ECOTROPICOS 20(2): 74-81 2007
Sociedad Venezolana de Ecología

COMPARING THE ANT FAUNA IN A TROPICAL AND A TEMPERATE FOREST CANOPY

COMPARACIÓN DE LA FAUNA DE HORMIGAS ENTRE UN DOSEL TROPICAL Y UNO TEMPERADO

Klaus Jaffe[1], Peter Horchler[2], Manfred Verhaagh[3], Cristina Gomez[1], Rene Sievert[2], Rodolfo Jaffe[1] and Wilfried Morawetz[+ 4]

[1]Universidad Simón Bolivar, Apartado 89000, Caracas 1080, Venezuela. Fax: 58-212-9063624. E-mail: kjaffe@usb.ve

[2]German Federal Institute of Hydrology, Department Ecological Interactions Am Mainzer Tor 1, 56068 Koblenz, Germany. E-mail horchler@bafg.de

[3]Staatliches Museum fur Naturkunde, Karlsruhe, Erbprinzenstraße 13, D-76133, Karlruhe, Germany.

[4]University of Leipzig, Department of Systematic Botany and Botanical Garden, Johannisallee 21-23, 04103 Leipzig, Germany

ABSTRACT

We studied the diversity and abundance of the ant fauna in the canopy and on the ground of a temperate forest (Leipzig Auwald, Germany) and compared the results with those from a Neotropical forest (Surumoni, Venezuela), using similar sampling methods, aided by two identical cranes that gave us ample access to both canopies. The data suggest the presence of approximately four times less ant species in the canopy of the temperate forest compared to the tropical one. In the temperate forest, the relationship between the species richness and presence of ants on the ground versus that found in the canopy, differ to that in the tropics: In the forest at Surumoni, ants were more diverse and had a larger presence in the canopy than on the ground, whereas this was not the case in the Auwald at Leipzig. These preliminary results shows the potential gains to be collected from deeper studies in comparative ecology, assessing the relative biomass of the different components of the ecosystem in the tropics and in temperate environments.

Key words: Canopy, forest, ants, ecology, diversity, abundance, tropical, temperate, crane, comparative ecology

RESUMEN

Estudiamos la diversidad de hormigas en el dosel y el suelo en un bosque temperado (Leipzig Auwald, Alemania) y la comparamos con levantamientos similares de un dosel Neotropical (Surumoni, Venezuela) utilizando los mismos métodos de muestreo y ayudados por dos grúas idénticas que nos daban acceso adecuado al dosel. Los datos sugieren que en el dosel del bosque templado hay aproximadamente cuatro veces menos especies de hormigas que en el dosel Neotropical. En el bosque temperado, la relación entre la frecuencia de ocurrencia de hormigas en el suelo y la del dosel difiere de la del Neotrópico. En el bosque de Surumoni, la ocurrencia de hormigas es más frecuente y más diversa en especies en el dosel que en el suelo; mientras que en el Auwald de Leipzig estos estratos no difieren entre si o la relación es inversa a la encontrada en Surumoni. Estos resultados preliminares muestran el potencial de estudios de ecología comparada referente a la biomasa relativa de los diferentes componentes del ecosistema entre bosques tropicales y templados.

Palabras clave: Dosel, bosque, hormiga, ecología, diversidad, abundancia, tropical, temperado, grúa, comparativo

INTRODUCTION

It is often stated that ants are the dominant component of the fauna in most ecosystems. After describing the dominance status of ants in some tropical ecosystems, Hölldobler & Wilson (1990) wrote: "Although comparable biomass measurements have not yet been made elsewhere, it is our subjective impression that the eusocial insects, ants foremost among them, are comparatively abundant in most other principal habitats around the world." This statement is very much supported by data coming from the tropics, but from temperate ecosystems no support for this affirmation is known. The little evidence available shows the other way: some studies, such as that by Seifert (1986) show that temperate ecosystems comprise often less than 10 ant species.

