Biodivers Conserv
DOI 10.1007/s10531-009-9596-4

ORIGINAL PAPER

Fuelling the biodiversity crisis: species loss of ground-dwelling forest ants in oil palm plantations in Sabah, Malaysia (Borneo)

Carsten A. Brühl · Thomas Eltz

Received: 26 March 2008 / Accepted: 5 February 2009

Abstract Oil palm plantations today cover large areas of former tropical lowland rain forest in Southeast Asia and are rapidly expanding on the island of Borneo. Study of the community of ground-dwelling ants in different plantations in Sabah, Malaysia, over 2 years using tuna baiting, revealed that the oil palm plantation ground ant community was severely reduced in species richness in comparison to the forest interior, regardless of age, undergrowth cover, or proximity to neighbouring forest. The results indicate that oil palm plantation habitats, now covering more than 15% of Sabah's land area, can sustain only about 5% of the ground-dwelling ant species of the forest interior. Nine of the 23 ant species baited in the plantations were never recorded inside forest. All numerically dominant ants were non-forest species. The most common species was *Anoplolepis gracilipes*, an invasive species present at 70% of all bait sites and known to cause 'ecological meltdowns' in other situations. The low frequency and species number of forest ground ants indicates that oil palm plantations act as effective dispersal barriers leading to community isolation in rain forest remnants. The replacement of natural forests with oil palm plantations poses a serious threat to the conservation of biodiversity on Borneo if similar results are confirmed in other taxa.

Keywords *Anoplolepis gracilipes* · Ants · Biodiversity · Dispersal barrier · Fragmentation · Isolation · Malaysia · Oil palm

Introduction

With the growing global demand for agricultural products landscapes throughout the tropics are increasingly dominated by agriculture (Tilman et al. 2001; Achard et al. 2002).

C. A. Brühl (✉)
Institute for Environmental Sciences, University Koblenz-Landau, Fortstr. 7, 76829 Landau, Germany
e-mail: Bruehl@uni-landau.de

T. Eltz
Department of Neurobiology, Sensory Ecology Group, University of Düsseldorf, Universitätsstr. 1, 40225 Düsseldorf, Germany
e-mail: Eltz@uni-duesseldorf.de

The increase in oil palm (*Elaeis guineensis*) cultivation is cited as a major driver of deforestation and biodiversity loss in tropical countries (Donald 2004; Koh and Wilcove 2007, 2008) and has also major impacts on global carbon balance (Danielsen et al. 2008). Oil palm plantations expanded almost exponentially in recent decades (Donald 2004), now covering over 13 million ha, primarily in Southeast Asia (Danielsen et al. 2008). Palm oil is now the world's most traded oilseed crop with uses from cooking oil to biofuel (Carter et al. 2007) and with over 37 million metric tons produced in 2005 (Turner et al. 2008). In 2006, 85% of the global palm oil crop was produced by Indonesia (43%) and Malaysia (42%) (FAOSTAT 2007), two countries whose combined annual forest loss is around 2 million ha (Danielsen et al. 2008). Malaysia has the highest levels of palm oil production per unit area but also the highest relative number of endangered species, and therefore impacts on biodiversity are expected. However, to date studies addressing this topic are few (Fitzherbert et al. 2008; Koh and Wilcove 2008; Turner et al. 2008).

In the Malaysian state of Sabah, oil palm plantations have been established on a large scale in the lowland areas that had previously been degraded by selective logging of variable intensity (McMorrow and Talip 2001). This valuable crop is currently grown on more than 1.2 million ha in Sabah equalling around 30% of the total of Malaysia's plantation area (MOPB 2007; FAOSTAT 2007) or ca. 15% of the total land area of Sabah. Oil palm plantations today stretch all along the coastal plains in Eastern Sabah and most of the lowland rain forest has been converted into an extensive monoculture of immense dimensions.

Before the establishment of an oil palm plantation, the forest must be completely cleared of vegetation. The wooden debris and trees easily catch fire, especially in dry El Niño years. The extensive fires in Borneo in 1998 were mostly associated with agricultural and land clearing operations (Chazdon 1998; Cao 2000; Dennis et al. 2005), in Sabah often related to the establishment of oil palm plantations. After clearing, the ground is terraced before planting the young oil palms. A humus and leaf litter layer is lacking in the newly established plantations because of erosion of the top soil associated with high surface water runoff, which reaches more than twice the amount measured on land under forest cover (MacKinnon et al. 1996). Lack of organic matter is the main factor determining the unfavourable change in soil properties in oil palm plantations, leading to a marked deficiency in most nutrients (Yeboua and Ballo 2000).

