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From rainforest to oil palm plantations: Shifts in predator population and prey communities, but resistant interactions

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ABSTRACT

Anthropogenic habitat change can dramatically alter biotic communities in tropical landscapes. Species that persist in human dominated landscapes are therefore likely to modify the way they interact. Although human impacts on community composition are relatively well studied, changes in species interactions are less well documented. Here we assess how logging of rainforest and conversion to oil palm plantations affects the populations of the ant-specialist giant river toad (*Phrynoidis juxtaspera*), and the availability and composition of its ant prey. We measured canopy cover as an estimate for the degree of disturbance and found that toad abundance decreased with increasing disturbance, and that retaining riparian vegetation should therefore help conserve this species. Both abundance and species richness of local ground-foraging ants increased with disturbance, and ant community composition was altered. Despite these changes, composition of ants consumed by toads was only weakly affected by habitat change, with the exception of the invasive yellow crazy ant (*Anoplolepis gracilipes*), which was positively selected in oil palm plantations. This suggests that predator–prey interactions can be mostly maintained with habitat disturbance despite shifts in the community composition of potential prey, and even that some predators are capable of exploiting new prey sources in novel ecosystems.

1. Introduction

The negative impacts of habitat loss and land conversion on a wide range of species are increasingly well documented (Hoekstra et al., 2004; Sala et al., 2000). However, our understanding of the impact of human activity on species interactions remains poor. Mutualisms and trophic interactions influence the structure of animal and plant communities, and affect the stability and function of ecosystems (Ives and Cardinale, 2004). Species interactions play essential roles in both natural and human-dominated ecosystems, providing services such as pollination (Klein et al., 2007) and pest control

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(Bianchi et al., 2006). Given the ecological and economic importance of ecological processes and associated ecosystem services, documenting the impact of human activity on interactions between species is a priority (Herrera and Doblas-Miranda, 2013). We need to understand the causes and consequences of changes in networks of interactions if we are to properly predict and manage human impacts on ecosystems (Morris, 2010; Tylianakis et al., 2010).

The complexity of ecological interactions may make it challenging to generate general rules for predicting the impacts of such changes (Tylianakis et al., 2008). For example, shifts in resource consumption following habitat fragmentation are likely to differ between generalists and specialists (Martinson and Fagan, 2014). Similarly, the removal of top predators can have a range of cascading effects on lower trophic levels (Ripple et al., 2014). Nevertheless, there is an increasing body of evidence indicating that resource extraction and land use change alter species interactions. For example, modification of tropical habitats reduces the diversity and breadth of host–parasitoid food webs (Tylianakis et al., 2007), alters the trophic position and narrows the niche breadth of bird communities (Edwards et al., 2013), and alters the trophic position of leaf-litter ant species (Senior et al., 2013; Woodcock et al., 2013). Understanding the variation in responses of different species interactions to habitat modification is potentially a greater challenge than documenting the changes in the communities themselves.

Our knowledge of how trophic interactions are altered by anthropogenic disturbance is particularly poor for tropical systems (Morris, 2010). This is a particular concern because tropical ecosystems exhibit high levels of biodiversity and are particularly vulnerable to on-going anthropogenic threats (Brooks et al., 2002). Southeast Asia, and Sundaland in particular, is an important biodiversity hotspot (Myers et al., 2000) threatened by habitat loss (Sodhi et al., 2004). In this region, the important drivers of changes in community structure and function are logging and subsequent conversion of degraded forest to oil palm plantation (Wilcove et al., 2013). There is a substantial body of evidence showing that the community composition of many species in Southeast Asian rainforest changes with logging and conversion to oil palm dominated landscapes (Danielsen et al., 2009; Fitzherbert et al., 2008; Foster et al., 2011), including abundant tropical meso-predators such as anurans (Faruk et al., 2013). Furthermore, there is some evidence that interactions of other ecologically important groups such as ants are altered by conversion to oil palm plantations (Fayle et al., 2013). However, the impact of oil palm expansion on species interactions and in particular on trophic interactions remains mostly unknown.

Habitat conversion is often accompanied by the introduction of non-native species (Ricciardi, 2007) and these invasions can also alter or inhibit interactions between native species (Traveset and Richardson, 2006). Understanding the effects of non-native species on food webs and trophic interactions is therefore of particular interest. We need to enhance our understanding of the interaction between land conversion and invasive species if we are to predict and manage species' responses to anthropogenic change. Knowing the extent to which native species can respond to the ecological changes caused by the presence of these introduced groups will help with predicting the resilience of communities and targeting conservation efforts (Didham et al., 2007).

