Seasonal variation in insect assemblages at flowers of *Balanites aegyptiaca*, an ecologically and socially important tree species in the Ferlo region of Senegal's Great Green Wall corridor

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Abstract

The Sahel is among the world's regions most affected by ecosystem degradation, caused by intensive land use and climate change. The importance of conserving biotic interactions is increasingly recognised in actions that attempt to counter and reverse this degradation, such as the Great Green Wall initiative in the northern Sahel. Interactions between flowers and flower-visiting insects play central roles in ecosystem functioning, ensuring pollination. Floral resources are also crucial for numerous other biotic interactions, as flower-visiting insects use them as fuel in their search for prey, hosts, breeding sites, and other resources. Despite their importance in ecosystem functioning, very little is known about insect-flower interactions in the northern Sahel. Using two capture methods, netting and pan traps, we studied interactions between insects and flowers of *Balanites aegyptiaca*, sampling in three sites in a single locality: a topographical depression with higher tree density, a

‘restored’ site with exclusion of livestock and an ‘unrestored’ site in intensively grazed rangeland. Each site was sampled at three different seasons to examine variation in this extremely harsh and seasonal environment. *Balanites aegyptiaca* is the region’s most abundant tree. Its open-access flowers, produced in multiple flowering events each year, are a critical resource for insects. This species also produces economically important resources for the region’s inhabitants. We found a surprisingly high diversity of insects visiting its flowers, comprising 371 morphospecies from 10 insect orders, with a predominance of Hymenoptera and Diptera. Insect abundance and diversity differed between seasons but only little between the different sites. Bees appear to be important pollinators. The bee fauna is dominated by solitary bees of the family Halictidae, which were abundant at all seasons. Diptera, particularly diverse families of small flies, were also frequent visitors and were particularly abundant and diverse in the wet season. Ants were abundant, but captures at flowers were frequent only in the dry season, when few resources other than flowers and flower-visiting insects were likely available to them. Insect abundance and observed diversity differed only little between sites, but estimated total diversity (Chao1 richness) was highest in the depression site. Insects visiting flowers of *B. aegyptiaca* included herbivores, decomposers, and parasitoids and predators of diverse arthropods, underlining the role of these floral resources in numerous facets of ecosystem functioning. The floral resources of *B. aegyptiaca* and other trees, which can flower throughout the year, are likely critical to assure the persistence of numerous insect species through the long dry season. It is crucial to integrate understanding of biotic interactions in management aimed at conservation and restoration of Sahelian ecosystems.

Keywords: *Balanites aegyptiaca*, biotic interactions, flower-visiting insects, Great Green Wall, insect-tree interactions, restoration, Sahelian ecosystems

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1. Introduction

The Sahel is among the world's regions most vulnerable to climate change. In the semi-arid savannas of the northern Sahel, the combination of climate change and land-use change, particularly intensive grazing and browsing, have led to widespread environmental degradation. Initiatives such as the United Nations Convention to Combat Desertification (UNCCD) and the pan-African "Great Green Wall" attempt to halt and reverse this degradation, with varying degrees of success (Delay et al., 2022; Turner et al., 2023). With recent calls to "accelerate" these initiatives (UNCCD, 2021; Diallo et al., 2023), it is essential to establish a more solid foundation for integrative approaches to ecosystem restoration. Work on restoration in the region has been plant-centred, with little attention to biotic interactions, which are crucial for ecosystem functioning and resilience (Carlucci et al., 2020; Dicks et al., 2021). A comprehensive approach to restoring pastoral ecosystems in the northern Sahel is currently lacking. Research has primarily focused on sustaining the productivity of silvopastoral systems, with little attention to the impact of management options on biodiversity (e.g., Touré et al., 2012; Rasmussen et al., 2018). Revegetation actions of the GGW, principally planting trees and encouraging their natural regeneration, can result in improved pollination services by increasing the amount and diversity of floral resources in space and time, but maximising their impact depends on selecting appropriate species, based on knowledge about how different tree species interact with flower-visiting insects (Kireta et al., 2024). Like other insects, flower-visiting species also require food resources for immature stages, which often feed at trophic levels different from adults, and suitable habitat for each stage in their complex life cycles (Buisson et al., 2024). Understanding biotic interactions is crucial for developing actions to maintain and restore biodiversity in the Sahel, especially given concerns that decreasing habitat connectivity could lead to a loss of rare species and of particular ecosystems (Menz et al., 2011).

Our research focuses on insect-flower interactions in the context of the Great Green Wall (GGW) initiative in the Ferlo region of northern Senegal. This focus provides an entry point to explore the diversity of biotic interactions and their contributions to ecosystem functions (Kevan, 1999). Insects play a crucial role in the pollination of angiosperms, making them key players in ecosystems, and maintaining their interactions with flowering plants is essential for successful ecological restoration (Dirzo et al., 2014; Genes & Dirzo, 2022). Floral resources are also crucial for many insects that may not be effective pollinators but that contribute to other ecosystem functions such as population regulation, decomposition and nutrient cycling (Medina-Serrano et al., 2025).

The northern Sahel is characterised by a long and harsh dry season. How does seasonality affect insect-flower interactions? The majority of insects in the seasonally dry tropics show seasonal variation in the activity of adult stages, but a minority do not. Furthermore, activity of some insects peaks in the wet season, but that of others peaks in the dry season (Kishimoto-Yamada & Itioka, 2015). Most studies of insect seasonality have compared rain forests and tropical dry forests. Few have been done in savanna, and to the best of our knowledge there have been no community-level studies of insect seasonality in semi-arid Sahelian savannas.

The entomological literature for the Ferlo region, and for the northern Sahel in general, is scattered across various specialist publications. Mirroring the situation for much of Africa, a comprehensive synthesis on insect diversity is lacking, particularly concerning insects involved in pollination (Rodger et al., 2004; Archer et al., 2014). A primary objective of our research is thus to characterise the diversity of flower-visiting insects in the Ferlo region over the annual cycle and assess their current status, an essential step in studying the impact of GGW actions on ecological restoration (Medina-Serrano et al., 2025). The present paper focuses on insects that visit the flowers of *Balanites aegyptiaca* (L.) Delile (the desert date; Zygophyllaceae), the most common woody species in the studied region. With more than three flowering periods

each year, the timing and duration of which vary across years, it is a major resource for flower-visiting insects. In addition to its ecological importance, this species supplies local people with fodder for livestock, edible fruits, and materials for construction. To understand how the region's extreme seasonality affects insect assemblages, we sampled the diversity of insects on flowers of this species in three different seasons: end of the dry season (June 2022), rainy season (August 2022) and middle of the dry season (February 2023). We also compared assemblages of flower visitors in three sites differing in their management history (benefiting, or not, from actions under the GGW initiative aimed at restoring ecosystem functioning and biodiversity) and in tree density. By focusing on this ecologically and socially important tree species, we aim to fill crucial knowledge gaps related to insect-flower interactions in the region and their role in ecosystem functioning and provision of ecosystem services (Ndong et al., 2015; Dendoncker et al., 2020).

Specifically, we ask: How does seasonality influence the abundance, the diversity, and the composition of assemblages of flower-visiting insects? Do restoration actions (in this case, exclusion of livestock) influence these parameters? Are there differences in insect assemblages between well-drained sites that dominate the landscape and scattered topographical depressions, in which tree density and diversity are much higher? Does the extreme seasonality of precipitation in our study area impact the abundance, diversity, and species composition of insect assemblages? To answer these questions, we compared the diversity and composition (both taxonomic and functional) of flower-visiting insects across seasons and sites.

2. Materials and Methods

(1) Study area

The study was conducted in the Ferlo region, northern Senegal, characterised by a semi-arid climate with average annual rainfall ranging from 300 to 500 mm, average temperature of approximately 28°C, and strong seasonality, with a 2-3-month rainy season and 9-10 months without any rain (Cissé et al., 2016). To monitor variation in weather conditions throughout the period of the study, we installed a sensor monitoring temperature and humidity every 30 minutes and a rain gauge, in the village of Koyli Alpha, about 1 km from the closest sampling site and 6 km from the furthest. Figure S1 shows the distribution of precipitation during our study period. Figure S2 shows that mean temperature does not vary much throughout the year, but that large diurnal differences in temperature and humidity were registered during the dry season. This variation is produced by the Harmattan, a cool dry wind from the northeast or east in the western Sahara that is strongest from late November to mid-March. Its arrival may cause air temperatures to fall to 9 °C. One of the biggest variations we measured was in December 2022, from 89.5% relative humidity and 17.7 °C at 7:00 am, to 19.5% relative humidity and 33 °C the afternoon of the same day.

The Ferlo is dominated by herbaceous plants, particularly grasses (Poaceae) and leguminous forbs (Fabaceae). Vegetation in the Ferlo is classified as tree/shrub savannah, in which *Balanites aegyptiaca*, *Vachellia tortilis* subsp. *raddiana* (Savi) Kyal. & Boatwr., and *Senegalia senegal* (L.) Britton (the two last species are both Fabaceae: Mimosoideae) are the most abundant woody species. Other common woody species in the area include *Boscia senegalensis* (Pers.) Lam. ex Poir. (Capparaceae) and *Calotropis procera* (Aiton) W.T. Aiton (Apocynaceae). Vegetation in the northern Ferlo is subjected to intensive grazing and browsing by cattle, sheep, and goats. Degradation of soils and desertification (i.e., irreversible degradation of ecosystems),

owing to the combined effects of climate change and human land use (mostly pastoralism in this region), are major environmental concerns (Miehe et al., 2010; Vincke et al., 2010).

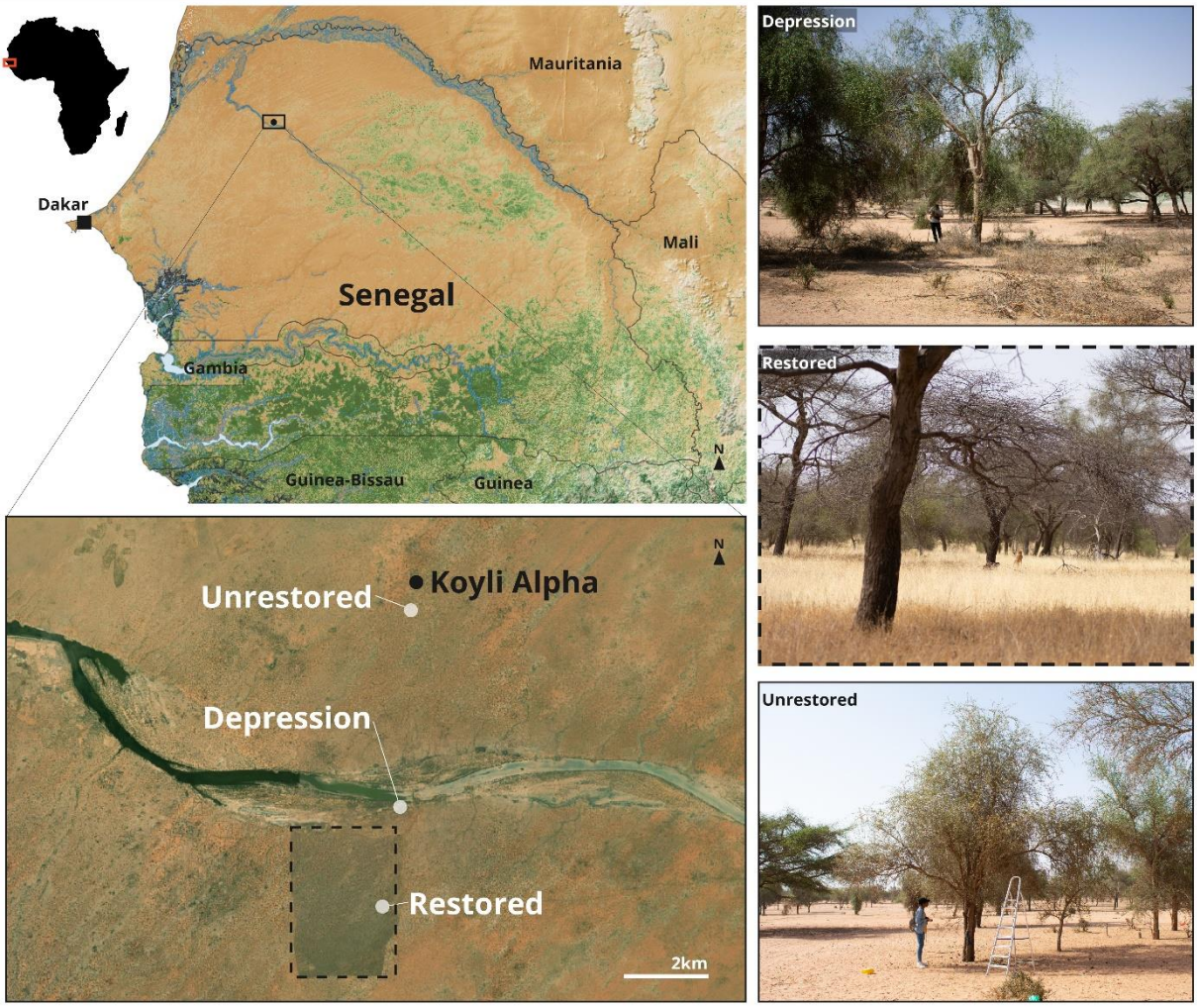

Figure 1. Location of the study area and sampling sites. The map was built under QGIS 3.28.3, using elevation SRTM data at 90m spatial resolution from the CGIAR-CSI database (Jarvis et al., 2008), hydrographic data from (Senegal PCS200, on Africa GeoPortal) and vegetation data from Hansen et al. (2013). Satellite photograph taken in 2019 of the Koyli Alpha landscape (Bing Maps), 15.666964°N, -15.524456°E, Alt 9.44 km. Photographs of the field sites were taken during the mid-dry season (February 2023). © N. Medina-Serrano.

The study area was located near the village of Koyli Alpha (Figure 1), situated in the southern part of the valley of the "Lac de Guiers". Within this locality, we studied three sites. The site characterised as "depression" is not within the restored area and is thus subjected to grazing and browsing by livestock, but is located in a topographical

depression. In such lower-lying areas, soils retain moisture into the dry season and tree density and diversity are higher than in the two other sites (Dendoncker & Vincke, 2020; Dendoncker et al., 2023). The two other sites are comparable in terms of soil and drainage but differ in intensity of grazing and browsing. The "restored" site is within the Koyli Alpha Community Natural Reserve, where livestock have been effectively excluded from an area of around 650 ha since 2017. Within the reserve, herders are allowed to cut and export herbaceous biomass at the end of the dry season. As most herbaceous plants in the region are annuals, this harvest occurs after production and dispersal of seeds and does not cause mortality of adult plants. The third site ("unrestored") is located in intensively grazed and browsed rangeland nearby (Figure 1).

