

# Commercial banana and macadamia plantations in a savanna matrix support high levels of arthropod diversity

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Expansion and intensification of agroecosystems is one of the major causes of habitat loss in the savanna biome in South Africa. As such, this study sought to determine the influence of commercial subtropical fruit plantations (banana and macadamia) on species richness, abundance, and composition of surface-active arthropods compared to the savanna biome. Given that pesticides and herbicides are applied from spring to early autumn in banana and macadamia plantations, we sampled in winter to reduce the potential impact of pesticides and herbicides. Surface-active arthropods were sampled using pitfall traps. Habitat type did not affect species richness and abundance of ants and spiders, as well as species richness of beetles. However, significantly greater abundance of beetles was recorded in the macadamia plantation compared to the banana and savanna. This could have been due to greater abundance of herbivorous beetles and other insects, which would have increased the diversity of predatory beetles. Furthermore, unlike the banana plantation, the macadamia plantation was characterised by a deep leaf litter layer and the presence of weeds and grasses, which probably increased abundance of beetles. Species composition indicated that the studied arthropod taxa associate with specific habitats, as demonstrated by the three habitats supporting different species composition. Despite savanna habitat not supporting high species richness or abundance of surface-active arthropods, we recorded the highest number of unique species of ants and spiders in the savanna rather than in the plantations. These results highlight the importance of natural landscapes in conservation of surface-active arthropods.

## INTRODUCTION

The vegetation in the savanna biome is characterised by high diversity of plant species composed of grasses, shrubs, and scattered trees (Rutherford et al. 2006). The mixture of herbaceous and woody plants is supported by the summer rainfall and gives the savanna biome a particularly complex structure (Rutherford et al. 2006), providing diverse microhabitats for many arthropod species (Botha et al. 2016). Different arthropod taxa prefer different environmental and habitat conditions (Yekwayo et al. 2017); therefore, high diversity of arthropods is likely to be associated with greater habitat heterogeneity. The availability of microhabitats, such as debris and logs, resulting from high diversity of plants in the savanna vegetation, increases food resources and nesting sites for surface-active arthropods (Loyola et al. 2006). Several studies have documented different surface-active arthropods, including, millipedes, scorpions, centipedes (Druce et al. 2007), termites (Doube 2018), ants, spiders, and millipedes (Mwabvu & Yekwayo 2020), and dung beetles (La Scaleia et al. 2018) in the savanna. Surface-active arthropods provide different ecosystem services that are crucial for the functioning of the savanna ecosystems (Marchant 2010) while also benefitting humans (Samways et al. 2012).

Despite the vital role of the savanna in biodiversity conservation, about 50% of savanna landscapes are now converted into agroecosystems to meet the demand of the growing human population (Lichtenberg et al. 2017; Riggio et al. 2013). Although the rate of conversion of the savanna biome is high, the low levels of endemism and the high number of protected areas within this biome makes the savanna biome a low priority for biodiversity conservation (Driver et al. 2005). However, the endemism level and conservation status of the savanna biome is based on assessments of plants, birds, and mammals (Driver et al. 2005), with relatively fewer studies focusing on arthropod groups, such as spiders (Cardoso et al. 2019; Foord et al. 2020).

Surface-active arthropods are sensitive to changes that occur in their habitats (Lichtenberg et al. 2017). Changes in habitats that are associated with the reduction in plant diversity decrease food resources and nesting sites for arthropods (Rhoades et al. 2018). Marasas et al. (2010) recorded low species richness and abundance of carabid beetles in wheat plots compared to semi-natural plots, which are likely to have more resources for surface-active arthropods. However, contrasting findings were reported by Magagula & Samways (2001), who found greater density and species richness of ladybirds in citrus orchards than in natural habitats, even though there were species unique to the natural habitats. Ladybirds dominated citrus orchards because of high abundance of prey and the high dispersal ability of some species, which allowed movement across habitats (Magagula & Samways 2001). However, many species of surface-active arthropods are characterised by low dispersal ability, as such the species may not be able to move to alternative

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## SUPPLEMENTARY MATERIAL

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habitats (Yekwayo et al. 2017). Thus, surface-active arthropods are affected by anthropogenic activities that result in habitat fragmentation (Moir et al. 2005).

