The influence of ants on the guild structure of Acacia insect communities in Mkomazi Game Reserve, north-east Tanzania

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Summary

A total of 41,099 insect specimens of 133 families and 492 morphospecies were collected from 31 trees of six species of Acacia in north-east Tanzania, representing one of the largest insect samples ever analysed from a tropical savannah habitat. Herbivores (sapsuckers and chewers) and parasitoids had the highest diversity shares, whereas the highest biomass shares were obtained by phytophagous chewers, ants and predators. The percentage biomass of ants was correlated positively with the diversity share of sapsuckers and negatively with the diversity share of tourists. A positive correlation was found with the residual biomass share of phytophagous sapsuckers, indicating a protective function of ants for this guild. Diversity and abundance share was much higher in egg and coccoid parasitoids compared to larval parasitoids, probably due to predation by ants on larval parasitoids. Their low diversity supports the hypothesis of a decline towards the equator in ichneumonid diversity.

Key words: Acacia canopies, ants, guild, insect, mist-blowing

Résumé

On a récolté un total de 41,099 insectes appartenant à 133 familles et 492 espèces morphologiques, dans 31 arbres de six espèces d’Acacia, au nord-est de la Tanzanie, ce qui constitue un des plus vastes échantillonnages d’insectes jamais étudiés dans un habitat de savane tropicale. Les herbivores (insectes suceurs et broyeurs) et les parasites représentaient la plus forte diversité, tandis que la plus grande biomasse était constituée par des phytophages broyeurs, des fourmis et des prédateurs. Le pourcentage de biomasse des fourmis a été lié positivement à la diversité relative des insectes suceurs, et négativement avec la diversité présentée par les voyageuses. On a trouvé une corrélation positive avec la part restante de biomasse formée par les phytophages suceurs, indiquant une fonction protectrice des fourmis pour ce groupe. La diversité et l’abondance relatives étaient plus élevées pour les œufs et les cocons de parasites que pour les larves de parasites, ce qui est probablement dû à une prédation des larves de parasites par les fourmis. Leur faible diversité était l’hypothèse d’un déclin de la diversité des ichneumonidés vers l’équateur.

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Introduction

Ants dominate the insect communities in tropical habitats in terms of biomass and abundance (Beck, 1971; Dejean et al., 1986; Hölldobler & Wilson, 1990). Their impact as the leading predators on food webs in terrestrial habitats is immense (Wilson, 1971; Sörensen & Schmidt, 1987).

During the last 15 years, a lot of research has focused on the insect diversity in tropical forest tree canopies (Erwin, 1982, 1983; Moran & Southwood, 1982; Adis et al., 1984; Morse et al., 1988; Basset & Kitching, 1991; Basset, 1996), but the tropical savannahs, although the most widespread habitat in the tropics (Solbrig, 1996), have not been studied in detail. Apart from the large literature on insects of medical and agricultural importance, only one large-scale study exists for the African continent (Erwin, 1995). As a by-product of the forest studies, the importance of ants in insect communities became evident (Wilson, 1959) and through the marvellous studies of Janzen (1966, 1969) the symbiosis between some *Acacia* species and ants was clearly demonstrated. However, ant–plant relationships are far from understood (Stork, 1991), especially for African *Acacia* species. Recently, applied entomologists have been assessing the impact of pesticides on the non-target faunas. The studies in mopane woodland in north-western Zimbabwe probably represent the largest insect sample ever analysed from an Afrotropical savannah system (Tingle et al., 1992; Douthwaite & Tingle, 1994). However, being largely based on pitfall trapping, these samples are somewhat selective.

This study deals with the largest insect sample ever analysed from the canopies of the trees in a tropical savannah habitat. The guild structure of 31 trees representing six *Acacia* species was analysed with regard to the association with ant abundance measured as biomass share.

Materials and methods

Study area

The Mkomazi Game Reserve is located in north-east Tanzania and lies adjacent to the Kenyan border and the Tsavo (West) National Park. It covers an area of ≈3250 km² with geographical borderlines of 37°35′–38°45′ E and 3°50′–4°25′ S. The area is part of the East African high plateau, with an altitude varying between 240 and 1609 m a.s.l. The climate is semi-arid (Coe, 1995) with a pronounced dry season and high mean temperatures between 23.1 and 37.8 °C. Precipitation ranges from 300 mm in the eastern part to 900 mm in the central and western parts of the reserve and shows a bimodal distribution, with the long rainy season between March and mid-May and the short rainy season between late October and December. The habitat is wooded grassland on the plains and woodland on the top of most hills; the most common tree species belong to the genera *Acacia* and *Commiphora*.

