

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

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Summary

1. 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 South-East Asia.

2. We 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. We 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, we 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.

3. 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.

4. Synthesis and applications. 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.

Key-words: agriculture, Bayesian modelling, climate change, herpetofauna, hierarchical regression, Indonesia, land-use change, Sulawesi

Introduction

Depending on the level of the world's future environmental resource consumption and overall population growth, global

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cropland may expand between 0.3 and 1.8 billion hectare 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; Tscharnkte *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 (see Perfecto *et al.* 2007; Philpott *et al.* 2008), whilst South-East Asian case studies, where deforestation and associated land-use change increased by 25% from 1990 to 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 South-East 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 South-East Asia's forest biota are highly sensitive to forest disturbance (Sodhi *et al.* 2009), 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 the nearby presence of pristine habitats to sustain high diversity (Klein, Steffan-Dewenter & Tscharnkte 2003; Bos, Steffan-Dewenter & Tscharnkte 2007; Schroth & Harvey 2007). By contrast, studies on amphibians and reptiles are scarce in South-East Asia and the limited results from other tropical regions revealed equivocal and regionally variable results (Gardner, Barlow & Peres 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, we 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, Mustafa & Henderson 2002). In addition, 55% of the available land is threatened by an ever increasing human immigration pressure (Sodhi *et al.* 2005). 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; T.C. Wanger, unpublished data).

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, Sodhi & Brook 2002). Here, we integrate a correlative and manipulative approach at various spatial scales (Hewitt *et al.* 2007). In a Bayesian model selection approach, we 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 2007) posed to explain diversity patterns in different taxa. Second, we 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). Our overarching aim was to determine whether local-scale alteration of habitat complexity can enhance the conservation value of cacao agroforestry for tropical amphibians and reptiles. We 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. S1 in Supporting Information). 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] (for climate diagrams, see Fig. S1). 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

We sampled 43 plots (40 × 40 m²) 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. We also determined the mean percentage canopy cover, 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, we 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 data loggers in the lower canopy of the cacao trees (for details on environmental variables, see Appendix S1 in Supporting Information).

SAMPLING PROTOCOL

All plots were sampled six times between December 2007 and July 2008 (258 total sampling sessions) covering the general rainy and dry seasons in Sulawesi respectively (Whitten *et al.* 2002). Sampling was conducted three times during the day and night always between 06:00 and 18:00, and 18:00 and 06:00 hours respectively. We 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 us to use average values in the analyses; to avoid pseudoreplication, we did not add results of each sampling. Because of the manipulation, we used only the first four sampling sessions in the Poisson regression analysis to determine environmental predictors of herpetological diversity patterns.

In the experimental approach, we evaluated temporal changes 26 days before (third and fourth sampling sessions) and 26 days after (fifth and sixth sampling sessions) 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, we found several species in the plots even hours after management activities have ceased (T.C. Wanger, unpublished data). We, therefore, assumed that the assemblage requires a relatively short time to recover from disturbance and that the time frame was suitable.

We 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 min per plot), we 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 assured 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). We also fitted models based on the Michaelis–Menten equation, a negative exponential equation, and a logistic model 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 (for equations, see Appendix S2; for an introduction to Bayesian model evaluation, see Appendix S3, Supporting Information). After calculating seven species richness estimators in ESTIMATE-S (Chao 1 & 2 estimators, Abundance-based Coverage Estimator, Incidence-based Coverage Estimator, Jackknife 1 & 2 estimators and Bootstrap estimator; see Magurran 2004; Colwell 2006), sampling effort was evaluated based on the percentage sampled compared with the estimate of the best-fit equation and the species richness estimators. Sampling effort was truncated to fit a sensible scale between 0% and 100%.

IDENTIFICATION OF ENVIRONMENTAL VARIABLES

We 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.* 2009). We 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 variables relevant only at the plantation scale (LLT, LOGS, stone blocks and 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 2007). 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.

We used an individual variable ranking method to avoid over-parameterization 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

We manipulated LLT and LOGS based on the results from the model selection. We 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, we 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.

We randomly excluded one plot for a balanced data set 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. We 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. We then prepared the plots following a standard protocol (for details on the spatial control, protocol and validation of the LLT treatments, see Appendix S4 and Table S1 in Supporting Information).

