Conservation Biology

Contributed Paper

Effects of Land-Use Change on Community Composition of Tropical Amphibians and Reptiles in Sulawesi, Indonesia

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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. We 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. We determined species richness, abundance, turnover, and community composition in all habitat types and related these to environmental correlates, such as canopy heterogeneity and thickness of leaf litter. 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 by canopy heterogeneity and cover in reptiles. Amphibians were 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 the 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.*

Keywords: amphibians, Bayesian modeling, cacao agroforestry, Indonesia, land-use change, reptiles, Southeast Asia

Efectos del Cambio de Uso de Suelo sobre la Composición de la Comunidad de Anfibios y Reptiles en Sulawesi, Indonesia

Resumen: *Se conoce poco de los efectos del cambio de uso de suelo antropogénico sobre los anfibios y reptiles en los biodiversos bosques tropicales del sureste de Asia. Estudiamos un gradiente de modificación de uso de suelo(bosque primario, bosque secundario, agrobosque de cacaco con sombra natural, agrobosque de cacao con sombra sembrada y áreas abiertas) en Sulawesis central (Indonesia). Determinamos la riqueza de especies, abundancia, recambio y composición de la comunidad en todos los tipos de hábitat y las relacionamos con variables ambientales como la heterogeneidad del dosel y grosor de la capa de hojarasca. La riqueza de especies de anfibios disminuyó sistemáticamente a lo largo del gradiente de modificación del uso de suelo, pero la riqueza y abundancia de anfibios fue mayor en los agrobosques de cacao con sombra natural. Los patrones de riqueza y abundancia de especies en el gradiente de perturbación fueron mejor explicados*

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Paper submitted April 25, 2009; revised manuscript accepted September 8, 2009.

Conservation Biology, Volume 24, No. 3, 795–802

DOI: 10.1111/j.1523-1739.2009.01434.x

por la cobertura del dosel y el grosor de la hojarasca en anfibios y por la heterogeneidad y cobertura del dosel en reptiles. Los anfibios fueron afectados más severamente que los reptiles por la perturbación del bosque en Sulawesi. Para facilitar el valor de conservación para ambos grupos, se debe mantener una cobertura de dosel heterogénea y una capa gruesa de hojarasca en las plantaciones de cacao. Para el uso a largo plazo y sustentable de plantaciones, permanentemente se deben mantener árboles de sombra podados para permitir el rejuvenecimiento del cacao y, por lo tanto, reducir presión sobre los bosques.

Palabras Clave: agroforestería de cacao, anfibios, cambio de uso de suelo, Indonesia, modelos Bayesianos, reptiles, sureste de Asia

Introduction

Increasing deforestation rates and subsequent land-use change in the tropics will force the majority of 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 either by comparing diversity patterns across gradients of land-use modification (i.e., open to pristine habitats; e.g., Barlow et al. 2007) or by examining the factors driving diversity patterns within agricultural habitats (e.g., Clough et al. 2009*a*). 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. 2009). Among the most-threatened vertebrate taxa globally (30% and 31%, respectively of all evaluated species until 2008 [IUCN 2008]), tropical amphibians and reptiles are highly sensitive to habitat modifications and climate change (e.g., Sodhi et al. 2008; Wake & Vredenburg 2008; Huey et al. 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 (e.g., Koh 2008). Although most studies on amphibians and reptiles in Southeast Asia show that canopy cover and leaf litter thickness are 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; 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 exposure to the sun.

We determined the patterns in amphibian and reptile species richness, abundance, and community composition across a land-use modification gradient in Sulawesi, Indonesia. We used Bayesian model selection to identify the best environmental predictors for amphibian and reptile species richness and abundance, including the lacunarity index as a measure of canopy heterogeneity. On the basis of our results, we provide recommendations for conserving amphibians and reptiles in cacao plantations.

Methods

Study Region

We conducted this study in Central Sulawesi with an annual average temperature of 24.0 °C (SD 0.16), a monthly average rainfall of 143.7 mm (SD 22.74), and no pronounced climatic seasons (equatorial wet tropics). Located around the village of Toro in the Kulawi valley (1°30′24″ S, 120°2′11″ E) the study area was surrounded by the 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 encompassed a habitat gradient with increasing disturbance and a sufficiently large control area of a pristine forest.