Leaf litter ants are considered useful indicators of ecosystem disturbance (Agosti et al. 2000; Underwood and Fisher 2006) and they have been found to show congruent patterns with other taxa in their responses to environmental change in different habitats (Lawton et al. 1998; Alonso 2000). The functional importance of ground-dwelling ants in the process of nutrient cycling due to their role in bioturbation (Gunadi and Verhoef 1993; Wilson 2000) and enhancement of microbial activity (Dauber and Wolters 2000) established their role as ecosystem engineers (Jones et al. 1994; Folgarait 1998). They are also recognised as main predators of other ground arthropods (Carroll and Janzen 1973; Hölldobler and Wilson 1990).

Selective logging in Sabah has resulted in a pronounced reduction in forest leaf litter ant diversity and density, and communities did not recover even 25 years after the logging impact (Brühl 2001). Ant diversity was also reduced in smaller primary forest fragments (Brühl et al. 2003) where the genetic diversity of forest litter ants was affected as well (Bickel et al. 2006), implying that ant populations in forest remnants were effectively isolated. Here, the ground ant community in surrounding oil palm plantations was studied to evaluate if this agricultural matrix is a suitable habitat for native forest ant species.

Methods

Study sites

Ground-dwelling ants were collected in four oil palm plantations in Eastern Sabah (Fig. 1): In the Mayvin oil palm estate (MOP) and in plantations near Tawai Hills Forest Reserve (THFR), Deramakot Forest Reserve (DFR) and Sepilok Forest Reserve (SFR). MOP is situated in the core of a very large plantation area (15 × 10 km) and was ~8–10 years old with palm trees reaching 8 m in height. Undergrowth consisted of various grasses and herbs (e.g. *Panicum* sp., *Mimosa pudica*). In all but the MOP location sampling transects extended from the forest edge into the oil palm plantation. The THFR plantation was 5–7 years old, palm trees were about 3–5 m in height and the undergrowth was sparse with bare ground mostly visible. A similar plantation type was present at the DFR site, bordered by heavily logged forest. The SFR transects ran from the edge of a primary forest remnant (42.9 km^2) into an old abandoned oil palm plantation (ca. 15–20 years old). The palm trees reached up to 10 m in height, and various herbs, bushes and saplings were present, forming a comparatively dense undergrowth. The soil in the oil palm plantations was mostly bare and no substantial leaf litter layer was present. For comparative purposes ants were also collected in the Danum Valley Conservation Area (DVCA), a contiguous primary rain forest of 438 km^2 ~80 km south of the plantation area (Fig. 1). The transect in DVCA was situated on the West Trail Transect ~1.5 km from the field center.

Sampling

Sampling transects were initially established in 1999 at two sites (SFR1, THFR1). Subsequently, in 2000, except for the single site established at MOP and the control site at DVCA, paired transects were established (SFR, THFR, DFR; see Table 1). Since the ant fauna in the plantations was found to be impoverished, some of the transects were operated at more widely spaced intervals (100 m) to detect potential turnover (see Table 1). The longest transects covered almost 1 km, which was the maximum length manageable for monitoring and sampling the bait sites.

All transects were sampled once in the morning from 8:00–10:00 hour, at least 2 days after rain in dry conditions in March and April. Ground-dwelling ants were attracted with baits consisting of a teaspoon of canned tuna in oil placed on tissue paper. Three tuna baits were placed at every bait site at a distance of 5, 10 and 15 m from the access trail to avoid possible disturbance by humans or machinery. Baits were left for 2 h to attract ants and were checked every 30 min. All ant species present at a bait site were collected using forceps and were pooled for a bait site sample. During the 2 h of active baiting the area was also searched for ants by hand collecting. During this process stones, twigs or palm leaves on ground level were turned and searched for ants. Ants were stored separately and later compared with the ants collected at baits.

The ants were sorted to genus level, then mounted following the convention of Bolton (1994) and finally sorted to morphospecies. Morphospecies classification was based on external morphological characters of the worker class visible under a dissecting microscope (Leica MZ8 16 × 14). Morphospecies labels were replaced by valid species names whenever possible. Voucher specimens have been deposited with the Entomology Section, Forest Research Centre, Sandakan, Sabah, the Department of Animal Ecology and Tropical Biology, University of Würzburg, Germany and are integrated in a web based ant identification key (www.antbase.net).

