The impact of logging and conversion to oil palm plantation on Bornean stream-dependent frogs and their role as meso-predators

Die Auswirkungen von Abholzung des Regenwalds und Umwandlung zu Ölpalmplantagen auf bachbewohnende Frösche und ihre Rolle als Mesoprädatoren in Borneo

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Slow loris (*Nycticebus menagensis*), Sabah (Malyasia) 2014

“What escapes the eye … is a much more insidious kind of extinction: the extinction of ecological interactions”

(Daniel H. Janzen)

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Affidavit

I hereby confirm that my thesis entitled "The impact of logging and conversion to oil palm plantation on Bornean stream-dependent frogs and their role as meso-predators" is the result of my own work. I did not receive any help or support from commercial consultants. All sources and / or materials applied are listed and specified in the thesis.

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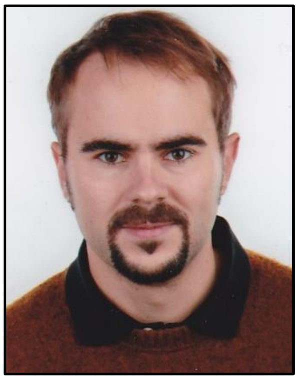

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Publication list

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Konopik, O., Steffan-Dewenter, I., Grafe, T. U. (under review) Effects of logging and oil palm expansion on stream frog communities on Borneo, Southeast Asia. *Biotropica*.

Konopik, O., Ahmad Sah, H. H., Keller, A., Wong, A., Grafe, T. U., Steffan-Dewenter, I. (submitted to Ecology) Logging and conversion to oil palm plantations alters trophic interactions and reduces multiples levels of anuran diversity.

Summary (English)

I. Nowadays, tropical landscapes experience large-scale land use intensification and land conversion driven by increasing demand for resourses. Due to the continuously high demand for tropical timber and politically intended step increase in palm oil production, multiple rounds of logging and subsequent conversion to oil palm plantations became a regionally wide-spread land conversion pattern in Southeast Asia. Although many tree species and some animals are highly threatened by logging, a great number of species groups, such as birds or mammals, have been shown to persist in logged forests. Accordingly, many ecosystem services, such as dung removal, seed dispersal or the activity of scavengers, are functionally maintained in logged forests. In contrast, oil palm plantations have been shown to not only dramatically alter the species composition and reduce biodiversity, but also curtail many crucial biotic and abiotic ecosystem functions. The focus of this dissertation was to investigate the response of anuran species richness and community composition to logging and conversion to oil palm plantation in northern Borneo (chapter II). I analysed the diet of various frog species and their change with habitat degradation. Furthermore, I assessed the shift in the trophic position of the anuran community as well as the response of anuran phylogenetic, dietary, and functional diversity to logging and conversion to oil palm plantations (chapter III). Finally, the resilience of the predator-prey interaction between an ant-specialist toad and its ant prey was analysed using shifts in species-level interactions (chapter IV).

II. This part of the study compares the species richness, relative abundance and community composition of stream anuran assemblages among primary forests, repeatedly logged forests and oil palm plantations. I used a highly standardised sampling setup applying transect-based sampling. Surprisingly, most of the anuran species native to primary forests were able to survive in logged forest streams. In contrast, on average only one third of the forest species richness was found in oil palm plantation streams. However, a high percentage of canopy cover above the plantation streams was able to mitigate this loss substantially. This study demonstrates the high conservation value of logged forests for Southeast Asian anurans. In contrast, the conversion to oil palm plantations leads to a dramatic decline of forest species. However, they have a mainly unused potential to contribute to the protection of parts of the regional anuran biodiversity if conservation-oriented management options are implemented.

III. In this part, I analysed the shifts in trophic position and multiple diversity layers of Southeast Asian stream-dependent anuran species across a gradient of disturbance from primary forest through intensively logged forest to oil palm plantation. For this purpose, I identified the diet composition of 59 anuran species by means of stomach flushing. Furthermore, I use diet composition of frog species as well as species traits to calculate dietary and functional diversity, respectively. I found that the trophic position of the entire anuran community is elevated in heavily disturbed habitats. Furthermore, species diversity, phylogenetic species variation, dietary diversity, and functional diversity were reduced. However, beyond the effect of the decreased species richness, only phylogenetic species variability and functional diversity were significantly impacted by land conversion, indicating a non-random loss of phylogenetic groups and functionally unique species. Overall, the observed changes to species interactions and functional composition suggest a greatly modified role of anurans in altered habitats and major foodweb reorganisation. Such far-reaching changes to the way species groups interact are likely to threaten local biodiversity and ecosystem functioning in natural and particularly modified habitats. However, I could also show, that small-scale habitat quality, provided by riparian reserves, is able to mitigate the negative consequences of land conversion considerably.

IV. Here I assess how logging of rain forest and conversion to oil palm plantations affect the populations of the ant-specialist giant river toad (*Phrynoidis juxtaspera*), and availability and composition of its ant prey. I measured canopy cover as an estimate for the degree of disturbance. I found that toad abundance decreased with increasing disturbance. At the same time, ant community composition was altered, and local ground-foraging ant species richness increased with disturbance. However, for a given amount of canopy cover, primary forest supported more ant species than altered habitats. 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 community composition, and even that some predators are capable of exploiting new prey sources in novel ecosystems.

V. I could show that anuran diversity and their trophic interaction is negatively impacted by logging and in particular by conversion to oil palm plantations. From species richness and community composition, my study expanded to phylogenetic, dietary and functional diversity. Furthermore, I investigated the interaction of a particular toad species with its preferred prey

(ants), on species level. This increasing degree of detail in my study provided comprehensive results, beyond the detail of many related studies. Overall, conservation of the remaining forest in Southeast Asia is urgently required to protect anuran biodiversity and their trophic interactions.

Zusammenfassung (German)

I. Durch den stetig steigenden Bedarf an vielfältigen Ressourcen stehen heutzutage vor allem tropische Ökosysteme unter enormem Druck hin zu intensiver Landwirtschaft und der Umwandlung von natürlichen Lebensräumen. Getrieben durch die hohe Nachfrage an Tropenhölzern und dem politisch gewollten Anstieg der Palmölproduktion, etablierte sich in Südostasien eine weit verbreitete Landnutzungsumwandlung charakterisiert durch wiederkehrende Holznutzung und die anschließende Umwandlung zu Ölpalmplantagen. Manche Tiergruppen und vor allem Baumarten sind dadurch stark gefährdet. Dennoch können andere Organismengruppen wie Vögel oder Säuger auch in genutzten Wäldern überleben. Auch Ökosystemdienstleistungen, wie Kotbeseitigung oder die Aktivität von Aasfressern bleiben vielfach in genutzten Wäldern erhalten. Im Gegensatz dazu stellen Ölpalmplantagen keinen geeigneten Lebensraum für viele Tier und Pflanzenarten dar und viele Ökosystemserviceleistungen können in diesen Plantagen nicht aufrecht erhalten werden. Ziel dieser Arbeit war die Auswirkungen dieser massiven Habitatumwandlung auf die Artenzahl und die Artenzusammensetzungen von Fröschen und Kröten in Nordborneo zu untersuchen (Kapitel II). Ich untersuchte die Nahrungszusammensetzung von mehreren Froscharten und wie sich diese mit Habitatumwandlung verändert. Zusätzlich habe ich die Stellung von Fröschen in der Nahrungskette sowie ihre phylogenetische, nahrungs- und funktionelle Diversität untersucht (Kapitel III). Schließlich habe die Interaktion von Fröschen mit ihrer Beute (in diesem Fall Ameisen) auch auf Artebene untersucht (Kapitel IV).

II. Dieser Teil der Arbeit vergleicht die Artenzahl, relative Häufigkeit und die Artenzusammensetzung der bachlebenden Froscharten zwischen Primärwäldern, genutzten Wäldern und Ölpalmplantagen. Dazu nahm ich die Froschbestände mit einer standardisierten Transektmethode auf. Ich fand heraus, dass die meisten Froscharten aus Primärwäldern auch in forstwirtschaftlich intensiv genutzten Wäldern überleben konnten. Im Gegensatz dazu wiesen Ölpalmplantagen nur durchschnittlich ein drittel der Froscharten aus Wäldern auf. Jedoch konnte dieser Artenschwund durch einen hohen Kronenschluss über den Plantagenbächen reduziert werden. Diese Studie belegt den hohen naturschutzfachlichen Wert von genutzten Wäldern in Südostasien und die geringe Bedeutung von Ölpalmplantagen in diesem Zusammenhang. Jedoch zeigt es auch Wege auf, wie Ölpalmplantagen naturschutzfachlich aufgewertet werden können.

III. Dieser Teil der Arbeit befasst sich mit den Auswirkungen der Habitatumwandlung auf die trophischen Interaktionen und mehrere Ebenen der Froschbiodiversität. Dazu untersuchte ich die Nahrungszusammensetzung von 59 Froscharten mittels Magenspülung. Darüber hinaus nutzte ich diese Daten um die Nahrungsvielfalt zu untersuchen und Daten aus der Literatur und die funktionelle Diversität zu erfassen. Dabei fand ich heraus, dass Frösche bei zunehmender Habitatzerstörung eine höhere Stellung in der Nahrungskette einnahmen. Darüber hinaus sank die allgemeine Diversität, die phylogenetische Verwandtschaft, die Nahrungsvielfalt und die funktionelle Diversität der Frösche. Also lässt sich schließen, dass diese tiefgreifenden Veränderungen eine deutlich andere Rolle der Frösche in den umgewandelten Habitaten zur Folge hat. Solche dramatischen Eingriffe in das Nahrungsnetz können negative Auswirkungen auf die Stabilität von Ökosystemen haben, jedoch zeigt sich auch hier, dass diese durch die Erhöhung des Kronenschlusses deutlich abgemildert werden können.

IV. In diesem Abschnitt befasse ich mich auf die Auswirkungen der Habitatumwandlung auf die Häufigkeit der Kröte *Phrynoidis juxtaspera*, ihre Beute (Ameisen), sowie die Interaktion von Räuber und Beute. Dabei fand ich heraus, dass die Kröte in ungestörten Bächen am häufigsten war und gleichzeitig mehr (und andere) Ameisenarten in Ölpalmplantagen vorkamen. Jedoch war die Artenzahl von Ameisen bei konstantem Kronenschluss in Primärwäldern immer höher als in Ölpalmplantagen. Im großen Gegensatz zu diesen Veränderungen, war die Nahrungszusammensetzung der verbleibenden Kröten in den Plantagenbächen kaum unterschiedlich im Vergleich mit Primärwaldbächen. Eine Ausnahme war ein deutlich gestiegener Anteil der invasiven Ameisenart *Anoplolepis gracilipes*. Diese Ergebnisse zeigen, dass die Räuber-Beute Interaktion unter Umständen unverändert die Habitatumwandlung überstehen können, aber auch in gewissem Umfang neue Ressourcen erschlossen werden können.

V. Mit dieser Arbeit konnte ich zeigen, dass sich die großflächige Habitatumwandlung von Wäldern hin zu Ölpalmplantagen negativ auf die Froschbiodiversität, wie auch die Räuber-Beute Interaktionen von Fröschen auswirkt. Ausgehend von Artenzahl und Artenzusammensetzung konnte ich in meiner Arbeit darüber hinaus auch die Biodiversität der Frösche auf verschiedenen Ebenen beleuchten und schließlich sogar die Räuber-Beute Interaktion auf Artebene untersuchen. Dadurch konnte ich diesen komplexen Zusammenhang in ganz besonderer Tiefe beleuchten. Insgesamt liefert diese Arbeit einen weiteren wichtigen

Beleg dafür, dass Primärwälder, aber neuerdings auch immer mehr genutzte Wälder entscheidend für den Erhalt von tropischer Biodiversität sind.

I. General introduction

Biodiversity describes the degree of variation in the biotic part of ecosystems. It is often confused with species richness (Stirling and Wilsey, 2001), which however is only a part of biodiversity. Genetic variation, the variety of habitats, and complexity of species interactions are also crucial parts of the variation in life (Noss, 1990). Whereas living organisms can be found across the globe, on all continents and in a vast spectrum of even the most extreme habitats, such as Antarctica or hydrothermal vents (Chown, 2012), global biodiversity is not equally distributed. In particular, terrestrial ecosystems tend to be more diverse around the equator, in humid tropical regions (Gibson *et al.*, 2011; Jenkins *et al.*, 2013; Pimm and Raven, 2000). The reasons for this mostly universal pattern are still part of scientific discussion, but include theories such as the mid-domain effect, niche conservatism or the species-energy hypothesis (Brown, 2014; Romdal *et al.*, 2013). Furthermore, especially tropical rainforest support an exceptionally high level of spatial and ecological niches provided by their composition comprising multiple strata (Slik *et al.*, 2003; Whitmore, 1990). These multiple and three-dimensional layers support individual sub-systems and unique species assemblages. Hence, many global biodiversity hotspots can also be found in the tropical regions, and particularly in tropical rainforests (Myers *et al.*, 2000).

Global biodiversity is nowadays threatened by a number of factors; many of them are typically summarised as ‘global change’ (Sala *et al.*, 2000). Global change describes the impact of the modern society on planet earth and include carbon cycle, energy development, or land use. Main drivers of global change are increased demand for resources and ultimately global population growth (Grimm *et al.*, 2008). Again, these causes and the effects of global change are not equally distributed (Lewis *et al.*, 2004). Whereas, population-rich and industrialised countries lead the global demand for resources, many of these need to be imported. Not uncommonly, tropical countries export products to satisfy global demand (Tucker, 2000). Typical tropical products include timber, soya bean, coffee, cocoa, and palm oil (FAO 2013).

Southeast Asia is an important tropical biodiversity hotspot (Myers *et al.*, 2000) with a natural vegetation of mainly tropical rainforests of various types. At the same time it is the tropical region with the world-wide highest deforestation rates (Miettinen *et al.*, 2011) and it is leading global palm oil production by far (FAO 2013). These processes have lead to massive changes to regional forests, with only a small percentage of primary forest remaining (Sodhi *et al.*, 2004). In contrast, the vast majority of the current forests have experienced (multiple) logging in the past (Reynolds *et al.*, 2011), particularly in the lowlands. Commonly, most logging in Southeast Asia is targeting economically important tree species from the family Dipterocarpaceae (Cannon, 1998). These are typically the tallest trees in the forests, shaping the composition of rainforest strata (Slik *et al.*, 2003). By their large-scale removal, the not to be underestimated collateral damage to other trees (Asner *et al.*, 2006), and the establishment of logging road infrastructures (Konopik *et al.*, 2014b; Laurance *et al.*, 2009), local biotic and abiotic characteristics are massively altered.

The effect of logging on Southeast Asian rainforests and its implications for conservation are controversially discussed in the scientific community. On the one hand, there is an apparent need for more large-scale protected areas (Barlow *et al.*, 2007a; Gibson *et al.*, 2011). These need to be established to protect the last remaining patches of mostly unlogged rainforest in Southeast Asia. On the other hand, the protection of large parts of biodiversity, habitats, and some large mammals will not be feasible if only protected areas remain, particularly in the light of climate change (Hannah *et al.*, 2007). Furthermore, most of the lowland forests in the region are nowadays (repeatedly) logged forests (Reynolds *et al.*, 2011). For a long time, conservation efforts have been trying to work out the differences between primary forests and logged forests, to focus conservation on these primary habitats. This has led to a premature policy, that the remaining logged forest, which supposedly has little conservation value, is eagerly and in large-scale converted to oil palm plantations (Wicke *et al.*, 2011). However, even repeatedly logged forests in Southeast Asia have an undeniably high biodiversity (Berry *et al.*, 2010), compared to plantation landscapes. As a result, conservation efforts are more and more focusing on protecting any kind of natural or semi-natural forest in the region (Edwards *et al.*, 2010; Putz *et al.*, 2012), to maintain large blocks of connected habitat.