Plot Characteristics and Environmental Variables

We sampled 31 plots (40 × 40 m) in five habitat categories: primary forest (six plots), secondary forest (seven), natural-shade cacao agroforest (with forest trees; seven), planted-shade cacao agroforest (with planted trees; six), and open areas (five). Unbalanced replicates resulted from difficulties with some locations (e.g., a church was built on one of the open-area plots). We classified all habitat categories on the basis of 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 (see Supporting Information). Secondary forest differed from primary forest in that large trees had been cut in the past and, for example, rattan and fire wood had been extracted. In complex natural-shade cacao agroforest, shade was provided by rainforest trees and canopy cover was higher there than in planted-shade cacao agroforest. In the latter, shade trees were mostly planted legume or fruit trees (e.g., *Glyricidia* sp. and *Musa* sp.). In Sulawesi, cacao trees are not only planted as undergrowth within near-primary forests, but also in secondary forest, coffee agroforests, clove plantations, or among annual crops. Open-area plots were an unshaded mosaic of grass and bare soil. All plots of one habitat type were surrounded by similar habitat (e.g., rainforest plots were located within a large area of pristine forest) and were at a minimum distance of 1 km from the next plot to increase statistical independence.

To characterize each plot, we measured distances to the forest (zero for primary forest plots) and the nearest water body; canopy cover and heterogeneity; leaf-litter cover and thickness; and understory shrub characteristics (height, density, and cover). Apart from the two distance measures, we 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, we 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. We also interviewed plot owners about pesticide use because these chemical compounds have been used increasingly over the last 10 years in the study region (Supporting Information).

Sampling Protocol

We 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 06:00 and 18:00 and 18:00 and 06:00, 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 us to use average values in the analyses. We 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) and sampled in a time-constrained manner (approximately 25 min in one plot). We inspected leaf litter, logs, branch piles, and looked underneath stones for amphibians and reptiles. We 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 reexamined to confirm identities. We 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., Rödel & Ernst 2004).

Assessment of Sampling Effort

We computed species accumulation curves on the basis of 50 randomly added sampling sessions of the original data and calculated a bootstrap estimator to determine the total species richness in the assemblage (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, we 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 suggested that it was appropriate to use the original data for subsequent analyses (Shahabuddin et al. 2005) because then there would be no deviation of the estimator data from the distribution of the original data.

Analysis of the Habitat Gradient

We calculated species richness for each plot as a response variable in our linear models to quantify the differences of amphibian and reptile species richness between habitat classes. For the analysis, we used a Bayesian hierarchical regression with hyperparameters that allows subdivision of variance in finer scales. This approach allows intuitive graphical evaluation of the results (Qian & Shen 2007). The same model structure was used to investigate changes in amphibian and reptile species abundance.

To determine the relative strength of evidence for environmental parameters driving species richness patterns across the habitat gradient, we chose an a priori set of candidate models on the basis of 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, we calculated the lacunarity index for all canopy pictures. Bayesian multimodel inference (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 [DIC]; Spiegelhalter et al. 2002).

We used additive biodiversity partitioning to determine species turnover and calculated species-rank-abundance curves to investigate community evenness in different habitats (Magurran 2004). The 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 advantage that it is more suitable for small sample sizes and hierarchical data (Golicher et al. 2006). We did not calculate the Simpson diversity index because a sample size of > 1000 individuals is required to obtain meaningful results (Magurran 2004).

Results

We 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 (Table 1).