The impact of habitat degradation on the trophic interaction between ants and is currently unknown. However, ants are an important part of the diet of some tropical anuran communities (e.g. Inger, 2009; Konopik et al., 2014; Toft, 1980). Here we assess the variation in the interaction between a common anuran predator, the giant river toad (*P. juxtaspera*) and the ground dwelling ants on which it feeds. We quantify changes in toad populations, ant communities, and predator–prey interactions across different land uses in Malaysian Borneo. Specifically, we ask the following questions:

(1) How does the abundance of the toad *P. juxtaspera* vary with degree of disturbance and stream characteristics?
(2) How does the abundance and species richness of ground dwelling ants vary with degree of disturbance and stream characteristics?
(3) How do the predator–prey interactions between the toad and ant communities change with degree of disturbance and stream characteristics?

2. Materials and methods

2.1. Study sites

The study was conducted in northern Borneo in the state of Sabah, Malaysia from April to June 2011. We sampled the abundance and diet of the giant river toad (*P. juxtaspera*) and corresponding ground-dwelling ant communities along streams in primary lowland dipterocarp rainforest, continuous logged forest and in oil palm plantations under the framework of the SAFE project (Stability of Altered Forest Ecosystems; Ewers et al., 2011).

Primary forest sites were located within the Maliau Basin Conservation Area (MBCA, 58,840 ha) and a patch (2200 ha) of mainly unlogged forest (lightly logged along its edges), which is continuous with both the SAFE project area and a major forest block (>1 million ha) of both logged and unlogged forest (Reynolds et al., 2011). Logged forest sites were located in the SAFE project area, which has undergone two rounds of selective logging. The forest structure in the SAFE project area is highly variable, ranging from open areas to those with closed canopies (Ewers et al., 2011). The oil palm plantation sites and their catchments were isolated by 1–5 km from the logged forests. All plantation streams were managed by the same company (Benta Wawasan Sdn Bhd) but had riparian reserves of differing vegetation and quality. These ranged from forested riparian strips shading the streams to shrubby and grassy, heavily degraded streamside vegetation. To standardise stream size, all data were collected at the outlets of 2.5 km^2 stream catchments, which were 1.5–9 km apart from each other.

However, one primary forest stream was located in MBCA, approximately 50 km from the other streams (note that this is one of only two large continuous blocks of primary forest in the vicinity).

2.2. Effects of habitat change on relative toad abundance

P. juxtaspera is the largest native anuran species found in SE Asia. Females can grow up to 215 mm snout-vent length (SVL), while males typically reach no more than 120 mm (Inger and Stuebing, 2005). Sexes are hard to distinguish in the field, other than by size (individuals >120 mm are females). It is a widespread, ground-dwelling species, which can frequently be found along streams and has been recorded from both primary rainforests and disturbed forests (Inger and Stuebing, 2005). To date there has been no systematic study of the diet of *P. juxtaspera*, although congeneric species are also known to feed primarily on ants (Inger, 2009).

Toads were sampled in a total of two primary forest streams, eight logged forest streams and seven oil palm plantation streams. To assess the relative abundance of toads we conducted six standardised visual encounter surveys at minimum intervals of one week per site (stream). We walked line transects in the streams, starting from the mouth of the 2.5 km^2 catchment at each site and leading 200 m upstream. Toads were actively searched for one hour by a single person using a headlamp (Petzl Myo RXP), always between 18:45 and 20:30. Stomach contents were collected from randomly selected individuals between 18:45 and 01:00 in the morning, using stomach flushing (Solé et al., 2005), which is a gentle method for obtaining dietary information without harming the toads. We only sampled subadult and adult toads (snout-vent length $>$ 60 mm), but did not distinguish between sexes. We applied high ethical standards (Beaupre et al., 2004) for handling the individuals and no toad was killed during our study.