Study sites

The field work for this study was conducted in northern Borneo between April 2011 and March 2014 for a total of 14 month. The study sites were located in the sultanate of Brunei Darussalam and the state of Sabah (Malaysia). Within the study sites multiple forest and plantation streams with a catchment size of 2.5 km^2 were studied (Fig. I.1). I sampled a total of seven streams in primary rainforests (Fig. I.2a, page 18), eight streams in logged forests (Fig. I.2b, page 18), and seven streams in oil palm plantations (Fig. I.2c, page 19).

Figure I.1: A typical primary forest stream that was included in this study (Sg. Injing, UTNP, Brunei Darussalam). All streams were rocky and typically free of vegetation. They are frequently subjected to heavy flash floods.

The Ulu Temburong National Park (UTNP) is located in the sparsely populated Temburong district in Brunei. It is characterised by a very rough terrain, gorges, the lack of roads, and by the major streams Sg. Temburong and Sg. Belalong (Cranbrook and Edwards, 1994). The forest in the park has never been logged, but there is some hunting within the park borders, mainly by the local population and tribes. The UTNP has been shown to be a local amphibian hotspot (Grafe and Keller, 2009) with far over 60 species known to occur within the park borders (Grafe *et al.*, 2010). The two intensively studied streams were within walking distance from the Kuala Belalong Field Studies Centre (Sg. Sibut) or only reachable by boat (Sg. Injing).


a)
b)

Figure I.2: The tree different types of landscapes included in this study. Primary dipterocarp lowland rainforests (page 18, a), logged lowland rainforests (page 18, b), and oil palm plantations (c).

Danum Valley Conservation Area (DVCA) is a 438 km^2 protected area in Sabah. Its forest consists of mainly undisturbed patches and some areas, which experienced logging in the past. However, there was historically no hunting within the park borders (Reynolds *et al.*, 2011), and many large mammals, including Bornean pygmy elephants and Orang Utans, can regularly be observed. All three studied streams (Sg. Tembaling, Sg. Rhino, West Stream) were located within primary forests. However, natural disturbance, mainly by elephants, was evident, particularly around West Stream. So far over 50 anuran species have been recorded from Danum valley (Sheridan *et al.*, 2012).

Maliau Basin Conservation Area (MBCA) is a remote protected area located in central Sabah. It covers an area of 588 km^2 and is dominated by a large natural basin, the source of Sg. Maliau. The inside of the basin is characterised by montane heath forests and tannin-rich streams (Hazebroek *et al.*, 2004). The studied stream is a tributary of Sg. Maliau and located outside the basin along its slopes.

The SAFE project area is located between DVCA (~50 km) and MBCA (~60 km). Its forest is continuous with a major protected forest block, including DVCA and MBCA. The 25 km^2 project area consist mainly of repeatedly logged forest. Forest quality is very patch and ranges from 16% to 63% forest cover remaining. Adjacent to the experimental area is a 2200 ha block of mainly unlogged forest (VJR) and oil palm plantations managed by Benta Wawasan Sdn Bhd. Hunting is common in the area, however elephants and Orang Utans can also frequently be observed. The SAFE project (http://www.safeproject.net) is a large-scale, international forest fragmentation project, led by Imperial College London and the Southeast Asian Rainforest Research Program by the Royal Society (Ewers *et al.*, 2011). A total of eight streams have been studied in the logged forest of the experimental area, one stream in VJR, and seven streams in the surrounding plantations.

DVCA, MBCA and the SAFE project area and the oil palm plantations are managed by the Sabah foundation (Yayasan Sabah).

Bornean frogs

To date more than 160 amphibian species have been described from Borneo (Inger, 2009). Salamanders and newts are absent from most of Southeast Asia, including Borneo, leaving anurans (frogs and toads) and caecilians (Gymnophiona). The latter is only represented by few species, all of which are mainly fossorial or aquatic and generally their specific taxonomy and ecology is mostly unknown (Nishikawa *et al.*, 2012). Hence, the vast majority of Bornean amphibian species are frogs and toads.

In 2009, a total of 156 frog species from 8 families are known to occur on Borneo (Inger, 2009). Bornean anurans are closely related to the anuran fauna of Sumatra and Peninsular Malaysia. These regions were connected during the last ice ages, leading to a limited species exchange (Inger and Voris, 2008). However, particularly in montane habitats Borneo has a mostly unique anuran fauna with a high overall percentage of endemic species. Most Bornean species can be found along streams and many have stream-living larval stages. However, various reproductive modes, including direct development, are represented amongst Bornean anurans (Das *et al.*, 2007; Inger, 2009). The community composition of Bornean stream-dependent frogs has been shown to depend greatly on environmental heterogeneity (Keller *et al.*, 2009). Borneo is also home to the so-called “flying frogs” (Fig. I.3), such as the charismatic Wallace’s Flying Frog and the mostly endemic foot-flagging frogs (Grafe and

Wanger, 2007) of the genus *Staurois*. Furthermore, the enigmatic lungless frog (*Barbourula kalimantanensis*) can be found exclusively on Borneo. So far it has only been found a few times in the Bornean central mountain range. It is the only known anuran that totally lacks lungs (Bickford *et al.*, 2008).

Some frog species are locally hunted in Borneo (Warkentin *et al.*, 2009). These are mostly large-bodied representatives of the genus *Limnonectes* and some large toads. Furthermore, the non-native Taiwanese Frog (*Hoplobatrachus rugulosus*) is locally farmed for food and has occasionally established free-living populations in highly modified landscapes (Inger and Stuebing, 2005).

Research questions

The impact of logging and conversion to oil palm plantations on anuran diversity in Southeast Asia is hardly understood. I want to investigate the effect of this regionally wide-spread land conversion pattern on:

1. **the species richness, abundance, and community composition of Bornean stream-dwelling amphibians;**
2. **other layers of anuran diversity, including phylogenetic diversity, and functional diversity;**
3. **the diet composition and dietary diversity of anuran communities;**
4. **the predator-prey interaction of the largest Bornean anuran (*Phrynoidis juxtaspera*) with its main prey (ants, Formicidae);**

Figure I.3: ***Rhacophorus borneensis*** **is a Bornean endemic belonging to the "flying frogs". It is rarely seen due to its life high up in the forest canopy.**

Methods

All methods, study sites, and materials are described in chapter II, III, and IV.

II. Effects of logging and oil palm expansion on stream frog communities on Borneo, Southeast Asia

This chapter is submitted as: Konopik, O., Steffan-Dewenter, I., Grafe, T. U. Effects of logging and oil palm expansion on stream frog communities on Borneo, Southeast Asia. *Biotropica*, in review

Running title: Species richness and community composition

Abstract

The conversion of tropical rainforests to oil palm plantations is a major threat to Southeast Asia’s rich biodiversity. Although primary forests have a unique role in conservation, improving biodiversity in secondary forests, agroforestry systems, or plantations is increasingly gaining attention. This study compares the species richness, density and community composition of stream anuran assemblages among primary forests, repeatedly logged forests and oil palm plantations in northern Borneo. We applied a standardised sampling setup using transect-based sampling. In primary forest streams, we recorded 19 frog species on average, compared to 15 species in logged forests and 11 species in oil palm plantation streams, respectively. However, a high percentage of canopy cover above the plantation streams was able to mitigate this loss to some extent. This study demonstrates the high conservation value of logged forests for Bornean stream-dependent anurans and supports the broadly assumed dramatic effects of oil palm plantations on the region’s biodiversity. However, oil palm plantations have a mainly unused potential to contribute to the protection of parts of the regional anuran biodiversity if conservation-oriented management options are implemented.

Keywords

amphibia; canopy cover; deforestation; riparian reserves; tropical rainforest

Introduction

Southeast Asia is among the world's most important biodiversity hotspots (Myers *et al.*, 2000) with a unique bio-geographical history. Presently, this diversity is severely threatened by a combination of factors, most notably the loss of primary forests and forest conversion (Sodhi *et al.*, 2004). Nevertheless, huge areas of forest of varying quality continue to be converted into oil palm plantations in the region (Koh and Wilcove, 2008). Southeast Asia generates over 80 percent of the global palm oil production (FAO 2013). Accordingly, palm oil plantations are taking up an increasingly high percentage of the region's land cover (Miettinen *et al.*, 2011), mostly at he expense of non-primary forests.

There is increasing evidence that most of Southeast Asia's animal species are able to survive in disturbed rain forests and even repeatedly logged forests and agroforestry systems (Berry *et al.*, 2010; Edwards *et al.*, 2010; Steffan-Dewenter *et al.*, 2007). The extensive distribution of these altered forests might even be advantageous for large scale forest habitat protection, particularly in the light of the massive expansion of oil palm plantations in the region (Wicke *et al.*, 2011). Thus, the importance of non-primary forest for conservation of tropical biodiversity is increasingly gaining attention (Wilcove *et al.*, 2013). However, primary forests are frequently considered a key element in overall conservation strategies as some animal species and in particular tropical tree species are severely threatened by logging (Gibson *et al.*, 2011) and conservation of original species communities is likely to depend on pristine frontier forests (Barlow *et al.*, 2007b).

In contrast to the protection of natural or semi-natural habitats, optimisation of agroforestry in converted landscapes (Chazdon *et al.*, 2009; Clough *et al.*, 2011), such as oil palm plantations, is seen as an alternative. Based on their great extent and on-going expansion, oil palm plantations should not be ignored by conservation efforts in Southeast Asia. Instead, plantations could be ecologically designed and optimised to increase the number of forest species that can survive in the altered habitat and to maintain important ecosystem services (Foster *et al.*, 2011). Hence, the identification of conservation measures for the different taxa and ecosystem functions is of particular importance for oil palm plantations.

Amphibians are among the most threatened taxa worldwide (Stuart *et al.*, 2004). Habitat loss, together with other factors like overexploitation, fragmentation, introduction of alien species, disease, pesticides, and climate change have been identified as important drivers of species decline (Beebee and Griffiths, 2005). In addition, the interaction of these factors has led to a dramatic loss of species richness (Stuart *et al.*, 2004; Wake and Vredenburg, 2008). Southeast Asian amphibians, in particular, have been shown to face a conservation crisis, caused by these factors (Bickford *et al.*, 2010; Rowley *et al.*, 2010). Nevertheless, until now amphibians in Southeast Asia have mainly been spared from enigmatic declines, such as chytridiomycosis (Kaiser and Grafe, 2011; Swei *et al.*, 2011). However, Southeast Asian anurans together with other taxa remain extremely vulnerable to habitat loss (Sodhi *et al.*, 2009).

Commonly, amphibians are characterised by complex life cycles involving both aquatic and terrestrial stages (Wells, 2007). However, there are also direct developing anuran lineages in Southeast Asia (Grosjean *et al.*, 2008) and in some species the reproductive mode is unknown. Although dependence on water bodies as breeding sites varies among species, many amphibians have been shown to be sensitive to changes in temperature, humidity, water quality or canopy cover (Wanger *et al.*, 2010). In particular, stream-breeding amphibians are susceptible to these environmental changes (Welsh and Ollivier, 1998). Furthermore, based on their high habitat specificity and exposure to diseases, they are assumed to have an underestimated extinction risk (Almeida-Gomes *et al.*, 2014). In the context of the considerable increase in temperature and decreased humidity in oil palm plantations (Luskin and Potts, 2011), stream-dependent anuran communities can be predicted to suffer from this land conversion.

In this study we compare Bornean stream frog communities along the gradient of the three major habitat types in the region: primary forest, logged forest, and oil palm plantations. Our aim is to understand the response of stream frog species richness, density and community composition to this regionally wide-spread land conversion pattern and the underlying factors causing this response. Specifically, we ask the following questions:

1) Are species richness and anuran density decreases by logging and conversion to oil palm plantations?

2) Does logging and conversion to oil palm plantation change the community composition by local extinction of forest species and immigration of generalist species?

3) Does local habitat quality (canopy cover provided by forested riparian strips) have a positive effect on persistence of anurans within logged forests and oil palm plantations?

Methods

Study sites

The study was conducted in northern Borneo (Fig. II.1). We sampled eight streams located in logged lowland dipterocarp rainforest and seven streams in oil palm plantations in the Malaysian state of Sabah. Sampling of logged forests and plantations was conducted within the framework of the SAFE project (Stability of Altered Forest Ecosystems) and the surrounding plantations (Ewers *et al.*, 2011). The SAFE project is a large-scale (7200 ha) ecological experiment investigating the impact of fragmentation of Southeast Asian rainforest and conversion to oil palm plantation. Within the project area, logged forest has undergone two rounds of selective logging in the past: once during the 1970s and again from the late 1990s-2000s. It is continuous with a major forest block (>1 million ha) of lowland rainforest forest, including Danum Valley and Maliau Basin (Reynolds *et al.*, 2011). The forest structure in the SAFE project area is highly variable, ranging from open areas to those with closed canopies. The terrain is generally very rough and fast flowing rocky streams are

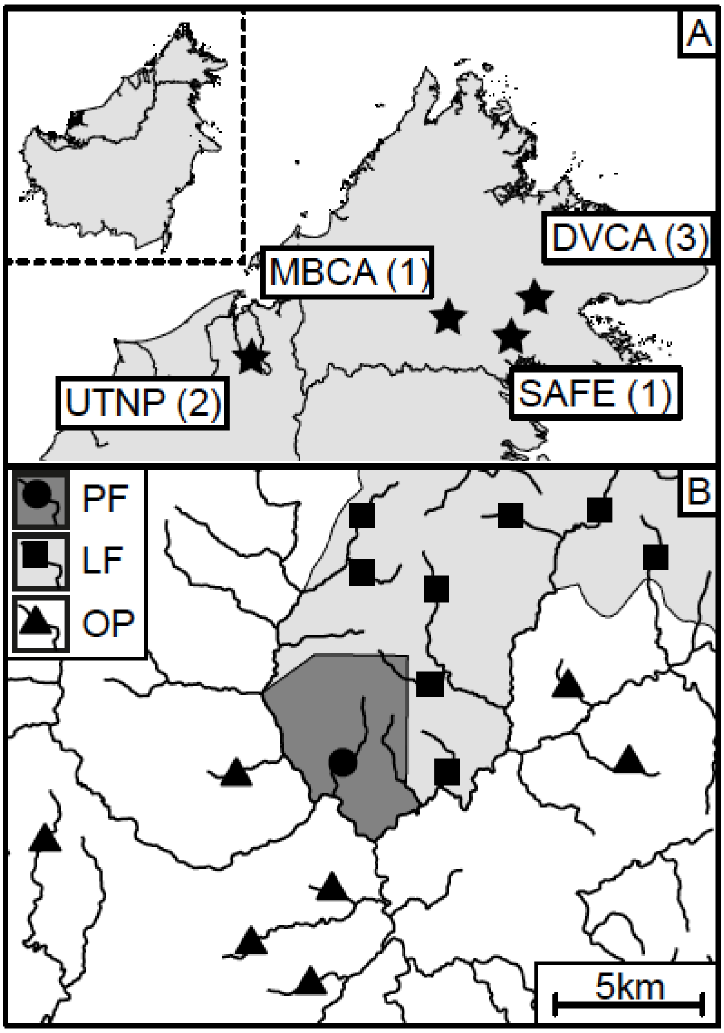

Figure II.1: Position of the study area on Borneo and the location of the sampling sites (A). Numbers in brackets indicate the number of sampled primary forest streams per site. The distribution of the sampled streams at the SAFE project site and the surrounding oil palm plantations is illustrated in detail (B). Shown are streams in a primary forest (PF) fragment, logged forest (LF) and oil palm plantations (OP).

embedded in steep valleys. This leads to a lack of natural ponds or standing water bodies apart from side pools next to streams. Mean annual precipitation at Danum Valley is about 2600 mm (Douglas, 1999).

