains evolved to withstand frequent flooding episodes, being adapted to live in inundated environments (Adis et al., 1997; Zerm & Adis, 2001; Kolesnikov et al., 2012; Marx et al., 2012). Such adaptations include the ability to swim, surviving long periods submerged or having the mobility to cross small, inundated areas to reach habitat refuges (Siepe, 1994; Kolesnikov et al., 2012). Apart from the small number of species with such capacities, most carabid beetles disperse to habitats away from the source of flooding (Zerm & Adis, 2001; Andersen, 2005; Kolesnikov et al., 2012).

Sensitive species may only survive in sheltered habitats further from the disturbance source (Kirichenko-Babko et al., 2020). In the case of the GNP, the miombo forested habitats are considerably less impacted by yearly flooding, especially the sites farthest from Lake Urema, and as such offer more stable conditions that benefit sensitive species. In accordance, miombo sites showed higher levels of diversity and activity-density the further they were from Lake Urema, and therefore from the floodplains. Additionally, a higher frequency of larger species was correlated with a greater distance to the lake, as they lack the capacity that smaller carabids have to both flee the flood and repopulate the plots that were disrupted (Gerisch, 2011). Smaller species are better able to utilize water surface tension to cross between flooded areas to reach trees or other structures that can serve as refuges from flooding (Sienkiewicz & Żmihorski, 2012). These findings support our hypothesis that seasonal flooding has an impact on carabid beetle communities, affecting the distribution of larger more sensitive species. Their lower dispersal capabilities, make them not as suitable to navigate flooded sites and as such limit them to more stable areas, less impacted by flooding.

According to our findings, the seasonal cycle of flooding is a significant influence in the dynamics of carabid populations within the park. In addition to controlling the range of vulnerable bigger species, it also plays a role in the nutrient cycle of transitional forests and grasslands, the two main habitats of the floodplains (Beilfuss et al., 2007). Due to playing such an important role on their activity and distribution, deep changes to the flooding patterns of Lake Urema could have a profound impact on carabid beetle populations, and even lead to local extinctions. The potential construction of dams in catchments that supply Lake Urema are a serious threat to the stability of this system and could significantly change the flooding extent, having devastating consequences for the adjacent habitats that carabid beetles depend on (McCartney & Owen, 2007). Besides direct man-made impacts, climate change also poses a significant threat to this cycle. Unprecedented severe flooding events could become more common, as consequence of the El Niño/southern oscillation exacerbated by climate change, which could greatly harm GNP's ecosystems and its carabid communities.

4.5. Habitat shelter as a refuge from drought and climate change

Future patterns of carabid beetle diversity are also anticipated to be directly impacted by climate change, primarily as a result of the longer and harsher dry spells (Ariza et al., 2021; Peterson et al., 2021). Forested habitats help carabids cope with the harsh environment of the dry season and may be essential for species survival during the extreme arid conditions derived from climate change. In temperate and Mediterranean ecosystems, these habitat types play a crucial role in protecting carabid beetle populations and governing community patterns from adverse conditions in landscapes with both forested and grassland environments (Woodcock et al., 2005; Zamora et al., 2007; Elek & Tóthmérész, 2010; Martins da Silva et al., 2011). Unlike those ecosystems, in Afrotropical habitats there is a lack of information on carabid beetle community dynamics during the dry season and the relative influence of habitat shelter in species survival and community compositions. By addressing these knowledge gaps, we will be able to better understand the role forested habitats might play in the survival of sensitive carabid species in the following decades, in a region that will be deeply affected by climate change.

Dense vegetation cover found in forested habitats fosters higher humidity levels, which, in turn, enables a greater number of species to occur in these areas when compared to unprotected open habitats (Niemelä, 1993; Máthé, 2006; Elek & Tóthmérész, 2010; Magura & Lövei, 2019; Marrec et al., 2021; Zajicek et al., 2021). In line with this, this study showed that during the dry season, habitat shelters were related with higher species richness of carabid beetles. Furthermore, higher levels of species richness in habitat shelters were correlated to increased functional diversity in terms of species' body size. As such, our results emphasize the critical role of refuges provided by vegetation structure, namely canopy and litter layers, in the protection of sensitive species from desiccation. Hygrophilous species found in the GNP, such as *Abacetus percoides* and *Metagonum insolitum*, will be dependent on these structures in order to survive the predicted harsher climate conditions.

Further emphasizing the important role of shelter habitats during dry spells, some species that occur in open environments during the humid periods, are confined to forested habitats when conditions are more arid. These species can expand their range to open habitats after the heavy rainfall starts and micro-habitat conditions, like soil humidity, become high enough for them to colonize less protected habitats (e.g. Brose, 2003; Holland et al., 2007; Marasas et al., 2010; Litavský et al., 2021). As such we predicted that, during the wet season, grasslands would have a higher average body size then during the dry season as species that were previously restricted to forest habitats during the latter would expand to open habitats with the rise in humidity. Our results partially corroborated this hypothesis, as we observed an increased community body size in grasslands following heavy rainfall, partially caused by the presence of certain larger species, such as *Anthia alternata*, which were previously limited to forest habitats. Alternatively, some beetle species found in grasslands during the heavy rains were absent in forest habitats during the dry season, likely remaining in diapause as eggs, larvae, or pupae until the beginning of the wet season to survive low moisture conditions (Lövei & Sunderland, 1996; Holland et al., 2007; Kotze et al., 2011; Kolesnikov & Malueva, 2015; Ariza et al., 2021; Fülöp et al., 2021).