In addition to habitat loss, intensive management practices, which are intended to increase yields in agroecosystems, can affect the diversity of surface-active arthropods negatively (Isbell et al. 2017). The application of pesticides may kill non-targeted beneficial surface-active arthropods (Olfert et al. 2002). For example, Hafsi et al. (2016) observed greater abundance of the Coccinellidae in peach plots that were not treated with pesticides than those that were treated. In addition, the use of herbicides along the plantation edges and between rows of crop plants reduces microhabitats for some surface-active arthropods (Sarabi 2019). Furthermore, high abundance of predatory arthropods was recorded in experimental plots that had weeds between apple trees compared to control plots that had no weeds (Wyss 1992). Variation in leaf litter depth also influences temperature, moisture, and prey abundance (Halaj et al. 2008). Therefore, clearing of leaf litter in agroecosystems can also affect surface-active arthropods negatively. For instance, in a wet tropical forest there was greater diversity of surface-active arthropods in sites that had a thick layer of leaf litter compared with sites that were bare (Sayer et al. 2006). However, in KwaZulu-Natal, Eckert et al. (2019) found that arthropod assemblages in grasslands and pine plantations were not influenced by the percentage of leaf litter cover. Thus, assessing communities of surface-active arthropods in agroecosystems is important for agricultural sustainability and mitigation of the negative effects of agricultural practices on ecosystem services.

Ecosystem services provided by surface-active arthropods can improve the production of crops in agroecosystems. These ecosystem services include, pollination (Bommarco et al. 2012), cycling of nutrients (Doube 2018), decomposition of organic matter (Ahmad & Ahmad 2009), control of pests (Poeydebat et al. 2017) and predation (Marie et al. 2018). For example, ants and certain beetles were recorded as pollinators in mango orchards in South Africa (Simba et al. 2018). Furthermore, dung beetles associate with specific mammalian dung, and protected areas are known to support greater diversity of mammals than forest plantations (Pryke et al. 2022). As such, the occurrence of high species richness of dung beetles in habitats with greater plant diversity, such as protected areas and wider corridors (van Schalkwyk et al. 2017) is not surprising considering the contribution of dung beetles in plant growth (Sitters et al. 2014). When these dung beetles remove and bury dung, they increase carbon and nitrogen storage in soils (Sitters et al. 2014). In another study, Pryke et al. (2013) recorded greater diversity of dung beetles in grassland and pine plantations compared to the natural forest. The activity of dung beetles and termites in the soil influences plant growth indirectly by improving the texture of the soil, aeration in the soil and infiltration of water (Doube 2018). Furthermore, even though activities of termites lead to the formation of mounds, there are plant species that have been reported to grow on those mounds (Kelly & Samways 2011), which may increase vegetation heterogeneity. Other important surface-active arthropods include natural enemies of pests, such as weaver ants that control the infestation of bagworm in oil palm orchards (Pierre & Idris 2013) and ground beetles that control the olive fruit fly in olive orchards (Albertini et al. 2017). Unfortunately, agroecosystems that are managed intensively can reduce the diversity of arthropods unlike natural landscapes (Luke et al. 2014).

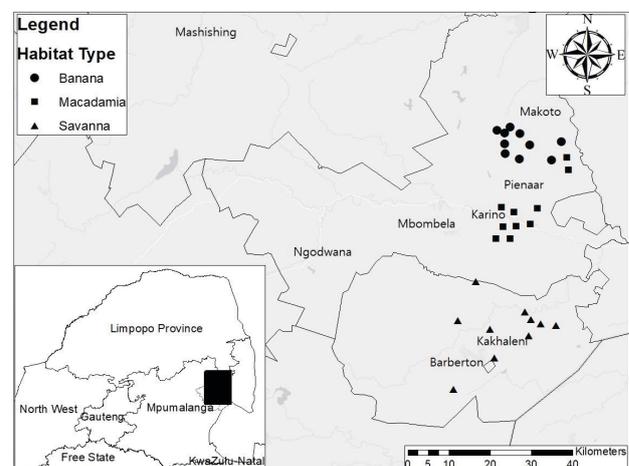
Amongst other agroecosystems, subtropical fruit plantations have been expanding rapidly (Granatstein et al. 2016; Pio et al. 2018) because of their high contribution to the economies of countries (Campbell 2018). Banana and macadamia are among the most widely produced subtropical fruits that contribute