The sampled oil palm plantation streams were of comparable characteristics and their catchments were isolated by 1km to 5km from the logged forests. Plantations varied in age but were generally established between 2000 and 2005. All plantation streams had riparian reserves (riparian strips or river reserves) of differing vegetation and quality. Under Malaysian law riparian reserves are required to extend at least 20m on both sides of the stream into the plantations (Sabah Water Resources Enactment 1998). However, the riparian reserves ranged from gallery forests shading the streams to shrubby and grassy vegetation on the streamside.

As primary forest control, we selected the closest accessible streams in continuous and undisturbed areas of comparable elevation, terrain, and natural vegetation. The closest (one stream) was a Virgin Jungle Reserve of 2200 ha, adjacent and continuous to the SAFE project area and the sampled oil palm plantations. Furthermore, we sampled streams in Danum Valley (three streams, 30km distance), Maliau Basin (one stream, 70 km distance), and Ulu Temburong National Park (two streams, 250 km distance).

Sampling

All sampled streams were independent first order streams. To standardise stream size, sampling was conducted where the stream catchments reached the size of 2.5 km^2. A line transect was then established starting from the point where the respective catchment is 2.5 km^2 and leading 200 m upstream, following the stream. Transect walks where performed walking in the streams.

To assess species richness and density of frogs we conducted six standardised visual and acoustic encounter surveys at intervals of at least one week per transect. Frogs were actively searched during the highest calling activity of most species (1845 h – 2030 h) by a single person within the stream bed using a headlamp (Petzl Myo RXP) for one hour. All audible and identifiable anuran calls that were heard from within the stream bed were recorded. Visual and acoustic records were treated equally and summed up to get final numbers. However, to avoid double counting of individuals of a respective species, we applied a conservative approach by discarding acoustic records from locations where individuals of the same species could already be visually recorded during the same transect walk. We only recorded adult and subadult individuals (both males and females) and metamorphs were excluded from the analysis. Finally, the average number of individuals per stream was used as a density estimate. However, these densities (abundances) should rather be treated as conservative estimates or relative densities compared to absolute densities. All frogs were identified in the field using morphological or acoustic characteristics following Inger & Stuebing (2005).

The date of sampling of the three habitat types was randomised as far as logistically possible to avoid confounding impact of the year of sampling or climate patterns. Primary forest streams were sampled between June and July 2011 (UTNP), April and July 2012 (DVCA, MBCA) and January to May 2013 (UTNP). Logged forests and oil palm plantations were sampled between April to June 2011 and January to April 2013. General sampling was planned to avoid dry seasons and extremely wet periods. Furthermore, sampling was discontinued during periods of heavy flooding or extensive dry spells.

To assess suitability of altered habitats for the forest frog community (primary forest species), we grouped the frog species into forest species and generalist species. Forest species were defined as the species, which were recorded from the primary forest sites. Species that could only be recorded in logged forest and oil palm plantations were treated as generalist species.

Habitat parameters

To account for the highly heterogeneous degree of disturbance in the logged forest, the differing age of the oil palm plantations and the different quality of riparian reserves in both habitats, we used the canopy cover above the stream as an estimate of the degree of disturbance. Canopy cover was obtained from canopy pictures taken from the ground. The 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). Subsequently, using Adobe Photoshop pictures were converted to black and white images and the percentage of the sky covered by vegetation (black pixels) was used as canopy cover (%).

In addition, we measured both width and slope of the streams. Stream width and slope have already been shown to shape Bornean anuran communities (Keller *et al.*, 2009), so we included these variables to account for differing stream characteristics. Stream width was measured at an intermediate water level. If the stream split up into two or more branches, their individual width was added up to get the total stream width. Stream slope was measured applying the principle of communicating vessels (LaPerriere and Martin, 1986). First, a 14 m water-filled translucent 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 ground (on the downstream end) was divided by the stream distance being measured to obtain the stream slope.

All habitat parameters were measured at intervals of ten m and once per transect. Individual values were averaged per transect to get overall values.

Data analyses, species richness estimation

To test the effect of habitat type and habitat parameters on species richness and frog density, we used analysis of variance (ANOVA) and applied linear models. We analysed the species richness and density of all frog species (overall species richness/ density) as well as the species richness and density of forest species. Furthermore, we used the average of two sample-based (sampling rounds) species richness estimators (Chao2, ICE) to estimate the total number of frog species per stream. Calculation of species richness estimators was done using EstimateS (Version 9, R. K. Colwell, http://purl.oclc.org/estimates).

For all statistical analyses we used the open source software R (R Development Core Team 2008). The respective full models contained habitat type and the three habitat parameters, as well as all interaction terms. To select the most parsimonious model we applied stepwise backward selection using likelihood ratio tests. Afterwards, we tested the significance of the predictors of our final models using analysis of variance (ANOVA). Finally, *post-hoc* tests (Tukey's HSD) were used to identify significant differences between habitat types. All parameters were tested for normality and collinearity before analysis.

Frog community composition was analysed using permutation-based multivariate analysis of variance (PerMANOVA). To calculate the distance matrix for the PerMANOVA, we used Bray-Curtis dissimilarity. To calculate the pseudo-F values and the p-statistic, we performed a total of 999 permutations of the raw matrix.

To display the variation in frog community composition among habitat types and the impact of habitat parameters we used non-metric multidimensional scaling (NMDS) using the same distance matrix as for the PerMANOVA. We set the program to generate 1,000 iterations to find the final ordination with minimum stress and best fit. All calculations of the frog community analyses were done using the “vegan” package for R (Oksanen *et al.*, 2013).

Results

We recorded a total of 5549 frogs and toads (32% acoustic records) belonging to 43 species (21 genera, 6 families) in the 22 streams sampled in this study. 37 species could be recorded in primary forests, 28 in logged forests and 19 frog species in oil palm plantations. Six frog species (*Fejervarya limnocharis*, *Limnonectes paramacrodon*, *Hylarana erythrea*, *Hylarana nicobariensis*, *Polypedates leucomystax*, *Polypedates otilophus*) were categorised as generalist species. They were mostly found in oil palm plantations and were never recorded in primary forests during our study.

Impact of land conversion on species richness

Estimated species richness varied among habitat types (ANOVA: $F_{2,18} = 25.8$, $P < .001$) and increased with stream slope (ANOVA: $F_{1,18} = 13.8$, $P = .0016$) but was unaffected by canopy

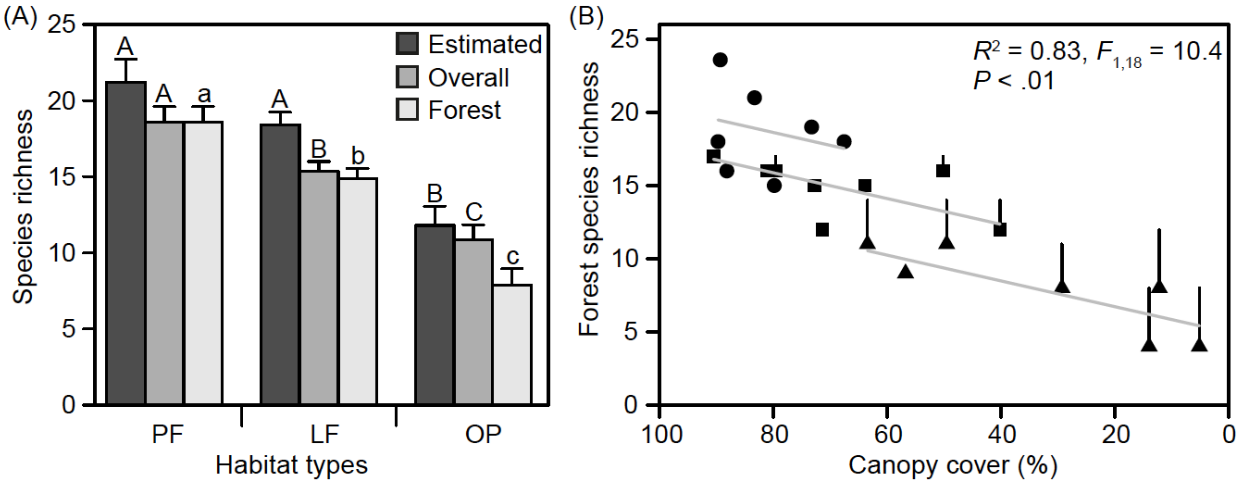

Figure II.2: Effect of habitat type (A) and canopy cover (B) on estimated, recorded, and forest species richness of stream-dependent anuran species. Shown are habitat means (± SE), respectively. Differing letters above bars indicate significant differences (at least *P* < 0.05) between groups. Vertical lines (in B) indicate the difference between forest species and overall frog species richness. Primary forest: PF (circles); logged forest: LF (squares); oil palm plantation: OP (triangles).

cover and stream width. Estimated species richness was highest in primary forest streams (21.2 ± 4.0). Furthermore, the highest species richness for all habitat types was estimated for the Maliau Basin primary forest stream (28.1). Estimated species richness dropped to 87 percent (18.4 ± 2.4) in logged forests and only 56 percent (11.8 ± 3.4) of the species richness of primary forests was calculated for oil palm plantations. Robustness of sampling was generally good. However, the six rounds of sampling per stream resulted in marginally different values per habitat type. On average 89 percent of the estimated species richness was recorded in primary forests, 84 percent for logged forests and 93 percent for oil palm plantation streams.

Overall species richness (recorded species richness) varied among habitat types (ANOVA: $F_{2,18} = 20.6$, $P < .001$), but was unaffected by stream characteristics. Habitat type was the only remaining significant predictor in this model. Recorded species richness was highest in primary forest streams (18.7 ± 2.7). Furthermore, the overall highest species richness was recorded from a primary forest stream in the UTNP (24). However, species richness dropped to 83 percent (15.4 ± 1.8) in logged forests, but this difference was only marginally significant (Tukey's HSD: $P = 0.046$). In contrast only 58 percent (10.9 ± 2.6) of the primary forest species richness could be recorded in oil palm plantations.

Accordingly, richness of forest species was depending upon habitat type (ANOVA: $F_{2,17} = 48.6$, $P < .001$), but also decreased with diminishing canopy cover ($F_{1,18} = 10.4$, $P = .0047$). Stream width and stream slope were not included in this model. Forest species richness was highest in primary forest streams (18.6 ± 2.8). It dropped to 80 percent (14.9 ± 1.9) in logged forests. However, we found considerably less species in oil palm plantations compared to primary forests. Only 42 percent (7.9 ± 2.9) of the primary forest species richness could be recorded in oil palm plantations. On average, forest species richness decreased by 0.9 species with ten percent reduction in canopy cover. Slopes were the same for all habitat types, because no interaction term remained in the final models. In summary, most forest species were found in primary forest streams with high levels of canopy cover and the lowest values were recorded for oil palm plantation streams with low canopy cover (Fig. II.2).

Impact of land conversion on frog density

Overall frog density was depending upon habitat type (ANOVA: $F_{2,17} = 6.1$, $P = .0101$), decreased with lost canopy cover ($F_{1,17} = 9.6$, $P = .0066$), and decreased with stream width

(ANOVA: $F_{1,17} = 8.6$, $P = .0093$). For all habitat types *Meristogenys* cf. *orphnocnemis* was the most abundant species. This species represented 15.4 percent of the individuals recorded in primary forests, 32.5 percent in logged forests, and 35.2 in oil palm plantations. However, it was totally absent from two plantations streams. Three frog species could only be recorded once during the whole study.

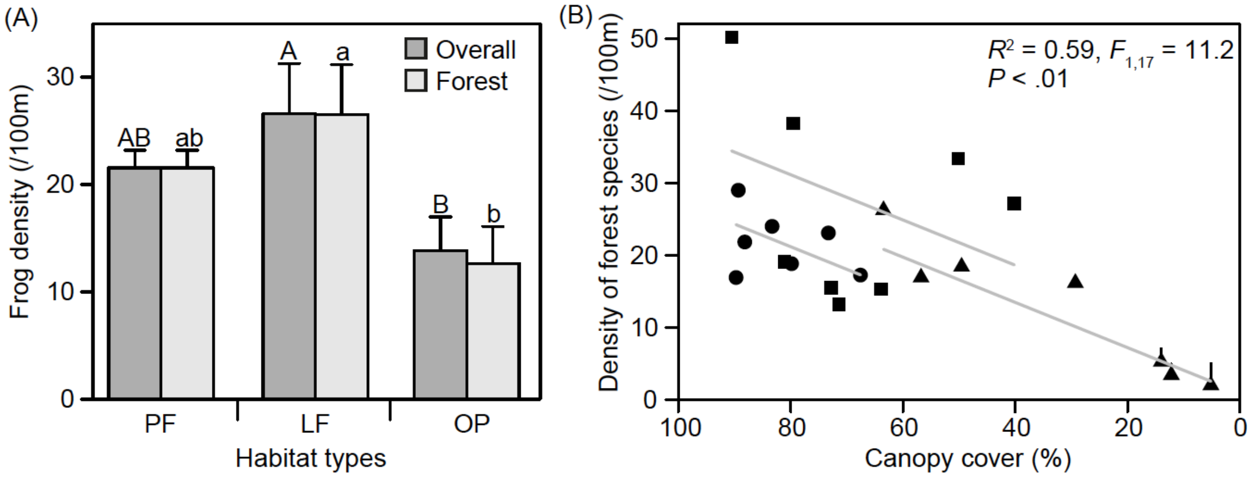

Figure II.3: Effect of habitat type (A) and canopy cover (B) on the density of overall and forest anuran species. Shown are habitat means (± SE), respectively. Differing letters above bars indicate significant differences (at least $P < 0.05$) between groups. Vertical lines (in B) indicate the difference between forest species and overall frog density. Primary forest: PF (circles); logged forest: LF (squares); oil palm plantation: OP (triangles).

Contrary to the pattern for species richness, the highest frog densities were recorded from logged forests. However, especially those logged forest streams featuring a high level of canopy cover had the highest overall densities. At the bottom of the canopy cover scale, oil palm plantation streams, with a canopy cover under 20 percent, had low frog densities between five and seven frogs per 100 m.

This pattern was consistent considering only forest species. Accordingly, forest species density varied with habitat type (ANOVA: $F_{2,17} = 7.3$, $P = .0052$), decreased with lost canopy cover ($F_{1,17} = 11.2$, $P < .0039$), and decreased with stream width (ANOVA: $F_{1,17} = 8.5$, $P = .0098$). Excluding the generalist species, the low frog density in oil palm streams becomes even more evident and dropped to two to five individuals per 100 m. Generally, there was a high variance of individual numbers between streams within habitat type, particularly in logged forests and oil palm plantations (Fig. II.3).

