

**Land-use change, tropical biodiversity, and ecosystem services –
Southeast Asian amphibians and reptiles in focus**

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Born 31st May 1981 in Marburg a.d. Lahn, Germany

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Australia

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Doctor of Philosophy

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To my parents.

“The fire had been violent, and now only smouldering black stumps remained. The aspect of the land was desolate. The great trees had toppled down, tearing up the soil and making deep pits. All the landscape was soiled with ash and soot. Smouldering trunks lay everywhere.”

Madelon H. Lulofs – *Rubber*. 1931

“Sometimes all it takes is a tiny shift of perspective to see something familiar in a totally new light”

Dan Brown – *The Lost Symbol*. 2009

Table of Content

Table of content	I
Summary	II
Originality statement	IV
Acknowledgements	V
Introduction. <i>Conserving Southeast Asian forest biodiversity and their services provided in human-modified landscapes</i>	1
Chapter 1. <i>Land-use change affects community composition of tropical amphibians and reptiles in Sulawesi (Indonesia)</i>	11
Chapter 2. <i>Conservation value of cacao agroforestry for amphibians and reptiles in Southeast Asia: combining correlative models with follow-up field experiments</i>	32
Chapter 3. <i>Amphibians and reptiles of the Lore Lindu National Park area, Sulawesi (Indonesia)</i>	61
Chapter 4. <i>Endemic predators, invasive prey, and native biodiversity; biocontrol by an endemic toad</i>	80
Chapter 5. <i>Pesticides and tropical biodiversity</i>	100
Conclusions	105
Appendix	107
Bibliography	134
List of publications as listed in this thesis	153
Complete list of publications including all resulting from this PhD work	154

Summary

In the tropics, global food demand and population growth have already led to conversion of more than 50 % of formerly forested areas into agricultural landscapes. Across all tropical regions, Southeast Asia suffers from the highest deforestation rates, where land-use change is mainly driven by rapid expansion of biofuel and cash crops such as cacao. The ecological effects of agricultural expansion on biodiversity and ecosystem services are little known, in particular, in chronically understudied areas like Sulawesi (Indonesia), the third largest cacao producer globally. Moreover, certain taxonomic groups such as amphibians and reptiles remain particularly poorly studied, yet are the most threatened vertebrate groups on the planet. My thesis targets the impact of land-use change on Southeast Asian amphibian and reptile diversity as well as their ecosystem services provided.

After an introduction to the research context, the first chapter shows how land use change from pristine forest to open areas impacts amphibians and reptiles. I use Bayesian modelling to examine environmental predictors of diversity patterns to then derive the first assessment of how amphibians and reptiles are affected by cacao farming in Sulawesi. In the second chapter, I assess the conservation value of cacao agroforest based on a two-step approach: (i) multi model inference is used to identify environmental predictors of herpetological diversity patterns in cacao agroforests; then (ii) a large scale experimental approach is used to test whether these predictors can realistically be implemented on a large scale by local farmers. In the third chapter, I compiled, for the first time, an extant species list, to make best use of the information on amphibians and reptiles in the region. I discuss how such species lists can be used by National Park authorities and local researchers to facilitate ecotourism and research activities. In the fourth chapter I show how endemic toads can control highly invasive “yellow crazy ants” and the likely implications this interaction may have for cacao yield. In the final chapter, I argue that pesticide use is a major driver of tropical biodiversity loss that currently has not received the attention it deserves.

In conclusion, this thesis revealed that there is still much to be learned about the impact of land-use change on amphibians and reptiles in Southeast Asia, their conservation, and the ecosystem services they can provide. Future research efforts need to incorporate pesticide impacts on amphibians and reptiles, to give realistic management recommendations for sustainable agricultural landscapes. In addition, the monetary value of herpetological ecosystem services must be identified in these secondary habitats. Only then, local small-scale farmers may be supportive of biodiversity conservation.

Originality statement

This work contains no material which has been accepted for the award of any other degree or diploma in any university or other tertiary institution to Thomas Cherico Wanger and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text.

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Date: 10/12/2010

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T.C. Wanger

Introduction

**CONSERVING SOUTHEAST ASIAN FOREST BIODIVERSITY IN HUMAN-
DOMINATED LANDSCAPES**

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Introduction - Conserving Southeast Asian forest biodiversity and their services provided in human-modified landscapes

Tropical biodiversity has been suffering substantially from habitat loss (Dirzo & Raven 2003), with the highest deforestation rates in Southeast Asia across all tropical regions (Sodhi *et al.* 2004; Sodhi & Brook 2006; Sodhi *et al.* 2010a). While – if unabated – this may result in massive extinctions (Brook *et al.* 2003; Cardillo *et al.* 2006; Lee & Jetz 2008), most of the region's residual biodiversity will be confronted with living in human-modified habitats such as agricultural areas (Ziegler *et al.* 2009). In fact, human population density correlates with deforestation and species endangerment in Southeast Asia (Sodhi *et al.* 2010a). Therefore, in addition to protecting relatively undisturbed forests, conservation biologists have to also develop strategies to make human-dominated areas more hospitable for forest biodiversity (Gardner *et al.* 2009; Koh & Gardner 2010; Peres *et al.* 2010). However, our current knowledge of how to facilitate biodiversity and ecosystem service conservation in these habitats differs vastly between taxonomic groups. In the following overview, I will look at the impact of agricultural intensification on invertebrates, birds, mammals, amphibians, and reptiles.

Agricultural intensification and animal biodiversity

Invertebrates comprise a dominant component of tropical diversity in terms of richness, abundance and biomass (Dunn 2005) and perform many important ecological functions (e.g. pollination). Due to their short generation times and rapid growth rates they are likely to respond quickly to habitat changes (Sodhi *et al.* 2009b). The response of invertebrates to forest disturbance is well studied for lepidopterans and seems to be dependent on the spatial scale considered (increasing richness and diversity at smaller spatial scale while the contrary is true for larger spatial scales; Spitzer *et al.* 1997; Hamer & Hill 2000; Vu 2009). Traits that

predict sensitivity are known but they differ between groups (Holloway *et al.* 1992). For less-studied groups, the responses are heterogeneous and generalizations seem difficult. In dung beetle assemblages, for example, selective logging had little effect on the diversity or community composition even six years after logging (Holloway *et al.* 1992). However, diversity was lower in logged compared to primary forest (Davis *et al.* 2001). Stingless bees were not affected within logged forest (Eltz *et al.* 2002; Samejima *et al.* 2004). In oil palm plantations, ants, bees, and moths had higher species richness compared to primary forest (Danielsen *et al.* 2009). However these data were not corrected for sampling effort and may likely reflect higher rates of species accumulation within oil palm. Other studies suggest that for example butterfly richness is reduced in oil palm plantations (Koh & Wilcove 2008). Across a land-use intensification gradient in Sulawesi, from rainforest to different agroforestry types, species richness of bees, wasps and their parasitoids peaked at intermediate levels of canopy cover, whereas canopy beetles and ants showed no significant correlation with canopy cover (Steffan-Dewenter *et al.* 2007; Clough *et al.* 2010).

Birds are the best studied taxonomic group in Southeast Asia with the highest estimate of long-term loss of forest species due to deforestation (Castelletta *et al.* 2000). A total of 274 forest bird species are confined to the lowlands of the Sundaic region (excluding Palawan), out of which 109 are adversely affected by forest disturbance (Lambert & Collar 2002). While disturbed forests support higher species richness of birds than undisturbed forests, this is likely due to common forest edge species (Johns 1996). Endemic forest species, understory insectivores, terrestrial insectivores, large canopy frugivores and/or bark foragers, are disproportionately affected by forest disturbance (Lambert 1992; Posa & Sodhi 2006; Cleary *et al.* 2007). Depending on the considered communities, birds tend to recover several decades after disturbance (Yap *et al.* 2007). Agricultural habitats are often lower in species richness and communities are very dissimilar to forests (Peh *et al.* 2005; Sodhi *et al.* 2005b; Aratrakorn *et al.* 2006). Few studies have been conducted to determine the effects of forest

disturbance on montane birds, but available data shows that their richness and density declines in human-dominated areas such as tree plantations and urban areas (Soh *et al.* 2006).

Mammals are generally more sensitive to forest disturbance than invertebrates and birds (Sodhi *et al.* 2009a). Agricultural practises, in particular those that involve burning of habitat needed for crop farming, and associated fragmentation of once-contiguous landscapes, have led to the substantial decline of large mammals in Southeast Asia (Kinnaird & O'Brien 1998). This has, for example, caused a reduction of 84% and 70% in Sumatran elephant and tiger populations in Riau, respectively (Uryu *et al.* 2008). In Indonesia, the encroachment and unregulated expansion of agroforestry plantations into National Parks are considered major threats to mammals (e.g. rhinos, tigers, elephants and orang-utans); this is through poaching and illegal logging activities, but also disruption of movement patterns around forest edges (Kinnaird *et al.* 2003; Wich *et al.* 2008). In agricultural landscapes, mammalian richness was found to be lower compared to pristine habitats (Laidlaw 2000; Fitzherbert *et al.* 2008).

Compared to other vertebrate taxa in Southeast Asia and work conducted in the Neotropics and Africa, few studies have addressed the impacts of human-dominated landscapes on the herpetofauna of Southeast Asia (Fig. I). These studies report declines in amphibian species richness, as habitat disturbance — or fragmentation (Alcala *et al.* 2004) — increases, while reptile species richness remains similar or increases (Inger & Colwell 1977; Gillespie *et al.* 2005; Wanger *et al.* 2009; for contrasting results see Alcala *et al.* 2004; Bowman *et al.* 1990; Inger 1980). Species composition was distinctly different in pristine habitats but similar between disturbed habitats (Inger & Colwell 1977; Gillespie *et al.* 2005). Habitats studied include secondary forests, rubber and cacao plantations, traditional gardens, rice fields and open areas, but rapidly expanding oil palm plantations have received no attention in herpetological studies. As in the Neotropics (e.g., Whitfield *et al.* 2007; Luja *et al.* 2008), species responses are mostly attributed to changes in leaf-litter thickness and temperature through reduced canopy cover (Inger 1980; Alcala *et al.* 2004; Wanger *et al.*

2009; Wanger *et al.* 2010a). Overall, resilience of forest herpetofauna to habitat disturbance seems to be lower in amphibians than reptiles and depends on sufficient pristine habitat remaining in the area (Gillespie *et al.* 2005; Wanger *et al.* 2009; Wanger *et al.* 2010a). Improving the conservation value of disturbed habitats for herpetological diversity appears to be scale dependent; for amphibians and reptiles, modifications at the plantation level and landscape level, respectively, have been suggested (Gillespie *et al.* 2005; Wanger *et al.* 2009; Wanger *et al.* 2010a).

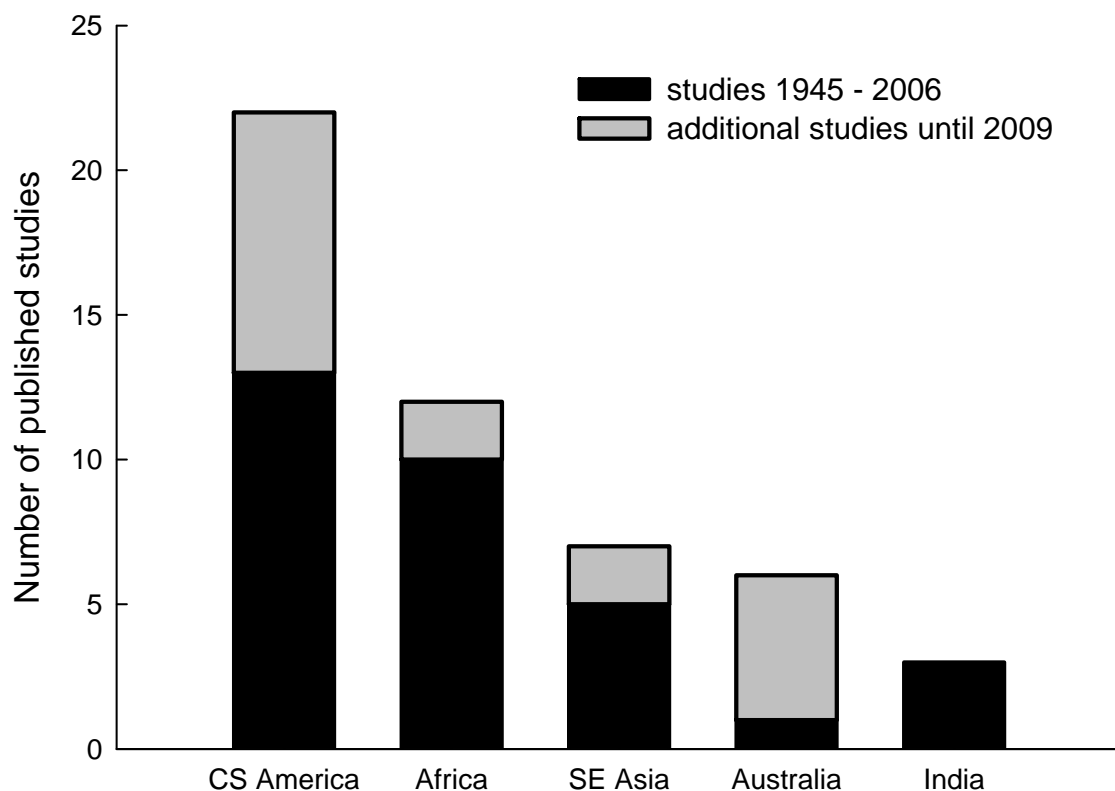


Figure I – Number of published studies on the impact of land-use change on amphibians and reptiles between 1945 and 2006/2009. I used the same search string in the ISI Web of Science as a comprehensive review on the topic in 2006 (Gardner *et al.* 2007) to make results comparable. I combined studies from Madagascar with Africa and those from the Philippines with Southeast Asia (*SE Asia*). *CS America* = Central and South America.

Habitat disturbance and ecosystem-functioning losses

Conservation strategies should aim to protect not only rainforests and biodiversity but also ecosystem services, i.e., the benefits people obtain from ecosystems (MEA 2005). Managing ecosystem services in human-dominated landscapes poses a major challenge because, rather than being independent, they interact (e.g., optimizing reforestation will reduce food production; Rodriguez *et al.* 2006). To ensure the maintenance of these multiple services, a landscape perspective is required (Chazdon *et al.* 2009). Agricultural land use is often focused on few species and local processes, but in dynamic, human-dominated landscapes, species diversity will substantially enhance resilience (i.e. the capacity to re-organize after disturbance). Hence, biodiversity and associated ecosystem services can be maintained only in complex landscapes with near-natural habitat supporting a minimum number of species dispersing across natural and managed systems (Tscharntke *et al.* 2005). This is exemplified by one of the best known ecosystem service, pollination, provided by bees. In Indonesian agroforestry systems, high levels of pollination and yield in coffee and pumpkin depend on a high diversity of bee species (Klein *et al.* 2003a; Hoehn *et al.* 2008), which is only available in heterogeneous environments including nearby forests providing natural bee habitats (Liw *et al.* 2001).

In a land use change context, we know little about the factors affecting amphibians and reptiles in particular in Southeast Asia. Even less is known about the services that these taxa provide. However, realistic management recommendations for sustainable agricultural landscapes require a good and general knowledge of the effects of land-use changes on biodiversity. Besides other factors, the effects of pesticide use on biodiversity are poorly known but must urgently be evaluated. I, therefore, conducted my research in Central Sulawesi (Indonesia), an equatorial island region of importance both for its exceptionally high endemism and because it is the second largest cacao producer globally. This combination implies an urgent need to understand land-use change impacts on Sulawesi's little studied

native fauna. In the following chapters, I will first focus on the response of amphibians and reptiles to different aspects of land-use change. Since very little is known about the herpetofauna of Sulawesi, I also review the literature and combine these findings with my own field research to the first species list of Central Sulawesi. This work clearly demarcates the region as a herpetological endemism hotspot. I then look into amphibians and reptiles as ecological service providers in Sulawesi's cacao plantations. Finally, I discuss the importance of pesticides for tropical biodiversity conservation in general.

T.C. Wanger

Chapter 1

**EFFECTS OF LAND USE CHANGE ON COMMUNITY COMPOSITION OF
TROPICAL AMPHIBIANS AND REPTILES IN SULAWESI, INDONESIA**

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Chapter 1 - Land-use change affects community composition of tropical amphibians and reptiles in Sulawesi (Indonesia)

Abstract

Little is known about the effects of anthropogenic land-use change on the amphibians and reptiles of the biodiverse tropical forests of Southeast Asia. I studied a land-use modification gradient stretching from primary forest, secondary forest, natural-shade cacao agroforest, planted-shade cacao agroforest to open areas, in central Sulawesi (Indonesia). I determined species richness and abundance, turnover, and community composition in all habitat types, and related these to environmental correlates, such as canopy heterogeneity and leaf litter thickness. Amphibian species richness decreased systematically along the land-use modification gradient, but reptile richness and abundance peaked in natural-shade cacao agroforests. Species richness and abundance patterns across the disturbance gradient were best explained by canopy cover and leaf litter thickness in amphibians, and canopy heterogeneity and cover in reptiles. I found amphibians to be more severely affected by forest disturbance in Sulawesi than reptiles. Heterogeneous canopy cover and thick leaf litter should be maintained in cacao plantations to facilitate their conservation value for both groups. For long-term and sustainable use of plantations, pruned shade trees should be permanently kept to allow rejuvenation of cacao and, thus, to prevent repeated forest encroachment.

Introduction

Increasing deforestation rates and subsequent land-use change in the tropics will force the surviving tropical biodiversity to reside in human-dominated landscapes such as agricultural areas (Bawa *et al.* 2004; Foley *et al.* 2005). The conservation value of agricultural habitats can be assessed by first comparing diversity-patterns across land-use modification gradients (i.e. open to pristine habitats) (e.g., Barlow *et al.* 2007) and then examining the factors driving diversity patterns within agricultural habitats (e.g., Clough *et al.* 2009b). Most scientific studies are, however, regionally and taxonomically restricted, with Southeast Asian amphibians and reptiles being the most poorly studied (Gardner *et al.* 2007; Sodhi *et al.* 2010a). Among the most threatened vertebrate taxa globally (30 % and 31 % of all evaluated species until 2008; IUCN 2009), tropical amphibians and reptiles are highly sensitive to habitat modifications and climate change (Sodhi *et al.* 2008; Wake & Vredenburg 2008; Huey *et al.* 2009; IUCN 2009). This makes mitigating the effects of land-use change on herpetological diversity in Southeast Asia a high conservation priority.

For better preservation of biodiversity in modified habitats, it is crucial to understand the environmental drivers of species responses to land-use changes (Koh 2008). Although most studies on amphibians and reptiles in Southeast Asia have found canopy cover and leaf litter thickness to be the most important drivers (e.g., Inger & Colwell 1977; Wanger *et al.* 2009), canopy cover may not be the most appropriate parameter to measure. For example, lizards thermoregulate by basking in open areas and, hence, several open patches in the canopy may sustain higher abundances than just one large open patch. Specific canopy heterogeneity (i.e., many small open patches vs. one large open patch in the canopy) may, thus, be a better predictor for species richness and abundance patterns in lizards. Contrastingly, a crude measure of canopy cover may be sufficient for amphibians as tropical frogs generally avoid direct sun exposure.

Here I determine the patterns in amphibian and reptile species richness, abundance, and community composition across a land-use modification gradient in Sulawesi. Bayesian model selection was used to identify the best environmental predictors for amphibian and reptile species richness and abundance, including the lacunarity index as a measure for canopy heterogeneity. Based on my results, I provide recommendations for conserving amphibians and reptiles in cacao plantations.

Material and Methods

Study region

I conducted this study in Central Sulawesi (Indonesia; Fig. 1.1), with an annual average (\pm SD) temperature of 24.0 (\pm 0.16) °C, a monthly average rainfall of 143.7 (\pm 22.74) mm, and no pronounced climatic seasons (equatorial wet tropics). The study area was located around the village of Toro, Kulawi valley (1°30'24" S, 120°2'11" E) surrounded by Lore Lindu National Park (231,000 ha pristine forest), old (> 10 years) cacao plantations of different farming intensity, and open areas for cattle grazing. Hence, this locality comprised a habitat gradient with increasing disturbance and a sufficiently large control area.

Plot characteristics and environmental variables

I sampled 31 plots (40 × 40 m) in five habitat categories: primary forest (6 plots), secondary forest (7), natural-shade cacao agroforest (with forest trees) (7), planted-shade cacao agroforest (with planted trees) (6), and open areas (5). Unbalanced replicates resulted from difficulties with some locations (e.g., a church was built on one of the open area plots). All habitat categories were classified based on canopy cover and heterogeneity, annual pesticide use, leaf litter cover and thickness, number of logs, shrub volume, and the number of trees in the plots (Tab. 1.1). Here I refer to secondary forest as degraded primary forest, where large trees had been cut in the past and for example rattan, and fire wood was extracted. In complex

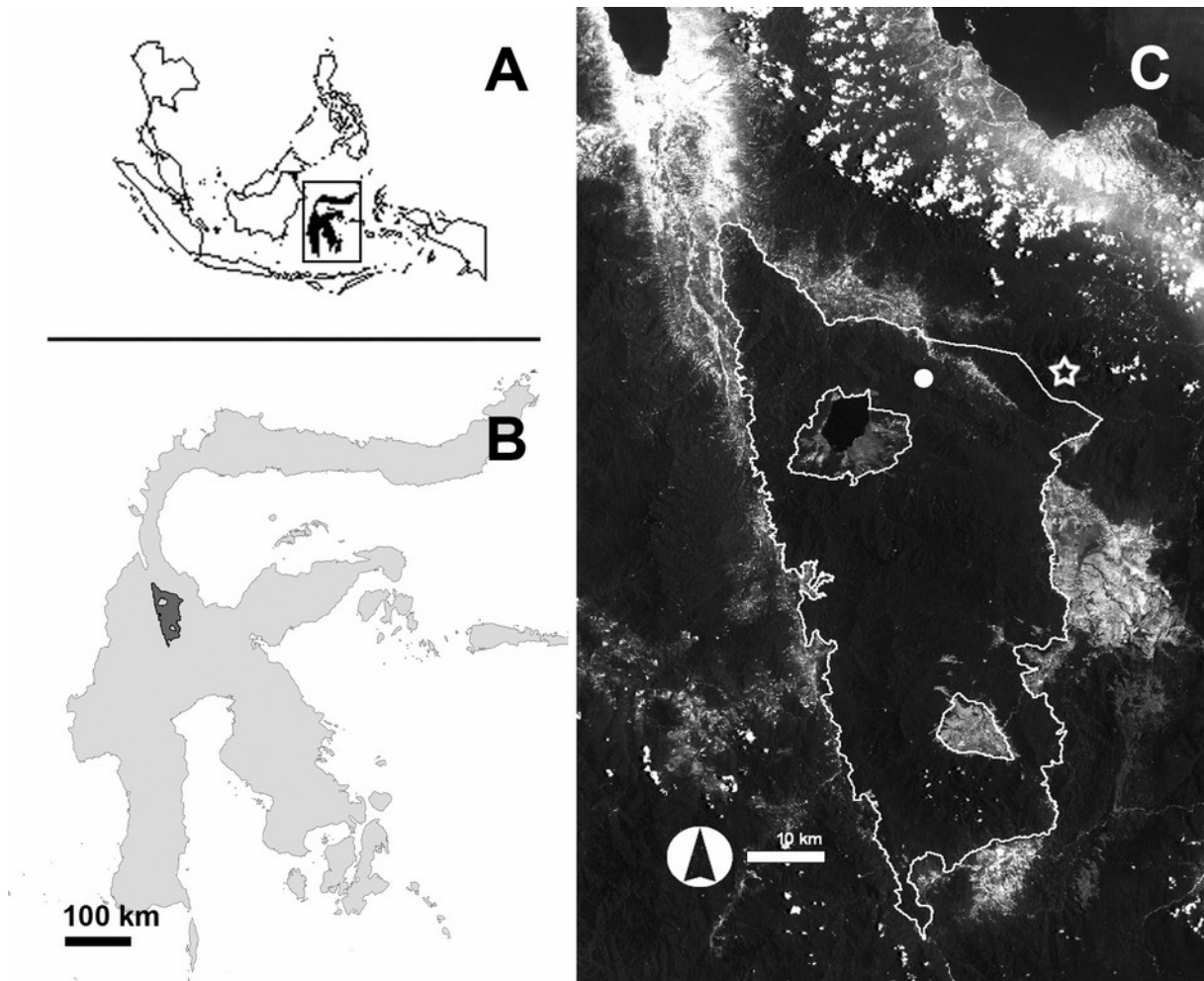


Figure 1.1 – Location of the study area around the Lore Lindu National Park on three different scales (in Southeast Asia (A); Sulawesi (B), and Central Sulawesi (C)). The map shows the mountainous terrain of Central Sulawesi with the two highest peaks, both inside (Mount Nokilalaki, 2357 m; white dot) and outside the LLNP (Mount Rore Katimbu 2610 m; star). Maps are oriented northwards.

natural-shade cacao agroforest, shade was provided by rainforest trees, with higher canopy cover than in simple planted-shade cacao agroforest. In the latter, shade trees were mostly planted legume or fruit trees (e.g., *Gliricidia* sp. and *Musa* sp.). In Sulawesi cacao trees are not only planted as undergrowth within near-primary forests, but also into secondary forest, coffee agroforests, clove plantations or annual cultures. Open area plots were an unshaded mosaic of grass and bare soil. All plots of one habitat type were surrounded by similar habitat

Table 1.1 – Habitat characteristics of all sampled habitats. Variables are as described in the text; *Shrub Volume* = shrub density * shrub height; *Number of trees* = number of trees in a plot with a diameter at breast height \geq 50 cm. Values are means (SD) per habitat. *NS-cacao agroforest* = natural shaded cacao agroforest; *PS-cacao agroforest* = planted-shaded cacao agroforest

	Canopy Cover [%]	Annual pesticide use [ml/plot]	Leaf litter cover [%]	Leaf litter thickness [cm]	Number of logs	Shrub Volume	Number of trees	Canopy heterogeneity
<i>Primary forest</i>	94.93 (1.17)	0 (0.00)	72.5 (27.59)	2.13 (0.97)	6.17 (2.71)	408.67 (228.01)	11.50 (5.99)	2.49 (0.27)
<i>Secondary forest</i>	87.01 (2.20)	21.43 (56.69)	70.29 (20.87)	2.40 (0.73)	9.43 (3.78)	370.57 (252.29)	9.00 (4.00)	2.72 (0.46)
<i>NS-cacao agroforest</i>	77.83 (4.41)	81.43 (103.51)	37.29 (19.54)	1.65 (0.94)	6.29 (4.68)	289.51 (217.74)	3.85 (3.52)	3.14 (0.26)
<i>PS-cacao agroforest</i>	65.95 (3.79)	145.00 (136.05)	29.00 (25.16)	1.02 (0.57)	6.67 (5.05)	240.93 (240.28)	2.67 (2.62)	2.63 (0.52)
<i>Open areas</i>	0.00 (0.00)	384.00 (411.01)	0.00 (0.00)	0.00 (0.00)	3.20 (1.64)	61.04 (24.91)	0.00 (0.00)	1.17 (0.00)

(e.g., rainforest plots were located within a large area of pristine forest) and had a minimum distance of 1 km to the next plot to increase statistical independence.

