A positive relationship between ant biodiversity (Hymenoptera: Formicidae) and rate of scavenger-mediated nutrient redistribution along a disturbance gradient in a southeast Asian rain forest

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Abstract

Human modification of pristine habitats almost always leads to the local extinction of a subset of the species present. This means that the ecosystem processes carried out by the remaining species may change. It is well documented that particular species of ants carry out important ecosystem processes. However, while much work has been carried out to investigate the link between biodiversity and ecosystem functioning in other taxa, this has received relatively little attention for ant communities. In particular, no attempt has been made to link levels of ant diversity with the rates of nutrient redistribution carried out by scavenging species. Here we investigate the impacts of anthropogenic disturbance on the rate of scavenger-mediated nutrient redistribution, using bait-removal rate as a surrogate measure. We found that although ant species richness, diversity, biomass and rates of bait removal did not change systematically across the disturbance gradient, the rate of bait removal was related to ant species richness. Sites with more ant species experienced a faster rate of bait removal. This is the first documented positive relationship between ant species richness and the rate of an ecosystem process. If these results are applicable at larger spatial scales for a wider range of nutrient sources, loss of ant species could lead to important changes in the way that ecosystems function.

Key words: Ecosystem function, ecosystem process, scavenging, baiting, Malaysia, Danum Valley, rainforest, disturbance, Formicidae, nutrient redistribution.

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Introduction

Habitat change is one of the main global drivers of species extinctions (VITOUSEK & al. 1997, TILMAN & al. 2001). One consequence of these species losses is radical and sometimes unexpected changes in the way that ecosystems function. For example, loss of pollinators may lead to declines in plant populations (BIESMEIJER & al. 2006), while higher diversity of predators may actually lead to increases in herbivore densities (FINKE & DENNO 2004). Because of this, there has been considerable interest in understanding the way that particular ecosystem processes are affected by the loss of biodiversity (BALVANERA & al. 2006).

Ants are highly abundant in tropical environments and are involved in a wide range of ecosystem processes. Many plants recruit ants to help distribute their seeds (BEATTIE 1985, DUNN & al. 2007), colonies of ground-nesting species can turn over large volumes of soil (LYFORD 1963, WHITFORD 2000) and predatory ants can control herbivore populations (e.g., DEJEAN & al. 1997). In ecosystems across the globe, some ants fill primary consumer niches, either by consuming extra-floral nectar or honeydew (BLÜTHGEN & al. 2003, DAVIDSON & al. 2003), or in the Neotropics by using harvested leaves to cultivate fungus (WILSON 1971). Since many species are also facultative scavengers the group as a whole is likely to play an important role in the cycling of nutrients (LAAKSO & SETALA 1998, BESTELMEYER & WIENS 2003).

A range of possible relationships between biodiversity and ecosystem processes have been proposed to explain how changes in diversity affect ecosystem services (NAEEM & al. 2002). However, relatively little work has been carried out explicitly linking ant biodiversity levels with rates of ecosystem processes. Of the existing work, most relates to ant-mediated seed dispersal. GOVE & al. (2007) found that removal rates of *Acacia blakelyi* (MAIDEN, 1917) seeds decreased with increasing ant species richness. This was due to the presence of a keystone ant genus, *Rhytidoponera*, which was confined to sites with low species richness. Other studies have also found the presence of one or two keystone ant species to drive seed dispersal rates (ZELIKOVA & BREED 2008, ZELIKOVA & al. 2008, NESS & al. 2009). GARRIDO *& al.* (2002) suggest that changes in abundance, rather than changes in species composition, are important in determining seed-dispersal success, although they did not test this directly. The only other ecosystem process that has been measured in relation to ant diversity is that of predation. JEANNE (1979) showed a simultaneous decrease in

the rate of predation of wasp larvae and in ant diversity towards higher latitudes, although this relationship did not hold at smaller scales.

No work has yet attempted to investigate the relationship between ant diversity and scavenger-mediated nutrient redistribution, although BESTELMEYER & al. (2003) found that a wide range of species contribute to this process and that there was variation between species in their scavenging activity. Furthermore, a positive link between ant diversity and any sort of ecosystem process has yet to be clearly demonstrated (FOLGARAIT 1998, PHILPOTT & ARMBRECHT 2006, GOVE 2007, CRIST 2009).