(2) Study species

Balanites aegyptiaca (Zygophyllaceae) is a drought-resistant tree species widely distributed in Sahelian ecosystems. The species can be found in various topographic conditions, including hilltops, slopes, and depressions, and can tolerate annual precipitation ranging from 200 to 900 mm, with an optimal rainfall of 400 mm (Dendoncker et al., 2020). Its evergreen foliage and ability to withstand aridity make it a vital component of the region's ecosystems. Beyond its ecological significance, the tree holds socioeconomic importance, providing construction wood known for its insect-resistant properties, edible fruits sold in local markets, and fodder for goats. This last use is particularly important in the dry season, when the lopped branches of *B. aegyptiaca* are among the few common sources of fodder. Different parts of this tree (fruits, leaves, bark) are also used in traditional medicine (Chothani & Vaghasiya, 2011). *Balanites aegyptiaca* typically grows to an average height of 5.7 m (up to 8-9 m) and features a spherical crown with supple, drooping branches adorned with straight spines measuring 8 to 10 cm in length. Its flowers, grouped in small axillary

racemes, are small, hermaphrodite and actinomorphic, offering open access to floral resources (nectar and pollen) by diverse insects. Flowering occurs throughout the year, in both wet and dry seasons. These characteristics underscore the tree's adaptability and its multifaceted contributions to ecosystem functioning and services provided to humans (Le Houérou, 1989; Arbonnier, 2000; Ndoye et al., 2004; Gebrekirstos et al., 2008; Dendoncker 2020; Dendoncker et al., 2020).

(3) Study design

Two sampling methods were employed: capture of flying insects using nets and capture of insects in coloured pan traps. These two complementary methods are frequently used in combination to study species assemblages of flower visitors (Westphal et al., 2008). Netting of insects was conducted daily at each site around five flowering individuals of the target tree species. Sampling was conducted for a duration of fifteen minutes at heights ranging from two to five meters. This procedure was repeated over three successive days, with the order of sampling rotated between trees. Pan trapping used round plastic pans (diameter 15 cm) sprayed with UV fluorescent paint (white, yellow, or blue) and containing water and a drop of unscented detergent. The three coloured pans were placed near inflorescences at mid-canopy level during 48h on three of the five individual trees sampled by netting in each site to attract and capture flower-visiting insects (Westphal et al., 2008). Use of traps of three different colours helped to limit bias in the identity of the insects collected (Vrdoljak & Samways, 2012). Sampling design is schematised in Figure 2.

The five flowering trees sampled were often not the same individuals in the three seasons. For each tree in each sampling period, we estimated the abundance of flowers on the tree (percentage of the tree’s canopy that bore flowers, semi-quantitative scale that varied from 5% to 85%). For each sampled tree, we also noted the 10 other trees

(height ≥ 4 m) closest to it, recording their species identity and the distance of each from the focal tree (Figure S3). This allowed estimation of tree species diversity and density in the neighborhood of each sampled tree.

Owing to logistical constraints, we were able to sample only three sites (one "depression", one "restored" and one "unrestored"). We recognise the limitation imposed by the lack of replication of sites, and attempted to mitigate it by sampling individual *Balanites* trees scattered in each site (distances between trees in the same site ranging from 1 to 15 m) and treating them as replicates. In each site, five individual trees were sampled. It was difficult to find more than five individuals with abundant flowers (≥ 10% of the tree's canopy) at the same time in a given site. To capture seasonal variation in insect diversity and activity patterns, we sampled in three different seasons when the trees were in flower: June 2022 (end of the dry season), August 2022 (rainy season), and February 2023 (middle of the dry season).

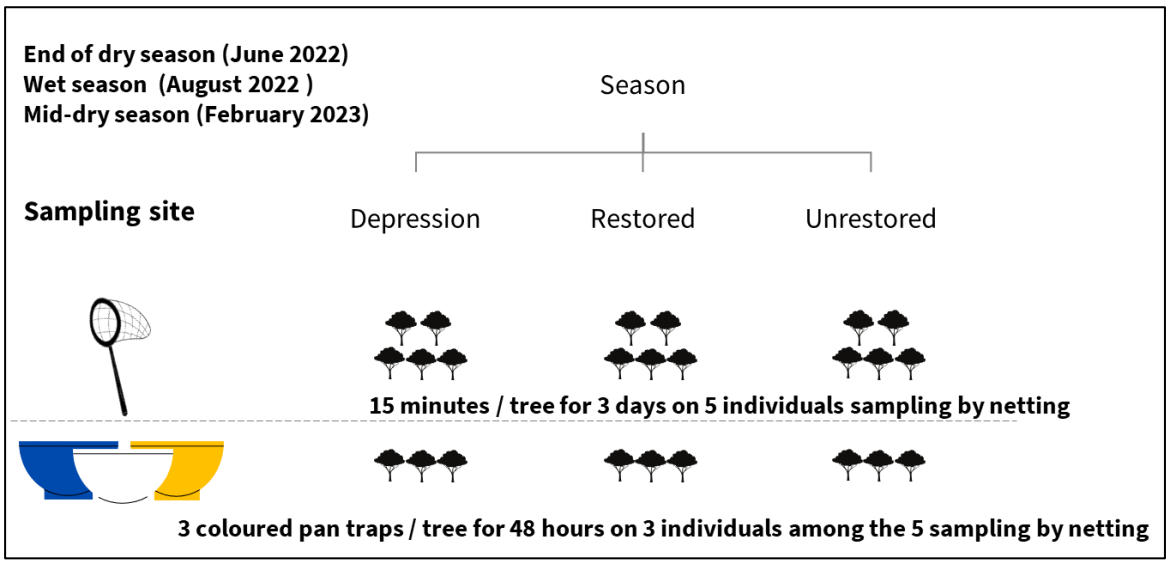

Figure 2. Sampling design for collection of insects visiting flowers of *Balanites aegyptiaca*. For net sampling, the order of sampling in the different sites was rotated each day to avoid a confounding effect of time of collection.

(4) Insect taxonomic and functional diversity

Determination of morphospecies involved several steps. First, insects were observed and, if necessary, photographed using a Leica stereomicroscope equipped with a Leica MC170 HD camera and connected to a computer. The identification of the specimens to family level was carried out using various resources, primarily Aberlenc (2021). Within each family, morphospecies were distinguished and assigned individual codes including the first six letters of the insect family name. The number of specimens per morphospecies was meticulously recorded, and one individual of each morphospecies was photographed for the purpose of documentation. As new morphospecies were recognised based on differences in size, colour, or other traits, the morphospecies list was updated accordingly. All samples are preserved in the personal collection of the first author at the Center for Functional and Evolutionary Ecology (CEFE) in Montpellier, France. All determinations were verified to the family level. For Diptera, we also consulted Kirk-Spriggs & Sinclair (2017-2021), with additional verifications for Chloropidae and Milichiidae performed by J.W. Ismay (Oxford University Museum of Natural History) at the end of the 2022 field campaign. Furthermore, Coleoptera collected were compared with those from the reference collection of the terrestrial invertebrate zoology laboratory at IFAN Ch. A. Diop on the UCAD campus in Dakar. For Lepidoptera, we tallied the numbers of individuals captured. Almost all were small moths. We lacked the time to spread and mount them, and it was not possible to distinguish morphospecies with ethanol-preserved specimens. We thus excluded Lepidoptera in our analyses of morphospecies diversity.

We also characterised insect functional diversity. In many cases, families correspond to broad functional groups. Assignment of morphospecies to functional groups was based on both the literature and our own field observations. Taxonomic and functional classification allowed a closer look at the ecological roles and interactions of the insect community within the study area.

We characterised functional groups based on the known ecology of each family (see Table 1). Specific classifications, such as "pollinators", emphasise the heavy reliance of these insects on floral resources (bees and flies are categorised separately, with bees relying exclusively on floral resources). Families in which species vary widely in their ecology are classified as "diverse." Our classification has obvious limitations. For example, Tachinidae (Diptera) are parasitoids but are frequently mentioned as flower visitors and potential pollinators, justifying their classification as "pollinators" along with other dipteran families whose adults are heavily dependent on floral resources. Similarly, species of families classed as predatory or as phytophagous are also known to contribute to pollination (e.g., predatory wasps). The group "parasitoids" encompasses insects whose hosts include a great diversity of arthropod species and life-cycle stages. Despite these limitations, we believe our classification provides a general idea of the guilds represented by the different groups visiting the flowers of *B. aegyptiaca*. We use our functional-group classification only to support discussion, and not statistical analyses.

(5) Analysis of global patterns of insect abundance, composition and diversity

All the following analyses presented were performed with R-Studio 2023.06.0 (R Core Development Team, 2016). To comprehensively describe the dataset, we first combined datasets from both sampling methods in all seasons and for all sites in global analyses of the abundance, diversity, and composition of insects visiting the flowers of *B. aegyptiaca*. We then standardised sample sizes for the two sampling methods using the method of Chao et al. (2014a) to calculate two indicators of diversity, species richness (Hill number= 0) and the Simpson index (Hill number= 2), utilising the INEXT R package (Hsieh et al., 2016).

(a) How complete was our sampling?

We assessed the sampling coverage of flower-visiting insects using rarefaction and cumulative curves. The Chao1 richness was computed to estimate true species richness, based on the observed richness and abundance distributions, with species ranked in order of abundance from the rarest to the most abundant for each season separately (Chao et al. 2014a).

Cumulative curves are shown for each method separately (net and pan-trap) and for each of the three seasons: end of the dry season (June), rainy season (August) and middle of the dry season (February), indicating the total number of individuals sampled and the number of species observed for each season. We then compared observed species richness and the Chao1 richness estimator for each season, both for the two methods combined and for net and pan-trap captures analysed separately.

Subsequently, to quantify the cumulative richness per site, we pooled data for all trees in each site ("restored", "unrestored", and "depression") for each sampling method separately. We then compared observed species richness and the Chao1 richness estimator for each site, both for the two methods combined and for net and pan-trap captures analysed separately.

Species abundance distributions are used to calculate estimated true species richness and diversity. Species-abundance distributions in our data (net and pan-trap captures combined) followed a log-normal distribution, characterised by many rare species and a few very abundant ones (see Figure S4). When dealing with small sample sizes, caution is needed in extrapolating the overall shape of a species abundance distribution from limited data. The negative binomial distribution is considered the best fit when there is a large proportion of rare species (Chao et al., 2014b: Callaghan et al., 2023). We thus computed our models of abundance using this distribution.

Data on insect abundance and diversity from each tree taken over three days were aggregated for analysis. Treating each tree as a replicate, we used Generalised Linear models (GLMs) and Linear models (LMs) to examine the influence of season and site. The GLMs were performed with the glm.nb function with the MASS package, which fits a negative binomial regression model (Ripley & Venables, 2009). The linear regression models were performed with the lm function using the log1p transformed data. Residuals of models were verified to confirm the appropriateness of the assumptions using the R package DHARMa (Brooks et al., 2017; Hartig & Lohse, 2020). Additionally, we conducted pairwise comparisons of the results of our models using the *pairs* function from the emmeans R package (Lenth, 2023). Owing to the limited number of observations, models were made as simple as possible, examining effects of only season and site and combining data from the two sampling methods.

(b) Effect of season

To assess how the abundance of flower-visiting insects varied across different seasons, we performed a Generalised Linear model(GLM). The model addresses potential overdispersion in the count data by employing the negative binomial distribution, which is more appropriate than the Poisson distribution for this type of data (Baldridge et al., 2016). Additional effects, such as the mean distance to the 10 closest trees (giving an estimation of local tree density; see Figure S3) and the % canopy flowering were tested in a second model with a Generalised Linear model (for more details see Table S1).

For the diversity indices, we used two linear regression models with log1p transformation of the data to examine the effect of season on species richness (Hill number 0) and Simpson diversity index (Hill number 2). We also examined the effects of season on the Shannon diversity index but as this analysis added no further

information, the results are not shown. We present only the analyses for species richness and Simpson diversity.

To illustrate overall patterns of seasonal variation in the morphospecies composition of the captured insects, we tabulated the number of morphospecies unique to each season and the number shared by each combination of seasons, constructing a Venn diagram. We then tested for effects of season on the abundance of each order and family to obtain a more detailed picture of the major seasonal patterns. These analyses were performed using a negative binomial GLM, following the methods cited above. We tested effects of season on abundance of the main flower-visitor orders Hymenoptera, Diptera, Hemiptera, and Coleoptera. Additionally, we were only able to test effects for three families (all Hymenoptera), Braconidae, Halictidae and Formicidae.

(c) Effect of site

We used Generalised Linear models (GLMs) with a negative binomial distribution to assess the effect of site on abundance and diversity of flower-visiting insects. For the first model we compared data from the restored, unrestored, and depression sites to assess the effect of site on insect abundance per tree in the model. The model was optimised using the bobyqa optimizer within the glmerControl function (Powell, 2009; Bates et al., 2015), which is suitable for handling convergence issues in complex models arising from a limited number of observations.

We used two Linear models to analyse the effect of site on indicators of diversity. In both models, the response variables were Hill numbers 0 and 2: species richness and the Simpson diversity index, log-transformed using the log1p function. This transformation helped manage skewness and outliers in the data. Additionally, we used two linear mixed models to analyse the effect of site on species richness and the

Simpson diversity index. We retained only the model assessing the effect of site on Simpson diversity, as only its results differed from those given by the previous model. In this model, we treated season as a random effect and fitted the model using lmer with Restricted Maximum Likelihood (Bates et al., 2015).

(d) Morphospecies communities

After investigating the effects of season and site on diversity indices, we examined the composition of the sampled insect assemblages. To continue to explore the effect of season and site, we conducted Redundancy Analysis (RDA) with the package *vegan* to explore the relationships between abundance of morphospecies and the two variables season and site, using two models and including the insects captured with the two sampling methods (Peres-Neto et al., 2006).

The first model introduced the combined effect of season and site, in order to understand the contribution of these two effects in the community composition. The second model introduced a conditional term, whereby the species abundance was analysed with respect to site, while controlling for season. Significance of each model was assessed using permutation tests with 199 permutations to determine the robustness of the associations identified (Legendre & Legendre, 2012).