2.3. Effects of habitat change on ant communities

Samples of the ground-foraging ant fauna were taken at the two primary forest streams, five (out of eight) logged forest streams and three (out of seven) oil palm plantation streams. At each site, ants were collected from 12 pitfall traps set in a grid adjacent to the river. Three traps were placed at 50 m intervals on each of four transects, with the first trap placed approximately 1 m above the high water line. Transects ran perpendicular to the river and were 100 m apart. Pitfall traps were plastic cups (dimension 8 cm top diameter, 5.5 cm bottom diameter, 12.5 cm depth), filled with a solution of water, salt and a small amount of detergent, and were collected after 48 h. The traps were baited with 25 g human dung, since they also formed part of a separate study surveying dung beetles (Gray et al., 2014). The mean distance between toad transects and ant sampling grids was 152.9 (range $\pm$ 96.7) m. The mean time between stomach content collection and the collection of the pitfall traps was 15 (range$\pm$14) d.

2.4. Ant identification

Ants from toad stomachs and the ground-foraging ant fauna were identified to genus using a binocular dissecting microscope (Fayle et al., 2014), divided into morphospecies, and assigned species names where possible (Pfeiffer, 2014). Ants from toad's stomachs were often surprisingly well-preserved, allowing the generation of a dry-mounted voucher collection. Body fragments were then compared with these entire specimens. Counts were based on numbers of alitrunks present. Reproductives and lone major workers were excluded from analyses, to prevent inadvertent splitting of species.

2.5. Habitat parameters

To capture variance in primary forests and especially the highly heterogeneous degree of disturbance in the logged forest, the differing age of the oil palm plantations and the different quality of riparian vegetation in both habitats, we used the canopy cover above the stream as an estimate of the degree of disturbance. A camera (Pentax K20D) was positioned at the centre of the stream at a height of 0.5 m above the water surface. Pictures were taken perpendicular to the stream and in full wide angle, using a fisheye lens (Pentax SMC DA 10–17 mm) facing upwards. Images were analysed using a graphics editor (Adobe Photoshop) and the percentage of the sky covered by vegetation was used as canopy cover (%).

In addition, we measured both width and slope of the streams, as these variables are known to influence Bornean anuran communities (Keller et al., 2009). Stream width was measured at an intermediate water level, and combined across both channels for sites where the stream split within the sampling area. Stream slope was measured applying the principle of communicating vessels (LaPerriere and Martin, 1986). First, a 14 m water-filled transparent hose was submerged in the stream. Then, the downstream end was lifted perpendicularly out of the water. Finally, the height of the water column from the water surface was divided by the stream distance being measured to obtain the stream slope. Canopy cover, stream width and slope were measured at intervals of 10 m and averaged to give a single value for each transect.

2.6. Statistical methods

We used linear models to analyse the impact of the degree of disturbance and habitat parameters on relative toad abundance. The impact on the number of ant species and number of ant individuals derived from pitfall traps and toads'

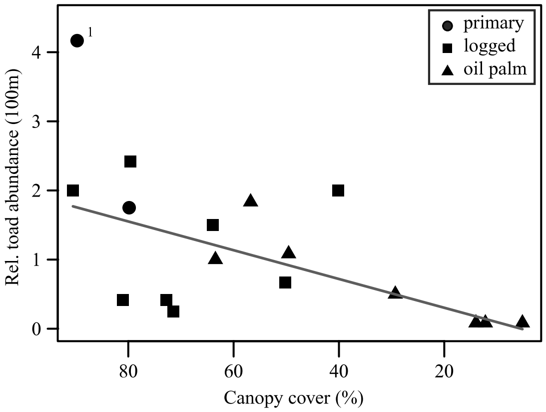

Fig. 1. Impact of canopy cover above the streams on the relative abundance of the giant river toad (*P. juxtaspera*). Abundance was significantly reduced with increasing habitat disturbance (z-value = 3.84; $P < 0.001$). The primary forest stream sampled at Maliau Basin Conservation area (1) was excluded from this analysis.

stomachs was analysed using mixed models with site (stream) as a random factor to account for non-independence of data points collected at the same stream. Hence, fixed factors for all models were stream width, stream slope, and canopy cover. Additionally, the distance between the traps and the stream was included for the trap-models, as well as the length of the toads (SVL) for the toad-models. Ant abundances were log-transformed to meet the assumptions of normality. Model selection was conducted using a model averaging approach. All combinations of explanatory variables were used and the models with the best fit were selected using the corrected Akaike's information criterion (AICc). A model was included if the difference in AIC of that model from the best model (ΔAICc) was <4 (Burnham and Anderson, 2002). All parameters were tested for normality and collinearity before analysis.