Lowland dipterocarp forest, one of the dominant habitat types in Sabah, Malaysia, supports an extremely diverse litter-dwelling ant community (BRÜHL & al. 1998). Southeast Asia has the highest relative rate of deforestation of any tropical region, the majority of which results from commercial logging and conversion of forest to oil palm plantation (SODHI & al. 2004, TURNER & al. 2008). This makes the ant communities of dipterocarp rain forest and nearby disturbed habitats an ideal system in which to study the relationship between ant diversity and scavenger-mediated nutrient redistribution.

Here we quantify the changes in ant biodiversity along a gradient of disturbance in Sabah, Malaysia, and assess how these changes are related to the ecosystem process of scavenging, using bait-removal rate as a surrogate measure.

Material and methods

Field methods: Field work was conducted in lowland dipterocarp forest around Danum Valley Field Centre, Sabah, Malaysia (5° 01' N, 117° 49' E) as a class field exercise during a Tropical Biology Association course. Baits were placed along five transects leading from closely-mown lawn (disturbed) through the border with the forest (edge) and then at three distances into the forest (10 m, 50 m and 100 m). Due to limitations on the availability of nearby lawn / forest borders, two pairs of transects started from points close to each other (Appendix, as digital supplementary material to this article, at the journal's web pages). Observations of ant activity and collections of ants were made along these transects on 7 October 2009 at 1030 h and 1410 h, and on 8 October 2009 at 0920 h, 1120 h and 1445 h. At each of the five positions on each transect, one tuna bait (1.000 g) and one crushed biscuit bait (0.500 g) were placed on the forest floor on 10.1 cm diameter Petri

dish lids 30 cm apart. The lids were placed flat side upper-most and the bases were taped to the lids during transport to prevent loss of bait. Baits were then observed for a one-hour period and numbers of individuals of all ant species feeding on the baits were recorded. Collections were made of as many species as possible. Baits were then re-weighed in order to assess rates of bait removal. The biscuit baits absorbed water from the humid environment and so the final biscuit weights were standardised by dividing them by the weight of the heaviest bait (which would have experienced least predation) and then multiplying by 0.5. This is a conservative correction, since it will slightly underestimate the rate of bait removal, as ants were observed feeding on all baits. Proportion of total mass removed was then calculated as the proportion of the total 1.5 g of bait of both types taken.

Ant identification: All collected ants were identified to genus (BOLTON 1994) and then separated into morphospecies. Where possible, species names were assigned using the antbase.net online image database (PFEIFFER 2009) and published keys (MOFFETT 1986, BOLTON 1992, RIGATO 1994, LAPOLLA 2009). Voucher specimens were deposited at Danum Valley Field Centre for use by future field courses. The body length of an individual of each species was recorded and total ant biomass at each pair of baits calculated using the standard regression equation $W = 0.021 * L^{2.31}$, where length is measured in mm and weight in mg (SCHOENER 1980).

Statistical analysis: First we assessed the way that ant species richness, Simpson's diversity (1-D, MAGURRAN 2004) and biomass changed across the disturbance gradient using Linear Mixed Models (LMMs). For all of these analyses, the ants found at both of the bait types were combined, i.e., species richness was recorded as the total number of ant species found at both baits at a transect position. For these analyses, transect position was included as a fixed factor, and transect number as a random factor. Although it is likely that time of day had an effect on the ants that attended the baits, there was not sufficient replication to include this in our analysis. Note that transect position was included as a factor, rather than a continuous variable due to the likely non-linear nature of responses across the disturbance gradient. Generalized Additive Models gave the same results as the Linear Mixed Models used here (data not presented).

Detrended Correspondence Analyses (DCA) were carried out to assess changes in ant-community composition across the disturbance gradient. The ordination was carried out on square-root transformed ant abundances for the samples combined in two ways. (1) Samples at each transect distance were combined across transects with bait types kept separate. (2) Samples were combined between the bait types, giving replication at each transect distance. This was done in order to increase sample sizes sufficiently to be able to carry out the ordination. We used a unimodal ordination technique, since levels of species turnover were relatively high (longest DCA-axis lengths of 4.1 and 13.2 respectively for the two analyses, LEPS & SMILAUER 2003). All univariate analyses were carried out using Minitab release 14 and multivariate analyses using CANOCO 4.5.