significantly to the economy of South Africa (Diczbalis et al. 2014). Although arthropods have been studied in subtropical fruit plantations, the focus has been on arthropods as pollinators (Bommarco et al. 2012), pests and their natural enemies (Grout et al. 2001; Pierre & Idris 2013). In addition, checklists of spiders have been produced in South African agroecosystems (Dippenaar-Schoeman et al. 2001, 2005, 2013). However, ecological data on ants, beetles and spiders in banana and macadamia, particularly in South Africa, remain limited. Therefore, this study aimed to determine if species richness, abundance and composition of ants, beetles and spiders will differ between the two fruit plantations that are under specific agricultural practices. Furthermore, we compared species richness, abundance, and composition of the three taxa between the fruit plantations and the savanna vegetation. Several studies have reported increased diversity of surface-active arthropods in natural vegetation because of greater habitat heterogeneity, which is driven by the high diversity of plants (Mauda et al. 2018; Rhoades et al. 2018; Marasas et al. 2010). Therefore, we expected high species richness and abundance of ants, beetles and spiders in the savanna vegetation compared with the two fruit plantations. Furthermore, we expected the species composition of the three taxa to vary amongst the three habitat types.

## MATERIAL and METHODS

### Study site

Surface-active arthropods were sampled from three habitat types, two in the Agricultural Research Council farms in Mbombela (macadamia) and Hazyview (banana and macadamia), and the savanna in Barberton Nature Reserve in the Mpumalanga province, South Africa (Figure 1). The two farms in Hazyview and in Mbombela are about 66 km apart. Barberton Nature Reserve is about 54 km from the farm in Mbombela and about 88 km from the farm in Hazyview. The macadamia and banana plots in Hazyview are between 15 and 20 years in age, while the macadamia trees in Mbombela are about 12 years old. Leaf litter depth was measured using a ruler. In the banana plantation leaf litter depth was 1.7–13.5 cm and in the macadamia plantation it was 4.5–14.7 cm, while in the savanna leaf litter depth was not measured due to its sparse distribution. However, leaf litter in macadamia sites in Hazyview was swept from under the tree canopies and piled up between the rows. Furthermore, the macadamia sites in Mbombela had grasses and up to six herbaceous plant species between rows of the trees, unlike banana and macadamia plantations in Hazyview which had no herbaceous plants nor grasses. The sites in Barberton Nature Reserve (BNR) were characterised by tall and short grass, scattered



**Figure 1.** Study area showing the sites in the three habitat types in Mpumalanga province

trees, and shrubs. In addition, BNR is rocky with some areas having steep slopes and dominated by shrubs of *Vachellia* spp.

The watering practices as well as control of pests and weeds in the two plantations differ between the two farms. Watering of the macadamia and banana plants in Hazyview occurs fortnightly in the dry winter compared with watering of the macadamia trees in Mbombela which occurs at higher frequency (weekly) between August and February. Both plantations in the two farms applied herbicides (glyphosate and paraquat) between September and March. However, in addition to the herbicides, two pyrethroid pesticides (beta-cyfluthrin and alpha cypermethrin) were applied in Mbombela.

### Study design

Each habitat type had ten sites that were 10 m × 10 m in size, making a total of 30 sites in the study (Figure 1). The sites in macadamia plantation and savanna vegetation were at least 300 m away from each other to prevent false replication (see Clark & Samways 1997). The banana plants are planted in smaller blocks that are separated by dirt roads that are about 8 m wide. Each block (minimum size about 8 000 m<sup>2</sup>) had a single site; thus, the roads were physical barriers between the sites; as Samways et al. (2010) indicated, sites or samples that are separated by a physical or geographical barrier can be considered independent of each other. However, we acknowledge the limitation (that we were unable to avoid) of having all banana sites in a single farm, as this may imply false replication (see Samways et al. 2010). To eliminate the edge effect, we adopted Gallé et al. (2020) methods and placed sites in macadamia plantation 10 m away from the edge, while sites in the banana were at the centre of the block. In all the vegetation types, each site was divided into four line transects, adjacent transects were about 2 m apart. In each line transect there were six pitfall traps, adjacent pitfall traps were about 2 m apart.

