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# Impact of land-use changes on ant communities and the retention of ecosystem services in Rashad District, Southern Kordofan, Sudan

The ecological consequences of biodiversity loss are usually the reduction of ecosystem functions. These responses, however, differ depending on the type of land-use change and the ecological setting. We investigated the impact of land-use type and ecosystem functions on the ant assemblage of Rashad District, Sudan. We analysed the effects of three different land uses (soy monoculture, pasture and organic production of vegetables) on the ant community by assessing ant composition in 176 different locations. The collection sites were conventional soy monoculture, pastures, organic agriculture, and native vegetation such as Campo, Kubos, and forests. We recorded 264 ant species on the soil surface of the Rashad District, where 342 to 354 species were thought to exist. Pastures and organic agriculture areas have 61% and 56% of the native myrmecofauna, respectively, while conventional soy monoculture areas are home to only 17% of native ant species. Forest areas present a unique community, and soy monoculture areas have the strongest pattern of biotic homogenisation. We also detected that rare species (of low frequency) were the chief promoters of richness in the Rashad District, and the most threatened with local extinction, due to their low density and low occurrence in agrosystems. Overall, we found that agricultural expansion reduces ant diversity, particularly in soybean crops, and can affect ecosystem functions. To mitigate the reduction in the ant assemblage, we recommend the conservation of multiple natural habitats.

**Significance:**

- Agricultural land conversion and climate change play a major role in shaping tropical landscapes, but the direct and indirect links to biodiversity and species community composition remain poorly understood.
- Ant richness is correlated with biomass, demonstrating that the effects on ecosystem function are dependent on the particularities of each assessed function (such as resource type), the types of land uses, and the abundance of ants in the region.
- Land-use effects on ant diversity were strongly scale dependent.
- The highest ant diversity occurred in soy monoculture areas.

## Introduction

Conservation efforts have primarily focused on plant and vertebrate groups. Norris et al.<sup>1</sup>, for example, determined the planet's 'hotspots' using only vascular plants and vertebrates. Although these groups are the most well known in terms of described species, they account for a small proportion of biodiversity.<sup>2</sup> Insects, which account for the majority of animal biodiversity, have received little attention in conservation studies, possibly due to the large number of species and/or the difficulty in identifying these species, which are frequently unnamed.<sup>2</sup>

Insects play a significant role in ecosystems through influencing the composition and size of populations of plants, herbivores, predators and detritivores.<sup>3,4</sup> Insect communities are influenced by fire<sup>5,6</sup>, vegetation heterogeneity<sup>7</sup>, seasonality<sup>8</sup>, fragmentation<sup>9</sup>, exotic species, and the effects of change in land use, more especially in recent decades, among other factors<sup>10,11</sup>.

Land conversion to agrosystems has been viewed as detrimental to biodiversity conservation.<sup>12</sup> The agricultural systems are derived from conversion of complex natural ecosystems to simplified ecosystems through intensive use of machinery, chemical and biological inputs, as well as improved and changed crops.<sup>10,13,14</sup> These agrosystems are a major cause of biodiversity loss because of fragmentation and destruction of native vegetation.<sup>15</sup> However, the effects of land-use change on native fauna depend on the size of divergence of pre- and post-land-use conversion ecological conditions.<sup>16</sup> There are thus agricultural systems that have a high impact on native fauna and flora, and other types of low-impact agricultural systems, which can play a key role in species conservation<sup>17</sup>, as the landscapes under low-impact agriculture can harbour much of the world's biodiversity<sup>14</sup>. According to Gareng<sup>13</sup>, before 1970, land use in the Rashad District was primarily cattle production over natural pastures. Since then, there has been an intense expansion of mechanised agricultural output to export soy and corn. Due to agricultural expansion, an estimated 40% to 80% of the natural Rashad area has been converted to agrosystems during the last five decades. However, these estimates are highly variable due to difficulties in discriminating in satellite images of areas of native vegetation and pasture areas.<sup>13</sup>

Recent research indicates that shifting land use to simpler and more intensively managed systems, such as soybean or corn plantations, reduces ant richness.<sup>10,18</sup> Less-intensive agrosystems, such as pasture, may have a species richness comparable to that of natural areas<sup>18</sup>, demonstrating that agricultural production areas are used for conservation of at least part of the biodiversity and/or are managed to reduce species loss. However,

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the presence of many native species in some types of agriculture does not guarantee the integral conservation of biodiversity. According to Cingolani et al.<sup>19</sup>, the number of species in a region (gamma diversity) is determined by the number of species in a location (alpha diversity) plus the exchange of species with other locations (beta diversity). It is critical to understand how diversity is distributed in the landscape and to determine conservation actions.

Rubene et al.<sup>20</sup> developed a method for deconstructing beta diversity or species exchange between sites into two distinct processes, which they refer to as species replacement or species loss. The beta diversity increases as a result of species exchange between sites (by different species) or because of a difference in the number of species due to nesting. This is nothing more than a pattern in which the community with fewer species is a subset of the communities with more species.<sup>21,22</sup>

According to Ebenman and Jonsson<sup>23</sup>, as the structure of the vegetation became more complex, the number of ant species increased, beginning with a gradient from footpath to Rashad. However, preserving only these complex habitats (with more species) far from ensures the full conservation of ant species, because the exchange of species between Rashad vegetation types accounts for 50% of the richness (beta diversity), and different areas of the same physiognomy account for 25%.<sup>23</sup> These studies were limited to a few areas, and the diversity patterns, as well as the ability of these species to maintain themselves in different environments altered by humans, have yet to be evaluated. The aim of this study was to determine how changes in land use affect the ant community and its ecological functions. Furthermore, we aimed to determine how the conversion of native vegetation affects the richness and composition of ant species based on the type of land use. We evaluated soy monoculture, pasture and organic agriculture in terms of patterns of local diversity, exchange of species between places, and regional diversity.