To characterize each plot, I measured the distance to the forest (zero for primary forest plots) and water body, canopy cover and heterogeneity, leaf litter cover and thickness, and understorey shrub characteristics (height, density, and cover). Apart from the two distance measures, I measured all variables in all four corners and the middle of the plots and used the mean of each parameter from all five locations. In addition, I counted the number of stone blocks (stones with diameter ≥ 50 cm) and log piles (dead tree trunks and branch piles of ≥ 15 branches with a diameter of ≥ 3 cm) on the plots. I also interviewed plot owners about pesticide use, because these chemical compounds have been increasingly used over the last 10 years in the study region (for details on the sampling habitat variables and pesticide surveys see Appendix 1).

Sampling protocol

I sampled all 31 plots six times between December 2007 and July 2008 [186 sampling sessions covering the general rainy and dry season in Sulawesi (Whitten *et al.* 2002)], three times during day and night between 0600 and 1800 h, and 1800 and 0600 h, respectively. Randomized sampling time of each plot and habitat category avoided repeated sampling of the same plot at the same time. Replicated samples of each plot allowed me to use average values in the analyses. I used both diagonals of the plots as a single transect (113 m length, 3 m width on each side; i.e., 43.4 % of the total plot area) that was sampled in a time-constrained manner (~ 25 minutes in one plot), and leaf litter, logs, branch piles, and stones inspected for amphibians and reptiles. I photographed, measured, weighed, and toe-clipped every animal found, the latter to avoid pseudoreplication. The animals were identified in the field and later photographs of all species were re-examined to confirm identities.

I did not use pitfall traps in this study because the diminishing accumulation of species numbers does not trade-off well against the resources required to maintain the trap setup (e.g., Roedel & Ernst 2004). For a discussion of the species I likely have missed see chapter 3.

Species accumulation curves – assessment of sampling effort

I computed species accumulation curves based on 50 randomly added sampling sessions of the original data and calculated a bootstrap resampling estimator to determine the total species richness in the assemblage (see Magurran 2004). Bootstrapping provides a measure of error in the total species richness estimated from a given number of iterations and is, therefore, considered more robust than other analytical estimators (Magurran 2004). To evaluate effectiveness of sampling effort, I used a Bayesian regression model to estimate the correlation between the randomized original and the bootstrap estimator data, for each sample. A strong correlation in all habitat classes suggests that it is appropriate to use the original data for subsequent analyses (Shahabuddin *et al.* 2005), because this indicates no deviation of the estimator data from the distribution of the original data.

Analysis of the habitat gradient

I calculated species richness for each plot as response variable in my linear models to quantify the differences of amphibian and reptile species richness between habitat classes. For the analysis, I used a Bayesian hierarchical regression analysis that allows subdivision of variance in finer scales using hyper-parameters; this approach allows intuitive graphical evaluation of the results (Qian & Shen 2008). I referred to an effect, trend, and no effect, if the credibility intervals did not overlap, overlap, and were centered on zero, respectively. The same model structure was used to investigate changes in amphibians and reptile species abundance. For a brief introduction to Bayesian model evaluation see Appendix 2.

To determine the relative strength of evidence for environmental parameters driving species richness patterns across the habitat gradient, I chose an *a priori* set of candidate models based on previous work in the study area (Wanger *et al.* 2009). Models incorporated information on leaf litter thickness, canopy cover, and the ratio between leaf litter and shrub cover. For a measure of canopy heterogeneity, I calculated the lacunarity index for all canopy pictures. Bayesian multi-model inference (hereafter MMI) with uninformative priors was then used to reveal the model(s) with the best fit to the data, after introducing a bias correction to account for additional fitted parameters (the deviance information criterion; Spiegelhalter *et al.* 2002).

I used additive biodiversity partitioning to determine species turnover and calculated Species-Rank-Abundance curves to investigate community evenness in different habitats (Magurran 2004). MMI was used to determine the appropriate abundance model fit to the Species-Rank-Abundance curves; the median of the posterior distribution was used as comparison limits for the slope-determining variables of the abundance model (Golicher *et al.* 2006). Using a Bayesian instead of a frequentist generalized linear model (GLM) approach to compare Species-Rank-Abundance curves has the advantages that it is suitable for small sample sizes and more amenable hierarchical data structures (Golicher *et al.* 2006).

Results

In total, I sampled eight amphibian and 12 reptile species (three pristine-forest specialist species each) comprising 63 (eight pristine-forest specialists) and 118 (43 pristine-forest specialists) individuals, respectively (Tab. 1.2). Note that of the species found, only 37.5 % and 0 % of all amphibian and reptile species, respectively, are evaluated in the IUCN Red List

Table 1.2 – Amphibian and reptile species encountered in all habitats. *Red List* classifications are as follows: NT = near threatened; LC = least concern; NE = not evaluated by the IUCN; *Specialist* [Y/N] = species considered pristine-forest specialist / disturbance-tolerant species; *Habitat encountered* abbreviations: *PF* = Rainforest; *SF* = secondary forest; *NAF* = Natural-shade cacao agroforest; *PAF* = Planted-shade cacao agroforest; *OA* = Open areas.

Species	Red List	Specialist*	Habitat encountered
Amphibians			
<i>Hylarana celebensis</i>	LC	N	PF, SF
<i>Ingerophrynus celebensis</i>	LC	N	PF, SF, NAF, PAF, OA
<i>Kaloula pulchra</i>	LC	N	PF
<i>Limnonectes</i> n. sp. 1	NE	Y	PF
<i>Limnonectes</i> n. sp. 2	NE	Y	PF
<i>Limnonectes</i> n. sp. 3	NE	N	PF, SF
<i>Limnonectes</i> n. sp. 4	NE	Y	NAF
<i>Oreophryne</i> n. sp.	NE	N	PF, SF
Reptiles			
<i>Boiga irregularis</i>	NE	N	NAF
<i>Cyrtodactylus famosus</i>	NE	Y	PF
<i>Eutropis grandis</i>	NE	N	SF, NAF, PAF, OA
<i>Eutropis multifasciatus</i>	NE	N	PAF, OA
<i>Eutropix rudis</i>	NE	N	PF, NAF, PAF
<i>Parvosцинus</i> sp.	NE	N	PF, SF, NAF, PAF
<i>Sphenomorphus textus</i>	NE	N	PF, NAF, PAF, OA
<i>Psammodynastes pulverulentus pulverulentus</i>	NE	N	SF
<i>Rhabdophis callistus</i>	NE	N	SF
<i>Sphenomorphus nigrilabris</i>	NE	Y	PF, SF, NAF, PAF
<i>Sphenomorphus variegatus</i>	NE	Y	PF, SF, NAF, OA
<i>Xenopeltis unicolor</i>	NE	N	NAF, PAF

*References: (Manthey & Grossmann 1997; de Lang & Vogel 2005; Gillespie *et al.* 2005; McKay 2006; D.T. Iskandar unpublished data)

Table 1.3 – Environmental determinants of amphibian and reptile species richness (*aSPR* and *rSPR*, respectively) and abundance (*aABD* and *rABD*). The deviance information criterion (*DIC*) is a Bayesian measure of relative model ranking; *pD* = number of effective parameters; % *Dev* = percent deviance explained (structural adequacy of model); *Dhat* = point estimate of the posterior deviance. Predictor parameter abbreviations are as follows: CAC = canopy cover; LLT = leaf litter thickness; HET = canopy heterogeneity; RAT = ratio between shrub and leaf litter cover. *Null* represents the mean (intercept) model.

Amphibians richness	Dhat	pD	DIC	ΔDIC	%Dev
aSPR ~ CAC	79.2	1.9	83.1	0.0	10.5
aSPR ~ CAC + LLT	80.2	2.0	84.3	1.2	9.4
aSPR ~ CAC + HET	79.1	2.8	84.7	1.6	10.6
aSPR ~ HET	82.8	1.9	86.6	3.5	6.5
aSPR ~ RAT	84.6	1.9	88.4	5.3	4.4
Null	88.5	1.0	90.5	7.4	0.0
Amphibians abundance	Dhat	pD	DIC	ΔDIC	%Dev
aABD ~ CAC + LLT	114.7	3.0	120.6	0.0	10.7
aABD ~ CAC	118.5	2.0	122.4	1.8	7.7
aABD ~ CAC + HET	116.9	2.9	122.8	2.2	8.9
aABD ~ HET	123.1	2.0	127.0	6.4	4.2
Null	128.4	1.0	130.4	9.8	0.0
aABD ~ RAT	128.5	1.0	130.5	9.9	-0.1
Reptiles richness	Dhat	pD	DIC	ΔDIC	%Dev
rSPR ~ HET	115.2	1.2	117.2	0.0	0.1
Null	115.3	1.0	117.5	0.3	0.0
rSPR ~ RAT	116.0	1.3	118.7	1.5	-0.6
rSPR ~ HET + CAC	116.2	2.1	120.5	3.3	-0.8
rSPR ~ CAC	123.5	1.1	125.7	8.5	-7.1
rSPR ~ LLT + CAC	121.7	2.1	125.8	8.6	-5.6
Reptiles abundance	Dhat	pD	DIC	ΔDIC	%Dev
rABD ~ HET	167.2	1.9	170.9	0.0	3.6
rABD ~ HET + CAC	163.8	3.6	171.0	0.1	5.6
rABD ~ RAT	172.0	1.7	175.4	4.5	0.9
Null	173.5	1.0	175.5	4.6	0.0
rABD ~ CAC	175.1	1.1	177.4	6.5	-0.9
rABD ~ LLT + CAC	172.7	2.5	177.7	6.8	0.5

Table 1.4 – Results of the Multi Model Inference for the two abundance models (Log normal and gamma)

Amphibians	Dhat	pD	DIC	ΔDIC
<i>Lognormal</i>	53.0	21.3	95.6	0.0
<i>Gamma</i>	87.5	18.9	125.3	29.7

Reptiles	Dhat	pD	DIC	ΔDIC
<i>Gamma</i>	114.8	26.9	168.5	0.0
<i>Lognormal</i>	114.5	36.2	186.8	18.3

assessments. As the original and the bootstrap estimator data were highly correlated for both groups in all habitat types (Appendix 3), I used the original data for further analyses.

For amphibians, mean species richness declined from structurally complex habitats towards structurally simple habitats (Fig. 1.2). I found a positive effect and trend of rainforest and secondary forest on species richness, respectively, and a negative effect and trend of planted-shade cacao agroforest and open areas, respectively. Abundance was also higher in structurally complex habitats compared to simpler habitats (I found effects of secondary forest and planted-shade cacao agroforest, and trends of primary forest and open areas, whereas natural-shade cacao agroforest did not lead to any response). Reptile species richness was highest in natural-shade cacao agroforest and showed only marginal changes in the other habitats (Fig. 1.2). Abundance, however, showed a negative effect in secondary forests and strong positive and negative trends in primary forest and open areas, and planted-shade cacao agroforest, respectively. Natural-shade cacao agroforest had no effect on abundance.

Patterns in amphibian species richness and abundance were best explained by models incorporating canopy cover (DIC weight (w) = 0.44), and canopy cover and leaf litter thickness (w = 0.56), respectively (Tab. 1.3). Canopy heterogeneity was only included in the third best model for amphibian richness (w = 0.20). Reptile species richness and abundance

were best explained by a model only including canopy heterogeneity ($w = 0.39$ and $w = 0.45$, respectively). Canopy heterogeneity and canopy cover were included in the second best model to explain reptile abundance ($w = 0.43$; Tab. 1.3). Note that in reptile species richness, the null model was the second most parsimonious model. Given the low Δ DIC value and percent deviance explained compared to the null model, the heterogeneity model cannot be considered robust. While canopy heterogeneity plays a more important role for reptiles, canopy cover is most relevant to amphibians.

Amphibian alpha diversity was highest in the primary forest (25 % of total γ -diversity) and declined towards disturbed habitats (5 %); this was paralleled by an increase in beta diversity (75 to 95 %). Reptile alpha diversity peaked in agroforestry systems (23 %) but was similar in all other habitat types (14.1 to 16.7 %). Beta diversity was, in contrast to amphibians, only lower in agroforestry (77 %) but remained the same in all other habitats (83.3 – 85.9 %; Fig. 1.3).

Amphibian and reptile species-rank-abundance curve evaluation was based on the commonly used log-normal and gamma abundance model, respectively (Fig. 1.4; Tab. 1.4). I refer to an effect or trend, if the credibility intervals do not overlap or overlap with the reference line, respectively. Amphibian curves showed strong positive and negative trends of sigma values in rainforest and open areas, respectively. This suggests a relatively even abundance for species in pristine habitats, whereas in disturbed habitats a few species predominate. Reptile curves indicated a strong negative trend and effect for rainforest and open areas, respectively, and positive trends for the remaining habitats. Hence, abundance was even across species in rainforest and open areas, but over-dominated by a few species otherwise.

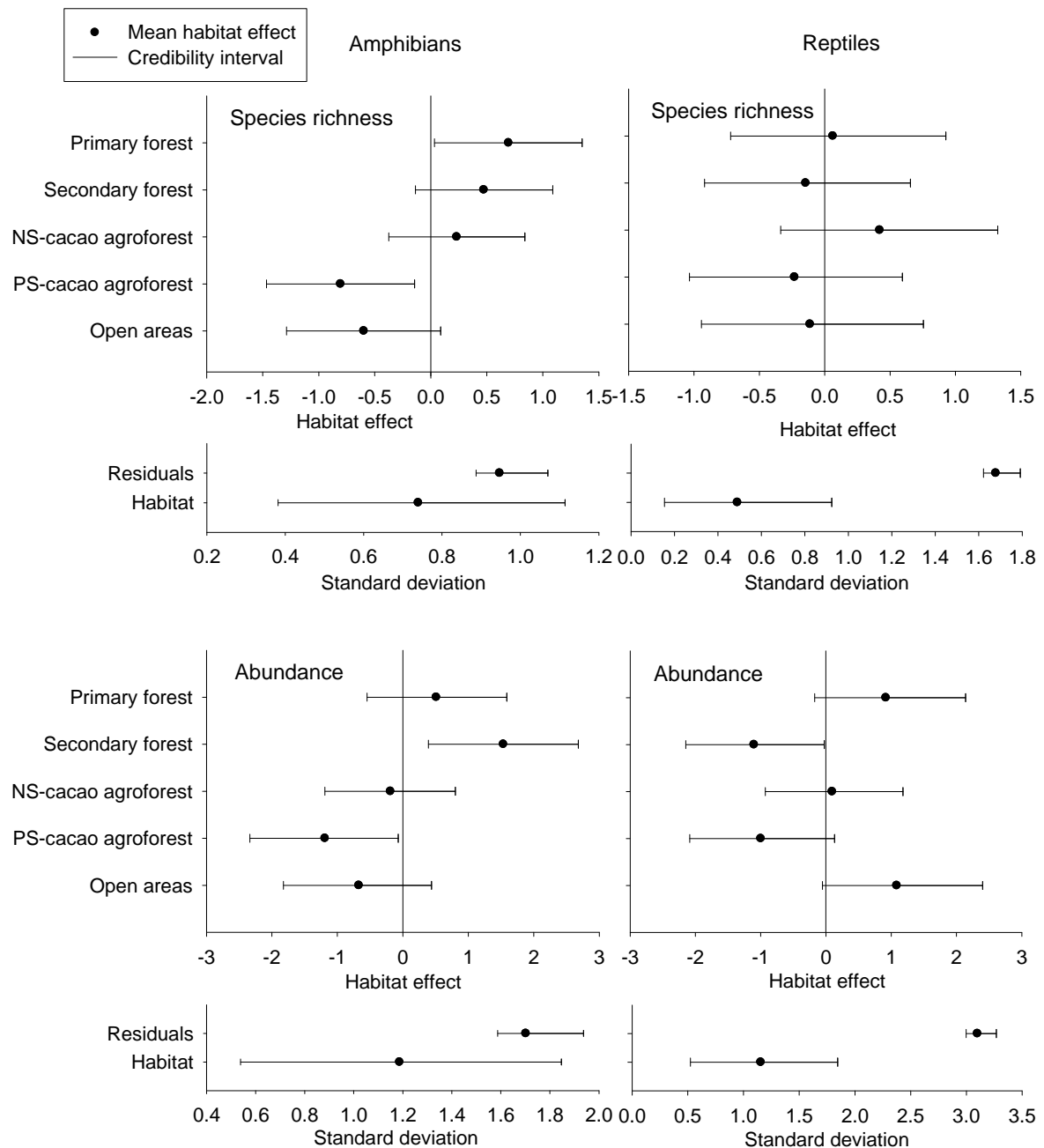


Figure 1.2 –Amphibian and reptile species richness and abundance changes across land-use gradient. The more the credibility intervals of the habitat effect means separate, the stronger is the difference between habitats; a wide overlap with zero means that the habitat had no effect on the investigated metric. The small sections show variance partitioning between habitat effects (*Habitat*) and residuals (*Residuals*). Abbreviations in all figures: *NS-cacao agroforest* = natural shaded cacao agroforest; *PS-cacao agroforest* = planted-shaded cacao agroforest

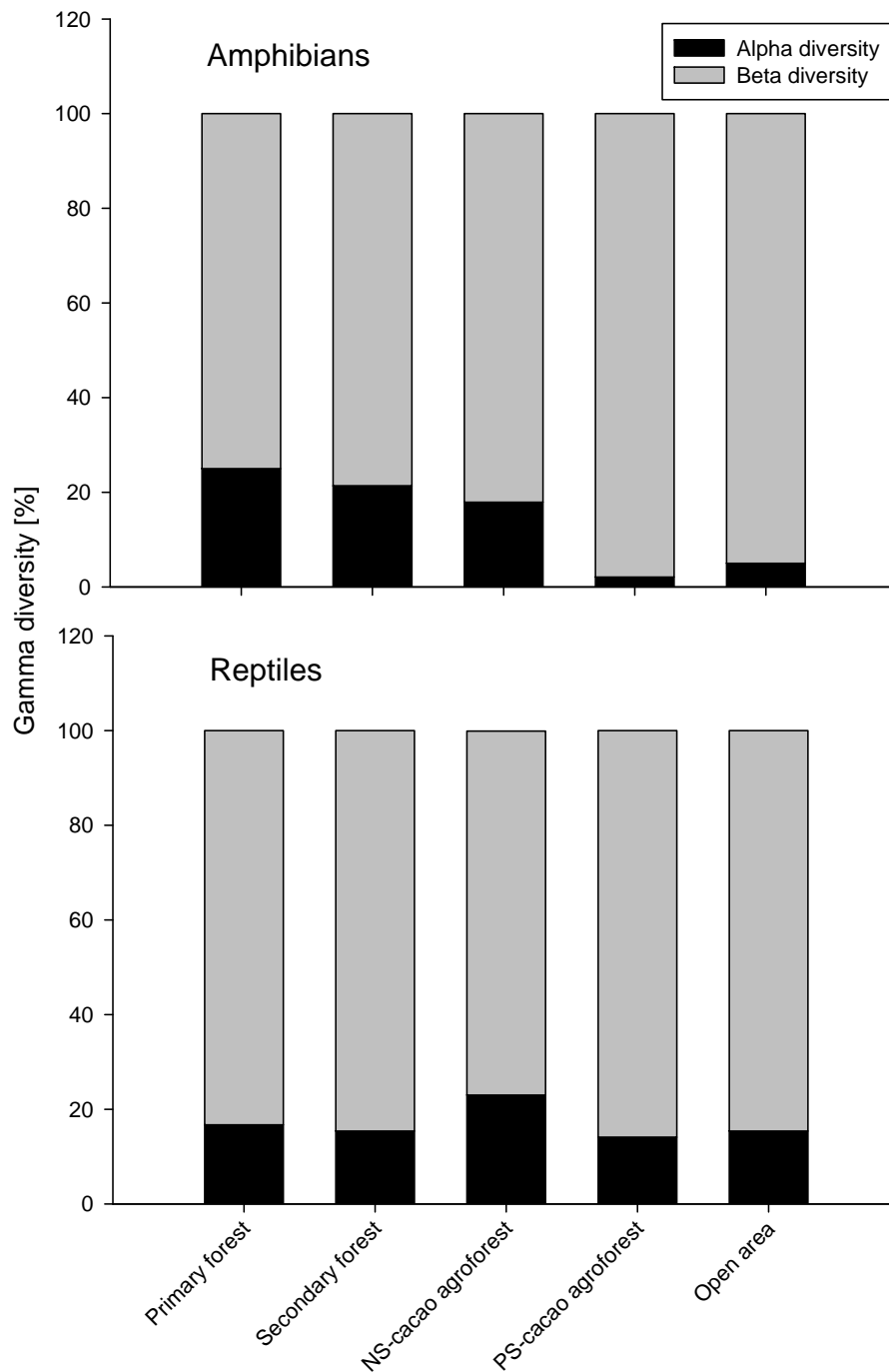


Figure 1.3 – Diversity partitioning of amphibian and reptile diversity in all habitat types.

Gamma diversity (i.e., the total diversity in the assemblage) is separated between mean alpha diversity per habitat (mean species richness of all replicate plots in a habitat category) and beta diversity (difference between gamma- and alpha-diversity). Beta-diversity is an indication of species turnover among habitat types.

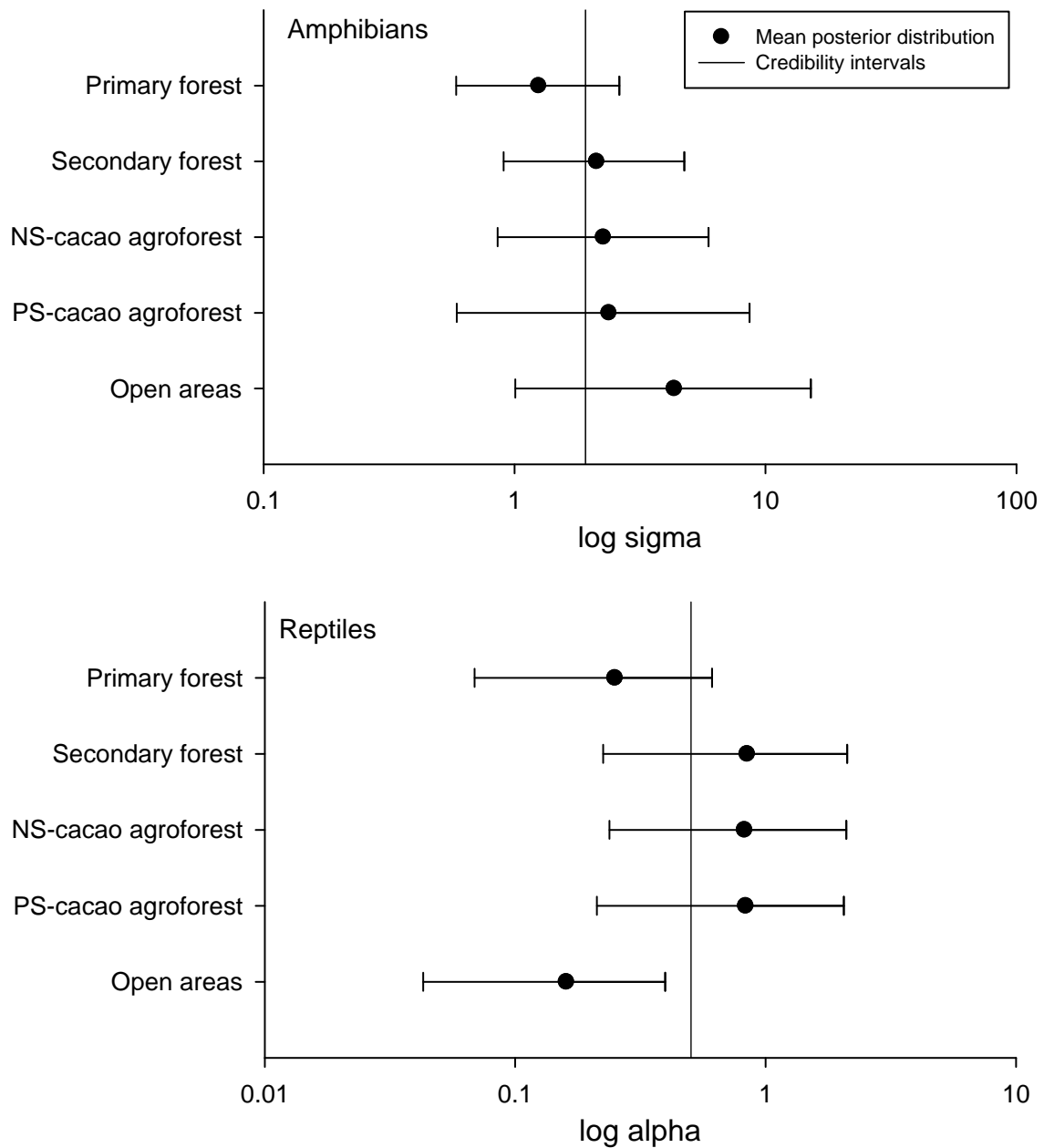


Figure 1.4 – Species rank-abundance plots comparison for amphibians and reptiles among habitat types. For amphibians and reptiles, the log-normal and gamma model, respectively, provided the best fit in the model selection; thus, I compared the parameters σ and α (black dots) for the log-normal model and the gamma model, respectively. A smaller and larger parameter value indicates a flatter and steeper curve, respectively. The former, hence, represents a community with even species abundance and the latter with few dominant species. Interpretation is as in Fig. 1.2.

