Basic and Applied Ecology 81 (2024) 35–43

Contents lists available at ScienceDirect

Basic and Applied Ecology

journal homepage: www.elsevier.com/locate/baae

RESEARCH PAPER

Functional traits mediate ant community assembly in a West African savannah-forest mosaic (Côte d'Ivoire)

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ARTICLE INFO

Keywords:
Ant diversity
Community composition
Bioindicators
Species richness
Community ecology
Functional traits
Tropical grassy biomes
Forest-savannah mosaic

ABSTRACT

African forest-savannah mosaics are complex landscapes holding mixtures of woody grasslands (savannah) and different forest systems (gallery forests and forest islands). In these landscapes, ants are highly diverse and perform essential ecosystem services, however, the assembly of ant communities in African forest-savannah mosaics is poorly understood. Here we showed the diversity and species overlap of ant communities in three habitats of the West African savannah and quantified the contribution of thermal tolerances and trophic ecology to community assembly. We investigated ant diversity in the West African Comoé National Park (Côte d'Ivoire) at 16 sites of three habitat types within a forest-savannah mosaic: continuous gallery forest, isolated forest islands and savannah. Across all sites, we collected a total of 91 species from 35 genera from three strata: trees, leaf litter, and soil. Additionally, we assessed differences in functional traits (trophic groups and thermal tolerance) between habitat types and strata. Though species richness was similar in all three habitats, there was a clear separation in species assemblages and functional traits between the two forest habitats and the savannah. Species assemblage shifts were primarily due to species turnover between savannah and forest habitats. In addition, the turnover in species assemblages from forests to savannah habitats was associated with a change in the thermal tolerance of species and in the proportion of trophobionts and predators. Forest and savannah habitats support distinct ant communities with different functional traits and contribute additively to the landscape-scale diversity of the West African ant fauna. Land-use and park management should focus on conserving both savannah and forest sites in tropical protected areas such as the Comoé National Park.

Introduction

Tropical landscapes are biodiversity hotspots, with two major distinct terrestrial biomes: tropical grassland or savannahs on the one hand and closed-canopy forests on the other (Murphy, Andersen & Parr, 2016). Though tropical forests receive more attention, both in research and in conservation efforts, tropical grassy biomes cover 20% of all tropical landscapes globally and provide critical ecosystem services (Parr et al., 2014). In fact, the species richness of vertebrates in savannahs is comparable to those of forest biomes despite lower plant diversity (Murphy, Andersen & Parr, 2016), while at the same time being more threatened and suffering a greater area reduction than rainforests (Hoekstra et al., 2004; Buisson et al., 2021). Especially West African savannahs are under high pressure and habitat reduction, endangering their biodiversity (Konaté & Kampmann, 2010). In grassy habitats, not only vertebrate megaherbivores are important: invertebrate animal groups such as termites and ants can be equal or greater in biomass than vertebrate herbivores and function as ecosystem engineers in these biomes (Schultheiss et al., 2022). Social insects are especially dominant in tropical landscapes, weighing 20% of the total human biomass and more than mammalian and avian wildlife combined (Schultheiss et al., 2022; Greenspoon et al., 2023), yet they are understudied compared to vertebrates in tropical grassy biomes.

Ants are important bioindicators and their key ecological functions,

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https://doi.org/10.1016/j.baae.2024.10.003
Received 4 December 2023; Accepted 8 October 2024

such as predation and nutrient cycling, influences natural and human-managed ecosystems (Crist, 2009). Habitat complexity plays a major role in ant diversity because of microhabitat specialization (Ribas et al., 2003; Vasconcelos & Vilhena, 2006). For example, in landscapes with a high density of trees, tree canopies can harbour a high diversity of invertebrates, and arboreal species richness is expected to be high in tropical landscapes, whereas in savannahs, invertebrate diversity is not primarily located in the canopy like tropical forests but in the grass and at ground level (Brühl, Gunsalam & Linsenmair, 1998). Yet, the contribution of arboreal ant fauna to overall ant diversity in savannahs is mostly unknown as it is understudied compared to tropical rainforests. Similarly, the subterranean fauna is diverse and abundant (Schmidt & Solar, 2010), but owing to difficulties in sampling, many studies did not investigate subterranean ant fauna (Berghoff et al., 2003). Therefore, to analyse composition of ants and their diversity in a tropical savannah-forest mosaic, all strata, including trees, leaf litter, and soil, should be included to increase the robustness of ant diversity studies.

Though differences in species richness between habitat types are expected, investigating species richness as the only metric of diversity has its limitations. With habitat differences and disturbance, certain species may be lost as they cannot persist in an unsuitable environment. Alternatively, species can be replaced by others – which can result in no net differences in species richness between distinct habitats. These two mutually exclusive processes, known as nestedness (species loss) or turnover (species replacement), can drive species assemblage shifts (Baselga, 2010). Changes in species community composition among habitats can be mediated by species whose functional traits are better fitting to certain habitat conditions. Two key functional traits are trophic ecology and thermal tolerance. In ants, trophobiotic species are usually found in open habitats or strata with direct sunlight, such as the canopy (e.g. Blüthgen, Mezger & Linsenmair, 2006; Crist, 2009). Generalist species are often superior under harsh conditions and fluctuating resources. In open grassland habitats, ants face much higher temperatures than in forests at ground level, with midday temperatures often exceeding critical thermal limits. As a result, ants living in these exposed habitats have to adapt physiologically or behaviourally to these hot environments.

Though the contribution of different habitat types in savannah-forest mosaics in West Africa has been studied before (e.g., Yeo et al., 2017; Vanthomme et al., 2017; Yode et al., 2023), these studies conflict in their findings. For example, Vanthomme et al., (2017) and Yode et al., (2023) found lower richness in savannah than in forested habitats, whereas Yeo et al., (2017) found no richness differences. However, these studies limited their sampling to one or two strata and did not investigate community functional traits in detail. The inclusion of additional strata in the sampling design as well as investigating ant functional traits as possible drivers could further elucidate diversity differences between habitat types in the tropical landscapes of West Africa.