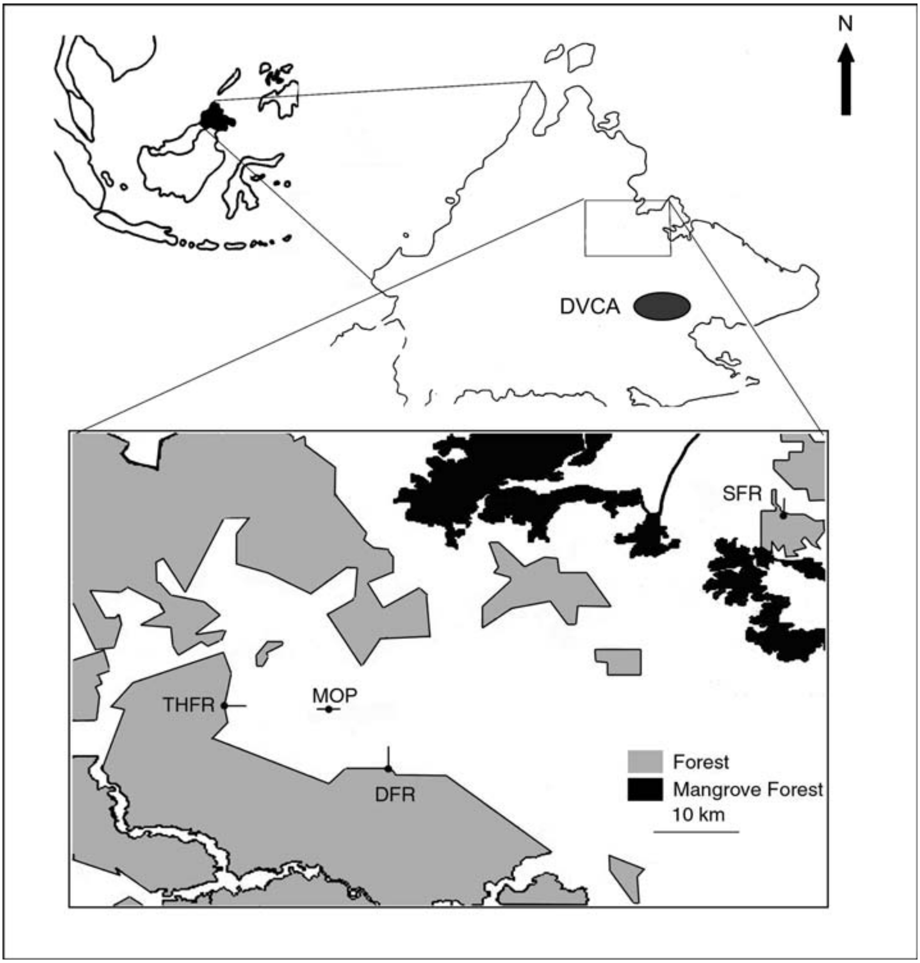

Fig. 1 Location of the four sampled oil palm plantations in East Sabah: plantation bordering the Tawai Hills Forest Reserve (*THFR*), the Deramakot Forest Reserve (*DFR*) and the Sepilok Forest Reserve (*SFR*). The Mayvin oil palm plantation (*MOP*) is situated in the center of a large plantation area. The primary forest site was located in the Danum Valley Conservation Area (*DVCA*)

Table 1 Transects used for tuna baiting of ground-dwelling ants in oil palm plantation (SFR, THFR, DFR, MOP) and primary forest (DVCA)

Transects	SFR1	SFR2	SFR3	THFR1	THFR2	THFR3	DFR1	DFR2	MOP1	DVCA
Sampling year	1999	2000	2000	1999	2000	2000	2000	2000	2000	1999
Number of bait sites	5	13	13	13	13	10	13	10	10	6
Distance between bait sites (m)	25	10	10	50	10	100	10	100	20	100
Transect length (m)	100	120	120	600	120	900	120	900	180	500

Statistical methods

Presence and absence of ant species at bait sites was analysed. Species accumulation curves for the different plantation transects were calculated using EstimateS 5.0 (Colwell 1997) randomising the data 100 times. Five species richness estimators were calculated for the total oil palm plantation ground ant community: ICE, Jackknife 1 and 2, Bootstrap, MMMean (Colwell and Coddington 1994; Colwell 1997). Sampling efficiency was obtained after dividing observed by estimated species number.

Results

In total 23 ant species in 14 genera were recorded along nine transects in oil palm plantations (Table 2). Most species belonged to the subfamily Myrmicinae (11 species) followed by the Dolichoderinae and Formicinae (five species each). Two Ponerinae species were also sampled. Hand collecting did not reveal any species not recorded at the tuna baits.

The randomised species accumulation curves of the oil palm plantation transects were much flatter than that of the primary forest transect, yielding lower species numbers (Fig. 2). The rate of increase in species with bait sites was low in all plantation transects. In the DFR1 transect only one species (*A. gracilipes*) was recorded at all 13 bait sites (Table 2). Observed species number in single transects was similar in the different plantation areas (Fig. 2), although longer transects (600–900 m, THFR1, THFR3, DFR2; Table 1) tended to yield more species.