3. Results

(1) Community of insects visiting flowers of *Balanites aegyptiaca*

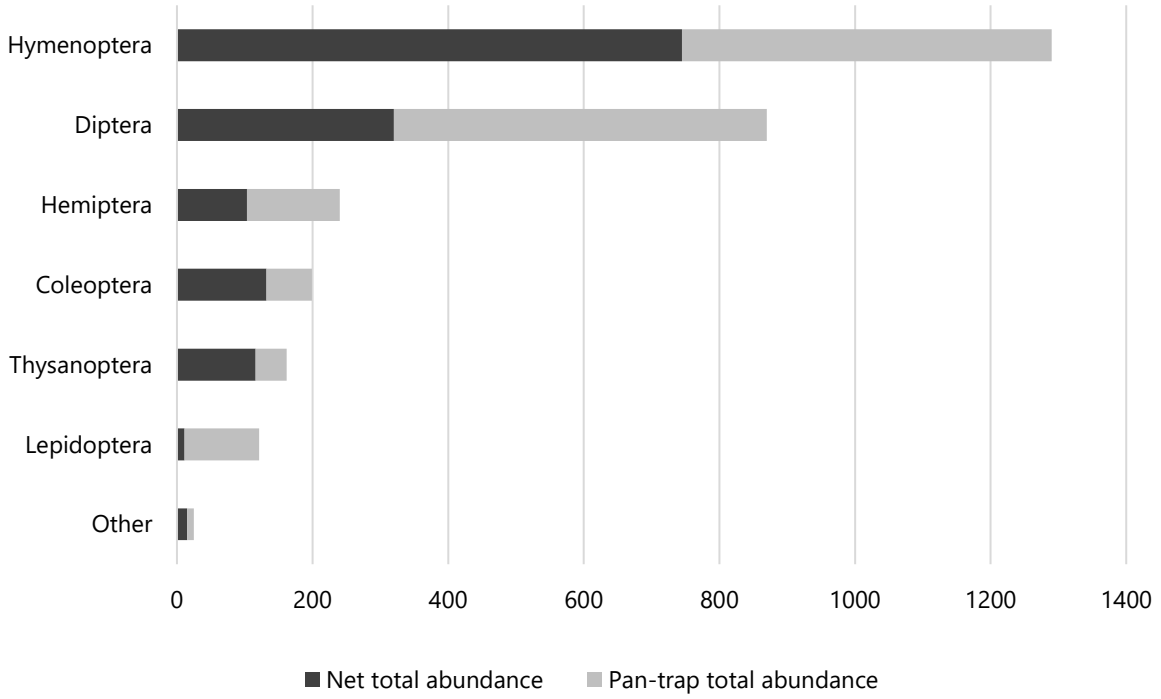

Figure 3. Barplot of the total abundance of insects of different orders captured at flowers of *Balanites aegyptiaca*. "Other" includes Ephemeroptera, Neuroptera, Orthoptera and Psocoptera. The two methods (net and pan-trap) combined for a total of 2907 individuals of at least 371 morphospecies (morphospecies not distinguished for Lepidoptera). A total of 1442 insects were collected by net sampling, and a total of 1465 insects were collected by pan-trap sampling.

We found an unexpectedly high diversity of insects at the flowers of this tree species in this extremely harsh environment. We captured 2907 individuals of a total of at least 371 morphospecies from 10 insect orders (Figure 3). The most abundant and diverse orders were Hymenoptera (1290 individuals, 180 morphospecies) and Diptera (870 individuals, 101 morphospecies), followed by Hemiptera (240 individuals, 30 morphospecies), Coleoptera (199 individuals, 39 morphospecies), Thysanoptera (162 individuals, 11 morphospecies), and Lepidoptera (121 individuals, morphospecies not

distinguished). Four other orders (Ephemeroptera, Neuroptera, Orthoptera and Psocoptera) contributed a combined total of 25 individuals and 10 morphospecies (Figure 3). Table 1 presents the families of flower-visiting insects encountered in the study and the taxonomic and functional categories we used to describe each family, functional group and order.

Table 1. Flower-visiting insects captured (pan-trap and net samples), grouped by orders, broad functional groups, and families. Biological information on families taken from Aberlenc (2021), Kirk-Spriggs & Muller (2017-2021), and Mawdsley et al. (2016).

Order	**Functional group**	**Family**
Coleoptera	polyphagous	Aphodiidae, Buprestidae, Chrysomelidae, Curculionidae, Dermestidae, Elateridae, Leiodidae, Lycidae, Meloidae, Mordellidae, Nitidulidae, Ptinidae, Staphylinidae
	predator	Carabidae, Cerylonidae, Coccinellidae
Diptera	unknown adult biology	Mycetophilidae, Psychodidae
	« diverse »	Anthomyiidae, Apsilocephalidae, Cecidomyiidae, Ceratopogonidae, Chaoboridae, Chironomidae, Chloropidae, Corethrellidae, Cryptochetidae, Culicidae, Dolichopodidae, Drosophilidae, Lonchaeidae, Muscidae, Odiniidae, Oestridae, Pseudopomyzidae, Phoridae
	pollinator	Bombyliidae, Mythicomyiidae, Rhiniidae, Rhinophoridae, Sarcophagidae, Syrphidae, Tachinidae
	predator	Asilidae, Carnidae, Chamaemyiidae, Ephydridae, Lauxaniidae, Milichiidae
	phytophagous	Tephritidae
Hemiptera	phytophagous	Achilidae, Aleyrodidae, Anthocoridae, Aphididae, Berytidae, Cicadellidae, Delphacidae, Miridae, Tingidae
Hymenoptera	generalist	Formicidae

	parasitoid	Aphelinidae, Bethylidae, Braconidae, Ceraphronidae, Chalcididae, Chrysididae, Chrysolampidae, Cleonymidae, Diapriidae, Dryinididae, Encyrtidae, Eulophidae, Eupelmidae, Eurytomidae, Eutrichosomatidae, Gasteruptiidae, Ichneumonidae, Liopteridae, Megaspilidae, Mymaridae, Ormyridae, Orussidae, Perilampidae, Platygastridae, Pteromalidae, Signiphoridae, Tetracampidae, Torymidae, Trichogrammatidae
	pollinator	Andrenidae, Apidae, Halictidae
	predator	Crabronidae, Mutillidae, Pompilidae, Scoliidae, Thynnidae
Neuroptera	parasitoid	Chrysopidae
	predator	Coniopterygidae
Orthoptera	phytophagous	Acrididae
	omnivorous	Rhaphidophoridae
Thysanoptera	phytophagous	Phlaeotripidae

There were some notable differences in the assemblages captured by the two methods (Figure 3). First, Lepidoptera, almost all of which were small moths, comprised only 0.8% of the net samples but 7.5% of pan-trap samples. This difference may reflect the nocturnal habits of most species captured. Netting was done only during the day, whereas pan traps sampled insects over 48 hours. Lepidoptera were captured primarily at the end of the dry season, with 85 individuals recorded in June, compared to 35 individuals during the mid-dry season and only 3 individuals during the rainy season. Secondly, the two most abundant orders, Hymenoptera and Diptera, were equally abundant in pan-trap samples but Hymenoptera were two times more abundant than Diptera in net samples.

As stated in the Methods section, Lepidoptera were not further analysed. Insects of all nine other orders were captured by both sampling methods. The two sampling methods contributed a roughly equal number of individuals to the total sample (pan traps: 1465; net: 1442). Note, however, that at each season and site, five trees were sampled by netting, while a subset of three of these trees was sampled using pan traps. The number of insects captured per tree was thus about 1.7 times higher for pan traps than for nets.

We first grouped the results from these two complementary methods to analyse global patterns in species richness. We then analysed diversity indices for the grouped results, after correcting for the difference in sampling effort between the two methods.

(2) Effects of season on abundance and diversity of flower-visiting insects

(a) Overview of seasonal patterns

The composition of insect assemblages varied greatly across seasons. Of 371 morphospecies recorded, only 21 (5.6%) were present in all three seasons. Each season had 46–60% of morphospecies unique to that period. The overlap in morphospecies composition (Sorensen index) was highest between the rainy and mid-dry seasons (20.0%), and lower between the mid-dry and end-dry seasons (14.7%) and the end-dry and rainy seasons (12.8%). The limited biological knowledge for individual morphospecies prevents further analysis of these patterns (see Figure 4).

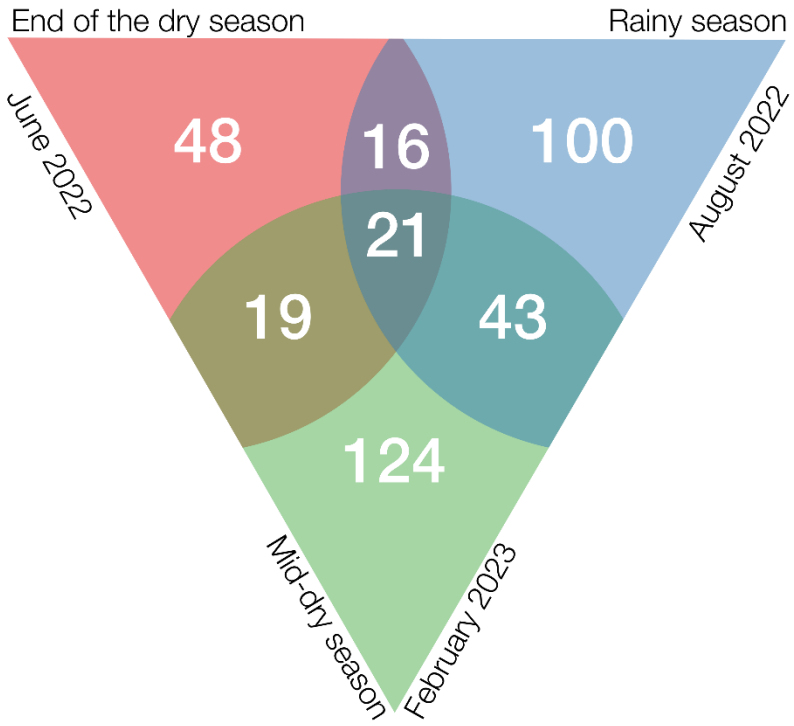

Figure 4. Venn diagram: showing great seasonal variation in composition of insect assemblages on *Balanites aegyptiaca*. In pink the end of the dry season, in blue the rainy season and in green the mid-dry season. The numbers give the number of species captured only in a single season, those captured in two seasons, and those captured in all three seasons.

(b) Seasonal variation in abundance and diversity metrics

Combining results from both sampling methods, there were no significant differences in the overall abundance of insects across seasons or between any pair of seasons (Figure 5). However, species richness varied significantly, being highest in the mid-dry season, lower (but not significantly so) during the rainy season, and significantly lower at the end of the dry season than in the other two seasons (Figure 5). Statistical models revealed the following:

1. Abundance: Generalised Linear models (GLM with a negative binomial distribution) found no significant effect of season on insect abundance, with non-significant

pairwise comparisons across seasons (Figure 5). We also tested, with a GLM, the effect on insect abundance at a tree as a function of the mean distance from that tree of the 10 closest neighbouring trees (i.e., an estimate of local density of trees) and of % canopy flowering. Results of the GLM showed that insect abundance at a tree significantly increased with greater mean distance to neighbouring trees (χ^2 = 5.81, df = 1, p = 0.016). However, there was no significant effect of canopy flowering percentage on insect abundance (see detailed statistical results in Table S1).

2. Species richness: Species richness was significantly higher during both the rainy season (August, p = 0.022) and the mid-dry season (February, p < 0.001) than at the end of the dry season (June) (see Figure 5 and detailed statistical results in Table S2).

The analysis of deviance showed that there was a significant difference among seasons (F = 7.55, df = 2, p = 0.002) and pairwise comparisons showed that species richness during the mid-dry season was significantly greater than at the end of the dry season (June) (p = 0.001). However, the difference between the rainy season (August) and the end of the dry season (June) was marginally non-significant (p = 0.055). Values for richness in the rainy season and the mid-dry season were not significantly different (p = 0.286). These results highlight seasonal shifts in species richness, with notable increases during the mid-dry (February) and rainy (August) seasons.

3. Simpson diversity: Simpson diversity was highest at the end of the dry season. The analysis of deviance showed there was a significant difference among seasons (F = 7.45, df = 2, p = 0.002) and pairwise comparisons confirmed that diversity was significantly higher at the end of the dry season than in both the rainy season (August, p = 0.018) and the mid-dry season (February, p = 0.002) However, no significant difference in Simpson diversity was found between the mid-dry season and the rainy season (p = 0.653; see Figure 5 and detailed statistical results in Table S2).

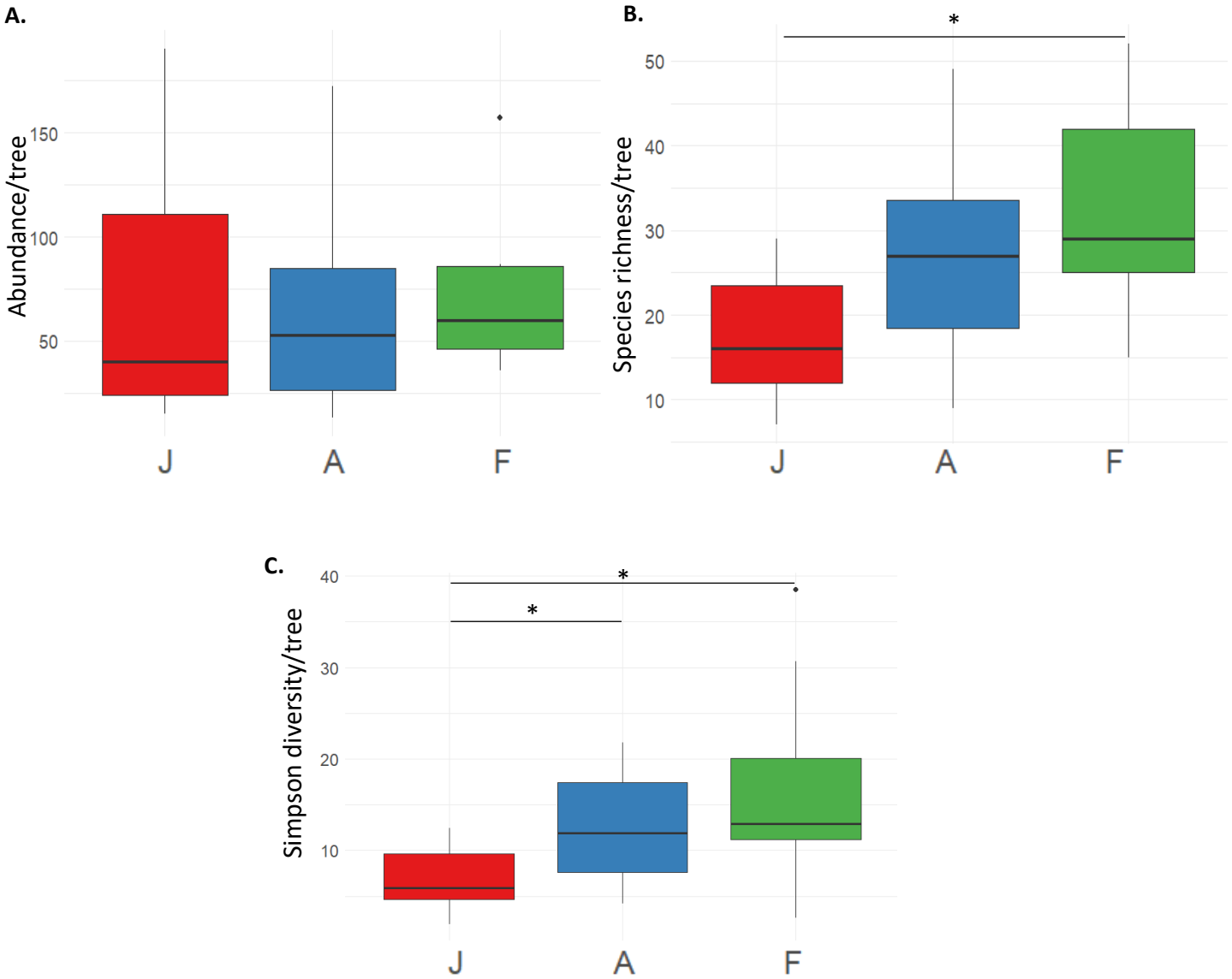

Figure 5. Boxplots showing the distribution of the mean abundance per tree (A), observed species richness per tree (B) and Simpson diversity index per tree (C) of insects at flowers of *Balanites aegyptiaca*. In red: J, June, end of the dry season; In blue: A, August, rainy season; In green: F, February, middle of the dry season. The central rectangle represents the interquartile range (IQR), showing the middle 50% of the data. The horizontal line shows the median and the whiskers show variability beyond the quartiles. Individual points outside the whiskers are considered outliers. See tables S1 and S2 for statistical details.