In order to understand how any changes in the ant-biodiversity variables in turn affected the rates of bait removal, we used a second set of LMMs. For these, the response var-
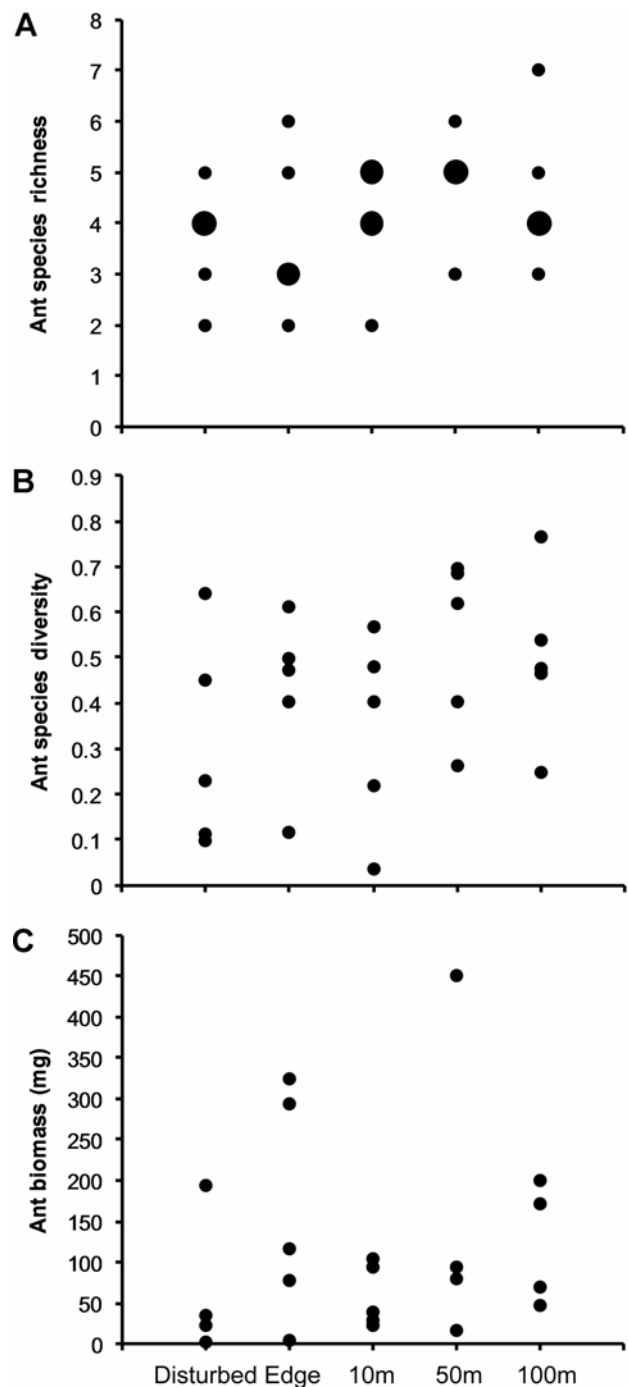

Fig. 1: Changes in ant species richness (A), ant species diversity (B) and ant biomass (C) across a disturbance gradient around Danum Valley Field Centre. In plot A, larger points denote two over-plotted data points. Simpson's index (1-S) was used to calculate species diversity. There was no change in any of the response variables across the disturbance gradient (see text for statistics).

iables from the first set of analyses were used in separate models as predictors, with transect position and transect number again being included in all models. If all ants scavenge at a rate proportional to their body size, and there is otherwise no difference between species in terms of scavenging rate, we would expect ant biomass to be the best predictor of rate of bait loss. On the other hand, communi-
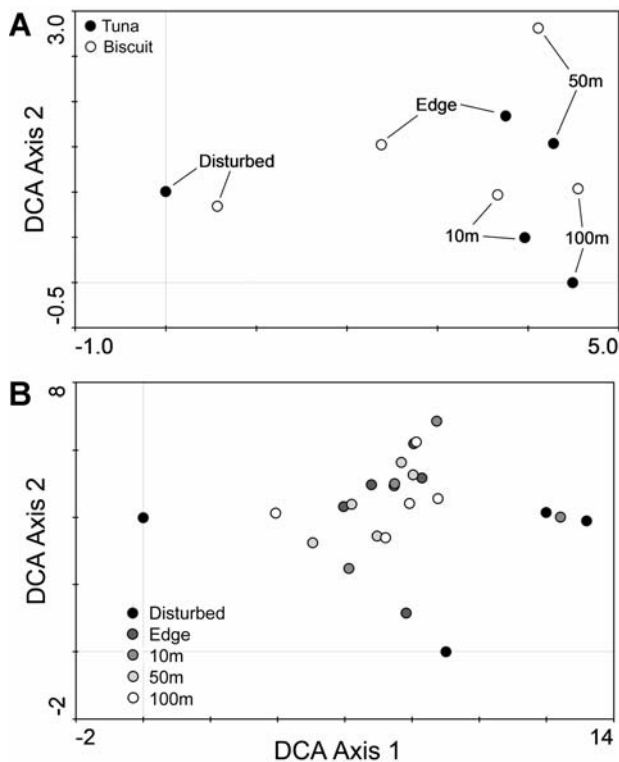
Fig. 2: Detrended Correspondence Analyses of species abundances for (A) combined samples across replicated transect distances and (B) combined samples from different bait types. Points close together represent communities with similar compositions, while those far apart represent communities with different species compositions.