The Comoé National Park in Côte d'Ivoire is one of the biggest protected areas in West Africa and an example of a complex savannah-forest mosaic landscape in the tropics. Its unique biodiversity has earned it the status of a UNESCO World Heritage Site. It is home to several charismatic mammal and bird species such as chimpanzees, ground hornbills and elephants, though the park's invertebrate fauna has received less attention. There are three main habitat types in the park: continuous gallery forests, savannah, and isolated forest islands. Here we investigate the contribution of each of these three habitat types on ant richness, community composition, and community functional traits, by thoroughly sampling ants from all strata: trees, leaf litter, and soil. With this, we wanted to test the following predictions:

I. Ant richness (α-diversity) is positively related to tree density and negatively to isolation from similar habitats. We therefore expect the highest richness in gallery forests and the lowest richness in savannah sites, with forest islands representing an intermediate state. We expect ant community composition to differ between the three habitat types. We expect community composition differences (β-diversity) between savannah and forest sites to be due to turnover (species replacement), but assemblage differences between the two forest habitats to be due to species loss between gallery forest and forest islands.

II. Community functional traits, specifically trophic group and thermal tolerance, differs between habitat types and strata. Due to differences in habitat characteristics, we expect open habitats, such as savannahs, to support proportionally more trophic generalists and species with higher thermal tolerances than in forests. Similarly, we expect differences in functional traits among strata. For example, we expect more specialist predators with a lower thermal tolerance in the soil traps compared to trees and the leaf litter, potentially due to the presence of soil-dwelling prey and shaded conditions (Baudier et al., 2015).

III. Tree, leaf litter and soil traps complement each other in the community composition of ants captured, therefore, we expect that ant community composition and the trophic groups captured from the three strata to be distinct.

Materials and methods

Study region and study sites

The study was conducted in the Comoé National Park, located in the North-eastern region of Côte d'Ivoire (Fig. 1A) at the Comoé National Park Research Station (8°46′N 3°47′W; Fig. 1B). The climate is tropical with temperatures over the year ranging from 20.6 to 32.2 °C and distinct dry and rainy seasons (Kampmann and Konaté 2010). The wet season lasts over 6 months distributed in two periods with a longer season from March to June and a shorter season from September to October. The annual precipitation ranges from 1500 to 2200 mm with the highest precipitation in June (180 mm) and October (120 mm) (Yeo et al., 2017).

The data was collected from May to July 2017 during the beginning of the rainy season, complemented by an opportunistic hand collection from August to November 2015. Data on thermal tolerance was collected from late April to June 2019. The sampled savannah was a grassland with shrubs and small trees dominated by the grasses of *Loudetia simplex* and *Hyparrhenia* spp., while the continuous gallery forest was near the Comoé River and its tributary Iringou with a high density of *Cynometra* trees. The study included five savannah plots, five gallery forest plots and six forest island plots (Fig. 1C), three nearby habitat types were considered nested in five areas. Forest islands were fully surrounded by savannah, while the gallery forest was a continuous forest, stretching on both sides of the Comoé River, with a width of up to ~375 m at either side of the river.

Ant community sampling

At each habitat within a sampling plot, 10 samples were taken in two parallel 40 m transect lines with at least a 50 m distance from the edge of the habitat and a 10 m distance between sampling points along the transects. For every sampling point three different sampling methods were used: (1) a Winkler trap with a collection area of 1 × 1 m for the leaf litter layer. This was done after the protocol of Agosti & Alonso (2000). The leaf litter samples were collected in the field, sifted, and transported to the laboratory in plastic bags. In the case of the savannah habitat, leaf litter samples consisted mainly of grass material rather than tree leaves. After transferring into mesh bags, each individual sample was dried for 48 h in the Winkler funnel with an ethanol filled cup. The extracted animals in the ethanol were sorted and counted in the laboratory. (2) A soil sample of a 30 × 30 × 30 cm area on the sample plot cleared by the Winkler trap to prevent collecting species from the surface. The soil samples were excavated with a shovel and sieved through over a white cloth to allow us to easily detect the ants which were then