### Sampling method

The spraying of pesticides and herbicides occurred between September and March in the two farms. Our target was to sample outside of the spraying season in order to ensure that the effects of pesticides on the activity of surface-active arthropods was reduced. As a result, sampling took place in July 2020. The pitfall trapping method was used because it is the most effective for sampling surface-active arthropods (Woodcock 2005; Samways et al. 2010). We sampled in three consecutive sampling events to ensure that the samples were representative in the study areas. Furthermore, sampling in three events increased the probability of capturing different species of ants, beetles and spiders, which are known to be active at different times depending on the behaviour of the species and environmental conditions (Samways et al. 2010). The pitfall traps were placed in the same location for all three sampling events. Each pitfall trap was half-filled with 50% ethylene glycol solution and inserted in the ground leaving the open end at the same level as the soil surface. Pitfall traps were collected after seven days because it is the appropriate minimum period for sampling arthropods (see Borgelt & New 2006). Traps were emptied into collection bottles, which had 100% ethyl alcohol. In the laboratory, specimens were extracted from the debris and stored in 70% ethyl alcohol. Species were identified to family and genus levels where possible, and assigned to morpho-species. Arthropods were identified using different guides (Dippenaar-Schoeman & Jocqué 1997; White 1998; Bouchard 2014; Dippenaar-Schoeman 2014; Fisher & Bolton 2016; Picker et al. 2019). Voucher specimens were housed temporarily in the Soil Invertebrates Laboratory at the University of Mpumalanga, and will be deposited for long-term storage at the KwaZulu-Natal Museum, Pietermaritzburg, South Africa. Leaf litter depth, which was measured randomly at four points in each site using a ruler was averaged.

### Statistical analyses

The samples from each sampling event, at each site were pooled for analyses. Data were analysed separately for each of the three taxa (ants, beetles and spiders). Due to the high number of singletons and doubletons in our datasets, we used two non-parametric estimators (Chao2 and Jackknife2) to determine the effectiveness of our sampling (Samways et al. 2010). Species richness was estimated in PRIMER 7.

Species richness and abundance datasets of each taxon were tested for normality using the Shapiro-Wilk test in R (R Core Team 2020). Given the close proximity of our sites, especially in the banana plantation, we accounted for spatial autocorrelation by using the generalised least squares (GLS) and generalised linear mixed models (GLMM) with the penalised quasilielihood estimation (Dorman et al. 2007). Species richness of ants and spiders, as well as abundance of spiders were analysed using GLS because these data were normally distributed. However, GLMMs were used for species richness of beetles and abundance of ants as well as beetles because these data were not normally distributed. The MASS package (Ripley et al. 2013) and Poisson distribution (Bolker et al. 2009) were used in GLMMs. In the models, GLS and GLMM, the longitude and latitude were included as a dummy variable with an exponential correlation (Dormann et al. 2007), which was the random factor. The type of habitats, banana, macadamia and savanna, was included in models as an explanatory variable. Boxplots were used to display significant differences in species richness and abundance among the three habitat types. Spearman's rank correlations in R (Crawley 2005) were used to determine significant correlation between response variables, species richness and abundance, of each taxon and leaf litter depth.

Variation in the composition of ants, beetles and spiders among the three habitat types were assessed with a multivariate generalised linear model using the “*manyGLM*” function in the *mvabund* package (Wang et al. 2012) in R. Arthropod abundance data were modelled as the response variable with a negative binomial distribution used as the best fit. Habitat type was modelled as an explanatory variable. The species composition of each taxon was visualised using the canonical analysis of principal coordinates in PRIMER 7 (Anderson & Willis 2003). In addition, similarities and dissimilarities in species unique to each habitat and those shared between and/or among habitats were visualised using Venn diagrams. Furthermore, the Jaccard index of similarity was calculated for each pair of habitat types. The formula used to calculate the Jaccard index of similarity is  $C_j = j / (a + b - j)$ , where  $C_j$  is the Jaccard index of similarity,  $j$  is the number of species shared between two habitats,  $a$  is the number of species unique to the first habitat, and  $b$  refers to the number of species unique to the second habitat.