Discussion

My results show that amphibians in Sulawesi were more strongly impacted by land-use changes than reptiles. Amphibian species richness and abundance declined parallel to the land-use modification gradient. Reptile species richness peaked in natural-shaded cacao agroforest between mildly (secondary forest) and strongly (planted-shade cacao agroforest) disturbed habitats. Abundance was high in pristine forest and open areas with different species composition, but low in secondary forest and planted-shade cacao agroforest. Similar responses of the two groups to humid forest disturbance are found in other studies, mostly from the Neotropics (Faria *et al.* 2007; but see King *et al.* 2007; Suaz-Ortuno *et al.* 2008). These patterns are often explained by changes in leaf litter thickness and, thus, in microhabitats (humidity and food-source abundance; Whitfield *et al.* 2007) or heat-exposure changes as canopy cover decreases (Pineda *et al.* 2005; Luja *et al.* 2008).

I found that canopy cover was included in all models as a predictor of amphibian species richness and abundance patterns. For reptile species richness and abundance, canopy heterogeneity was represented in the best supported models. This may be explained by different modes of thermoregulation; while amphibians do not bask, this behavior is crucial for tropical lizards in open areas (Huey *et al.* 2009). Using a crude measure of canopy cover may, hence, be sufficient for amphibians because as canopy cover decreases, their sensitivity increase. For lizards, in contrast, the canopies of two separate plots may have the same cover, but differ in heterogeneities (spatial aggregation of closed and open areas). The one with higher heterogeneity will provide more basking spots that are also close to shady retreats, and hence, support more home ranges than the homogenous one. In snakes, this effect often depends on the size of the species; larger snakes (e.g., Brown tree snake [*Boiga irregularis*]) often are top predators and, hence, do not occur in high abundances, whereas medium sized species may do so (e.g., Boettger's Keelback [*Rhabdophis callistus*]). Based on my results I posit that canopy heterogeneity is a more useful attribute to measure than only canopy cover,

for reptiles and lizards in particular. I caution, however, that the canopy heterogeneity model determining reptile species richness still leaves much of the between-plot deviance unexplained and so should not be relied upon as the primary measure of habitat suitability.

Species turnover is an important indicator for conservation planning. High beta diversity was characteristic for amphibians, with disturbed habitats dominated by a few species. This suggests that conservation decisions predicated on species diversity and functionality must consider the whole landscape (Clough *et al.* 2007) rather than just plantation scales (Pineda & Halffter 2004). In contrast, similar beta diversity across habitat types implies that conservation strategies on the plantation level may be sufficient. This is the case in reptiles, where natural-shade cacao agroforestry harbors more species with equal abundance, suggesting that reptiles may already benefit from being able to use natural-shade cacao agroforestry in addition to primary and secondary forest. Differences in beta diversity between the two species groups may be explained by lower disturbance sensitivity of reptiles (Wanger *et al.* 2009), leading to species homogenization across the landscape. Note, however, that not using pitfall traps may have led to missing more species in some but not other habitats. Depending on the strength of this effect, it may have biased my estimates of additive diversity.

For both groups, natural-shade cacao agroforestry may enhance resilience against extensive species loss, at least if sufficient pristine habitats remain in the landscape in my study region; for reptiles, it may provide a valuable habitat on its own. However, herpetological studies on land-use gradients find different results within and between taxa. This makes it difficult to generalize conservation management recommendations for both groups (Gardner *et al.* 2007). In addition, a recent experimental study on cacao agroforestry habitats in my study region identified leaf litter thickness, logs, a ratio between plant and leaf litter cover, and temperature as main drivers of herpetological diversity patterns (Wanger *et al.* 2009). Taken together with the identified abiotic drivers for herpetological species richness

and abundance from my study, herpetological diversity patterns are not necessarily driven by the same variables across and within habitats. Hence, results from both approaches are most valuable when integrated.

Conclusions

Sulawesi provides 65% of Indonesia's cacao (Perkebunan 2008) and cacao comprises an important part of local farmer income. Cacao plantations cover almost a million ha on the island (Perkebunan 2008) and thus constitute important potential secondary habitats. I could show that in order to sustain herpetological diversity, complex canopy from natural shade trees and leaf litter cover in the plantations is essential. Recommending establishment of cacao plantations in the understorey inside the forest instead of burning areas for new plantations may not be sustainable for herpetofaunal diversity. This is because shade trees are essential only for young cacao trees but later cut because shade reduces yield in older plantations. Farmers then further encroach into the forest as yields decrease in aging plantations (Clough *et al.* 2009a). Thus low-intensity cacao agroforests with natural-shade trees need to be supported, e.g. by premium prices to offset yield declines. Moreover, farmers need to be trained to maintain yields in shaded conditions and to rejuvenate plantations on site.

The very low evaluation rate in the IUCN Red List assessments of all species considered here suggest that little is still known about the Sulawesi herpetofauna. However, if habitats are not sufficiently preserved and managed, many species may vanish before they are properly studied.

T.C. Wanger

Chapter 2

**CONSERVATION VALUE OF CACAO AGROFORESTRY FOR AMPHIBIANS AND
REPTILES IN SOUTHEAST ASIA: COMBINING CORRELATIVE MODELS WITH
FOLLOW-UP FIELD EXPERIMENTS**

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STATEMENT OF AUTHORSHIP

CONSERVATION VALUE OF CACAO AGROFORESTRY FOR AMPHIBIANS AND REPTILES IN SOUTHEAST ASIA: COMBINING CORRELATIVE MODELS WITH FOLLOW-UP FIELD EXPERIMENTS

Journal of Applied Ecology – 2009, 46, 823-832

Wanger, T.C. (Candidate)

Prepared and conducted the data collection, analysed the data, interpreted the results, wrote the paper and acted as corresponding author.

I hereby certify that the statement of contribution is accurate.

Signed

Date 12/11/2010

Saro, A.

Helped with the field sampling of amphibians and reptiles and coordinating the experiment.

I hereby certify that the statement of contribution is accurate and I give permission for the inclusion of the paper in the thesis.

Signed

Date 12/11/2010

Iskandar, D.T.

Helped with species identification and gave recommendations for proper sampling of the animals in the field. Also discussed and commented on the manuscript.

I hereby certify that the statement of contribution is accurate and I give permission for the inclusion of the paper in the thesis.

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Date 18 November 2010

Brook, B.W.

Provided support when analysing the data and discussed and commented on the manuscript.

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Date 15/11/2010

Sodhi, N.S.

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Date 12/11/2010

Clough, Y.

Contributed to the discussion of the manuscript and helped in the field and initial preparations in Indonesia

I hereby certify that the statement of contribution is accurate and I give permission for the inclusion of the paper in the thesis.

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Date 12/11/2010

Tscharntke, T.

Helped with initial preparations, site selection, and discussing the manuscript.

I hereby certify that the statement of contribution is accurate and I give permission for the inclusion of the paper in the thesis.

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Date 12/11/2010

Chapter 2 - Conservation value of cacao agroforestry for amphibians and reptiles in Southeast Asia: combining correlative models with follow-up field experiments

Abstract

Although agricultural expansion is a primary threat to tropical biodiversity, experimental studies evaluating the conservation value of tropical agricultural habitats are scarce. In particular, little is known about the sensitivity of amphibians and reptiles to habitat disturbance in areas of very high diversity such as Southeast Asia. I used a two-step approach to determine the relationship between habitat complexity and conservation value of cacao agroforestry for herpetological diversity in Sulawesi (Indonesia). Indonesia is the third largest cacao-exporting country globally and forest conversion to cacao plantations is a major threat to its biodiversity. I first sampled 43 cacao plantations six times to determine the environmental variables that best explained herpetofaunal diversity patterns using a Bayesian model selection approach. Based on these results, I experimentally manipulated leaf-litter thickness (LLT), number of branch piles (LOGS), and LLT + LOGS combinations in the cacao plots. The experimental data were analysed using Bayesian hierarchical regression. The best-supported correlative models incorporated LLT, LOGS, air temperature, and the ratio between leaf litter and shrub cover, showing the importance of habitat heterogeneity and suggesting climate change sensitivity. The subsequent structural manipulation of these attributes changed amphibian and reptile species richness, and reptile abundance, but only addition of leaf litter did so in a biologically meaningful way, providing microhabitat resources. However, the main beneficiaries were common disturbance-tolerant reptiles. The different results from the correlative model and the independent manipulative experiments showed how important such a combined approach is to derive adequate conservation

management recommendations. Increasing leaf litter in cacao agroforestry will work best if implemented on a landscape scale to incorporate sufficient environmental variation and species life histories. This will mainly enhance the richness and abundance of disturbance-tolerant species, which still may maintain ecosystem functions such as pest removal. Particularly for rare species, native forests remain critical for herpetological richness. The direct temperature sensitivity suggests that future climate change impacts may be severe for herpetological diversity in plantation habitats and, hence, demand further research.

Introduction

Depending on the level of the world's future environmental resource consumption and overall population growth, global cropland may expand between 0.3 and 1.8 billion ha by 2050 (Kitzes *et al.* 2008). This additional land clearance for agriculture will occur mainly in the tropical developing countries (Tilman *et al.* 2001). The resulting loss in biodiversity (Brook, Sodhi & Bradshaw 2008) will be paralleled by a decline in associated ecosystem functions and services (e.g. crop pollination; Tscharntke *et al.* 2005), and a weakened resilience against other threats such as climate change (Hooper *et al.* 2005). Understanding the value of the agricultural landscape for native biodiversity, therefore, not only assists sustainable management, but also poverty alleviation through changing crop yields (Steffan-Dewenter *et al.* 2007; Perfecto & Vandermeer 2008).

Most research on the impact of agriculture on biodiversity in humid forests comes from the Neotropics (Perfecto *et al.* 2007; Philpott *et al.* 2008), whilst Southeast Asian case studies, where deforestation and associated land-use change increased by 25 % from 1990 – 2005, are still few (Sodhi & Brook 2006; Koh 2007). While Indonesia, for example, comprises two global biodiversity hotspots (Myers *et al.* 2000) and contains most of Southeast Asia's old growth forests, it is also the third largest cacao *Theobroma cacao* Linné producer in the world with an annual net forest loss of 0.3 % (Koh 2007; ICCO 2008). Thus, studies targeting the poorly documented conservation value of cacao agroforests are needed, to understand how best to mitigate its negative impacts on biodiversity. Given that Southeast Asia's forest biota are highly sensitive to forest disturbance (Sodhi *et al.* 2009a), they are expected to be negatively affected by extensive cacao expansion.

Most studies determining the effects of agriculture on tropical biodiversity focus on birds or invertebrates, and highlight the importance of rainforest trees or nearby presence of pristine habitats to sustain high diversity (Klein *et al.* 2003b; Bos *et al.* 2007; Schroth & Harvey 2007a). In contrast, studies on amphibians and reptiles are scarce in Southeast Asia

and the limited results from other tropical regions revealed equivocal and regionally variable results (Gardner *et al.* 2007). This makes it difficult to develop sensible, evidence-based management recommendations – a cause for concern given that amphibians and reptiles are both the most threatened vertebrate taxa on the planet and particularly susceptible to habitat destruction and climate change (Gibbons *et al.* 2000; Whitfield *et al.* 2007; Sodhi *et al.* 2008).

In this study, I assess the conservation value of cacao agroforestry for the herpetofauna of Sulawesi (Indonesia). This large equatorial island is an ideal study area requiring urgent attention, because 76 % and 33 % of its amphibian and reptile species, respectively, are globally endemic (Whitten *et al.* 2002). In addition, 55 % of the available land is threatened by an ever increasing human immigration pressure (Sodhi *et al.* 2005a). Some migrants have been converting primary forest to cacao plantations in central Sulawesi (Steffan-Dewenter *et al.* 2007; Weber *et al.* 2007). Such land-use changes are likely to affect amphibians and reptiles severely (Gillespie *et al.* 2005; Wanger *et al.* 2010a).

Numerous correlative studies have been conducted to identify environmental variables conducive for species and communities (Garnett & Brook 2007; Koh 2008) but few experimental studies have pin-pointed causality (e.g., Yap *et al.* 2002). Here, I integrate a correlative and manipulative approach at various spatial scales (Hewitt *et al.* 2007). In a Bayesian model-selection approach I first identify the environmental parameters that best describe herpetological diversity patterns in 43 cacao plantations in central Sulawesi. Eight different *a priori* candidate models address predictors at three different scales (plantation, landscape, and a mixture of both) and capture former hypotheses (Schroth & Harvey 2007a) posed to explain diversity patterns in different taxa. Secondly, I experimentally manipulate the best predictor variables derived from the correlative models on the plantation scale to test cause-effect relationships on herpetological diversity patterns (i.e. changes in community structure, species richness and abundance). My overarching aim is to determine whether local-scale alteration of habitat complexity can enhance the conservation value of cacao

agroforestry for tropical amphibians and reptiles. I then discuss how habitat modifications can be successfully implemented at the landscape scale.

Materials and Methods

Study region

The study area is located in the Kulawi (167292.444 E; 9831667.769 N) and Palolo (174486.085 E; 9869691.209 N) valleys in Central Sulawesi, Indonesia (see Fig. 1.1). This region lacks clearly defined seasonal variation in climate with relatively constant annual average (\pm SD) temperatures and monthly average (\pm SD) rainfall (24.0 (\pm 0.16) °C and 143.7 (\pm 22.7) mm, respectively). Besides rice cultivation, cacao farming is the major source of income; small-scale farmers transform pristine forests into cacao agroforests and use large rainforest trees to provide shade for cacao tree seedlings. Shade trees are later removed to increase plantation productivity.

Plot characteristics and environmental variables

I sampled 43 plots (40 x 40 m) in cacao plantations, heterogeneous in environmental variables relevant to ground dwelling and arboreal amphibians and reptiles, but each surrounded by structurally similar habitat. For each plot, distance to the nearest intact forest patch was obtained from recent GIS maps based on satellite imagery, while distance to the nearest water body was measured in the field. I also determined mean percentage canopy cover, the mean percentage leaf litter cover, mean leaf litter thickness (LLT), and mean percentage understorey shrub cover in all plots. The importance of different above-ground strata was measured as the ratio of shrub cover to leaf litter cover (COVER). Moreover, I counted the number of stone blocks and log piles (LOGS; dead tree trunks and branch piles) on the plots. Mean annual temperature in the plantations was obtained from ThermoChron® data loggers

(DS1921G-F5#, Maxim, Dallas, USA) in the lower canopy of the cacao trees (for details on environmental variables see Appendix 1)

Sampling protocol

All plots were sampled six times between December 2007 and July 2008 (258 total sampling sessions) covering the general rainy and dry season in Sulawesi, respectively (Whitten *et al.* 2002). Sampling was conducted three times during day and night always between 6.00 and 18.00 h, and 18.00 and 6.00 h, respectively. I randomized sampling time of each plot and treatment category to avoid repeated sampling of the same plot at the same time. Six replicated samples of each plot allowed me to use average values in the analyses; to avoid pseudoreplication I did not add results of each sampling. Because of the manipulation I used only the first four sampling sessions in the Poisson regression analysis to determine environmental predictors of herpetological diversity patterns.

In the experimental approach, I evaluated temporal changes 26 days before (third and fourth sampling session) and 26 days after (fifth and sixth sampling session) the manipulation. This time period between manipulation and re-sampling reflects the time between monthly management activities in the plantations (leaf litter removal, tree pruning, and weeding; Y. Clough unpublished data). Extension of this time period may have either resulted in repeated disturbance through plantation management or in unrealistically stable habitat conditions. Additionally, I found several species in the plots even hours after management activities have ceased (T.C. Wanger unpublished data). I, therefore, assumed that the assemblage requires a relatively short time to recover from disturbance and that the timeframe was suitable.

I used both diagonals of the plots as a single transect (113 m) with a width of 3 m on each side (i.e. 43.4 % of the total plot area). While transects were sampled in a time-constrained manner (~ 25 minutes per plot), I thoroughly searched the leaf litter and turned logs, branch piles, and stones. Animals found were photographed, measured, and toe-clipped,

the latter to avoid pseudoreplication. After the animals were identified to species in the field, photographs of all species were later examined by D.T. Iskandar to confirm identities; this double identification process re-confirmed correct identification.

Assessment of sampling effort

Sampling effort was assessed with species accumulation curves for all sampling sessions, randomly re-shuffled 50 times to smooth curves and account for environmental variation (Colwell & Coddington 1994). I also fitted models based on the Michaelis-Menten equation

$$SPR = (a*x)/(b+x),$$

a negative exponential equation

$$SPR = a*(1-e^{-b*x}),$$

and a logistic-model

$$SPR = b*\log(x)-a$$

(for all equations; *SPR*= species richness; *x* = number of sampling sessions; *a* = asymptotic value; *b* = constant value) to the data for curve extrapolation and used the Deviance Information Criterion (DIC) in a Bayesian Multi Model Inference (hereafter “model selection”) procedure to assess the best model fit. The first two equations were chosen because they are the most commonly used ones to extrapolate species accumulation curves, whilst the third was based on an educated guess given the apparent shape of the distribution. After calculating seven species richness estimators in EstimateS (Chao 1 & 2 estimators, Abundance-based Coverage Estimator, Incidence-based Coverage Estimator, Jackknife 1 & 2 estimators, and Bootstrap estimator; see Magurran 2004; EstimateS website at <http://purl.oclc.org/estimates> (accessed Sept. 2008)) sampling effort was evaluated based on the percentage sampled compared to the estimate of the best fitting equation and the species richness estimators. Sampling effort was truncated to fit a sensible scale between 0 and 100 %.

Identification of environmental variables

I use observed species richness as a response variable in a Bayesian Poisson regression to capture the community response to disturbance. Species richness facilitates comparability between studies because it is widely used as a diversity surrogate and is an indicator for ecosystem change when used for multiple taxa (Sodhi *et al.* 2009a). I defined *a priori* a set of eight candidate models that can be subdivided into three groups, also incorporating previous hypotheses on factors driving diversity patterns in agroforestry systems. The first incorporates only variables relevant at the plantation scale (LLT, LOGS, stone blocks, COVER). The second incorporates variables relevant at the landscape scale (distance to the nearest forest patch and water body), and the third incorporates a mixture of both. In terms of hypotheses, results from agroforestry systems in the Neotropics showed increasing herpetological diversity when percentage canopy cover and proximity to pristine habitats increase (Schroth & Harvey 2007b). Diversity responses were also assumed to be related to temperature changes under the canopy (Perfecto *et al.* 2007). The eight candidate models were then challenged in a DIC-based model selection.

I used an individual variable ranking method to avoid over-parameterisation of the models but to still determine the relative deviance explained by each variable in the data (Garnett & Brook 2007). Each variable is first dropped from the saturated model and then added to the null model. For both, changes in deviance explained relative to the saturated and null model are calculated and then summed as total deviance. Total deviance is rescaled to sum up to one (relative deviance) and variables are ranked according to the relative deviance explained.

Manipulation

I manipulated LLT and LOGS based on the results from the model selection. I expected that increasing structural complexity will enhance species richness; abundance of species should increase and decrease in the adding and removal treatments, respectively, following the availability of microhabitats. Although the predictor variable COVER was included in the best models, I did not manipulate it as it would have drastically reduced sample size per treatment. As shrub ground cover changes quickly, manipulation of this variable would have been extremely difficult.

I randomly excluded one plot for a balanced dataset and then used a full factorial design with 42 plots divided into six treatments (removal of (*rem*) *LLT*, *rem-LOGS*, *rem-LLT & LOGS*, addition of (*add*) *LLT*, *add-LOGS*, and *add-LLT & LOGS*) and a spatial control (controlling for manipulation effects *per se*), with six plot replicates each. The plots for the manipulation were selected *a priori* and plots of each category were equally distributed across the study region. I incorporated information about the individual plots (species richness; LLT, COVER, stone blocks, canopy cover, etc.) from the first two sampling sessions in December 2007 to balance spatial variation in these characteristics equally across categories. I then prepared the plots according to the following standard protocol:

Removal of LLT: to achieve effects that would have sufficient impact as to be measurable on a short-return time scale but within the natural scale of plantation management, I removed all leaf litter from the plots so that only shrubs and bare soil remained on the plot. The leaf litter was packed in rice bags and stored for a maximum time period of two nights to use the same leaf litter for the *addition of LLT* treatment. In total I removed 408 and 398 rice bags with leaf litter from the Palolo and Kulawi valley cacao plots, respectively. Branches from the pruning were removed whilst old branches remained in the plot. *Addition of LLT:* 67 rice bags with leaf litter were allocated to each *addition of LLT* plot at random, to avoid effects that were related to the leaf litter of a particular plot *per se*. In particular, to avoid animal exchange of the target groups and their prey species (arthropods)

between plots, leaf litter was sieved before transferring it between plots (see section below). I removed branches from the pruning but kept old ones in the plot. *Removal of LOGS*: For this treatment, I cleared each *removal of LOGS* plot from all branches and logs resulting from the pruning and those already on the plot. Leaf litter was rearranged. *Addition of LOGS*: I used branches from the pruning to erect 10 x 1 m³ piles on each *addition of LOGS* plot, as several reptiles were previously found in similar microhabitats (T.C. Wanger unpublished data). In addition, all other branches and logs remained on the plot. The leaf litter was rearranged. *Removal of LLT & LOGS* and *addition of LLT & LOGS* were additive treatments of the individual treatments. *Control*: in the control plots, all treatments were conducted and then restored to normal as far as this was possible, given temporal constraints with the manipulation. Leaf litter was raked and rearranged but not removed and added again. For the LOGS treatments, trees were pruned the same way in the control plots and in the treatment plots, and old LOGS rearranged. I then removed the cutting and left the old and rearranged LOGS in the plantations.

As I was interested in changes in herpetological diversity related to treatment effects I used a 4 m² wooden frame with a wire mesh (mesh diameter = 3.5 cm; hereafter “shaking frame”) to shake the leaf litter. This removed organisms before transferring leaf litter between plots. In addition to testing one rice bag of each removal plot, I tested 12 more bags from 12 different locations; in total I validated the shaking frame with 24 rice bags. Leaf litter was raked from a 5 x 5 m area in different microstructural habitats differing in (i) distance to forest, (ii) distance to the nearest rainforest tree in the plantation, and (iii) leaf litter thickness towards a plastic cover on which the shaking frame was placed. This allowed larger animals such as spiders and lizards to leave the leaf litter piles. The leaf litter was then evenly spread (~10 cm thickness) on the shaking frame and shaken for 60 seconds. However, I found that even shaking for 30 seconds yielded a 100 % removal rate for most groups. I then immediately searched the leaf litter on the plastic cover with two people and evaluated the

rough number of all animals found. The animal numbers found were used as the pre-value for the shaking frame validation. After removing all fall out leaf litter from the plastic cover and carefully checking for remaining animals, the leaf litter from the shaking frame was transferred onto the plastic cover and searched for remaining animals (by the same two people). The animal number found was used as the post-value for the shaking frame method. On average (\pm SD), I had removal success of 98 (\pm 3) % (Appendix 4).

I measured LLT before and after the removal and addition of the LLT treatment in all four corners and in the middle of the plot. My LLT treatments resulted in strong manipulation effects: on average (\pm SD), LLT was 77.4 (\pm 109.6) times lower and 4.5 (\pm 2.6) times higher after removal and addition of leaf litter, respectively.

To quantify the experimental treatment effects on amphibian and reptile species richness, I calculated pre- and post-manipulation species richness for each plot and used the pair-wise difference as response variable in my Bayesian hierarchical regression model. This approach allows subdivision of variance in finer scales using “hyper-parameters” and adjustment of the model to the data (Gelman & Hill 2006; Qian & Shen 2008). The same model structure was used to investigate changes in abundance patterns.

To visualize changes in relative abundance before and after the manipulation, I show the three most abundant species per treatment level. Changes in beta diversity across all treatment groups were haphazard compared to alpha diversity (probably the number of replicates was too small to reliably calculate turnover) and, therefore, results are not included here.

Results

General pattern

I found 6 amphibian and 17 reptile species comprising 90 (5 pristine-forest specialists) and 374 (39 pristine-forest specialists) individuals, respectively. Based on all sampling sessions on

all plots, an average (\pm SD) of 1.0 (\pm 1.0) amphibian species was found (min = 0; max = 3) and mean amphibian abundance was 2.1 (\pm 2.7) individuals (min = 0; max = 12) per plot. Of these six amphibian species, three were pristine-forest specialists. Reptile species richness was higher, comprising an average of 3.3 (\pm 1.5) species (min = 1; max = 7) and an average reptile abundance of 8.7 (\pm 5.3) individuals (min = 1; max = 22) per plot. Four reptile species were exclusive pristine-forest specialists (Tab. 2.1).

Evaluation of sampling effort

Model selection revealed that the Michaelis-Menten and the logistic model fitted the amphibian and reptile species richness data best, respectively (Fig. 2.1; Tab.2.2). The estimated asymptote for amphibian richness is marginally above the observed number of detected species ($a = 6.2$), whilst the credibility intervals reveal 86 to 100 % detection (95 % CI = 5.6 to 7.0). The eight estimates for species richness suggest sampling completeness was between 64 % and 100 % (mean (\pm SD) = 86 (\pm 15) %). In reptiles, the asymptote was estimated at 18.3 species with the credibility intervals revealing 89 to 97 % detection (95 % CI = 17.5 to 19.0). The species richness estimators revealed a completeness of sampling effort between 68 % and 100 % (mean (\pm SD) = 85 (\pm 13) %; Appendix 5). The completeness of sampling effort was, therefore, similar between the groups. Overall, both curves suggest that sampling of the species assemblages probably was not exhaustive, but due to the same relative sampling effort in all 43 plots, results are directly comparable.

Table 2.1 – Species list and characteristics (G = disturbance tolerant generalist; S = pristine forest specialist); Reproduction of all amphibians is aquatic and that of reptiles terrestrial. Evaluation based on Manthey & Grossmann 1997; de Lang & Vogel 2005; Gillespie *et al.* 2005; McKay 2006; data base from Sodhi *et al.* 2008; D. T. Iskandar unpublished data; Wanger *et al.* unpublished data).