When all samples were combined in order to estimate total projected ground ant species number in oil palm plantations the highest estimate was 48 (Jack2), the lowest 25 species (MMMean) with sampling efficiencies of 47.9 and 92.0%, respectively (Table 3).

Discussion

Loss of forest ants in oil palm plantations

The ground-dwelling ant communities of oil palm plantations were found to be highly impoverished with respect to forest taxa and, instead, were dominated by a small number of, partly invasive, non-forest species. Species richness and community composition did not vary much between the four plantations. This was unexpected since the SFR, THFR and DFR transects were directly connected to forest, in the case of SFR a primary forest fragment. Proximity to closed forest could theoretically promote an influx of forest ant species into the plantations (Laurance and Bierregaard 1996). Instead species numbers were similar to the MOP transect which was isolated in the core of a large oil palm plantation. Also, there seemed to be no effect of plantation age or undergrowth structure on ant species richness: The abandoned SFR plantation, with old palm trees, dense vegetation and no mechanical or chemical treatment, harboured as few ant species as the young plantations near THFR, where the ground had been completely cleared of forest just 4–5 years prior to sampling. Slightly more species were only recorded in the three longer transects THFR1, THFR3, and DFR2, indicating that monitoring of ants might need to consider larger spatial scales in monocultures.

The species accumulation curve of the tuna bait samples in the primary forest had a steep slope revealing that sampling of the ground ant community was far from complete.

Table 2 Occurrences of ground-dwelling ant species and cumulative species number at the different oil palm transects (maximum number of bait sites)

Species	SFR1 (5)	SFR2 (13)	SFR3 (13)	THFR1 (13)	THFR2 (13)	THFR3 (10)	DFR1 (13)	DFR2 (10)	MOP1 (10)	Total (100)
Pachycondyla b			1						1	2
Odontoponera denticulata		1				3		4	3	11
Dolichoderus sp. 1						1			2	3
Dolichoderus sp. 2				1	9	6		1		17
Technomyrmex sp. 1									1	1
Technomyrmex sp. 2				4		5		2		11
Technomyrmex sp. 1						1			2	3
Oecophylla smaragdina	1									1
Anoplolepis gracilipes	5	10	10	11	4	2	13	5	10	70
Paratrechina longicornis			3	1		1			2	7
Paratrechina sp. 1		1								1
Paratrechina sp. 2				1						1
Crematogaster sp. 1								1		1
Recurvidris sp. 1									1	1
Lophomyrmex bedoti		3	1	2						6
Tetramorium noratum				1						1
Monomorium floricola	1			2	1	3		1	2	10
Monomorium sp. 1				1	1					2
Monomorium sp. 2				1		3				4
Solenopsis sp. 1								1		1
Pheidole sarawakana			1							1
Pheidole sp. 1				4	2	1				7
Pheidole sp. 2			1							1
Number of species	3	4	6	11	5	10	1	7	9	23

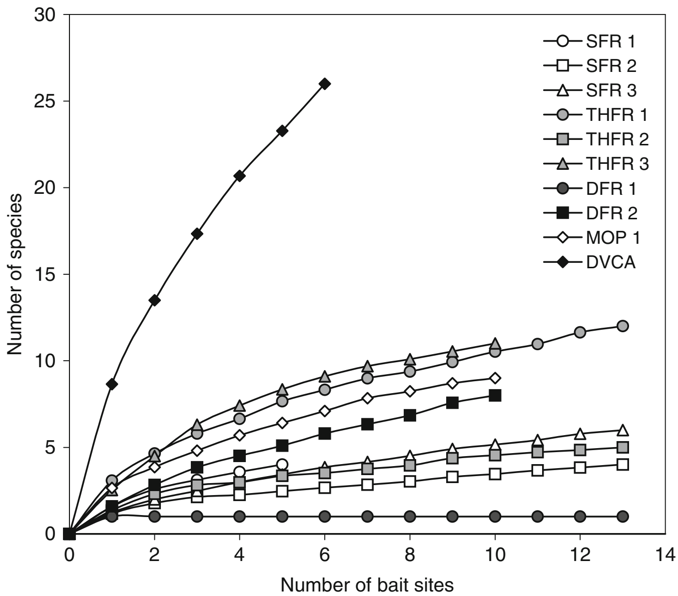

Fig. 2 Randomised species accumulation curves (100 runs) of the sampled transects in the different oil palm plantations (*SFR*, *THFR*, *DFR*, *MOP*) and the primary forest (*DVCA*)

Table 3 Observed and estimated species and sampling efficiency (%) of the ant communities for all bait sites ($N = 100$) in the oil palm plantations

	Observed species	ICE	Jack 1	Jack 2	Bootstrap	MMMean
Total oil palm	23	38 (60.5)	33 (69.7)	48 (47.9)	27 (85.2)	25 (92.0)