Canopies are thought to be especially favorable to ants (Erwin 1983). Yet comparative studies of temperate and tropical canopies, using comparable sampling techniques are lacking. Studies on ant diversity use different collection methods and therefore the data available for different ecosystems are not directly comparable. Regarding canopies, Hölldobler & Wilson (1990) claim that ants might be much more abundant on trees. Ants are certainly an important component of the canopy fauna in tropical systems (Blüthgen *et al.* 2000, Jaffe *et al.* 2003, Floren *et al.* 2002, Wagner 1996, for example). Equivalent studies on the dominance status of ants in the canopy of temperate forests are rare, although some results from fogging with insecticides of parts of tree canopies exist (Floren & Otto 2002, Floren personal communication). Yet again, each study used different collecting methods and thus the available data is not directly comparable.

Taking advantage of two identical cranes, one placed in Leipzig, Germany, and another in Surumoni, Venezuela, we got ample access to a temperate and a Neotropical canopy, which allowed for a pilot comparative study of the ant fauna in both localities, using the equivalent collecting methods and the same collector. This pilot comparative study should serve as a first approach to unveil the potential of these comparative studies, in order to eventually motivate financing and executing of more ambitious studies in comparative ecology.

Regarding collection methods for ants that are useful for comparative purposes, previous studies (Romero & Jaffe 1989) showed that direct collecting by hand is the simplest and most reliable method. Regarding collection using traps or baits, ants have a peculiar characteristic that makes collecting them different from collecting other insects. They are social, and therefore, the capture of a single specimen of an ant, indicates the probable presence of a colony of that species in the neighborhood, but so does the capture of a large number of specimens in a single trap. The probability of finding one or many workers in a given trap or site depends on the foraging and recruitment behavior of a given ant species and not on its abundance. That is, absolute numbers of individual worker ants captured while foraging does not give a good estimate for ant abundance. Yet relative frequencies of capture, noting only the presence or absence of workers of a given species in a trap or site, is a far more reliable indicator for the prevalence of a given ant species in an ecosystem (Romero & Jaffe 1989). The use of frequency of capture to estimate ant abundance also minimizes difference due to seasonal variations in foraging activity. Most ant species maintain foraging activity during the summer and autumn in temperate regions, and during most of the year in the tropics, so that direct sampling for assessing frequency of capture of ant species during these periods minimizes errors due to particular climatic or seasonal characteristics during collection.
Temperature and seasonality are the main abiotoc factors explaining differences in biodiversity between temperate and tropical regions. These should affect canopies and soil strata equally. In order to detect some additional characteristics affecting biodiversity, the differential assessment of biodiversity in a tropical and a temperate ecosystems in two strata (canopy and soil), seems adequate.

The aims of the present research were:
1- Optimize trapping procedures for ants in the Leipziger Auwald canopy, trying to use trapping methods that are equivalent to those used in Surumoni for the assessment of ant species diversity.
2- Design methods that allow for rough estimates of access to resources by ants in the canopy and on the ground, which can be used both in the tropics and in temperate forests.
3- Re-analyze data available from Surumoni so as to have equivalent trapping procedures and

collecting efforts for a more meaningful ant fauna comparison.
4- Compare the ant fauna, regarding diversity and ecological dominance, using different collecting methods, from a temperate and a tropical canopy, in order to unveil some putative fundamental ecological differences between both ecosystems.

METHODS

The temperate forest studied was the Auwald floodplain forest at the canopy-crane project of the University of Leipzig in Central-East Germany, where no flooding had been reported for the last 50 years. The tropical forest was located in southern Venezuela in the Orinoco basin at a floodplain bordering the river Surumoni where flooding did occurred frequently. Thus, collection of ground ants at Surumoni was undertaken some 5 Km from the crane in an area where flooding was not reported to have occurred during the last 50 years. Both sites had identical cranes. The temperate Auwald, located in Central-East Germany, Leipzig at 51° 20´N, 12° 22´E, and 102 m. a. s. l. is a formerly inundated floodplain forest. Detailed descriptions of the site are given in (Morawetz and Horchler 2002, Morawetz *et al.* 2003). The Neotropical rain forest located in Southern Venezuela at the upper Orinoco at 3°10' N, 65°40' W and 105 m. a. s. l. is a partly regularly inundated floodplain forest. Detailed description of the site is given in (Winkler & Listabarth 2002). It has to be noted that the Leipzig crane is situated in a managed forest close to an urban landscape, whereas Surumoni is a far remote wild area. This fact may add to differences in biodiversity.