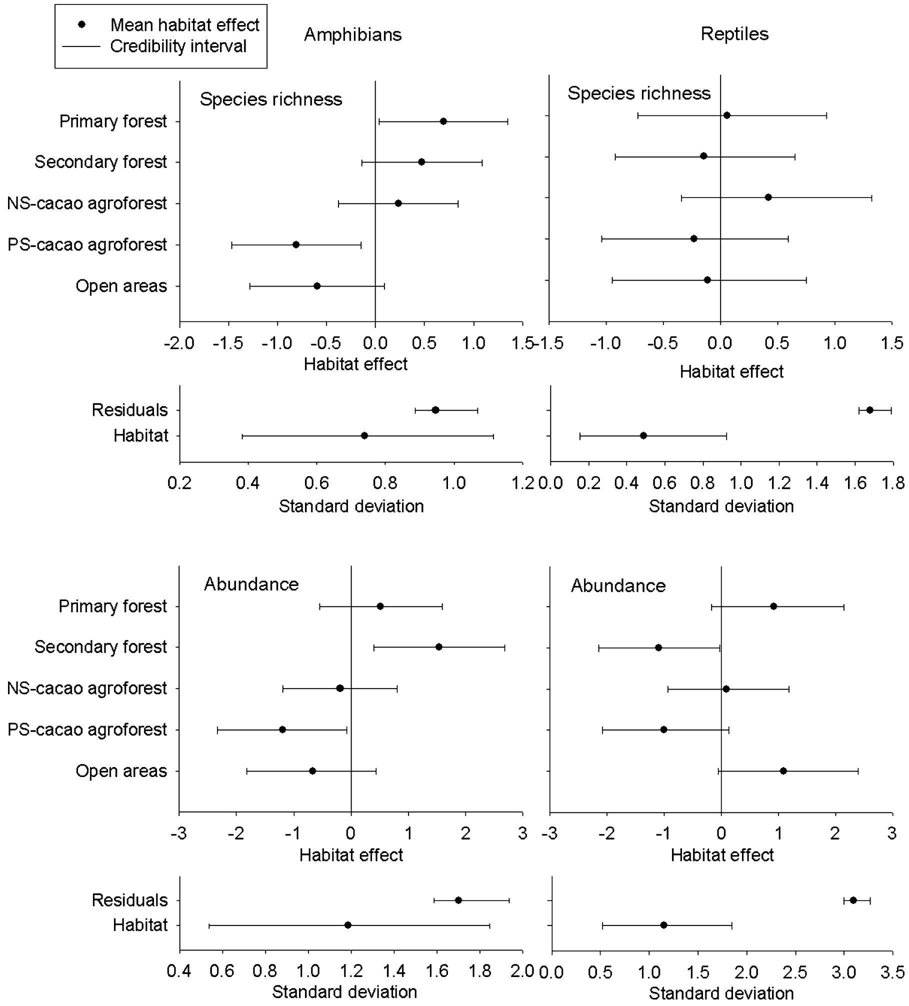

Figure 1. Amphibian and reptile species richness and abundance across the land-use gradient from pristine rainforest to open areas. The more the credibility intervals of the habitat-effect means are separated, the stronger the difference between habitats; a wide credibility overlap with zero means the habitat had no effect on species richness or abundance. The smaller graphs show variance partitioning between habitat effects (habitat) and model residuals (residuals) (NS-cacao agroforest, natural-shade cacao agroforest; PS-cacao agroforest, planted-shade cacao agroforest).

Because the original and the bootstrap estimator data were highly correlated for both groups in all habitat types (Supporting Information), we used the original data for further analyses.

Amphibian mean species richness declined from pristine rainforest toward open areas (i.e., from structurally complex to structurally simple habitats, respectively; Fig. 1). Abundance was higher in structurally complex habitats compared with simpler habitats. To evaluate the results of the analysis, we referred to an effect, trend, and no effect if the credibility intervals did not overlap, overlapped, or were centered on zero, respectively (Qian & Shen 2007). We 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 was only marginally different in the other habitats (Fig. 1). Abundance, however, showed a negative effect in secondary forests and strong positive and negative trends in primary forest and open areas and in 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 that incorporated canopy cover (DIC weight [*w*] = 0.44) and canopy cover and leaf litter thickness (*w* = 0.56; Table 2). 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 that included only canopy heterogeneity (*w* = 0.39 and *w* = 0.45, respectively). Canopy heterogeneity and canopy cover were included in the second-best model that explained reptile abundance (*w* = 0.43; Table 2). In reptile species richness, the null model was the second-most parsimonious model. Given the low ΔDIC value and percent deviance explained compared with the null model, the heterogeneity model was not robust. Although canopy heterogeneity played a more important role for reptiles, canopy cover was most relevant to amphibians.

Amphibian alpha diversity was highest in the primary forest (25% of total gamma diversity) and declined toward disturbed habitats (5%); this pattern was paralleled by an increase in beta diversity (75 to 95%; Appendix 3). Reptile alpha diversity peaked in agroforestry systems (23%), but was similar in all other habitat types (14.1 to 16.7%). Beta

Table 1. Amphibian and reptile species encountered in all surveyed habitats.