To quantify the experimental treatment effects on amphibian and reptile species richness, we calculated pre- and post-manipulation species richness for each plot and used the pair-wise difference as response variable in our Bayesian hierarchical regression model. This approach allows subdivision of variance in finer scales using ‘hyperparameters’ and adjustment of the model to the data (Gelman *et al.* 2004; Qian & Shen 2007). The same model structure was used to investigate changes in abundance patterns.

To visualize changes in relative abundance before and after the manipulation, we show the three most abundant species per treatment level. Changes in beta diversity across all treatment groups were

haphazard compared with alpha diversity (probably the number of replicates was too small to reliably calculate turnover) and, therefore, results are not included here.

Results

GENERAL PATTERN

We found six amphibian and 17 reptile species comprising 90 (five 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 (Table S2).

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. 1; Table S3 Supporting Information). 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 5.6–7.0). The eight estimates for species richness suggest that 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 89–97% detection (95% CI 17.5–19.0). The species richness estimators revealed a completeness of sampling effort between 68% and 100% [mean (\pm SD) 85 (\pm 13)%; Figs S2 and S3 Supporting Information]. 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.

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), LLT and the ratio between leaf litter cover and shrub cover (COVER; Table 1). 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 (Table 2). The remaining variables explained less than 5% relative deviance. In reptile species richness, the most parsimonious model included the parameters LOGS, LLT, COVER and annual temperature of the plots (Table 1). The

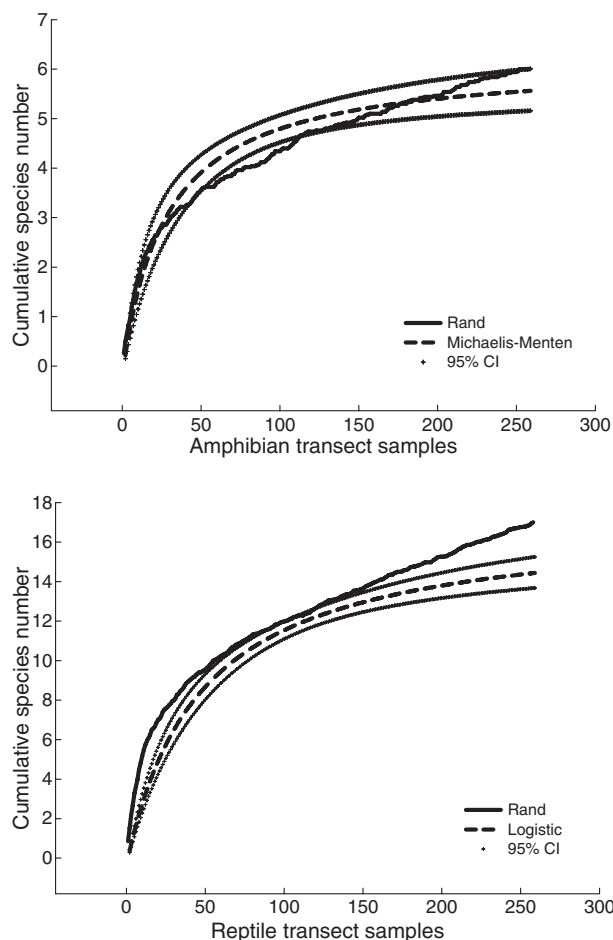


Fig. 1. Species accumulation curves for amphibians (above) and reptiles (below). Shown are the randomized original data (*Rand*) based on all sampling sessions conducted in the cacao plantations ($n = 258$), the best equations determined by DIC-based model selection (*Michaelis–Menten* equation for amphibians; *Logistic* model for reptiles), and the 95% credibility intervals (95% CI).

second and third models, excluding annual temperature of the plots and including stone blocks, respectively, were still plausible models for explaining variation in reptile species richness (i.e. Δ DIC ≤ 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% (Table 2). Notably, all models incorporating landscape effects (such as distance to forest and to the nearest water body) were ranked the 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].

Table 1. Amphibian and reptile species richness in the Bayesian model selection

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

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: *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: *Dhat*, point estimate of the Bayesian posterior deviance; *DIC*, deviance information criterion; *ADIC*, 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.

MANIPULATION

The three most abundant species for each treatment before and after the experimental manipulations show distinct patterns (Fig. 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 top). 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 bottom). All of these species 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.