In both sites, ants were collected by hand using forceps (direct collection) whenever an ant was sighted. The trees were explored from a gondola moved at will with the crane, which allowed access to the borders of the canopy and to holes in the canopy that lead to main branches and sometimes the trunk of trees. All collections were done at daytime. Collecting of ants in Leipzig was done during May to October of 2001 (Sievert 2002), and from August 21 to September 6, 2002, summing up approximately 12 hours/men of effective collecting effort. Ant collecting at Surumoni was performed irregularly during three years, but only data from the first collections, summing up the same collecting effort as that undertaken in Leipzig, were used here. For canopy data, only collections at over 15 m above the ground are used. Data from the ground are from ants collected on the soil and from plants growing up to 1.5 m above ground.

The estimate the ant density is very tricky as estimates of amount of workers is not equivalent to estimates of nest densities. As the number of ants captured depends on the recruitment habits of the ant species in question, the frequency of occurrence of ants on baits was used to estimate ant prevalence (see Romero & Jaffe 1989 for details).

In Leipzig, we placed either tuna or honey on the branches, and examined the foraging ants present at different time intervals, in collections made from August 21 to September 6, 2002 on 20 baited sites (10 baits at 15 m and additional 10 at approximately 30 m above the ground). On a given day on the crane, baits were placed in 6 to 8 sites and were evaluated during the whole day. New sites were explored on different days. The same collecting effort was performed on the ground (10 baits were placed on the ground and 10 at about 1.2 meter above the ground). The ecological importance of the ant species collected was estimated by the frequency of specimens of a given species captured in relation to the total number of traps. None of the trees was flowering during our collection period.

In Surumoni, natural baits, represented by nectar secreting flowers, were used as baits for collecting ants. Ant densities were so high that all tuna and all honey baits tested attracted ants. In most baits the attracted ant was an aggressive dominant ant that excluded other ants from the bait. As no competition between ants was observed in Leipzig, we looked for sampling methods were baits were not saturated by ants and no strong competition for baits was evident. Thus, data from ants collected at 20 inflorescences in the canopy and 20 located at less than one m above the ground were used. More information of the Surumoni ant ecology can be found in Jaffe *et al*. (2003).

RESULTS

The ant fauna found in the canopy and on the ground in Surumoni is given in Table 1. More data on the ant fauna of Surumoni is given in Jaffe *et al.* (2003). As can be observed from the table, one *Azteca* ant was dominant in the forest canopy of Surumoni, being present in half of the collecting sites, followed in frequency of collection by

Cephalotes atratus. Much fewer ants were collected on flowers than on the leaves of plants growing on the ground. The most frequent ant on flowers on the ground was a *Camponotus* species which occurred in only 15 % of the flowering plants examined.

The ant fauna found in the Leipziger Auwald is given in Table 2. Ants collected are from only 4 species. The most dominant ant species, *Lasius brunneus*, was collected in only 10 percent of the baits, most of them close to the ground. In addition to *L. brunneus*, only *Dolichoderus quadripunctatus* was collected on baits at 15 m above the ground or higher. All other ant species were only found close to the ground. Other insects collected on the baits include Hymenoptera (wasps, bees) Arachnida, Coleoptera, Hemiptera, Dermaptera, among others. More intensive collecting effort, with direct collection by hand, revealed the presence of two more ant species than those collected on baits. Although only six ant species were collected with the methods used, we are aware that at least two more species have been reported from this forest.

In total, using direct collection methods, we found 19 ant species in the canopy at Surumoni

Table 1. Ants collected in the forest canopy and on the ground. Numbers indicate the percentage of times a given ant species was found on a given location.

Ant species (Surumoni)	**Canopy**	**Ground**
Azteca sp.	50	0
Cephalotes atratus (Linne)	35	0
Crematogaster sp.	25	10
Camponotus sp.	25	15
Pseudomyrmex simplex (F.Smith)	10	5
Daceton armigerum (Latreille)	10	0
Cephalotes spinosus (Mayr)	5	0
Crematogaster sp2	5	0
Dolichoderus bidens Linne	5	0
Dolichoderus bispinosus (Olivier)	5	0
Dolichoderus sp.	5	0
Pachycondyla villosa (Fabricius)	5	0
Paraponera clavata Fabricius	5	0
Paratrechina sp.	5	5
Pheidole sp.	5	5
Procryptocerus sp.	5	0
Pseudomyrmex cf. flavidus	5	0
Pseudomyrmex sp.	5	0
Solenopsis sp.	5	0
Ectatomma ruidum Roger	0	10
Ectatomma tuberculatum (Olivier)	0	5
Cephalotes pusillus (Klug)	0	5
Ant species (Leipzig)	**Canopy**	**Ground**
Lasius brunneus (Olivier)	0	29
Lasius emarginatus (Latreille)	5	0
Dolichoderus quadripunctatus (Linne)	0	5
Leptothorax corticalis (Schenck)	5	0
Leptothorax affinis Mayr	5	0
Myrmica ruginodis Nylander	5	5