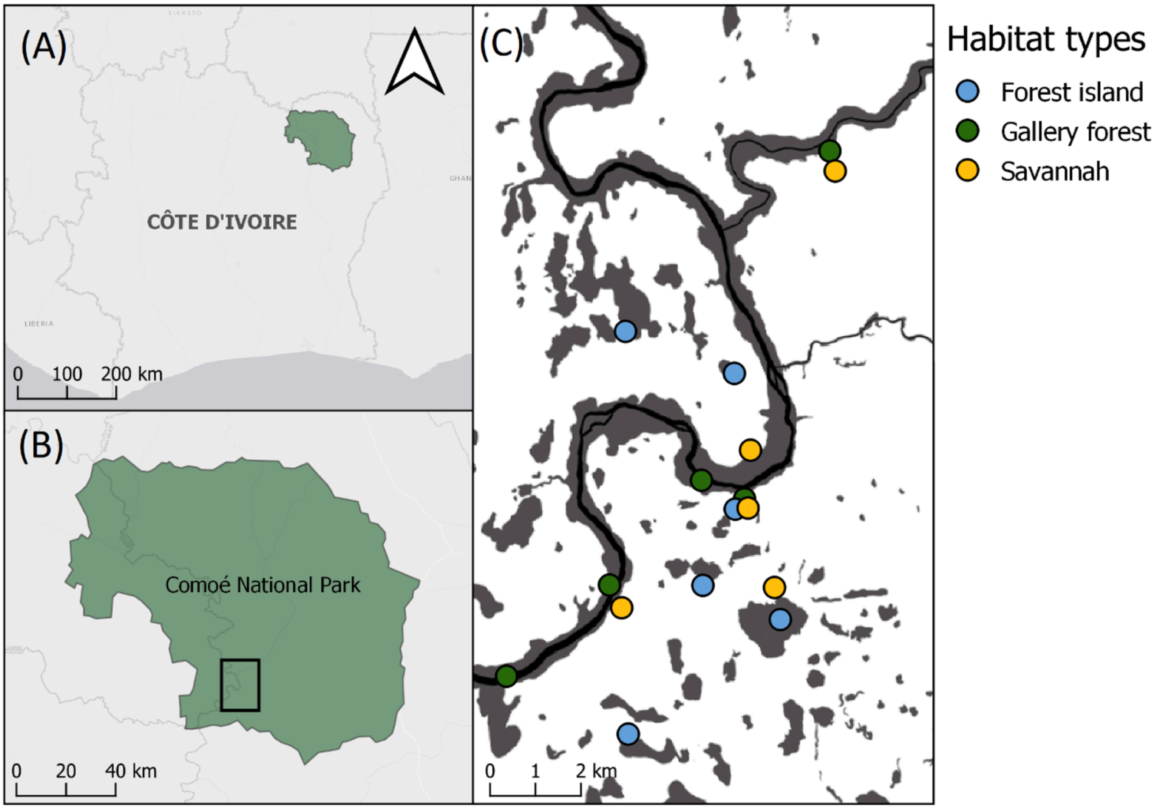

Fig. 1. Map showing (A) the location of the Comoé National Park (in green) within Côte d'Ivoire, (B) the location of the sampling area within the Comoé National Park (indicated by the black rectangle) and (C) the location of the sample sites within the sampling area. In (C) the Comoé River is indicated in black, forested habitats, including the gallery forest along the Comoé River and the forest islands are indicated in grey, and the savannah is indicated in white.

individually placed in alcohol. (3) A honey bait, consisting of a petri dish with a drop of local unprocessed honey attached to a tree trunk with a diameter at breast height of at least 15 cm and a maximum distance of 1 to 4 m from the Winkler sample. The honey baits with ants were collected after one hour and stored in plastic bags and were frozen in the local lab. In the laboratory, all ants were extracted from samples and identified to genus and morphospecies level on the basis of "The Ants of Africa and Madagascar: A Guide to the Genera" by Fisher and Bolton (2016) and stored at the University of Würzburg (Germany).

Trophic groups

We assigned trophic groups (generalists, generalist predators, specialist predators, trophobiotic ants, and cryptic ants) at the genus level using descriptions of the habits and biology of the genera in Fisher and Bolton (2016) and additional information from "Ants: standard methods for measuring and monitoring biodiversity" by Agosti et al., (2000). We considered ants generalists if they were described to have a diet that to some extent combines animal prey, plant matter, extrafloral nectar and/or honeydew produced by other insects. Generalist predators are ants that consume no plant matter but may consume a variety of animal prey, whereas in contrast, specialist predators consume only a single animal prey group. Trophobiotic ants primarily consume honeydew produced by other insects. We do not include ants that are opportunistically trophobiotic in this group, these species would be considered generalists. Finally, cryptic ants are genera with small workers restricted to leaf litter, soil or rotting organic material. For four detected genera, specifically *Bothroponera, Dicroaspis, Euponera*, and *Nesomyrmex,* very little is known about their habits and biology, and we therefore could not assign them a trophic group (Table S1).

Thermal tolerance

Ants for thermal tolerance analysis were collected by hand or with an aspirator. Foragers, rather than nest workers, were collected as these are more likely to be exposed to heat stress at the surface. We collected foragers opportunistically in each habitat type from early morning to midnight. At least ten individuals of each foraging colony were collected. Ambient temperature at the time of collection was noted.

Upon collection, ants were immediately tested for their critical thermal maximum (CT_{max}). Each individual was placed in individual tubes. Tubes were sealed with moist cotton wool to prevent ants from dying from drought or lack of oxygen. The tubes were then placed in an Eppendorf© heating block. Tests started at 34 °C (i.e. a temperature tolerated by all ants in pre-experiments), and the temperature was increased by 1 °C every 10 min. Every 10 min, we examined the tubes to check if the ants were still alive. When 50 % of the ants (5 individuals) had died, we ended the experiment and the temperature was noted as the CT_{max} for this species. Ants collected for thermotolerance analysis were also identified using the key in Fisher and Bolton (2016).

Statistical analysis

All statistical analyses were conducted in R version 4.1.0 (R Core Team, 2021).

Species richness and community composition differences between habitat types

First we assessed if the sampling coverage was comparable across the three habitat types using the package 'iNEXT' (Hsieh, Ma & Chao, 2016). We found overall sampling coverage by plot to be comparable across the habitat types: for forest islands = 81.1 % (mean 83.47 ± 9.93 % sampling cover at plot level), gallery forest = 76.4 % (mean 83.87 ± 4.82 %

sampling cover at plot level) and savannah = 74.4 % (mean 64.86 ± 8.02 % at plot level) (Figure S1). To test for differences in ant species richness between the three habitat types (forest islands, gallery forests or savannah), we used the cumulative species richness of ants across the sampling methods in each habitat type plot per area. We used generalized linear mixed models with a Poisson distribution using the 'glmmTMB' function from the 'glmmTMB' package (Brooks et al., 2022). Since habitat types were nested in an area, we used area as a random effect in the model. If habitat differences were detected, we tested pairwise differences between habitat types using the 'emmeans' function from the 'emmeans' package (Lenth et al., 2021). To validate if our observed patterns were not due to differences in sampling coverage, we repeated our analysis using the estimated richness ($q = 0$) calculated by 'iNEXT' (Table 1). As we found similar patterns, we further report only observed richness in this study.

To test differences in community composition between habitat types, we generated a presence/absence matrix for the species in each habitat type plot per area. We then calculated a permutational multivariate analysis of variance (PERMANOVA) with the Chao-Jaccard dissimilarity index (suitable for presence/absence matrices) and 999 permutations, using the 'adonis2' function from the 'vegan' package (Oksanen et al., 2020). We included 'strata = area' to account for the nestedness of the three habitat types within areas. We visualized the ant species community composition using non-metric multidimensional scaling (NMDS).