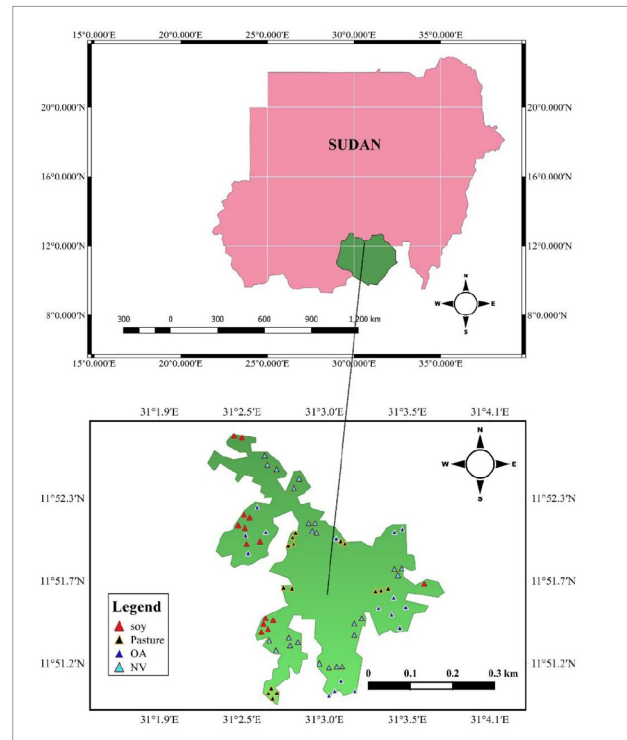
## Materials and methods

### Study area

This study was conducted in the Rashad District from February to June 2019 and February to May 2020. The study area was 7872 km<sup>2</sup>, and was located in the centre of the Kordofan State between latitudes 10° and 13° N and between longitudes 29° and 33° E (Figure 1). The study site included areas such as pasture, soy monoculture and organic agriculture, as well as areas of native vegetation (see Supplementary table 1). In total, 69 sites were sampled: 14 conventional soy monoculture sites, 15 pastures, 16 organic agriculture areas (14 vegetable plantations and 2 organic soy plantations, OA-15 and OA-16) and 24 native vegetation areas. From the 24 areas of native vegetation, we chose 7 rural formations, 8 Kubos areas (old-growth forests), and 9 forest formations to collect the three most common phytophysiognomies. The annual rainfall of the study area is between 500 mm and 800 mm. The majority of the basement complex in the area is overlaid with Nubian sandstone. Vegetation cover in the Rashad area consists of legumes dominated by the *Acacia* genus annual grasses, and shrubs. The vegetation, on the other hand, varies with rainfall patterns and soil structure. According to Hassan and Ibrahim<sup>24</sup>, the total population in the study area is estimated to be 240 000 persons. There are two main livelihood groups in the study area, including minor livestock holders and agriculturalists.

### Sample design

We sampled three 20-m-long transects in each location (sample plot) (Figure 2a). Each sample plot was made up of a grid of 12 pitfall traps, which were arranged in three rows with four traps each, with a 2-m spacing between them (Figure 2b). The pitfall traps used were 200-mL plastic cups filled up to 1/3 with water and detergent, and were active in the field for 24 h. There were 12 pitfalls per plot, 36 per location, and 2484 in 69 locations (Figure 2c).



Habitats: OA, organic agriculture; soy, soy monoculture; NV, Native vegetation

Figure 1: Map of the study area showing distribution of sampling sites.

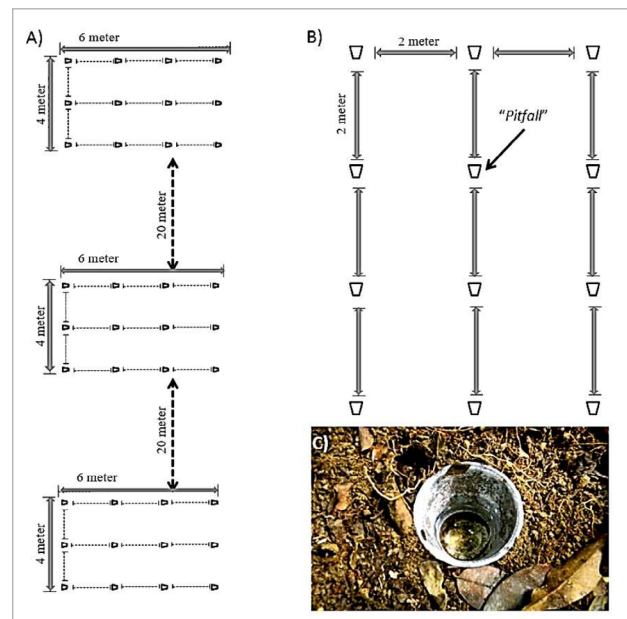


Figure 2: Method used to collect ants. (A) Distribution of sample plots in each location. (B) Distribution of pitfalls in each sample plot. (C) Photograph of a pitfall in the field.