To assess the dietary selectivity of the toad we used the Jacobs's Electivity Index (Jacobs, 1974) on ant genus-level data. The index reaches "+1" for a taxon or prey category exclusively selected by the toad but rare in the environment and "−1" if the taxon is completely absent from the toads diet, but frequently found in the environment. Consequently, a value of "0" indicates an equal frequency of the respective ant genus in pitfall traps and the toads' diet. Finally, we conducted chi-square tests on the original count data for each ant species in the toads' stomachs versus in the pitfall traps, using Bonferroni corrections to account for multiple comparisons.

To compare the composition of the ant community obtained from traps and toads, we used a permutation-based multivariate analysis of variance (PerMANOVA), specifying Bray–Curtis dissimilarity and 999 permutations. To display the variation in species composition of ants derived from traps and toads among habitat types and the impact of habitat parameters we used non-metric multidimensional scaling (NMDS) on the same distance matrix calculated for the PerMANOVA. We set the program to generate 999 iterations to find the final ordination with minimum stress and best fit. To test for possibly confounding effects of the differing distances between the traps and the stream on both the genera composition and the species composition found in the traps, we used the same PerMANOVA setup. We ran general linear mixed models to test for differences in the species richness and abundance of ants in the pitfalls versus the stomach contents.

All statistical analyses and graphics were conducted using the open source software R (R Core Development Team 2008) with the packages *MuMIn* (Bartoń, 2014), *nlme* (Pinheiro et al., 2014) and *vegan* (Oksanen et al., 2013).

3. Results

3.1. Effects of habitat change on relative toad abundance

The giant river toad (*P. juxtaspera*) was found in all studied streams and transects. The average number of recorded toads was higher in streams with more canopy cover (Fig. 1) and also in narrower streams (Table 1). Stream slope had no significant influence on the average number of recorded individuals of *P. juxtaspera*.

3.2. Effects of habitat change on ant communities

We identified 65,886 individuals from 56 ant genera and 140 morphological species. In the pitfall traps, the ant genera *Diacamma, Leptogenys, Lophomyrmex, Odontoponera* and *Pheidologeton* were commonly found in forest samples (logged forest and primary forest). The genera *Cardiocondyla, Monomorium, Ochetellus, Plagiolepis* and *Solenopsis* were nearly exclusively obtained from oil palm plantations. *Pheidole* and *Tetramorium* were abundant genera in all habitat types. The ant species with the highest frequency in forested habitat were *Camponotus gigas* and *Odontoponera rixosus*. In contrast the yellow crazy ant (*Anoplolepis gracilipes*) and *Monomorium floricola* were the species most frequently found in oil palm plantations.

The number of ant species per trap increased slightly with decreasing canopy cover (Table 1). Although we did not include habitat in the models due to collinearity with canopy cover, there was a trend for more ant species in primary

