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Responses of tropical forest herpetofauna to moderate anthropogenic disturbance and effects of natural habitat variation in Sulawesi, Indonesia

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ABSTRACT

Tropical forest destruction is a major contributor to global biodiversity loss, with much of remaining forests subject to extensive subsistence use. Compared to forest clear-felling and conversion, the impacts of these less intense but complex disturbance regimes on biodiversity remain poorly understood. Given the challenges of protecting pristine tropical forests for conservation in developing regions, there is a strong imperative to understand the role of altered forests with a range of low to moderate disturbance regimes in long term biodiversity conservation. We sampled tropical rainforest reptile and amphibian diversity over a nine year period along a gradient of moderate anthropogenic disturbance to intact primary rainforest in Sulawesi, Indonesia. We evaluated the relative influences of anthropogenic disturbance proxies and natural habitat variability on species richness and assemblage composition. Reptile and amphibian species richness were affected by natural variability in a range of habitat characteristics, but not by moderate anthropogenic disturbance. In contrast, species composition varied with both natural and anthropogenic disturbance metrics. Our results indicate that even low to moderate levels of anthropogenic disturbance have measurable, pervasive, impacts on tropical herpetofaunal diversity. However, moderately disturbed and altered forests that retain relatively high canopy cover and habitat complexity still retained most species associated with primary forest, indicating that they provide a significant contribution to herpetofaunal biodiversity conservation. Management implications from these findings complement those for birds and large mammals in tropical Asia, in that sustainable biodiversity conservation is likely to be best achieved by maintaining larger forest areas of variable disturbance and usage regimes around more remote, minimally disturbed core areas.

1. Introduction

Tropical forest destruction is a major contributor to global biodiversity loss (Sodhi et al., 2010). Southeast Asia is currently experiencing some of the world's highest rates of deforestation (Miettinen et al., 2011). Additionally, much remaining forest is affected by secondary disturbances and habitat alteration from harvesting of forest resources (McMorrow and Talip, 2001; Fitzherbert et al., 2008). Historically, equatorial tropical forests have been subjected to extensive subsistence use, including slash and burn agriculture, selective logging, firewood collection and rattan harvesting (Freeman, 1955; Fretes, 1992; Fox, 1995; Hoang et al. 2011), resulting in ecosystems experiencing multiple disturbance regimes. Whilst many of these disturbance processes are arguably less severe than clear-felling, their impacts on biodiversity remain poorly understood (Sodhi et al., 2010; Burivalova et al. 2014).

Some have argued that maximizing tropical biodiversity conservation depends mainly on retention of primary forest (Giam et al., 2011a; Giam et al., 2011b; Gibson et al., 2011). However, remaining tracts of primary tropical forest continue to be eroded and altered, including those within protected areas (Miettinen et al., 2011). Due to the limited extent and effectiveness of protected areas and the poor prospects for long-term conservation of remaining large tracts of primary forest (De Fries et al., 2005), degraded or altered forests need to be incorporated into conservation planning (Giam et al., 2011a;

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Giam et al., 2011b; Fisher et al. 2011). As biodiversity conservation in Southeast Asia becomes increasing dependent on management of habitats with varying levels of anthropogenic disturbance, a greater understanding is needed of the relationships between forest structure, disturbance processes, and the biota (Gillespie et al. 2005).

Until recently, the conservation value of disturbed or secondary tropical forests has been largely ignored (Giam et al., 2011a; Giam et al., 2011b). Management strategies that attempt to balance sustainable multiple-use forest management with biodiversity may lead to more sustained conservation outcomes in developing countries, where population pressures and resource demands on forests are large and resources to protect them are small (De Fries et al., 2005; Wright, 2010). Reptiles and amphibians are important components of the vertebrate diversity of tropical forests. Collectively they exhibit high species richness (e.g. Zug et al., 2001); may attain very high densities (Rodda et al., 2001; Zug et al., 2001); and play important roles in food webs (Heatwole and Taylor, 1987; Wells, 2007). Due to high diversity of life history strategies, trophic levels and microhabitat niches, the sensitivities of different taxa or guilds to varying disturbance regimes are expected to be complex (Gardner et al. 2007a).