Community composition

Habitat type had significant impact on the composition of the frog communities (PerMANOVA: $F_{2,16} = 1.9$, $R^2 = 0.13$, $P = .043$). Both canopy cover and stream slope were significant covariates explaining a considerable amount of this variation. The influence of canopy cover on the community composition was strongest (PerMANOVA: $F_{1,16} = 7.6$, $R^2 = 0.24$, $P < .001$). Yet, the composition of anuran communities of oil palm plantation streams with high canopy cover was more similar to forested streams (both logged and primary forest) than to oil palm streams with low canopy cover. Furthermore, stream slope explained a minor part of the variation (PerMANOVA: $F_{1,16} = 2.5$, $R^2 = 0.08$, $P < .033$) and stream width did not have a significant impact at all (Fig. II.4).

The recorded frog species were typical for the hilly parts of northern Borneo. Furthermore, the species overlap between the sampled primary forest control streams was generally high. However, in MBCA we found one unique species (*Huia cavitympanum*) and in the UTNP several frog species were replaced by ecologically similar sister species (e.g. UTNP: *Ansonia longidigita* and *Rhacophorus belalongensis*, East-Sabah: *A. spinulifer* and *R. gauni*).

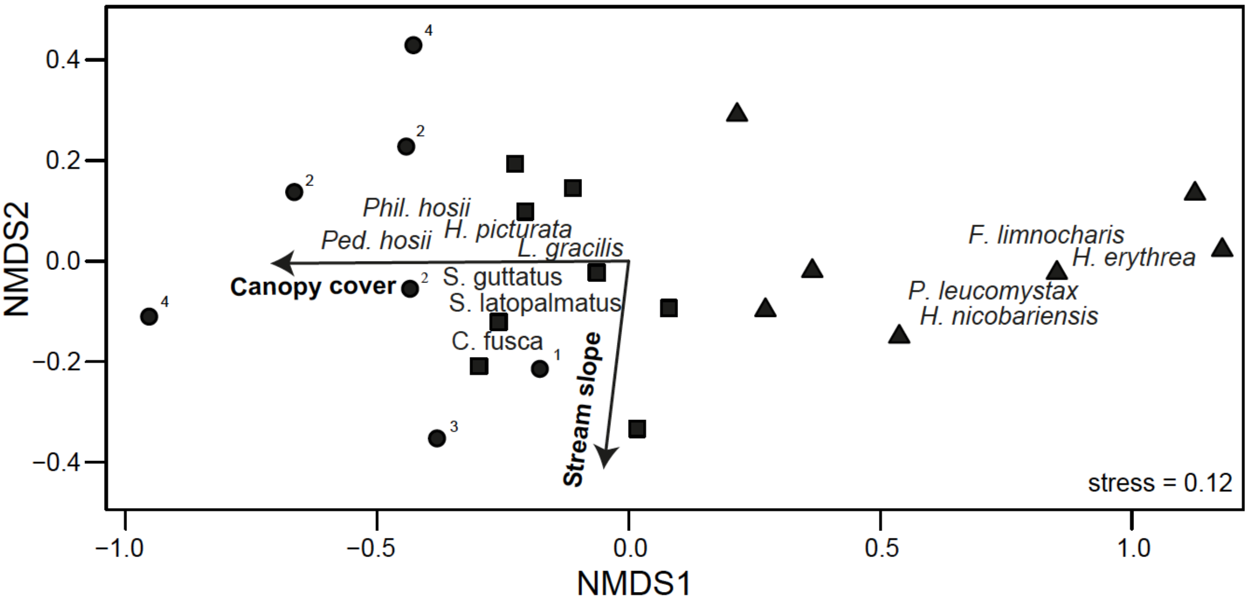

Figure II.4: Ordination (non-metric multidimensional scaling) of the anuran community composition of the primary forest streams (circles), logged forest streams (rectangles) and oil palm plantation streams (triangles). Primary forest streams are tagged according to the respective sampling site (1: SAFE; 2: DVCA; 3: MBCA; 4: UTNP). Included are significant (*P* < 0.05) environmental vectors. Additionally, only significant frog species that act as indicator species (Dufrêne and Legendre, 1997) for both forest types or oil palm plantation are displayed.

In contrast, frog communities in oil palm plantations were clearly differing from communities of forested habitats. *Staurois* spp. were mostly absent from plantation streams and five species (*F. limnocharis, L. paramacrodon*, *H. erythrea*, *H. nicobariensis, P. leucomystax*) were exclusively found in oil palm plantation streams and (less abundant) in logged forests. Only two species (*Phyrnoidis juxtaspera*, *Limnonectes kuhlii*) were found in every sampled stream, independent of habitat type.

Stream characteristics

Overall, stream width (ANOVA: $F_{2,19} = 0.4$, ns) and stream slope (ANOVA: $F_{2,19} = 0.3$, ns) did not differ between the three habitat types. Average stream width was 4.0 m and average slope was 6.4 m per 100 m stream segment. In contrast to the width and slope of the streams, canopy cover was significantly different between habitats (ANOVA: $F_{2,19} = 14.8$, $P < .001$), but was not highly correlated (< 0.7) with habitat type. Primary forest streams had the highest percentage of canopy cover and were more homogenous (81.6 % ± 7.9). Mean canopy cover in logged forest (68.7% ± 15.6) and oil palm plantation streams (32.9% ± 21.9) were considerably lower and more variable compared to primary forest streams.

Discussion

Our study on the impact of land conversion in Southeast Asia on frog species richness, density, and community composition has several important implications for anuran conservation and the design of oil palm plantations. Whereas primary forests, from various protected areas, and logged forests were mostly comparable in respect to their species richness and community composition, oil palm plantations did not provide suitable habitat for two thirds of the original forest species. However, we showed that high canopy cover, provided by riparian reserves, was able to mitigate this loss to some extent.

The value of secondary forest

Our results indicate that repeated logging has an impact on anurans in hilly Bornean rain forests. However, in terms of species richness and community composition we showed that logged forests are only subjected to a minor loss of the original species and a small shift in the community composition, which is rather based on altered abundances than on altered species occurrences.

This is in line with other studies, showing that light or selective logging does not have strong effects on tropical amphibian communities (*e.g.* Vallan *et al.* 2004, Fredericksen & Fredericksen 2004). However, the logged forest in our study has experienced at least two rounds of intensive logging, which has, in parts, resulted in heavily degraded landscapes. Hence, Bornean stream anuran assemblages seem to be partially resistant to logging, as long as riparian reserves are spared from harvesting. Nevertheless, in other tropical regions logging has also been shown to have a significantly negative effect on amphibian communities (*e.g.* Ernst *et al.*, 2006). Furthermore, stream amphibians are generally assumed to be highly sensitive to habitat modification (Konopik *et al.*, 2014b; Welsh and Ollivier, 1998) and physical as well as chemical stream properties should be highly affected by logging (Gomi *et al.*, 2006). In fact, long-term effects have not been the focus of this study and extinction debts (*e.g.* caused by further degradation or isolation of forest fragments) might lead to a significant meltdown of forest species in the long term (Kuussaari *et al.*, 2009).

Oil palm plantations

Gillespie *et al.* (2012) and Faruk *et al.* (2013) found no difference in overall species richness between forests (logged forests) and oil palm plantations in Peninsular Malaysia and Sabah (Borneo), respectively. However, both studies found a shift in anuran community composition between forested habitats and oil palm plantations. Our study provides further evidence for this major species turnover. Furthermore, we are able to confirm this effect for hilly areas with fast flowing, rocky streams, which are typical for central Borneo and other regions in Southeast Asia. However, in contrast to the previous studies we found considerably lower species richness in oil palm plantations compared to forested habitats (both primary and logged forest). Additionally, we expanded this comparison by including primary forests and showed that species richness in primary forests is slightly higher compared to logged rainforests.

We explain this differing result with a combination of three factors. First, we suggest that amphibian communities from flat and swampy habitats might have some kind of preadaptation to plantation habitat. Most likely, they utilise the numerous ditches, ponds and drainages in a typical tropical plantation landscape (*e.g. Limnonectes finchi* in Sabah).

Second, forests of lowland areas do not contain the same full complement of species as found in more hilly terrain (Gillespie *et al.*, 2012). In particular, the hilly lowland rainforest in Borneo is known to be a diversity hotspot for anurans (Grafe and Keller, 2009). Third, our study suggests that even logged forests with canopy cover comparable to pristine forests, have lower frog species richness, compared to primary forest.

Our study clearly highlights the importance of canopy cover for riparian amphibian communities. Oil palm plantation streams with high percentage of canopy cover had a significantly higher species richness, frog density and the community composition was closer to those from forested habitats. However, other habitat parameters such as water temperature or pesticide use are likely to be correlated with canopy cover and hence, have to be taken into consideration. Especially the use of agricultural chemicals is known to threaten amphibians worldwide (Mann *et al.*, 2009). Furthermore, the effect of terrestrial pesticide exposure on amphibians has recently been shown to be highly underestimated (Brühl *et al.*, 2013). Presumably, the use of agricultural chemicals in oil palm plantations is widespread. Potential pollutants include palm oil mill effluent, fertilisers, insecticides, rodenticides and herbicides (Fitzherbert *et al.*, 2008). How these factors influence frog communities in oil palm plantations remains to be studied.

However, we could also show that canopy cover plays an important role in logged forests and even primary rainforests. Therefore, in habitat types which should not be affected by agricultural chemicals. This supports the high importance of an intact or semi-natural canopy above logged forest and oil palm plantation streams. In fact, this suggests possibilities to improve oil palm plantation habitat by maintaining or even restoring riparian reserves. Especially against the background of high drainage densities of about 20 km/ km^2 in the region (Clarke and Walsh, 2006), riparian reserves could contribute significantly to enhancing biodiversity in oil palm plantations. However, according to our experience many streams in conventional oil palm plantations are effectively lacking adequate riparian reserves, although these practices are mostly integrated in local legislation (*e.g.* Sabah Water Resources Enactment 1998). Furthermore, appropriate riparian reserves could not just help protect frog species. They are also known to provide other ecologically important functions, such as connecting habitats (Tabarelli and Gascon, 2005) or reduce soil erosion (Gomi *et al.*, 2006). However, they cannot be seen as an alternative to large scale protected areas (Marczak *et al.*, 2010).

Conclusions

Our study outlines that Bornean stream-dependent anurans are highly impacted by the on-going large-scale land conversion in the region. However, we show that even repeatedly logged forests have high conservation value for Southeast Asian anurans. Furthermore, we conclude that the conversion to oil palm plantation dramatically reduces the original species richness. Thus, the conversion of large tracts of repeatedly logged forest into palm oil plantations will lead to a decline of anuran species richness. However, a solid implementation of riparian reserves along oil palm plantation streams together with large-scale protected areas could mitigate this species loss to a great extent

III. Logging and conversion to oil palm plantations alters trophic interactions and reduces multiple levels of anuran diversity

This chapter is submitted as: Konopik, O., Ahmad Sah, H., Keller, A., Wong, A., Grafe, T. U., Steffan-Dewenter, I. Logging and conversion to oil palm plantations alters trophic interactions and reduces multiple levels of anuran diversity. Submitted to *Ecology*

Running title: Trophic interactions and anuran biodiversity

Abstract

Global change is known to dramatically impact the diversity and composition of amphibians, particularly in the tropics. However, anthropogenically driven impacts on functional diversity and trophic interactions of amphibians are mainly unknown. Here, we analysed the shifts in trophic position, functional and phylogenetic diversity of Southeast Asian stream-dependent anuran species across a gradient of disturbance from primary forest through intensively logged forest to oil palm plantation. We determined the diet composition of 59 anuran species by means of stomach flushing. Furthermore, we use diet composition of frog species to calculate dietary diversity. The trophic position of the entire anuran community was elevated in heavily disturbed habitats. Furthermore, species phylogenetic, dietary, and functional diversity were reduced. However, beyond the effect of the decreased species richness, only phylogenetic species variability and functional diversity were significantly impacted by land conversion, indicating a non-random loss of phylogenetic groups and functionally unique species. Overall, the observed changes in species interactions and functional composition suggest a massively modified role of anurans in altered habitats and a major reorganisation of foodwebs. Such far-reaching changes to the way species groups interact are likely to threaten local biodiversity and ecosystem functioning in heavily disturbed natural and particularly in human-modified habitats. However, we could also show, that small-scale habitat quality, provided by riparian reserves, is able to mitigate the negative consequences of land conversion considerably.

Introduction

The negative impacts of land conversion and the consequent habitat loss on a wide range of species are increasingly well documented (Hoekstra *et al.*, 2004; Sala *et al.*, 2000). Understanding the anthropogenic impact on biotic communities is vital to answering questions about the ecological consequences of species extinctions and shifts community composition on trophic cascades and ecosystem functioning (Flynn *et al.*, 2011). Predation, competition, and mutualism influence the structure of animal and plant communities, and affect the stability and function of ecosystems (Ives and Cardinale, 2004; Petchey *et al.*, 2008). Species interactions play essential roles in both natural and human-dominated ecosystems, providing key services such as pollination (Klein *et al.*, 2007) and herbivore control (Bianchi *et al.*, 2006; Wielgoss *et al.*, 2014). 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 to complex species interactions, such as foodwebs to properly predict and manage human impact on ecosystems (Morris, 2010; Reiss *et al.*, 2009; Tylianakis *et al.*, 2010).

Trophic interactions are known to link spatially separated subsystems, such as aquatic and terrestrial habitats or aboveground and belowground systems (Kupfer *et al.*, 2006; Wardle *et al.*, 2004). Particularly predators play a key role in these foodwebs by having so-called “cascading effects” on lower trophic groups, such as herbivores or lower trophic mesopredators (Duffy *et al.*, 2007; Ritchie and Johnson, 2009). The impacts of these trophic cascades on ecosystems are far-reaching, yet the strength of these impacts differ among particular foodwebs and species communities (O’Gorman and Emmerson, 2009). Generally, removing (apex) predators from ecosystems, or adding them (e.g. Ripple and Beschta, 2012), can have far-reaching impacts on the composition of the remaining species assemblage and the overall appearance of ecosystems (Estes *et al.*, 2011). However, the impact of an altered (meso) predator community, such as amphibian communities, on foodwebs and trophic interactions is less clear. Only recently, first studies have shown that amphibian predation can have indirect effects on plant growth or inhibit dung removal (González-Bernal *et al.*, 2013; Wu *et al.*, 2014).

It has been proposed that the trophic position of organisms is mainly explained by phylogeny and adaptation (Cattin *et al.*, 2004). These main drivers of food web structure result in specific traits characterising species and species communities. Hence, traits based on trophic interactions, such as body size, activity pattern, and most notably feeding type, are often used to determine the functional diversity (FD) of animal communities (McGill *et al.*, 2006). Generally, FD can be seen as ‘the number, type and distribution of functions performed by organisms within an ecosystem or within a specific species group (Sandra and Cabido, 2001). FD is a crucial part of biodiversity, affecting available ecosystem function (Cadotte *et al.*, 2011; Griffin *et al.*, 2009; Hoehn *et al.*, 2008) and improving ecosystem stability, particularly in a changing world (Johnson *et al.*, 1996).

FD has widely been shown to decrease following anthropogenic disturbances, such as land use intensification (Flynn *et al.*, 2009), logging (Ernst *et al.*, 2006), or forest conversion to oil palm plantations (Edwards *et al.*, 2014). These processes are widespread in SE Asia, a highly threatened and globally important biodiversity hotspot (Myers *et al.*, 2000; Sodhi *et al.*, 2004).