To assess if any differences in species community composition were due to turnover (replacement of species between habitat types), nestedness (species loss between habitat types), or a combination of both, we created an aggregated species matrix for the three habitat types (i.e., the cumulative species matrix for the three habitat types across areas). In our analyses, we chose to follow the framework proposed by Baselga, (2010). Though other methods of partitioning β-diversity exist, we chose this framework as it is a commonly applied method of partitioning β-diversity as it allows easy comparison with similar studies and is suitable for the partitioning of presence/absence species data. Then, from the 'betapart' package, we used the function 'beta.multi' to compute the total dissimilarity between the habitats, and the function 'beta.pair' to calculate pairwise differences between habitat types (Baselga & Orme, 2012). For both functions, we used Jaccard dissimilarity.

Trophic group and thermal tolerance differences between habitat types

To test the effect of habitat type (savannah, forest island and gallery forest) on the proportional representation of trophic groups in the community composition (Table S1) we accumulated the number of species per trophic group per plot within each area. Since cryptic ants were only very poorly represented in the species pool (2 out of 26 potential species at a site), we limited our analyses to generalists, generalist predators, specialized predators and trophobiotic ants. In addition, the biology of four genera is poorly understood, and we were therefore unable to confidently assign them trophic groups. However, this affected only 5 species found in our study. To test whether there are differences between habitat types in the proportion of species represented by these three trophic groups, we calculated generalized linear mixed models with a Beta distribution (suitable for proportional data), again using 'glmmTMB' from the 'glmmTMB' package, with habitat type as a fixed effect and area as a random effect. If we detected habitat type differences, we again used 'emmeans' to test pairwise differences between habitat types. To test the effect of habitat type on the trophic group composition in the community, we calculated a proportion matrix of all five trophic groups and used a PERMANOVA, but this time using the Bray-Curtis method (suitable for proportional matrices) and 999 permutations. Again, we included 'strata = area' to account for the nestedness of the habitat types within areas.

To test the differences in thermal tolerance of ants (as defined by their critical thermal maximum: CT_{max}), between habitat types (forest islands, gallery forest and savannah), trophic groups, and strata (soil, leaf litter and trees) we used linear models testing CT_{max}, against these three predictors. If group differences were detected, we again used 'emmeans' to detect pairwise differences between habitat types, trophic groups and/or strata. To test how closely the CT_{max} values match the ambient temperature at which the species were collected (and thus were active), we used a linear model testing CT_{max} against ambient temperature at the time of collection.

Trap efficacy at different strata

To test the efficacy of the traps in different strata (soil, leaf litter and trees), we calculated the cumulative species richness per trap and habitat type (savannah, forest islands, and gallery forest) within an area. We then calculated a generalized linear mixed effects model with a Poisson distribution using trap type in interaction with habitat type as fixed effects and area as a random effect. Similarly, to test the probability of collection of different trophic groups in the traps in different strata we calculated a binomial model testing the proportion of generalists, generalist predators and specialist predators against strata with site as a random effect. To test whether different traps catch different species communities (and therefore, complement each other when catching the whole species communities at a plot) and trophic groups, we calculated a presence/absence species matrix for soil and leaf litter traps, and a proportion matrix of the trophic groups accumulated across the habitat types. Tree traps were excluded as they captured only a very limited number of species. We then used a PERMANOVA using the

Table 1

Model results. (*) = $p < 0.100$. * = $p < 0.050$. ** = $p < 0.010$. *** $p < 0.001$. DF_{num} = numerical degrees of freedom. DF_{den} = denominator degrees of freedom. R^2 is the conditional/marginal R^2 (in the case of GLMMs) or adjusted R^2 (in the case of LMs). For zero-inflated Beta distributions, no R^2 values are reported. LM = linear model. GLMM = generalised linear model.

Predictors	Response	Chi^2-value	p-value	DF_{num}, DF_{den}	R_c^2/R_r^2	Model type
Habitat type	Species richness	4.91	**0.086(*)**	2, 12	0.26/0.26	GLMM with Poisson distribution
	Estimated richness (q = 0)	3.06	0.216	2, 12	0.16/0.17	LMM
	Proportion of generalists	6.10	0.408	2, 11	0.25/0.31	GLMM with Beta distribution
	Proportion of generalist predators	19.10	**< 0.001*****	2,10	n.a.	GLMM with zero-inflated Beta distribution
	Proportion of specialist predators	12.55	**0.002****	2, 10	n.a.	GLMM with zero-inflated Beta distribution
	Proportion of trophobionts	27.00	**< 0.001*****	2, 10	n.a.	GLMM with zero-inflated Beta distribution
Strata	Species richness	63.37	**< 0.001*****	2, 14	0.53/0.89	GLMM with Poisson distribution
	Proportion of generalists	6.34	**0.042***	2, 13	0.53/0.82	GLMM with Beta distribution
	Proportion of generalist predators	1.45	0.485	2, 12	n.a.	GLMM with zero-inflated Beta distribution
	Proportion of specialist predators	5.88	**0.053(*)**	2, 12	n.a.	GLMM with zero-inflated beta distribution
	Proportion of trophobionts	17.92	**< 0.001*****	2, 12	n.a.	GLMM with zero-inflated beta distribution
Ambient foraging temperature	Critical thermal maximum (CT_{max})	7.71	**0.007****	1, 60	0.10	Linear model
Habitat type	Critical thermal maximum (CT_{max})	8.72	**< 0.001*****	2, 68	0.47	Linear model
Strata		0.08	0.913	2, 68		
Functional group		4.32	**0.008****	2, 68		

Jaccard method for species community composition. Jaccard dissimilarities are suitable here because we used the sampling effort between soil and leaf litter traps, which were equal across sites. For community functional groups we used the Bray-Curtis method. Each PERMANOVA had 999 permutations, again using strata = area to account for nestedness.

All models were checked individually for collinearity and overdispersion (of residuals). Any remaining model assumptions were checked visually using the 'performance' package (Lüdecke et al., 2021). We detected no violation of model assumptions.