Species	Habitat	Reproduction
<i>Amphibians</i>		
Bufonidae		
<i>Duttaphrynus melanosticus</i>	G	aquatic
<i>Ingerophrynus celebensis</i>	G	aquatic
Ranidae		
<i>Hylarana celebensis</i>	G	aquatic
Microhylidae		
<i>Limnonectes</i> sp. nov.	S	aquatic
<i>Limnonectes</i> sp. nov.	S	aquatic
<i>Limnonectes</i> sp. nov.	S	aquatic
<i>Reptiles</i>		
Agamidae		
<i>Bronchocela celebensis</i>	G	terrestrial
Gekkonidae		
<i>Cyrtodactylus</i> cf. <i>famosus</i>	S	terrestrial
<i>Cyrtodactylus jellesmae</i>	S	terrestrial
Scincidae		
<i>Eutropis grandis</i>	G	terrestrial
<i>Eutropis multifasciatus</i>	G	terrestrial
<i>Eutropis rudis</i>	G	terrestrial
<i>Eutropis</i> sp.	G	terrestrial
<i>Eutropis</i> sp.	G	terrestrial
<i>Parvoscincus</i> sp. nov.	G	terrestrial
<i>Parvoscincus</i> sp.	G	terrestrial
<i>Sphenomorphus</i> cf. <i>textus</i>	G	terrestrial
<i>Sphenomorphus nigrilabris</i>	S	terrestrial
<i>Sphenomorphus variegatus</i>	S	terrestrial
Colubridae		
<i>Ahaetulla prasina</i>	G	terrestrial
<i>Dendrelaphis pictus pictus</i>	G	terrestrial
<i>Rhabdophis callistus</i>	G	terrestrial
Xenopeltidae		
<i>Xenopeltis unicolor</i>	G	terrestrial

Table 2.2 – DIC based model selection for the species accumulation curve equations.

Model selection parameters are as follows: $Dhat$ = point estimate of the Bayesian posterior deviance; DIC = Deviance Information Criterion; ΔDIC = Difference between the model with the lowest DIC value and the model of interest; pD = number of effective parameters.

Amphibians	Dhat	DIC	ΔDIC	pD
<i>Michaelis Menten equation</i>	883.30	887.20	0.00	2.0
<i>Logistic model</i>	884.00	887.30	0.10	1.6
<i>Exponential rise function</i>	934.00	937.80	50.60	1.9

Reptiles	Dhat	DIC	ΔDIC	pD
<i>Logistic model</i>	1181.00	1185.00	0.00	1.8
<i>Michaelis Menten equation</i>	1185.00	1189.00	4.00	2.0
<i>Exponential rise function</i>	1371.00	1375.00	190.00	2.0

Identification of environmental parameters

The most parsimonious model explaining the variation in amphibian species richness included the number of branches and log piles in the plantations (LOGS), leaf litter thickness (LLT), and the ratio between leaf litter cover and shrub cover (COVER; Tab. 2.3). While the best model explained 9.59 % of the deviance in the amphibian species richness, the second most parsimonious model including the average annual temperature of the plots explained 9.65 % of the deviance. The variable ranking revealed that COVER, LLT, and distance to the nearest river explained 51, 41.13, and 8.49 % relative deviance, respectively (Tab. 2.4). The remaining variables explained less than 5 % relative deviance. In reptile species richness, the

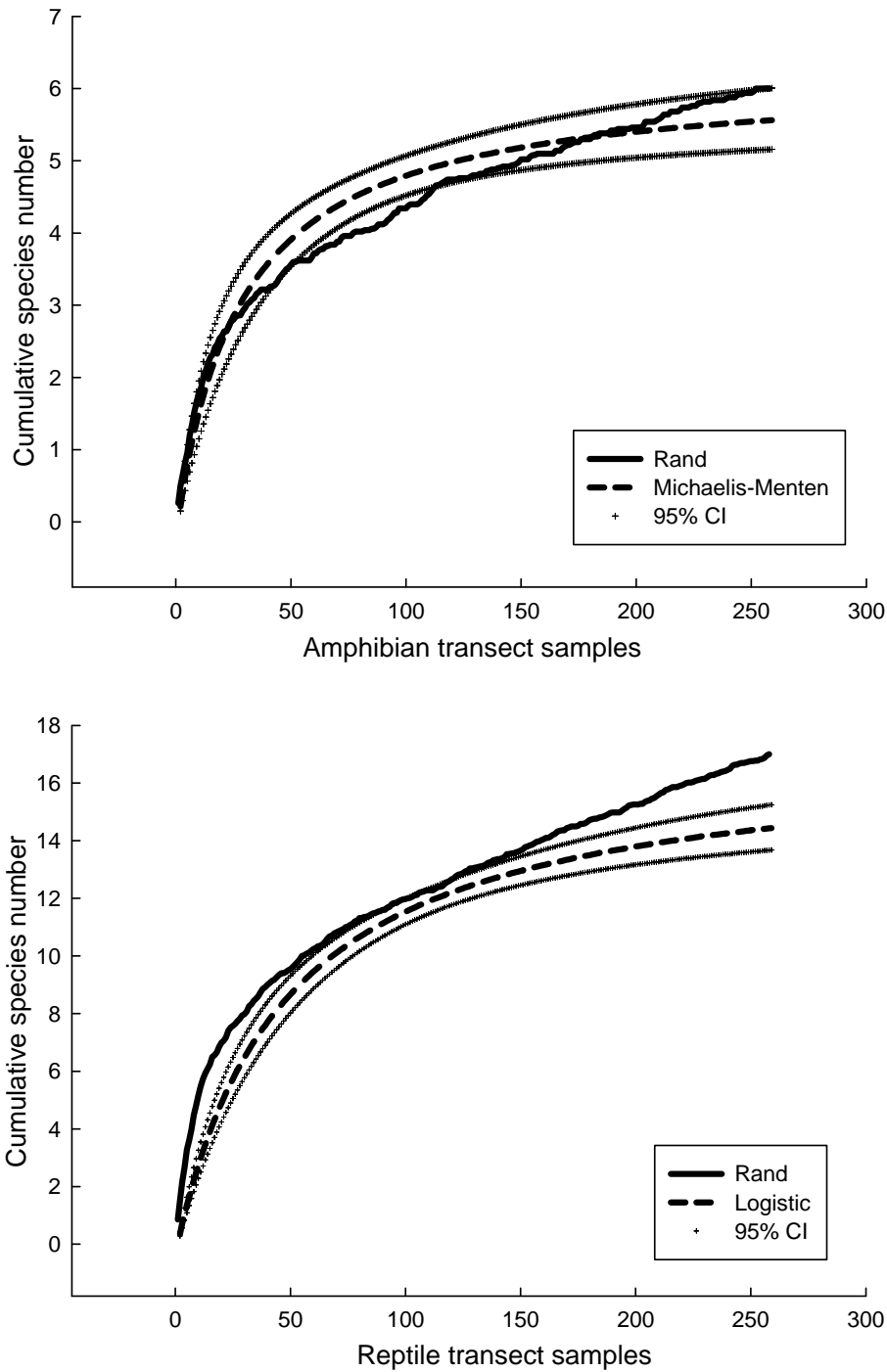


Figure 2.1 – Species accumulation curves for amphibians (above) and reptiles (below). Shown are the randomized original data (*Rand*) based on all sampling sessions conducted in the cacao plantations ($n = 258$), the best equations determined by DIC-based model selection (Michaelis-Menten (Michaelis-Menten) equation for amphibians; Logistic-model (Logistic) for reptiles), and the 95 % credibility intervals (95 % *CI*).

Table 2.3 – Amphibian (aSPR) and reptile species richness (rSPR) in the Bayesian model selection. The best-supported models are in bold/italics. The saturated model includes all predictor variables while the null model only includes the interaction term. Abbreviations are as follows: *COVER* = ratio between leaf litter cover and shrub cover; *LLT* = leaf litter thickness; *LOGS* = number of logs and branches; *TEMP* = mean annual temperature in the plantation; *STB* = number of stone blocks; *Dist2Water* = distance to the nearest water body; *Dist2Forest* = distance to the nearest forest patch; *CanCov* = canopy cover; Model selection parameters are as follows: *Dhat* = point estimate of the Bayesian posterior deviance; *DIC* = Deviance Information Criterion; Δ *DIC* = Difference between the DIC values of the model of interest and the best-supported model; *pD* = number of effective parameters; *%Dev* = percentage deviance explained, indicating structural goodness-of-fit.

Amphibians					
Model	Dhat	DIC	ΔDIC	pD	%Dev
<i>aSPR ~ LOGS + LLT + COVER</i>	87.67	95.48	0.00	3.9	9.59
<i>aSPR ~ LOGS + LLT + COVER + TEMP</i>	87.61	97.32	1.84	4.9	9.65
<i>aSPR ~ LOGS + LLT + STB</i>	90.74	98.51	3.03	3.9	6.42
<i>Null model</i>	96.97	98.98	3.50	1.0	0.00
<i>aSPR ~ LOGS + LLT + STB + COVER + TEMP</i>	87.68	99.19	3.71	5.8	9.58
<i>aSPR ~ Dist2Forest + Dist2Water</i>	96.80	102.7	7.22	2.9	0.18
<i>Saturated model</i>	86.35	103.3	7.82	8.5	10.95
<i>aSPR ~ CanCov + Dist2Water + Dist2Forest</i>	96.84	104.6	9.12	3.9	0.13
Reptiles					
Model	Dhat	DIC	ΔDIC	pD	%Dev
<i>rSPR ~ LOGS + LLT + COVER + TEMP</i>	145.10	155.00	0.00	4.9	6.81
<i>rSPR ~ LOGS + LLT + COVER</i>	147.90	155.90	0.90	4.0	5.01
<i>rSPR ~ LOGS + LLT + COVER + STB + TEMP</i>	145.10	156.90	1.90	5.9	6.81
<i>Null model</i>	155.70	157.70	2.70	1.0	0.00
<i>rSPR ~ LOGS + LLT + STB</i>	153.60	161.60	6.60	4.0	1.35
<i>rSPR ~ Dist2Forest + CanCov</i>	155.60	161.60	6.60	3.0	0.06
<i>Saturated model</i>	144.30	162.00	7.00	8.8	7.32
<i>rSPR ~ Dist2Forest + Dist2Water + CanCov</i>	155.00	162.90	7.90	4.0	0.45

Table 2.4 – Individual explanatory strength of predictor variables. Variables were deleted from the saturated model and added to the null model; the changes in deviance (% Dev) were then summed and rescaled to give the explained relative deviance (Rel. Deviance) as indication of variable explanatory strength. The three parameters with the largest contribution to the relative deviance are in bold / italics. Variable abbreviations and description of *Dhat* are as in Tab. 2.3. Negative deviances indicate a poorer fit than the null model.

Amphibians	Variable deletion		Variable addition		Rel deviance	
	Variable	Dhat	% Dev	Dhat		% Dev
	<i>COVER</i>	89.36	3.10	89.65	7.55	0.511
	<i>LLT</i>	88.31	2.02	90.61	6.56	0.411
	<i>Dist2Water</i>	87.84	1.54	96.74	0.24	0.085
	<i>LOGS</i>	86.49	0.14	96.94	0.03	0.009
	<i>STB</i>	86.41	0.06	96.97	0.00	0.003
	<i>Dist2Forest</i>	86.30	-0.05	97.03	-0.06	-0.005
	<i>TEMP</i>	86.21	-0.14	96.95	0.02	-0.006
	<i>CanCov</i>	86.22	-0.13	96.99	-0.02	-0.007

Reptiles	Variable deletion		Variable addition		Rel deviance	
	Variable	Dhat	% Dev	Dhat		% Dev
	<i>COVER</i>	148.00	2.38	148.10	4.88	0.526
	<i>TEMP</i>	147.10	1.80	152.00	2.38	0.302
	<i>LLT</i>	144.40	0.06	154.00	1.09	0.084
	<i>Dist2Forest</i>	145.00	0.45	155.70	0.00	0.033
	<i>Dist2Water</i>	144.30	0.00	155.10	0.39	0.028
	<i>STB</i>	144.30	0.00	155.30	0.26	0.019
	<i>LOGS</i>	144.30	0.00	155.60	0.06	0.004
	<i>CanCov</i>	144.30	0.00	155.60	0.06	0.004

most parsimonious model included the parameters LOGS, LLT, COVER, and annual temperature of the plots (Tab. 2.3). The second and third model, excluding annual temperature of the plots and including stone blocks, respectively, were still plausible models for explaining variation in reptile species richness (i.e. $\Delta\text{DIC} \leq 2$). As for amphibian species richness, the most parsimonious models all contained LOGS, LLT, and COVER. Ranking of

the environmental variables revealed that COVER, annual temperature of the plots, and LLT explained 52.57, 30.2, and 8.4 %, respectively, of the relative deviance in reptile species richness. The other variables explained less than 5 % (Tab. 2.4). Notably, all models incorporating landscape effects (such as distance to forest and to the nearest water body) were ranked lowest in both animal groups. In the variable ranking, however, distance to the nearest water body was the third most important variable in amphibians.

While COVER values $\gg 1$ indicate benefits of taller above-ground cover and potential protection from predators, values $\ll 1$ stress the importance of the leaf litter stratum and its microclimate. For both groups, COVER had a negative coefficient in the variable ranking (-1.9 ± 1.5 credibility intervals (95 %; CI); 1 ± 0.7 CI, respectively).

Manipulation

The three most abundant species for each treatment before and after the experimental manipulations show distinct patterns (Fig. 2.2). For amphibians, *Ingerophrynus celebensis* (Günther), *Duttaphrynus melanostictus* (Schneider), and *Hylarana celebensis* (Peters) were the most abundant species across all treatments, both before and after the manipulation (Fig. 2.2 above). All of these species were disturbance-tolerant. Before the manipulation, *D. melanostictus* was the most abundant species in most *add-treatment* plots whilst *I. celebensis* was dominant in all *rem-treatment* plots. After the manipulation, *I. celebensis* dominated in all but the *add LLT & LOGS* plots and the control. The abundance patterns are similar before and after the manipulation for *add-LLT* and *add-LOGS* and *rem-LLT*, but entirely different for abundance distributions for all other treatments and the control. For reptiles, *Eutropis grandis* Howard *et al.*, *Parvosцинus* spp., *Sphenomorphus* cf. *textus* (Müller) and *Eutropis multifasciatus* (Kuhl) were the most abundant species before the manipulation with *E. grandis* being the most abundant species in all treatment groups (Fig. 2.2 below). All of these species

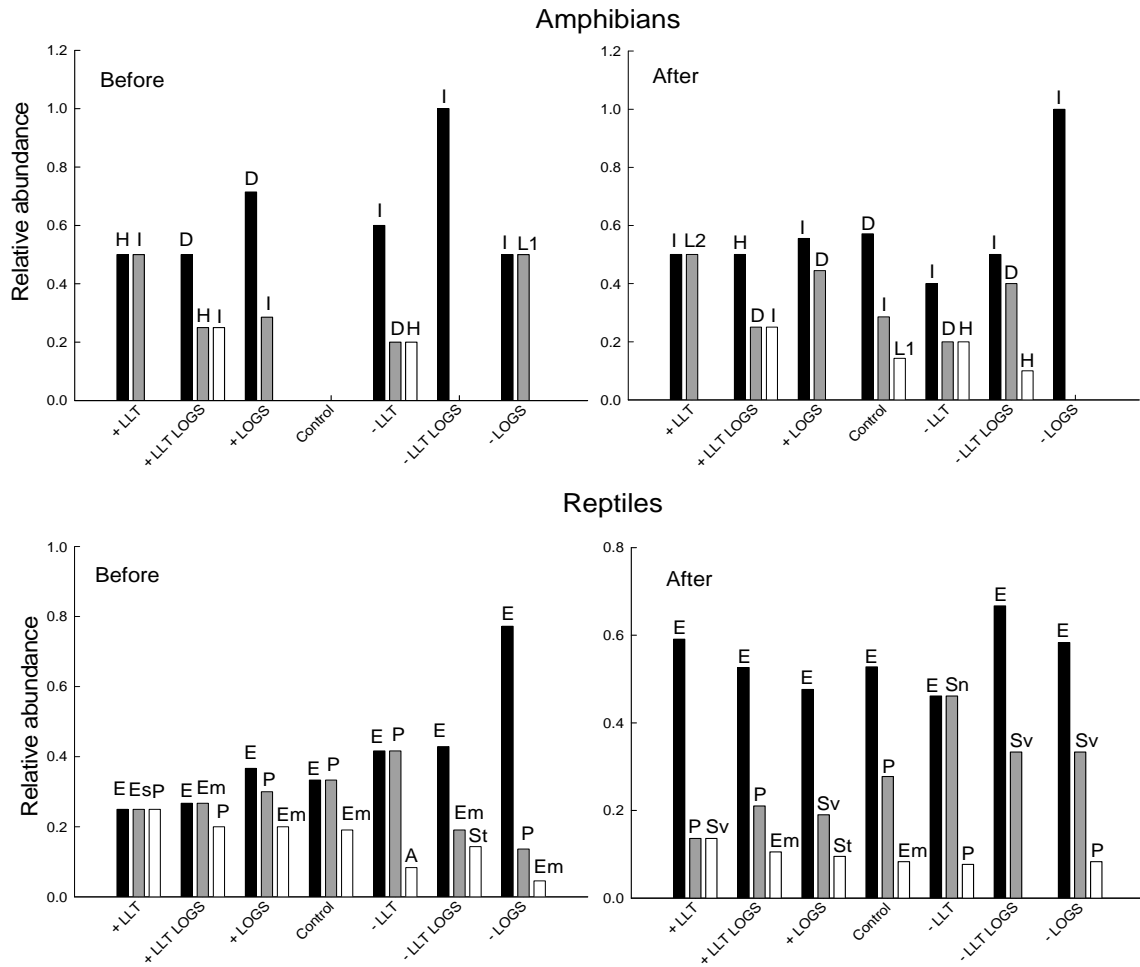


Figure 2.2 - Amphibian and reptile abundance before and after the experimental manipulation. Black, grey, and white bars represent species with 1st, 2nd, and 3rd highest abundance, respectively. Abbreviations for the treatments are *LLT* = leaf litter thickness; *LOGS* = branches and logs; *LOGS LLT* = additive treatment of both factors; +/- = addition/removal of treatment. Species codes on top of the bars are the same for all graphs and defined as follows: *H* = *Hylarana celebensis*; *D* = *Duttaphrynus melanostictus*, *I* = *Ingerophrynus celebensis*; *L1* = *Limnonectes* sp. nov; *L2* = *Limnonectes* sp. nov; *E* = *Eutropis grandis*; *Es* = *Eutropis* sp.; *P* = *Parvosцинus* spp.; *Em* = *Eutropis multifasciatus*; *A* = *Ahaetulla prasina*; *St* = *Sphenomorphus* cf. *textus*; *Sv* = *Sphenomorphus variegatus*; *Sn* = *Sphenomorphus nigrilabris*.

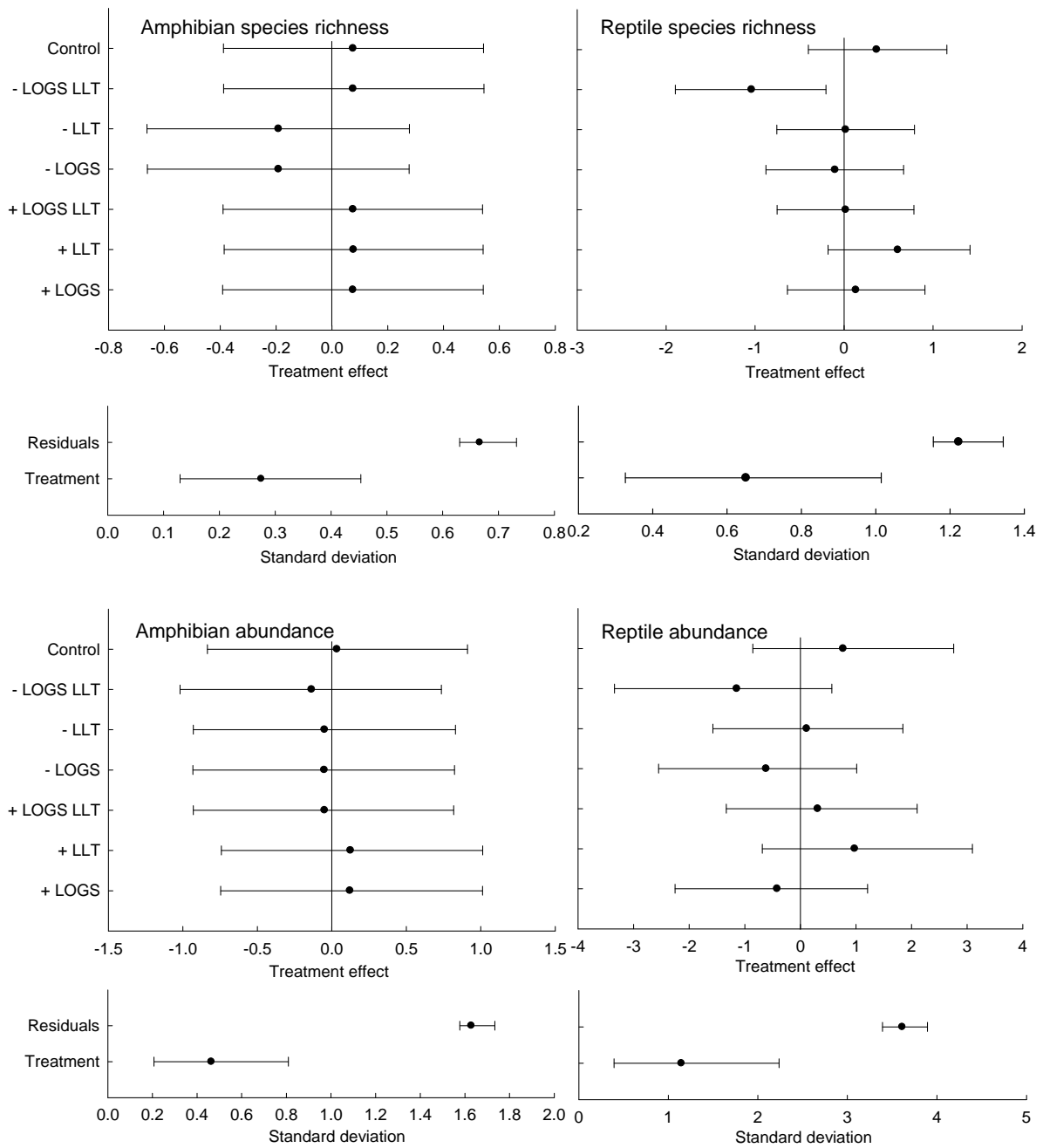


Figure 2.3 – Manipulation results for amphibian and reptile species richness and abundance. Small sections of the graphs represent variance explained by residuals and treatment effects. Dots represent means of the posterior distribution of the treatment effect for each treatment. Error bars are 95 % credibility intervals. For abbreviations of the treatments (y-axis) see Fig. 2.2.

were disturbance-tolerant. After the manipulation, pristine-forest specialists (*Sphenomorphus variegatus* (Peters) and *Sphenomorphus nigrilabris* (Günther)) increased in all but two treatments (*add LLT & LOGS* plots and the control). Whilst before the manipulation three species were mostly co-dominant, *E. grandis* was mostly over-dominant after the manipulation.

I found a decreasing trend of the individual removal treatments on amphibian species richness. All other treatments did not cause a detectable effect (upper sections Fig. 2.3). Reptile species richness decreased following the combined *removal LOGS* and *LLT* treatment and increased in response to the *add-LLT* treatment; all other treatments did not show an effect. Whilst amphibian abundance did not change when the plots were manipulated, reptile abundance decreased in response to the *rem-LOGS* and the combined removal treatment, and increased when *LLT* was added. The other treatments did not cause effects. Overall, treatment effects explained considerably less variance in the data than was contained in the residuals (lower sections Fig. 2.3).

I analysed data separately for pristine-forest specialists but given their absence in several treatments and low abundance in others, results of the analysis were statistically nonsensical. I, therefore, do not present these results here.

Discussion

I used a two-step, correlative-to-manipulative approach, to reveal the factors determining the conservation value of cacao agroforestry in Sulawesi, Indonesia. I first conducted surveys and identified the predictors of amphibian and reptile diversity patterns with a Bayesian modelling approach. I then manipulated the variables identified to be most important to determine the causal relationship between habitat complexity and changes in herpetological diversity.

Modelling environmental determinants

A model selection approach may – in the best-case scenario – give clear directions to improve the conservation value of agroforestry habitats. Candidate models hypothesizing that microstructure components (i.e., leaf litter thickness, logs and branches, and the ratio between leaf litter and shrub cover [LLT, LOGS, and COVER, respectively]) enhance amphibian and reptile diversity clearly fit the data better than models pointing towards landscape effects. This contrasts with other studies stressing the importance of landscape effects (e.g. distance to the nearest forest patch; Gillespie *et al.* 2005; Schroth & Harvey 2007b). The responses found here could have been expected given the ecological preferences of most disturbance-tolerant species found (e.g., Manthey & Grossmann 1997).

Mean annual temperature of the cacao plantations was always included in the most parsimonious models and explained most of the deviance of all favourable candidate models; therefore, temperature is a driving force for species richness patterns when land-use is intensified. Other studies also suggest temperature sensitivity of amphibians and reptiles in plantation habitats (Perfecto *et al.* 2007; Luja *et al.* 2008). Mechanistically, for example skin brightness of species increases from pristine habitats to disturbed open canopy habitats (as found in my study area; T.C. Wanger unpublished data). Darker pristine-forest specialist species have to commit more physiological performance for acclimatization in open-canopy environments and less for feeding or mating. Hence, as canopy opens, species get more exposed to heat stress, which intensifies as future climatic conditions intensify. These findings stress the importance of monitoring the impacts of climate change in plantation habitats.

My results provide recommendations that can be readily implemented by local farmers, because leaf litter removal and cacao tree pruning are common practice in plantation management. This would, hence, allow easy adjustment of LLT and LOGS, and – when incorporated with weeding – COVER. However, findings of the manipulation approach

suggest that the choice of management actions are species-specific and general recommendations based on model predictions are difficult to make.