We found a decreasing trend of the individual removal treatments on amphibian species richness. All other treatments did

Table 2. Individual explanatory strength of predictor variables

Variable	Variable deletion		Variable addition		Rel. deviance
	Dhat	% Dev	Dhat	% Dev	
Amphibians					
COVER	89.36	3.10	89.65	7.55	0.511
LLT	88.31	2.02	90.61	6.56	0.411
Dist2Water	87.84	1.54	96.74	0.24	0.085
LOGS	86.49	0.14	96.94	0.03	0.009
STB	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					
COVER	148.00	2.38	148.10	4.88	0.526
TEMP	147.10	1.80	152.00	2.38	0.302
LLT	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

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 an 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 Table 1. Negative deviances indicate a poorer fit than the null model.

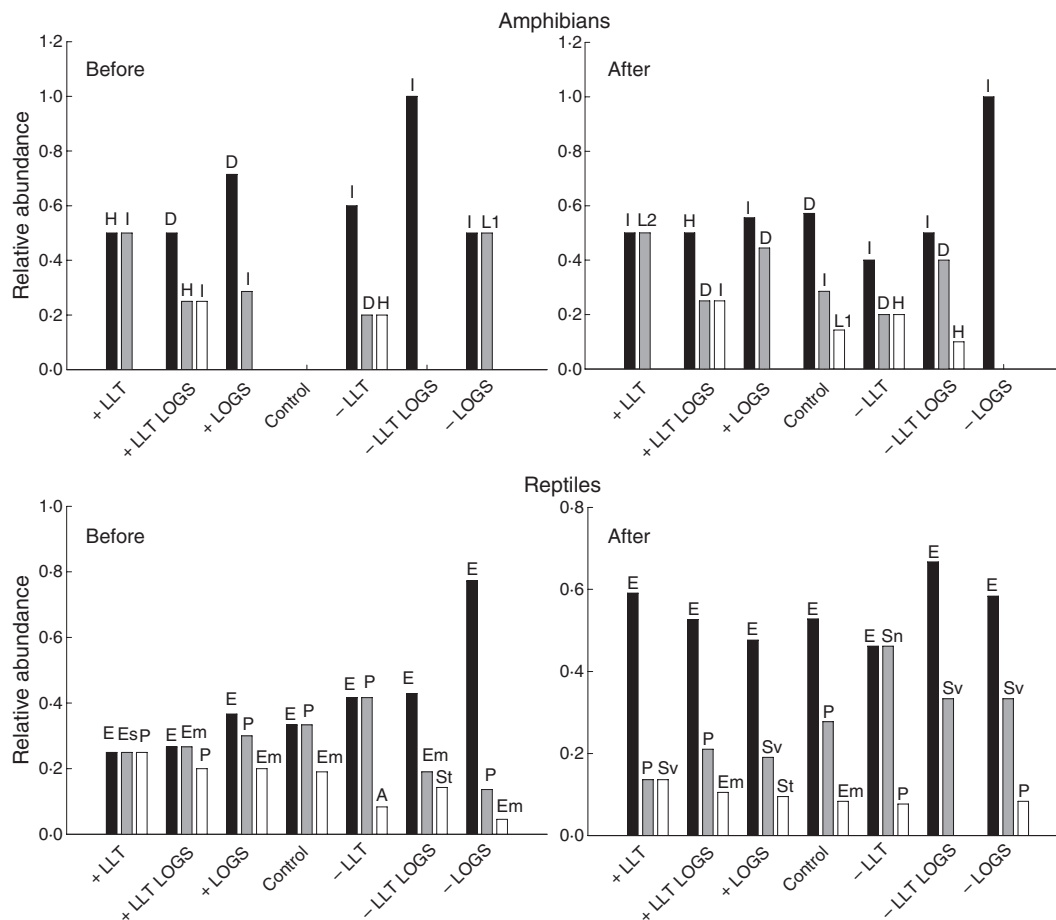


Fig. 2. Amphibian and reptile abundance before and after the experimental manipulation. Black, grey and white bars represent species with first, second and third highest abundance respectively. Abbreviations for the treatments are *LLT*, leaf litter thickness; *LOGS*, branches and logs; *LOGS LLT*, additive 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*, *Parvosincus* spp.; *Em*, *Eutropis multifasciatus*; *A*, *Ahaetulla prasina*; *St*, *Sphenomorphus* cf. *textus*; *Sv*, *Sphenomorphus variegatus*; *Sn*, *Sphenomorphus nigrilabris*.

not cause a detectable effect (upper sections Fig. 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 any effect. Overall, treatment effects explained considerably less variance in the data than was contained in the residuals (lower sections Fig. 3).