Table 2. Frequency of ant species collected by hand; and frequency of occurrence of ants on tuna and honey baits in the canopy of the Liepziger Auwald forest. The frequencies given represent the number of times, in percent, at least one representative of the species was found in relation to the total number of samples in that category.

Ant species (Leipzig)	Collected without baits (Frequency of abundance)	Collected on baited sites (% of sampled baits)
Lasius brunneus (Olivier)	0.5	10
Lasius emarginatus (Latreille)	0.4	0
Dolichoderus quadripunctatus (Linne)	0.3	1
Leptothorax corticalis (Schenck)	0.2	0
Leptothorax affinis Mayr	0.1	1
Myrmica ruginodis Nylander	0.1	1

versus 8 ant species on the ground. These numbers were 4 and 6 respectively for the Leipziger Auwald. The total number of ant species known for Surumoni is greater than 25, whereas that for the Leipziger Auwald is 8.

Of the three exposure times tested in the Leipziger Auwald (0.25, 4 and 24 h), the best time of exposure of the baits before looking for ants was 4 h for both types of baits, for both, ants (Figure 1a) and other arthropods (Figure 1b). This was partly due to the fact that tuna became dry, and honey became hydrated and trickled away after exposures longer than 4 hours. Data of insects on baits presented in Table 2 are for baits exposed for only 4 h.

The comparison of the number of ants and other arthropods collected at different heights in the canopy at Leipzig are presented in Figure 2. The results show that ants forage more frequently in the lower strata than in the higher canopy area. This could be connected with the nest localities of the examined three species. The same ant species were captured with similar frequencies at 15 and 30 m above the ground. The other arthropod groups collected in baited traps, comprising a high percentage of flying insects, appeared more or less equally distributed in the various height strata of the forest. It should be noted that our collection method did not captured all ants present in the environment and that many more can be expected (see Blüthgen *et al.* 2000 for ants in Surumoni). The collecting effort made in both ecosystems, however was the same.

The relative importance of ants in the two strata: canopy and soil, was estimated as the likelihood to find an ant on a food sources in each strata. This likelihood was 95 % in the Surumoni canopy vs. 45% near the Surumoni soil; and 5 % in the Auwald canopy vs. 40 % near the Auwald soil. Due to the different attractiveness of the baits used in Surumoni and Leipzig, the data for Leipzig might be overestimated whereas those for Surumoni might be underestimated. This difference, however applies to both canopy and soil, so that the relative data for each strata are significantly different between both ecosystems.

DISCUSSION

The most reliable collecting method found, which could be used for comparing ant abundance or ant dominance in both forests, is direct collecting of foraging workers. This confirms results from previous efforts in comparing sampling methods for ants (Romero & Jaffe 1989). The ant fauna were so different, that a method like tuna or honey