These findings highlight the importance of habitat shelter to carabid beetle survival during dry spells, and as such these refuges have the potential to help mitigate the impacts of drought exacerbated by climate change on carabid communities. In response to climate and habitat changes, larger and wingless species may be more threatened, leading to range contractions and possibly extinctions (Staunton, 2013; Homburg et al., 2014; Kirichenko-Babko et al., 2020; Ariza et al., 2021). On the other hand, generalist species that are smaller in size and have a greater capacity for dispersal will benefit from these changes, and likely expand their range (Ariza et al., 2021; Zajicek et al., 2021). The preservation of habitats with dense vegetation cover needs to be accounted for the protection of carabid beetle diversity in the GNP. If these forested habitats were to decrease in range, beetles would not only be exposed to more arid conditions, but also to increased competition and predation in the remaining wooded shelter patches due to higher densities, which would further stress their population (Shibuya et al., 2011; Bouchard & Hébert, 2016). Given the expected long-term decline of Gorongosa forested habitats, namely the miombo due to human impacts like fires and agriculture, as well as the anticipated dryer climate, land management regarding the conservation of forested areas is essential (Massad & Castigo, 2016; Herrero et al., 2020). Due to their ecological roles, disruptions in carabid beetle communities can lead to deep ecosystem imbalances in the GNP, highlighting the importance of conserving and restoring refuge habitats to support beetle diversity and ecosystem resilience.

5. Conclusion

The GNP registered a diverse community of almost 100 carabid beetle species across main habitat types, the majority of which were first records for the park. Our results highlight the importance of seasonal climatic conditions and habitat characteristics in shaping the richness and composition of carabid communities. Almost all habitats were shown to have higher species richness in the wet season, with hygrophilous species being more frequent due to more favorable conditions, such as increased humidity. Additionally, the higher precipitation of the wet season induces the flooding of Lake Urema which also significantly impacts carabid activity. While smaller species that are better adapted to survive in flooded areas are common near Lake Urema, bigger-sized species become increasingly more frequent the further away from the floodplains. Moreover, the distribution of woodlands also shapes carabid communities, as during the dry season, areas with dense vegetation cover support higher species richness and functional diversity. These forested habitats are more capable of retaining moisture and as such are necessary for the survival of hygrophilous species during dry spells.

In this study we also conducted the first survey of carabid beetle communities in the GNP, spanning the four main habitats, unveiling crucial information for population studies in a poorly studied region. By divulging data about the composition and diversity of carabid beetle communities, we provide baseline information for future studies that assess the effects of climate change and other impacts on population trends. As these beetles play a key role in tropical food webs, protecting them is vital for maintaining ecological balance and the overall health of the GNP’s ecosystems, also endangered by the climatic instability anticipated for Mozambique. Our results highlighted how habitat shelters enabled carabid species, especially larger wingless beetles, to survive the harsh conditions of the dry season. As a result, land management that focuses on forested patches in the park is imperative to assure the future survival of its carabid communities. Such preservation is needed given the expected decline of GNP’s habitats, due to both human factors, like deforestation for agricultural practices, and prolonged droughts, anticipated to particularly impact miombo forests. Several common tree species of the park have limited resistance to water stress and will greatly suffer under the more severe climate change scenarios. To address this issue, nurseries for drought-sensitive native trees should be established within the park to replant weakened forested areas in the future. Possible future conservation programs for carabids need to consider the crucial role of closed habitat patches as critical safeguards against the potential disastrous consequences of changing climate.

6. References

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7. Appendix

Table S1 - Traits of all carabid species recorded: wing typology (Yes - macropterous, or No - apterous/brachypterous); body size (in cm).

Species	**Wings fully developed**	**Medium length (cm)**
Abacetus cursor	Yes	5
Abacetus denticollis	Yes	9.25
Abacetus discolor	Yes	7
Abacetus nigrinus	Yes	10
Abacetus percoides	Yes	10.75
Abacetus perturbator	Yes	5.75
Abacetus pseudomashunus	Yes	14
Anaulacus madagascariensis	Yes	6.5
Anthia alternata	No	40.5