Insect sampling and analysis

A total of 31 trees of six *Acacia* species (*etbaica, mellifera, nilotica, reficiens, senegal* and *tortilis*) were sampled between 30 December 1995 and 18 January 1996. Samples were taken using a ‘Hurricane Minor’ petrol-driven mist blower (Cooper-Pegler Ltd), with an ultra-low-volume delivery nozzle. A mist of undiluted Pybuthrin 216,
a pyrethroid formulation synergised with piperonyl butoxide, was sprayed into the canopy in still conditions with dry leaf surfaces. Only trees under 10 m high were sprayed and spraying time was 30 s, with three bursts from different directions. After a standard drop-time of 1 h, insects were collected in 1-m² funnel-shaped trays. Catches were brushed into collecting jars, separated from debris and plant material and stored in 70% alcohol. All trays put under one tree were lumped to form a sample.

The material was sorted into taxonomic order and family by group specialists. Individuals were classified into recognizable taxonomic units (RTU). Larvae were not identified and were excluded from the RTU-level analysis. Each RTU was assigned to an ecological guild (Root, 1973). Larvae were grouped as a whole in the phytophagous chewers guild, because the overwhelming majority collected were caterpillars. Following the classification of Moran & Southwood (1982), eight guilds were recognized. In addition, adult Lepidoptera were placed in their own guild, the phytophagous nectarivores (pn): 1, phytophagous chewers (pc); 2, phytophagous sapsuckers (ps); 3, phytophagous nectarivores (pn); 4, epiphyte grazers (e); 5, scavengers (s); 6, predators (p); 7, parasitoids (pa); 8, ants (a); 9, tourists (t).

The body length of five randomly selected individuals of each RTU was measured to the nearest 0.01 mm using a binocular microscope with a calibrated eyepiece graticule. The median was taken to calculate the dry weight biomass using the allometric approximation used by Moran & Southwood (1982). Two-tailed significance boundaries were chosen, although the association of ant biomass was expected to be negative with all guilds except for the phytophagous sapsuckers (Hölldobler & Wilson, 1990). Pearson’s correlation coefficient was used as a parametric test to look for a linear correlation and Spearman’s rank correlation coefficient was used as a non-parametric test to look for a non-linear correlation. If the data were not normally distributed, only Spearman’s correlation coefficient was used.

To avoid spurious correlation between biomass shares, the biomass of the guilds was calculated as a percentage of non-ant biomass and then correlated with ant biomass.

Results

A total of 41,099 insect specimens, belonging to fourteen orders, 133 families and 492 RTUs were recognized. The nine guilds contributed unequally to the total RTU richness (Fig. 1a). The four most diverse guilds (phytophagous sapsuckers, chewers, parasitoids and predators) contributed over 80% of the total RTU richness. The situation was different for the biomass distribution (Fig. 1b). With the larvae included, the pc guild had the largest biomass share, followed by the ants and the predators. The four main guilds combined (pc, a, p and ps) had a biomass share of over 90%. The ant biomass share was significantly correlated with the percentage RTUs in the phytophagous sapsuckers and the tourist guild (Table 1), revealed by both the parametric and non-parametric test. The association was positive with the phytophagous sapsuckers guild, but negative with the tourists’ guild. With the exception of the phytophagous sapsuckers guild, all associations were negative, as expected. For both cases (Fig. 2a,b) the best fit was provided by a linear regression.

With regard to the biomass shares of the guilds, ant biomass share was significantly correlated with the biomass shares of the phytophagous sapsuckers guild (Table 2),
Fig. 1. (a) Distribution of RTUs among the nine recognized guilds in this study. The bar labelled ‘unknown’ refers to two RTUs (Coleoptera, Tenebrionidae) which could not be reliably assigned to a guild, and (b) distribution of biomass among the guilds.

<table>
<thead>
<tr>
<th>Guild</th>
<th>$r$</th>
<th>$P$-value</th>
<th>$r_s$</th>
<th>$P$-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Epiphyte grazers</td>
<td>-0.098</td>
<td>0.602</td>
<td>-0.072</td>
<td>0.701</td>
</tr>
<tr>
<td>Predators</td>
<td>-0.057</td>
<td>0.762</td>
<td>-0.106</td>
<td>0.571</td>
</tr>
<tr>
<td>Parasitoids</td>
<td>-0.053</td>
<td>0.776</td>
<td>-0.099</td>
<td>0.596</td>
</tr>
<tr>
<td>Phytophagous chewers</td>
<td>-0.225</td>
<td>0.224</td>
<td>-0.181</td>
<td>0.331</td>
</tr>
<tr>
<td>Phytophagous nectarivores</td>
<td>-0.048</td>
<td>0.796</td>
<td>-0.001</td>
<td>0.999</td>
</tr>
<tr>
<td>Phytophagous sapsuckers</td>
<td>0.406</td>
<td>0.024</td>
<td>0.364</td>
<td>0.045</td>
</tr>
<tr>
<td>Scavengers</td>
<td>-0.099</td>
<td>0.594</td>
<td>-0.086</td>
<td>0.648</td>
</tr>
<tr>
<td>Tourists</td>
<td>-0.364</td>
<td>0.045</td>
<td>-0.361</td>
<td>0.047</td>
</tr>
</tbody>
</table>
Fig. 2. (a) Correlation between the percentage ant biomass and the percentage RTUs in the ps (phytophagous sapsuckers) guild, and (b) correlation between the percentage ant biomass and the percentage RTUs in the t (tourists) guild.