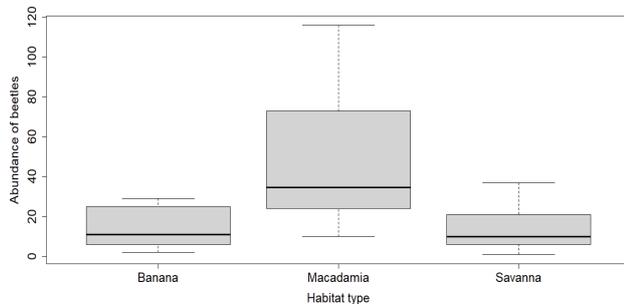
### RESULTS

Ants had the highest number of individuals (4 368), followed by spiders (1 031) and beetles (733). The species accumulation curves did not reach an asymptote for ants (observed = 55, Chao2 = 63.45 ± 6.13, Jackknife2 = 70.69), beetles (observed = 73, Chao2 = 198 ± 54.19, Jackknife2 = 158.99) and spiders (observed = 95, Chao2 = 263.2 ± 70.35, Jackknife2 = 196.19). Furthermore, beetles had the highest number of singletons and doubletons contributing 73% of the total number of morpho-species, followed by spiders at 63%, while ants had the lowest percentage (27%).

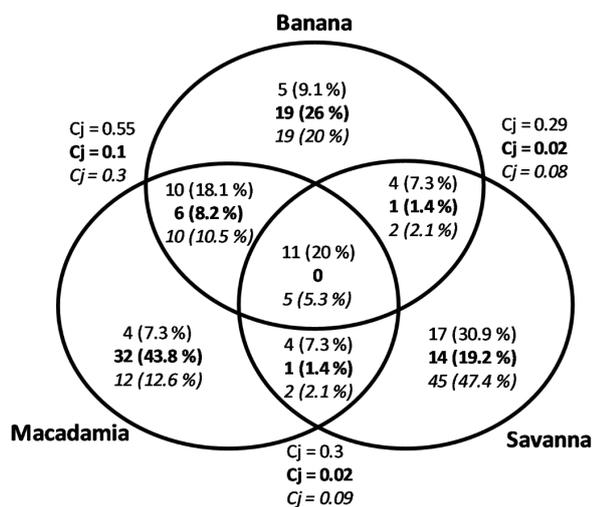
The three taxa showed varying responses to the type of habitat. Significantly greater abundance of beetles was recorded in the macadamia compared with the savanna and the banana (Table 1, Figure 2). Although species richness of beetles was nearly significant ( $p = 0.046$ ), the macadamia had the highest percentage of unique morpho-species (43.8%) compared with the

**Table 1.** Summary of the generalised least squares, generalised linear mixed models (for species richness and abundance), as well as multivariate generalised linear models (for species composition) showing the response of ants, beetles and spiders to habitat type

	Ants			Beetles			Spiders		
	SE	<i>t</i>	<i>p</i>	SE	<i>t</i>	<i>p</i>	SE	<i>t</i>	<i>p</i>
Species richness	3.08	0.04	0.97	0.42	2.98	0.046	3.19	-0.73	0.47
Abundance	0.23	0.61	0.56	0.36	3.21	0.003	17.85	-1.48	0.15
	dev	df	<i>p</i>	dev	df	<i>p</i>	dev	df	<i>p</i>
Species composition	402.2	27	< 0.001	343	27	< 0.001	575.2	27	< 0.001