(c) Seasonal variation by taxonomic group

Both season and sampling method affected variation in abundance of different insect orders (Figure 6). Seasonal effects were significant for Hymenoptera (χ^2 = 15.02, df = 2, $p < 0.001$, Diptera (χ^2 = 12.95, df = 2, $p = 0.002$), and Hemiptera (χ^2 =15.82, df = 2, $p < 0.001$) but not for Coleoptera (χ^2 = 3.80, df = 2 , $p = 0.15$). Pairwise comparisons highlighted significant differences between the rainy season and the end-dry season for Hymenoptera ($p < 0.001$), Hemiptera ($p <0.001$), and Diptera ($p < 0.001$). Additionally, significant differences were found for Hymenoptera ($p = 0.036$) and Diptera ($p = 0.017$) between the rainy season and the mid-dry season (see Figure 6 and Table S3). These results suggest that while Hymenoptera, Hemiptera, and Diptera showed more or less strong seasonal shifts, Coleoptera exhibited less seasonal variation.

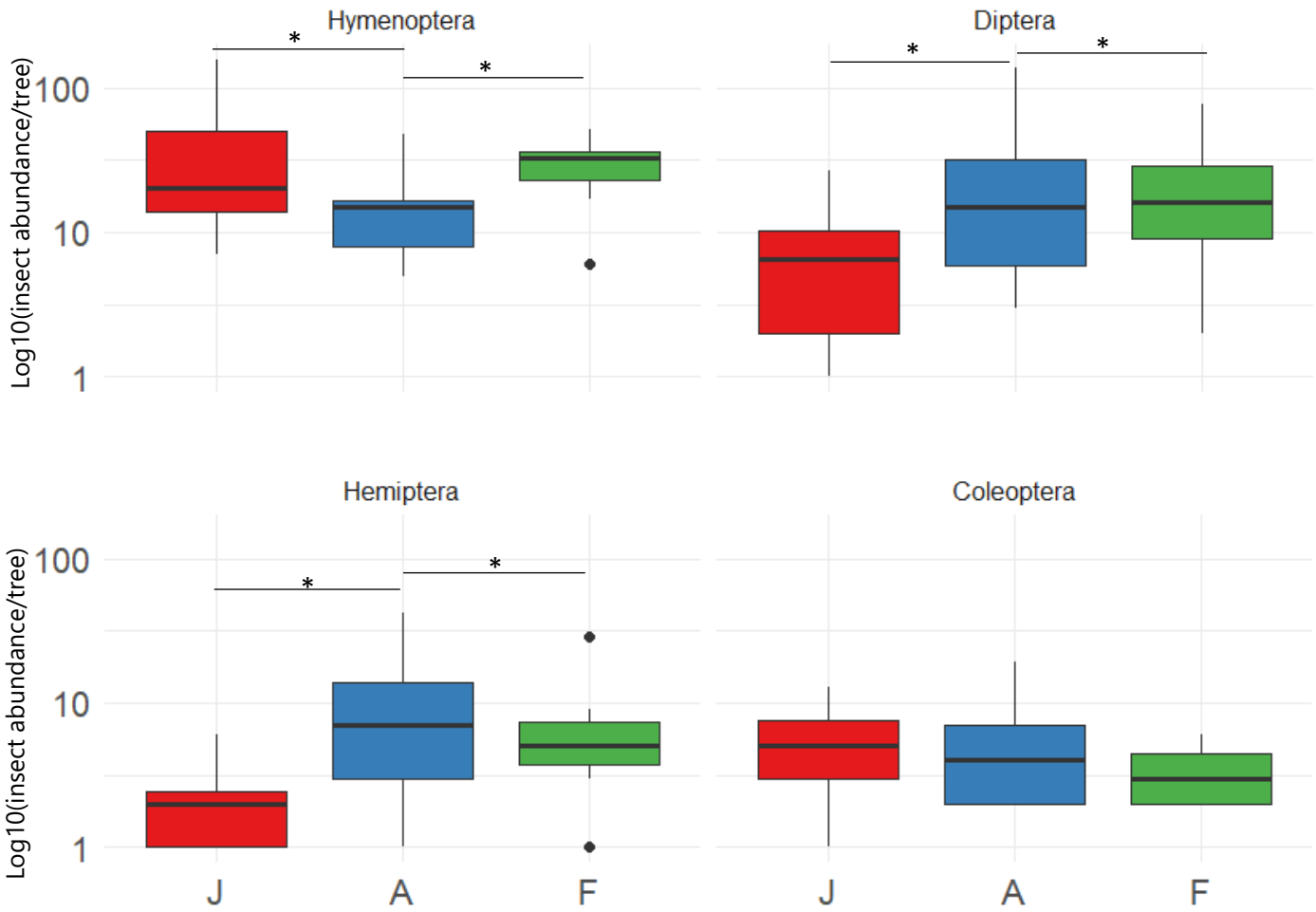

Figure 6. Boxplots showing the distribution of the mean abundance per tree of four orders of insects visiting flowers of *Balanites aegyptiaca* (Hymenoptera, Diptera, Hemiptera and Coleoptera) (the two sampling methods grouped). In red: J, June, end of the dry season; In blue: A, August, rainy season; in green: F, February, middle of the dry season. The central rectangle represents the interquartile range (IQR), showing the middle 50% of the data. The horizontal line shows the median and the whiskers show variability beyond the quartiles. Individual points outside the whiskers are considered outliers. See Table S3 for statistical details.

(d) Patterns in selected families

To provide biological insights, seasonal variation in abundance was examined for four insect families based on their ecological and biological characteristics (Figure 7). Significant seasonal differences were observed for all four families studied.

1. Halictidae: These bees were abundant year-round due to the consistent availability of the floral resources on which they rely. However, they were significantly more abundant at the end of the dry season (June) than in the rainy season (August; χ^2 = 8.44, df = 2, p = 0.015), a difference confirmed by a post-hoc pairwise comparison (p = 0.013; see Figure 7 and for statistical details Table S4).

2. Rhinophoridae: These flies were restricted to the rainy season, reflecting their dependence on moist microhabitats that support woodlice, the hosts of these parasitoids (Wood et al., 2018). Rhinophoridae were almost exclusively captured using pan traps (see Figure 7 and for statistical details Table S4).

3. Braconidae: Abundance of these parasitoid wasps varied significantly among seasons (χ^2 = 16.31, df = 2, p < 0.001). They were significantly more abundant at the end of the dry season than in both the rainy season (p = 0.011) and the mid-dry season (p = 0.001; see Figure 7 and Table S4 for statistical details). All Braconidae sampled in our study belonged to the subfamily Microgastrinae, all of which are parasitoids of diverse Lepidoptera (Whitfield et al., 2018). Their abundance coincided with a strong peak in abundance of Lepidoptera (see section 3.1. above). Lepidoptera likely increase during the flush of plant growth before the onset of the rainy season (Ryan et al., 2017).

4. Formicidae: Ant abundance also varied significantly among seasons (χ^2 = 23, df = 2, p < 0.001). Ants were significantly more abundant at the end of the dry season than in both the rainy season (p < 0.001) and the mid-dry season (p < 0.001; see Figure 7 and for statistical details Table S4). Seasonal patterns for ants likely reflect variations in

availability of different kinds of resources rather than population changes, as these social insects maintain long-lived colonies. Their peak of abundance at flowers is likely tied to the low availability of resources other than flowers (and the other insects that visit them) at the end of the dry season.

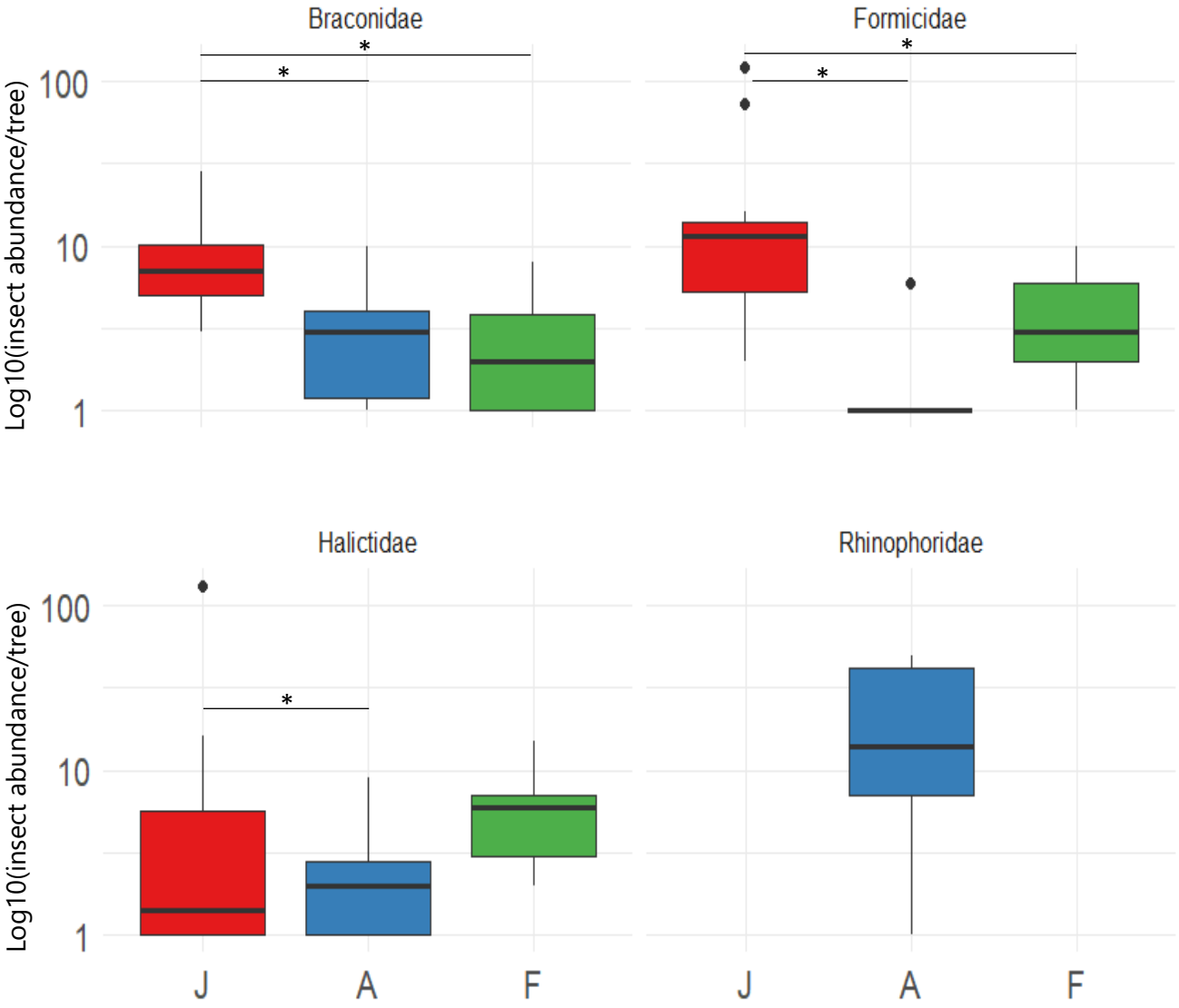

Figure 7. Boxplots showing the distribution of the mean abundance per tree of the four families (Braconidae, Halictidae, Formicidae and Rhinophoridae) visiting flowers of *Balanites aegyptiaca* (combined results for the two sampling methods). In red: J, June, end of the dry season; in blue: A, August, rainy season; in green: F, February, middle of the dry season. The central rectangle represents the interquartile range (IQR), showing the middle 50% of the data. The horizontal line shows the median and the whiskers show variability beyond the quartiles. Individual points outside the whiskers are considered outliers. See statistical details in Table S4.

(e) Comparison of observed and estimated species richness

For pan-trap and net captures combined, the observed and estimated species richness varied across months (Table S3). However, each method showed a distinct pattern of seasonal variation, so we also analysed them separately. For pan-trap captures, June (end of dry season) showed the lowest values for both observed species richness (61 species) and estimated richness (ChaoRichness 110.9). August (rainy season) showed higher values for both observed (103 species) and estimated richness (ChaoRichness 169.6). February (mid-dry season) showed the lowest observed richness (88 species), but the highest estimated richness of all samples (ChaoRichness 230). Net captures presented slightly different patterns. Similar to pan-trap captures, June showed the lowest values for both observed (67 species) and estimated species richness (ChaoRichness 100.1); August showed intermediate values of both observed (117 species) and estimated species richness (ChaoRichness 227.9); and February showed the highest values for both observed (152 species) and estimated species richness (ChaoRichness 304.1). June showed the highest values of sample coverage (SC) for both pan-trap (0.951) and net captures (0.939). SC in August samples was somewhat lower (pan-trap: 0.915; net: 0.837). SC in February was low for both net captures (0.867) and pan-trap captures (0.787, lowest of all samples) (Figure 8).