Nonetheless, species richness in the primary forest site was on average five times higher than that of the plantation sites. Furthermore, sampling with tuna baits is likely to underestimate the true diversity of ground-dwelling ants in forest habitats. Sampling with litter sifting, a technique that is more appropriate to sample habitats rich in leaf litter, revealed 187 ground-dwelling ant species at the same primary forest locality (Danum Valley, Brühl et al. 2003). More than 250 species were obtained by litter sifting along an altitudinal transect from primary lowland to subalpine forest in Northwestern Sabah (Brühl et al. 1999). In plantations, where no substantial leaf litter is available, litter sifting is not a feasible approach to collect ground-dwelling ants; instead tuna baiting is a very efficient alternative (Agosti et al. 2000). This is confirmed by our study. Sampling at tuna baits along the various transect was evidently efficient since intensive hand collecting did not reveal additional species at the respective sites. Thus, despite differences in the methodology that was used in the forest and plantation studies, we conclude that oil palm plantations retain only a small fraction (perhaps <5% of species) of the forest ground-dwelling ant community.

Two factors are likely responsible for the loss of ground-dwelling ants in oil palm plantations. First, the almost complete absence of leaf litter reduces the availability of nest sites for litter-nesting species (Carvalho and Vasconcelos 1999). Second, hot and dry conditions possibly prevent colony establishment and reduce colony survival of shadeadapted taxa. Microclimate is an influential factor on the distribution and competitive performance of ground-dwelling forest ants (Torres 1984; Perfecto and Vandermeer 2007; Brühl 2001). Forest ants have a lower tolerance to high temperature than ants from non-forested areas (Torres 1984). This may explain their absence in oil palm plantations, where conditions are warmer and drier and the unprotected soil layer can become extremely hot especially during the establishment phase of plantations. In addition to not providing a suitable habitat for forest ants, oil palm plantations likely form a dispersal barrier between forest populations. Queens of forest ants may be killed by adverse climatic conditions during dispersal between forest remnants. Forest ant populations that persist in small Virgin Jungle Reserves in Eastern Sabah may therefore be effectively isolated (Brühl et al. 2003). This was indicated by the lack of gene flow between fragmented populations of two forest ant species in Sabah (Bickel et al. 2006).

Our results on ground-dwelling ants are in good general agreement with findings concerning the arboreal ant community of oil palm plantations. Arboreal ants were studied by Pfeiffer et al. (2008), who intensively sampled from oil palm stems and freshly cut palm fronds. They recorded 53 species of ants with 17 species accounting for 95% of all species incidences. Thus, arboreal ant species richness in oil palm plantations was also dramatically lower than that of primary forest in Sabah, where 385 ant species were recorded in the lower vegetation and canopy (Brühl et al. 1998). Similar to our findings for ground-dwelling ants, almost 50% of all species occurrences represented tramp ant species, and at least four of these 12 species were invasive (Pfeiffer et al. 2008).

Ant community shift in oil palm plantations

Besides the evident reduction in species richness of forest ants, there was a pronounced shift in community composition towards non-forest taxa. Nine species of oil palm plantation ants were never observed in forest leaf litter in an extensive sampling program (Brühl 2001): *A. gracilipes, Dolichoderus* sp. 1 and 2, *Odontoponera denticulata*, *Monomorium* sp. 2, *Technomyrmex* sp. 2, *Oecophylla smaragdina*, *Paratrechina* sp. 2, and *Crematogaster* sp. 1. The 14 remaining species, which were also recorded in forest leaf litter (Brühl 2001; Brühl et al. 2003), were all rare in the plantations. Even *Lophomyrmex bedoti*, a common ant in highly disturbed logged-over forest in Sabah (Brühl 2001) was not frequently observed in oil palm plantations (six of 100 bait sites). The oil palm plantation ground ant community was numerically dominated by three species not occurring in forest habitats: *O. denticulata*, *Dolichoderus* sp. 2, and *A. gracilipes* (Table 2). The yellow crazy ant, *A. gracilipes*, was the most abundant species, collected at 70 out of 100 bait sites. It was present in all oil palm plantations and was the only species collected along the transect DFR1. *A. gracilipes* was also recognised as the dominant arboreal ant in oil palm plantations in Sabah and Peninsular Malaysia (Pfeiffer et al. 2008) and in cocoa agroforests in Sulawesi (Bos et al. 2008). The presence of *A. gracilipes* may in itself be responsible, by means of predation or competitive exclusion, for the very low ant diversity in some of the transects (especially DFR1). The yellow crazy ant has been recognised as an invasive tramp ant species (Wetterer 2005) and is documented as a dominant species in many ant communities in disturbed habitat all over the world (Majer 1993; Wetterer 2005; Bos et al. 2008). Its ecological impact was studied especially on islands (Lester and Tavite 2004) where it has revealed the potential to influence a wide variety of fauna and flora, negatively affecting ant communities but also other insects, spiders and, in the case of Christmas Island, the land crab *Gecaroidea natalis*. The reduction of the crab resulted in mutitrophic-level distortions in the ecosystem causing an invasional 'meltdown' with changes in forest structure and tree composition (O'Dowd et al. 2003; Abbott and Green 2007). *A. gracilipes* is also known to directly attack hatchling birds and reptiles and preys upon small livestock (Wetterer 2005). Reduced breeding success and behavioural changes were observed in birds on Christmas Island in the presence of *A. gracilipes* (Davis et al. 2008). *A. gracilipes* supercolonies reach densities of up to 2,250 ants per m^2 (O'Dowd et al. 2003; Abbott and Green 2007) and cover large areas. Supercolonies consist of interrelated nests that show no or very low levels of intraspecific aggression, which is a key feature for the ecological dominance of *A. gracilipes* (Hölldobler and Wilson 1990). The population structure of *A. gracilipes* was recently studied in Malaysian Borneo and a mosaic of supercolonies and expanding, newly introduced propagules was revealed (Drescher et al. 2007). Although the direct and indirect impacts of *A. gracilipes* on vertebrates have not been studied outside an island context, it seems possible that this species not only affects the ant community in oil palm plantations but also poses more wide-ranging threats to the residual amphibian, reptile, bird and mammal fauna. Another tramp species, *Monomorium floricola* (Schultz and McGlynn 2000) was also fairly common in the plantations and present at 10% of all bait sites. This species was also recorded in disturbed forests in Sabah (Brühl 2001).