Before sorting, the contents of each trap were sieved (in a fine mesh to reduce the loss of tiny invertebrates) and preserved in a container filled with 75% alcohol. We combined all 12 pitfalls from each sample plot into a single composite sample to shorten the screening time. As a result, each locality has three sub-samples, each of which was screened for Formicidae. Specimen processing and identification included keys used for genus and species level identification, comparison with voucher specimens, and comparison with type images available at AntWeb and AntWiki. To reduce the impact of the weather on the sampling, we

collected data on days when rain was not forecast. Furthermore, we sampled two to three locations at the same time (Supplementary table 1), diluting any climatic effects amongst the many categories investigated.

### Data analysis

We compared the richness of ant species between native vegetation environments and different agricultural systems in order to estimate the potential loss of species due to conversion of native areas into agricultural systems. We plotted species accumulation curves and estimated the richness using Jack1 and Chao2 to determine how much of the expected total number of ant species was sampled and whether the richness per habitat type differed between systems. EstimateS 9.1.0<sup>25</sup> was used for all of the analyses. To determine whether changes in land use affected the richness of ants in the locality (alpha diversity), an ANOVA with a Tukey post-hoc test<sup>26</sup> was used, with the habitat factor being divided into 'native vegetation', 'pasture', 'soy monoculture', and 'organic agriculture'.

Species composition was analysed between habitats presence-absence matrix by location (176 species x 69 locations). The first analysis was a PERMANOVA, with 999 permutations, using the *adonis* function of the *vegan* R package<sup>27</sup> (R Development Core Team 2016). We used this analysis because it is the most robust for unbalanced data.<sup>28</sup> However, as the PERMANOVA analysis cannot determine which habitats differ from one another, non-metric multidimensional scaling was performed<sup>29</sup> using the *metaMDS* function of the *vegan* package<sup>27</sup>, grouping the collection points by their similarities. Indicator value (*IndVal*) analysis was used to show associated species and a particular habitat with a significance value.<sup>30</sup> The *interval* function of the *labdsv* package was used for this final analysis.<sup>29</sup> Aside from difference in species occurrence, we did a functional group analysis, adapting the classification proposed by Divieso et al.<sup>31</sup> The ant species were classified into:

1. Arboreal – species that nest in tree and shrub vegetation
2. Attini – a tribe that includes all ants that grow on fungus
3. Camponotini – a tribe that includes all species of the genus *Camponotus*
4. Correction – a group of migratory species that forage in large columns (many individuals, one next to the other), and are incredibly greedy, with records of predation on small rodents
5. Specialist – a group of species that have particular morphological or ecological characteristics (in general, their recording frequency is low, with most predators being specialists of a specific taxon)
6. Generalist – a group that includes species with great ecological and omnivorous plasticity, composed of most species of the genera *Pheidole*, *Solenopsis*, and *Brachymyrmex*, in addition to exotic species
7. Dominant generalist – a group composed of three omnivorous species with characteristic large recruitment of individuals to monopolise the resource found in relation to other competitors
8. Opportunistic – a group capable of foraging, which forages in the warmer periods and monopolises the food source in the face of competitors
9. Large predator – large species, some of which are specialist predators

Following classification, we assessed the frequency of occurrence of each functional group in different habitats. For that, we analysed generalised linear models using the *glm* function of R.<sup>32</sup> In this analysis, we counted the number of records per location and recorded the number of plots including each species within each location.

To assess the richness of ant species, an additive partition diversity analysis was used at three hierarchical levels: sample plot, location, and habitat type. The sum of alpha diversity (average number of species in the sample plot) plus each of the components of beta diversity (number of different species between locations and habitat types) must equal

the total diversity of ant species collected (i.e. 176). We created a null model to see if any factor was influencing ant diversity by changing the values of alpha and beta diversity more than what would be expected at random. We created this null model by randomising the data in the field 2000 times, and from these randomisations, generating a pattern that we defined as random. After this step, we compared the pattern found in the field, with the pattern considered at random; if the probability of the pattern found in the field had a less than 5% chance of having occurred due to chance, we considered this pattern to be different, and thus influenced by some factor.<sup>33</sup> For this type of analysis, the *adipart* function of the *vegan* package was used.<sup>27</sup>

Beta diversity ( $\beta$ ) is divided into two components that are distinct ecological processes: nesting ( $\beta_{nes}$ ) and species exchange ( $\beta_{sim}$ ).<sup>21</sup> We calculated  $\beta$  diversity pairwise between the localities with Sorensen ( $\beta_{sor}$ ) and Simpson ( $\beta_{sim}$ ) indexes. We calculated  $\beta_{sor}$  by taking into account the species identity and incorporating information from both the turnover and species nesting.  $\beta_{sim}$  was calculated from the probability of capturing a specific species as a function of the total species (regardless of their identity), and calculating only the species exchange. Therefore, the difference between the calculated indices provides the beta diversity value due to nesting<sup>21</sup>:

$$\beta_{nes} = \beta_{sor} - \beta_{sim}$$

To detect differences between agrosystems and native vegetation, we made comparisons between the values of  $\beta_{sor}$ , then between those of  $\beta_{sim}$  and between those of  $\beta_{nes}$ , using T-tests.<sup>21</sup> We made the same comparison between habitats (soybean, pasture, organic agriculture, field, savanna, and forest), but using the Kruskal–Wallis non-parametric test with Kruskal–Nemenyi post-hoc test of the package *PMCMR*.<sup>34</sup> In this Kruskal–Wallis test, equal values within the database were ranked randomly to avoid nodes (ties) in the analysis. Then, using the Mantel analysis in the *vegan* package, compare the dissimilarity matrix generated by the beta. A multifunction and a distance matrix between the locations were used to determine whether the distance between the points affects the species exchange. Where the result was significant, we performed a Pearson correlation to determine the direction and strength of the relationship.