Large scale manipulation experiment

Large scale experimental approaches in tropical agricultural habitats are scarce, despite offering important insights into ecological and conservation theory (but see Cruz-Angon *et al.* 2008; Greenberg *et al.* 2008). Difficulties arise in complex habitats, where results may be obscured by strong temporal and spatial variation (Hewitt *et al.* 2007; Dumbrell *et al.* 2008). My results show that manipulation of structural complexity on the plantation level can modify amphibian and reptile species richness. Whilst reptile abundance followed the changes in reptile species richness, amphibian abundance remained similar to pre-manipulation levels.

Effects on amphibian species richness were restricted to individual removal treatments. The absence of a response to the combined removal treatment may be explained by the differential disturbance tolerance of species. Half of the six species found are disturbance-tolerant, two of which are toads and one is a frog. The combined treatment may have had a negative effect on the more sensitive ranid species (*H. celebensis*) that was then readily replaced by one of the robust toad species (e.g. *D. melanostictus* is invasive in Bali and occurs in strongly disturbed habitat; McKay 2006), thus obscuring effects of the treatment on species richness. In the individual removal treatments, however, sensitive *Limnonectes* species were not found and then replaced by other species after the manipulation. In terms of abundance, the toads (*I. celebensis* and *D. melanostictus*) appear to benefit from disturbance even when structural complexity is reduced. The same relative abundance of these species in all treatments may result from migration patterns of the common bufonids following their prey (Ryall & Fahrig 2006), as was shown in birds and carabid beetles (Winder *et al.* 2001; Fink *et al.* 2009). This is probably the case in these common amphibians (T.C. Wanger

unpublished data). Given the high abundance of common disturbance-tolerant species, they seem to have an overriding effect on patterns observable in specialized species.

Reptile species richness response patterns were paralleled by less clear patterns in abundance. The removal of LOGS & LLT and adding LLT decreased and increased species richness, respectively. In reptiles, four of the 17 species found are specialized on primary habitats. Manipulation of a single structural component alone may not be sufficient to decrease occurrence of strongly disturbance-tolerant species (e.g. *E. multifasciatus* and *E. grandis*, although the latter was described as a rare obligate arboreal species; Howard *et al.* 2007). An explanation that species richness only increased after addition of LLT, but not in the LOGS treatment, may be competitive exclusion. If all available niches are already occupied by the most abundant species (*E. grandis* and *E. multifasciatus*), immigration of new species is difficult (for examples on skinks and tropical snakes see Langkilde & Shine 2004; Luiselli 2006). Surprisingly, *Sphenomorphus* spp. were found in most treatments only after the manipulation. Given that these lizards are considered forest species, this may have resulted from a change in prey abundance or other temporal variation.

Although model setup and study design were carefully planned to incorporate and minimize temporal and spatial variation, I make a caveat that indirect abiotic changes (e.g. climatic conditions), varying resource availability (Hewitt *et al.* 2007), and processes such as facilitation, inhibition, and competition (Bruno *et al.* 2003) between plots and sampling events may have slightly altered control treatment effects. This may, hence, have influenced manipulation results. I am, however, confident that detection probability was not compromised through the treatment effects but eventually through variation in shrub cover between plots. As the latter was randomly spread between plots of the different treatment groups and the control, this should not have influenced my results.

Taken together, the addition of LLT was the only treatment that caused the expected effect on reptile diversity at sufficient magnitude to be detected, whilst amphibian diversity

was not enhanced by any treatment. LLT has been shown to be an important determinant for tropical amphibians and reptiles by providing important microhabitat resources (e.g. humidity and prey; Whitfield *et al.* 2007). However, the manipulation approach may be obscured by temporal and spatial variation. My results suggest further that disturbance-tolerant species are dominant in the plantations and, therefore, determine the response to the manipulation.

Conclusions

Low species richness and abundance paralleled by exceptionally high endemism distinguish Sulawesi from other tropical regions. An additional difference is reflected in the results of my observational modelling where, in contrast to other studies, plantation rather than landscape-environmental factors enhance the value of cacao agroforests for herpetological diversity. Implementation of the correlative results in field experiments has revealed reduced pristine-forest specialist diversity in plantations; as disturbance-tolerant species dominate the assemblage, improving the conservation value of cacao agroforestry for herpetological diversity will, therefore, mostly benefit these common species. The limited presence of pristine-forest specialists is not ideal, and implies that even cacao agroforests managed for biodiversity cannot replace natural habitat. However, common species probably fulfil – and their conservation thus assures maintenance of – important ecosystem functions (Gaston & Fuller 2008). Abundant lizards, for example, help to control insect pest species in coffee plantations (Borkhataria *et al.* 2006). In strongly modified habitats, where forest specialists are less abundant, sustaining functionality through the preservation of abundant species is crucial.

The environmental predictors found to be important on the plantation scale are easily implemented by the local farmers during management practices. However, my manipulation approach suggested that large scale variation prevented, in part, detection of a clear pattern. Therefore, to make cacao agroforests more hospitable to herpetological diversity, plantation-

scale modifications focused on increasing leaf litter thickness have to be integrated at a larger scale with many farmers participating in such an approach. For pre-emptive buffering of climate change impacts, canopy cover in plantations should be supplemented with fast growing leguminous trees (e.g. *Gliricidia sepium*), to maintain a suitable microclimate. Although more studies are needed for sound management recommendations, such habitat changes may positively affect the adaptation potential of plantations towards future climate change impacts (Scherr & McNeely 2008). Predictive modelling approaches incorporating field data of climate-driven changes in these habitats should be used to lay the path for successful future management recommendations.

*Land-use change, tropical biodiversity, and ecosystem services –
Southeast Asian amphibians and reptiles in focus*

T.C. Wanger

Chapter 3

**AMPHIBIANS AND REPTILES OF THE LINDU NATIONAL PARK AREA,
SULAWESI (INDONESIA)**

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Salamandra – 2010, in press

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I hereby certify that the statement of contribution is accurate.

Signed

Date 12/11/2010

Motzke, I.

Helped with the field sampling of amphibians and reptiles and handling, and discussed and commented on the manuscript.

I hereby certify that the statement of contribution is accurate and I give permission for the inclusion of the paper in the thesis.

Signed

Date 12/11/2010

Shahabuddin

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Date 12/11/2010

Iskandar, D.T.

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Date 18/11/2010

Chapter 3 - The amphibians and reptiles of the Lore Lindu National Park area, Sulawesi (Indonesia)

Wanger, T.C., Motzke, I., Shahabuddin, & Iskandar, D.T. (2011) Amphibians and reptiles of the Lindu National Park area, Sulawesi (Indonesia).

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NOTE:

This publication is included on pages 64-79 in the print copy of the thesis held in the University of Adelaide Library.

*Land-use change, tropical biodiversity, and ecosystem services –
Southeast Asian amphibians and reptiles in focus*

T.C. Wanger

Chapter 4

ENDEMIC PREDATORS, INVASIVE PREY, AND NATIVE DIVERSITY

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Date 12/11/2010

Chapter 4 - Endemic predators, invasive prey, and native diversity; biocontrol by an endemic toad

Abstract

Interactions between native diversity and invasive species can be more complex than currently understood. Invasive ant species often substantially reduce native ant diversity that act as natural control agents for pest insects. In Indonesia (on the island of Sulawesi), the third largest cacao producer worldwide, I show that a predatory endemic toad (*Ingerophrynus celebensis*) controls invasive ant (*Anoplolepis gracilipes*) abundance, and positively affects native ant diversity. I call this the invasive-naïvety effect, an opposite of enemy-release, whereby alien species may not harbour anti-predatory defences against a novel native predator. A positive effect of the toads on native ants may facilitate their predation on insect vectors of cacao diseases. Hence toads may increase crop yield but further research is needed on this aspect. Ironically, amphibians are globally the most threatened vertebrate class and are strongly impacted by the conversion of rain forest to cacao plantations in Sulawesi. It is, therefore, crucial to manage cacao plantations to maintain these endemic toads, as they may provide critical ecosystem services, such as invasion resistance and preservation of native insect diversity.

Introduction

Cacao is the largest international trade commodity after petroleum and coffee, and currently covers eight million ha in the tropics (FAO 2009). Cacao plantations, despite their structural similarities to natural tropical forests, harbour reduced biodiversity, especially when shade trees are removed to maximise crop yields (Schroth & Harvey 2007b; Clough *et al.* 2009a). The effects of land use change can be further intensified when these agricultural areas are subsequently colonised by invasive species, particularly on remote islands with high endemism (Roemer *et al.* 2002; Wagner & Van Driesche 2010). Structural simplification in plantations can also compromise the ecosystem services provided by native biodiversity. Natural ant diversity, for example, has been shown to regulate insect vectors of cacao pests and decrease the risk of disease outbreaks (Philpott & Armbrrecht 2006). Introductions of the Yellow Crazy Ant (*Anoplolepis gracilipes*) are known to affect native biodiversity and ecosystem processes on islands (O'Dowd *et al.* 2003; McNatty *et al.* 2009). As a result, *Anoplolepis gracilipes* is ranked amongst the top 100 invasive species worldwide (GISD 2007).

An ubiquitous yet expensive and often unsuccessful approach to controlling invasive ant species in poor, developing countries is the heavy application of pesticides, which can also damage native biodiversity and human health (Wanger *et al.* 2010b). Theoretically, native diversity could provide free services by controlling invasive ants and mitigating pesticide use (Chivian & Bernstein 2008). This requires that native predators become effective predators of invasive ants (Fig. 4.1). Further, the native predator should be abundant, ground living, and ideally, be ant specialist. The Common Celebes Toad (*Ingerophrynus celebensis*), and a skink (*Eutropis grandis*), are the most abundant ground-living vertebrates in the cacao plantations of Sulawesi (Wanger *et al.* 2009). To assess their role as an invasive ant control agent, I first determined dietary preferences of these two species and then experimentally excluded ant predating specialists (the toads) from cacao plantations. I tested the hypothesis that an

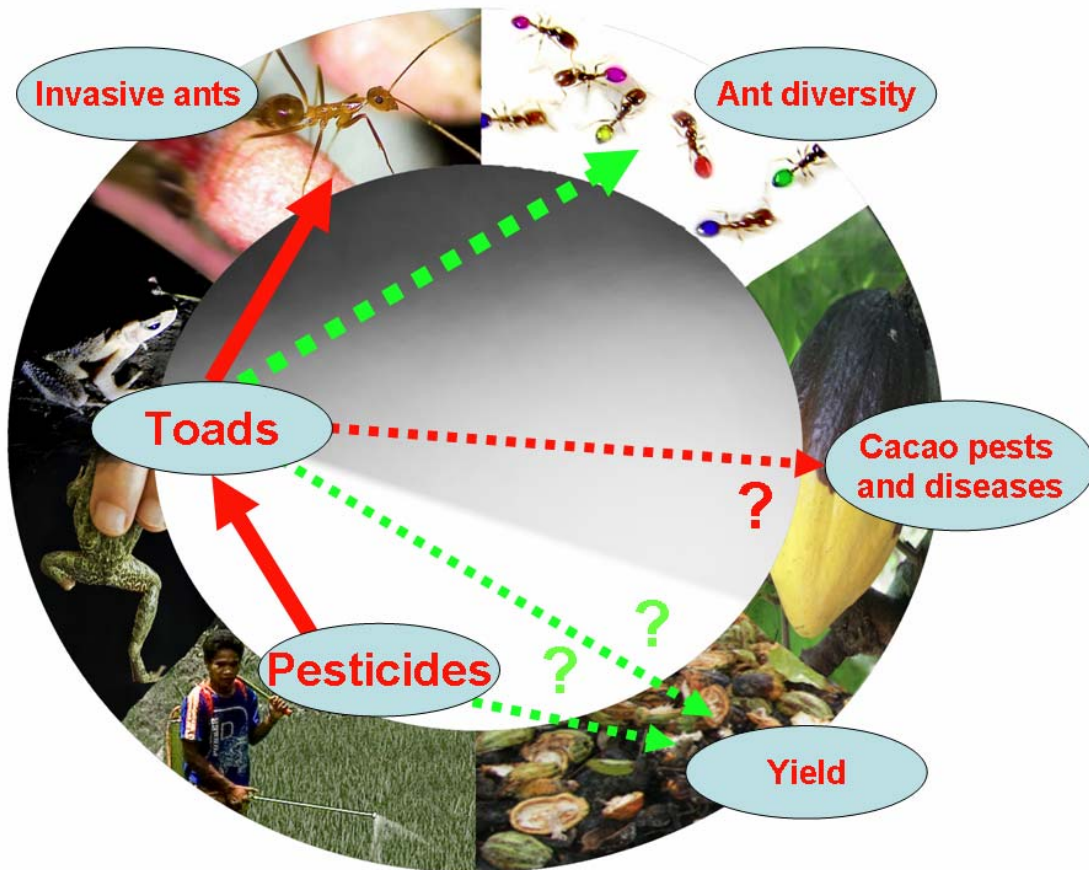


Figure 4.1 – Toad abundance reduces invasive ant abundance and thereby positively affect native ant diversity (red and green dashed arrow, respectively, in dark grey area). The literature suggests that a decline in native ant diversity increases disease outbreak frequency (light grey area) that likely affects crop yield. However, excessive pesticide application may hamper toad ecosystem services (red arrow). Effects of the toads on cacao disease and yield are not yet confirmed (question marks). Thickness of arrows indicates strength of an effect; dashed arrows resemble an indirect effect. Red arrows mean a negative, green a positive relationship between two groups.

endemic amphibian species can control an invasive ant and thereby alleviate its impact on natural ant diversity.

Material and Methods

Amphibian, reptile, and ant sampling

To predict toad and lizard abundances by different ant species abundances and richness, I collected data from 43 cacao plots (40 x 40 m; 21 cacao agroforest and 22 cacao monoculture plantations) around the Lore Lindu National Park in Central Sulawesi (Indonesia; Fig. 1.1). Amphibians and reptiles were sampled three times during day and night with visual and acoustic encounter surveys (Wanger *et al.* 2009). Ants were sampled with observation plates (10 on the ground and 10 in the trees) on each plantation, baited with tuna and sugar solution. For ant recruitment rates (hereafter I refer to ‘ant abundance’ for clarity) and species richness, I counted the number of ant individuals and species on each plate every 15 minutes for 1h. I used the mean maximum number of all plates as a measure of ant abundances per plot. For ant diversity, I used the total number of species encountered in the plot (Wielgoss *et al.* 2010).

Biomass analysis – faeces and reference data from the cacao plantations

I collected faeces samples of amphibians and reptiles between December 2007 and August 2009 and analysed arthropod species composition. All individuals captured in the 43 plots were kept in plastic containers for 12 h and faeces were collected. I identified the prey items found in faeces samples to order whenever identifiable species parts were available, and where possible I quantified individual numbers (e.g., counting the number of heads, thoraxes, etc.). I equated hymenopterans with ants, because I mainly identified ant remnants in the faeces; thus, I assume that bees and wasps are less likely prey items for these lizard and toad species. I used five Barber traps randomly placed within a plot equipped with a 1:1 ethylene:glycol solution. The traps were emptied twice (once every four weeks) over a period of two months. I identified the samples to taxonomic order and measured dry weight. The summed biomass of all traps within a plot was used for standardisation of the faeces biomass.

Toad enclosure

The toads migrate through the plantations to form calling choruses in the rice fields roughly every three months. They stay in the plantations for an average of one week where their abundance can reach up to 300 toads per hectare (T.C. Wanger and I. Motzke pers. observ.). In contrast to the control plots, I expected that by excluding the toads from treatment plots, *Anoplolepis* abundance would increase due to a lack of toad predation. If this is a long lasting effect, removal of the enclosure would not change ant abundance patterns when few or no toads are present in the plantations. Therefore enclosures were removed.

For the fence enclosure experiment, 14 plots (10 x 10 m; for environmental details see Tab. 4.1) with *Anoplolepis* present were sampled four times in cacao agroforests. Ant abundances were determined once in the evening and morning over seven days; on the first day before an enclosure fence had been established, the third and fifth day after the fence had been established, and on the seventh day after the fence had been removed. Seven plots were randomly assigned to treatment and control groups. While the control plots were only disturbed on the edges for all sampling sessions, I built 50 cm tall enclosures of 3 mm wide plastic mesh on the treatment plots. Fences and enclosures were maintained every day and checked every night for toads inside the fence. In all plots and sampling sessions, ant diversity and *Anoplolepis* abundance – as the only invasive species present – was determined with four sampling plates per plot, baited with tuna and sugar solution (Wielgoss *et al.* 2010). I only used four plates because increasing the number of plates may have resulted in unrealistic abundances due to overabundant food sources. Time frames were chosen so that the evening sample was conducted before the toads moved through the experimental area and the morning sampling was after the toads had finished feeding in the area. For the analysis, I pooled abundance data from morning and evening sampling sessions for higher robustness of samples (e.g., climatic variation between morning and evening sessions may potentially lead to changes in ant abundances).

Table 4.1 – Characteristics of the 14 sample sites. Variable definitions and acquisition: *C* – Control plot; *T* – treatment plot; *SD* – Standard deviation; *No. cacao trees* – counted number of cacao trees in the plots; *Distance to forest* – distance to the nearest forest edge, measured in the field; *Distance to rice field* – distance to the nearest rice field; *Leaf litter thickness* – thickness of leaf litter layer in the plot, measured with a ruler; *No. logs* – number of branch piles in the plot; *plant density* – counted number of plant stems in five 1 x 1 m subplots in the plots; *No. trees* – number of trees other than cacao in the plot.

Treatment/Control plot	No. cacao trees	Distance to forest [m]	Distance to rice field [m]	Leaf litter thickness [cm]	No. logs	Plant density [No. / m²]	No. trees
C	8	200	8	2	2	32	1
C	10	170	16	3.5	1	18	0
C	8	230	2	2.5	1	1	1
C	6	140	3	0.5	1	8	0
C	8	80	12	2	3	39	2
C	8	80	8	2	2	48	2
C	9	90	5	2.5	1	25	0
Mean	8.1	141.4	7.7	2.1	1.6	24.4	0.9
SD	1.2	60.9	5.0	0.9	0.8	16.8	0.9
T	9	200	8	1.5	1	45	0
T	8	180	13	3.5	1	25	0
T	9	150	12	2	1	17	0
T	9	190	6	4	1	12	0
T	9	200	2	3	0	3	1
T	6	140	2	1	1	4	1
T	8	75	15	1	2	43	1
Mean	8.3	162.1	8.3	2.3	1.0	21.3	0.4
SD	1.1	45.1	5.3	1.2	0.6	17.3	0.5

I sampled the plots for one week to minimize confounding climatic effects in the field rather than accounting for it in the models with limited sample size. Only 14 sites were sampled because each site had to fulfil a strict set of requirements for a robust sampling design: 1) toads had not moved through the cacao plot prior the first sampling session (all candidate sites were checked every night over a 3 month period); 2) toads were moving through the plots until the third sampling session was completed; 3.) climatic conditions were suitable and similar for the ants (i.e., no rain or wet soil) to minimize confounding climatic effects on the results.

Analysis

I used Bayesian linear modelling with multi-model inference to determine whether individual ant species abundances and general fossorial ant diversity were drivers for toad and lizard abundance. I defined three *a priori* main hypotheses that were challenged in a Bayesian Multi Model Inference approach (i.e., that either (a) cumulative abundance of large ants [of *Anoplolepis gracilipes*, *Paratrechina longicornis*, *Pheidologeton* sp., *Philidris* sp.], (b) individual large ant abundances, or (c) ground dwelling ant species richness, drive abundance patterns in the most common amphibian and reptile species). For an introduction of Bayesian model evaluation, see McCarthy (2007) and Appendix 2.

The enclosure experiment and its impact on ant diversity was analysed with a Bayesian repeated-measures ANOVA, where the first sampling session was specified as reference level, and site was coded as a random effect to account for spatial differences not accounted for in the fixed effects. The treatment effect was modelled as an interaction with sampling session, because I was interested in the enclosure effects over time and not a treatment effect *per se*. To reduce the predictors in the model, I used the relative abundance and relative native ant species richness (i.e., difference between treatment and control plots) as response variables.

Results

Dietary analyses revealed that ants dominated arthropod biomass (74%; standardised by plantation arthropod biomass) in the faeces samples of the toad. In the skink faeces, ants played a minor role and prey items were evenly distributed between arthropod orders (Fig. 4.2). A comparison of arthropod biomass removal between cacao agroforest and monoculture plantations revealed that *I. celebensis* had the highest impact on ant biomass (i.e., 45%) in both habitats. *E. grandis* had the greatest impact on orthopterans and dermapterans (i.e., 26 and 65% in cacao agroforest and monocultures, respectively; Fig. 4.3). Based on behavioural observations of toads feeding on ants (see also Clarke 1974), I am confident that results from the faecal analysis are not strongly biased (i.e., soft-bodied prey items are unlikely to be fully digested and thus overlooked).

Bayesian regression modelling showed that abundance of *Anoplolepis* ants was the strongest predictor of toad abundance; the model explained 19.4% of the deviance in the data, and was >1,000,000 more likely than the null relationship (Tab. 4.2). Skink abundance was predicted by abundance of large ant species in general, but the relationship was weaker, with 7.7% deviance explained. These results suggest that – as an *Anoplolepis* predator - the toads choose plantations with higher *Anoplolepis* abundance, and are abundant in cacao plantations during regular migration to their breeding grounds in rice fields at night.

A Bayesian repeated measures ANOVA revealed a treatment (i.e. toad exclosure) effect over time relative to the reference sample (i.e., the first sampling session (*Session 1*) before the exclosure-fence was built; Fig. 4.4). I found measurable effects at all four sample sessions; the credibility intervals do not overlap with zero. While the relationship between treatment and control plots at the reference sample is negative (*Session 1*; -11.9 [-22.5 to -1.2]), this relationship inverts over time (*Session 2*; 3.5 [0.6 to 6.9]) and remains positive even after the fence is removed in the last sampling session (as suggested by the overlapping

Table 4.2 – Effect of ant species abundances and richness on amphibian and reptile abundance. Common Celebes Toad (*Ingerophrynus celebensis*) abundance was best predicted by Yellow Crazy Ant (*Anoplolepis gracilipes*) abundance. Large ant species abundances were the best predictor for the common lizard (*Eutropis grandis*). The best models, selected based on the smallest Deviance Information Criterion (*DIC*) statistic, are indicated in *bold-italics*. The saturated model (*Saturated*) comprises all, the null model (*Null*) none of the explanatory variables tested. Model variables: *ICA* – toad abundance; *EGA* – lizard abundance; *an* – *Anoplolepis gracilipes* abundance; *pe* – *Pheidologethon* sp. abundance; *p* – *Paratrechina longicornis* abundance; *ph* – *Philidris* sp. abundance; *foss.spr* – large fossorial ant species richness. Model selection parameters: *Dbar* – point estimate of the deviance; *DIC* – deviance information criterion; Δ *DIC* – difference between the DIC values of the model of interest and the best supported model; *pD* - number of effective parameters; *%Dev* - percentage deviance explained, indicating a structural goodness of fit.

<i>Ingerophrynus celebensis</i> abundance	Dbar	DIC	ΔDIC	pD	%Dev
<i>ICA ~ an</i>	120.9	122.9	0.0	2.0	19.4
ICA ~ Saturated	119.7	125.3	2.4	5.6	20.2
ICA ~ pe + ph + p + an	120.9	125.6	2.7	4.8	19.4
ICA ~ pe	147.5	149.3	26.4	1.9	1.7
ICA ~ ph	148.7	150.7	27.8	2.0	0.8
ICA ~ foss.spr	149.0	150.9	28.0	1.9	0.7
ICA ~ Null	150.0	150.9	28.0	1.0	0.0
ICA ~ p	150.8	152.7	29.8	2.0	-0.5
<i>Eutropis grandis</i> abundance	Dbar	DIC	ΔDIC	pD	%Dev
<i>EGA ~ pe + ph + p + an</i>	200.2	205.1	0.0	4.9	7.7
<i>EGA ~ Saturated</i>	200.1	206.1	1.0	6.0	7.8
EGA ~ an	206.3	208.4	3.2	2.0	4.9
EGA ~ foss.spr	208.7	210.7	5.5	2.0	3.9
EGA ~ ph	213.7	215.7	10.6	2.0	1.5
EGA ~ Null	217.0	218.0	12.9	1.0	0.0
EGA ~ p	217.0	218.9	13.8	1.9	0.0
EGA ~ pe	217.6	219.7	14.5	2.1	-0.3

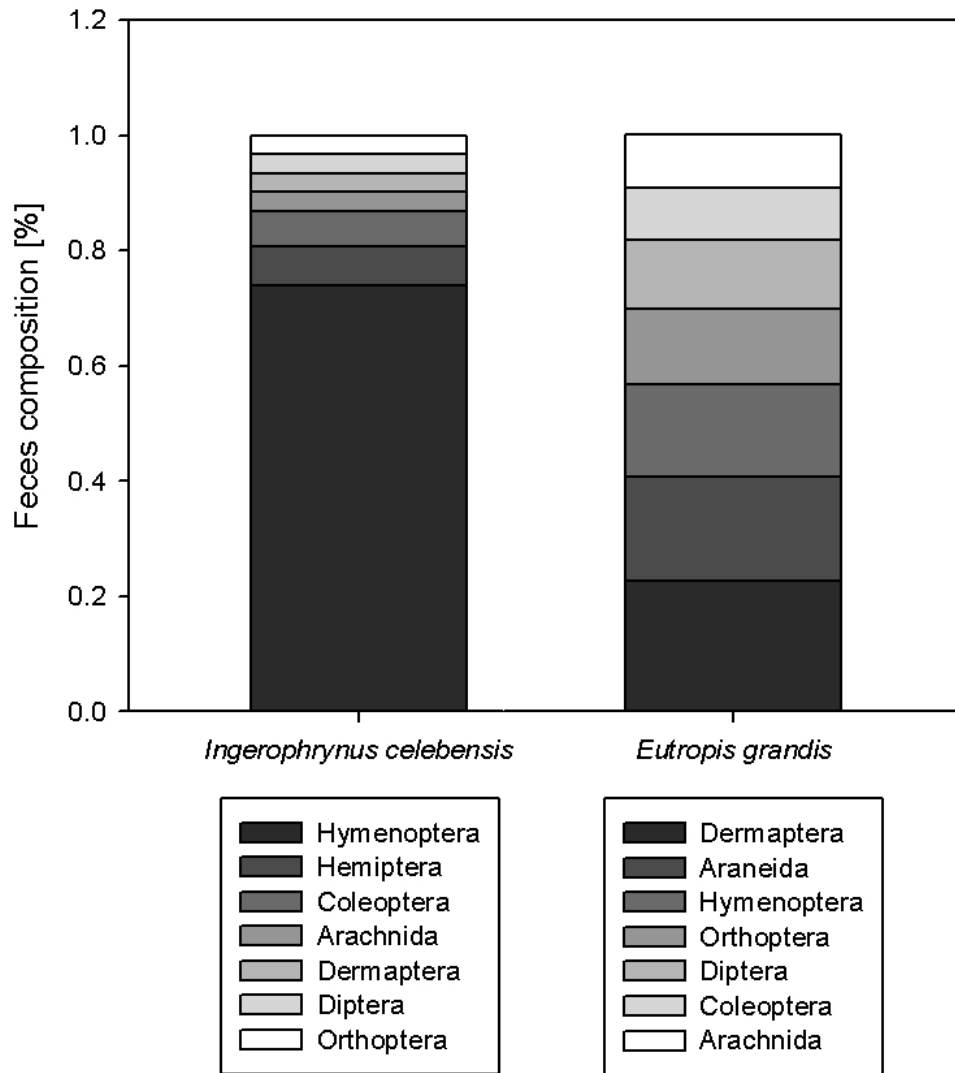


Figure 4.2 – Faeces composition of the two common amphibian (*Ingerophrynus celebensis*; n = 41) and reptile species (*Eutropis grandis*; n = 34). Note the strong dominance of Hymenoptera in the toad’s diet and the equal spread of the lizard diet. I equated hymenopterian preference with ants, because toads are highly unlikely to prey upon bees and wasps, and identified fragments were mainly ants.