Conclusion

The ground-dwelling ant communities of oil palm plantations were found to be highly impoverished with respect to forest taxa and, instead, were dominated by a small number of, partly invasive, non-forest species. The latter also included *A. gracilipes*, an invasive tramp species that is known for its adverse effects on biodiversity on tropical islands. Therefore it seems important to evaluate the ecological impact of this ant species in oil palm plantations, not only on other ants and insects but also on vertebrates.

The low abundance and species richness indicates that oil palm plantations cannot serve as a refuge for ground-dwelling forest ants. Furthermore, oil palm plantations are likely to act as dispersal barriers for forest taxa leading to community isolation in rain forest remnants. There is a clear need for more research to understand how animal and plant populations of the remaining forest fragments are affected by the surrounding plantation. A shift of the current focus in conservation biology from large mammals and birds towards arthropods that make up the bulk of the biodiversity in tropical rain forests would be desirable.

Acknowledgments We want to thank K. Eduard Linsenmair and Brigitte Fiala for discussions of many aspects of this research and Tobias Bickel for his help with tuna baits. We are also thankful to Chey Vun Khen, Arthur Chung, Robert Ong, Hubert Petol and Ruben Nilus of the Forest Research Center in Sandakan for all their support during our stay in Sabah. Permission to conduct research in Sabah was granted by the Economic Planning Unit, the Forestry Department Sabah and the Danum Valley Committee and is gratefully acknowledged. Three anonymous reviewers improved the quality of the paper. This study is project number DV163 of the Danum Valley Rainforest Research and Training Programme and was supported through a DAAD scholarship and DFG travel grant to CAB and by GTZ (TÖB) funding to TE.

References

Abbott KL, Green PT (2007) Collapse of an ant-scale mutualism in a rainforest on Christmas Island. Oikos 116:1238–1246. doi:10.1111/j.0030-1299.2007.15629.x

Achard F, Eva HD, Stibig H-J, Mayaux P, Callego J, Richards T, Malingreau J-P (2002) Determination of deforestation rates of the world's humid tropical forests. Science 297:999–1002. doi:10.1126/science.1070656

Agosti D, Majer J, Alonso E, Schultz TR (2000) Ants: standard methods for measuring and monitoring biodiversity. Biological diversity handbook series. Smithsonian Institution Press, Washington DC, 280 pp

Alonso LE (2000) Ants as indicators of diversity. In: Agosti D, Majer J, Alonso E, Schultz TR (eds) Ants: standard methods for measuring and monitoring biodiversity. Biological diversity handbook series. Smithsonian Institution Press, Washington DC, pp 80–88

Bickel TO, Brühl CA, Gadau JR, Hölldobler B, Linsenmair KE (2006) Influence of habitat fragmentation on the genetic variability in leaf litter ant populations in tropical rainforests of Sabah, Borneo. Biodivers Conserv 15:157–175. doi:10.1007/s10531-004-4248-1

Bolton B (1994) Identification guide to the ant genera of the world. Harvard University Press, London, 1689 pp