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

Discussion

We used a two-step, correlative-to-manipulative approach, to reveal the factors determining the conservation value of cacao

agroforestry in Sulawesi, Indonesia. We first conducted surveys and identified the predictors of amphibian and reptile diversity patterns with a Bayesian modelling approach. We 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 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 2007). We found the occurrence of LLT, logs and branches, and the ratio between leaf litter and shrub cover (LLT, LOGS and COVER respectively), the latter suggesting

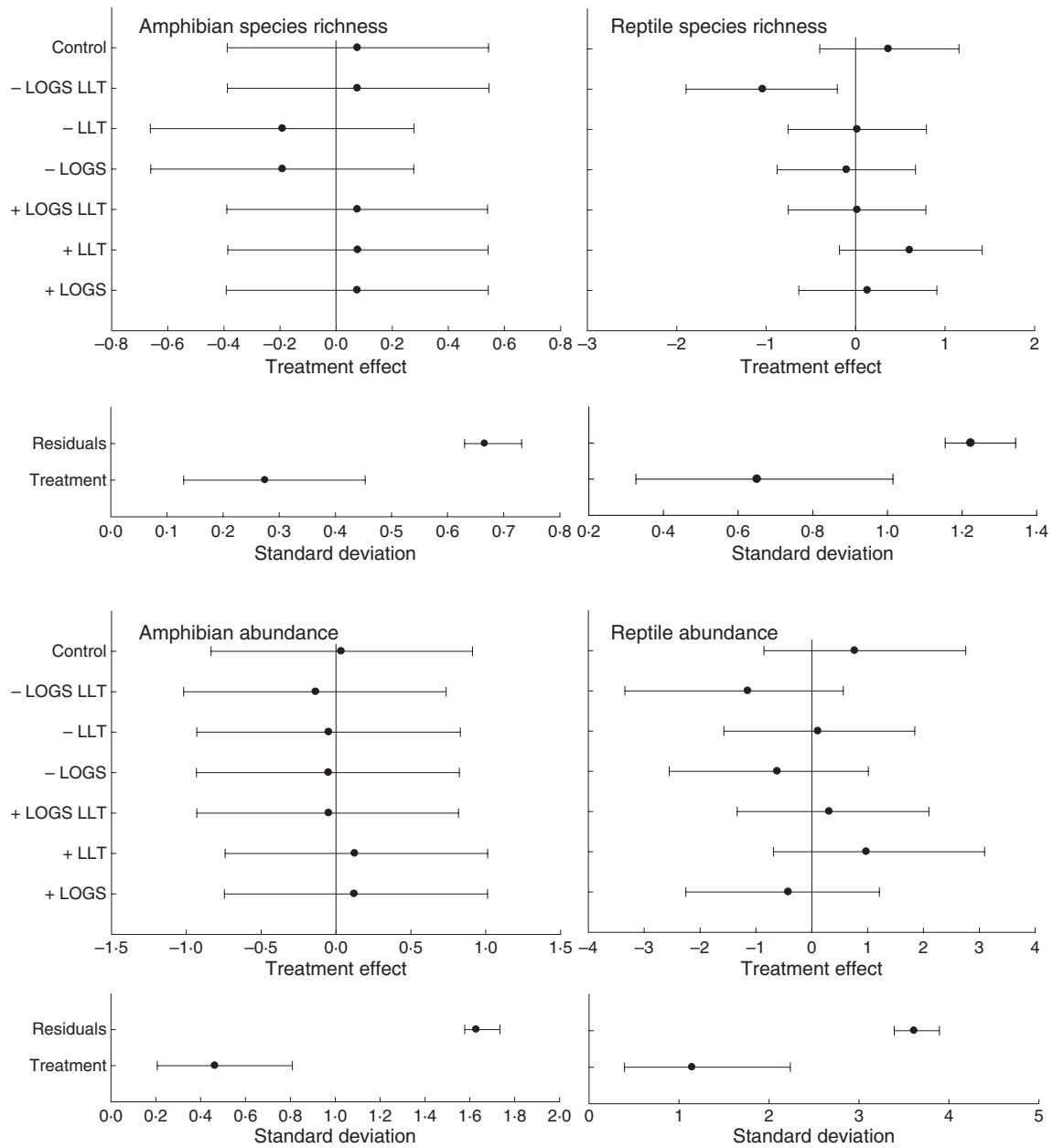


Fig. 3. Manipulation results for amphibian and reptile species richness and abundance. Small sections of the graphs represent variance explained by residuals and treatment effects. Dots represent means of the posterior distribution of the treatment effect for each treatment. Error bars are 95% credibility intervals. For abbreviations of the treatments (y-axis), see Fig. 2.