Species	*Threat category*[a]	*Specialist*[b]	*Habitat encountered*[c]
Amphibians			
Hylarana celebensis	LC	N	PF, SF
Ingerophrynus celebensis	LC	N	PF, SF, NAF, PAF, OA
Kaloula pulchra	LC	N	PF
Limnonectes n. sp. 1	NE	Y	PF
Limnonectes n. sp. 2	NE	Y	PF
Limnonectes n. sp. 3	NE	N	PF, SF
Limnonectes n. sp. 4	NE	Y	NAF
Oreophryne n. sp.	NE	N	PF, SF
Reptiles			
Boiga irregularis	NE	N	NAF
Cyrtodactylus famosus	NE	Y	PF
Eutropis grandis	NE	N	SF, NAF, PAF, OA
Eutropis multifasciatus	NE	N	PAF, OA
Eutropis rudis	NE	N	PF, NAF, PAF
Parvoscincus sp.	NE	N	PF, SF, NAF, PAF
Sphenomorphus textus	NE	N	PF, NAF, PAF, OA
Psammodynastes pulverulentus pulverulentus	NE	N	SF
Rhabdophis callistus	NE	N	SF
Sphenomorphus nigrilabris	NE	Y	PF, SF, NAF, PAF
Sphenomorphus variegates	NE	Y	PF, SF, NAF, OA
Xenopeltis unicolor	NE	N	NAF, PAF

[a] *From International Union for Conservation of Nature Red List: LC, least concern; NE, not evaluated.*

[b] *Abbreviations: Y, species considered pristine-forest specialist; N, disturbance-tolerant species. References: Manthey & Grossmann 1997; de Lang & Vogel 2005; Gillespie et al. 2005; McKay 2006.*

[c] *Abbreviations: PF, rainforest; SF, secondary forest; NAF, natural-shade cacao agroforest; PAF, planted-shade cacao agroforest; OA, open areas.*

diversity was, in contrast to amphibians, only lower in agroforestry (77%), but remained the same in all other habitats (83.3–85.9%; Supporting Information).

Amphibian and reptile species-rank-abundance curve evaluation was based on the commonly used log-normal and gamma abundance model, respectively (Fig. 2; Supporting Information). 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 of rainforest and open areas, respectively, and positive trends for the remaining habitats. Hence, abundance was even across species in rainforest and open areas, but overdominated by a few species otherwise.

Discussion

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

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 the different modes of thermoregulation between the two groups; whereas amphibians do not bask, this behavior is crucial for tropical lizards in open areas (Huey et al. 2009). Hence, use of a crude measure of canopy cover may be sufficient to predict amphibian diversity patterns because as canopy cover decreases, amphibian heat sensitivity increases. 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,

Table 2. Environmental determinants of amphibian (aSPR) and reptile (rSPR) species richness and abundance (aABD and rABD, respectively) in Sulawesi, Indonesia.*

Predictor variable	*Dhat*	*pD*	*DIC*	*ΔDIC*	*%Dev*
Amphibian richness					
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
Amphibian abundance					
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
		2.0			
Reptile richness					
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
Reptile abundance					
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

**Abbreviations: DIC, deviance information criterion (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; CAC, canopy cover; LLT, leaf litter thickness; HET, canopy heterogeneity; RAT, ratio between shrub and leaf litter cover; Null, mean (intercept) model.*

and hence, support more home ranges than the homogenous canopy. 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 be abundant (e.g., Boettger's keelback [*Rhabdophis callistus*]). On the basis of our results we posit that canopy heterogeneity is a more useful attribute to measure than canopy cover only, for reptiles and lizards in particular. We 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 on as the primary measure of habitat suitability.

Species turnover is an important indicator for conservation planning. Beta diversity of amphibians was high and disturbed habitats were dominated by a few species. This suggests that conservation decisions predicated on species diversity and functionality must consider the entire landscape rather than areas at the plantation level (Clough et al. 2007; Pineda & Halffter 2004). In contrast, similar beta diversity across habitat types implies that conservation strategies on the plantation level may be sufficient. This was the case for reptiles; natural-shade cacao agroforestry harbored more species with equal abundance than the other habitat types, which suggests reptiles may 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). As a result, species in this group may homogenize across the landscape.

Natural-shade cacao agroforestry may enhance resilience of both amphibians and reptiles against extensive species loss, at least if sufficient pristine habitats remain in the landscape in our study region. For reptiles, natural-shade cacao agroforestry may provide a valuable habitat on its own. Nevertheless, herpetological studies on land-use gradients show different results within and between taxa. This makes it difficult to generalize recommendations for conservation management for both taxa (Gardner et al. 2007). In addition, a recent experimental study on cacao agroforestry habitats in our study region identified leaf-litter thickness, the amount of logs, the ratio between plant and leaf-litter cover, and temperature as main