## Results

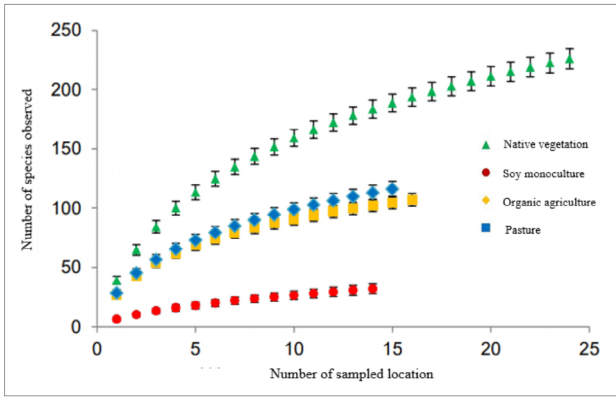
### Diversity of ant assemblages

In total, 176 ant species were recorded, accounting for 74% to 78% of the species estimated on the soil surface for the Rashad area using the diversity estimators Jack1 (342 species) and Chao2 (354 species). An average of 3965 ants (in 58 genera and 8 subfamilies) were recorded from the sites (Supplementary table 1). Myrmicinae was the most diverse subfamily (101 species), and Tetramorium was the most diverse genus (27 species) (occurring in 97% of the locations). The subfamily Formicinae was the second most diverse (34 species), and had the second most diverse genus, *Crematogaster* (10 species). Genera *Cataulacus*, *Monomorium* and *Pheidole* also are notable for having between 17 and 10 species, all belonging to the subfamily Myrmicinae, except for *Brachymyrmex* of the subfamily Formicinae.

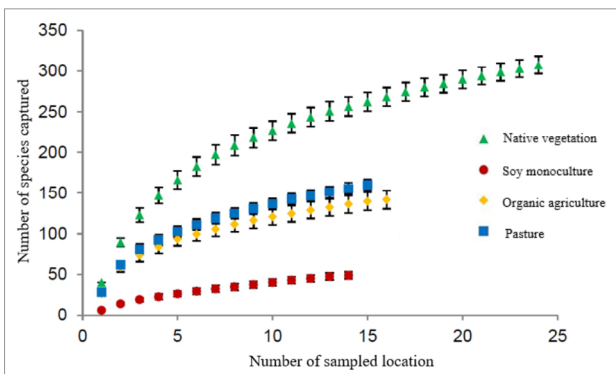
### Ant species richness in different land-use classes

Species richness at the site scale was highest in soy monoculture areas (83%), followed by organic farming areas (44%), and pastures (39%) (Figure 3). These values are comparable with the values calculated using the Jack1 wealth estimator, that is, 40% for pasture, 47% for organic agriculture areas and 82% for soy monoculture (Figure 4).

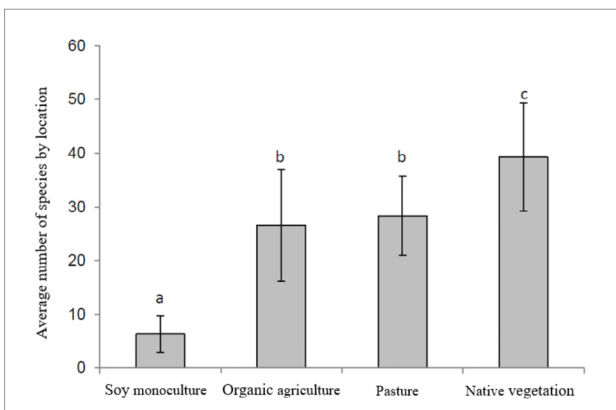
The analysis of local wealth, which corresponds to the average number of species collected in each of the 69 locations, also reveals that there is a difference between areas of native vegetation and organic agriculture systems. Soy monoculture areas had fewer species than organic agriculture systems and pastures ( $F_{3,65} = 66.96$ ;  $p < 0.001$ ), which had the same number of species (Figure 5). Areas of native vegetation had more species than all managed areas combined.



**Figure 3:** Accumulated number of ant species by sampled locations with the respective standard deviation based on data collected between May 2019 and August 2020 in the Rashad District.



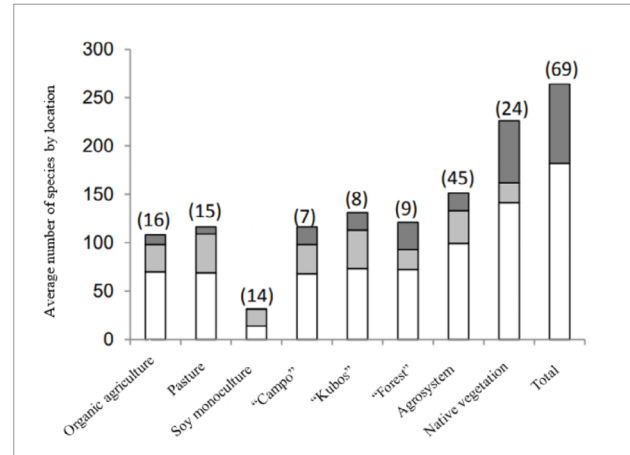
**Figure 4:** Estimated number of ant species by number of sampled locations using the Jack1 estimation with the respective standard deviation based on collections made between June 2019 and August 2020 in the Rashad District.