Anurans are particularly vulnerable to the wide-spread land conversion pattern found in Southeast Asia (Faruk *et al.*, 2013; Gillespie *et al.*, 2012; Wanger *et al.*, 2010; chapter II). However, despite documented decreases in species richness and abundances, the shifts in anuran functional diversity in SE Asia is currently unknown. Moreover, globally the functional diversity of anuran communities has hardly been studied (but see Ernst *et al.*, 2006), or refers to larval anurans (Strauss *et al.*, 2010).

Typically, FD and species richness are closely correlated. Hence, FD of communities depends on the number of species present in the particular system. However, independent effects of land use intensification have been shown for some small mammal and bird communities (Flynn *et al.*, 2009).

In this study we investigate the changes to the anuran diversity and particularly the trophic ecology of anuran communities caused by the widespread conversion of rainforest into palm oil plantations in Borneo. Based on the quantity and composition of their diet, we (1) categorise anuran species from primary lowland tropical rainforest, logged forest, and oil palm plantations based on their diet; (2) identify the trophic position of the community and its response to logging and conversion to oil palm plantation.

Furthermore, we hypothesise that (3) phylogenetic diversity, dietary diversity and functional diversity of the anuran community decrease in logged forests and oil palm plantations, following the expected drop in species richness.

Methods

Study sites

The study was conducted in northern Borneo in the state of Sabah, Malaysia and the sultanate Brunei Darussalam between April 2011 and May 2013. Anurans were sampled along seven streams in primary lowland dipterocarp rainforest, eight streams in continuous logged forest and seven streams in oil palm plantations. Logged forest and oil palm plantation streams were sampled under the framework of the SAFE project (Stability of Altered Forest Ecosystems; Ewers *et al.*, 2011).

Primary forest sites were located within the Ulu Temburong National Park (UTNP, Brunei Darussalam, 55 000 ha), Danum Valley Conservation Area (DVCA, 43 800 ha), Maliau Basin Conservation Area (MBCA, 58 840 ha), and an isolated patch (2200 ha) of mainly unlogged forest (lightly logged along its edges), which is continuous with 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, with canopy cover ranging from 16% to 71% (Ewers *et al.*, 2011). The oil palm plantation sites and their catchments were isolated by 1 - 5 km from continuous forests. All plantation streams were managed by the same company (BentaWawasan 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 km² stream catchments. Furthermore, all sampled streams were independent first order streams.

Sampling anuran community and relative densities

To assess species richness and abundance of frogs we conducted six standardised visual and acoustic encounter surveys at intervals of at least one week per transect (chapter II). Surveys were performed using a line transect starting from the point where the respective catchment was 2.5 km^2 and leading 200 m upstream, following the stream. Transect walks were performed while walking in the streambed. Frogs were actively searched for by a single person using a headlamp (PetzlMyo RXP) between 1845 h and 2030 h for one hour. Visual and acoustic records were treated equally and summed up to get final numbers. Finally, the average number of individuals per stream was used as averaged relative abundance. However, these abundances (densities) should rather be treated as conservative estimates or relative densities. All frogs were identified in the field using morphological or acoustic characteristics (Inger and Stuebing, 2005). Sampling was planned to avoid dry seasons and extremely wet periods and was discontinued during periods of heavy flooding or extensive dry spells.

Phylogenetic relatedness

To compare the degree to which anurans in a stream community are phylogenetically related we calculated phylogenetic species variability (PSV), which is independent of the number of species occurring in the different communities (Helmus *et al.*, 2007). We used the amphibian phylogeny published in Pyron and Wiens (2011) to construct a subtree of the species occurring in our study. If a particular species was not present in the initial tree (about 1/3 of the species), we subsidised these species with congeneric species, where possible. However, since these substitutions were mainly at the genus level, they are likely to have a negligible effect on the main outcome.

Diet sampling and categorisation

Stomach contents were collected from randomly selected individuals at night between 18:45 h and 01:00 h by means of stomach flushing (Solé *et al.*, 2005). Stomach flushing is a gentle method to get dietary information, without harming anurans. Furthermore, we adhered to high ethical standards (Beaupre *et al.*, 2004) for handling the individuals to prevent handling-based injuries or overheating. Male and female individuals were sampled according to their abundance in the field, but were treated equally throughout the analysis. Amplecting individuals were spared from sampling.

Prey items were counted, analysed and identified as far as possible based on their condition, but at least to order level, using a dissection microscope. Generally, in holometabolic insects we distinguished between larval stage and imago to account for possible dietary and ecological shifts between these stages. Beetles were assigned to families where possible and ants were identified to subfamilies. Finally, the volume of the remains of each prey item was estimated by measuring length and width and applying volumetrical formulas of the respective general shape (e.g. sphere, ellipsoid body, cylinder).

All anuran species were clustered according to their dietary composition and grouped into feeding types. We applied "ward" clustering for displaying purposes and prey item categories were weighted after the square root of their overall volumetrical percentage. We used the diet composition of frogs, based on functional prey categories, and ecological traits to calculate the dietary diversity as well as the functional diversity, respectively. For functional diversity (FD) we collected trait data for all species in our study (Inger and Stuebing, 2005). Both indices were calculated using the tree-based method described in Petchey and Gaston (2007). Empty samples were excluded from the analysis for dietary diversity.

Data analysis

All prey items were grouped into functional categories and assigned to either predators (including parasites and parasitoids) or non-predators (mainly herbivores). In some cases of highly heterogeneous insect groups, such as beetles or ants, generalisations were necessary. For example, coleopterans were assigned to the respective groups based on the general feeding ecology of their respective family (Crowson, 1981). For coleopterans that could not be assigned to families due to progressed digestion, the same predator-ratio as for the family-identified coleopterans was used. Furthermore, ants were grouped based on their main carbon source (Andersen, 1995; Blüthgen *et al.*, 2003). For example, the subfamily Ponerinae was categorised as predator and the subfamily Formicinae was categorised as non-predator, based on their affiliation with honeydew-producing insects. Finally, parasitic groups that were likely gastric parasites of anurans, such as nematodes, were excluded from the analysis.

We used beta regression to test the effect of habitat type and canopy cover on the percentage of predatory prey consumed by the anuran communities per stream. We averaged all samples collected per stream and species to get mean diet compositions (including empty samples). Subsequently, these averaged diet compositions were weighted by each anuran species' density. Finally, the sum of these averaged and weighted diet compositions was used as the overall composition of the respective anuran community (per stream).

Species richness and diversity indices were analysed using linear models. To test for the effect of species richness on the diversity indices, species richness was also used as covariate in the respective models. Post-hoc tests (Tukey HSD) were used to identify significant ($p < 0.05$) differences between habitat types.

The statistical platform R (R Development Core Team, 2012) was used for calculations and to produce graphics. We used the R-packages “betareg” (Cribari-Neto and Zeileis, 2010) to perform beta-regression, “vegan” (Oksanen *et al.*, 2013) for calculations of functional indices, and “MuMIn” (Bartoń, 2014) for model selection and model averaging.

Results

We collected a total of 3532 diet samples of 59 anuran species, belonging to 29 genera and 7 families. 73 048 different prey items were identified in total including predatory prey, such as spiders, centipedes or lizards and non-predatory prey, such as caterpillars, true bugs or stick insects. Ants represented 70% of the total number of prey items solely. Overall mean sample size of stomach content samples per species was 59 ± 83 and varied between five for extremely rare species and 251 for the most common anuran species. For single streams sample size was ranging from 1 to 51 for each occurring frog species.

Based on the functional clustering, anuran species could be divided into two main categories comprising species specialised on social insects (ants and termites) and a second, more heterogeneous group. The latter can be further subdivided into species with a vertebrate-focused diet (mainly other anurans and lizards), a group of species with a generalist feeding pattern, and ant avoiders (Fig. III.1).

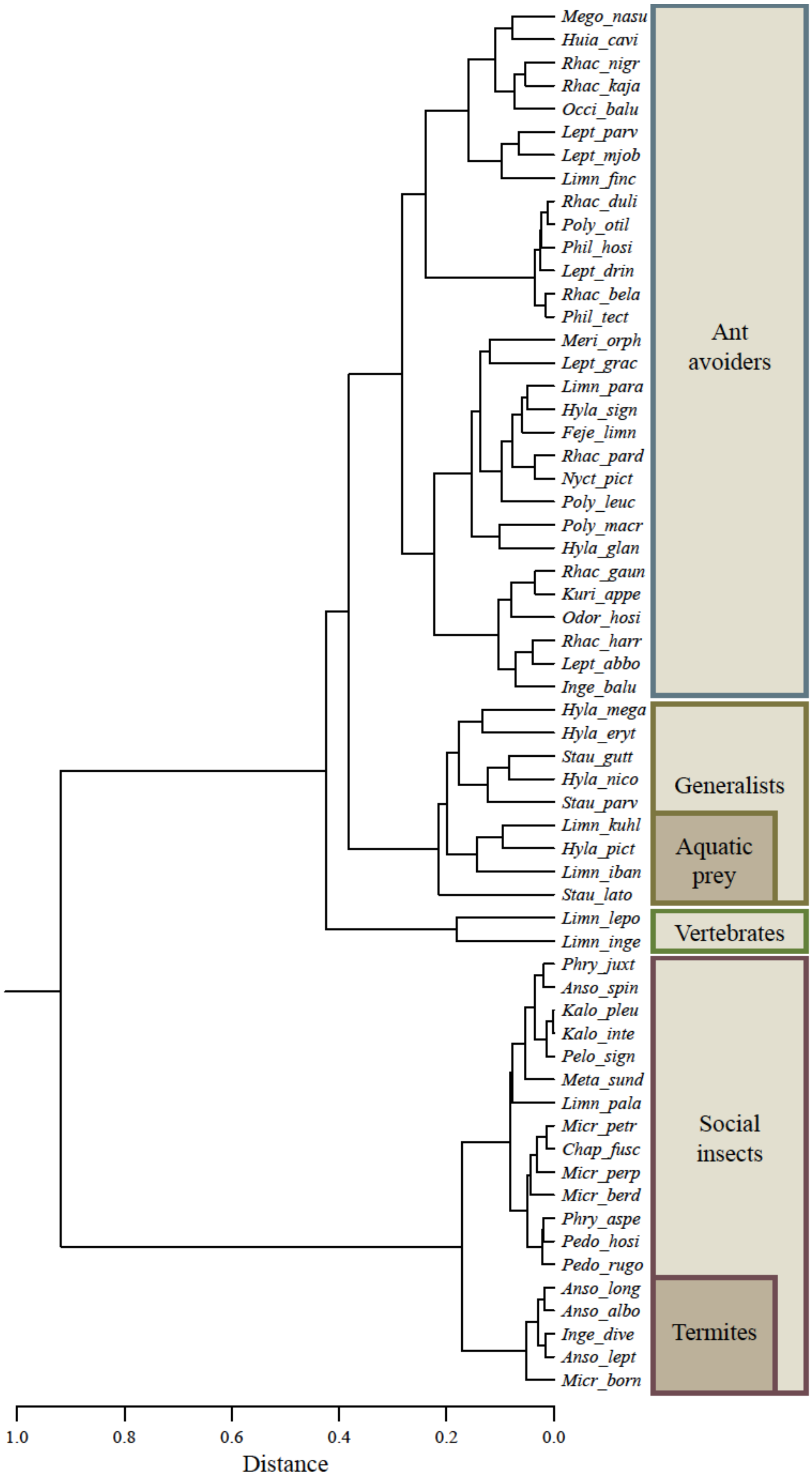

Figure III.1: Dietary clustering of 59 anuran species sampled in the study areas.

Effect of habitat change on the predator-non-predator ratio

Non-predatory prey was the main dietary component of the anuran community in primary forests, logged forests, and oil palm plantations. However, the volumetrical percentage of predatory prey significantly decreased with canopy cover (z-value= 9.628, p < 0.001; Fig. III.2). Yet, habitat type did not have a significant effect on predator percentage (z-value= 1.567, n.s.). Accordingly, the volumetrical percentage of non-predatory prey (100% - "percentage of predators") increased with the percentage of canopy cover, but was independent of habitat type (Tab. III.1).

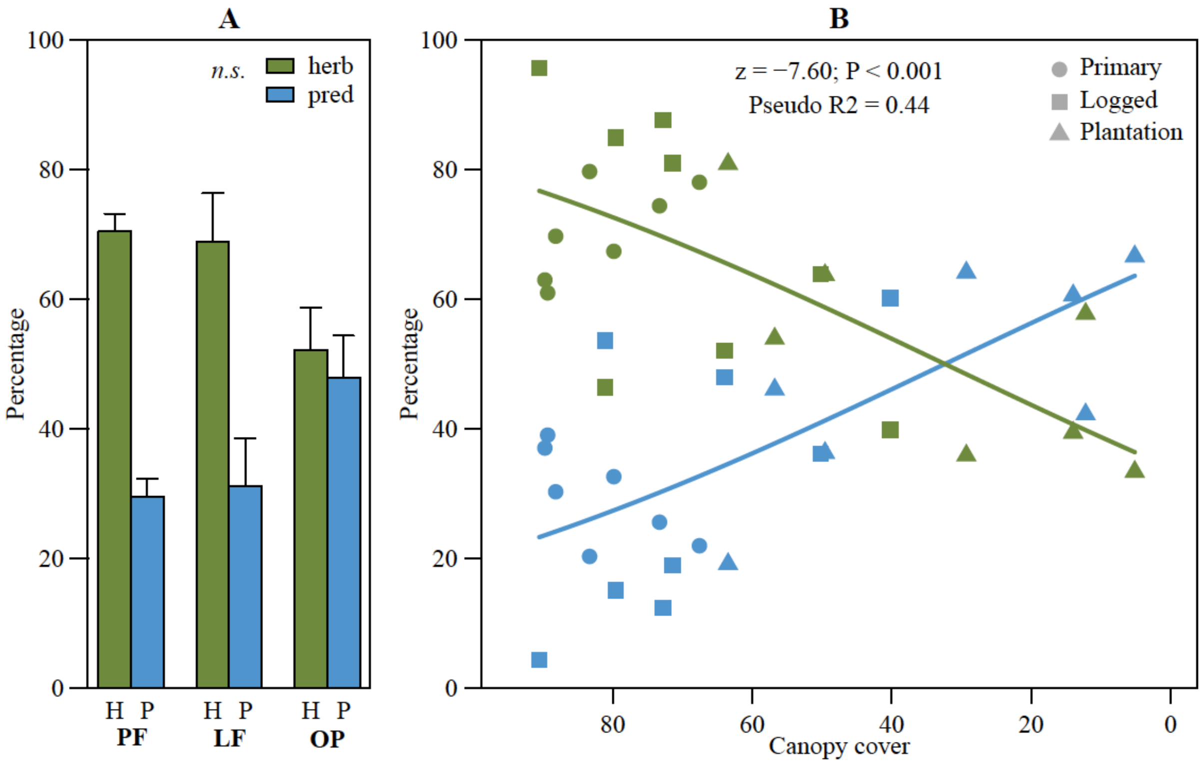

Figure III.2: The effect of logging and conversion to oil palm plantation (A) as well as the small-scale habitat quality (B) (provided by riparian reserves, shading the streams) on the percentages of predatory (blue) and non-predatory prey (green) of the anuran community.