**Figure 2.** Effect of habitat type on abundance of beetles

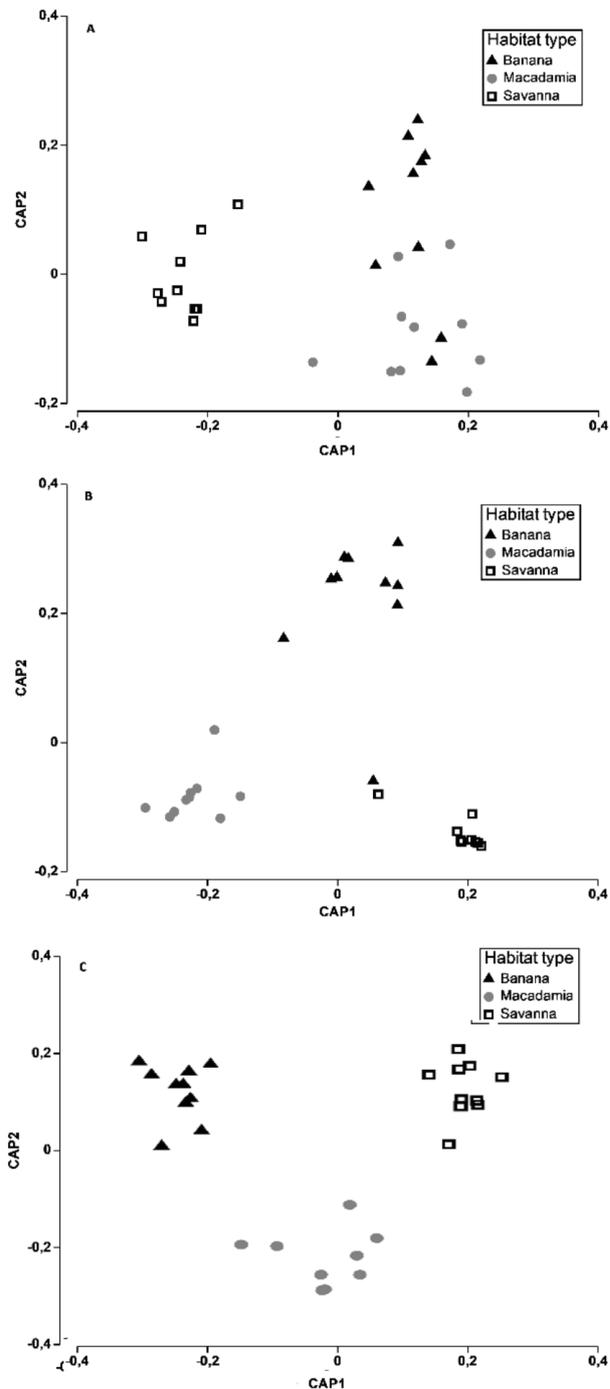


**Figure 3.** Number (percentage) of species unique to each habitat type, those shared between habitat types and those that occurred in all habitat types, as well as the Jaccard index of similarity (*C<sub>j</sub>*) for each taxon. Non-italic and not bold = ants; bold = beetles; and italics = spiders

banana and the savanna (Figure 3). Even though no significant differences were recorded in species richness and abundance of ants and spiders among the three habitats (Table 1), the savanna had the highest percentage of unique species for both taxa (Figure 3).

Spearman's rank correlation showed that the effect of leaf litter depth on species richness and abundance is taxon-dependent. Species richness ( $r = 0.58, p = 0.0007$ ) and abundance ( $r = 0.43, p = 0.02$ ) of beetles positively correlated with leaf litter depth. However, a negative correlation between species richness of ants and leaf litter depth ( $r = -0.41, p = 0.02$ ) was observed. On the other hand, leaf litter depth was not correlated with the abundance of ants (correlation =  $-0.03, p = 0.87$ ) and spiders (correlation =  $-0.18, p = 0.33$ ) nor species richness of spiders (correlation =  $-0.19, p = 0.32$ ).

The multivariate generalised linear models showed that species composition of ants, beetles and spiders was significantly different among the three habitat types (Table 1; Figures 3, 4). However, the Jaccard index of similarity ( $C_j = 0.55$ ) and canonical



**Figure 4.** Canonical analysis of principal coordinates (CAP) of (A) ants, (B) beetles and (C) spiders across the three habitats

analysis of principal coordinates displayed an overlap in assemblages of ants between the banana and macadamia plantations (Figures 3, 4a).

## DISCUSSION

Contrary to our expectations, the savanna vegetation did not support significantly greater species richness nor abundance of arthropods compared to the two plantations. Instead, species richness and abundance of ants and spiders, as well as species richness of beetles did not differ among the three habitat types. Although there are specialist species of ants and spiders, there are many generalist predators also (Abera-Kalibata et al. 2007; Dippenaar-Schoeman et al. 2001, 2005; Herwina et al. 2013; Pekár & Toft 2015). Species richness and abundance of arthropods may have increased in different habitat types because of the predatory nature of spiders and some species of ants and beetles, which are affected mostly by prey availability. Subtropical fruit plantations support high abundance of herbivorous insects (Herwina et al. 2013; Michalko et al. 2019), which may increase the abundance and species richness of predatory spiders (Herwina et al. 2013; Michalko et al. 2019; Tsai & Pekár 2019). Similarly, Bolu & Özgen (2018) reported a positive correlation between the abundance of aphids and *Camponotus* species that prey on aphids. Furthermore, ants are species rich and abundant in agricultural, natural, and urban landscapes, where they nest in microhabitats, such as rotten trunks, twigs, logs, leaf litter, plant roots and underneath rocks (Fisher & Bolton 2016; Herrera et al. 2020). Similarly, some salticids and thomisids have been recorded underneath loose bark and beneath leaves (Dippenaar-Schoeman et al. 2001). Furthermore, diverse species of spiders thrive in natural habitats (Foord et al. 2011), as well as, in subtropical fruit plantations (Dippenaar-Schoeman et al. 2001, 2005).