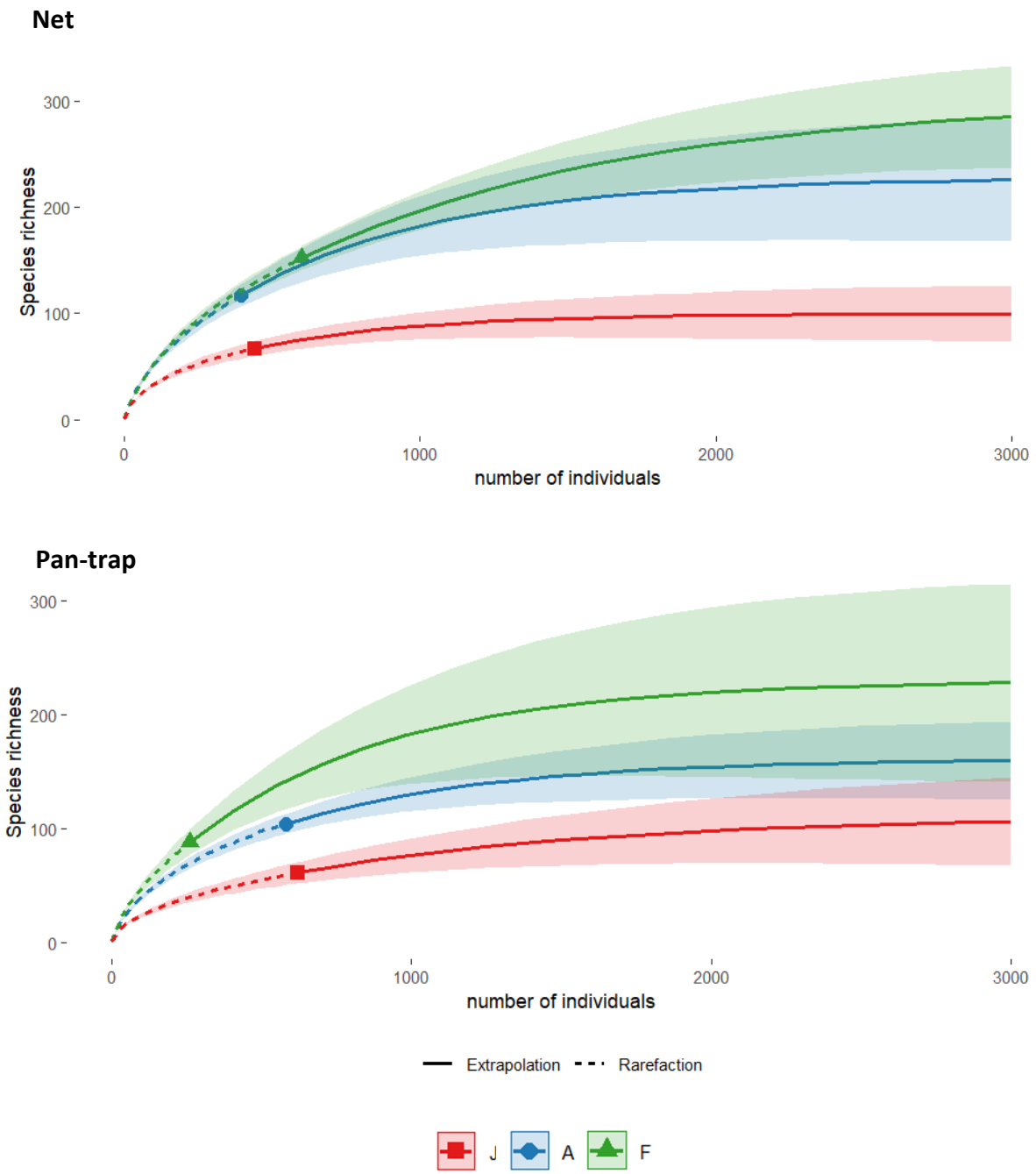

Figure 8. Accumulation curves for net and pan-trap captures, showing seasonal variation in morphospecies richness on *Balanites aegyptiaca*. Red represents J: June, the end of the dry season; blue represents A: August, the rainy season; and green represents F: February, the mid-dry season.

(3) Effect of site

(a) Diversity metrics across sites

The analysis using Generalised Linear models (GLMs) revealed that effects of site on insect abundance or diversity were much weaker than the effects of season. Low insect capture rates in some seasons precluded robust statistical comparisons of site-level captures when treating season as a random effect. We thus used models that took into account only the effects of site. In these tests, effects of site were still mostly non-significant. However, observed abundance of insects per tree was significantly lower in the depression site than in the restored site ($F = 8.14$, $df = 2$, $p = 0.017$) (estimate (SE) = -0.669 ± 0.233, $p = 0.011$, but not significantly different from that in the unrestored site (see Figure 9 and for more details Table S5).

Some insect families exhibited a trend to greater abundance in the restored site compared to the unrestored site. However, there was no consistent trend indicating higher insect abundance or diversity in the depression site, despite its greater tree density and tree diversity. In the Linear model (LM), Simpson diversity was significantly higher in the depression site than in the restored site (estimate (SE) = 0.451 ± 0.214, $p = 0.0417$), but post-hoc pairwise comparisons showed no significant differences between the two sites in either species richness or Simpson diversity. However, in the linear mixed model, where season was treated as a random effect ($\chi^2 = 6.05$, $df = 2$, $p = 0.049$), the Simpson diversity index was significantly higher in the depression site than in the restored site ($p = 0.049$; see Table S5).

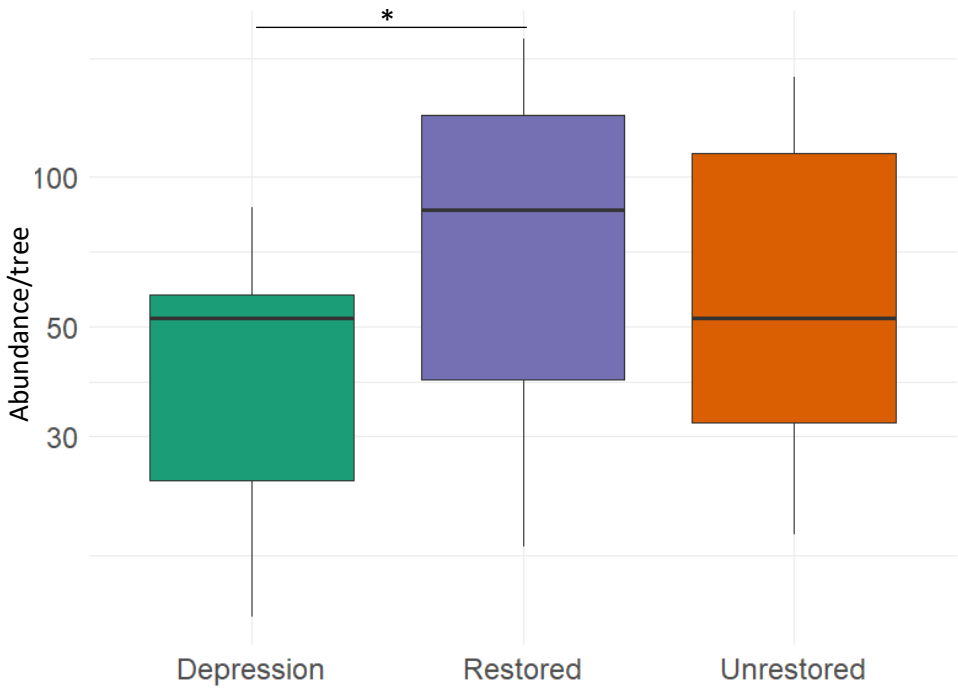

Figure 9. Boxplots showing mean abundance per tree of insects at flowers of *Balanites aegyptiaca* for each site (three seasons combined). The central rectangle represents the interquartile range (IQR), showing the middle 50% of the data. The horizontal line shows the median and the whiskers show variability beyond the quartiles. See statistical details in Table S5.

(b) Comparison of observed and estimated species richness across sites

Observed species richness tended to be lower in the unrestored site (176 species) and similar in the restored and depression sites (205 and 209 species, respectively). Estimated richness (ChaoRichness) was also lowest in the unrestored site (283 species). However, in contrast to their similar observed richness, estimated richness was much higher in the depression site (417 species) than in the restored site (320 species).

Effects of site on observed and estimated species richness showed somewhat different patterns between the two capture methods. For pan-trap captures, both observed and estimated richness were highest in the restored site (112 species and 214.3, respectively), followed by the depression site (97 species; 204.8) and the unrestored site (97 species; 173.6). For net captures, both observed and estimated richness were highest for the depression site (148 species and 333.3, respectively), followed by the restored site (131 species; 234.5) and the unrestored site (117 species ; 222.4) (Figure 10).

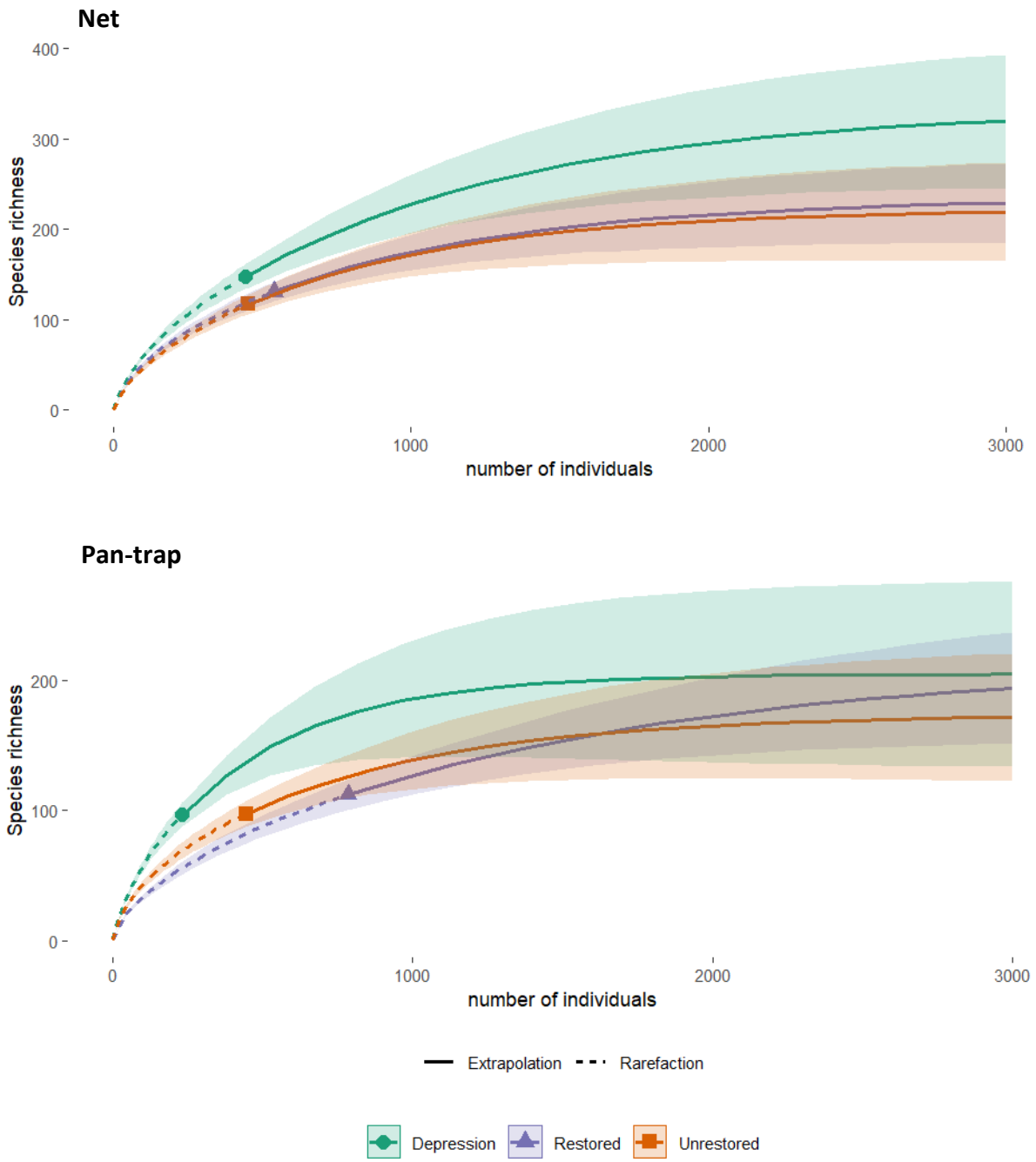

Figure 10. Accumulation curves for net and pan-trap captures separately showing variation among sites in morphospecies richness on *Balanites aegyptiaca*. In green the depression site, in purple the restored site, and in orange the unrestored site.

(c) Morphospecies communities and RDA analysis

We tested the effects of season and site on morphospecies composition of our samples using redundancy analysis, which estimates the distribution of inertia (variance) among the components of the RDA model. With the redundancy analysis we tested the effects of season and site on the morphospecies composition in our sampling. We found that season (condition) explained 26.41% of the total variance, site explained only 6.18% (the constrained component), and the remaining unconstrained variance accounted for 67.41% (see Figure S5).

4. Discussion

(1) The surprising diversity of flower-visiting insects

The flowers of the desert date (*Balanites aegyptiaca*) provide freely accessible nectar and pollen, resources that should be exploitable by insects of various sizes, morphologies, and behaviours. This study showed that the diversity of insects visiting its flowers was in fact very high, comprising at least 371 morphospecies from 10 insect orders. For a semi-arid ecosystem near the southern edge of the Sahara, intensively grazed and browsed by livestock, this diversity is surprisingly high. For comparison, in a study of the overall assemblage of flower visitors to plants in a more humid savanna in Kenya with less extreme seasonality, greater plant species richness, and no livestock, Guy et al. (2021) found around 300 insect morphospecies. Furthermore, estimations based on species abundance distributions suggest that the true species richness of visitors to *B. aegyptiaca* flowers in the northern Sahel is substantially higher than the observed richness. Ongoing analysis by barcoding of our morphospecies confirms our identifications.

We found that the two sampling methods we used captured somewhat different insect assemblages. We first analysed results for these two methods separately to understand these differences. Small, rapidly flying insects such as halictid bees and many flies were difficult to capture by netting but were easily captured with pan traps, whereas larger insects were more easily captured by netting and non-flying insects such as ants were easily captured by both methods. Each of these methods also has other biases (Wilson et al., 2008; Vrdoljak & Samways, 2012; Westerberg et al., 2021). Together, they capture a greater diversity of insects than either method separately (Popic et al., 2013). We thus combined samples from these two complementary methods to investigate global patterns.

The two most abundant and diverse orders, Hymenoptera and Diptera, accounted for a large proportion (77 %) of all individuals of flower-visiting insects. The most abundant insects at flowers were ants. Ants play diverse roles as flower visitors, consuming nectar and preying upon other floral visitors (florivores or pollinators; Romero & Vasconcellos-Neto, 2004), but for most plants they are unlikely to be important pollinators. Ants are followed in abundance by solitary bees (Halictidae). Small flies belonging to a diverse set of Diptera families were next in abundance. All of these groups showed strong seasonal variation in abundance and, for Diptera, in diversity as well.

To our knowledge few studies have sampled the abundance and diversity of flower-visiting insects over multiple periods in such a highly seasonal environment. Despite strong logistical constraints, we sampled not only during the short rainy season but also during the middle and near the end of the dry season, and showed that each of these periods was characterised by a highly distinct insect fauna. Sampling at additional periods (e.g., beginning of the dry season, or during the transition between the dry and rainy season when trees begin their vegetative activity) might yield an even finer-scale picture of seasonal variation in insect diversity.

(2) Predominance of solitary bees, mostly Halictidae

Exclusively dependent on floral resources throughout all life stages, bees are often considered the most important of all pollinators. A striking feature of the bee fauna visiting the flowers of *B. aegyptiaca* is the virtually complete absence of eusocial bees. Only two individuals of *Apis mellifera* and no meliponine bees were recorded. *Apis* is generally very rare in the region (N. Medina-Serrano, unpublished data). The bee fauna is completely dominated by solitary bees, predominantly Halictidae. Development and maintenance of colonies of eusocial bees requires long flight periods and a continuous supply of floral resources during the flight period. Seasonal scarcity of floral resources may lead to their relative rarity in dry environments like the northern Sahel (Medina-Serrano et al., 2025). Also, in contrast to tropical eusocial bees, solitary bees are mostly ground-nesting. The rarity of soil-dwelling fungal pathogens in arid environments favours ground-nesting species.