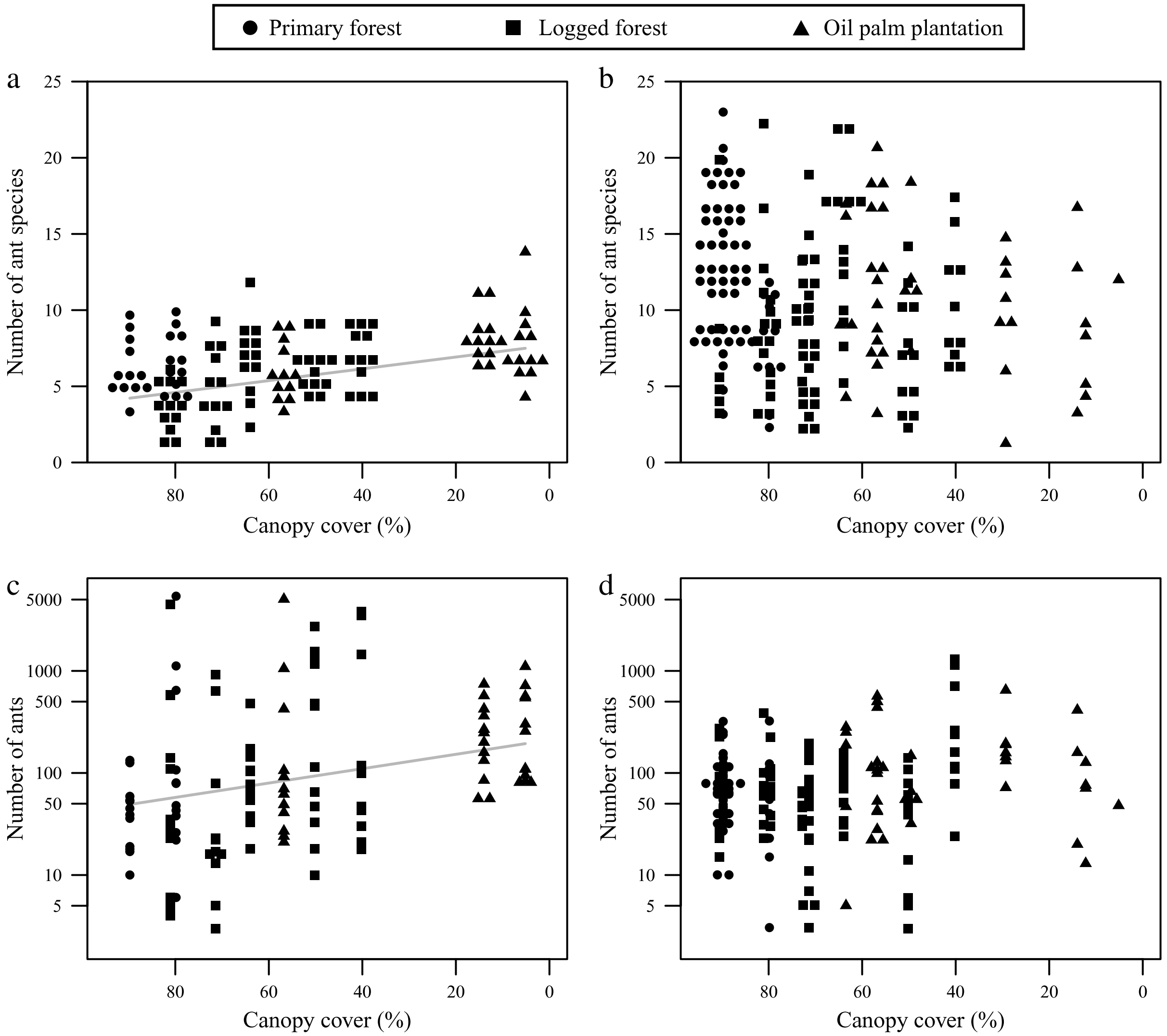

Fig. 2. Impact of the degree of disturbance (canopy cover) on the number of ant species (a, b) and the number of individuals (c, d) of samples derived from baited pitfall traps (left) and stomach content samples from *P. juxtaspera* (right).

forest, compared to logged forest and oil palm plantations at a given degree of canopy cover. Local scale ant species richness was highest in oil palm plantations (7.3 ± 2.2), followed by primary forest (6.3 ± 1.9) and logged forest (5.6 ± 2.5). Hence, the highest local ant species richness was found at streams with low canopy cover in oil palm plantations (Fig. 2(a)). The total number of individuals per trap also increased significantly with decreasing canopy cover (Fig. 2(c)).

3.3. How does toad diet change in converted habitats?

For dietary analysis, we sampled a total of 189 toads with an average snout-vent length of 86.9 mm (±34). There was no significant size difference between toads sampled in primary forests, logged forest, and oil palm plantations (ANOVA: $F_{2186} = 0.59$, n.s.). Sixty four toads were sampled in primary forests, 84 toads in logged forest, and 41 toads in oil palm plantations. From the stomach contents we identified 16,840 individuals belonging to 57 ant genera and 224 morphological species. In general, ants made up 82% of the recovered prey items. We were able to obtain stomach content from all sampled toads. Furthermore, all samples contained ants. The number of ant species found in toads' stomachs varied only with the size of the toad (see Table 1 for statistics, Fig. 2(b)). There was no significant relationship between the number of individuals recovered from the toads' stomachs and any explanatory variable (Fig. 2(d)).

3.4. Comparing shifts in toad diet with changes in ground-dwelling ant communities

There was a significant interaction between land use type and the origin of ant communities (stomach vs. pitfall traps) on the composition of both ant genera (PerMANOVA: $df = 2$, Residuals $= 255$, $F = 4.2$; $R^2 = 0.02$; $p < 0.001$) and species

Table 1
Average model coefficient estimates (β) with average standard errors (SE), and P-values for variables explaining changes in relative toad abundance, ant species richness, and ant abundance in response to ecologically important explanatory variables.