Bos MM, Tylianakis JM, Steffan-Dewenter I, Tscharntke T (2008) The invasive yellow crazy ant and the decline of forest ant diversity in Indonesian cacao agroforests. Biol Invasions 10:1399–1409. doi:10.1007/s10530-008-9215-4

Brühl CA (2001) Leaf litter ant communities in tropical lowland rain forests in Sabah, Malaysia: effects of forest disturbance and fragmentation. Dissertation, Julius-Maximilians-Universiät, Würzburg, Germany, 168 pp. Available from http://www.opus-bayern.de/uni-wuerzburg/

Brühl CA, Gunslam G, Linsenmair KE (1998) Stratification of ants (Hymenoptera, Formicidae) in a primary rain forest in Sabah, Borneo. J Trop Ecol 14:285–297. doi:10.1017/S0266467498000224

Brühl CA, Maryati M, Linsenmair KE (1999) Altitudinal distribution of leaf litter ants along a transect in primary forests on Mount Kinabalu, Sabah, Malaysia. J Trop Ecol 15:265–277. doi:10.1017/S0266467499000802

Brühl CA, Eltz T, Linsenmair KE (2003) Size does matter—fragmentation of tropical rain forest in Sabah Malaysia and the effects on the leaf litter ant community. Biodivers Conserv 12:1371–1389. doi:10.1023/A:1023621609102

Cao KF (2000) Water relations and gas exchange of tropical saplings during a prolonged drought in a Bornean heath forest, with reference to root architecture. J Trop Ecol 16:101–116. doi:10.1017/S0266467400001292

Carroll CR, Janzen DH (1973) Ecology of foraging by ants. Annu Rev Ecol Syst 4:231–257. doi:10.1146/annurev.es.04.110173.001311

Carter C, Finley W, Fry J, Jackson D, Willis L (2007) Palm oil markets and future supply. Eur J Lipid Sci Technol 109:307–314. doi:10.1002/ejlt.200600256

Carvalho KS, Vasconcelos HL (1999) Forest fragmentation in central Amazonia and its effects on litter-dwelling ants. Biol Conserv 91(2–3):151–157. doi:10.1016/S0006-3207(99)00079-8

Chazdon RL (1998) Tropical forests-log'em or leave'em. Science 281:12–13. doi:10.1126/science.281.5381.1295

Colwell RK (1997) EstimateS: statistical estimation of species richness and shared species from samples. Version 5. http://viceroy.eeb.uconn.edu/esimates

Colwell RK, Coddington JA (1994) Estimating terrestrial biodiversity through extrapolation. Philos Trans R Soc Lond Ser B 345:101–118. doi:10.1098/rstb.1994.0091

Danielsen F, Beukema H, Burgess ND, Parish F, Brühl CA, Donald PF, Murdiyarso D, Phalan B, Reijnders L, Struebig M Fitzherbert EB (2008) Biofuel plantations on forested lands: double Jeopardy for biodiversity and climate. Conserv Biol. doi:10.1111/j.1523-1739.2008.01096.x

Dauber J, Wolters V (2000) Microbial activity and functional diversity in the mounds of three different ant species. Soil Biol Biochem 32:93–99. doi:10.1016/S0038-0717(99)00135-2

Davis NE, O'Dowd DJ, Green PT, Mac Nally R (2008) Effects of an alien ant invasion on abundance, behavior, and reproductive success of endemic island birds. Conserv Biol 22(5):1165–1176. doi:10.1111/j.1523-1739.2008.00984.x

Dennis RA, Mayer J, Applegate G, Chokkalingam U, Colfer CJP, Kurniawan I, Lachowski H, Maus P, Permana RP, Ruchiat Y, Stolle F, Suyanto S, Tomich TP (2005) Fire, people and pixels: linking social science and remote sensing to understand underlying causes and impacts of fires in Indonesia. Hum Ecol 33:465–504. doi:10.1007/s10745-005-5156-z

Donald PF (2004) Biodiversity impacts of some agricultural commodity production systems. Conserv Biol 18:17–38. doi:10.1111/j.1523-1739.2004.01803.x

Drescher J, Blüthgen N, Feldhaar H (2007) Population structure and intraspecific aggression in the invasive ant species *Anoplolepis gracilipes* in Malaysian Borneo. Mol Ecol 16:1453–1465. doi:10.1111/j.1365-294X.2007.03260.x

FAOSTAT (2007) Online statistical service. FAO, Rome. Available from http://faostat.fao.org/. Accessed January 2008