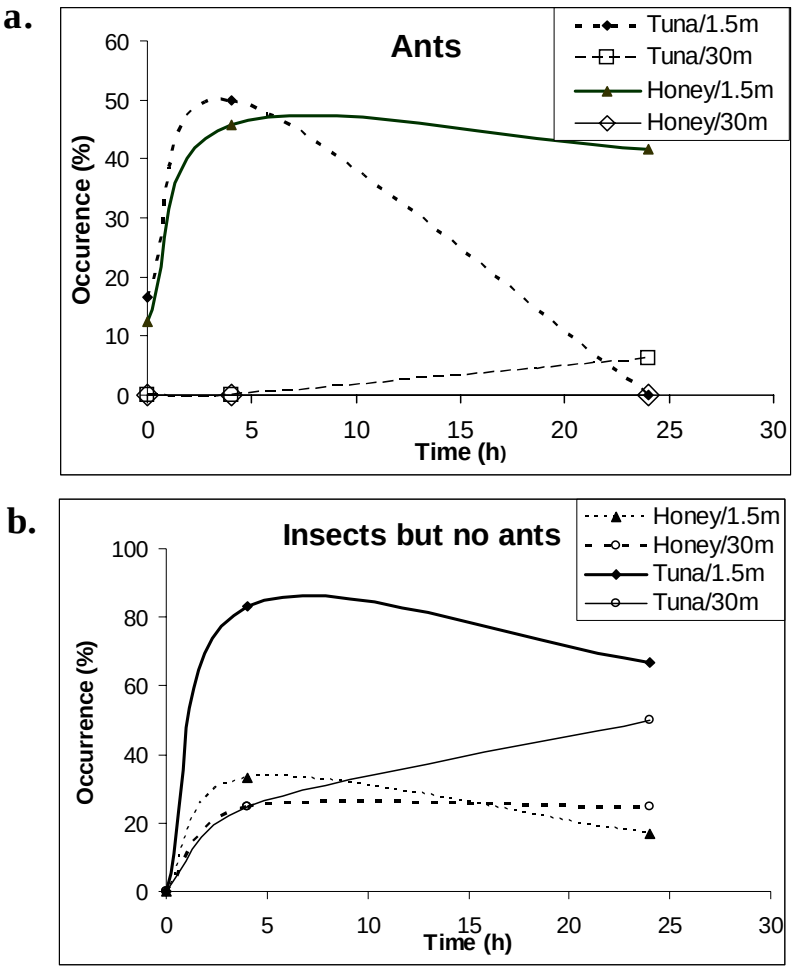

Figure 1. The duration of the attractive effect of baits measured by the occurrence of ants (**a**) and other insects (**b**), found on tuna or honey baits, at different times (0.5, 4 and 24 h), for baits placed at different heights above the ground (1.5 or 30 m) in the forest canopy of the Leipziger Auwald.

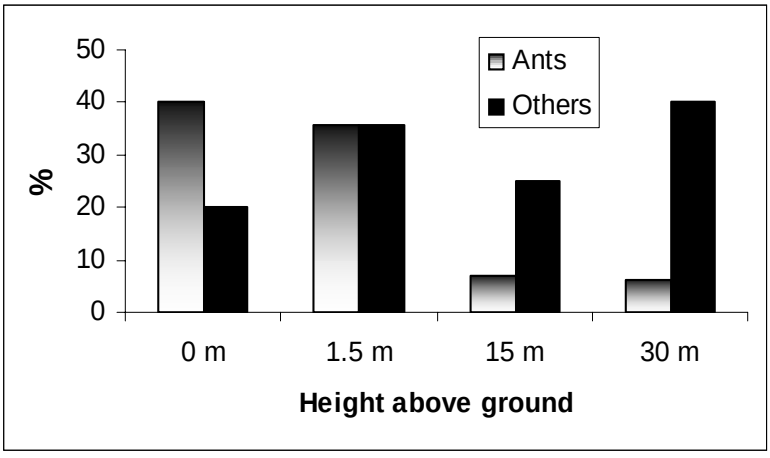

Figure 2. Frequency of capture (%) of ants (red) and other arthropods (blue), on all baits at different levels in the forest canopy (1.5, 15 and 30 meters above the ground) in the Leipziger Auwald.

baits, worked rather well in Leipzig and was unusable in Surumoni due to a much larger presence of ants. Thus, only data from direct sampling can be compared directly between both sites. The estimate for the relative ant species richness in Surumoni using this method is 19 ant species in the canopy vs. 8 ant species on the ground, compared with Leipzig where the numbers were 4 vs. 6. That is, ants were 2.4 times more species rich in the Surumioni canopy than on the ground, whereas in Leipzig they were 0.7 times more species in the canopy compared to the ground.

These results suggest that ants are conspicuously few in the temperate canopy ecosystem at the Leipziger Auwald, compared to Surumoni. This was despite the fact that the forest at Surumoni is not an especially ant rich ecosystem compared to other forests in the tropics (Blüthgen *et al.* 2000, Jaffe *et al.* 2003). Although more recent data on tropical ecosystems seem to give a picture for ant diversity in tropical canopies that is much lower than that estimated by the first quantitative reports published from the Neotropics (see reviews in Basset *et al.* 2003). In fact, the ant diversity found in the Surumoni canopy seems to be rather among the average diversity reported for tropical canopies.