ties with more species of ant, or those with a more even distribution of individuals between species, might be able to better exploit the baits, in which case species richness and species diversity (Simpson's index) respectively would be the best predictors of bait loss. Ant biomass was used rather than ant abundance since ants varied in size by over an order of magnitude (*Camponotus gigas* (LATREILLE, 1802), 19.5 mm; *Carebara* MS10, 1.0 mm) and larger individuals would be expected to remove more bait.

Ant communities composed of species with a more diverse range of body sizes might be expected to remove more bait than those with a less diverse range of body sizes. To investigate this, for models where a significant relationship between biodiversity response variables and bait-removal rates was found, we added variance in size of ant species found at a baiting site as a predictor. Biomasses were $\log_{10}(x)$ transformed for all analyses. All residuals were checked and found to be normally distributed and homoskedastic.

Results

We observed a total of 6826 ants from 47 species in 27 genera feeding on the baits (Tab. 1). Myrmicines and to a lesser extent formicines dominated the baits (24 spp. and 12 spp., respectively), with smaller numbers of ponerines (6 spp.), dolichoderines (4 spp.) and ectatommines (1 sp.).

There was no change in ant species richness, diversity or biomass along the disturbance gradient (LMM, richness: $F_{4,16} = 0.41$, $P = 0.797$; diversity: $F_{4,16} = 1.32$, $P = 0.305$; biomass: $F_{4,16} = 0.90$, $P = 0.486$; Fig. 1 A, B, C). However,

ant community composition did change across the disturbance gradient (Fig. 2 A). For samples summed over replicates of the same transect distance, DCA axis 1 separated out sites on the basis of transect position, with forest communities having high axis scores, the disturbed site having a low axis score and the edge an intermediate score, although being closer to the forest sites. But for the data summed between bait types the pattern was less clear, with no particular clumping of samples from the same transect distance, although samples from the more disturbed end of the gradient appeared to be more heterogeneous (Fig. 2 B). There was no systematic difference in the ant communities at the two bait types (Fig. 2 A).

There was a positive relationship between the total amount of bait collected (tuna and biscuit combined) and ant species richness (LMM, richness: $F_{1,15} = 4.96$, $P = 0.042$; Fig. 3 A), but no relationship between amount of bait collected and ant diversity or ant biomass (LMM, diversity: $F_{1,15} = 2.27$, $P = 0.153$; biomass: $F_{1,15} = 2.93$, $P = 0.057$; Fig. 3 B, C). There was no change in bait-collection rate across the disturbance gradient for any of these analyses (LMM, richness: $F_{4,15} = 1.42$, $P = 0.274$; diversity: $F_{4,15} = 2.27$, $P = 0.153$; biomass: $F_{4,15} = 2.93$, $P = 0.057$).

There was no relationship between variance in size of ant species found at a bait and the amount of bait taken when this predictor was added into the richness model (LMM, $F_{1,14} = 0.41$, $P = 0.534$).

Discussion

There was no detectable change in ant species richness, diversity or biomass across the disturbance gradient, nor any change in the amount of bait taken. However, ant species richness was related to the amount of bait collected (Fig. 3 A). This indicates that variation in species richness, that is itself not correlated with the disturbance gradient, is driving the relationship between biodiversity and the rate of this ecosystem process in the system.