Fitzherbert EB, Struebig MJ, Morel A, Danielsen F, Brühl CA, Donald PF, Phalan B (2008) How will oil palm expansion affect biodiversity? Trends Ecol Evol 23:538–545. doi:10.1016/j.tree.2008.06.012
Folgarait PJ (1998) Ant biodiversity and its relationship to ecosystem functioning: a review. Biodivers Conserv 7:1221–1224. doi:10.1023/A:1008891901953
Gunadi B, Verhoef HA (1993) The flow of nutrients in a *Pinus merkusii* forest plantation in Central Java; the contribution of soil animals. Eur J Soil Biol 29:133–139
Hölldobler B, Wilson EO (1990) The ants. Belknap Press of Harvard University Press, Cambridge MA, 733 pp
Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69:373–386. doi: 10.2307/3545850
Koh LP, Wilcove DS (2007) Cashing in palm oil for conservation. Nature 448:993–994. doi: 10.1038/448993a
Koh LP, Wilcove DS (2008) Is oil palm agriculture really destroying tropical biodiversity? Conserv Lett 1:60–64. doi:10.1111/j.1755-263X.2008.00011.x
Laurance WF, Bierregaard RO (1996) Fragmented tropical forests. Bull Ecol Soc Am 77:34–36
Lawton JH, Bignell DE, Bolton B, Blowmers GF, Eggleton PM (1998) Biodiversity inventories, indicator taxa and effects of habitat modification in tropical rain forest. Nature 391:72–76. doi:10.1038/34166
Lester PJ, Tavite A (2004) Long-legged ants, *Anoplolepis gracilipes* (Hymenoptera: Formicidae), have invaded Tokelau, changing composition and dynamics of ant and invertebrate communities. Pac Sci 58:391–401. doi:10.1353/psc.2004.0031
MacKinnon K, Hatta G, Halim H, Mangalik A (1996). The ecology of Kalimantan—Indonesian Borneo, Vol. 3. Periplus Editions, Singapore, 802 pp
Majer JD (1993) Comparison of the arboreal ant mosaic in Ghana, Brazil, Papua New Guinea and Australia—its structure and influence on arthropod diversity. In: La Salle J, Gauld ID (eds) Hymenoptera and biodiversity. CAB International, Wallingford, pp 115–141
McMorrow J, Talip M (2001) Decline of forest area in Sabah, Malaysia: relationship to state policies, land code and land capability. Glob Environ Change 11:217–230. doi:10.1016/S0959-3780(00)00059-5
MOPB (2007) Malaysian oil palm statistics 2006, 26th edition. Malaysian Palm Oil Board. Available from http://econ.mpob.gov.my. Accessed June 2008
O'Dowd DJ, Green PT, Lake PS (2003) Invasional 'meltdown' on an oceanic island. Ecol Lett 6:812–817. doi:10.1046/j.1461-0248.2003.00512.x
Perfecto I, Vandermeer J (2007) The agricultural matrix and a future paradigm for conservation. Conserv Biol 21:274–277. doi:10.1111/j.1523-1739.2006.00582.x
Pfeiffer M, Ho CT, Teh CL (2008) Exploring arboreal ant community composition and co-occurrence patterns in plantations of oil palm *Elaeis guineensis* in Borneo and Peninsular Malaysia. Ecography 31:21–32. doi:10.1111/j.2007.0906-7590.05172.x
Schultz TR, McGlynn TP (2000) The interactions of ants with other organisms. In: Agosti D, Majer J, Alonso E, Schultz TR (eds) Ants: standard methods for measuring and monitoring biodiversity. Biological diversity handbook series. Washington DC, Smithsonian Institution Press, pp 35–44
Tilman D, Fargione J, Wolff B, D'Antonio C, Dobson AP, Howarth R, Schindler D, Schlesinger WH, Simberloff D, Swackhammer D (2001) Forecasting agriculturally driven global environmental change. Science 292:281–284. doi:10.1126/science.1057544
Torres JA (1984) Diversity and distribution of ant communities in Puerto Rico. Biotropica 16:296–303. doi: 10.2307/2387938
Turner EC, Snaddon JL, Fayle TM, Foster WA (2008) Oil palm research in context: identifying the need for biodiversity assessment. PLoS One 3:e1572. doi:10.1371/journal.pone.0001572
Underwood EC, Fisher BL (2006) The role of ants in conservation monitoring: if, when, and how. Biol Conserv 132(2):166–182. doi:10.1016/j.biocon.2006.03.022
Wetterer JK (2005) Worldwide distribution and potential spread of the long-legged ant, *Anoplolepis gracilipes* (Hymenoptera: Formicidae). Sociobiology 45:1–21
Wilson EO (2000) Foreword. In: Agosti D, Majer J, Alonso E, Schultz TR (eds) Ants: standard methods for measuring and monitoring biodiversity. Biological diversity handbook series. Smithsonian Institution Press, Washington DC
Yeboua K, Ballo K (2000) Caractéristiques chimiques du sol sous palmeraie. Cahiers d'études et de recherches francophones/Agricultures 9:73–76