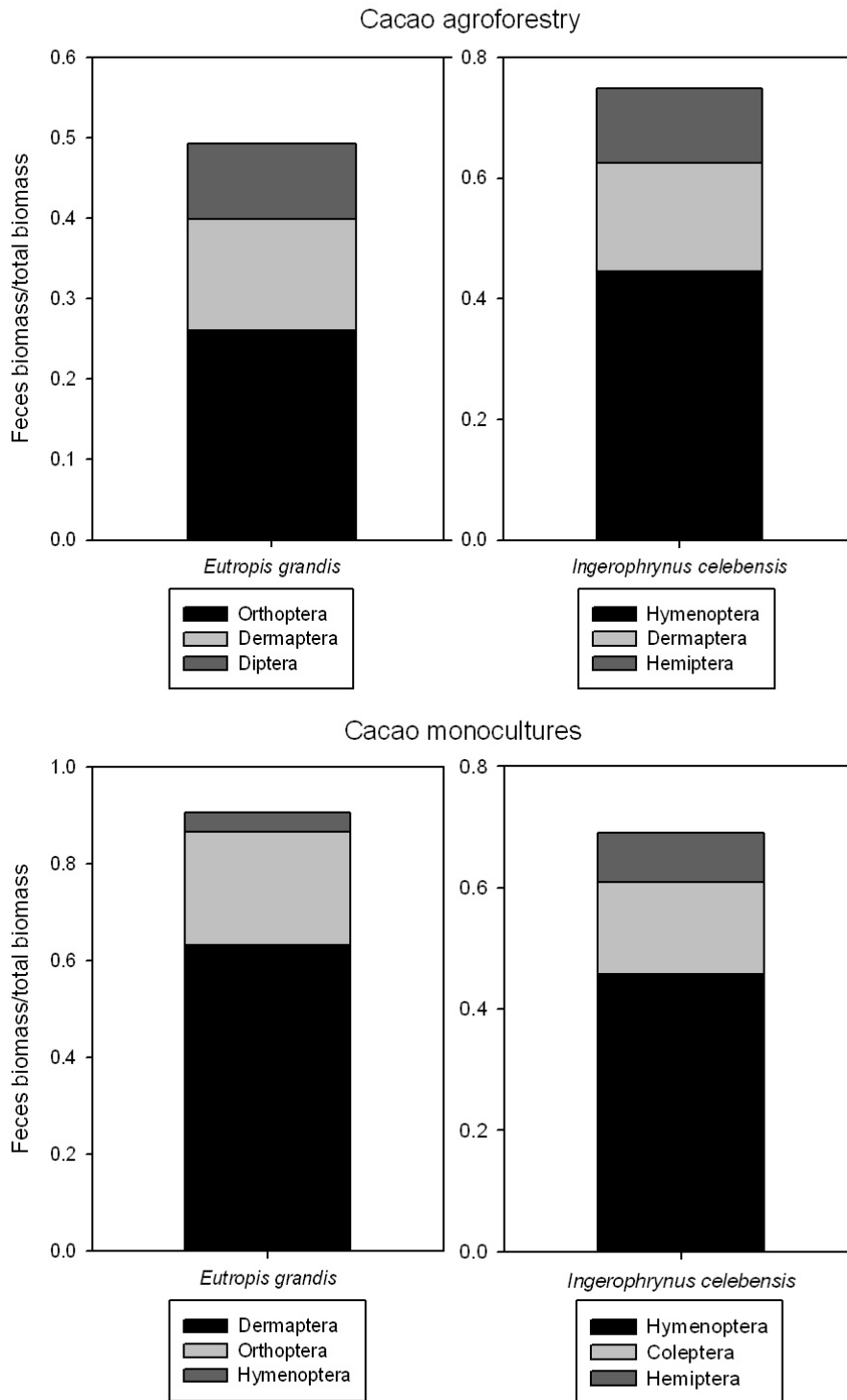


Figure 4.3 – Biomass removal of *Eutropis grandis* and *Ingerophrynus celebensis* between cacao agroforest and cacao monocultures. The skink is rather a generalist feeder whilst the toad is specialized on ants (hymenopterans; shown are the three most encountered arthropod orders). I equated hymenopteran preference with ants, because toads are highly unlikely to prey upon bees and wasps, and identified fragments were mainly ants. The two habitat types were defined from the 43 cacao plantations; cacao monocultures had a canopy cover of less than 25 %.

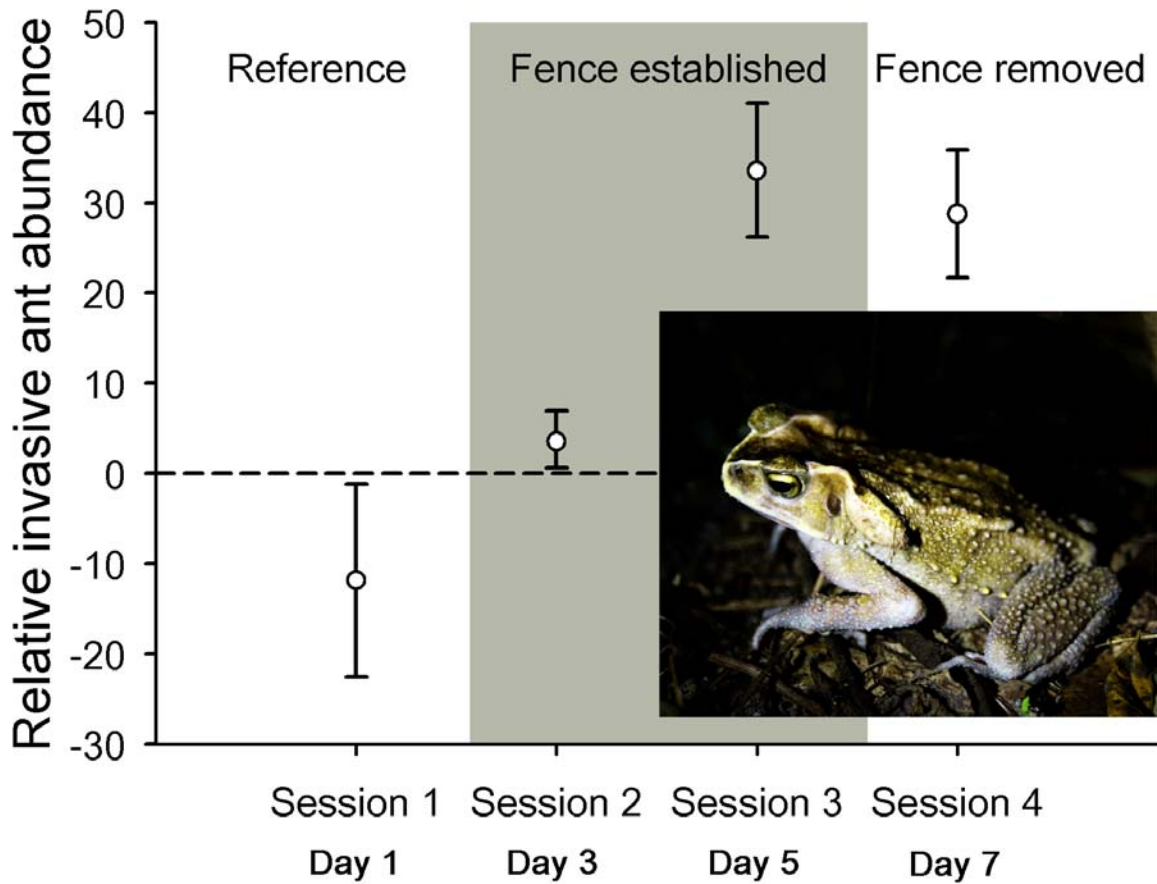


Figure 4.4 – Effects of native toad exclosure on invasive Yellow Crazy Ant (*Anoplolepis gracilipes*) abundance. Shown is the treatment effect of the exclosure fence (Session 2 and 3, grey) relative to the reference (Session 1). Fence removal (Session 4) served to show persistence of ant abundance changes over time. The photo shows a female Common Celebes Toad (*Ingerophrynus celebensis*). The means (black dots \pm 95 % credibility intervals) represent the relationship of ant abundance between treatment and control plots as derived from a Bayesian linear mixed effects model.

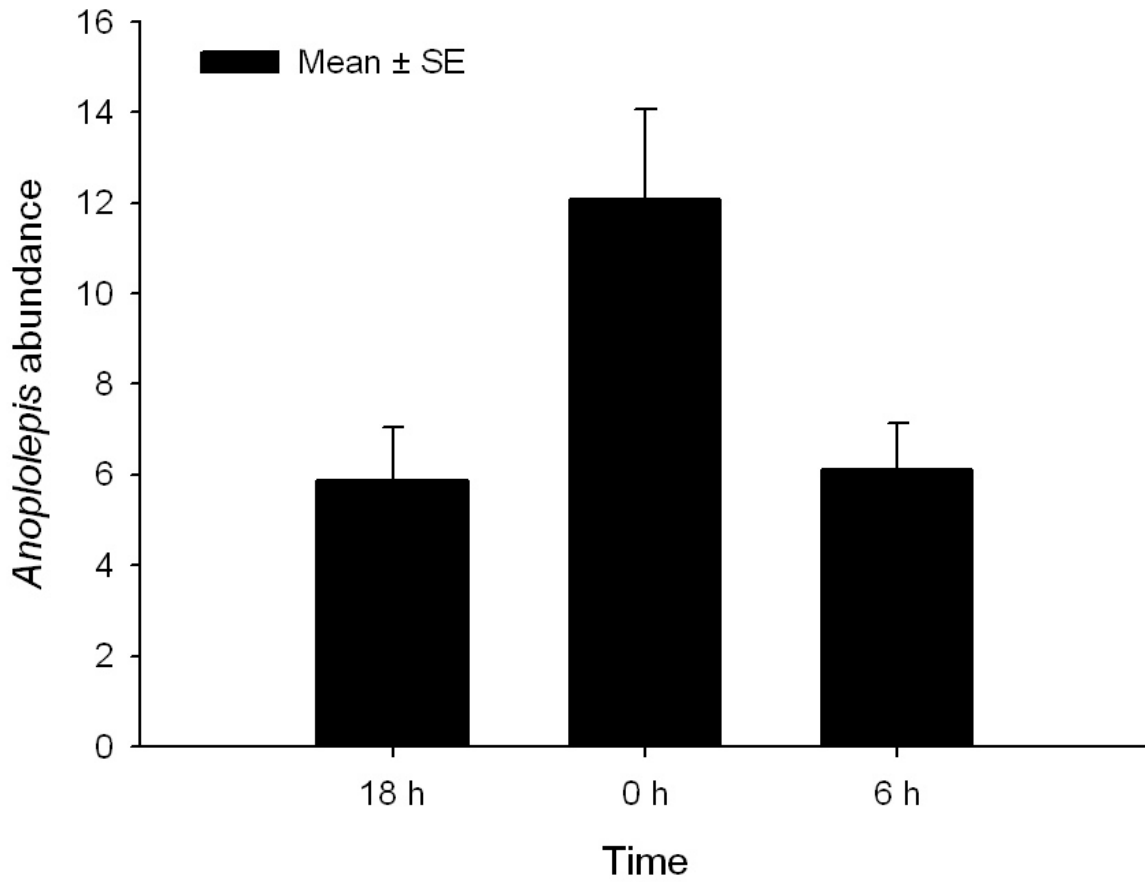


Figure 4.5 – *Anoplolepis* activity in the study region over night. I determined *Anoplolepis* abundance at six sites for one hour for each time step (i.e., at 18h, 0h, 6h). Throughout the day, however, activity patterns were found to be constant (Suwabe *et al.* 2009).

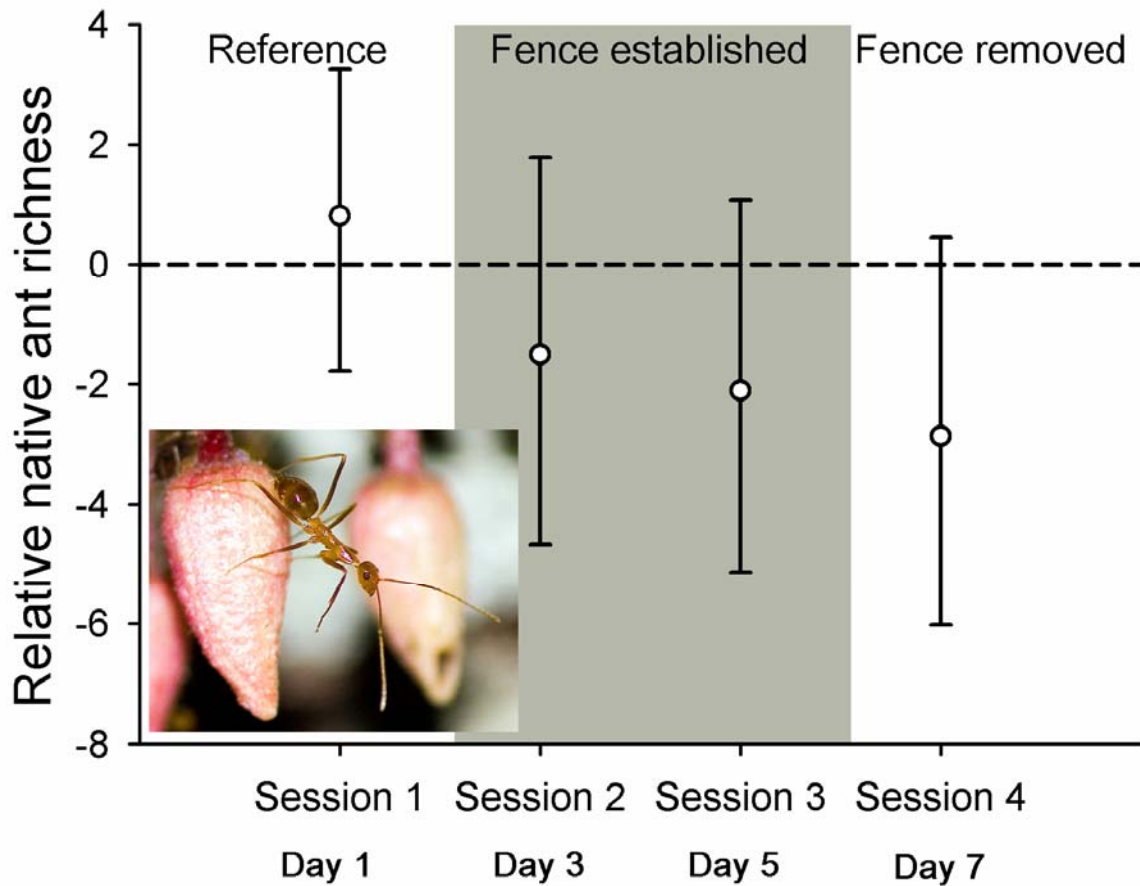


Figure 4.6 – Effects of toad exclusion on native ant diversity. Shown is the treatment effect of the enclosure fence (Session 2 and 3, grey) relative to the reference (Session 1). As in Fig. 4.4, fence removal (Session 4) served to show persistence of ant abundance changes over time. The photo shows *Anoplolepis gracilipes* on a cacao flower, where this species is tending homoptera (T.C. Wanger pers. observ.). The means (black dots \pm 95 % credibility intervals) represent the relationship of native ant species richness between treatment and control plots as derived from a Bayesian linear mixed effects model.

credibility intervals in the last two sessions *Session 3* and *Session 4*; 33.6 [26.2 to 41.1]), 28.7 [21.7 to 35.9]). These effects were not confounded by presence of the skink, because it is diurnal and not specialised on ants. In contrast, toads forage most actively at midnight, because their calling period has ended and their energy requirements are at their highest (T.C. Wanger and I. Motzke, pers. observ.; Wells 2001). *Anoplolepis* activity also peaked around midnight but was constant throughout the day (Fig. 4.5).

I found that overall mean ant diversity did not measurably differ between treatment and control plots in the reference sampling session, but decreased over time (0.8 [-1.8 to 3.2]; -1.5 [-4.7 to 1.8]; -2.1 [-5.1 to 1.1]; -2.9 [-6.0 to 0.45]; Fig. 4.6). As the credibility intervals of all sampling sessions overlap with zero, I found a strong trend but no effect of the manipulation (and, hence, *Anoplolepis* abundance) on ant diversity over time.

Discussion

Island endemics are often claimed to be inferior competitors to invasive species, because they have been released from selective pressures (Simberloff 2010). I show that an island endemic toad (*I. celebensis*), as a predator, negatively affects the noxious invasive *A. gracilipes*, and this, in turn, mitigates the impact of *A. gracilipes* on natural ant diversity. Thus, in contrast to an enemy-release effect, this is an invasive-naïvety effect: the alien prey species may not harbour anti-predatory defence against the novel endemic predator. This effect may be widespread and so offer resistance to biotic invasions.

For an invasive-naïvety effect to occur, the native species must possess certain defensive and dietary traits. The invasive success of the ant *A. gracilipes* is grounded in its tendency to aggregate in high densities, aggressiveness, and chemicals used for attack (Holway *et al.* 2002; Kenis *et al.* 2009). Bufonids have a tough skin capable of producing potent toxins (Zug *et al.* 2001), and amphibian skin can be distasteful for ants (Fritz *et al.* 1981). In addition, toads are sit-and-wait predators, sometimes exclusively feeding on ants

(Clarke 1974). As endemic toads likely have been ant specialists *before* the invasion occurred, their prey search image may be “pre-set” for an *Anoplolepis*-type of prey. Density dependence predation of the toads on the abundant invasive ants may be a likely explanation of the reduction of *A. gracilipes* abundance. In addition, there may be nutritious preferences for the invasive to the native ants such as essential amino acid composition. A preference for *A. gracilipes* may lead to reduction in their abundance due to toad predation. Based on skin defences and potential predefined feeding preference of many toads, there may be a general potential for bufonids as biocontrol agents; this area of conservation and invasion biology needs further research.

Intuitively, toads can only provide useful ecosystem services if they are abundant – yet, (endemic) amphibians are the most threatened vertebrates on the planet (Rowley *et al.* 2009). If toad populations are reduced as a result of land-use change and pesticide use (Relyea 2005; Wanger *et al.* 2010a), my results suggest that *A. gracilipes* can flourish as “ecosystem transformer” (Fig. 4.1). In Sulawesi, rapid expansion of these ants drastically depletes natural ant diversity (Bos *et al.* 2008). This may have a real economic impact because native ants in Southeast Asia have been shown to provide various ecosystem functions, including biocontrol of insect-mediated cacao pests (see Table 1 in Philpott & Armbrrecht 2006). On other islands, *A. gracilipes* affects litter decomposition and nutrient cycling (Dunham & Mikheyev 2010), trophic cascades (O'Dowd *et al.* 2003) and even the tourism industry (via displacement of a bird species; Feare 1999). These negative impacts may, however, take several decades to unfold fully; on Christmas Island, Yellow Crazy Ant populations exploded 60 years after its introduction (Abbott 2005).

The economic magnitude of the toad’s biocontrol service in cacao agroforestry systems is, however, conditional on parameters affecting cacao yield and *Anoplolepis*’ effectiveness as a predator of cacao pest insect vectors. In Sulawesi, both pest and disease occurrence are important determinants of cacao yield (Juhrbandt *et al.* 2010). Thus, the less effective

Anoplolepis is as a predator on disease vectors relative to the native ant species, intuitively more economical it is to have the toads in cacao plantations. It is possible that the time period to detect an effect of invasive ants on the native ant species in my study may be too short. However, it has previously been shown that *A. gracilipes* depletes native ant diversity in Sulawesi's cacao plantations (Bos *et al.* 2008); thus, I believe that my results indicate effects that will be evident over the long term.

Clearly then, it is important to maintain toads and other amphibian populations in cacao plantations to sustain ecosystem services in the future. Plantation management for leaf litter cover, and maintenance of intact canopy structure to buffer against temperature fluctuations, will benefit amphibian diversity (Wanger *et al.* 2009). This will also facilitate toad abundance in cacao agroforest and, hence, translate into ant biomass removal. In contrast, *A. gracilipes* invasions are facilitated by thinned canopy, which alters microclimatic conditions in cacao plantations and enhances the frequency of cacao disease outbreaks (Bos *et al.* 2008). It is through the beneficial effect for the toads in cacao agroforest that biomass removal of ants will increase. Managed sensibly, native biodiversity offers great potential to provide invasion resistance (Carlsson *et al.* 2009) and likely contributes to sustainable, pesticide-reduced crop production.

*Land-use change, tropical biodiversity, and ecosystem services –
Southeast Asian amphibians and reptiles in focus*

T.C. Wanger

Chapter 5

PESTICIDES AND TROPICAL BIODIVERSITY

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Frontiers in Ecology and the Environment – 2010, 4,178-179

STATEMENT OF AUTHORSHIP

PESTICIDES AND TROPICAL BIODIVERSITY

Frontiers in Ecology and the Environment – 2010, 4,178-179

Wanger, T.C. (Candidate)

Collected the pesticide information in Indonesia, had the initial idea, wrote the paper, and acted as corresponding author.

I hereby certify that the statement of contribution is accurate.

Signed

Date 12/11/2010

Rauf, A.

Contributed to the general discussion of the manuscript and helped to establish contacts with the relevant institutions to gather pesticide information.

I hereby certify that the statement of contribution is accurate and I give permission for the inclusion of the paper in the thesis.

Signed

Date 15/11/2010

Schwarze, S.

Supervised household surveys, analysed data on pesticide expenditures, and contributed to the general discussion of the manuscript.

I hereby certify that the statement of contribution is accurate and I give permission for the inclusion of the paper in the thesis.

Signed

Date 12/11/2010

Chapter 5 - Pesticides and tropical biodiversity

The UN declared 2010 as the “International Year of Biodiversity” to raise awareness of both the value of biodiversity for improved human well-being, and human impacts on the world’s ecosystems (www.cbd.int/2010/welcome/). Besides informing readers about threats to biodiversity such as climate change and habitat loss, the website provides recommendations on how various stakeholders and interested parties can help protect biodiversity. Wise consumption choices – using products obtained through sustainable production – is listed as a top priority.

Actions such as the “International Year of Biodiversity” and articles about the tropical biodiversity crisis (Bradshaw *et al.* 2009) are invaluable for communicating related threats and addressing potential mitigation. However, the debate has so far largely neglected one issue that is gaining greater importance in tropical ecosystems – namely, increased pesticide application. Pesticide expenses in tropical countries with the highest deforestation rates increased from US\$2 million in 1980 to US\$73.1 million in 2006 (FAO 2009). Small-scale farmers in the tropics may be more likely to use pesticides excessively if, for instance, pesticide prices remain stable or decrease in parallel because producers often sell pesticides with expired patents at low cost. In Sulawesi (Indonesia) between 2000 and 2006, pesticide prices remained stable (US\$3.30 L⁻¹; Balai Penelitian Teknologi Pertanian Palu, pers. comm.) but pesticide use increased (US\$7.20 to US\$9.00 ha⁻¹; $n = 279$ households; unpublished data). As a result, pesticides may be applied as often as once every 2 weeks, while application is recommended by the manufacturer once every 4 months (Fig. 5.1). Such intensified pesticide use has substantial negative impacts on the early reproductive stages of non-target organisms (Relyea 2005), and may also counteract the beneficial effects of tree-shaded crop production that can be of high conservation value for maintaining biodiversity.

In expanding tropical agricultural lands, such as those devoted to cacao, oil palm, or soy, pesticides are likely to play a key role for “biodiversity friendly” production. In the

tropical biodiversity debate, pesticide effects are, however, critically under-represented. To my knowledge, through an ISI Web of Science search (http://thomsonreuters.com/products_services/science/science_products/a-z/web_of_science, performed on 31 March 2010), 36 published studies have investigated pesticide effects on – mostly invertebrate – tropical biodiversity, and only two such studies have been conducted in Southeast Asia. The benefits to biodiversity from tree-shaded cacao production are well known. However, future management recommendations should include results from experimental studies evaluating the dosage or application threshold of pesticides in tropical agricultural landscapes, for a more realistic assessment of the biodiversity–pesticide relationship. Ultimately, farmers should pursue organic crop production to preserve some of the remaining biodiversity and related ecosystem services. Nevertheless, these efforts must yield better prices than non-organic production and succumb to stringent control of the producer so that further cropland expansion is less likely.



Figure 5.1 – Pesticide applications in cacao plantations in Sulawesi, Indonesia.