Results

Across all traps, we detected 91 (morpho)species from 35 genera and 5 subfamilies (Table S1). We found 53 species in the savannah, 45 species in the forest islands and 57 species in the gallery forest (Figure S2). 52 species were found in the soil, 23 in trees and 74 in the leaf litter across all habitats. For thermal tolerance analyses, we collected a subset of 39 of these species (11 in forest islands, 16 in the gallery forest and 23 in the savannah). Additionally, 46 species (12 in forest islands, 14 in gallery forests and 20 in savannahs) were collected opportunistically by hand (Table S1). Twenty-seven of these species were not detected in the traps, bringing the total number of species detected in this study for the Comoé National Park to 118 ant species of 7 subfamilies.

Species richness and community composition differences between habitat types

Gallery forests had the highest mean species richness (21.4 ± 4.62 species per plot; 57 species across all five gallery forest plots), whereas forest islands had the lowest mean species richness (15.7 ± 5.20 species per plot; 45 species in total), with savannah habitats having an intermediate mean species richness (19 ± 2.55 species per plot; 53 species in total). However, species richness was not significantly different between the habitat types (Fig. 2a; Table 1; Table S2). Community composition, in contrast, differed strongly between savannah habitats and the two forest habitats (Fig. 2B; Table 2). The dissimilarity between the forest islands and gallery forests was much lower than dissimilarities between savannah and the two forest habitats, and dissimilarities were driven by species turnover, rather than nestedness (Fig. S3; Table 3).

Table 3
Pairwise comparison of Jaccard dissimilarity between the habitat types.

Total dissimilarity		Contrast		Dissimilarity
Total dissimilarity (β_{JAC})	0.64	Forest island	Gallery forest	0.47
		Forest island	Savannah	0.67
		Savannah	Gallery forest	0.71
Turnover (β_{JTU})	0.68	Forest island	Gallery forest	0.36
		Forest island	Savannah	0.63
		Savannah	Gallery forest	0.70
Nestedness (β_{JNE})	0.04	Forest island	Gallery forest	0.11
		Forest island	Savannah	0.04
		Savannah	Gallery forest	0.01

Trophic group and thermal tolerance differences between habitat types

The proportional representation of different trophic groups in the ant species community differed significantly between the different habitat types (Table 1). Overall, generalists were the best represented in the community (proportion: 0.54 ± 0.10), followed by generalist predators (proportion: 0.16 ± 0.07), trophobionts (proportion: 0.13 ± 0.15), and specialist predators (proportion: 0.12 ± 0.07). Cryptic species were very rare in the ant community (proportion: 0.03 ± 0.04). Generalists were equally common in all 3 habitats (Fig. S4a). While generalist predators

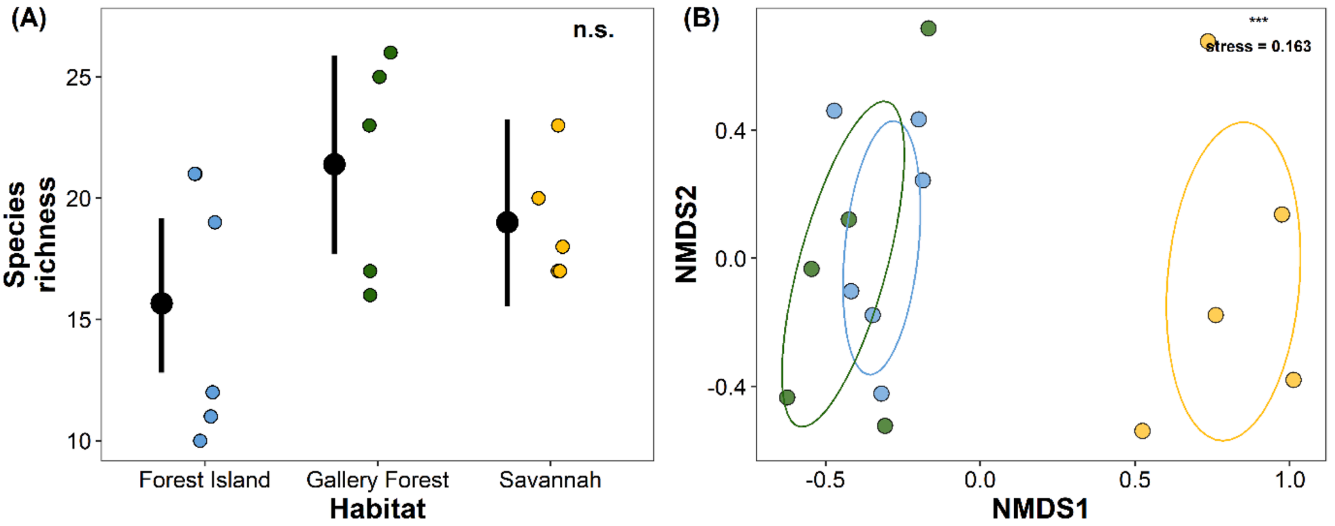

Fig. 2. (A) Species richness in the three habitat types (Tables 1 & S2), and (B) species community composition (Table 2). Blue = forest island (n = 6), green = gallery forest (n = 5) and yellow = savannah (n = 5; n = 16 total sites). In (A) black dots indicate the predicted mean and the vertical lines indicate the 95% confidence interval of the prediction. In (B) ellipses represent the standard deviation from the centroid of the habitat clusters. Coloured dots represent individual datapoints. n.s. = $p > 0.05$, *** = $p < 0.001$.

Table 2
Results of the PERMANOVAs assessing species or trophic community composition differences. DF= degrees of freedom. (*) = $p < 0.100$, * = $p < 0.050$, ** = $p < 0.010$.