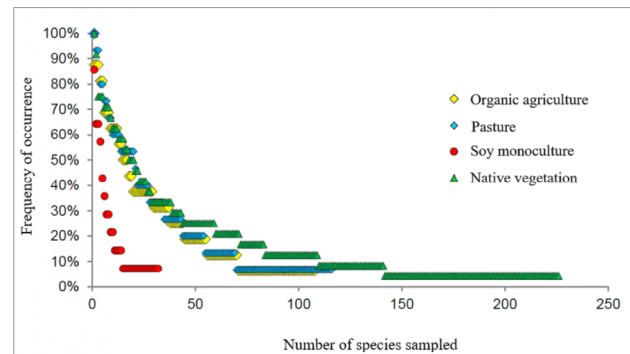
**Figure 5:** The average number of ant species per location, collected in different habitat types in the Rashad District between June 2019 and August 2020 using a pitfall trap. The bars represent the standard deviation and different letters indicate significant differences ( $p < 0.05$ ).

We found that the presence of rare species influenced both the richness and composition of species in native vegetation areas (Figure 6 and Figure 7). We classified rare species as those that occurred only once in a specific type of organic agriculture and native vegetation phytophysiology, and unique species as those that appeared only once throughout the study. Unique species accounted for 30% of

the species found in both agrosystems and native vegetation areas (Figure 6). However, areas of native vegetation had more unique species than did organic agriculture systems (Figure 7). It is also worth noting that species with a high frequency of occurrence were sampled, that are capable of surviving both in areas of native vegetation and in organic agriculture, but as the species' frequency decreased, they showed a preference or exclusivity for a specific type of habitat.

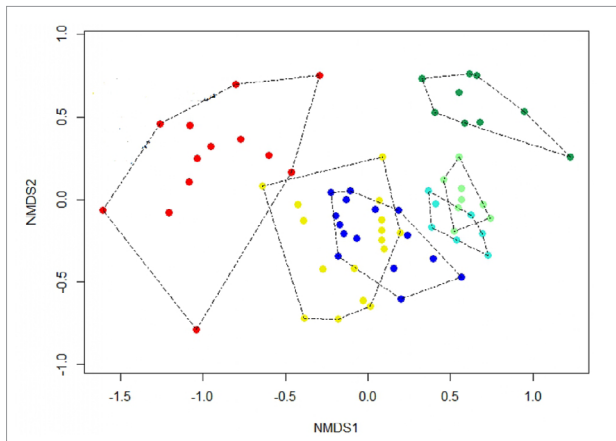


**Figure 6:** Occurrence of common, rare and unique species collected in the Rashad District between June 2019 and August 2020 with pitfall traps in different types of habitats. Numbers in parentheses indicate the number of sampled locations in each habitat. White bars indicate species considered typical, that is, that occurred more than once within the habitat; light grey bars indicate rare species that occurred only once in the habitat but that occurred in other habitats; and dark grey bars indicate species that occurred only once in the entire study. 'Campo' refers to rural formations, 'Kubos' refers to old-growth forests, and 'Forest' refers to forest formations.



**Figure 7:** Frequency of occurrence of species collected in the Rashad District between June 2019 and August 2020 using pitfall traps in different habitat types. The species were ordered in descending order, according to their frequency of occurrence in the 69 sampled locations.

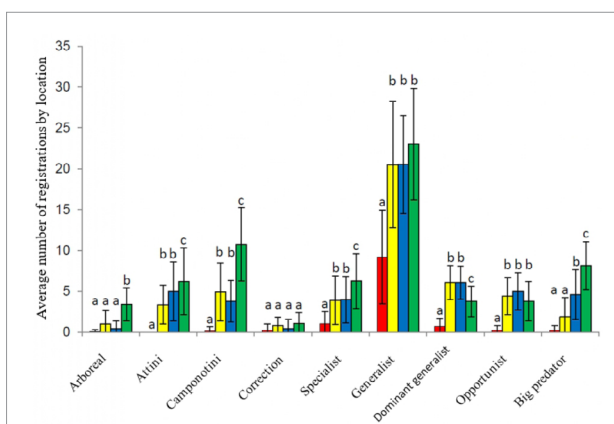
The PERMANOVA analysis revealed a significant difference in species composition ( $F_{3,68} = 10.697$ ;  $p < 0.001$ ). The ranking (Figure 8) demonstrates that, in addition to richness, there are differences between the species composition of native vegetation systems and that of organic agriculture systems. There is a visible gradient of change, with soy monoculture and forest areas having distinct communities (different from all others). Furthermore, two additional groups formed Rashad and the countryside, with two natural phytophysionomies that are much more similar to each other than between forest areas. Pasture and organic agriculture areas also have a similar community.



**Figure 8:** Non-metric multidimensional scaling (NMDS) based on the presence and absence matrix approximates the locations with the composition of ants most similar to each other. Forest (green), soy monoculture (red), pasture (blue), Kubos (light green), Campo (cyan), and organic agriculture (yellow) species.

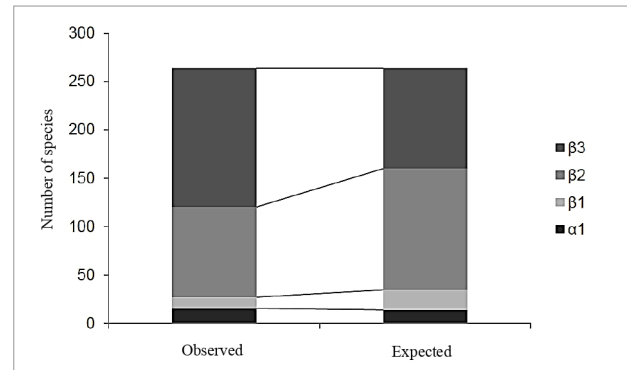
We found further evidence of the change in the pattern of distribution and abundance of species in the results obtained from the Indval analysis, which detected 76 species with significant indication values, ranging from 1% to 75% (Supplementary table 2). For example, *Pheidole andrieui* has a 59% chance of occurring in a soybean monoculture area, *Pheidole termitophila* has a 61% chance of occurring in organic farming areas, and *Dorylus aethiopicus* includes a 46% chance of occurring in pastures. It is important to note that the number of indicator species in native phytophysiognomies is almost three and a half times higher than that in agricultural areas.