Conclusions

In summary, this work shows that land-use change has a profound impact on amphibians and reptiles, with the former more sensitive and heavily impacted than the latter. If shade and leaf-litter structure of the plantations are properly maintained, they substantially facilitate protection of herpetological diversity. However, the increasing use of pesticides poses a substantial threat beyond structural habitat modification, because non-target organisms are poisoned outright and killed, and, hence, plantations lose conservation value for biodiversity. From studies conducted in temperate regions, amphibians, and reptiles to a lesser extent, are sensitive to pesticide application. It has been shown, for example, that application of the commonly used pesticide atrazine is a powerful endocrine disruptor (e.g., it de-masculinizes male frogs) and, hence, it interferes with population structure (Hayes *et al.* 2010). Glyphosate, the most commonly used herbicide, has led to substantial mortality in amphibians and is also known to cause genetic damage in reptiles at higher concentrations (e.g., Relyea 2005; Sparling *et al.* 2006).

A recently conducted pilot study in Sulawesi indicated severe negative pesticide effects on both taxa; even moderate herbicide application of >2.5 l/ha and >0.5 l/ha substantially depleted richness and dominant species abundance of amphibians and reptiles, respectively. Experimental trials revealed that amphibians are unable to persist in plantation habitats if either herbicide or insecticides are applied. The same is true for reptiles, but this taxon seems to be less sensitive towards insecticides (Wanger *et al.* in prep). Besides increasing knowledge of how amphibians and reptiles respond to land-use change, I strongly recommend the targeting of pesticide effects when structural improvements of agricultural plantations are assessed. Otherwise, effective preparation of agricultural landscapes for biodiversity conservation will be very difficult, if not impossible.

I also show for the first time that amphibians control invasive ants with effects on native ant diversity. These predator-prey interactions in Sulawesi's cacao plantations may potentially have implications for crop yield. If future research activities can experimentally establish the link between endemic toads and cacao yield, it provides an even more important argument for amphibian conservation than this study does. While valuing nature is not without criticism and can only be part of the conservation puzzle (e.g., Redford and Adams 2009), its use depends on the region and specific situation. Sulawesi's unique herpetofauna is of little interest for smallholder farmers primarily interested in increasing their monthly income from cacao. If anything is to change in the perception of local people, then biodiversity must have an obvious (economic) value to them. To date, the main benefit from amphibians to humans has been in the nature of a genetic resource. For instance, they are used as model organisms in the laboratory and they provide skin peptides to produce medical products (Smith & Stoskopf 2007). In addition to addressing the effects of pesticide use on amphibians and reptiles, much more research is needed on the ecosystem services that they provide to humanity.

Appendix

Appendix 1 – Acquisition of environmental variables

Distance to forest was evaluated based on recent GIS maps while distance to the nearest water body (i.e., flowing water body with a width >50 cm) was measured in the field. To evaluate the percentage of canopy cover, I took five 180° photographs of the canopy using a fisheye lens on a digital camera (Canon Powershot, 5 megapixels). The camera was set up on a 1.70 m tripod and pointed directly towards the sky. Pictures were then analyzed using the ImageJ software (<http://rsbweb.nih.gov/ij>). I determined canopy heterogeneity using the lacunarity measure of the same pictures using the FracLac plug-in in ImageJ. Percent leaf litter cover was estimated visually in these five patches by two people independently, and results compared afterwards; an area was classified as having 0 % leaf litter cover if only the bare ground was visible – conversely, an area had 100 % leaf litter cover if no ground was visible. Other percentages were rated between these two extremes. To measure leaf litter thickness, leaf litter was removed down to the soil from a 10 cm patch within these five areas and the distance from the soil to the top of the leaf litter measured with a ruler. To estimate shrub height from these five locations, I used the average height of 10 representative plants. For an estimate of shrub density I counted the number of plants in a 50 x 50 cm square in corner of the plot and used the mean of all five locations. I estimated shrub cover as – 0 % shrub cover means no plants in the locations and only leaf litter and/or bare soil is visible. In contrast, 100 % shrub cover means no leaf litter and bare soil are visible in the locations. Again, other percentages were rated between these two extremes. For 12 plots, leaf litter and shrub cover estimates were validated with 180° photographs of the five locations. I only counted stones for the stone block variable when the diameter was ≥ 50 cm.

Pesticide-use interviews - details

Plot owners were asked for the pesticide brand used and the number of pesticide container caps applied per month per plot. I then asked the owner to show me the original container and checked (1) the amount of pesticide per cap of the container; (2) the amount of caps / 10 liters of water as indicated in the manual; and (3) dosage instructions. Based on these values, I calculated the amount of pesticide applied per plot per year.

Appendix 2 – Bayesian model evaluation – a brief overview

Although Bayesian methods are increasingly used in ecology, I feel that many readers may not be familiar with the interpretation of my results and, therefore, provide a short overview. The smallest Deviance Information Criterion (DIC) value indicates the model that best (i.e., most parsimoniously) approximates reality based on a set of *a priori* candidate models given the data to hand and any prior information (Spiegelhalter *et al.* 2002). Here, I used uninformative priors due to lack of relevant previous work in this area, such that these assessments were strictly data based. The Δ DIC is the difference between the DIC values of the “best” model and the model of interest. Similar to the Akaike Information Criterion (AIC), a Δ DIC ≤ 2 indicates good support for a model relative to others in the model set (Burnham & Anderson 2002; McCarthy 2007).

The results of the hierarchical regression are displayed graphically as recommended by Qian and Shen (2008), because it allows easier assessment of manipulation changes. Points represent the mean of the posterior distribution (“mean” in this paragraph) while lines are 95% credibility intervals. When evaluating the results of the hierarchical regression, the difference of the mean and credibility intervals (the interval within which there is a 95% probability that the true value resides), in relation to zero, is important. The further the mean is away from zero, the stronger the tendency (trend) of an effect. When credibility intervals do not overlap zero, a true effect can be confidently assigned. For more details on Bayesian statistics see for example McCarthy (2007).

Appendix 3 – Results of the Bayesian correlation of the randomized original data (Sobs) and the Bootstrap species richness estimator (Boot)¹.

		Amphibians			Reptiles		
		<i>mean</i>	<i>Low95%CI</i>	<i>Up95%CI</i>	<i>mean</i>	<i>Low95%CI</i>	<i>Up95%CI</i>
Primary forest	<i>CorCoef</i>	0.989	0.9316	0.9997	0.5348	-0.4547	0.9617
	<i>mSobs</i>	3.699	1.864	5.417	0.8079	0.3682	1.241
	<i>mBoot</i>	5.913	2.921	8.697	0.9944	0.5405	1.445
Secondary forest	<i>CorCoef</i>	0.7816	0.2066	0.9752	0.9721	0.8608	0.9979
	<i>mSobs</i>	3.142	2.162	4.133	4.619	2.874	6.406
	<i>mBoot</i>	4.064	3.039	5.096	6.982	4.623	9.392
NS-cacao agroforest	<i>CorCoef</i>	0.9836	0.9149	0.9988	0.9131	0.5696	0.9915
	<i>mSobs</i>	2.131	1.381	2.86	5.867	3.828	7.847
	<i>mBoot</i>	2.908	1.992	3.797	8.085	5.801	10.32
PS-cacao agroforest	<i>CorCoef</i>	0.6355	-0.1659	0.9591	0.933	0.5995	0.9969
	<i>mSobs</i>	0.7393	0.3959	1.086	4.575	2.427	6.718
	<i>mBoot</i>	1.065	0.6382	1.499	7.15	4.095	10.18
Open areas	<i>CorCoef</i>	0.5348	-0.4547	0.9617	0.8931	0.2907	0.9981
	<i>mSobs</i>	0.8079	0.3682	1.241	2.805	1.489	4.02
	<i>mBoot</i>	0.9944	0.5405	1.445	3.92	2.016	5.707

¹ Interpretation of the results; high positive values of the correlation coefficient (CorCoef) indicate a positive correlation between the two variables of interest. To assess the strength of the correlation between two variables, the overlap of the credibility intervals (Low95%CI and Up95%CI) is of interest; the higher the overlap of the intervals, the stronger the correlation. *NS-cacao agroforest* = natural shaded cacao agroforest; *PS-cacao agroforest* = planted-shaded cacao agroforest

Appendix 4 – Validation of LLT treatment. Removal success of all groups found, based on 24 rice bags.

	<i>Reptilia</i>	<i>Amphibia</i>	<i>Hymenoptera</i>	<i>Coleoptera</i>	<i>Lepidoptera</i>	<i>Myriapoda</i>	<i>Arachnida</i>	<i>Total</i>
Mean removal success [%]	100%	100%	94%	97%	100%	100%	97%	98%
SD	0%	0%	6%	6%	0%	0%	8%	2%

Appendix 5

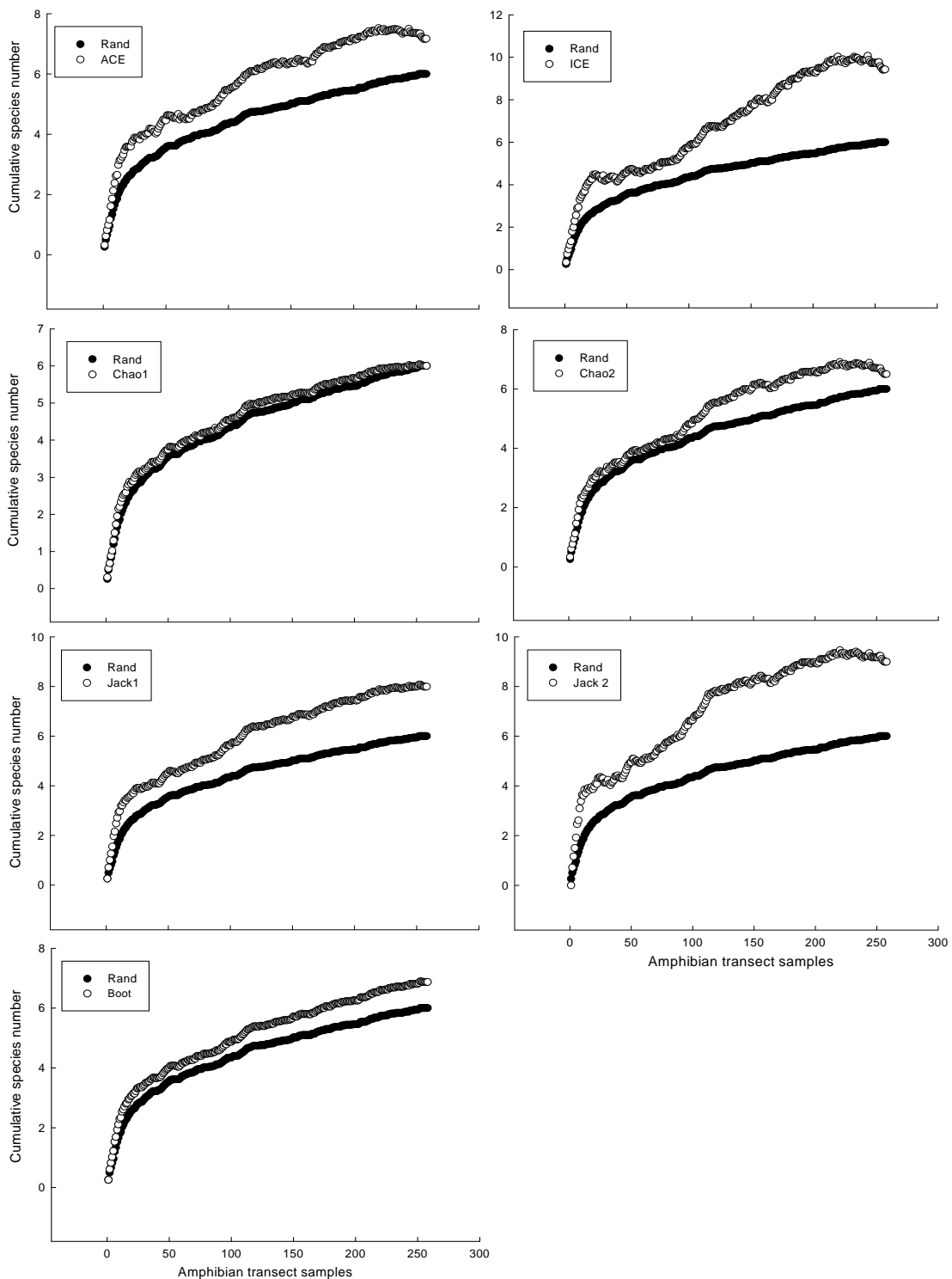


Figure A1 – Species richness estimators (Abundance-based Coverage Estimator (ACE), Incidence-based Coverage Estimator (ICE), Chao 1 estimator (Chao1), Chao 2 estimator (Chao2), Jackknife 1 estimator (Jack1), Jackknife 2 estimator (Jack2), and Bootstrap estimator (Boot)) and the randomized original amphibian data (Rand).

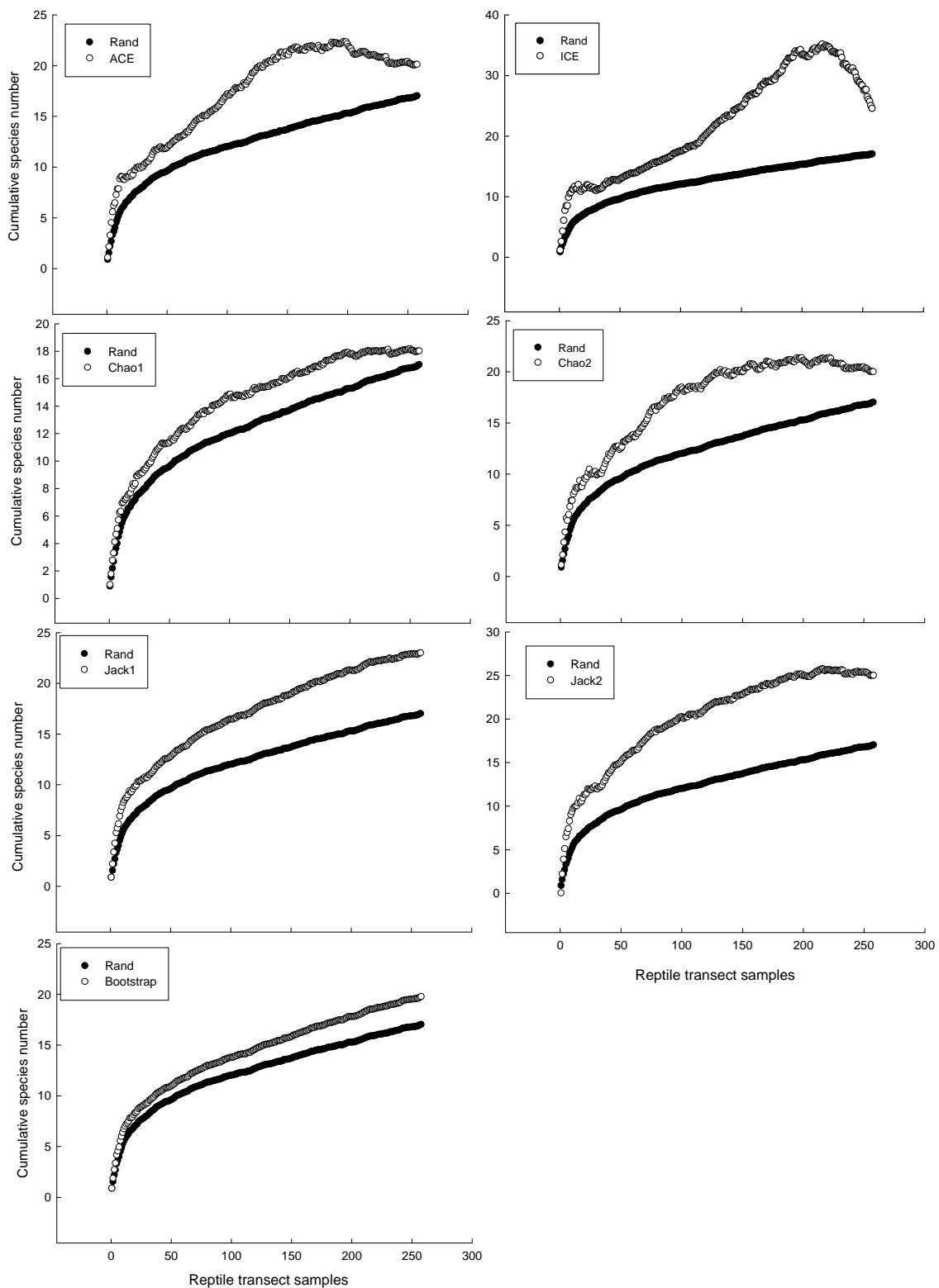
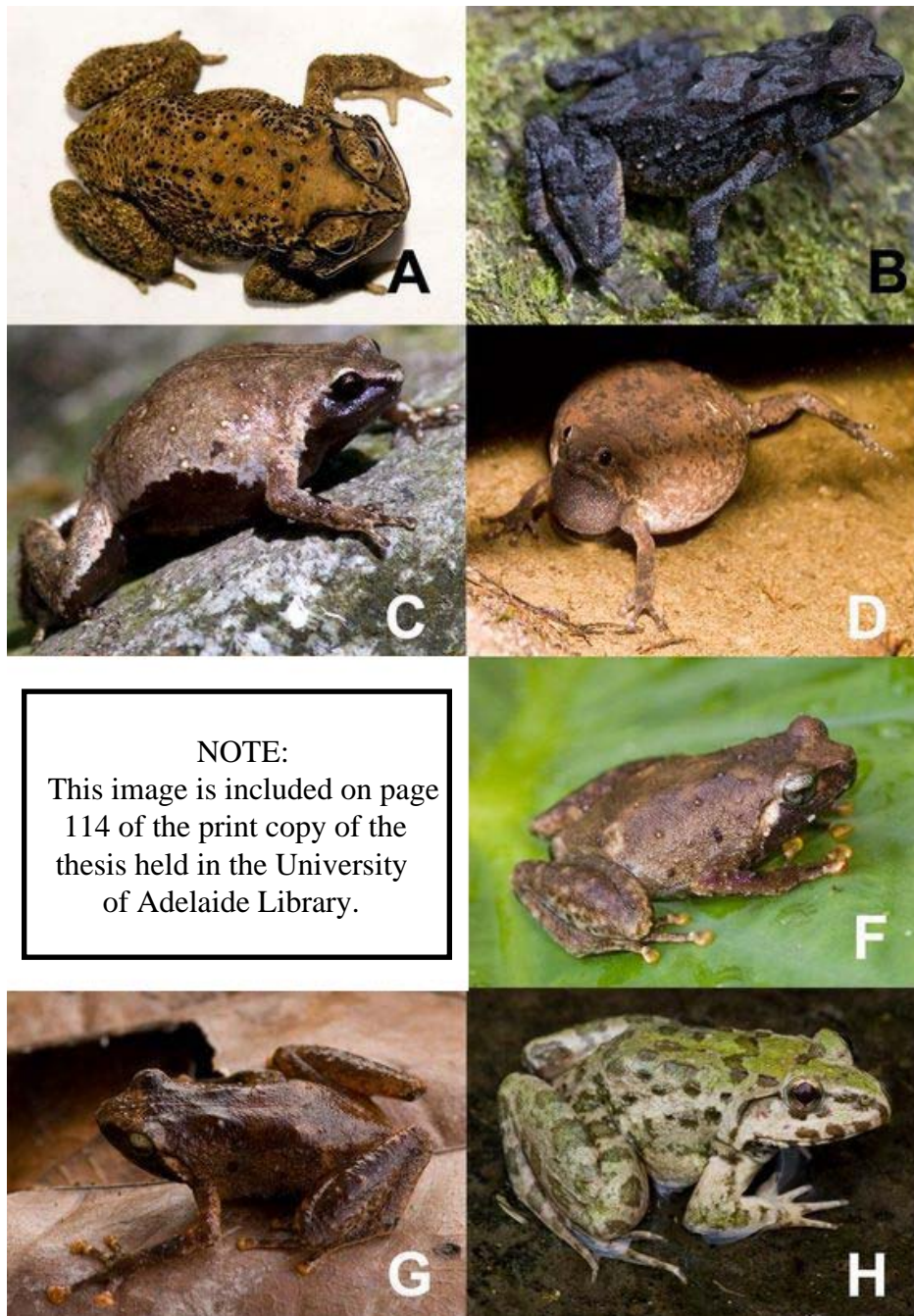
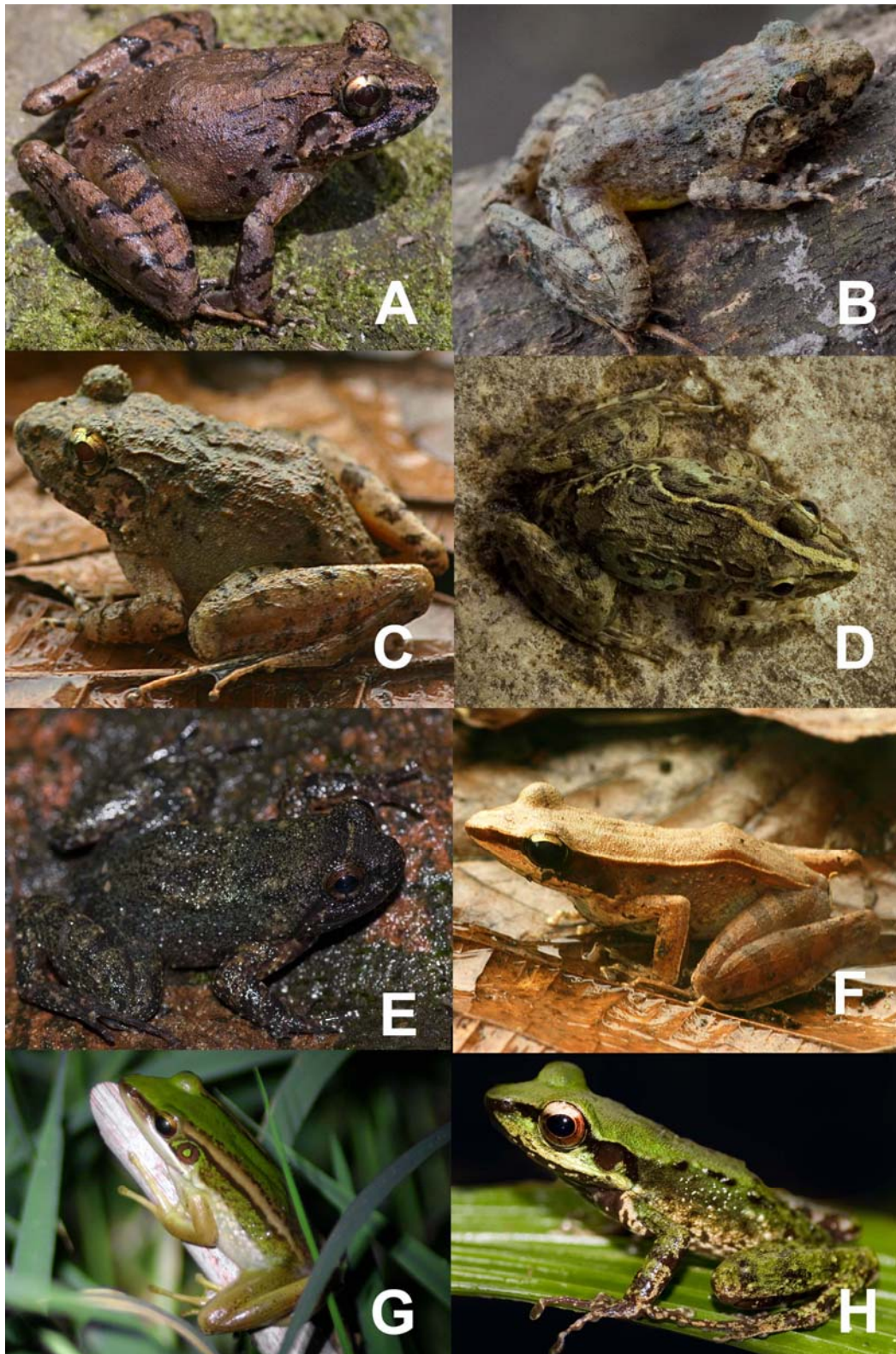


Figure A2 – Species richness estimators and randomized original reptile data (Rand).
 Abbreviations are the same as in Fig. A1.

Appendix 6



Panel 1 - Bufonidae: A = *Duttaphrynus melanostictus*; B = *Ingerophrynus celebensis* (juvenile); **Microhylidae:** C = *Callulops* n. sp.; D = *Kaloula baleata*; E = *Kaloula pulchra* (West Malaysia; Photo by U. Manthey); F = *Oreophryne* n. sp.1; G = *Oreophryne* n. sp.2; **Dicroglossidae:** *Fejervarya cancrivora*



Panel 2 – Dicroglossidae: A = *Limnonectes* cf. *modestus*; B = *Limnonectes* cf. *arathooni*; C = *Limnonectes* cf. *heinrichi*; D = *Fejervarya limnocharis*; E = *Occidozyga semipalmata*; **Ranidae:** F = *Hylarana celebensis*; G = *Hylarana erythraea*; H = *Hylarana macrops*.



NOTE:

This image is included on page 116 of the print copy of the thesis held in the University of Adelaide Library.

Panel 3 – Ranidae: A = *Hylarana mocquardii*; **Rhacophoridae:** B = *Polypedates leucomystax*; C = *Rhacophorus* sp. (Photo by J.A. McGuire)



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Panel 4 – Agamidae: A = *Bronchocela celebensis*; **Gekkonidae:** B = *Gecko gecko* (West Malaysia; Photo by U. Manthey); C = *Cyrtodactylus jellesmae*; D = *Cyrtodactylus spinosus* (reproduced with permission from the authors and Allen Press); E = *Cyrtodactylus wallacei* (reproduced with permission from the authors and Allen Press); F = *Gecko monarchus* (West Malaysia; Photo by U. Manthey); G = *Gehyra mutilata* (Photo by G. Gillespie); H = *Hemidactylus frenatus* (Thailand; Photo by U. Manthey)

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Panel 5 – Gekkonidae: A = *Hemidactylus platyurus* (Thailand; Photo by U. Manthey);
Scincidae: B = *Emoia atrocostata* (Photo by G. Gillespie); C= *Eutropis* n. sp.; D = *Eutropis multifasciatus*; E = *Eutropis rudis*; F = *Parvosцинus* sp.; G = *Sphenomorphus* cf. *textus*; H = *Sphenomorphus nigrilabris*.