Primary forest streams had the highest percentage of canopy cover (81.6% ± 7.9). It dropped to 68.7% (± 15.6) in logged forests and was lowest in oil palm plantation streams (32.9% ± 21.9). However, there was a wide variation in canopy cover within each habitat type.

Table III.1: Model-averaged coefficients of the remaining explanatory variables explaining the percentage of predators. (ΔAICc< 4)

	Estimate	SE	z-value	P value	RelVar Imp	N cont mod
Percentage of predators						
(Intercept)	0.63	0.13	4.87	< 0.001	-	-
Canopy cover	**-0.018**	**0.0019**	**9.63**	**< 0.001**	**1**	**2**
Habitat type	-0.089	0.057	1.57	0.12	0.43	1

Effect of habitat type and canopy cover on anuran diversity

Species richness, Shannon diversity, phylogenetic species variability, dietary diversity, and functional diversity were significantly higher in primary forests, compared to oil palm plantations (Fig. III.3, Tab. III.2). However, compared to logged forests, phylogenetic species variability as well as functional diversity of primary forests was not significantly higher. At the same time, logged forest had only significantly higher values for species richness and functional diversity compared to oil palm plantations.

Accordingly, all indices were significantly dropping with reduced canopy cover. However, only for phylogenetic species variability and functional diversity, this trend was independent of species richness.

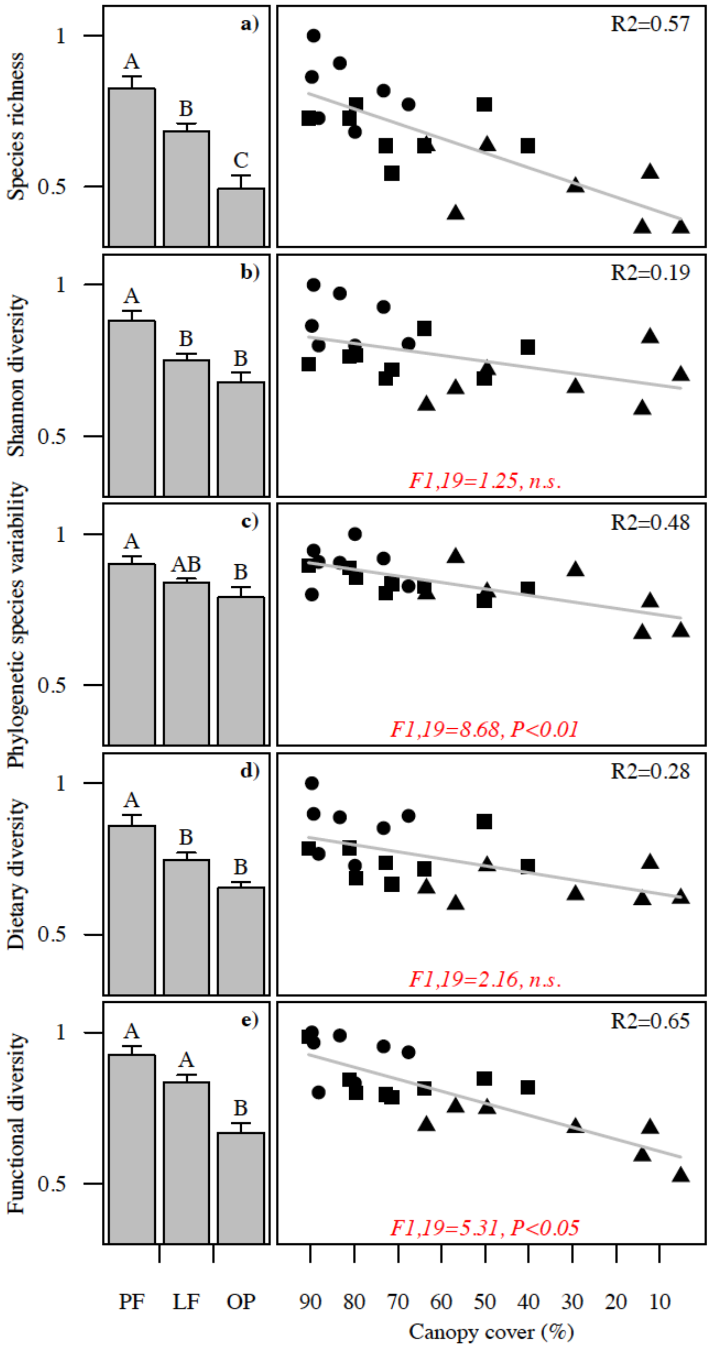

Figure III.3: Effect of forest conversion on multiple measurements of anuran diversity and functional diversity. Differences between primary rainforests (PF, circles), logged forests (LF, squares), and oil palm plantations (OP, triangles) are shown on the left. The right hand side displays the relative impact of the percentage of the remaining canopy cover above the sampled streams (as continuous measurement of habitat degradation) on the diversity. Species richness (a), Shannon diversity (b), phylogenetic species variability (c), dietary diversity (d), and functional diversity (e) are declining with habitat degradation. However, if species richness is included in the models, only phylogenetic species variability and functional diversity remain significantly declining with habitat degradation (red). See Tab. III.2 for statistics.

Discussion

This is the first study testing the effects of logging and the conversion to oil palm plantations on different components of diversity and trophic interactions of anuran communities in parallel. We show that forest conversion leads not only to a loss of species richness but also to a significant reduction in phylogenetic and functional diversity. The diet of anuran communities changed from a dominance of herbivorous prey in forests streams with high canopy cover to an increased preference of predatory prey in low canopy cover streams indicating strong shifts in food web interactions with consequences far beyond the loss of species richness of this globally endangered group of amphibians.

Especially with respect to the high abundance of anurans in tropical SE Asia (chapter II.), the changes to the trophic ecology of the studied anuran community is likely to have cascading effects on arthropod mesopredators, and ultimately herbivores in the studied semi-natural and agricultural systems.

Systematic studies on the feeding ecology of anurans are rare and typically focus on single species or subsets of communities (e.g. Toft, 1981). So far, the knowledge on the feeding ecology of SE Asian anurans was mostly based on anecdotal observations (e.g. Dehling, 2009) and a few ecological studies involving diet (Inger and Greenberg, 1966; Inger, 2009).

We studied the diet of an entire anuran community systematically and identified six distinct feeding guilds. The vertebrate feeding guild and the aquatic feeding guild contained only few species. However, the other guilds were represented by many more species. Taxonomic clustering was evident, but not strong. For instance, all studied bufonids and microhylids were represented in a group specialised on social insects. The only representative of another anuran family in this feeding guild was the dicroglossid *L. palavanensis*. Myrmecophagy is known from several bufonids and microhylids (Mebs *et al.*, 2010; Toft, 1980), but has so far only rudimentarily been shown for true frogs (Hirai and Matsui, 2000). Furthermore, *L. palavanensis* is characterised not only by a divergent feeding pattern, but also by a regionally exceptional behaviour of male parental care (Inger and Voris, 1986). The cluster of anurans with a vertebrate focused diet was represented by two species only (*L. ingeri*, *L. leporinus*). This is in accordance with other studies showing that large representatives of the genus Limnonectes are able to feed an large-bodied prey, such as vertebrates (Dehling, 2009; McLeod, 2009). The remaining species were more or less ordered in the clusters of ant avoiders and generalist species, with *Staurois latopalmatus* and few other species being remarkable exceptions in being specialised on aquatic prey. Aquatic prey is common for purely aquatic anurans, such as pipid frogs (Carreño and Nishikawa, 2010). However, it is unusual for terrestrial and semi-aquatic frogs to prey on aquatic organisms (Duellman and Trueb, 1994), but has occasionally been documented (Hirschfeld and Rödel, 2011). Most likely and with care, our classification of feeding guilds could be extrapolated to other frog species occurring on Borneo and SE Asia, analogous to feeding guilds in the Neotropics (Toft, 1980). However, the region is also home to anuran species with unusual habitats and traits, such as the lungless frogs (*Barbourula* spp.), crab-eating frog (*Fejervarya cancrivora*), or fossorial species (e.g. *Gastrophrynoides* spp.). The composition of their diet is likely to differ greatly and is certainly a promising goal for future research.

Changes to functional composition and amount of anuran prey

The detailed study of the anuran diets along a disturbance gradient provides the possibility to analyse the trophic response of the entire anuran community. The increased percentage of predatory prey and vice-versa decreased percentage of non-predatory prey (most notably herbivores) in highly modified habitats, indicates a massive shift in the trophic position of the anuran community. From a first order predator, mainly feeding on herbivores, in primary forests and logged forests with high canopy cover, anuran communities became higher order predators in highly disturbed, low canopy cover habitats, such as oil palm plantations. The reasons for this shift could be based on the habitat change directly or the local extinction of other relevant predators, such as the pangolin (Pantel and Chin, 2008). So far, changes in the trophic position of anuran communities caused by land conversion have not been documented, and few studies have been published on other terrestrial organisms, such as tropical birds (D. P. Edwards *et al.*, 2013) or ants (Woodcock *et al.*, 2013) indicating altered trophic position with increasing habitat disturbance. Yet, the loss of trophic interactions or changes by introduced species is known to affect ecosystem services (Dobson *et al.*, 2006) and biodiversity (Ritchie and Johnson, 2009). Accordingly, the changes we found are likely to interact with other key mesopredator groups, such as ants or spiders, which contribute a considerably larger part of the anurans' diet in heavily disturbed habitats. In particular, by shifting the dietary focus of the anurans to these mesopredators, this inverted preference is likely to further release herbivores from predation pressure. However, both invertebrate abundance and anuran abundance has been shown to be reduced in oil palm plantations (chapter II.; Turner and Foster, 2008), so ultimately predictions can only be made tentatively and require the study of both predator and prey abundances simultaneously (Konopik *et al.*, 2014a). The trophic interaction between apex predators, several levels of mesopredators, and ultimately herbivores is broadly known to be crucial for ecosystem regulation and stability (Estes *et al.*, 2011; Martin *et al.*, 2013; O'Gorman and Emmerson, 2009; Ritchie and Johnson, 2009). However, particularly the response of the hyper-diverse tropical species communities to altered trophic interactions is complex and hard to predict (Lewis, 2009).

So far the impact of adult anurans on trophic interactions and related ecosystem functions such as herbivore regulation and primary productivity have mainly been ignored. However, recently it could be shown that anurans have an indirect effect on plant growth via the predation of detritivores (Wu *et al.*, 2014) and invasive cane toads have been shown to inhibit dung removal by preying on dung beetles in Australia (González-Bernal *et al.*, 2013). These single species approaches highlight the importance and potential far-reaching effects of our findings. However, the actual consequences of these complex cascading effects on the local ecosystems can only be analysed by large-scale exclusion experiments (e.g. Klimes *et al.*, 2011). Such exclusion experiments will be essential to ultimately understand the impact of the presented shift in the trophic role of an entire anuran community on plant-herbivore-antagonist interactions in natural and human-altered ecosystems.

Loss of multiple layers of anuran diversity following land conversion

Species richness in logged forests and oil palm plantations declined following the loss of canopy cover (chapter II.). Beyond species richness we showed that multiple layers of anuran diversity are reduced with land conversion and the degree of disturbance. This highlights the enormous loss of biodiversity beyond species richness. Whereas all of these different layers of diversity should be justifiably viewed on its own, some are closely connected to the initial loss of anuran species. If species richness was considered as covariate, Shannon diversity and dietary diversity were no longer significantly reduced with the degree of disturbance. In contrast, canopy cover has an independent positive effect on phylogenetic species variability, which is by its nature already independent of species richness (Helmus *et al.*, 2007), as well as functional diversity. The first indicates that species in heavily disturbed habitats are more likely to be related to each other. This can be traced back to the absence of some genera (e.g. *Staurois*) and entire families (Ceratobatrachidae, Microhylidae) and vice-versa the dominance of the true frogs (Dicroglossidae, Ranidae) in Bornean oil palm plantations. Especially the loss of microhylids has also been reported in other studies from the region (Gillespie *et al.*, 2012), whereas disturbance resistant microhylid lineages exist in peninsular Malaysia (Faruk *et al.*, 2013) or on Sumatra (pers. obs.).

Dietary diversity was highest in primary forests, where all major dietary groups where present in all studied streams. Dietary diversity in logged forests and in oil palm plantations was comparable. However, representatives of all main feeding types were present in both forests and oil palm plantations, with the exception of vertebrate predators, which were lacking in most oil palm streams. Additionally, *P. juxtaspera*, a species that has been shown to prey on more than 200 ant species (Konopik *et al.*, 2014a), was mostly the only remaining ant specialist in oil palm streams. The assessment of the dietary diversity of entire anuran communities is a novel approach, and hence, lacks comparison.

The loss of FD in oil palm plantations follows the anuran species richness decline with land conversion (chapter II), and the altered community composition (Faruk *et al.*, 2013). However, beyond amphibians, functional diversity has been shown to be greatly reduced in oil palm plantations for other taxa, such as dung beetles (Edwards *et al.*, 2014), ants (Luke *et al.*, 2014) or birds (F. A. Edwards *et al.*, 2013). By following the same pattern, anurans join this list of ecologically important animal groups with greatly reduced functional diversity in oil palm plantations.

Additionally, we were able to disentangle the effect of species richness and habitat conversion on functional diversity. An independent effect of habitat degradation was so far mostly known from bird and mammal communities (Flynn *et al.*, 2009). Beyond the effect of species richness, functional diversity was driven by habitat quality (canopy cover) and ultimately by land conversion. This indicates, that anuran species sensitive to logging and land conversion are more likely to have unique functional traits and hence, ecological function. This implicates, that by increasing canopy cover (via riparian reserves) in oil palm plantations streams, not only forest frog species richness can be increased (chapter II), but also the functional diversity.

Conclusions

We showed that multiple layers of anuran biodiversity are heavily impacted by a wide-spread and important land conversion pattern. Logging and subsequent conversion of degraded forest to oil palm plantation alters the trophic position and reduces the diversity of anuran communities. However, the positive effect of (small-scale) habitat quality, such as canopy cover associated with riparian reserves, mitigates these negative consequences to some extent. By enhancing anuran diversity and their trophic interactions, riparian reserves showed potential in interacting with natural pest control in oil palm plantations. This suggests that management efforts should focus on maintenance and restoration of high quality riparian forests in human-modified tropical habitats. Conservation of anuran biodiversity and the maintenance of their trophic interactions require the protection of the remaining forests in Southeast Asia and urgent actions to improve habitat quality in existing oil palm plantations.

Table III.2: ANOVAs and linear models describing the impact of habitat type (primary forest, logged forest, oil palm plantation) and the degree of habitat degradation (canopy cover) on species richness, Shannon diversity, phylogenetic species variability, dietary diversity, and functional diversity of Bornean anurans. Red: Models with species richness as covariate.