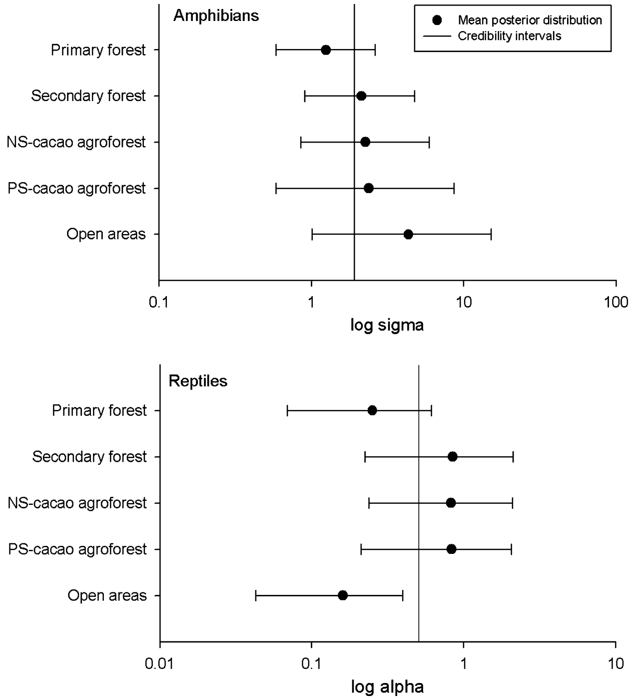

Figure 2. Comparison of species rank abundance for amphibians and reptiles among habitat types. For amphibians and reptiles, the log-normal and gamma models, respectively, provided the best fit in the model selection; thus, we compared the parameters σ and α (black dots) for the log-normal model and the gamma model, respectively. A smaller and larger parameter value indicates a flatter and steeper curve, respectively. Hence, the former represent a community with even species abundance and the latter a community with few dominant species. Interpretation is as in Fig. 1 (NS-cacao agroforest, natural-shade cacao agroforest; PS-cacao agroforest, planted-shade cacao agroforest).

drivers of patterns of herpetological diversity (Wanger et al. 2009). Taken together with the abiotic drivers of herpetological species richness and abundance we identified in the present study, herpetological diversity patterns are not necessarily driven by the same variables across and within habitats. Hence, results from both across-habitat gradients and within secondary habitat are most valuable when integrated.

Conclusions

Sulawesi provides 65% of Indonesia's cacao (Direktorat Jenderal Perkebunan 2008), and cacao is an important part of the income of local farmers. Cacao plantations cover almost 1 million ha on the island (Direktorat Jenderal Perkebunan 2008) and thus constitute important potential secondary habitats. Our results show that, to sustain herpetological diversity, complex canopy from natural shade trees and leaf-litter cover in plantations is essential. Like the practice of burning areas for new plantations, establishment of cacao plantations in the understory inside the forest may not sustain herpetofaunal diversity. This is because shade trees are essential only for young cacao trees, but in older plantations they are cut because their shade reduces yield. Farmers then further encroach into the forest as yields decrease in aging plantations (Clough et al. 2009*b*). Thus, low-intensity cacao agroforests with natural shade trees need to be supported by, for example, setting premium prices for biodiversity-friendly cacao production. Moreover, farmers need to be trained to maintain yields in shaded conditions and to rejuvenate plantations on site.

The very low rate of IUCN evaluations of the species we assessed in this study suggests little is known of the Sulawesi herpetofauna; only 37.5% and 0% of all amphibian and reptile species, respectively, have been evaluated. If habitats are not sufficiently preserved and managed soon, many species and ecosystem services they provide may vanish before they are even known.

Acknowledgments

We thank all our local assistants in Sulawesi for supporting the fieldwork, Kementerian Negara Riset dan Teknologi Republik Indonesia (RISTEK) and Lembaga Ilmu Pengetahuan Indonesia (LIPI) for issuing the relevant permits (to T.C.W. 1899/FRP/SM/VIII/2008 and 7374a/SU/KS/2007, respectively), and two anonymous reviewers for their comments. Field research was funded by the German Science Foundation to the SFB 552 STORMA (www.storma.de). T.C.W. received financial support through an Endeavour International Postgraduate Research Scholarship and a University of Adelaide Scholarship.

Supporting Information

Additional information on habitat characteristics, acquisition of environmental variables, and pesticide-use interviews (Appendix S1); results of the Bayesian correlation of the randomized original data and the bootstrap species richness estimator (Appendix S2); diversity partitioning of amphibian and reptile diversity in all habitat types (Appendix S3); and results of the model selection for the abundance models (Appendix S4) are available as part of the online article. The authors are responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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