	β	SE (β)	z-value	P-value
Relative toad abundance (linear model)				
Canopy cover	**0.252**	**0.059**	**3.84**	**<0.001**
Stream width	**−6.84**	**1.84**	**3.38**	**<0.001**
Stream slope	−0.0014	0.0028	0.44	0.66
Ant species richness in pitfall traps (mixed model)				
Canopy cover	**−0.031**	**0.011**	**2.32**	**<0.05**
Stream width	−0.750	0.333	1.88	0.06
Stream slope	0.0004	0.0003	1.09	0.27
Distance	−0.001	0.0048	0.228	0.82
Ant species richness in toads stomachs (mixed model)				
Canopy cover	−0.0008	0.027	0.027	0.98
Stream width	−0.538	0.599	0.825	0.41
Stream slope	0.0005	0.0004	1.151	0.25
Size of toad (SVL)	**−0.032**	**0.011**	**2.784**	**<0.01**
Number of ants in pitfall traps (log-transformed, mixed model)				
Canopy cover	**−0.016**	**0.006**	**2.107**	**0.04**
Stream width	−0.458	0.218	1.755	0.08
Stream slope	−0.0001	0.0002	0.619	0.54
Distance	−0.0028	0.0035	0.780	0.44
Number of ants in toads' stomachs (log-transformed, mixed model)				
Canopy cover	−0.006	0.006	0.996	0.32
Stream width	−0.187	0.154	1.265	0.21
Stream slope	0.00004	0.0001	0.301	0.76
Size of toad (SVL)	−0.002	0.003	0.859	0.39

(PerMANOVA: $df = 2$, Residuals $= 255$, $F = 3.8$; $R^2 = 0.02$; $p < 0.001$). Ant communities found in pitfall traps in logged forest and primary forest sites showed similar compositions, but both were different from oil palm plantations, whereas the composition of ants found in toad stomachs was not strongly affected by land use change (Fig. 3). The distance of the pitfall traps from the stream did not have a significant impact on the composition of ant genera and ant species.

Some ant genera were found significantly more frequently in stomach content samples of *P. juxtaspera*, compared to their frequency in pitfall traps, whereas others were found significantly less frequently (significant positive and negative electivity values respectively, Fig. 4). In cases where ant genera were found significantly more frequently or less frequently in stomach content samples of *P. juxtaspera*, these trends were constant across land uses and hence not affected by logging or land conversion to oil palm plantation. However, in some cases positively "selected" ant genera from primary forest simply did not occur in plantations. There were twelve genera that in at least one habitat were significantly more frequently recorded in the toads' stomachs than in pitfall traps (*Anochetus, Anoplolepis, Camponotus, Crematogaster, Gnamptogenys, Lordomyrma, Myrmicaria, Nylanderia, Odontoponera, Pachycondyla, Platythyrea, Polyrhachis*) and four genera that were found significantly less frequently (*Euprenolepis, Loweriella, Pheidologeton, Plagiolepis*). In particular, the invasive species *A. gracilipes* (the only species in the genus *Anoplolepis* at our study sites) was significantly more commonly found in the toads' stomachs than in the traps. However, this genus was absent from primary forest sites and very rare in logged forest.

4. Discussion

Because logging and conversion to oil palm plantation generally alters the species composition of both frogs and ants (e.g. Brühl and Eltz, 2009; Faruk et al., 2013; Woodcock et al., 2011), we expected there to be changes in the diet of the ant specialist toad *P. juxtaspera*. However, we found that interactions between these trophic levels remained relatively constant despite significant changes in the community composition of ants.

Our results indicate that the degree of habitat disturbance (as measured by the remaining canopy cover) has a strong effect on the abundance of this toad species. However, the abundances in high canopy cover streams in oil palm plantations were comparable with logged forest streams. This suggests that retaining canopy cover adjacent to rivers (in riparian buffers or reserves) may help conserve the toad species. Interestingly, we found that the decrease in toad abundance with loss of canopy cover occurs despite increases in the abundance of potential prey items. This indicates that other factors, such as changes in breeding habitat availability, microclimate or pesticides are more likely to be driving the decline in giant river toad numbers than a shortage of prey.