Predictors	Response	Method	F-value	p-value	DF	R^2
Habitat type	Species community composition	Chao - Jaccard	2.18	**< 0.001*** **	13	0.88
	Trophic group composition	Bray – Curtis	9.30	**0.003** **	13	0.59
Trap type (soil vs. leaf litter)	Species community composition	Jaccard	1.97	**0.031***	10	0.84
	Trophic group composition	Bray – Curtis	3.64	**0.031***	10	0.27

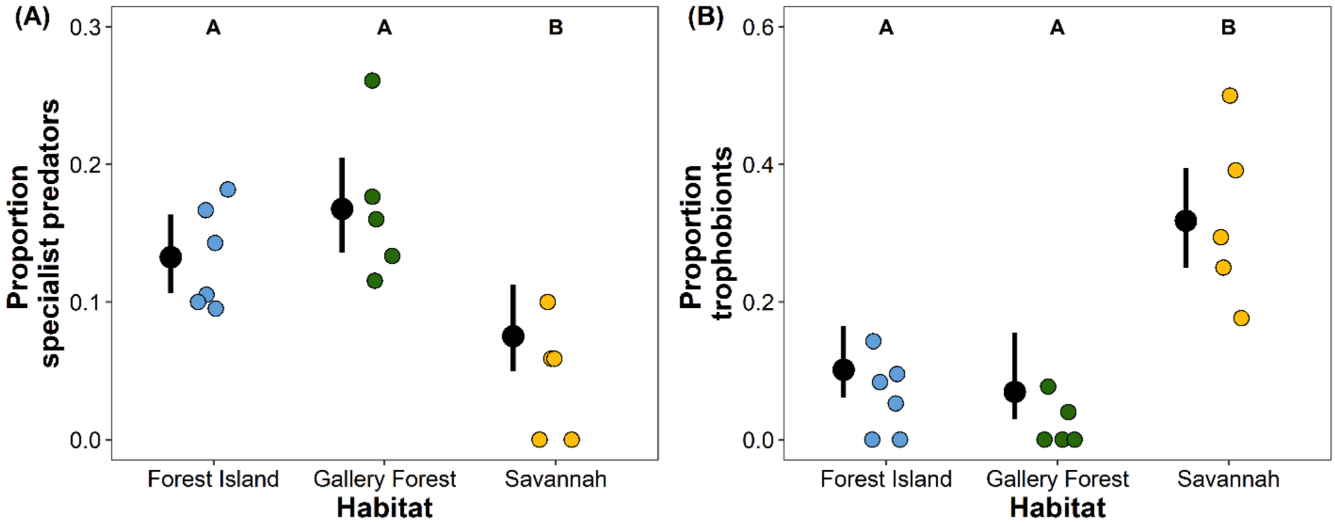

Fig. 3. (A) The proportion of specialist predators in the three habitat types (Tables 1 & S2), and (B) the proportion of trophobionts in the three habitat types (Table 1 & S2). Blue = forest island (n = 6), green = gallery forest (n = 5) and yellow = savannah (n = 5; n = 16 total sites). Black dots indicate the predicted mean and the vertical lines indicate the 95% confidence interval of the prediction, letters indicate significant group differences ($p < 0.05$). Coloured dots represent individual datapoints.

(Fig. S4b) and specialist predators (Fig. 3A) were both least represented in savannah habitats and best represented in gallery forests and forest islands. Trophobiotic species showed an inverse pattern: they were relatively more abundant in savannah habitats than either forest habitat (Fig. 3B, Table S2). The trophic group composition differed therefore significantly between habitat types (Fig. S4c; Table 2).

The observed critical thermal maximum ($\mathrm{CT}_{\mathrm{max}}$) of ants was positively related to the ambient temperature at which they were foraging (Fig. 4B; Table 1). The $\mathrm{CT}_{\mathrm{max}}$ of ants differed significantly between habitat types (Fig. 4a) and between ant trophic groups, but not between strata (Fig. S5a; Table 1). Ants from savannah habitats had a higher thermal tolerance than ants collected in forest habitats (Fig. 4A). Overall, trophobionts had a higher thermal tolerance than generalists and specialist predators, whereas generalist predators had an intermediate thermal tolerance (Fig. S5b; Table S2).

Trap efficacy from different strata

Tree, leaf litter, and soil traps (placed in their respective strata) differed significantly in the species richness of ants caught. Tree traps performed most poorly (3.79 ± 1.19 species), followed by soil traps (7.63 ± 3.28 species) and leaf litter traps (13.38 ± 4.27 species) (Fig. S6a). Community composition captured by soil and leaf litter traps also differed significantly (Fig. S6b; Table 2). Generalist predators were equally common across all three strata (Table 1 & S2). Generalists were best captured in trees, with lower proportions captured in soil and leaf litter (Fig. S6c). In contrast, specialist predators were best captured in leaf litter, with low proportions in soil samples (Fig. S6e). Only at one plot were specialist predators detected on trees (Fig. S6e). Trophobiotic ants were best captured from trees and were less common in leaf litter and soil samples (Fig. S6f). The composition of trophic groups therefore differed between soil and leaf litter traps (Fig. S6d, Table 2).