It is also obvious that the conversion of native areas to agricultural systems had an impact on functional groups or the type of land use (Figure 9). Of the several functional groups, 'Correction' was the only group that showed no significant difference in occurrence between the different habitats; however, this is a nomadic and rare group. The 'Dominant generalists' were the only group for which there was a higher number of records in organic agriculture and pasture when compared to native vegetation. Native vegetation areas had higher numbers than agricultural systems for all other groups except 'Generalists' and 'Opportunists'.



**Figure 9:** The average number of records per location of ants belonging to different functional groups, collected between June 2019 and August 2020 in the Rashad District using pitfall traps. Error bars indicate standard deviations and different letters indicate significant differences ( $p < 0.05$ ) between habitats.

When we analysed additive diversity partition (Figure 10) with all hierarchical systems and phytophysiognomies, we observed that the alpha richness ( $\alpha_1$ ) is greater than expected (5.8%). The exchange of species between the plots of each location is 29% lower than expected, and the exchange of species between locations within the same system or phytophysiognomy was 14% lower than expected. The exchange of species between the different systems and phytophysiognomies ( $\beta_3$ ) had the greatest importance for the pattern of diversity observed, being 15.9% greater than expected at random.



**Figure 10:** Analysis of additive partition of ant diversity in the Rashad District.  $\alpha_1$  is the average number of species in the plots.  $\beta_1$  is the exchange of species between plots within the exact location.  $\beta_2$  is the exchange of species between locations belonging to the same type of agroecosystem or phytophysiognomy.  $\beta_3$  is the exchange of species between different types of agroecosystems and phytophysiognomies. For all observed values, the difference was significant ( $p < 0.001$ ) compared to the expected model.

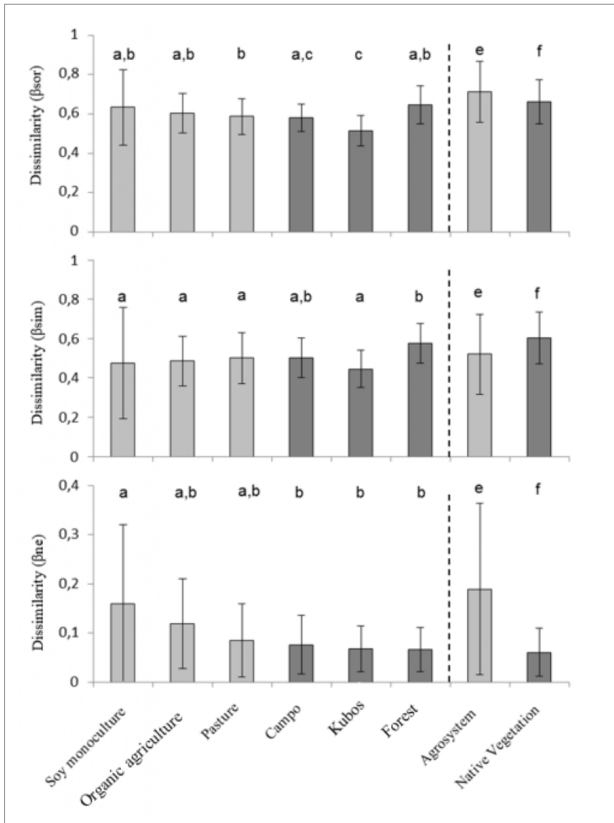
We also performed additive partition of diversity analyses for each system or phytophysiognomy (Supplementary figure 1). The additive partition patterns of diversity are similar, regardless of the system or phytophysiognomy. All of them differed from what we expected at random, with the alpha diversity (richness within each plot) about 2.3% higher than expected. Beta1 diversity, or the difference in species between pitfall plots within each location, is 4.1% lower than expected, indicating homogeneity on this scale. The exchange of species between locations is 4.1% higher than expected; beta diversity ( $\beta_{sor}$ ) may group two distinct processes: the exchange of species (turnover) and/or nesting (loss of species). The analysis of multiplicative diversity separated these two factors, revealing that the majority of the diversity is due to the exchange of species ( $\beta_{yes}$ ), with little influence from nesting ( $\beta_{nes}$ ) (Figure 11). However, nesting for agrosystems is three times that of native areas, indicating greater homogenisation in agricultural areas. In addition, Mantel's analysis between the level of dissimilarity and the distance between the points shows that, only for the agrosystems, the greater the distance, the greater the exchange of species (Figure 12).