Four morphospecies of Halictidae were among the most abundant species in all surveys, with three species present in every season and at almost every site. The year-round presence of these species suggests they may have multiple generations per year. The halictid species present all belong to the subfamily Nomioidinae. Solitary and usually ground-nesting, bees of this subfamily are relatively insensitive to habitat degradation (Williams, 2011). They are the most abundant bees in the Sahara Desert and are predominant pollinators in these ecosystems (Pesenko & Pauly, 2005). Halictidae species captured in our study appear to belong to the genera *Nomioides* (halict 1, 2, 3) and *Ceylalictus* (halict 17). They could be effective pollinators of *B. aegyptiaca* and other trees in the ecosystem. Pesenko & Pauly (2005) describe the presence of *Ceylalictus muiri* (to which halict 17 appears to correspond) on *Acacia* trees and *Nomioides* species on *Vachellia tortilis* subsp. *raddiana*, another dominant tree species in our study area.

(3) Seasonal variation in bee abundance and in the availability of floral resources

Because bees rely entirely on floral resources for food in both immature and adult stages, their seasonal patterns are expected to reflect the availability of floral resources. Halictidae of subfamily Nomioidinae are polylectic, i.e., they visit flowers and consume pollen of many plant species. Their abundance should thus reflect variation in abundance of overall floral resources, rather than being tied to the flowering phenology of a single tree species such as *B. aegyptiaca*. Bees were most abundant in our samples in the dry season, coinciding with the flowering period of most tree species in the region (Arbonnier, 2000). Seasonal variation in bee abundance thus indeed appears to be correlated with variation in the availability of floral resources.

Whereas flowering of herbaceous plants is restricted to the rainy season, the only period when their shallow root systems can access water, the deep roots of trees can access water year-round, permitting flowering at any time of year. Numerous tree species in the seasonally dry tropics are characterised by peak flowering in the dry season (Janzen, 1967). The most general hypothesis to explain this pattern is that vegetative competition with neighbouring trees demands maximum investment in growth during the rainy season, a small proportion of resources being stored for flowering in the dry season, when growth stops and competition is relaxed (Janzen, 1967). This hypothesis would appear not to apply in the northern Sahel, where trees are usually scattered. However, many tree species of the northern Sahel also occur in closed-canopy dry forests further south, and their phenology may have evolved in adaptation to those environments. Also, dry-season flowering has other advantages that apply not only in closed-canopy dry forest but also in thinly wooded savannas. For example, flowers of trees are an important source of water and energy for wasps, bees, flies and butterflies that pass the dry season as adults, and selective pressure to maintain pollinator populations may contribute to driving dry-season flowering peaks.

Also, with greater evaporation of nectar in the dry season, bees and other insects must visit a larger number of flowers to meet their requirements for water (Janzen, 1967).

(4) Diverse seasonal patterns in flower-visiting insects other than bees

Other flower-visiting insects depend on diverse resources, often using nectar, pollen, or both as fuel in their search for these resources. Our study revealed that the floral visitors of *B. aegyptiaca* included insects with a great diversity of biologies: predators, parasitoids, phytophagous insects, and detritivores (decomposers). The highly varied seasonal patterns in availability of the resources exploited by these insects may contribute to explaining the diverse seasonal patterns in their abundance and diversity. For example, most Hemiptera captured were Cicadellidae (leafhoppers) and other plant-sucking insects. Insects of these groups on tree hosts are frequently dependent on young growth, and this may explain their greater abundance in the rainy season. In studies of seasonality in dry tropical forest reviewed by Kishimoto-Yamada & Itioka (2015), leafhoppers and other plant-sucking Hemiptera were found to have peak activity in the wet season. Larval stages of many Diptera are dependent on humid environments, and this may similarly explain their greater abundance in the rainy season. Adults of Coleoptera found in our study often had thick cuticles, and this may help explain their apparently lower sensitivity to seasonal variation in precipitation and humidity. However, beetles have very diverse lifestyles, and in tropical dry forests, representatives of several families have peak activity in the rainy season (Kishimoto-Yamada & Itioka, 2015).

Ants were the insect group most frequently captured at flowers, represented by 10 morphospecies and a total of 350 individuals. They were much more abundant at flowers in June (end of the dry season) than in the two other months sampled. Three morphospecies, each belonging to a different genus, together accounted for 275

individuals (78.6%). Of these, *Monomorium* sp. (204 individuals) and *Crematogaster* sp. (21) were captured only in June. Of the 50 individuals of *Tetraponera* sp., 46 were captured in June (end of the dry season). This seasonal variation probably reflects not a change in the abundance of these generalist predators and omnivores, which live in year-round and perennial colonies, but rather seasonal differences in the diversity and abundance of the different kinds of resources available to ants. A wider variety of insect prey is likely to be available in the rainy season, associated with plant growth, whereas flowers and the insects attracted to them may be the only sources of water, energy, and protein for ants in the dry season (Rico-Gray & Oliveira, 2007).

Other flower-visiting insects are less long-lived, and seasonal patterns likely reflect real variation in their abundance and diversity. For some of these, the observed seasonal patterns can be plausibly explained by features of their biology. Diptera tended globally to be most abundant in the rainy season. This could be related to the reliance of larval stages of Diptera of many families on moist habitats. One Diptera family whose abundance in, and restriction to, the rainy season is particularly easily explicable in terms of larval resources is the Rhinophoridae. These flies are specialist parasitoids of woodlice (Isopoda) (Wood et al., 2018). These litter-dwelling detritivorous crustaceans have gills (inherited from their marine ancestors) that must be kept moist. In xeric environments they tend to be nocturnal and are most likely to be active at the soil surface only in the rainy season (Hornung, 2011). However, one Diptera family, Mythicomyiidae, was abundant in the middle of the dry season, and captured almost exclusively in that season. We can offer no explanation for this notable exception, because very little is known about the biology of these vastly understudied small flies. Records for a few species indicate they may be parasitoids of diverse insects. They are particularly abundant and diverse in arid environments and are frequently observed at flowers (Evenhuis & Lamas, 2017). Diverse other small Diptera, belonging to families Chloropidae, Phoridae, and Milichiidae, were also abundant visitors of *B. aegyptiaca* flowers. Owing to their small size, their likely small

flight ranges, and their low density of body hairs, these species are unlikely to be efficient pollinators of *B. aegyptiaca*, but given their abundance their contribution to pollination may nevertheless be significant (Kirk-Spriggs & Muller, 2017).

Other insect groups, such as hymenopteran parasitoids, attack diverse life stages (eggs, larvae, pupae) of very diverse insects, each with its own annual cycle, and this is reflected by their diverse phenologies. Lack of knowledge about their biology prohibits interpretation of seasonal patterns, with one possible exception. Braconid wasps of the subfamily Microgastrinae showed a pronounced seasonal peak at the end of the dry season, about four times higher than in the two other seasons sampled. These wasps are exclusively parasitoids of diverse lepidopteran larvae (Fernandez-Triana et al., 2020). Interestingly, Lepidoptera were captured in our samples (pan-trap only) almost exclusively in this same season.

A fundamental problem in interpreting seasonal patterns in flower-visiting insects is that little appears to be known about how different insects in the region survive unfavourable seasons (for most, the dry season). If this knowledge exists, it has never been synthesised. Several strategies have been documented, including seasonal migration and passing the dry season as active adults (Medina-Serrano et al., 2025), but for most groups nothing seems to be known, or at least has not been synthesised.

(5) Variation among sites

For several families (Diptera: Ceratopogonidae, Chloropidae, Phoridae, Rhinophoridae; Hymenoptera: Crabronidae, Formicidae, Halictidae, Platygastridae), the number of individuals captured in the restored site (within the Koyli Alpha Community Natural Reserve) was somewhat higher than in the unrestored site (intensively grazed and browsed rangeland near the reserve). One of these families, Rhinophoridae, was captured almost exclusively in the restored site. Redundancy analysis also indicated

modest divergence not only among seasons, but also among sites in the patterns of occurrence of insect morphospecies. However, our results tell us little about the effects of restoration actions on assemblages of flower-visiting insects. The lack of replication prevents any conclusions. In any case, restoration actions have probably not been in place long enough to produce detectable effects. The Koyli Alpha reserve was inaugurated only seven years ago. Few studies of ecological restoration in other environments report a recovery in insect diversity before a decade or so (Suding, 2011). Working in another site within the area of GGW projects in Senegal, Brandt et al. (2020) showed that the number of trees in restored parcels was higher than in surrounding unrestored areas, but that trees in the these parcels were smaller and that tree cover was consequently lower. This suggests that tree cover will increase in the GGW parcels, with likely positive impacts on biodiversity of flower-visiting insects.

One of our sites was located in a topographical depression, where soils remain humid longer into the dry season. Such sites harbour greater density and species richness of trees and are seen as refugia for biodiversity in the face of intensive land use and climate change (Dendoncker et al., 2023). Like almost all tree species in the region, trees in these sites are insect-pollinated. If their greater tree species richness also reflects higher functional diversity, they should support greater diversity of flower-visiting insects (Kireta et al., 2024). We found surprisingly little indication that flower-visiting insects were more abundant in these tree-rich and relatively humid sites. In fact, abundance of insects in the depression site was lower than in the restored site. Interestingly, we found that insect abundance was positively correlated with mean distance to the 10 closest neighbouring trees (section **2**.*b* above). This mean distance varied among sites, being significantly lower in the depression site than in the two other sites (Figure S6). As insect abundance was also lower in the depression site (Figure 9 ; Table 5), we cannot separate an effect of site on insect abundance from an effect of mean distance to neighbouring trees.

Curiously, insect abundance was much less variable among trees in all seasons in the depression site than in the two other sites (Figure S7). We have no explanation for this difference. In contrast to abundance, observed species richness was as high in the depression site as in the restored site.

Furthermore, estimated richness (ChaoRichness) was much higher in the depression site than in the restored site, especially for flying insects captured by nets. This (along with the somewhat contrasting patterns of observed species richness and Shannon diversity between these two sites) suggests that observed richness particularly underestimates expected richness in the depression site, underscoring the likely importance of topographical depressions in this region as a refuge not only for rare plant species (Dendoncker et al., 2023) but also for insect diversity.

The finding that insect abundance at a tree was significantly positively correlated with the mean distance from neighbouring trees (i.e., significantly negatively correlated with proximity to neighbouring trees) is puzzling. Because we do not know if neighbouring trees were flowering in each of the sampling periods, we cannot judge whether this pattern is related to distribution of floral resources. The finding does suggest, however, that further analyses should take into account larger spatial scales (e.g., Musters et al., 2021).

5. Perspectives, open questions

Our study reveals several critical gaps in knowledge about interactions between plants and flower-visiting insects in the Sahel. These must be addressed to effectively guide the maintenance, and if necessary the restoration, of the diverse ecosystem functions performed by these components of biodiversity.

First, we need to know much more about the basic biology of flower-visiting insects in the region. What is the range of plant species with which each interacts? This study

was focused on the insects visiting flowers of a single common tree species. Like *B. aegyptiaca*, flowers of other common trees of the region offer pollen and nectar freely accessible to diverse insects (Medina-Serrano et al., 2025). Studies in progress on some of these other trees show that they share many floral visitors with *B. aegyptiaca* but that assemblages also differ (N. Medina-Serrano, M. Hossaert & D. McKey, in preparation).

How are flower-visitor networks structured across tree species? Unlike trees, forbs (non-graminoid herbaceous plants) of the region flower only during the brief rainy season. The assemblages of insects visiting their flowers are unknown. While many have 'open-access' flowers like those of the region's trees, in many others morphological traits restrict access to floral rewards. These include the "bee flowers" of many faboid legumes, as well as flowers apparently adapted to hawkmoths, to settling moths, or to butterflies (Medina-Serrano et al., 2025). Are trees and forbs associated with distinctive subnetworks of flower visitors that differ in their structure and functioning?

Halictid bees appear to be among the most important pollinators in the region. The species we found are polylectic, exploiting pollen and nectar of a broad range of flowers. The presence of each species in all seasons suggests that they are long-lived or are multivoltine, or both. Knowing their host range, life history, and behavioural ecology is key to understanding the dynamics and resilience of their populations. Are these same species also pollinators of forbs in the rainy season?

The importance of Diptera as pollinators is globally underestimated (Ollerton, 2017). In Africa, Diptera reach their greatest diversity in seasonally arid environments (Kirk-Spriggs & Stuckenberg, 2010), and we recorded diverse families of small flies as abundant visitors to flowers of *B. aegyptiaca*. Little is known about the biology of many of these flies. An outstanding example is the Mythicomyiidae, tiny flies, highly diverse and vastly understudied, with numerous species awaiting description. Very little appears to be known about their reproductive ecology.

Biological investigations require accurate species identifications. The dearth of taxonomists is particularly severe in Africa, especially for difficult groups such as small Diptera. There is a great need for integrative taxonomy, combining morphology, behaviour, and molecular barcoding.

This study has produced a one-time snapshot of insect abundance and diversity at flowers of the most common tree species in the northern Sahel. Extending this snapshot to long-term monitoring will be essential for effective conservation strategies. How will climate change and continued ecosystem degradation affect insect-flower interactions? Can restoration actions carried out in initiatives such as the Great Green Wall maintain the biodiversity of flower-visiting insects? Finally, insect-flower interactions are only one facet of the interactions in which biodiversity ensures the functioning of healthy ecosystems. Each of the trees and insects we studied here is linked by other biotic interactions in interlocking networks of herbivory, predation, parasitism, seed dispersal, and the cycling of nutrients (Pilosof et al., 2017). Efforts to conserve and restore Sahelian ecosystems must embrace and understand this complexity and integrate it into management actions.

Climate change is altering insect phenology in many ways, with manifold potential consequences for interactions between insects and flowers. Whereas shifts in phenology in response to climate change are beginning to be documented in insects of temperate regions, there is a dearth of information on how insect phenology responds to climate change in the seasonal tropics. In these regions, where temperature varies relatively little across seasons, phenology is less likely to be tied to temperature and the consequences of warming for phenology are less clear (Forrest, 2016). Careful, long-term studies of tropical insect phenology are needed to investigate correlations between seasonal activity and environmental variables that are affected by warming, such as seasonal precipitation patterns (Valtonen et al., 2013).