that leaf litter microhabitats as an above-ground stratum are more important than shrubs for both groups. These responses 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 our 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 exposed to more heat stress, which intensifies as future climatic conditions intensify. Our findings stress the importance of monitoring the impacts of climate change in plantation habitats.

Our 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, Sillett & Greenberg 2008; Greenberg, Perfecto & Philpott 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). Our 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.* 2008). 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 the 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 set-up and study design were carefully planned to incorporate and minimize temporal and spatial variation, we 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, Stachowicz & Bertness 2003) between plots and sampling events, may have slightly altered control treatment effects. This may, hence, have influenced manipulation results. We are, 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 our 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. Our 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. Results of our observational modelling reflect this, as in contrast to other studies, plantation rather than landscape environmental factors are demonstrated here to 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, Collazo & Groom 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, our 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 LLT 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 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.

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References

- Borkhataria, R.R., Collazo, J.A. & Groom, M.J. (2006) Additive effects of vertebrate predators on insects in a Puerto Rican coffee plantation. *Ecological Applications*, **16**, 696–703.
- Bos, M.M., Steffan-Dewenter, I. & Tscharntke, T. (2007) The contribution of cacao agroforests to the conservation of lower canopy ant and beetle diversity in Indonesia. *Biodiversity and Conservation*, **16**, 2429–2444.
- Brook, B.W., Sodhi, N.S. & Bradshaw, C.J.A. (2008) Synergies among extinction drivers under global change. *Trends in Ecology & Evolution*, **23**, 453–460.
- Bruno, J.F., Stachowicz, J.J. & Bertness, M.D. (2003) Inclusion of facilitation into ecological theory. *Trends in Ecology & Evolution*, **18**, 119–125.
- Colwell, R.K. (2006) ESTIMATE S. v8.0.0. <http://viceroy.eeb.uconn.edu/estimates>. (accessed September 2008).
- Colwell, R.K. & Coddington, J.A. (1994) Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, **345**, 101–118.
- Cruz-Angon, A., Sillett, T.S. & Greenberg, R. (2008) An experimental study of habitat selection by birds in a coffee plantation. *Ecology*, **89**, 921–927.
- Dumbrell, A.J., Clark, E.J., Frost, G.A., Randell, T.E., Pitchford, J.W. & Hill, J.K. (2008) Changes in species diversity following habitat disturbance are dependent on spatial scale: theoretical and empirical evidence. *Journal of Applied Ecology*, **45**, 1531–1539.
- Fink, R.D., Lindell, C.A., Morrison, E.B., Zahawi, R.A. & Holl, K.D. (2008) Patch size and tree species influence the number and duration of bird visits in forest restoration plots in Southern Costa Rica. *Restoration Ecology*, in press, DOI: 10.1111/j.1526-100X.2008.00383.x.
- Gardner, T.A., Barlow, J. & Peres, C.A. (2007) Paradox, presumption and pitfalls in conservation biology: the importance of habitat change for amphibians and reptiles. *Biological Conservation*, **138**, 166–179.
- Garnett, S.T. & Brook, B.W. (2007) Modelling to forestall extinction of Australian tropical birds. *Journal of Ornithology*, **148**, 311–320.
- Gaston, K.J. & Fuller, R.A. (2008) Commonness, population depletion and conservation biology. *Trends in Ecology & Evolution*, **23**, 14–19.
- Gelman, A., Carlin, J.B., Stern, H.S. & Rubin, D.B. (2004) *Bayesian Data Analysis*, 2nd edn. Chapman & Hall, Boca Raton, FL.