	Habitat type (ANOVA)		Canopy cover (linear model)			
	F	P	Estimate	SE	t	P
Species richness						
Canopy cover	18.2	< 0.001	0.0049	0.00091	5.37	< 0.001
Shannon diversity						
Canopy cover	13.4	< 0.001	0.0020	0.00081	2.44	< 0.05
Phylogenetic species variability						
Canopy cover	4.4	< 0.05	0.0021	0.00048	4.49	< 0.001
Dietary diversity						
Canopy cover	14.5	< 0.001	0.0023	0.00076	3.05	< 0.01
Functional diversity						
Canopy cover	21.3	< 0.001	0.0040	0.00062	6.35	< 0.001
Shannon diversity						
Species richness	30.3	< 0.001	0.0280	0.0067	4.22	< 0.001
Canopy cover	2.2	n.s.	-0.0010	0.0009	-1.12	n.s.
Phylogenetic species variability						
Species richness	7.4	< 0.05	-0.0010	0.0056	-0.19	n.s.
Canopy cover	0.8	n.s.	0.0023	0.0008	2.96	< 0.01
Dietary diversity						
Species richness	60.6	< 0.001	0.0312	0.0050	6.25	< 0.001
Canopy cover	1	n.s.	-0.0010	0.0007	-1.15	n.s.
Functional diversity						
Species richness	74.9	< 0.001	0.0212	0.0053	3.98	< 0.001
Canopy cover	2.3	n.s.	0.0017	0.0007	2.30	< 0.05

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

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Running title: Species level interactions

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 rain forest 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.

Keywords

Southeast Asia; riparian reserves; invasive species; deforestation; amphibia

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 (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; Millennium Ecosystem Assessment 2005). 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 foodwebs (Tylianakis *et al.*, 2007), alters the trophic position and narrows the niche breadth of bird communities (D. P. 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 frogs is currently unknown. However, ants are an important part of the diet of some tropical anuran communities (e.g. Inger, 2009; Konopik *et al.*, 2014b; Toft, 1980). Here we assess the variation in the interaction between a common anuran predator, the giant river toad (*Phrynoidis 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?

Figure IV.1: *Phrynoidis juxtaspera* is the larges anuran species on Borneo. Females can grow up to 215 mm snout-vent length. It occurs throughout the lowlands, both in primary rainforests and various disturbed habitats including oil palm plantations.

Materials and Methods

<u>*Study sites*</u>

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 (*Phrynoidis 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, with canopy cover ranging from 16% to 71% (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).

Effects of habitat change on relative toad abundance

P. juxtaspera (Fig. IV.1, page 59) 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>120mm are females). It is a widespread, ground-dwelling species, which can frequently be found along the 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.

Effects of habitat change on ant communities

Sampling of the ground-foraging ant fauna was conducted 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 hours. 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± 96.7) m. The mean time between stomach content collection and the collection of the pitfall traps was 15 (range± 14) days.

Ant identification

Ants from frog 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 frog 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.

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 reserves 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 sloped were measured at intervals of 10 m and averaged to give a single value for each transect.

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 pitfalls traps and toads’ 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 Jacob'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 frogs' 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).

Results

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. IV.2) and also in narrower streams (Tab. IV.1). Stream slope had no significant influence on the average number of recorded individuals of *P. juxtaspera*.

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.

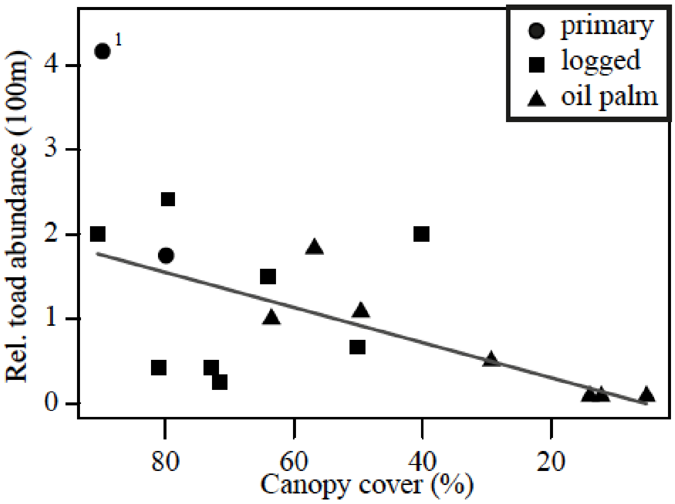

Figure IV.2: Impact of canopy cover above the streams on the relative abundance of the giant river toad (*Phrynoidis juxtaspera*). Abundance was significantly reduced with the degree of habitat disturbance (z-value = 3.84; P < 0.001). The primary forest stream sampled at Maliau Basin Conservation area (1) was excluded from this analysis.

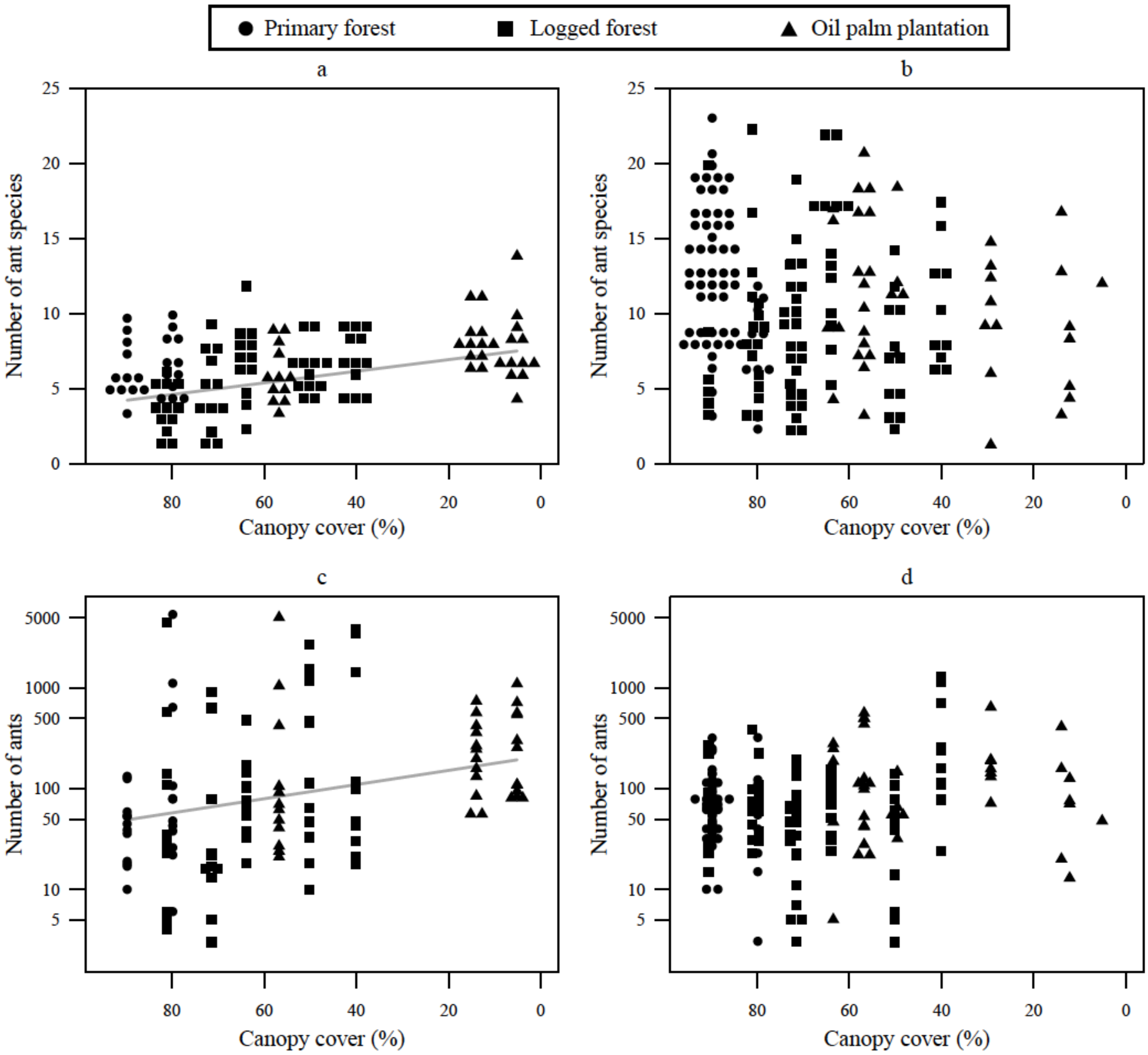

Figure IV.3: Impact of the degree of disturbance (canopy cover) on the number of ant species (a,b) and the number of individuals (c,d) of samples derived from baited pitfall traps (left) and stomach content samples from *Phrynoidis juxtaspera* (right).

The number of ant species per trap increased slightly with decreasing canopy cover (Tab. IV.1). Whilst we did not include habitat in the models due to collinearity with canopy cover, there was a trend for more ant species in primary 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. IV.3a). The total number of individuals per trap also increased significantly with decreasing canopy cover (Fig. IV.3c).

Table IV.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

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 86.9mm (±34). There was no significant size difference between toads sampled in primary forests, logged forest, and oil palm plantations (ANOVA: $F_{2,186}$=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 frogs’ stomachs varied only with the size of the toad (see Tab. IV.1 for statistics, Fig. IV.3b). There was no significant relationship between the number of individuals recovered from the toads’ stomachs and any explanatory variable (Fig. IV.3d).

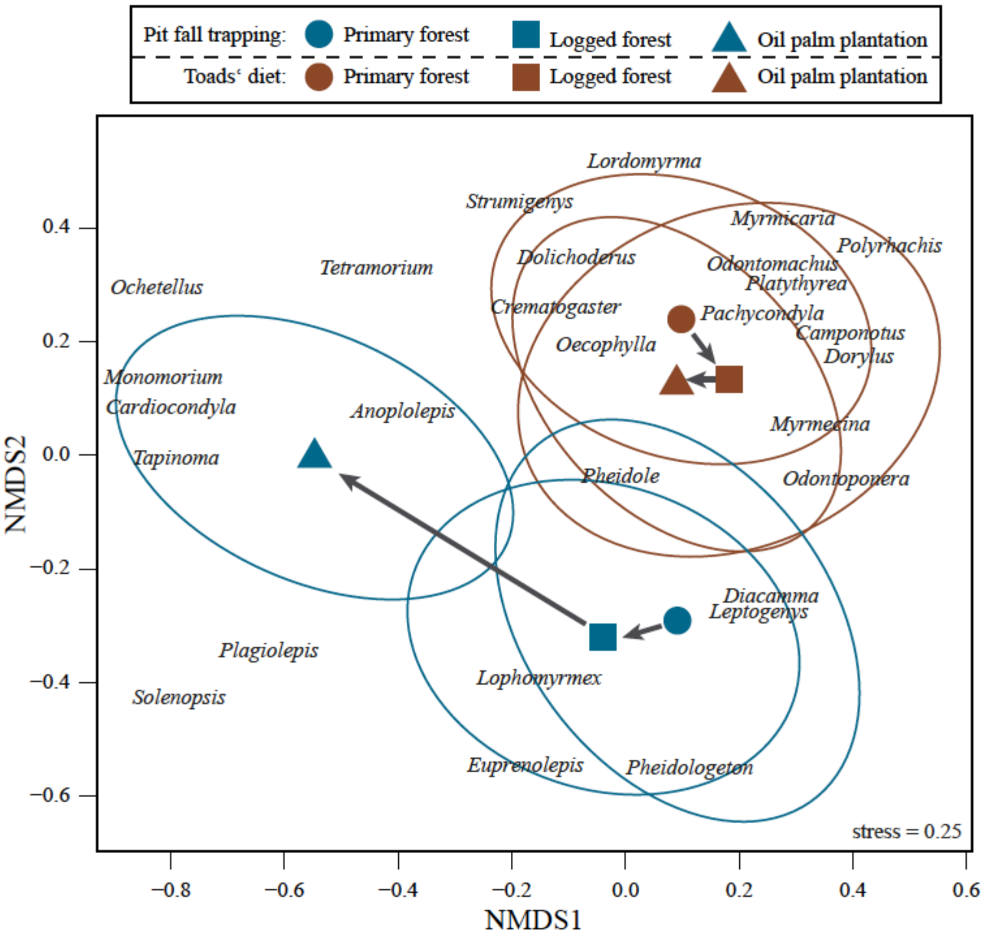

Figure IV.4: Non-metric multidimensional scaling showing difference on genera composition. Displayed are the centroids of the pitfall data (blue) and the data derived from the stomach contents of the ant-specialist toad *Phrynoidis juxtaspera* (red). Ellipses around the centroids indicate standard deviation 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.

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 (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. IV.4). 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. IV.5). 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 *Anoplolepis 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.

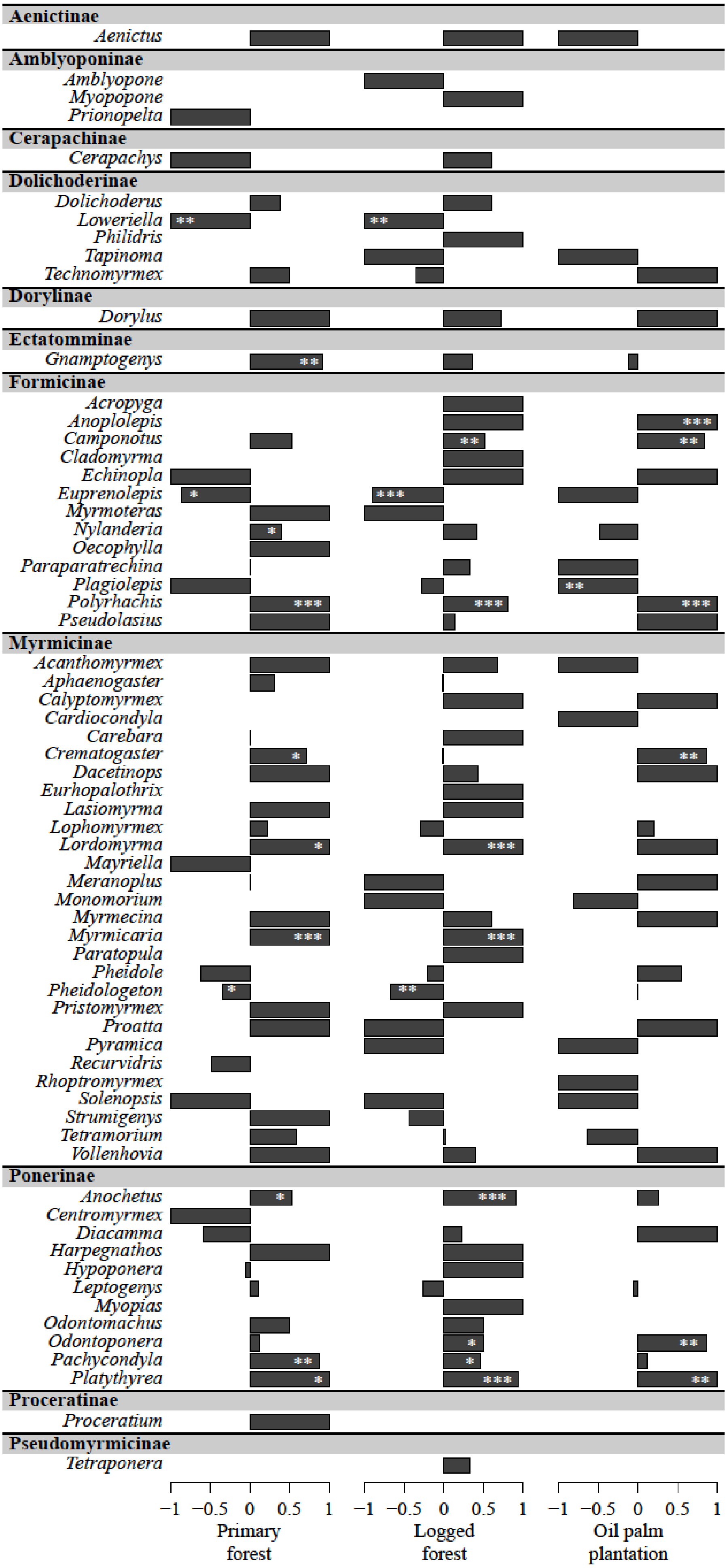

Figure IV.5: Electivity of *Phrynoidis juxtaspera* for different ant genera per habitat type in relation to the ground-foraging ant fauna. Values of +1 indicate a preference for this genus and values of -1 indicate a complete absence of this genus from the toad's diet.