The changes in the ant community that we observed are consistent with previous findings that invasive species become more abundant in disturbed habitats (Didham et al., 2007; Dukes and Mooney, 1999). However, we found a higher local ant species richness in heavily modified habitats. This contrasts with previous observations that ant fauna are less species

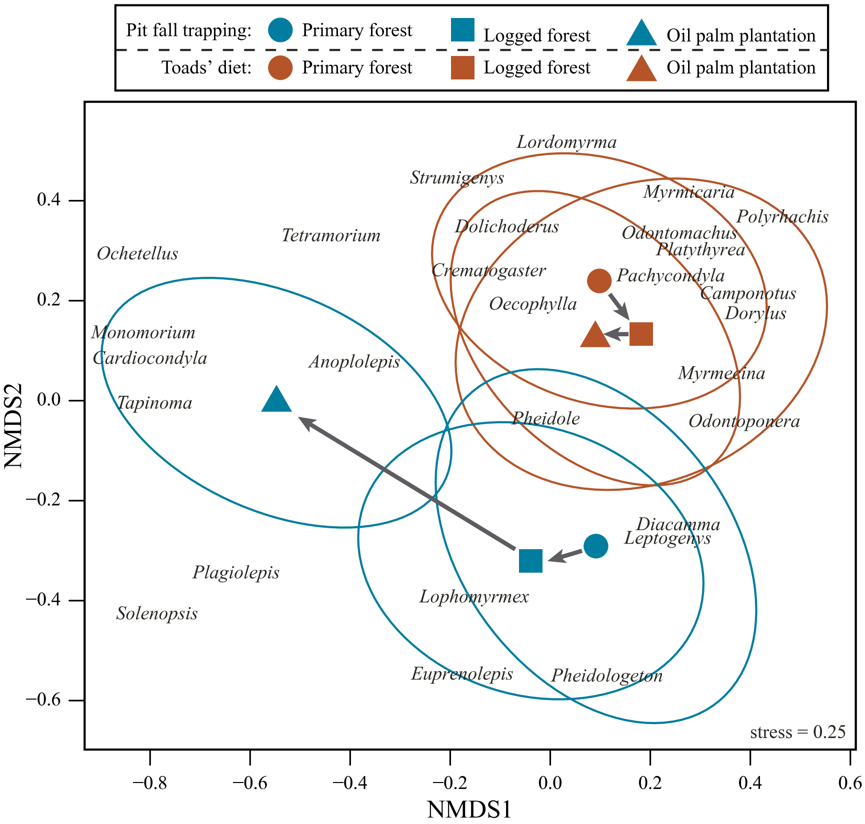

Fig. 3. Non-metric multidimensional scaling showing differences in ant genera composition. Displayed are the centroids of the pitfall data (blue) and the data derived from the stomach contents of the ant-specialist toad *P. juxtaspera* (red). Ellipses around the centroids indicate standard deviation of the respective categories. Arrows indicate shifts in composition between land-uses (primary forest – logged forest – oil palm plantation). Only the most frequent ant genera are displayed. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

rich in degraded tropical forest compared to undisturbed habitats, both in terms of ground foraging (Brühl and Eltz, 2009; Woodcock et al., 2013) and arboreal communities (Klimes et al., 2012; Widodo et al., 2004). There are several possible explanations for this result. First, our use of a trapping method that assesses combined activity and density of ants (the former of which may be high in oil palm, due to elevated temperatures (Turner and Foster, 2006)), coupled with the small scales at which we analysed our data (the scale relevant to a single toad), could result in higher records of species richness and abundance with decreasing canopy cover. Second, we used baited traps that could potentially have differing degrees of attractiveness between habitat types and hence lead to this unexpected pattern. Third, the variation in riparian vegetation at oil palm sites could mean that the range of microhabitats available for ants adjacent to oil palm streams was higher than that in forested streams. As a result, there would be higher beta diversity within the area covered by the pitfall transects at oil palm sites, leading to a higher species richness overall. Lastly, it is possible that the increase in local species richness is due to the simplification of the vegetation structure forcing arboreal species down to nest and/or forage at lower heights. Therefore even if both ground foraging species and arboreal species decline with habitat degradation, the merging of these communities could potentially result in an increase in terrestrial ant species richness. Indeed, the microclimate in logged forest and in particular in oil palm plantation has been shown to be more extreme (Luskin and Potts, 2011) and hence resembles the conditions in the canopy layer. This could favour canopy-adapted ant genera and decrease the number of leaf-litter ants on the forest floor.