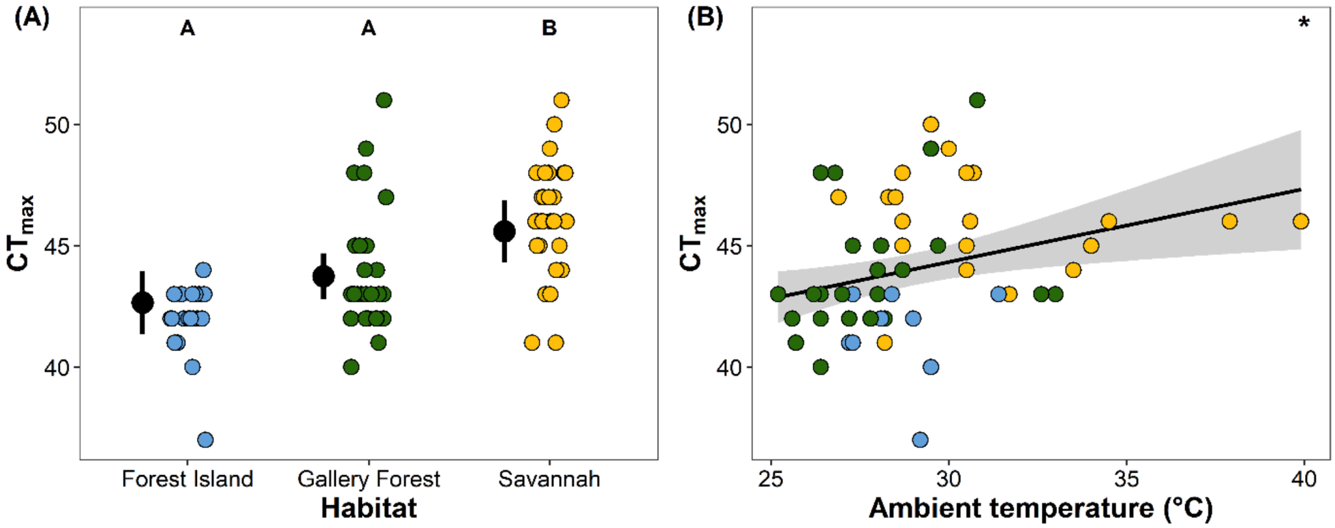

Fig. 4. (A) Critical thermal maximum ($\mathrm{CT}_{\mathrm{max},}$ in°C) of ants collected in the different habitat types (forest island n = 20; gallery forest n = 29; savannah n = 34; total n = 83), and (B) relationship between the measured critical thermal maximum ($\mathrm{CT}_{\mathrm{max}}$) of the collected ants and the ambient temperature at which they were collected (n = 75; $R^2 = 0.10$; tables 1 & S2). In (A) black dots indicate the predicted mean and the vertical lines indicate the 95% confidence interval of the prediction, letters indicate significant group differences ($p < 0.05$). In (B) the black line indicates the predicted trend and the grey area the 95% confidence interval of the prediction. Coloured dots represent individual datapoints. * = $p < 0.05$.

Discussion

Species richness and community composition differences between habitat types

A high distinctness between savannah and forest ant community composition in landscapes where they co-occur is a worldwide pattern (Fisher & Robertson, 2002; Vasconcelos & Vilhena, 2006; Cuissi et al., 2015; Yeo et al., 2017), and we confirm this pattern for the West African savannah-forest mosaic. In addition, our parallel assessment of functional traits suggests that these species composition shifts might, at least in part, be facilitated by species-specific functional traits (trophic niches, thermal tolerance), which significantly differ among ant communities of forest and savannah habitats. Though we expected higher richness in the forest habitats because of their more complex vegetation structure (Stein & Kreft, 2015), differences were not significant.

There were no significant differences between gallery forest and forest islands in terms of species richness and community composition, and limited differences in community functional groups, but we found that overall, forest islands had the lowest species richness of all three habitats. Despite the relative under-appreciation of tropical grasslands compared to tropical forests as biodiverse habitats, the distinct communities between forest and savannah habitats was caused by species turnover, further emphasizing that savannahs are valuable habitats in their own right and support a unique ant fauna (Yeo et al., 2017; Strömberg & Staver, 2022). In addition, we do not find evidence for lower richness in West African savannah habitats (in contrast to, e.g., Yode et al., 2023). In contrast with savannahs, that supported 23 unique species, forest islands had only 4 species unique to that habitat type, and 78% of species found in forest islands were also found in gallery forests. Despite the lower species richness, in their current state, forest islands are valuable for conserving forest ant communities within the savannah matrix. However, with continued isolation forest island communities may become increasingly distinct from continuous gallery forest habitats. For example, ant communities in the Amazon rainforest had both distinct communities as well as lowered species richness in isolated forest islands compared to continuous forests (Vasconcelos & Vilhena, 2006). The currently high overlap between forest islands and the gallery forest may possibly be due to low isolation, ants with high dispersal ability and a similar forest vegetation. Therefore, size and isolation of forest islands could further elucidate the effects of habitat fragmentation in West Africa on ant communities in future studies.

Trophic group and thermal tolerance differences between habitat types

Mirroring the patterns in ant communities among the three habitat types, we find distinctions between the representation of trophic groups and the thermal tolerance of the species in the three habitat types. This reflects differences in conditions among the habitat types and suggests that functional traits are important drivers of ant community responses to habitat differences (Mauda et al., 2018).

We show that savannah habitats clearly support proportionally fewer predators and more trophobionts than forest habitats. Differences in ant functional groups between forests and savannah may be caused by different disturbances in different habitat types and related landscape management, such as fire in savannah habitats (Kone et al., 2018), or more continuous vegetation and microclimatic conditions between wet and dry seasons (Konaté & Kampmann, 2010). For predators, structurally complex forest habitats could support a higher abundance of suitable animal prey (Parr, Gray & Bond, 2012). In addition, specialised trophic groups in forests are particularly sensitive to vegetation changes. Cryptic species, such as *Calyptomyrmex* spp. foraging in soil and leaf litter, and large specialist predators such as *Psalidomyrmex* spp., which are usually solitary and active hunters are expected to decline with increased disturbances such as those common in savannah habitats (Hoffmann & Andersen, 2003). In contrast, flowering plants and honeydew-producing insects might be more common on savannah-specific vegetation, like grasses or acacias. This is additionally supported by the fact that we found the highest proportion of trophobionts in trees, rather than at ground level. Higher occurrences of trophobiotic ants in the canopies is a worldwide pattern and found in many types of habitats (Blüthgen, Mezger & Linsenmair, 2006; Crist, 2009). Generalists seem to have no clear habitat preference, as they are adaptable and can persist in a wider range of conditions (Vanthomme et al., 2017). In contrast, both predatory and trophobiotic ants' interactions with other organisms, such as prey species or mutualists determine the ability of these trophic groups to survive in these habitats. Investigating the habitat requirements of ant prey or mutualists can be an important next step to optimise management for invertebrate diversity.