## Discussion

### Effects on richness

The findings show that converting native areas of the Rashad District into agrosystems resulted in the loss of local diversity, with the magnitude of this loss determined by the type of agrosystem used, as soy monocultures caused a greater loss of diversity than pastures or organic agriculture. Ribeiro et al.<sup>35</sup> use the term 'divergence from ecological conditions' to explain why some land uses have a greater impact on biodiversity than others. This term attempts to portray that the lower the expected diversity is, the more different the post-conversion condition is from the original vegetation simplifying or increasing the intensity of system management. These findings are consistent with those found in the scientific literature; several studies with various taxa show that conversion of natural habitats and intensification of agrosystems leads to species reduction and changes in composition, as well as changes in the structure and functioning of the ecosystem.<sup>36-38</sup> Among the several

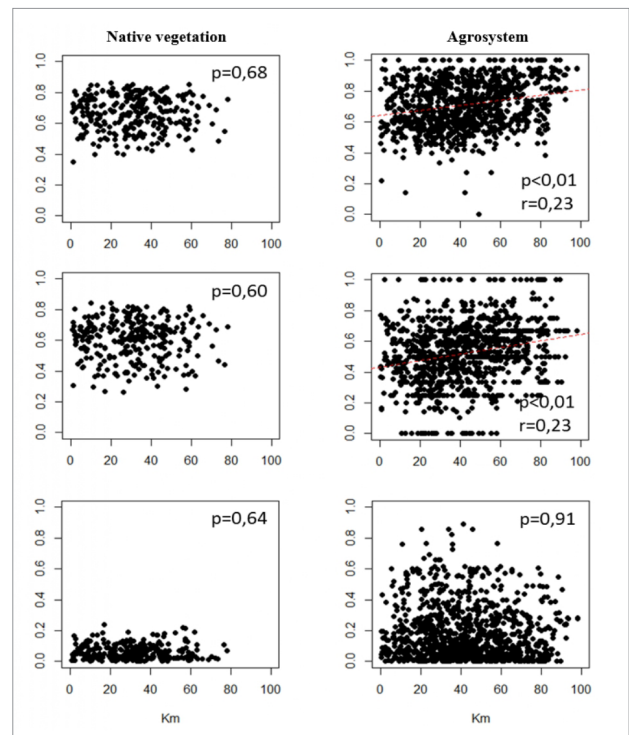
examples in the literature of how conversion of native areas for food production affected the local fauna, perhaps the best studied is that of coffee production in Latin America, according to which a reduction in the diversity of ants was noted in a review by Eldridge et al.<sup>39</sup> However, the magnitude of this reduction was dependent on the type of land management (monoculture of coffee or coffee in the shade of native trees), in addition to considering ecological services.<sup>14,40</sup> Similar patterns of reduction in ant diversity or richness in planting systems were also found in the Amazon<sup>41</sup>, Argentina<sup>42,43</sup>, Australia<sup>44</sup>, Africa<sup>45</sup>, and China<sup>46</sup>. Despite the fact that the loss of species due to conversion of native vegetation into agrosystems is a well-known global occurrence, the magnitude of this effect and its interaction with the different agrosystems remain unknown. The reduction in diversity observed in the current study is greater than that described by Bremer and Farley<sup>10</sup> and Moranz et al.<sup>11</sup>



**Figure 11:** Values of beta diversity based on data of presence and absence of ant species collected using pitfall traps between June 2019 and August 2020 in the Rashad District.  $\beta_{sor}$  represents the sum of  $\beta_{sim}$  and  $\beta_{nes}$ .

This work depicts that soy monocultures – with their application of pesticides, ploughing and harrowing the soil, off-season periods without live soil cover and pre-planting desiccation – are forms of management that make these fields environments that are difficult for pest insects to survive in (which is the main reason for some of these management activities, such as application of pesticides and pre-planting desiccation), but consequently make it a difficult environment for insects to survive in. Many authors have used the term ‘intensification of land use’ to describe this process, which is a way of characterising the management of these areas as a cause of the different riches found in these environments, regardless of the crop planted.<sup>12</sup>

Pastures are not managed, and thus have a greater diversity of ant species than soybean fields (as previously described by Bremer and Farley<sup>10</sup>), as grazing has little effect on ant diversity.<sup>47</sup> The most important effect in these areas is the indirect effect of occupation of exotic grass species, which outcompete native grasses and reduce floral and faunal diversity.<sup>48</sup>



**Figure 12:** Relationship between ant fauna dissimilarity ( $\beta_{sor}$ ,  $\beta_{sim}$ , and  $\beta_{nes}$ ) and the distance between the locations of native vegetation and agrosystems. Pearson’s correlation ( $r$ ) and the significance computed using Mantel’s analysis are displayed within the graphs. The points correspond to the comparison values between the sampling locations.

Organic agriculture areas are as diverse as grazing areas, suggesting that pesticides, as well as management techniques, reduce diversity in conventional organic agriculture areas.<sup>49</sup> In addition to the restriction in using pesticides, organic areas have a high level of local heterogeneity, planting of flowers to provide an alternative resource for predators, and year-round irrigation to ensure that there is always green matter, and herbivores and other organisms that can serve as a source of food for ants (Eisawi, personal observation). Furthermore, unlike what is found in soy monocultures, organic agriculture areas have bands of land with perennial plants and trees where the soil is not disturbed, and which act as a refuge for ants that nest in the soil or in the trees themselves.<sup>10</sup>

### Effects on composition

In terms of composition, the species that persist in organic agriculture were distinguishable by being generalists, recruiting to monopolise available resources in the field and/or exhibiting dominant behaviour, such as the genera *Pheidole* and *Solenopsis*.<sup>11</sup> Other common species in the studied agrosystems are opportunistic ants with high temperature tolerance, such as those of the genera *Dorymyrmex* and *Linepithema*.<sup>50,51</sup> In addition to these, there are tiny generalist ants (~1.5 mm) such as *Brachymyrmex* and the so-called ‘thief ants’, also of the genus *Solenopsis*, which occur in both natural and disturbed environments, including residences in urban areas.