Using the total number of species collected with all methods, the numbers do not differ very much. The total number of species collected in the Surumoni canopy was about 4 times larger than that found in Leipzig. Over 22 species were collected in the canopy in Surumoni vs. 6 ant species in Leipzig, suggesting that more sampling efforts, using the same methods, should not change these values very much. The use of fogging, though, might produce quite different numbers, as they will sample not only diurnal ants, but also nocturnal and cryptic ant species.

Regarding the methods used for estimating the ecological importance of ants, assessed through the likelihood of find an ant on a honey baits or nectar sources, they could only provide data for intra-site comparisons as they differed between sites. Therefore, these values were used only for comparing relative ant presence between canopy and soil in each site. These estimates showed that in Surumoni, a spot in the canopy is 2.1 times more likely to be visited by ants than a spot on the ground, compared to 0.125 times in Leipzig.

Of course, our sampling method had many weaknesses and shortcomings, but these were the same in both strata (canopy and ground) in each site and similar in both sites. Fogging studies in temperate forest confirm our findings by showing that there are only few ants in temperate canopies compared to tropical canopies (Floren, personal communication). Yet our results clearly show a conspicuous huge relative scarcity of ants in temperate canopies relative to the ground. This difference does not apply for other arthropods collected in the Leipziger Auwald. The study in Leipzig found that other arthropods, feeding on honey and/or tuna baits, were found with equal abundance on the ground and in the canopy. Certainly, harsh winters (relative to the tropics) limit the nesting possibilities of ants in the canopy. In any case, this limitation may be stronger in the canopy than in the soil.

Although no definitive general conclusion can be drawn from the comparison of a couple of sites, our data hint to enormous ecological differences in respect to the ant fauna between temperate and tropical forests. Tropical canopies are much more important, in ecological terms, for ants than temperate canopies. This qualitative difference between tropical and temperate canopies should have consequences in the ecological interactions occurring in them. An indirect test as to the evolutionary importance of the reduced number of ants in temperate forest canopies is that we could expect that competition among foraging workers in the canopy should be rare, and therefore, the few ants that occur in this canopy should show little or no intra-specific aggression. In certain temperate pine forests, *Formica* ants dominate the insect fauna and are known to engage in aggressive interspecific combats (Elton 1932, Mabelis 1979, for example). In this case, the hypothesis would predict reduced aggression the higher up in the canopy ant encounters occurs. Other consequences are very likely to be uncovered as more comparative research enhances our understanding of such ecosystem differences.

However, alternative hypothesis might prove true. It might be assumed that canopies always will provide a reduced amount of resources or at least a limited number of possible accesses to this resource. In case temperate forest provide in poorer resources to ants than tropical forests, competition may be likely even in canopies with few species (Yanoviack & Kaspari 2000)

The preliminary results presented here are based on two very specific sites, and future studies

on different temperate and tropical sites might show different results. The present study, hopefully, will stimulate more and better studies in comparative ecology between tropical and temperate forests, as our results may reflect a more general ecological situation, rather than a particular exception.

ACKNOWLEDGEMENTS

We thank Dr. Erik Arndt (Hochschule Anhalt) for the identification of the ants; Dr. Andreas Floren (Universität Würzburg); and anonymous referees for helpful criticism of the paper.

LITERATURE CITED

BASSET, Y., V. NOVOTNY, S. MILLER and R. KITCHING (ed.). 2003. Arthropods of Tropical Forests: Spatio-Temporal Dynamics and Resource Use in the Canopy. Cambridge University Press.

BLÜTHGEN N., M. VERHAAGH, W. GOITÍA, K. JAFFÉ, W. MORAWETZ and W. BARTHLOTT. 2000. How plants shape the ant community in the Amazonian rainforest canopy: the role of extrafloral nectaries and homopteran honeydew. Oecologia (125): 229-240.

ELTON, C. 1932. Territory among wood ants (*Formica rufa* L.) at Picket Hill. Journal of Animal Ecology 1, 69-76

ERWIN, T.L. 1983. Tropical forest canopies: the last biotic frontier. Bulletin of the Entomological Society of America (29): 14-19.