We found that ants living in savannah habitats tolerated higher temperatures (critical thermal maxima) than those living in forest islands and gallery forests. Moreover, we found a positive correlation between the environmental temperatures and the critical thermal maxima of ants. These findings corroborate the general pattern that ants' critical thermal limits are positively associated with the habitat temperature to which they are exposed (Roeder, Roeder & Bujan, 2021). There are two principal mechanisms which could explain this pattern. First, ants living in savannah habitats have acclimatized to higher temperatures (Roeder, Roeder & Bujan, 2021). Second, ant species living in savannah habitats show adaptations to warmer temperatures, e. g. higher molecular expression levels of heat shock proteins or morphological adaptations like larger body sizes (Peters et al., 2016; González-Tokman et al., 2020). The high species turnover observed between forest and savannah habitats, the generally extreme temperatures in savannah habitats, together with the high sensitivity of ant species to temperature, suggests that the thermal environment acts as an environmental filter for species. Surprisingly, stratum had no influence on the maximum thermal limit of ants in our study. In contrast, for Australian forest ants, stratum or arboreality was found to be important for temperature adaptation (Leahy et al., 2022). To our knowledge, our study's unique combination of different natural habitat types with stratum and thermal tolerance has not been previously investigated. Other studies on thermal tolerance have typically focused on a single factor, such as stratum (e.g., Kaspari et al., 2015) or elevation gradients (e.g., Bishop et al., 2017). However, in (sub)tropical Asian forest ecosystems, vegetation characteristics, climatic parameters and the thermal tolerance of the ants shaped their community (Lee et al., 2021; Leong et al., 2023), suggesting that similar pathways of environmental filtering act across different biogeographic regions. However, further experiments will be needed to fully understand the causal relationships between habitat type, thermal tolerances and community assembly in West African savannah-forest mosaics.

Trap efficacy at different strata

By collecting ant samples from three strata: soil, leaf litter, and trees, we found 91 species from 35 genera, comparable to other studies from similar habitats across the world (Fisher & Robertson, 2002; Neves et al., 2013; Cuissi et al., 2015), and we find clear differences among the strata. The arboreal diversity in this study was relatively low, though some unique species such as *Cataulacus* spp. and *Crematogaster* spp. were collected only from trees. While our arboreal diversity is lower compared to that reported by Yode et al., (2023), their study additionally employed beating and other traps on trees in a similar forest-savannah landscape. For example, *Oecophylla smaragdina* was less frequently sampled in our study, despite its high abundance and widespread distribution observed elsewhere (Yode et al., 2023). In addition, soil samples contained a lower species richness than leaf litter samples. More importantly, we show that soil and leaf litter traps contain a completely distinct community of ant species and trophic groups, which allows for a more complete understanding of ant diversity. Our results are consistent with Yeo et al.'s (2017) findings of distinct soil and leaf litter communities. Similar studies from West Africa usually resulted in lower species numbers than our study (Vanthomme et al., 2017; Kone et al., 2018; Yode et al., 2023), as these studies often used one or two trap types and sampled single strata. Our study, finding a higher richness than previous studies in the region where one would expect a similar richness, emphasises the necessity for thoroughly sampling all strata in the habitats. Although the total number of species in the three strata is slightly lower than in the study by Yeo et al., (2017) from the Lamto Scientific Reserve in Côte d'Ivoire, the inclusion of species from hand collections gives a similar number. Combining our results and other studies from that region, West Africa remains less sampled than other seasonal savannah-forest mosaics, such as the Cerrado in Brazil or the regions of central and northern Australia, yet it still exhibits impressive biodiversity.

This diversity has implications for our understanding of the ecological functions of these ant communities. For example, in West Africa, ground-dwelling species like *Dorylus* ssp. are only collected in soil samples and can have a great impact on other ground-dwelling insects. Subterranean *Dorylus* are one of the few animals that can wipe out entire termite colonies of *Macrotermes* (Schöning & Moffett, 2007), affecting ecological functions such as nutrient cycling, soil quality and vegetation structure. Therefore, we argue that in future studies, complementary trapping methods should be applied to gain a full understanding of ant communities. In addition, complex interactions between stratum and habitat recovery on ant community traits has been found in the neotropics (Hoenle et al., 2023). As the habitats sampled in the Comoé are naturally formed, we suspect parallel trends for the three strata in response to habitat type. Though the aim in this study was to demonstrate the complementarity between collection methods in different strata, a detailed future study into possible interactions between strata and habitat characteristics on ant diversity and functional traits may be warranted.

Conclusion

Tropical grassy biomes, such as the savannah-forest mosaic in the Comoé National Park in Côte d'Ivoire, are important but underappreciated biodiversity hotspots (Strömberg & Staver, 2022). Insects such as ants comprise most of the faunal biodiversity, yet the distribution of species across habitat types of forest-savannah mosaics and its drivers are not well known. Our study demonstrates that despite of a similar ant species richness in forest and savannah habitats, community composition, trophic groups and thermal tolerances are distinct between savannahs and forest habitats. For land and park management, conservation should focus on all habitats to secure a high diversity. Due to the distinctness of species community composition a destruction of the gallery forest or forest islands, or in contrast, encroachment of forests in savannahs, would result in a considerable loss of species in the national park. A good park management needs to protect all habitat types within grassland-forest mosaics with ants as a potential bioindicator for invertebrate community diversity and health.

Open research statement

All data included in this manuscript will be made public upon acceptance.

CRediT authorship contribution statement

Cassandra Vogel: Writing – original draft, Visualization, Formal analysis, Data curation. **Nils-Christian Schumacher:** Writing – original draft, Methodology, Investigation, Formal analysis. **Marcell K. Peters:** Writing – review & editing, Supervision, Formal analysis. **Karl Eduard Linsenmair:** Supervision, Funding acquisition, Conceptualization. **Erik T. Frank:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

CV was funded by a SCIENTIA postdoctoral scholarship. ETF is funded by the DFGs Emmy Noether Programme (n°: 511474012). We thank the Comoé National Park Research Station for the use of their facilities and park management of Office Ivoirien des Parcs et Réserves (OIPR) for the permission to conduct field research in the park. We further thank David Kouassi Kouame, Koffi Kouadio, Inza Ouattara, Lakado Maizan and Richard Ouattara for their assistance in this study. We thank Phillipp Hönle for providing the data of the hand-collected ants. We also thank Viesturs Leibold, Paula Schmidt and the students of the Comoé excursion 2019 for collecting the ants and data for the thermal tolerance analyses.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.baae.2024.10.003.

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