Arboreal ants, large predators, specialists and the Attini and Camponotini tribes suffered a reduction in their occurrence with conversion of native areas into organic agriculture systems (Figure 8). This reduction is due to both environmental changes and, with ants belonging to the Attini tribe, to direct combat (that is, management to reduce the population). It is also clear that the type of land use affects the occurrence of certain functional groups of ants to varying degrees of magnitude. Soy planting had the most negative effects on almost all functional groups, whereas organic agriculture and pasture had intermediate effects. However, we associate the significant difference found in the composition of

ants between agrosystems and native vegetation with rare species or those that occurred only once. As shown in Figure 6, areas of native vegetation have 3.5 times more unique species (sampled only once) than agrosystems, despite the fact that the sampling effort in these areas was nearly half that of agrosystems. These rare species show some aspect of morphology, ecology or specialised behaviour.<sup>52,53</sup> Mohammed et al.<sup>54</sup> demonstrated that the Rashad ant fauna is characterised by a large proportion of rare ants (45% of the species occur in less than 5% of the samples), compared to the Australian savannah (where 27% of the species are rare). This makes the advance of agrosystems over native areas even more worrying, because rare species are the most vulnerable to extinction due to their low density and limited ability to persist in disturbed environments.<sup>55</sup>

Many studies have discussed the factors that can limit the colonisation of an agricultural area, and most seem to assume a limiting factor is the nesting place, which can be, in addition to the soil, litter, branches fallen on the soil, and the stratum.<sup>56,57</sup> Conservationists should emphasise the change in composition caused by the collected native phytophysiology<sup>23</sup>, which further increases the importance of conserving multiple native areas. Except for invasive species, all species found in agricultural systems can survive in native systems in theory; however, the reverse is not true: environments converted to agricultural systems do not contain species which are common in natural environments. This becomes clear when we examine the species composition of the forest formation, which contains the largest number of unique indicator species. This means that there are many unique species in forest areas that cannot survive in agricultural systems or in more open native vegetation areas. We also found similar results in the Rashad District for Drosophilids; Mohammed et al.<sup>54</sup> argue that, although gallery forests occupy less than 10% of the Kubos area, a large portion of the diversity exhibits a preference for or association with this environment.

Areas of native vegetation in the Rashad and countryside also contain some unique species, which would become extinct if these areas were converted into agricultural systems. Even though pasture and organic agriculture have a lower impact on ant biodiversity, they have a different composition than native areas, which contain a greater number of arboreal, cryptic, specialist predators and species of relative size, small and large. Crist<sup>58</sup> also reported these changes in the number of species of different sizes of birds, beetles and ants.

### **Additive and multiplicative partition of diversity**

The most abundant species persist in most habitats and, as they become rare, they show a pattern of habitat preference. The analysis of the additive diversity partition reveals that the presence of a greater diversity of habitats is the most important factor for the diversity of ants in the Rashad District.

Separating the beta diversity into two factors, which affect the exchange of species between different locations, we found that the magnitude of the  $\beta$  difference between agricultural systems and native phytophysiology is small, but significant (Figure 11). There is a greater exchange of species ( $\beta$  dissimilarity) in agricultural systems compared with native phytophysiology, and this dissimilarity is more a function of nesting ( $\beta$ nes) than of the species exchange itself ( $\beta$ sim). Similar results were found by Schoeman and Samways<sup>59</sup> in the Amazon, but with twice the nesting values found in the Rashad. This demonstrates that increased intensification of land use in the Rashad agricultural production areas has resulted in biotic homogenisation.<sup>60</sup>

In addition, a second pattern was found in  $\beta$  diversity, but we associated this pattern only with species exchange ( $\beta$ sim) and agrosystems. We observed that the dissimilarity between agricultural locations grows as they become more distant from one another (Figure 12), that is their location influenced diversity. The change in composition due to geographical position is an expected finding, but not over such short distances as 100 km. Morton and Law<sup>21</sup> also found an influence of distance on the dissimilarity variables ( $\beta$ sim,  $\beta$ nes and  $\beta$ nes), but for a distance of nearly 3000 km.

## **Conclusions**

The conversion of native Rashad vegetation into agricultural production systems caused a local loss in diversity and change in myrmecofauna composition. This loss is associated with the type of agricultural system, with soy monoculture causing a more significant decrease in local wealth than organic agriculture and pastures.

In general, the groups of ants that present the most significant specificity, such as nesting in trees or having a food specialisation, are the ones that show the most considerable reduction in their frequency of occurrence. These groups that present specialisations, in most cases, are already naturally rare species (of low frequency), are the leading promoters of biodiversity, and are, potentially, the species most threatened with local extinction in the Rashad District. Another critical factor in conservation is that different native physiognomies of Rashad have a distinct species composition. The areas of forest formation present the most exclusive fauna, with many unique species that do not occur in native Kobus areas (old-growth forests), in the countryside, and mainly in agrosystems. On the other hand, despite having only unique species, the Kobus (old-growth forests) and Campo areas have a subset of species capable of persisting or colonising agricultural systems.

Two practical implications of this work are to: (1) reassess how the management of agricultural areas, mainly soy monoculture, is being carried out to reduce its impact; and (2) consider that, in future conservation actions, pasture areas and organic agriculture may be preferential or encouraged production systems around conservation areas or in those areas of relevant biodiversities, such as impact amortisation zones or even corridors between fragments of Kobus *stricto sensu* and Campo.

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## **Competing interests**

We have no competing interests to declare.

## **Authors' contributions**

K.A.E.E.: Conceptualisation, study design, field data collection, data analysis and interpretation. I.P.S. and T.S.: Writing – initial draft. H.H.: Supervision, study design, writing – revisions. All authors read and approved the final manuscript.

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