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 frog *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 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.*, 2014b).

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 amongst 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 (*Anoplolepis 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.

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.

Table IV.A1: Output of the PerMANOVA testing the effect of the distance between traps and the stream on the genera composition and species composition

	df	F-Model	R2	P-Value
Genus level				
Habitat type	2	14.51	0.19	< 0.001
Stream	7	2.47	0.11	< 0.001
Distance	1	1.28	0.01	0.28
Residuals	109			
Species level				
Habitat type	2	10.75	0.15	< 0.001
Stream	7	2.43	0.11	< 0.001
Distance	1	1.54	0.01	0.07
Residuals	109			

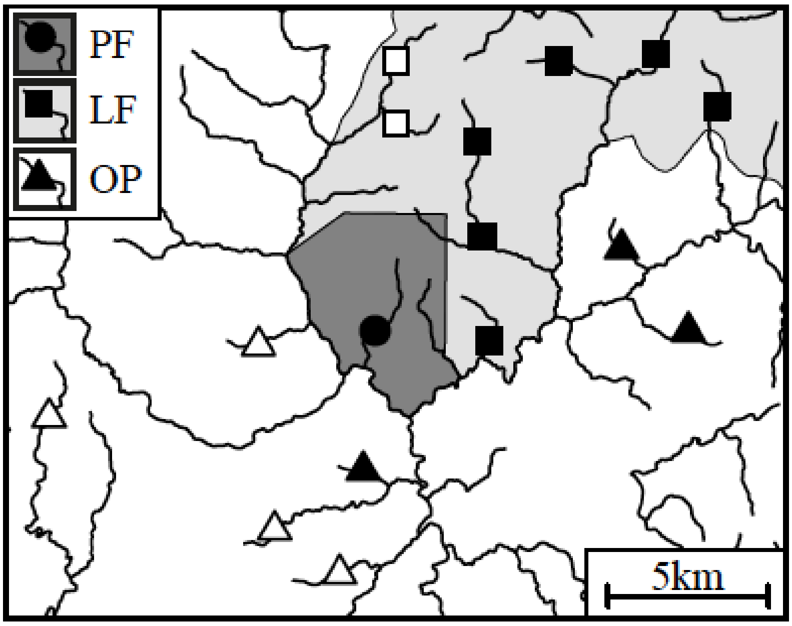

Figure IV.B1: Map of the study area. White symbols represent streams where only toads have been sampled and black symbols show streams with both toad and ant data. Symbols represent primary forest streams (PF), logged forest streams (LF), and oil palm plantation streams (OP). The primary forest stream from Maliau basin (both toad and ant data) is not shown, as it is 50 km to the east of the other sites.

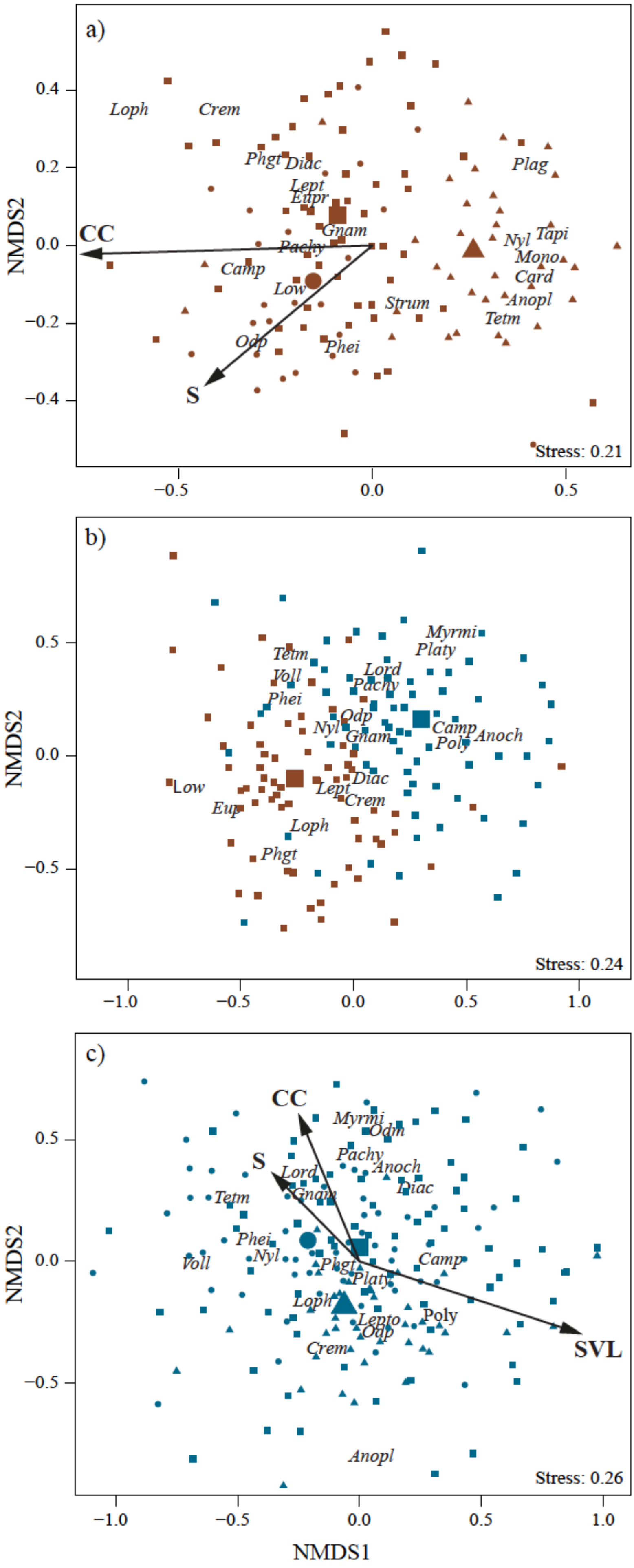

Figure IV.B2: Non metric multidimensional scaling of ant community composition obtained from (a) pitfall traps from primary forest, logged forest and oil palm plantations and (b) pitfall traps together with toad stomach content ant communities from logged forest. In addition, the ant communities derived from stomach content samples over the habitat gradient is shown (c); each time the 20 most abundant ant genera are displayed.

CC: canopy cover; S: slope of stream; SVL: length of toads. circles: primary forest, squares: logged forest; rectangles: oil palm; large symbols represent the respective centroid of the point cloud. Red from pitfall traps, blue from toad stomach content samples

V. General discussion

In my PhD-thesis, I was investigating the response of different aspects of anuran diversity and their trophic interactions to logging of lowland rainforest and subsequent conversion to oil palm plantations. First, I was looking at the response of species richness, abundance, and community composition of anurans (chapter II). I found a significant decline of anuran species and a major shift of the community composition towards wide-spread disturbance-tolerant frog species following land conversion. Forest frog species were found to be particularly vulnerable to habitat change. Second, following this decline in species richness, phylogenetic diversity, dietary diversity, and functional diversity were also negatively impacted by disturbance (chapter III). Yet, phylogenetic diversity and functional diversity was reduced by the degree of disturbance beyond the effect of species richness. Furthermore, by investigating the dietary composition of over 50 anuran species along the habitat gradient I was able to provide detailed ecological information for the studied species and to show that the trophic position of the anuran community is heavily altered by land conversion. Third, a detailed prey analysis of an ant-specialised toad revealed a certain robustness of trophic interactions on species level to land conversion (chapter IV). However, these interactions were crucially depending on the conservation of riparian reserves.

The value of logged forest

I could show that (repeated) logging has various impacts on Bornean anuran diversity and their trophic interactions. However, species richness, dietary diversity and community composition were only subjected to a minor loss of the original forest species and a minor loss in dietary diversity as well as a small shift in the community composition, which is rather based on altered abundances than on altered species occurrences. Furthermore, phylogenetic species variability and functionally diversity, albeit lower in logged forest, were statistically not different from primary forests.

My results line up with other studies, showing that light or selective logging does not have significant effects on tropical amphibian diversity (*e.g.* Vallan *et al.* 2004, Fredericksen & Fredericksen 2004). However, the logged forest in the SAFE project area has experienced at least two rounds of intensive logging (Ewers *et al.*, 2011), which has, in parts, resulted in heavily degraded landscapes. Hence, Bornean anuran diversity and their trophic ecology seem to be partially insensitive to logging, as long as riparian reserves are spared from harvesting. In particular, canopy cover above the streams significantly improved anuran diversity and their trophic interactions in logged forests. Nevertheless, in other tropical regions logging has also been shown to have a significantly negative effect on amphibian communities and functional diversity (*e.g.* Ernst *et al.*, 2006). Furthermore, stream amphibians are generally assumed to be highly sensitive to habitat modification (Konopik *et al.*, 2014b; Welsh and Ollivier, 1998) and physical as well as chemical stream properties should be highly affected by logging (Gomi *et al.*, 2006). In fact, long-term effects have not been the focus of this study and extinction debts (Kuussaari *et al.*, 2009), which could be caused by further degradation or isolation of forest fragments, and long-term cascading effects in the trophic ecology (Estes *et al.*, 2011; Ripple and Beschta, 2012) might lead to a significant meltdown of anuran diversity in the long term.

Anuran diversity and trophic interactions in oil palm plantations

In contrast to the rather mild effect of logging, the conversion of oil palm plantations has dramatic effects on multiple levels of anuran diversity and their trophic ecology. In fact oil palm plantations have been named the “greatest immediate threat to biodiversity in Southeast Asia” (Wilcove and Koh, 2010) and many studies demonstrate their negative effect on species richness (Brühl and Eltz, 2009; Fayle *et al.*, 2010) and functional diversity (Edwards *et al.*, 2014; F. A. Edwards *et al.*, 2013; Luke *et al.*, 2014; Senior *et al.*, 2013) of local ecosystems. Hence, my results that anuran diversity and functional diversity are greatly reduced in oil palm plantations match these studies.

However, until now anuran diversity was thought to be comparable in oil palm plantations and forests, albeit with a different composition of species. In particular, Gillespie *et al.* (2012) and Faruk *et al.* (2013) found no difference in overall species richness between forests (logged forests) and oil palm plantations in Peninsular Malaysia and Sabah (Borneo), respectively. However, both studies found a shift in anuran community composition between forested habitats and oil palm plantations. My study provides further evidence for this major species turnover. However, in contrast to the previous studies (Faruk *et al.*, 2013; Gillespie *et al.*, 2012) I found considerably lower species richness in oil palm plantations compared to forested habitats (both primary and logged forest). Furthermore, my study is the first study comparing anuran diversity between oil palm plantations and (true) primary forests.

Hence, I explain this differing result by a combination of three factors. First, I suggest that amphibian communities from flat and swampy habitats (habitats where other studies have focused on) might have some kind of preadaptation to plantation environment. Most likely, they utilise the numerous ditches, ponds and drainages in a typical tropical plantation landscape (*e.g. Limnonectes finchi* in Sabah). Second, forests of lowland areas do not contain the same full complement of species as found in more hilly terrain (Gillespie *et al.*, 2012). In particular, the hilly lowland rainforest in Borneo is known to be a diversity hotspot for anurans (Grafe and Keller, 2009). Third, my study suggests that even good secondary or logged forests have lower frog species richness, compared to pristine forest.

Riparian reserves mitigate the negative effects of land conversion substantially

All parts of this study showed that the presence and quality of riparian reserves (Fig. V.1, page 79) along the studied streams had a positive effect on all levels of anuran diversity and interactions. Riparian reserves are forest strips on both sides of the streams. They are a legal requirement in Malaysia and have to cover 30 m on both sides of the stream. However, many streams in the existing oil palm plantations in fact lack riparian reserves. Moreover, existing riparian reserves hardly reach the legal requirements and continuous logging of trees within the reserves significantly reduces canopy cover above the streams.

Riparian reserves are typically established to reduce run-off into the streams and hence, aquatic organisms usually benefit greatly (Mayer *et al.*, 2007; Sweeney *et al.*, 2004). Furthermore, beyond aquatic organisms, riparian reserves are also known to support terrestrial forest species (Marczak *et al.*, 2010) and ecosystem services, such as dung removal (Gray *et al.*, 2014). Rodríguez-Mendoza and Pineda (2010) found that riparian reserves improve the habitat quality for frogs in Mexico. My results expand these findings into Southeast Asia and show for the first time that riparian reserves also support a high phylogenetic, dietary and functional diversity of anurans as well as their trophic interactions. The (only partially enforced) protection and legal requirement together with their linear and hence, connecting character make riparian reserves an important tool for protection of biodiversity in agricultural landscapes. They contribute to the urgent need (Foster *et al.*, 2011) to improve biodiversity and ecosystem functions in oil palm landscapes. However, the required size of the reserves and their enforcement, remain critical open questions and objectives for the future. They demand more research (which has already been initiated by the SAFE project) and a policy change by decision makers. Hence, my results suggest that (1) riparian reserves should be maintained in a mostly undisturbed condition, providing sufficient canopy cover for the streams and (2) in plantations which lack riparian reserves, these need to be restored to improve anuran diversity and enable crucial ecosystem services.

Chances and perspectives for future research

The outcome of my research answered several urgent questions concerning the resilience of anuran diversity and trophic interactions to the regionally important land conversion pattern. However, the consequences of the reduction of anuran diversity, dietary diversity, functional diversity and the shifting trophic position on the local ecosystems remain theoretical. Ideally, large-scale exclusion experiments of anurans should be used to determine their impact on local ecosystems and how this shifts with habitat degradation. Some studies have already shown that anurans can have indirect effects on plant growth or interact with other ecosystem services, such as dung removal (González-Bernal *et al.*, 2013; Wu *et al.*, 2014).

Furthermore, the conservation value of logged forests needs long-term verification and the extent (width and length) as well as the isolation of riparian reserves requires more research to ensure their ecological functionality. The SAFE project (Ewers *et al.*, 2011) is under way to answer these questions and the data gathered during my study should be used as a base line for further research.

Conclusions

Southeast Asia and Borneo in particular is home to a great diversity of frog species, both in terms of species richness and functional diversity. Furthermore, Bornean anuran communities comprise various feeding types, including ant-specialised or vertebrate-specialised species. This diversity is highest in undisturbed primary forests. However, logging of these forests leads only to a minor loss of anuran diversity and hence logged forests have a great potential for the conservation of the regional anuran diversity. Particularly in the light of the small areas of remaining and protected primary forests, logged forests are essential for anuran conservation in large parts of Southeast Asia. In contrast, the conversion of forests to oil palm plantations leads to a dramatic loss of anuran diversity and trophic position. However, species-level interactions can be resilient to this disturbance. Additionally, high quality riparian reserves are able to mitigate the negative effects of oil palm plantations considerably. Hence, riparian reserves must be spared from logging and should be reinstalled in plantations where they have previously been removed.

Figure V.1: Riparian reserve alongside a stream within an oil palm plantation (Merbau estate, Benta Wawasan Sdn Bhd, near SAFE project).

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