Although there were no significant differences in species richness of ants or spiders among the three habitats that we studied, the savanna had the highest percentage of unique species for both taxa, unlike beetles which were most rich in the macadamia plantations. This high number of unique species in the savanna compared with the other habitat types could have been due to greater vegetation diversity and density in the savanna compared to the two plantations. Downie et al. (1995) found a positive correlation between the distribution of species of spiders and the vegetation density. The high percentage of ant and spider species that were restricted to the savanna emphasises the importance of natural landscapes in the conservation of arthropods. Previous studies have also reported a decrease in species richness of ants in cultivated monocultures compared to heterogeneous natural vegetation (Perfecto 1990; Roth et al. 1994; Perfecto & Snelling 1995).

Leaf litter depth is among the variables that influence species richness and abundance of some arthropods. For instance, Moses et al. (2021) reported that species richness of ants in an undisturbed forest in Papua New Guinea increased with leaf litter depth, while abundance of ants decreased with leaf litter depth. However, another study that compared arthropod abundance and diversity in plots with different levels and quality of leaf litter found that arthropod diversity did not differ between heterogeneous and homogenous leaf litter (Donoso et al. 2010). In our study, leaf litter depth did not influence species richness of ants and spiders, probably because of the generalist nature of these taxa. However, we recorded that species richness and abundance of beetles correlated positively with leaf litter depth. Out of the three habitats, the macadamia plantation was characterised by a deeper layer of leaf litter, which would have provided a suitable habitat for beetle species that require leaf litter. Furthermore, a deep layer of leaf litter influences beetles, such as, ground beetles because of the reduced ground temperature and increased availability of prey within the leaf litter (Magura et al. 2005). Greater leaf litter depth also increases the abundance of dung beetles (da Silva & Hernández 2016).

As such, high abundance and the number of unique species of beetles that we recorded in the macadamia may have been due to greater leaf litter in most of our study sites.

The greater abundance and number of species in the macadamia were attributed to herbivorous beetles in the Curculionidae and Chrysomelidae, as well as predatory beetles (e.g. Coccinellidae) (Table S1). In addition, within the Curculionidae there is a seed weevil (*Kuschelorrhynchus macadamiae*) that has been reported as a threat to macadamia production (Khun et al. 2020). The presence of coccinellids is highly dependent on the presence of their prey (Magagula & Samways 2001) that would be expected to occur in both plantations. Furthermore, most species of beetles in fruit orchards are pests and their natural enemies (Sutton et al. 2014), as such, it is not surprising that we recorded significantly greater abundance and greater percentage of species that were unique to the macadamia.

Despite that habitat type did not affect abundance and species richness of ants and spiders, as well as species richness of beetles, species composition of all the three taxa were affected significantly. Variation in species composition amongst the three habitat types indicates some level of specialisation even among predatory arthropods. For example, carabids, which are natural enemies of pests in agricultural crops (Matta et al. 2017; Wyckhuys & O'Neil 2006), were represented by three morpho-species, one unique to the savanna, the other to the macadamia, while the third one occurred in both the banana and macadamia plantations (Table S1). Our results supported studies, which reported variation in species composition of ants in banana, macadamia, citrus and palmito (Matlock & de la Cruz 2003), as well as between natural vegetation and agricultural landscapes (de Castro Solar et al. 2016).