Table 2. Correlation between the percentage ant biomass and the residual biomass shares (ant biomass excluded) of the other guilds per sample. Significant correlations are highlighted in bold.

<table>
<thead>
<tr>
<th>Guild</th>
<th>$r$</th>
<th>$P$-value</th>
<th>$r_s$</th>
<th>$P$-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Epiphyte grazers</td>
<td>0.233</td>
<td>0.207</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Predators</td>
<td>−0.030</td>
<td>0.871</td>
<td>0.032</td>
<td>0.863</td>
</tr>
<tr>
<td>Parasitoids</td>
<td>−0.156</td>
<td>0.403</td>
<td>−0.073</td>
<td>0.695</td>
</tr>
<tr>
<td>Phytophagous chewers</td>
<td>−0.232</td>
<td>0.210</td>
<td>−0.191</td>
<td>0.303</td>
</tr>
<tr>
<td>Phytophagous nectarivores</td>
<td>−0.103</td>
<td>0.582</td>
<td>0.011</td>
<td>0.952</td>
</tr>
<tr>
<td>Phytophagous sapsuckers</td>
<td>0.435</td>
<td>0.014</td>
<td>0.483</td>
<td>0.006</td>
</tr>
<tr>
<td>Scavengers</td>
<td>0.143</td>
<td>0.444</td>
<td>0.236</td>
<td>0.201</td>
</tr>
<tr>
<td>Tourists</td>
<td>−0.306</td>
<td>0.094</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

regardless of the test used. For the ps guild, the best fit was provided by a power regression (Fig. 3). The other correlations are weak and in line with the expectations, except for the epiphyte grazer and scavenger guilds (Table 2).

Comparison between larval parasitoids and the egg and coccus parasitoids (Fig. 4) showed that the RTU and abundance share was much higher for the egg and coccus parasitoids, whereas the biomass share was much bigger for the larval parasitoids. This was due to the fact that the two largest hymenopteran RTUs belonged to the family Ichneumonidae, and contributed over 25% to the total parasitoid biomass.

Discussion

The influence of ants on insect communities is well known (Wilson, 1959), but still not comprehensively understood. Although they formed only a small part of the RTU richness in this study (2.8%), their impact is probably the result of high
Ants and insect guild structure

Ants and insect guild structure abundance. Stork (1991) found a very similar diversity share (3.2%) in Borneo. Ant biomass share was also a good predictor of insect biodiversity (Krüger, 1997).

It has been shown by Wilson (1971) and Sørensen & Schmidt (1987) that ants are among the leading predators in terrestrial habitats. This is especially true for tree species which are in symbiosis with ants (Janzen, 1966, 1969; Bentley, 1977). Basset (1996) reported that ant abundance was one of the best predictors of the abundance and biomass of leaf-chewing herbivores from the rain forest in Papua New Guinea and showed a strong negative association.

The results of this study emphasize that ants might also play an important role on Acacia species which are not in obvious symbiosis with ants. Most correlations found in this study are in line with expectations. However, the percentage of the variance explained by ant biomass is not large, indicating that there must be other important factors. Ants often protect insect species in the phytophagous sapsucker guild (Hölldobler & Wilson, 1990), therefore the positive association with diversity and residual biomass in this guild might be a result of manipulation by ants. The negative association with the diversity in the t guild might result from the efficiency of ants as predators. The exclusion of larvae in the diversity analysis is likely to be of negligible importance for the conclusions, because the diversity shares would not change much, as most caterpillars presumably belong to very few species. The negative influence of ants on larval parasitoid species is stressed by the result that larval parasitoids are much rarer compared to egg and coccoid parasitoids. This has also been reported by Stork (1991) from Borneo and Askew (1985) in a comparison between the tropics and temperate regions. The rarity of ichneumonids in the samples seems to support the hypothesis that the species richness and abundance declines towards the equator (Owen & Owen, 1974; Janzen & Pond, 1975; Janzen, 1981; Gauld, 1986; Stork, 1991). Explanations for this phenomenon include the level of predation by ants as a factor (Rathcke & Price, 1976; Stork, 1991).

More research is needed to describe and understand the correlational evidence reported here in order to understand the importance of ants in savannah tree canopies. However, these results suggest that the influence of ants on insect communities might be even greater than previously expected.

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References