- Gibbons, J.W., Scott, D.E., Ryan, T.J., Buhlmann, K.A., Tuberville, T.D., Metts, B.S., Greene, J.L., Mills, T., Leiden, Y., Poppy, S. & Winne, C.T. (2000) The global decline of reptiles, déjà vu amphibians. *BioScience*, **50**, 653–666.
- Gillespie, G., Howard, S., Lockie, D., Scroggie, M. & Boeadi (2005) Herpetofaunal richness and community structure of offshore islands of Sulawesi, Indonesia. *Biotropica*, **37**, 279–290.
- Greenberg, R., Perfecto, I. & Philpott, S.M. (2008) Agroforests as model systems for tropical ecology. *Ecology*, **89**, 913–914.
- Hewitt, J.E., Thrush, S.F., Dayton, P.K. & Bonsdorff, E. (2007) The effect of spatial and temporal heterogeneity on the design and analysis of empirical studies of scale-dependent systems. *American Naturalist*, **169**, 398–408.
- Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J. & Wardle, D.A. (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, **75**, 3–35.
- Howard, S.D., Gillespie, G.R., Riyanto, A. & Iskandar, D.T. (2007) A new species of large Eutropis (Scincidae) from Sulawesi, Indonesia. *Journal of Herpetology*, **41**, 604–610.
- ICCO (2008) Production of cocoa beans. *ICCO Quarterly Bulletin of Cocoa Statistics*, **34**, Table.
- Kitzes, J., Wackernagel, M., Loh, J., Peller, A., Goldfinger, S., Cheng, D. & Tea, K. (2008) Shrink and share: humanity's present and future Ecological Footprint. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **363**, 467–475.
- Klein, A.M., Steffan-Dewenter, I. & Tscharntke, T. (2003) Pollination of *Coffea canephora* in relation to local and regional agroforestry management. *Journal of Applied Ecology*, **40**, 837–845.
- Koh, L.P. (2007) Impending disaster or sliver of hope for Southeast Asian forests? The devil may lie in the details. *Biodiversity and Conservation*, **16**, 3935–3938.
- Koh, L.P. (2008) Can oil palm plantations be made more hospitable for forest butterflies and birds? *Journal of Applied Ecology*, **45**, 1002–1009.
- Langkilde, T. & Shine, R. (2004) Competing for crevices: interspecific conflict influences retreat-site selection in montane lizards. *Oecologia*, **140**, 684–691.
- Luiselli, L. (2006) Resource partitioning and interspecific competition in snakes: the search for general geographical and guild patterns. *Oikos*, **114**, 193–211.
- Luja, V.H., Herrando-Perez, S., Gonzalez-Solis, D. & Luiselli, L. (2008) Secondary rain forests are not havens for reptile species in tropical Mexico. *Biotropica*, **40**, 747–757.
- Magurran, A.E. (2004) *Measuring Biological Diversity*. Blackwell Publishing, Oxford.
- Manthey, U. & Grossmann, W. (1997) *Amphibien und Reptilien Südasiens*. Natur und Tier Verlag, Münster.
- McKay, J.L. (2006) *A Field Guide to the Amphibians and Reptiles of Bali*. Krieger Publishing Company, Malabar.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853–858.
- Perfecto, I. & Vandermeer, J. (2008) Biodiversity conservation in tropical agroecosystems – a new conservation paradigm. *Annals of the New York Academy of Science*, **1134**, 173–200.
- Perfecto, I., Armbrecht, I., Philpott, S.M., Soto-Pinto, L. & Dietsch, T.V. (2007) Shaded coffee and the stability of rainforest margins in northern Latin America. *Environmental Science and Engineering* (eds T. Tscharntke, C. Leuschner, M. Zeller, E. Guhardja & A. Bidin), pp. 227–263. Springer Verlag, Berlin.
- Philpott, S.M., Arendt, W.J., Armbrecht, I., Bichier, P., Dietsch, T.V., Gordon, C., Greenberg, R., Perfecto, I., Reynoso-Santos, R., Soto-Pinto, L., Tejeda-Cruz, C., Williams-Linera, G., Valenzuela, J. & Zolotoff, J.M. (2008) Biodiversity loss in Latin American coffee landscapes: review of the evidence on ants, birds, and trees. *Conservation Biology*, **22**, 1093–1105.
- Qian, S.S. & Shen, Z. (2007) Ecological applications of multilevel analysis of variance. *Ecology*, **88**, 2489–2495.
- Ryall, K.L. & Fahrig, L. (2006) Response of predators to loss and fragmentation of prey habitat: a review of theory. *Ecology*, **87**, 1086–1093.
- Scherr, S.J. & McNeely, J.A. (2008) Biodiversity conservation and agricultural sustainability: towards a new paradigm of 'ecoagriculture' landscapes. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **363**, 477–494.