One explanation for the lack of a change in biodiversity across the gradient might be that even the transect positions farther into the forest were still quite disturbed, as demonstrated by the presence of two non-native species, *Monomorium floricola* (JERDON, 1851) (100 m position) and *Paratrechina longicornis* (LATREILLE, 1802) (50 m position). However, note that both of these species have been found occasionally in natural habitats (WETTERER 2008, 2010). Baiting tends to attract ant species with more generalist diets (BESTELMEYER & al. 2000) and so this technique will not detect declines of species with more specific dietary requirements, which may be those that are most susceptible to disturbance. Alternatively, differences in diversity may simply not be apparent at the small scales that

| Subfamily	Genus	Species	Disturbed	Edge	10 m	50 m	100 m
Dolichoderinae	*Iridomyrmex*	MS48	1 / 1				
	Tapinoma	*melanocephalum* (FABRICIUS, 1793)*	127 / 1	270 / 1			
	Technomyrmex	MS21		3 / 1			20 / 1
	Technomyrmex	MS30				1 / 1	
Ectatomminae	*Gnamptogenys*	*binghamii* (FOREL, 1910)	1 / 1				3 / 1
Formicinae	*Anoplolepis*	*gracilipes* (SMITH, 1857)*	313 / 1	20 / 1			
	Camponotus	*gigas* (LATREILLE, 1802)		2 / 1	1 / 1		3 / 1
	Camponotus	MS35		123 / 1			
	Camponotus	MS9		6 / 1			
	Euprenolepis	*variegata* LAPOLLA, 2009			1 / 1		
	Myrmoteras	MS14					3 / 1
	Paratrechina	*longicornis* (LATREILLE, 1802)*				12 / 1	
	Paratrechina	MS11					120 / 1
	Paratrechina	MS31			10 / 1	65 / 1	
	Paratrechina	MS57	20 / 1				
	Paratrechina	MS58	30 / 1				
	Polyrhachis	MS40			1 / 1		
Myrmicinae	*Acanthomyrmex*	*ferox* EMERY, 1893					14 / 1
	Aphaenogaster	MS47					170 / 2
	Cardiocondyla	MS32	4 / 1				