FLOREN A. and S. OTTO. 2002. Beeinflußt die Anwesenheit der Waldameise *Formica polyctena* FOERSTER die Artenzusammensetzung und Struktur von Spinnengemeinschaften auf Eichen? Arachnologische Mitteilungen (24): 1-18.

FLOREN, A., A. BIUN and K. E. LINSENMAIR. 2002. Arboreal ants as key predators in tropical lowland rainforest trees. Oecologia (131): 137–144.

HÖLLDOBLER, B. and E. O. WILSON. 1990. The Ants. Harvard University Press.

JAFFE, K., J. V. HERNANDEZ, W. GOITÍA, A. OSIO, F. OSBORN, H. CERDA, A. ARAB, J. RINCONES, R. GAJARDO, L. CARABALLO, C. ANDARA and H. LOPEZ. 2003. Flower ecology in the neotropics: a flower-ant love-hate relationship. Pp. 213-219, *in* Y. Basset, V. Novotny, S. Miller and R. Kitching (eds.): Arthropods of Tropical Forests: Spatio-Temporal Dynamics and Resource Use in the Canopy. Cambridge University Press,

MABELIS, A.A. 1979. Wood ant wars. Neth. J. Zool. (29): 451-620.

MORAWETZ, W. and P. HORCHLER. 2003. Leipzig Canopy Crane, Germany. Pp. 54-47, *in* Mitchell, A.W., Secoy, K. & Jackson, T. (eds.): The Global Canopy Handbook. Techniques of Access and Study in the Forest Roof. Global Canopy Program, Oxford.

MORAWETZ, W. and P. HORCHLER. 2003. Leipzig Canopy Crane Project (LAK), Germany. Pp. 79-85, *in* Basset, Y., Horlyck, V. & Wright, S.J. (eds.): The International Canopy Crane Network: Studying Forest Canopies and Understanding their Value. Smithsonian Tropical Research Institute, Panama.

MORAWETZ, W., J. WESENBERG and P. HORCHLER. 2003. Vegetation characteristics of the Surumoni Site. Pp. 133-136, *in* Basset, Y., Horlyck, V. & Wright, S.J. (eds.): The International Canopy Crane Network: Studying Forest Canopies and Understanding their Value. Smithsonian Tropical Research Institute, Panama.

MORAWETZ, W. & HORCHLER, P.J. 2004. The Leipzig Canopy Crane Project -Biodiversity, Ecology and Function in a Temperate Deciduous Forest. Sidebar, Chapter 20, Pp 374-376, *in* Lowman, M. & Rinker, B. (Editors): Forest Canopies. 2nd edition. Academic Press.

ROMERO, H. and K. JAFFE. 1989. On methods for sampling of Formicidae in savannahs. Biotropica (21): 348-352.

SEIFERT, B. 1986. Vergleichende Untersuchungen zur Habitatwahl von Ameisen im mittleren und südlichen Teil der DDR. Abh Ber Naturkundemus Görlitz (59): 1-124.

SIEVERT, R. 2002. Biodiversität von Arthropoden in der Kronenregion eines Leipziger Auwalds. unpublished diploma work at the University of Leipzig.

WAGNER, T. 1996. Artenmannigfaltigkeit baumkronenbewohnender Arthropoden in zentralafrikanischen Wäldern, unter besonderer Berücksichtigung der Käfer, Rheinische Friedrich-Wilhelm-Universität Bonn.

WINKLER, H. and C. LISTABARTH. 2002. The Surumoni Canopy Crane Project. Pp. 80-84, *in* Mitchell, A.W., Secoy, K. & Jackson, T. (eds.): The Global Canopy Handbook. Techniques of Access and Study in the Forest Roof. Global Canopy Programme, Oxford.

WINKLER, H. and C. LISTABARTH. 2003. The Surumoni Canopy Crane Project. Pp. 126-132, *in* Basset, Y., Horlyck, V. & Wright, S.J. (eds.): The International Canopy Crane Network: Studying Forest Canopies and Understanding their Value. Smithsonian Tropical Research Institute, Panama.

YANOVIAK S.P. and M. KASPARI. 2000. Community structure and the habitat templet: ants in the tropical Forest canopy and litter. Oikos (89):259-266.

Recibido 05 de enero de 2006; revisado 01 de mayo de 2006; aceptado 24 de octubre de 2007.