- Schroth, G. & Harvey, C.A. (2007) Biodiversity conservation in cocoa production landscapes: an overview. *Biodiversity and Conservation*, **16**, 2237–2244.
- Sodhi, N.S. & Brook, B.W. (2006) *Southeast Asian Biodiversity in Crisis*. Cambridge University Press, Cambridge.
- Sodhi, N.S., Koh, L.P., Prawiradilaga, D.M., Tinulele, I., Putra, D.D. & Tan, T.H.T. (2005) Land-use and conservation value for forest birds in Central Sulawesi (Indonesia). *Biological Conservation*, **122**, 547–558.
- Sodhi, N.S., Bickford, D., Diesmos, A.C., Lee, T.M., Koh, L.P., Brook, B.W., Sekercioglu, C.H. & Bradshaw, C.J.A. (2008) Measuring the meltdown: drivers of global amphibian extinction and decline. *PLoS ONE*, **3**, e1636.
- Sodhi, N.S., Lee, T.M., Koh, L.P. & Brook, B.W. (2009) A meta-analysis of the impact of anthropogenic forest disturbance on Southeast Asia's biotas. *Biotropica*, **41**, 103–109.
- Steffan-Dewenter, I., Kessler, M., Barkmann, J., Bos, M.M., Buchori, D., Erasmi, S., Faust, H., Gerold, G., Glenk, K., Gradstein, S.R., Guhardja, E., Harteveld, M., Hertel, D., Höhn, P., Kappas, M., Köhler, S., Leuschner, C., Maertens, M., Marggraf, R., Migge-Kleian, S., Moge, J., Pitopang, R., Schaefer, M., Schwarze, S., Sporn, S.G., Steingrebe, A., Tjitsoedirdjo, S.S., Tjitrosoemito, S., Twele, A., Weber, R., Woltmann, L., Zeller, M. & Tscharnk, T. (2007) Tradeoffs between income, biodiversity, and ecosystem functioning during tropical rainforest conversion and agroforestry intensification. *Proceedings of the National Academy of Sciences*, **104**, 4973–4978.
- Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., Schindler, D., Schlesinger, W.H., Simberloff, D. & Swackhamer, D. (2001) Forecasting agriculturally driven global environmental change. *Science*, **292**, 281–284.
- Tscharntke, T., Klein, A.M., Krüss, A., Steffan-Dewenter, I. & Thies, C. (2005) Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecology Letters*, **8**, 857–874.
- Weber, R., Faust, H., Schippers, B., Mamar, S., Sutarto, E. & Kreisel, W. (2007) Migration and ethnicity as cultural impact factors on land-use change in the rainforest margins of Central Sulawesi, Indonesia. *Environmental Science and Engineering* (eds T. Tscharntke, C. Leuschner, M. Zeller, E. Guhardja & A. Bidin), pp. 417–436. Springer Verlag, Berlin.
- Whitfield, S.M., Bell, K.E., Philippi, T., Sasa, M., Bolanos, F., Chaves, G., Savage, J.M. & Donnelly, M.A. (2007) Amphibian and reptile declines over 35 years at La Selva, Costa Rica. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 8352–8356.
- Whitten, A.J., Mustafa, M. & Henderson, G.S. (2002) *The Ecology of Sulawesi*, 2nd edn. Gadjah Mada University Press, Yogyakarta.
- Winder, L., Alexander, C.J., Holland, J.M., Woolley, C. & Perry, J.N. (2001) Modelling the dynamic spatio-temporal response of predators to transient prey patches in the field. *Ecology Letters*, **4**, 568–576.
- Yap, C.A.-M., Sodhi, N.S. & Brook, B.W. (2002) Roost characteristics of invasive Mynas in Singapore. *The Journal of Wildlife Management*, **66**, 1118–1127.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1. Map of the study area including climate diagrams.

Fig. S2. Species richness estimators and the randomized original data – amphibians.

Fig. S3. Species richness estimators and the randomized original data – reptiles.

Table S1. Validation of the leaf litter thickness treatment

Table S2. Species list and characteristics

Table S3. Deviance information criterion-based model selection for the species accumulation curve equations

Appendix S1. Determination of environmental variables – details

Appendix S2. Equations used for extrapolation

Appendix S3. Bayesian model evaluation – a brief overview

Appendix S4. Preparation protocol for the manipulation, validation of shaking frame and LLT treatment

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