	Cardiocondyla	MS52	18 / 1				
	Carebara	MS10			57 / 1	10 / 1	
	Crematogaster	MS41				55 / 1	
	Lophomyrmex	*bedoti* EMERY, 1893		642 / 4	654 / 2	562 / 3	197 / 2
	Monomorium	*floricola* (JERDON, 1851)*	75 / 1				17 / 1
	Myrmicaria	*carinata* (SMITH, 1857)				31 / 1	
	Pheidole	*angulicollis* EGUCHI, 2001			43 / 1	123 / 1	87 / 1
	Pheidole	*cariniceps* EGUCHI, 2001	154 / 1		56 / 1		
	Pheidole	MS18		159 / 2	6 / 1	212 / 1	20 / 1
	Pheidole	MS2	23 / 2				
	Pheidole	MS4		70 / 2	177 / 1	36 / 1	342 / 1
	Pheidole	MS50				30 / 1	
	Pheidole	MS54			63 / 1	31 / 1	77 / 1
	Pheidole	MS55			101 / 1		
	Pheidole	MS56		12 / 1	165 / 1		225 / 1
	Pheidole	*quadricuspis* EMERY, 1900					87 / 1
	Pheidologeton	MS20				13 / 1	269 / 1
	Proatta	*butteli* FOREL, 1912			35 / 1		
	Recurvidris	*browni* BOLTON, 1992		10 / 2		130 / 2	
	Recurvidris	MS28					145 / 1
	Tetramorium	MS13	79 / 1				
Ponerinae	*Diacamma*	*intricatum* (SMITH, 1857)		23 / 1		7 / 1	3 / 2
	Diacamma	*rugosum* (LE GUILLOU, 1852)	2 / 1				
	Leptogenys	MS42			1 / 1		
	Leptogenys	MS8				7 / 1	
	Odontoponera	*transversa* (SMITH, 1857)	2 / 1	31 / 1	7 / 2	94 / 2	
	Pachycondyla	*leeuwenhoeki* (FOREL, 1886)				2 / 1	
Not collected	Not collected (1)	NA			1 / 1		
	Not collected (2)	NA			1 / 1		
	Not collected (3)	NA	1 / 1				
	Not collected (4)	NA	1 / 1				
	Not collected (5)	NA	1 / 1				
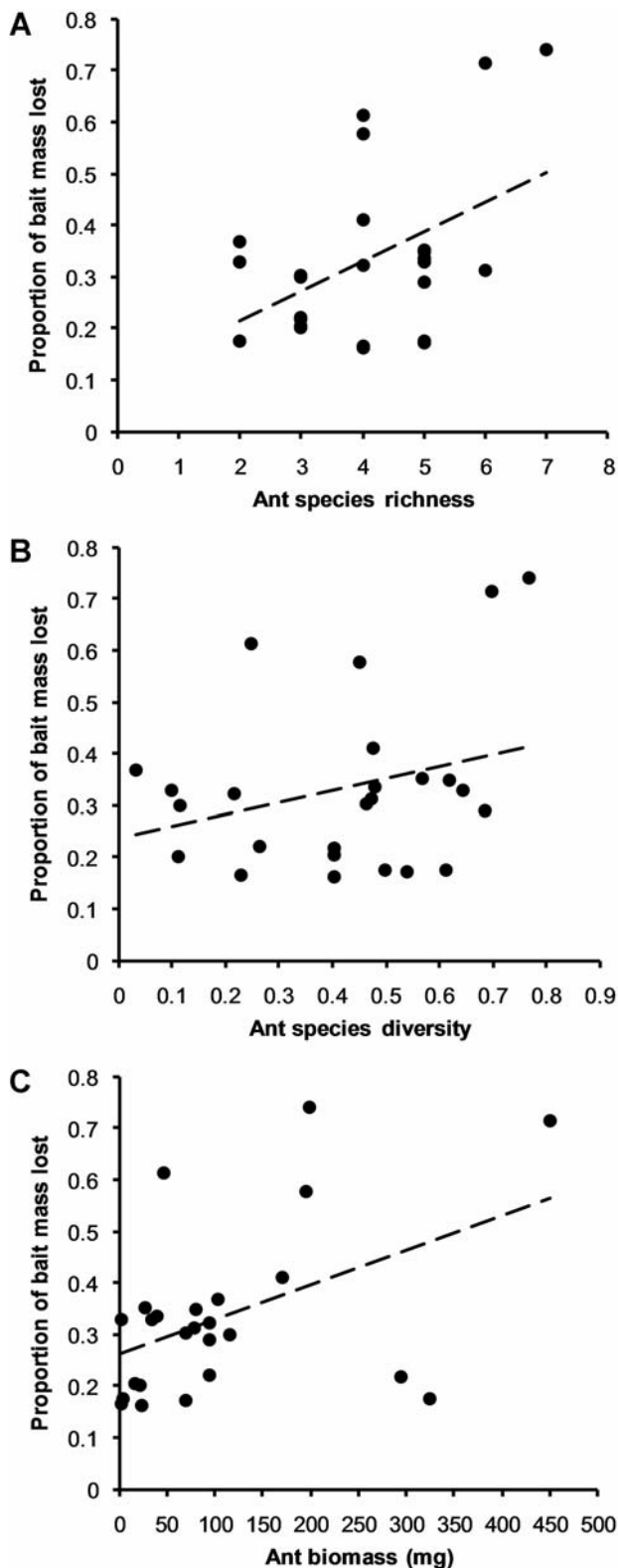
Fig. 3: The relationship between amount of bait removed in one hour and (A) ant species richness, (B) ant species diversity and (C) ant biomass. There was a positive relationship between bait-mass loss and ant species richness, but no relationship between bait-mass loss and ant species diversity or biomass.