The change in local ant species richness, ant abundance, and ant community composition with land use was not reflected in the trophic interaction between the giant river toad and its prey. None of the significant positive or negative electivity patterns for ant genera differed between the habitat types, indicating that the toad shows a high degree of niche-fidelity. Even though the toad feeds on a great variety of ants (including predatory and marauding ants, such as *Dorylus* spp. and *Leptogenys* spp.) this niche fidelity suggests that the toad is not feeding on the ant species that drive the changes in ant community composition when habitats are converted. This feeding preference-fidelity could be explained by overlapping micro-climatic niches between the predator and its natural prey together with avoidance of extreme microclimates in disturbed habitats. However, testing this hypothesis would require a more detailed autecological study, e.g. involving radio tracking of the toads in different habitat types (e.g. Konopik et al., 2014).

Fig. 4. Electivity of *P. juxtaspera* for different ant genera across habitat types in relation to the ground-foraging ant fauna. Values of +1 indicate a preference for this genus and values of −1 indicate a complete absence of this genus from the toad's diet.

We have also demonstrated that *P. juxtaspera* specialises on ants and that it preys on a great variety of different genera and species. Both small-bodied (e.g. *Crematogaster, Loweriella*) and large-bodied ant genera (e.g. *Polyrhachis, Euprenolepis*) were among the positively and negatively selected genera, respectively. Furthermore, well-defended ant genera such as *Crematogaster* and many of the Ponerines were part of the toads' diet and were also found in the pitfall traps. This indicates that toads are not basing prey selection exclusively on ant body size or defences.

The toad also displays an interesting ability to adapt to the novel ecosystems created by the oil palm plantations. In contrast to its generally niche-conservative feeding behaviour, the toad showed a significant positive preference for the invasive yellow crazy ant (*A. gracilipes*) in oil palm plantations. This finding does not necessarily contradict the mostly stable dietary pattern that we found for the remaining ant species, which is likely to be due to restriction of the toad to remaining high quality habitat patches. In heavily degraded habitats such as oil palm plantations, *A. gracilipes* is typically not restricted to the plantation, but rather invades remaining high quality habitat patches, such as riparian strips. This overlap with the toads' foraging habitat could explain the inclusion of *A. gracilipes* into the toad's diet despite the lack of inclusion of other non-native ant species. The yellow crazy ant has been linked to dramatic changes to local ecosystems (Holway et al., 2002) and it is a widespread tropical invasive species, particularly in Southeast Asia (Wetterer, 2005). It is known to thrive in plantations and suppress native ant species (Bos et al., 2008). We did not find this species in primary forest, however it is highly abundant in oil palm plantations (Brühl and Eltz, 2009). Our results indicate that the toad could be an effective native predator of this invasive species. Southeast Asian native toads have already been shown to promote native ant diversity and potentially increase crop yields in cocoa plantations (Wanger et al., 2011), and it is possible that they also deliver a similar ecosystem service in oil palm plantations. However, the low densities of this native predator in highly altered landscapes, such as conventional oil palm plantations together with its restriction to remaining high quality habitats for foraging, is likely to limit the extent to which it can help to control hyper-abundant invasive ants. Nevertheless, we demonstrated that *P. juxtaspera* is able to establish populations in oil palm streams reaching similar abundances to primary and logged forests as long as riparian reserves provide high canopy cover. This suggests that promoting populations of this toad species by increasing the quality of riparian strips could have both conservation and pest-control benefits.

5. Conclusions

We found that the abundance of the giant river toad declines with reductions in canopy cover, and at the same time the ground foraging ant communities increase in local species richness. However, despite these changes in the populations of both predator and prey, the feeding preferences of the toad remained mostly constant across different land uses. Our study indicates that predator–prey interactions can be somewhat robust to anthropogenic pressures, and highlights the importance of understanding food web structure for predicting and managing the responses of communities and ecological processes to increasing human impact. However, the ability of the giant river toad to exploit the highly invasive yellow crazy ant, coupled with its sensitivity to habitat quality, indicates the potential of high quality riparian reserves in altered habitats for conservation of native anurans and the biological control of invasive species.

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at http://dx.doi.org/10.1016/j.gecco.2014.10.011.

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