Anthia burchelli petersi	No	46.5
Anthia circumscripta circumscripta	No	44.5
Anthia fornasinii fornasinii	No	40.5
Anthia omoplata	No	38
Apotomus annulaticornis	Yes	3.5
Apristus latipennis latipennis	Yes	3.5
Brachinus distans	Yes	10
Brachinus laetus	Yes	8
Brachinus leprieuri	Yes	4
Calosoma planicolle	Yes	35
Chlaenius conformis	Yes	13
Chlaenius cosciniophorus	Yes	11.75
Chlaenius cylindricollis	Yes	14
Chlaenius discopictus nuncius	Yes	14.75
Chlaenius dusaultii diagraphus	Yes	16.5
Chlaenius fulvicollis	Yes	11.25
Chlaenius kirki kirki	Yes	15
Chlaenius lugens	Yes	18.75
Chlaenius notabilis	Yes	12
Chlaenius paenulatus	Yes	8
Chlaenius peringueyi	Yes	15.5
Chlaenius zanzibaricus giganteus	Yes	29
Cimbionotum schueppelii	Yes	4
Crepidogaster langenhani	No	10.75
Crepidogaster longelineata	No	4.65
Crepidogaster protuberata	No	9.75
Cymindoidea regularis	No	8.5
Cypholoba alveolata ranzanii	No	28
Cypholoba graphipteroides bilunata	No	25
Cypholoba rutata	No	22.5
Cypholoba semisuturata vassei	No	22.5
Distichus bisquadripunctatus	Yes	11.5
Distichus picicornis	Yes	9.5
Dromica dolosa latepolita	No	9.9
Eccoptoptera mutilloides mutilloides	No	15.5
Elaphropus aethiopicus	Yes	2
Elaphropus haemorrhoidalis	Yes	2.5
Elliptica compressicornis compressicornis	Yes	17
Galerita angustipennis	No	22.5
Graphipterus horni staudingeri	No	12
Graphipterus lineelus	No	11.5
Graphipterus tristis	No	12
Manticora latipennis	No	52.5
Megacephala asperata	No	24.5
Melaenus elegans	Yes	9
Melanchiton lucidulus	Yes	10.5
Mesolestes sp.	Yes	2
Mesolestes machadoi	Yes	2.65

Mesolestes nigrocephalus	Yes	2.65
Metagonum insolitum	No	10.75
Microlestes flavipes micromys	Yes	2.65
Microlestes zambezianus	Yes	2.75
Omostropus mandibularis	Yes	8.5
Parophonus tomentosus	Yes	15
Paussus cultratus	Yes	5
Paussus pseudoklugi	Yes	5
Pentaplatarthrus gestroi	Yes	8
Perigona schmitzi	Yes	2.85
Pheropsophus dregei	Yes	17
Pheropsophus insignis insignis	No	15.5
Pheropsophus mashunus	No	14.5
Pheropsophus stenopterus	Yes	19
Planetes quadricollis	Yes	11
Platytarus tesselatus	No	6.5
Prothymidia angusticollis	No	9
Scarites polyphemus	No	26
Scarites tenebricosus molossus	No	30
Siagona caffra	Yes	22
Siagona levasseuri	Yes	15
Siagona partita	Yes	9
Singilis africaorientalis kenyacus	Yes	4
Siopelus lucens	Yes	9
Styphlomerus neavei neavei	Yes	10.5
Systolocranius goryi	Yes	20
Tachys iridipennis	Yes	2.7
Tefflus carinatus carinatus	No	35
Tetragonoderus immaculatus	Yes	5
Triaenogenius carinulatus carinulatus	No	20

Table S2 - Habitat features, the resulting Shelter Index (SI) and distance to lake Urema of sampling sites (Mean ± SD) per habitat where tiger- and ground-beetle' communities were collected: Different capital letters indicate significant differences between habitats (General Linear Hypotheses tests (p< 0.01)) after Analysis of Deviance comparing mean values of distance to lake Urema and Shelter Index.

	Grassland	**Transitional Forest**	**Mixed Forest**	**Miombo Forest**
Distance to Lake Urema[a]	8.2 (3.3)A	5.6 (2.7)A	13.9 (4.3)B	28.7 (2.8)C
Canopy Area[b]	0 (0)	49.9 (23.6)	58 (23.2)	31.1 (20.1)
Bare Soil[c]	1 (0.9)	1 (1.1)	0.1 (0.3)	0.8 (1.1)
Herbaceous Cover[c]	2.7 (0.6)	1.6 (1)	1.92 (0.9)	2 (0.9)
Herbaceous Height[c]	1.1 (0.4)	1 (0.7)	1.2 (0.7)	1.6 (1)
Shrub Cover[c]	0.4 (0.5)	1.1 (1)	1.2 (0.6)	0.7 (0.5)
Litter[c]	1.2 (0.5)	2.6 (0.7)	2.7 (0.6)	2.2 (0.9)

Shelter Index[d]	5.5 (1.9)A	13.6 (4.6)BC	16.3 (3.5)B	11.3 (4.4)C

a - Variable expressed in km; b - Variable expressed in %; c - Variable ranges from 0 to 3; d - Variable ranges from 0 to 24.

Table S3 - Summary of GLM analysis with the fixed effects of wing development (species with not fully developed wings – apterous/brachypterous - used as reference) on Caraboidea body size (response variable).

Response	**Fixed effects**	**Estimate**	**Std. Error**	**t value**	**P value**	**$F_{(1,188)}$**	**P value**
Body size	Macropterous spp.	-8.43	0.97	-8.67	< 0.001	105.9	< 0.001