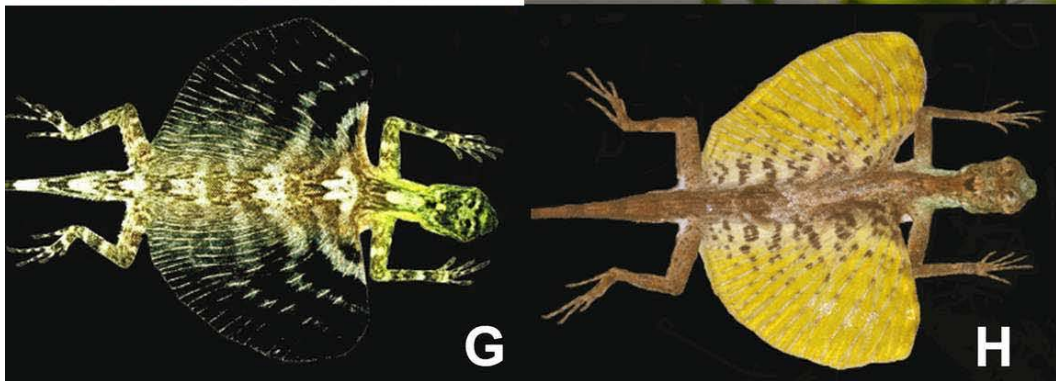
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Panel 6 – Scincidae: A = *Sphenomorphus tropidonotus* (Photo by G. Gillespie); B = *Sphenomorphus* cf. *variegatus*; C = *Tropidophorus baconi* (Photo by J.A. McGuire); D = *Lamprolepis smaragdina* (Photo by S. Howard); **Dibamidae:** E = *Dibamus celebensis* (Photo by G. Gillespie); **Varanidae:** F = *Varanus salvator*; **Agamidae:** (both pictures reproduced with permission from the authors and Allen Press): G = *Draco walkeri*; H = *Draco spilonotus*.

Appendix 7 – Journal Cover of Journal of Applied Ecology. Chapter 2 was the cover article of the August 2009 issue.

NOTE:

This appendix is included on page 120 of the print copy of the thesis held in the University of Adelaide Library.

Appendix 8 – Media features of Chapter 4. Included are the links to various news articles and the article featured by Science News; [ScienceNews](#), [Wired Science](#), [JakartaGlobe](#), [KeSimpulan \(in Bahasa\)](#), [FinancialTimes](#) (German), [Süddeutsche Zeitung](#) (German) , [FocusOnline](#) (German), [Bild](#) (German), [Deutschlandfunk](#) (German), [n*tv](#) (German), [Scinexx](#) (German), [Greenpeace](#) (German).

NOTE:

This appendix is included on pages 121-122 of the print copy of the thesis held in the University of Adelaide Library.

Appendix 9 – PhD thesis corrections after examination

I thank the two examiners for their positive feedback and insightful comments on my thesis.

My responses are given below the comments and where necessary they were also included in the thesis. Please note that my thesis is a ‘thesis-by-publication’, and as such I was advised to use the published manuscripts and to only make minor changes on methods (avoid repetition, include supplementary material information where necessary), citations, and general style. The introduction and conclusion section are the only exceptions, because the former had to be more specific than the original paper for the thesis, and the latter is the only unpublished part of the thesis.

I include additional references in the reference list below only if they had not been listed in the main thesis document.

This document is included with the thesis as Appendix 9.

Thomas C. Wanger, Stanford, 04 May 2011

Examiner 1

Introduction

1. I was confused by the fact that the text presented here is not, in fact, the text of the Sodhi et al. (2010) paper. Some parts are clearly experts and it is missing a lot. It should be made clear to the reader that this chapter draws from, but is not the same as, Sodhi et al.

The introduction is based on the published Sodhi et al. 2010 Biological Conservation paper. It is not an exact copy of this paper, because the focus was too broad and I felt it needed to be more focused to blend in with this thesis.

2. Some of the concepts discussed in very vague terms. For example on Page 9 you state that *“but in dynamic, human-dominated landscapes, only a diversity of species can guarantee resilience”* ... what is actually meant by this? How does a diversity of species guarantee resilience? And what in fact is a diversity of species? Are no other factors important? Also I agree that the wording of the sentence was not clear. The sentence now reads: *“Agricultural land use is often focused on few species and local processes, but in dynamic, human-dominated landscapes, species diversity will substantially enhance resilience (i.e. the capacity to re-organize after disturbance)”*.

3. There are also some rather vague and unsubstantiated claims – for example on Page 9 you state that *“While the factors affecting invertebrates and the services they provide are comparatively well understood ... “* .. do you really believe this? It is patently untrue given that invertebrates make up the vast majority of faunal diversity in a tropical forest. You don't need to overstate the case to explain how important it is to study amphibians and reptiles. You need to provide an accurate and objective context to your work. Elsewhere on Page 9 you state that good management requires *“good knowledge of the effects of land-use changes and drastically increasing pesticide use on biodiversity, is crucial”*. This is a very limited perspective and biased towards your research focus. What about invasive species? Climate change? Fertilizers? Hormones? Trade in wild species??

The sentence is changed and now reads:

“In a land use change context, we know little about the factors affecting amphibians and reptiles in particular in Southeast Asia. Even less is known about the services that these taxa provide. However, realistic management recommendations for sustainable agricultural landscapes require a good and general knowledge of the effects of land-use changes on biodiversity. Besides other factors, the effects of pesticide use on biodiversity are poorly known but must urgently be evaluated.”

Chapter 1.

1. As for the Introduction the text here is not the same as the final version published in Wanger et al. (2010) *Con Biol*. Why?

The text is not identical with the published paper, because I felt that it was necessary to include parts of the supplementary material of the paper in the methods section (see also initial remarks above).

2. Page 15, opening sentence. This is a strange claim. Most of tropical forest biodiversity is simply incapable of being able to survive in agricultural areas .. so rather than being forced to survive there it will simply go extinct.

The opening sentence now reads:

“Increasing deforestation rates and subsequent land-use change in the tropics will force the surviving tropical biodiversity to reside in human-dominated landscapes such as agricultural areas (Bawa *et al.* 2004; Foley *et al.* 2005).”

3. Page 15. It is not clear to me how the conservation value of agricultural habitats can be assessed by “*examining the factors driving diversity patterns within agricultural habitats*” ... this would simply tell us which factors drive diversity in agricultural habitats (possibly dominated by generalist species) .. not whether such habitats hold species that are important to conservation. Comparison to less disturbed areas is essential for assessments of conservation value, followed by detailed assessments of environmental correlates of species of conservation concern.

The sentence was clarified and now reads:

“The conservation value of agricultural habitats can be assessed by first comparing diversity-patterns across land-use modification gradients (i.e. open to pristine habitats) (e.g., Barlow *et al.* 2007) and then examining the factors driving diversity patterns within agricultural habitats (e.g., Clough *et al.* 2009b).”

4. Page 16. You state that all habitat categories are based on canopy cover and heterogeneity. What is meant by heterogeneity here?

As stated on p.15, canopy heterogeneity refers to the patchiness of the canopy (i.e., “many small open patches vs. one large open patch in the canopy”). In the methods section on p.21, I state briefly that “[f]or a measure of canopy heterogeneity, I calculated the lacunarity index [from] all canopy pictures.”

5. Page 16. Your definition of secondary forest is not true secondary forest (clear felled and left to recover) but of degraded (through resource extraction) primary forests. There is an important distinction

I do agree that it would be more appropriate to refer to degraded primary rather than secondary forest. In order to keep the chapters closer aligned to the published papers I kept using the term secondary forest but rephrased the sentence giving the distinction between primary to secondary forest as follows:

“Here, I refer to secondary forest as degraded primary forest, where large trees had been cut in the past and for example rattan, and fire wood was extracted.”

6. Some measure of the size of the different habitat areas would be useful to aid interpretation

It is difficult to provide areas for the sampled habitats due to severe habitat conversion from primary forest into plantation habitats. The values available from the study area are from 2002 but do not include all sampled habitats: broad-leafed forest – 6103 km²; perennial crops (coffee and cocoa) – 190 km²; grassland – 220.5 km² (Erasmí and Priess 2007). Because these values are outdated and not available for all habitats, I did not include them in the thesis.

7. Page 19. How do you classify a water body? Does it need to be of a minimum size?

The definition of a water body, as used in the thesis, is that it had to be flowing water and wider than 50 cm. I now mention this also in Appendix 1.

8. What is the motive for landowners to apply pesticide to secondary forests?

This is an important question. This is unfortunately not known, hence the reason why these plots were excluded from an analysis of pesticide effects on vertebrates and invertebrates in Sulawesi in a forthcoming paper. Further discussion with the landowners may shed light on this question.

9. I am impressed that you managed to identify all individuals in the field. Were no voucher specimens needed to be taken for more difficult groups of small frogs for example?

I did identify species in the field and took pictures of all species in the field laboratory that were sent to the leading expert in the region for confirmation. While I certainly tried my best to get the most accurate identification possible, I do agree that I might have missed cryptic species.

10. The question of pitfall trap utility depends on your objective more than anything else.

Generally speaking pitfall traps collect different species to active searches. They are also considerably less biased to observer effects. Your captures (83 and 118 amphibians and reptiles respectively) of active searching methods are extremely low which limits the inferences you can draw from the data.

As I briefly state, the reason for not using pitfall traps was that I did not have the resources to maintain a statistical robust pitfall trap setup. On p.67 I also provide more details on which species I likely have missed. In addition, one has to keep in mind that herpetological diversity in Sulawesi is generally lower compared to its neighbouring islands such as Borneo, for example.

11. You should provide more justification for some of your analytical methods. What, for example, are the advantages of using Bayesian correlation to test matching between observed and estimated measures of species richness?

While there may be no obvious advantages to use Bayesian correlations to test for matching of observed and estimated measures of species richness, there is justification to use Bayesian methods for other analysis conducted in this study and thesis (model is fitted to the data rather than vice a versa; it is easier and more intuitive to code models and represent uncertainty; ways to present results graphically; as mentioned in the text, the approach used to compare species rank abundance curves is more suitable for small sample sizes). To follow one consistent analytical approach throughout, I decided to use Bayesian analysis for the whole study and thesis, and not to mix up different statistical methods.

12. Page 21. You have a comprehensive array of analyses here. Your choice of analytical approaches seems sensible but you should try and give more background on why you are doing certain analyses in the first place. What makes them interesting and important? You don't need to explain why you didn't calculate the Simpson diversity index as you have not first made it clear that it would be desirable to do so.

See my response to comment 11.). I deleted the statement of the Simpson index.

13. Page 24. Some of your sentences do not make sense here – e.g. “I found a positive effect and trend of rainforest and secondary forest on species richness” what is meant by this?

This sentence interprets the results from the Bayesian modelling. I explain Bayesian Model evaluation (i.e. trend and effect) in Appendix 2.

“When evaluating the results of the hierarchical regression, the difference of the mean and credibility intervals (the interval within which there is a 95% probability that the true value resides), in relation to zero, is important. The further the mean is away from zero, the stronger the tendency (trend) of an effect.”

14. I sometimes get the impression that you have needlessly complicated analyses. For example it would be far more intuitive, I feel, to present simple species-abundance curves instead of the comparing credibility intervals of parameters for log-normal and gamma models. It is unnecessarily complex and provides the same result. You need to be careful about using methods just because they are available rather than being necessary to draw the strongest and clearest inferences.

The reason I used the approach for species rank abundance models is:

“Using a Bayesian instead of a frequentist generalized linear model (GLM) approach to compare Species-Rank-Abundance curves has the advantages that it is suitable for small sample sizes and more amenable hierarchical data structures (Golicher *et al.* 2006).”

.. And in addition I wanted to try something novel.

15. In discussing results, especially patterns of beta-diversity, recognition needs to be made of the possible bias from your low levels of capture success. It is difficult to imagine that there are not substantially more species awaiting to be sampled in the primary forest habitat (and this would not be shown by your accumulation curves and estimators as your sampling method only evaluates a subset of the total community)

Indeed, as mentioned in chapter 3, there are tenth of species awaiting formal description and some species likely have been missed. By not using pitfall traps I likely have missed certain species – with a bias towards more species-rich habitat. This may have caused a bias in the results of beta diversity patterns. In the thesis I write now:

“Note, however, that not using pitfall traps may have lead to missing more species in some but not other habitats. Depending on the strength of this effect, it may have biased my estimates of additive diversity.”

Chapter 2

1. It is quite a big claim to link studies on patterns of biodiversity in agricultural landscapes to poverty alleviation ...

If we agree that biodiversity loss results in loss of ecosystem function/services and resilience of a system against climate change, I think it is a valid claim to make that biodiversity protection will “assist [...] poverty alleviation” by affecting crop yield.

2. Same questions regarding definition of habitat variables and site description as for previous chapter

Please refer to my answers to the comments about habitat classification and site description in chapter 1.

3. Page 41. Your double identification process is helpful but it doesn’t “assure” identification .. there are doubtless various cryptic and poorly described species from this region

The sentence now reads:

“[...] this double [photo] identification process re-confirmed correct identification.”

4. **Page 41. Why was it necessary to employ so many richness estimators? Especially when you then go on to use observed species richness.**

I wanted to circumvent the selection-problem of one of several appropriate estimators by employing a selection of the most suitable estimators. Evaluation of sampling completeness seems more realistic to a range rather than a fixed estimated value.

5. **Page 48. Remember that your estimates of completeness of sampling effort refer only to the subset of species that are susceptible to this sampling method ... and not the fauna as a whole**

It is true that the results of sampling completeness may be biased because the number of species missed due to the sampling method in primary compared to disturbed habitats is likely larger.

6. **Page 55. Why do you think that you failed to find any strong landscape effects? Have the most sensitive species already been filtered from the cacao plantations diluting any possible effect?**

As mentioned in the text, pristine forest specialists are not if at all abundant in cacao plantations. Therefore, I agree with you that a lack of pristine forest species may be partially responsible for landscape variables not being a good predictor.

7. **Line 59. It is not clear why importance of plantation over landscape factors reflects high endemism and low richness and abundance of Sulawesi herpetofauna ???**

I agree that the original sentence was confusing. It now reads:

“Low species richness and abundance paralleled by exceptionally high endemism distinguish Sulawesi from other tropical regions. An additional difference is reflected in the results of my observational modelling where, in contrast to other studies, plantation rather than landscape-environmental factors enhance the value of cacao agroforests for herpetological diversity.”

8. **Line 59. In discussing the importance of preserving common, disturbance tolerant species to maintain ecosystem functions – is there any evidence that these species are actually depleted in strongly modified habitats? I.e. is there actually any need to invest in their preservation?**

A pilot study I conducted last year in Sulawesi showed that pesticides, for example, will strongly affect common species. On a broader scale, the review by Gaston and Fuller (2008) points out that even small decline of common species may result in larger losses of ecosystem functions and services. As such, there is definitely a reason for thinking about the protection of common species.

9. **You recommend increasing leaf litter depth as a management approach. But what would be the social and economic costs of doing this? This needs to be worked out before a responsible management recommendation can be made. At a broader scale the relative costs of investing in cacao manipulation need to be balanced against costs and benefits of investing potentially competing funds into stronger protection of remaining areas of primary forest.**

I propose increasing leaf litter depth as a means to enhance the conservation value of cacao plantations for herpetological diversity. I do agree that further economic aspects have to be taken into account before conclusive recommendations can be given.

Realistically, however, such an approach will have to be based not only on predictors for one but multiple taxonomic groups and take multiple structural parameters, pesticides, and fertilizer into account that affect yield. Two recent studies did this for my study region in Sulawesi (Tschardt et al. 2011; Clough et al. 2011).

In Sulawesi's cacao plantations, it has also been shown that there is no trade off between high biodiversity and high yield but that a combination of both is possible under the right management regimes (Clough et al. 2011). This suggests that investing in suitable management of agroforests may sustain biodiversity and spare natural habitat.

- 10. Overall it would be interesting to have seen your thoughts on the relative importance/value of the manipulative approach? You already knew that leaf litter was important from the correlative studies (and the literature). Were the experiments therefore a failure? What can the discrepancy in results tell us about relative difficulties of a priori model testing and field scale manipulations?**

The manipulative approach was a good way to challenge the statistical modelling results. It was not a failure but rather illustrated satisfactorily that translating modelling results into the real world is not straightforward, because there is a lot of temporal and spatial variation.

The modelling and experimental manipulation was done on the same plots but in different time frames. For the modelling approach, however, "snapshots" of the habitat and species were taken at two points in time. In contrast, the manipulative experiment was based on a comparison of sampling sessions over a longer period of time. As such, minimizing variation and detecting actual biological effects rather than statistical artefacts in the manipulative experiment is more difficult.

Chapter 3

- 1. How confident are you that there are no cryptic species that could only be identified from voucher specimens?**

As I point out above (point 10, chapter 1), I likely have missed (cryptic, secretive, and fossorial) species.

- 2. Page 67. Pitfall traps would almost certainly have added to your total species list**

I agree. Please see my responses to this comment above and the statement given in chapter 3.

- 3. Page 78. Is there such a thing as pristine forest cover in Sulawesi?**

There is – rapidly dwindling – forest in pristine condition in the Lore Lindu National Park and other parts of Sulawesi.

Chapter 4

- 1. Page 86. Is it possible that there is a bias in your method for assessing diet by examining thesis rather than (less processed) stomach contents?**

I do agree that there may be a potential bias towards soft-bodied animals in using faeces rather than stomach content for diet analysis. I assume, however, that this is unlikely, because I have more than 600 mins of behavioural video recording from different males in their natural habitats at night (from a different project). In these video recordings, I hardly

ever saw the toads feeding on soft-bodied animals, which will be most of the ones I missed.

2. **Figure 4.4. Not clear how the values for the reference sample itself were calculated, if the remaining sample values were all calculated in reference to it ...**

As mentioned in the methods section, I was interested in the treatment-over-time effect. The first sampling session was used as a reference level against which the subsequent sampling sessions were evaluated (i.e., the estimated effect parameter of the first sampling session was included in calculating the effect parameters for subsequent sampling sessions).

3. **The invasive naivety effect is probably quite strong in many places in so far as it doubtless explains the absence of many potential invaders (failures) to successfully establish**
I fully agree!

4. **Page 99, first sentence. Your theory depends entirely on the crazy ant not being effective as a predator on disease vectors Yet you brush over this question very fast and do not provide any evidence or reference to other studies to suggest that this may be the case ..**
This is right and the reason is that to my knowledge this is not known. A PhD student in Göttingen is currently working on this topic.

5. **Generally throughout the paper ... you need to be careful in referring to ecosystem services ... native ants may provide a regulating service (i.e. benefit to humans) IF they have a negative impact on disease vectors sufficient to impact yield in a way that is comparable or favourable to pesticide. You do not provide any data on these linkages so as it stands you are talking only about an ecological function that is hypothesised to provide indirect benefits to humans.**

I do agree that it is a critical point. This paper only shows experimentally the link between the toads as opponent of invasive and native ants, which I tried to make clear in Fig. 4.1. It shows the parts of the “toad biocontrol service” that come from experimental work in this study and those that come from the literature and have to be tested explicitly in the future. I do believe, however, that while pointing out the conditions for such a service, it is correct to speculate on indirect human benefits, hence, indirect biocontrol services.

Chapter 5

This is a very short chapter indeed. What findings have emerged from the 36 studies that have focussed on pesticide biodiversity impacts? There is no mention here. Also to be truly useful future research recommendations need to include assessments on pesticide use/dosage on yields compared to biocontrols that are facilitated by canopy cover of shade trees. Also what are the cultural/social motivations and drivers behind the exceptionally high (beyond manufacturer’s recommendations) usage of pesticide in some areas?

The comments on the conclusions drawn and future research recommendations are highly relevant. As mentioned in the initial remarks section, this chapter – published as a letter – was not modified. A full review paper on the impacts of pesticides on biodiversity and ecosystem services in the tropics including extensive future research recommendations is under peer-review (Wanger et al. submitted). I found for example that less than 0.1 % of all pertinent pesticide papers deal with tropical vertebrates, highlighting a priority for

future research activities. A comparison of pesticide sensitivity of temperate against tropical amphibian and fish species suggests higher susceptibility in tropical amphibians but not fish. Pollination and pest control services in the tropics seem to be substantially imperilled by pesticide usage. Besides ecotoxicological research on a broad spectrum of substances and tropical model organisms, integrated pest management (an ecological approach of controlling pests for most economic benefit with physical, cultural, biological and chemical methods and by reducing side effects) should be the long-term goal for sustainable crop production.

Conclusions

1. **Page 105. Lots of loose language. What is meant by “interferes with population structure” and “known to affect reptiles” and “substantially affected amphibians and reptiles”? It is also not clear why this focus on pesticides is suddenly presented in the conclusions of the entire thesis and not in Chapter 5.**

I now provide more details in the criticized sentences. The sentence now reads:

“It has been shown, for example, that application of the commonly used pesticide atrazine is a powerful endocrine disruptor (e.g., it de-masculinizes male frogs) and, hence, it interferes with population structure (Hayes *et al.* 2010). Glyphosate, the most commonly used herbicide, has led to substantial mortality in amphibians and is also known to cause genetic damage in reptiles at higher concentrations (e.g., Relyea 2005; Sparling *et al.* 2006).”

And

“[...] even moderate herbicide application of >2.5 l/ha and >0.5 l/ha substantially depleted richness and dominant species abundance of amphibians and reptiles, respectively.”

Besides summarizing the results from the thesis, I put a focus on pesticide impacts on biodiversity in the conclusions. After having written Chapter 5, a review on pesticide impacts on biodiversity and ecosystem services in the tropics (Wanger *et al.* submitted, mentioned in the Chapter 5 comment above), and a paper on the impacts of pesticides on Sulawesi’s vertebrates and invertebrates (Wanger *et al.* in preparation), I feel that this area is amongst the most important ones, where we need to focus our research efforts if agricultural habitats are to be made more sustainable for biodiversity.

2. **Page 105. You have no evidence that the control of crazy ants by toads affects crop yield. This is hopeful speculation. It is also a somewhat empty argument to state the need for economic valuation of biodiversity when all you have shown is a hypothetical link between one endemic toad and a potentially valuable return for people. Even if this link is shown people may, in theory, be motivated to cut down remaining forests and replace with cacao plantations populated by thousands of hand reared toads. Careful and balanced arguments are needed before making sweeping statements on the vital importance of economic valuation for conservation arguments.**

Please see my response to comment 5.) in chapter 4. In addition, I did rephrase the last part of the conclusion:

“I also show for the first time that amphibians control invasive ants with effects on native ant diversity. These predator-prey interactions in Sulawesi’s cacao plantations may potentially have implications for crop yield. If future research activities can experimentally establish the link between endemic toads and cacao yield, it provides an even more important argument for amphibian conservation than this study does. While

valuing nature is not without criticism and can only be part of the conservation puzzle (e.g., Redford and Adams 2009), its use depends on the region and specific situation. Sulawesi's unique herpetofauna is of little interest for smallholder farmers primarily interested in increasing their monthly income from cacao. If anything is to change in the perception of local people, then biodiversity must have an obvious (economic) value to them. To date, the main benefit from amphibians to humans has been in the nature of a genetic resource. For instance, they are used as model organisms in the laboratory and they provide skin peptides to produce medical products (Smith & Stoskopf 2007). In addition to addressing the effects of pesticide use on amphibians and reptiles, much more research is needed on the ecosystem services that they provide to humanity."

Examiner 2

Note that I extracted the comments from a longer paragraph, commenting – very positively – on the individual chapters. This is why the original comment is not shown here.

Chapter 1

Future experiments for leaf litter thickness and canopy variables

I agree that it is best to complement correlative evidence with experimental tests. In the second chapter I test how leaf litter thickness will affect diversity patterns in cacao plantation habitat. The reason for not testing the effects of canopy variables and leaf litter thickness on amphibian and reptile diversity along the land use gradient was simply that it was logistically not feasible to manipulate these (e.g. accessibility of the plots) and sample size per habitat group was not large enough for a full-factorial design.

Pesticide results not in the model

This is a valid point. The pesticide data was not included in the modelling for two reasons. First, the paper should focus only on the structural adjustments required to make cacao plantations more sustainable, because pesticide use intensified only after I first started my field experiments around the Toro village in Sulawesi (the study region). I then wanted to write an additional manuscript (which is currently in preparation) that also includes experiments to specifically show effects of common pesticides on amphibians and reptiles to present the whole picture.

Leaf litter effects on other organism groups

A recent study (Clough et al. 2011) investigated environmental correlates of various species groups including plants, fungi, vertebrates as well as invertebrates in Sulawesi's cacao agroforests. It was found that a thick leaf-litter stratum was a predictor of amphibian, reptile, and endemic bird species richness but there was no negative relationship with thinner leaf litter cover and species richness of any other taxonomic group.

Chapter 4

Which sugars are used for attracting ants (ref needed)

For ant sampling I used saccharose (common table sugar), which is a disaccharide. Saccharose is readily available and the applied sampling technique with this sugar has been shown to be successful in previous ant studies in Sulawesi. The method is explained in detail in the cited study by Wielgoss et al. (2010).

Clarify future research needs

Given that parts of this study are based on evidence from the literature and not shown yet in an experimental approach, I do agree that more research on amphibian pest control services is needed. Further comments on this point are made in response to the other referee's queries.

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List of publication as listed in this thesis

- Introduction published as** N.S. Sodhi, Koh, L.P., Clements, R., **Wanger, T.C.**, Hill, J.K., Hamer, K.C., Clough, Y., Tscharntke, T., Posa, M.R.C., Lee, T.M. (2010): Conserving Southeast Asian forest biodiversity in human-modified landscapes. **Biological Conservation**, 143,2375-2384. doi:10.1016/j.biocon.2009.12.029.
- Chapter 1 published as T.C. Wanger**, Iskandar, D.T., Motzke, I., Brook, B.W., Sodhi, N.S., Clough, Y., Tscharntke, T. (2010): Effects of land-use change on community composition of tropical amphibians and reptiles in Sulawesi (Indonesia). **Conservation Biology**, 24,794-802. doi:10.1111/j.1523-1739.2009.01434.x
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- T.C. Wanger**, Wielgoss, A.C., Motzke, I., Clough, Y., Brook, B.W., Sodhi, N.S., Tscharrntke, T. (2010): Endemic predators, invasive prey, and native diversity. **Proceedings of the Royal Society - B.**, 278,690-694. doi: 10.1098/rspb.2010.1512
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