6. Conclusion

Flowers of *B. aegyptiaca* in the intensively grazed and browsed rangelands of the northern Sahel are visited by an unexpectedly high diversity of insects. The abundance of this tree, the ease with which insects of varying size, morphology and behaviour gain access to its nectar and pollen, and its year-round flowering, combine to make it a critical resource for many insect species, which in turn play diverse roles in many other biotic interactions. The biology of insects visiting the flowers of *B. aegyptiaca*, even the most abundant ones, is very poorly known. Abundance, diversity, and species composition of assemblages of flower-visiting insects vary across seasons. As in tropical dry forests (Kishimoto-Yamada & Itioka, 2015), some insects have peak activity in the rainy season, but for others peak activity occurs in the dry season, which in the northern Sahel is exceptionally long and harsh. While some of this variation can be explained based on what we know about the functional traits of insects, our sparse knowledge of the biology and ecology of insects in the northern Sahel limits our interpretation of patterns. Knowledge of the biotic interactions that underpin ecosystem functioning, and how they vary across seasons, is crucial for monitoring, understanding, and managing the impacts of ecosystem degradation, restoration actions, and climate change on Sahelian ecosystems.

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8. Data availability statement

The scripts of the analyses carried out and the raw data are available in Zenodo: https://doi.org/10.5281/zenodo.15041362

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10. Conflict of interest disclosure

Authors declare no conflict of interest.

11. Ethics approval statement

Senegal adheres to the Nagoya protocol, but no official procedure has yet been initiated. The transportation of sampled specimens was carried out with the agreement of the institutions (ASERGMV and Institut Fondamental d'Afrique Noire Cheikh Anta Diop).

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13. Supporting information

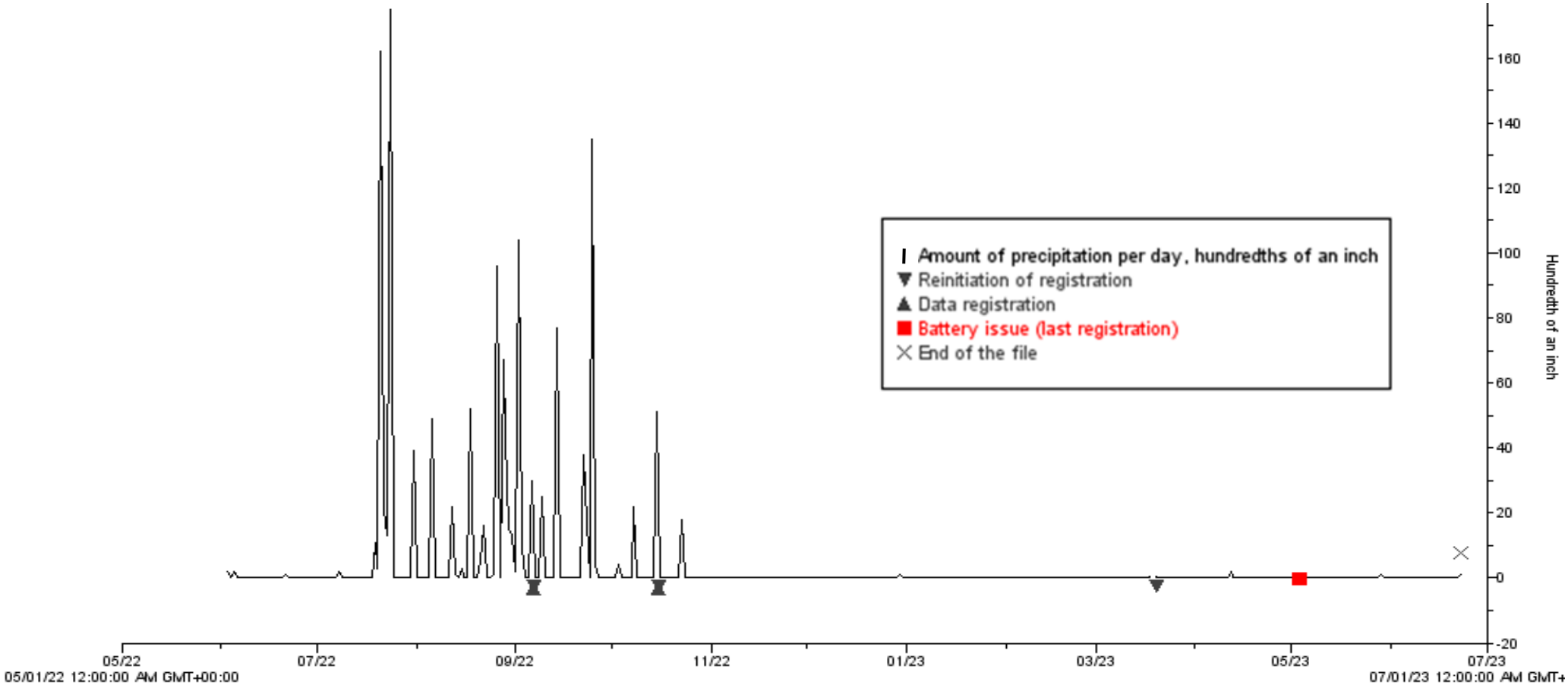

Figure S1. Daily precipitation at Koyli Alpha between 1 May 2022 and 30 July 2023. Each spike represents the amount of precipitation each day, recorded in hundredths of an inch (0.01 inches). Product: HOBO UA-003-64 Pendant Temp/Event. Onset's HOBO Data Loggers (2018).

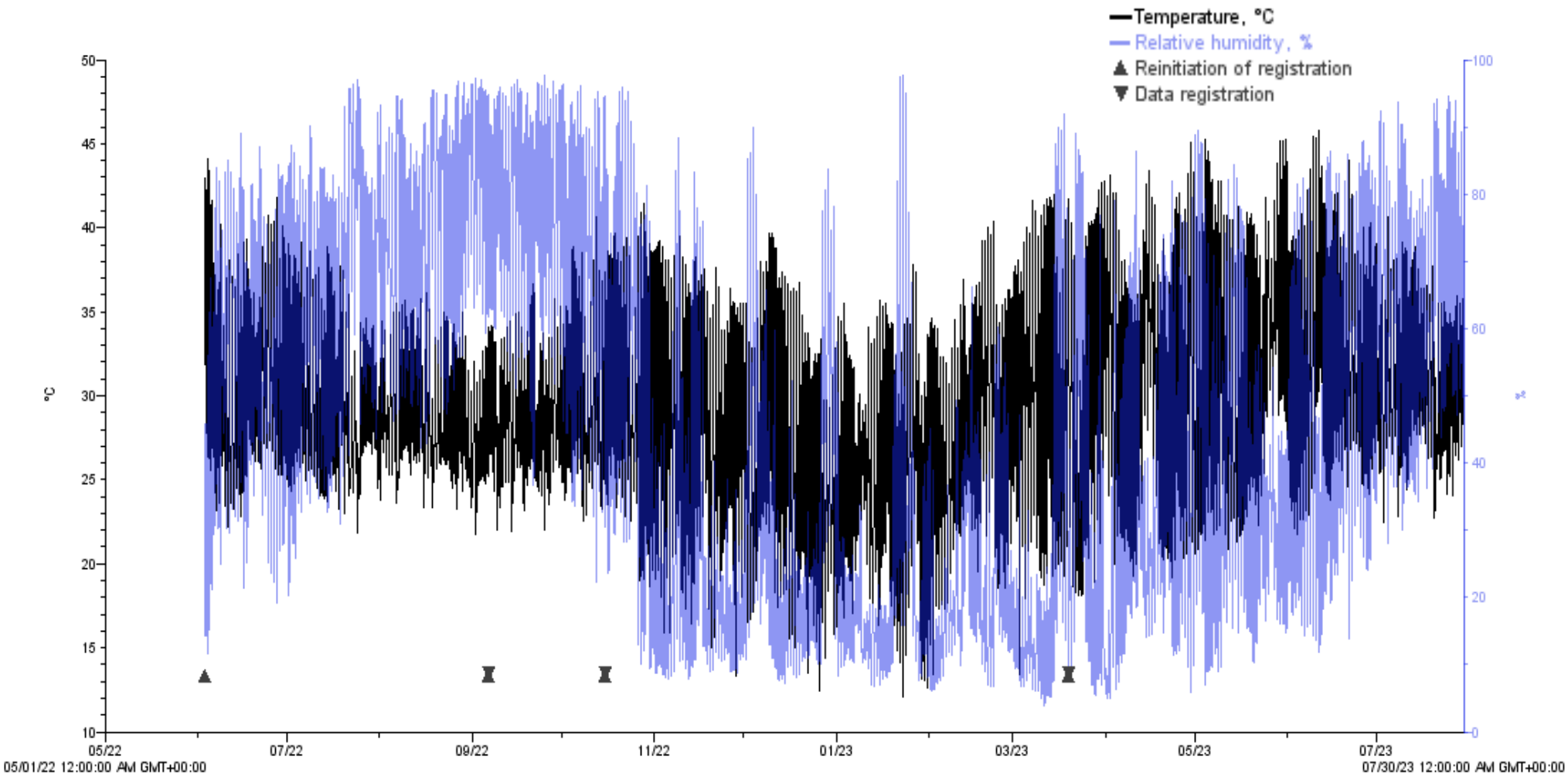

Figure S2. Diurnal variation in temperature and relative humidity measured at Koyli Alpha each day between 1 May 2022 and 30 July 2023. Note the strong diurnal variation in relative humidity during the dry season (November-March). Product: HOBO U23-001A Temp/RH. Onset's HOBO Data Loggers (2018).

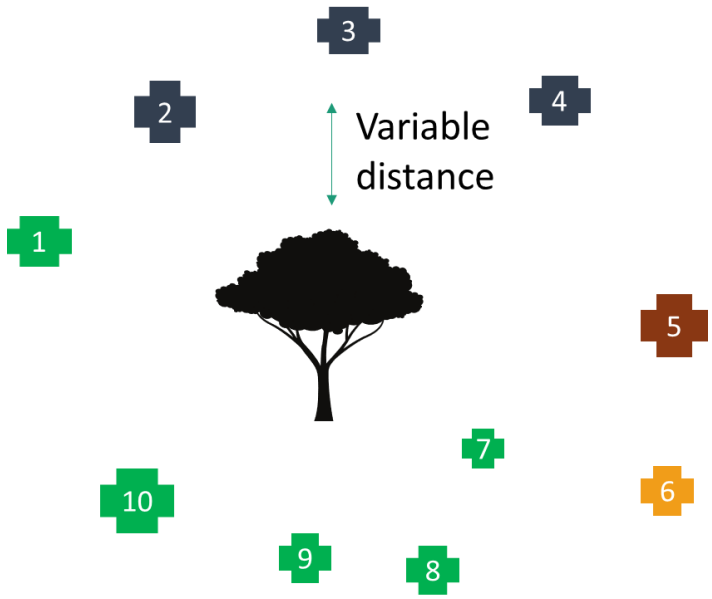

Figure S3. Schema showing estimation of local tree density and diversity around a sampled individual *Balanites aegyptiaca*. The 10 closest trees to each focal tree included 2-4 tree species. The crosses represent the 10 trees, and the different colours of crosses indicate different tree species. Size of the cross indicates relative size of the tree.

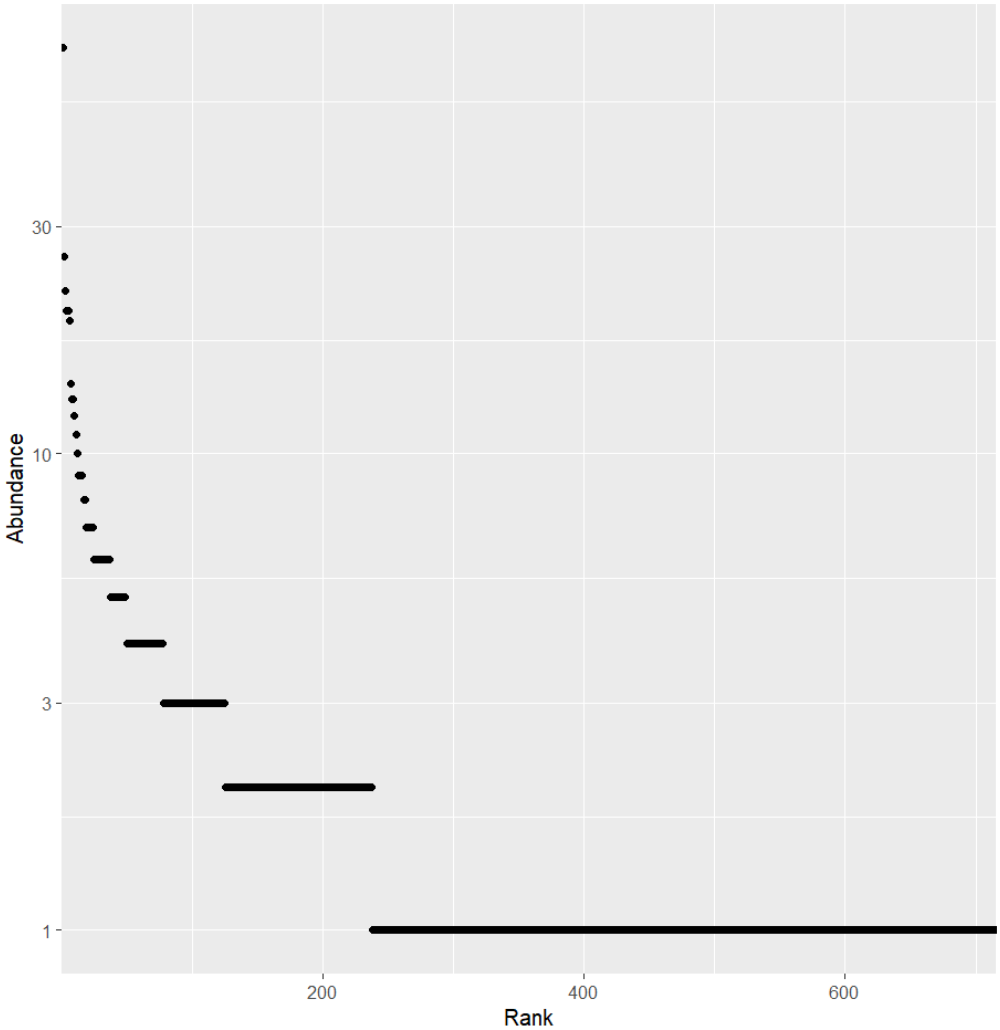

Figure S4. Rank-abundance curve of different morphospecies in the community of insects, combining net and pan-trap samples and data for all three seasons. The curve follows a log-normal distribution. The curve was done using the package entropart (Marcon & Hérault, 2015).