sampling was carried out. If the main component of diversity is between patches (beta diversity), rather than within

them (alpha diversity), sampling at this spatial grain would not be expected to reveal any consistent pattern in ant biodiversity across the gradient. Despite this, there were differences in the ant community composition along the gradient (Fig. 2). *Tapinoma melancephalum* (FABRICIUS, 1793) and *Anoplolepis gracilipes* (SMITH, 1857) both occurred at high abundance in the disturbed and edge habitats and not in the forest (Tab. 1). *Lophomyrmex bedoti* (EMERY, 1893) occurred in all habitats except the disturbed one, while there were only three occurrences of *Pheidole* species in the disturbed habitat compared to five or six occurrences at all the other transect positions.

The rate of bait removal was only related to species richness and did not change systematically across the gradient. It is interesting to speculate on the factors potentially driving this relationship. Since there was some (unquantified) variation in the sizes of food particles within baits, one would predict that with more species, there would be a wider range of body sizes, meaning that the community should utilise the food source more efficiently, on the assumption that there is some level of size matching between ants and food particles (PFEIFFER & al. 2006). But variance in body size had no effect on the amount of bait taken in any analysis, both including and excluding species richness as a covariable. Differences in preference of bait type could also cause this pattern, since sites with higher species richness would be more likely to contain at least one species on both baits. But there was no obvious difference in the communities on the different bait types (Fig. 2). Nor was there any difference in species richness, diversity or abundance between the bait types (data not presented). This leaves the simple explanation that where there are more ant colonies in an area, the rates of scavenging will be higher.

This result is in contrast to what has been found in studies of seed removal, where ant species richness is either negatively correlated with the rate of the process (GOVE & al. 2007) or there is no apparent relationship (ZELIKOVA & BREED 2008, ZELIKOVA & al. 2008). This is because, despite the fact that many species of plant have their seeds dispersed by ants, in any one community a single ant species dominates this process (NESS & al. 2009), and the presence of this species is either independent of overall ant species richness, or even negatively correlated with it. On the other hand, baiting often attracts many generalist scavenger species, and the more colonies of these species that are present the higher is the rate of ant-scavenging-mediated nutrient redistribution. JEANNE (1979) found a similar result for rates of predation of wasp larvae, which is presumably also a relatively unspecialised mode of feeding.

While we did not find decreases in species richness with increasing disturbance, such a pattern has been well documented at larger scales. In Sabah, although selective logging of primary forest leads to only minor reductions in species richness of ants (WIDODO & al. 2004), it seems likely that repeated logging cycles have a more extreme effect, and conversion of forest into oil palm plantation reduces ant species richness drastically (ROOM 1975, TAYLOR 1977, DEJEAN & al. 1997, BRÜHL & ELTZ 2010, FAYLE & al. 2010). If the results of our small-scale study were found to be applicable across these larger scales, we would expect ant-scavenging-mediated nutrient cycling to progress at slower rates in these degraded habitats. Carbon

flux has been tentatively linked to termite and nematode diversity (LAWTON & al. 1996) and habitats that have undergone varying intensities of disturbance have been found to have different rates of litterfall-related cycling (GAIROLA & al. 2009), but this has not yet been investigated in any system for ants.

Although this study is a preliminary one, we have demonstrated that even in a system where simple measures of ant biodiversity are robust to disturbance, these measures predict changes in the rate of an important ecosystem process. It is hoped that these results will stimulate further work on the potential implications of changes in ant biodiversity for ecosystem functioning at larger scales.

Acknowledgements

Zusammenfassung

Veränderungen ursprünglicher Lebensräume durch den Menschen führen fast immer zum lokalen Aussterben eines Teils der anwesenden Arten. Das kann die von den verbleibenden Arten ausgeführten Ökosystemprozesse verändern. Es ist belegt, dass bestimmte Ameisenarten wichtige Ökosystemprozesse ausführen. Aber während der Zusammenhang von Biodiversität und Ökosystemfunktion bei anderen Taxa intensiv untersucht worden ist, haben Ameisengemeinschaften diesbezüglich vergleichsweise wenig Aufmerksamkeit erfahren. Insbesondere wurde bisher nicht versucht, das Ausmaß von Ameisendiversität mit der Rate der Umverteilung von Nährstoffen durch Aas fressende Arten in Beziehung zu setzen. Wir untersuchen hier die Auswirkungen anthropogener Störung auf die Rate der Nährstoffumverteilung durch Aas fressende Ameisen, indem wir die Entnahme von Köder als Ersatzmaß verwenden. Wir stellten fest, dass sich zwar Artenreichtum, Diversität und Biomasse der Ameisen sowie auch die Köderentnahme über den Störungsgradienten hinweg nicht systematisch änderten, dass aber die Rate der Köderentnahme mit dem Artenreichtum in Beziehung stand. Stellen mit mehr Ameisenarten wiesen eine höhere Rate der Köderentnahme auf. Das ist die erste dokumentierte positive Beziehung zwischen Ameisenartenreichtum und der Rate eines Ökosystemprozesses. Falls diese Ergebnisse auch für ein größeres Spektrum von Nährstoffquellen und in größeren räumlichen Maßstäben gelten, könnte der Verlust von Ameisenarten zu bedeutsamen Veränderungen der Funktionsweise von Ökosystemen führen.

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