The three habitat types in our study had different characteristics. The savanna vegetation had tall grasses, herbaceous plants, scattered shrubs, and trees; unlike the macadamia plantations which, besides the about 5 m tall macadamia trees, had grasses and herbaceous plants and a layer of leaf litter (in some sites). The banana plantations had about 4 m tall banana plants growing in wet soil due to constant irrigation, a layer of leaf litter and scattered patches of bare soil. The differences in microhabitats within the three habitat types could have caused each habitat type to support different species of arthropods. Although both the banana and macadamia had leaf litter, the type and density were different, and may have caused the significant differences in assemblages between these plantations. However, it is important to note that the Jaccard index of similarity and the canonical analysis of principal coordinates revealed overlap of ant assemblages between the two plantations, thus supporting Mauda et al. (2018) who reported that cultivated landscapes often share dominant species of ants. The overlap of ant assemblages between the macadamia and banana plantations could be due to generalist species (such as, those in *Pheidole* and *Tetramorium*) that are adapted to disturbed areas (García-Martínez et al. 2015). Generalist predators adapt well because when disturbance decreases the abundance of the preferred prey they can feed on any other prey that is available (Kwon et al. 2013; Mollot et al. 2012). Furthermore, a shift in prey preference is possible for predators, such as ants, because many species nest and feed on a variety of items. However, Eckert et al. (2022) indicated that the effect of environmental variables on ants vary depending on the vegetation type. For instance, in a natural forest, leaf litter cover and soil pH were the important variables affecting ant assemblages, while in a grassland, variables that mattered were soil compaction, pH, carbon, nitrogen and sulphur (Eckert et al. 2022).

The dominance of lycosids in the fruit plantations may be due to them being early colonisers of disturbed areas (Samu & Szinetár 2002). Unlike many surface-active arthropods, lycosids

have greater dispersal ability, which facilitates invasion of, and thriving in disturbed habitats (Saqib et al. 2020). Species that were unique and abundant in the banana included a morpho-species in the Anthicidae, two in *Copa* and one in the Oonopidae. Most species of the Anthicidae are detritivores that are associated with agroecosystems that have high plant residues on the soil surface (Araújo et al. 2018). Furthermore, the Anthicidae is associated with high soil moisture (Telnov & Ghahari 2018), which was readily available in the banana compared with the other habitats. Similarly, species of *Copa* (Haddad 2013) and the Oonopidae (Ubick et al. 2005) are associated with leaf litter. Furthermore, oonopids feed on mites and springtails (Tiwari et al. 2021), which were common in the banana plantation. Therefore, irrigation and the layers of leaf litter in the banana plantation may have increased and retained soil and leaf litter moisture, thereby providing suitable habitats for mites and springtails and increased microbes on which they fed. The Nitidulidae are known to feed on the sap in fruits (Emekci & Moore 2015) and macadamia trees produce a lot of sap (Olesen et al. 2008), so the four morpho-species of nitidulids may have been feeding on the sap in the macadamia. Two nitidulids were in the banana and none were recorded in the savanna (Table S1).

Morpho-species of ants that were restricted to the savanna included species in genera that are associated with nesting in the ground and/or under rocks, e.g., *Bothroponera* sp. (Joma & Mackay 2017), *Lepisiota* sp. (Sharaf et al. 2020); *Ocymyrmex* sp. and *Polyrhachis* sp. (Andersen et al. 2000). These genera of ants build colonies in the ground and under rocks, this may explain their association with the savanna habitat where there is less disturbance. Furthermore, the restriction of *Odontomachus* sp. to the savanna habitat could be because the species feed on a variety of invertebrates (Raimundo et al. 2009), small vertebrates (Facure & Giaretta 2009), plant and insect exudates, and nutrient-rich fleshy fruits (Passos & Oliveira 2002, 2004). Thus, the savanna vegetation is more likely to have the preferred food resources for *Odontomachus* sp. compared with the two plantations. Furthermore, the abundance of scarabids in the savanna is probably a result of the continuous input of organic matter, such as leaf litter (although scattered) and the presence of mammalian dung on which scarabids depend (Pompeo et al. 2016). Most scarabids are sensitive to anthropogenic activities (Barretto et al. 2019). Therefore, their occurrence in the savanna habitat, which is less disturbed, was not surprising. Although morpho-species in the Gnaphosidae were present in all habitat types, there were morpho-species unique to each, with the savanna having the highest number. The occurrence of gnaphosids in all habitat types could be attributed to the fact that they are ant-eating spiders (Pekár 2004), and ants were abundant in the three habitats.

Our findings indicate that the conversion of savanna landscapes into subtropical fruit plantations does not reduce species richness and abundance of some predatory arthropods (ants and spiders). However, subtropical fruit plantations alter species composition of ants, beetles and spiders, as we found differences in assemblages among the three habitat types. Our results demonstrate that maintenance of diverse microhabitats in agroecosystems enhances arthropod conservation (see Geldenhuys et al. 2021). Considering the increasing habitat modification, and the importance and global decline in biological diversity, management practices in subtropical fruit plantations are critical in conserving surface-active arthropods.

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