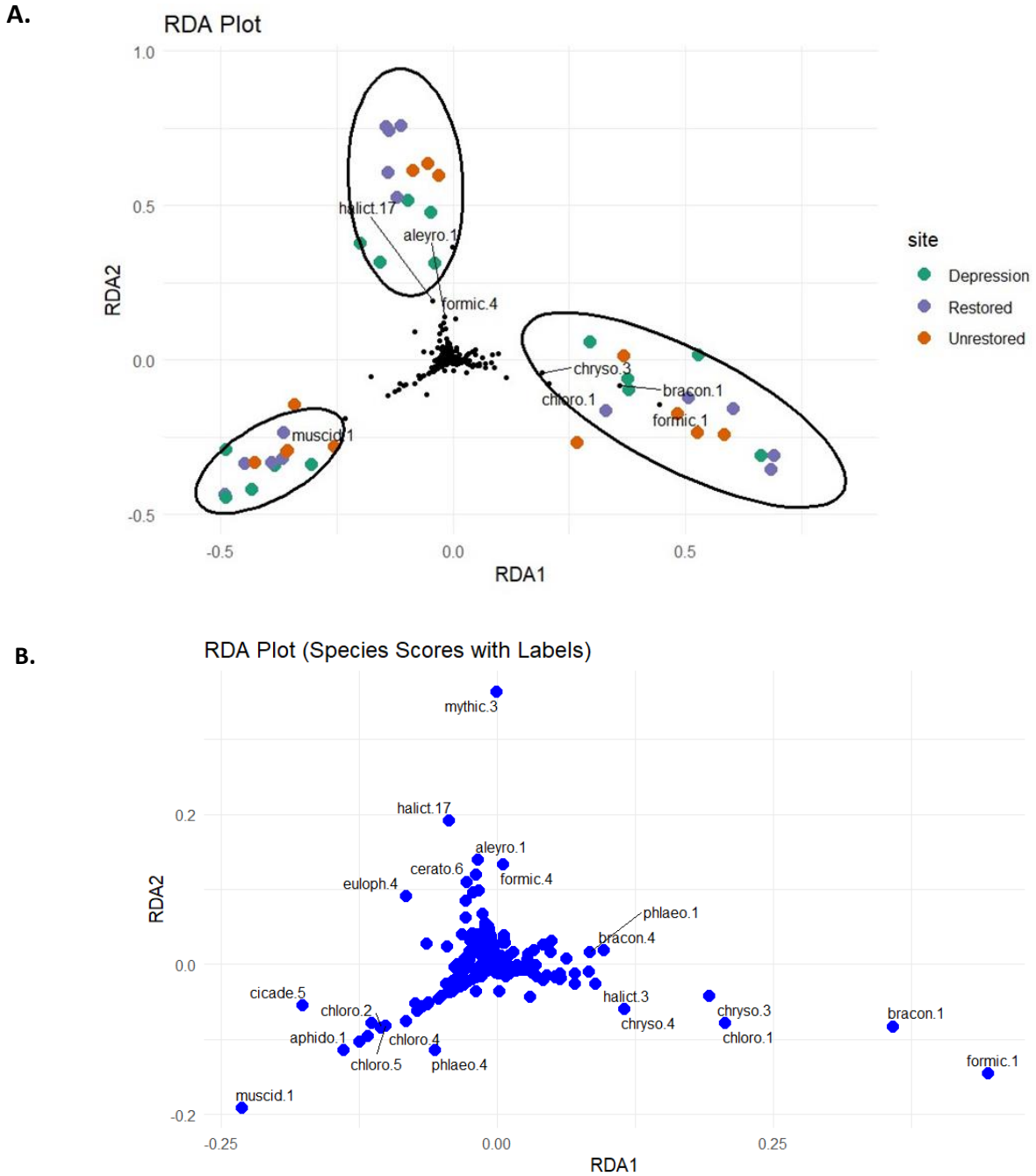

Figure S5. Redundancy analysis (RDA, using Hellinger transformation) of the influence of season and site on morphospecies composition of insect assemblages at flowers of *Balanites aegyptiaca*. (A.) Ellipses group observations of insects at trees in the different seasons while the coloured dots represent observations of insects at trees in different sites. The influence of site was formulated as a categorical variable representing the different sites and the influence of season as a conditioning variable of the model used. (B.) Each blue dot represents a morphospecies on a larger scale.

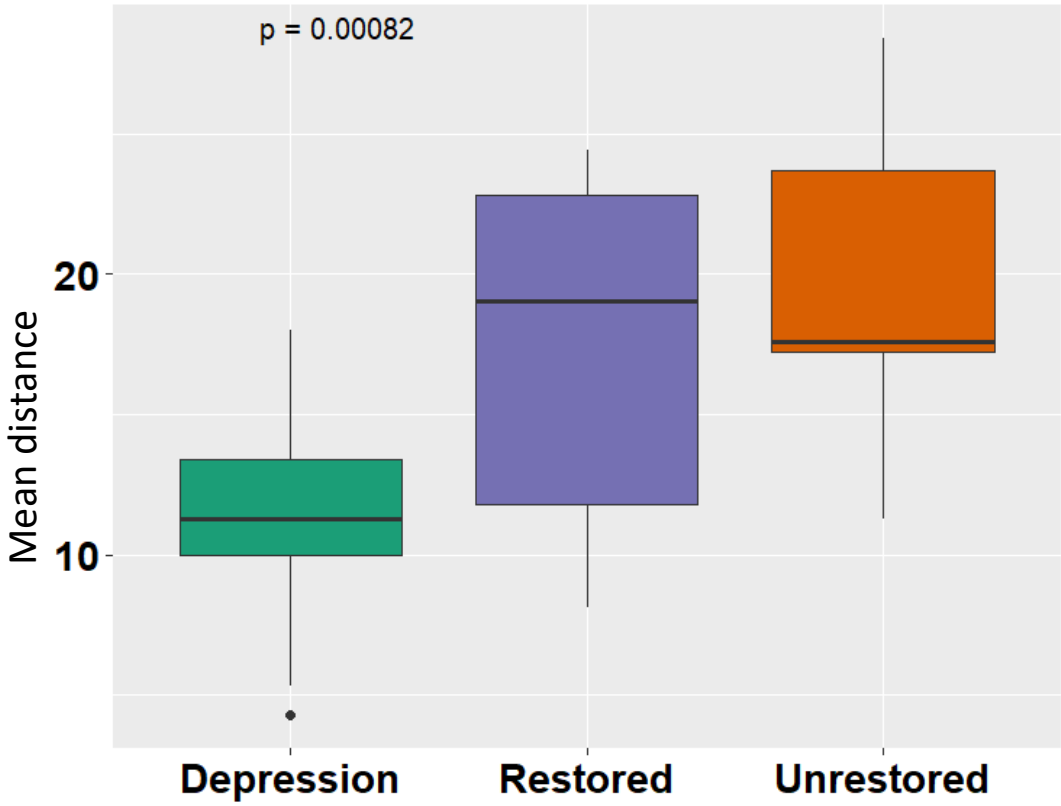

Figure S6. Boxplots showing the mean distance to the 10 closest trees for each site. The central rectangle represents the interquartile range (IQR), showing the middle 50% of the data. The horizontal line shows the median and the whiskers show variability beyond the quartiles. Individual points outside the whiskers are considered outliers. Note the significant variation in mean distance at the depression site, as determined by the Kruskal-Wallis test ($\chi 2$= 14.21, df = 2, p-value = 0.0008).

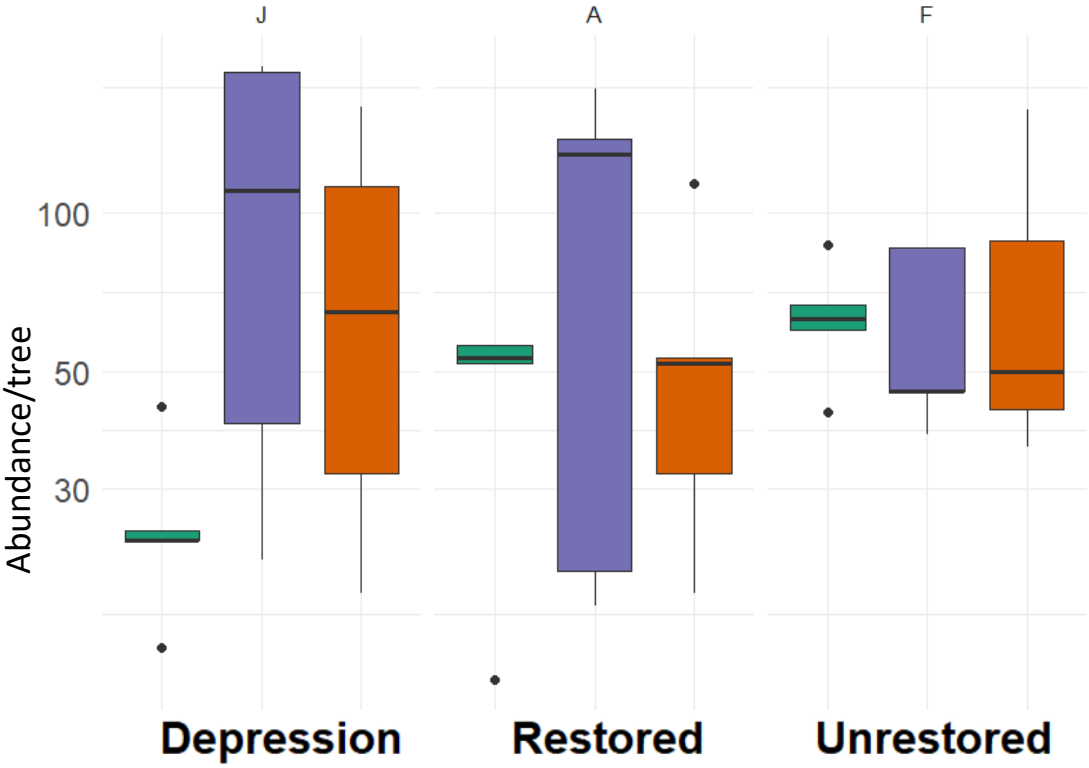

Figure S7. Boxplots showing mean abundance per tree of insects at flowers of *Balanites aegyptiaca* for each season and site. The central rectangle represents the interquartile range (IQR), showing the middle 50% of the data. The horizontal line shows the median and the whiskers show variability beyond the quartiles. Individual points outside the whiskers are considered outliers. For J: June, end of the dry season; for A: August, rainy season; for F: February, middle of the dry season. Note the very low variation in abundance in all three seasons in the depression site, a pattern for which we have no explanation.

Table S1. Results of the two different Generalised Linear models used to explore the effect of season, mean distance to the 10 closest trees and the % canopy flowering of the sampled tree on insect abundance (insects from the two sampling methods were grouped).

Model	Formula	AIC	Lognormal R^2	Predictor	Likelihood Ratio χ2	df	p-value
Generalised Linear Model	Abundance ~ season + flowering + mean distance	**442.28**	0.2119	Season	1.26	2	0.5330
				Flowering	1.16	1	0.2819
				Mean distance	5.81	1	**0.0160**
Generalised Linear Model	Abundance ~ season	445.21	0.0036	Season	0.13	2	0.9386

Table S2. Results of the Linear models used to explore the effect of season on species richness and Simpson index (insects from the two sampling methods were grouped). For J: June, end of the dry season, A: August, rainy season and F: February, middle of the dry season.

Model	Formula	R^2	Pairwise Comparisons (p-values)	Analysis of variance
Linear Model	Log1p (Species richness) ~ season	0.2377	June – August: 0.0554 June – February: **0.0012** August – February: 0.2858	F = 7.55, df = 2, p = **0.0017**
Linear Model	Log1p (Simpson diversity) ~ season	0.2351	June – August: **0.0177** June – February: **0.0021** August – February: 0.6534	F = 7.45, df = 2, p = **0.0018**

Table S3. Results of the Generalised Linear models comparing the seasonal effects for Hymenoptera, Diptera, Coleoptera and Hemiptera (same model, testing the different order) and insects from the two sampling methods were grouped.

Model	Formula	Lognormal R^2	Analysis of variance	Pairwise comparisons (p-values)
Generalised Linear Model	Hymenoptera abundance ~ season	0.3247	LR $\chi2$ = 15.02, df = 2, p = 0.0005	August-February: **0.0360**, August-June: **0.0002**, February-June: 0.3748
Generalised Linear Model	Diptera abundance ~ season	0.3391	LR $\chi2$ = 12.95, df = 2, p = 0.0015	August-February: 0.6839, August-June: **0.0007,** February-June: **0.0166**
Generalised Linear Model	Coleoptera abundance ~ season	0.1140	LR $\chi2$ = 3.80, df = 2, p = 0.1497	August-February: 0.2044, August-June: 0.9937, February-June: 0.1706
Generalised Linear Model	Hemiptera abundance ~ season	0.4614	LR $\chi2$ = 15.82, df = 2, p = 0.0004	August-February: 0.7709, August-June: **0.0002,** February-June: **0.0095**

Table S4. Results of the Generalised Linear models comparing effects of season for Braconidae, Halictidae and Formicidae (insects from the two sampling methods were grouped).

Model	**Formula**	**Lognormal R^2**	**Analysis of variance**	**Pairwise Comparisons (p-values)**
Generalised Linear Model	Formicidae abundance ~ season	0.6024	LR $\chi2$ = 23, df = 2, p < **0.0001**	August-February: 0.427, August-June: **0.0001,** February-June: **0.0005**
Generalised Linear Model	Halictidae abundance ~ season	0.3332	LR $\chi2$ = 8.44, df = 2, p = **0.0147**	August-February: 0.450, August-June: **0.0125,** February-June: 0.156
Generalised Linear Model	Braconidae abundance ~ season	0.3713	LR $\chi2$ = 16.31, df = 2, p = **0.0003**	August-February: 0.810, August-June: **0.0113,** February-June: **0.0010**

Table S5. Results of the models (Generalised Linear Model, Linear Model and Linear Mixed Model) used to explore the effect of site (depression, restored, unrestored) on abundance, species richness and Simpson diversity index (combining results from the two sampling methods).

Model	Formula	R^2	Restored - Depression Estimate (SE, p-value)	Unrestored - Depression Estimate (SE, p-value)	Analysis of variance	Pairwise Comparisons (p-values)
Generalised Linear Model	Abundance ~ site	Lognormal R^2 = 0.1934	0.6686 (0.2329, p = **0.0041**)	0.4234 (0.2421, p = 0.0803)	LR $\chi2$ = 8.14, df = 2, p = **0.0171**	Depression - Restored: **0.0114** Depression - Unrestored: 0.1871 Restored - Unrestored: 0.5648
Linear Model	Log 1p (Species richness) ~ site	R^2multiple = 0.0059	0.08439 (0.17786, p = 0.638)	0.0606 (0.1846, p = 0.744)	F = 0.12, df = 2, p = 0.888	Depression - Restored: 0.8837 Depression - Unrestored: 0.9424 Restored - Unrestored: 0.9909
Linear Model	Log 1p (Simpson diversity) ~ site	R^2multiple = 0.1026	-0.4505 (0.2141, **p = 0.0417**)	-0.2988 (0.2222, p = 0.1862)	F = 2.29, df = 2, p = 0.1148	Depression - Restored: 0.1017 Depression - Unrestored: 0.3793 Restored - Unrestored: 0.7746
Linear Mixed Model with lmer using REML (Restricted Maximum Likelihood)	Log1p (Simpson diversity) ~ site + (1|season)	R^2c = 0.3913	-0.4505 (0.1838, **p = 0.019**)	-0.2585 (0.1915, p = 0.1848)	$\chi2$ = 6.05, df = 2, p = **0.0487**	Depression - Restored: **0.0487** Depression - Unrestored: 0.3775 Restored - Unrestored: 0.5803