Major alterations to forests, such as clear-felling and conversion to agro-forestry, have severe effects on tropical herpetofaunal diversity (e.g. Gillespie et al. 2005; Gardner et al. 2007b; Burivalova et al. 2014). Recent studies have begun to examine the conservation value of altered forests for herpetofaunal species with disturbance regimes less severe than clear-felling (e.g. Wanger et al., 2009, 2010; Hilje and Aide, 2011; Gillespie et al., 2012). However, entire communities have rarely been examined, and studies have typically focused on relatively major disturbance processes, such as agricultural conversion or commercial forestry (see Wanger et al. 2010; Burivalova et al. 2014).

To assess the conservation value of forests subjected to less intense anthropogenic disturbance we need to better understand how low to moderate anthropogenic disturbances affect different taxa and guilds, and how such disturbances might differ from natural disturbances and habitat heterogeneity. We explored these questions by examining patterns of herpetofauna diversity along a forest disturbance gradient in Sulawesi, Indonesia. We expected that structural habitat characteristics influencing herpetofaunal species richness and/or composition would correspond to the level of anthropogenic disturbance, proxies of which would be the distance to the nearest road and/or distance to the nearest village. We also expected the responses to such structural habitat differences to vary amongst guilds.

2. Methods

2.1. Study site

This study was undertaken within and adjacent to the Lambusango and Kakenauwe Forest Reserves (Fig. 1) on Buton Island, the largest (approx. 4400 km^2) offshore island, approximately 6 km from southeast Sulawesi, Indonesia. Kakenauwe and the production forest zone north of Lambusango are close to villages and are bisected by a narrow road. Contemporary and historic disturbances are evident near the road and villages, including selective logging, evidenced by the presence of cut stumps, felled tree trunks, and absence of large trees of commercial value; numerous well-used human trails through the forest; trapping snares (typically targeting Red Jungle Fowl, *Gallus gallus*, and Anoa, *Bubalus* sp.); firewood collection; and removal of rattan, a climbing palm used to make furniture (Fretes, 1992). Further south into the Lambusango reserve, signs of these disturbances diminish. No visible signs of selective logging are evident more than approximately 3 km south of the road; large trees of high commercial value are more prevalent; forest trails are few and less established, and snares are rarely encountered. However, rattan harvesting has occurred extensively well beyond this area, throughout all but the most remote parts of the island (B. Carlisle unpublished data) and local villagers have indicated that hunting occurs over a similarly wide area.

2.2. Sampling design

We established 75 sampling sites spread across a gradient of anthropogenic disturbance from primary rainforest through to moderately disturbed forest that, although never clear-felled or replaced with other land uses, had a long history of subsistence use. The study area was bisected by one vehicle road, with sampling sites spanning ~1 km north-west into the Kakenauwe Reserve, and 5 km south into the Lambusango Reserve (Fig. 1). With the exception of the road, sites were within continuous forest, thus avoiding potential confounding effects of edges and fragmentation (see Fischer et al. 2006). Throughout this anthropogenic-disturbance gradient, sites were selected by on-ground inspection; on ridges, mid-slopes with varying aspects, gullies and riparian terraces, ranging from 118 to 337 m above sea level. Site locations were recorded using a GPS (Garmin Map62s). Distance between sites varied but maintained a minimum of 200 m and undulating terrain ensured that no adjacent sites had similar landscape habitat attributes. Sampling was undertaken from June to September from 2001 to 2010, except 2003, coinciding with the transition from wet to dry season (Gillespie et al., 2005). Undertaking repeated sampling over multiple years minimized biases in site-based measures of community composition potentially resulting from annual fluxes in species populations or imperfect detection.

We used three methods to sample herpetofauna:

1. Pitfall traps consisted of five plastic buckets, embedded in the ground 4-5 m apart, connected with a plastic fence, 50 cm high and 30 m long, passing across each bucket, with the bottom edge embedded in the ground. Due to local availability, each site used three 60-l (57 cm deep) and two 70-l (65 cm deep) buckets. Traps were checked every morning. Traps were closed during periods of heavy rain. Between 25 and 48 sites were sampled each year. The combination of sites sampled each year varied in order to minimize temporal confounding sampling effects. Each site was sampled three to six of the nine sampling seasons, resulting overall in 14,094 trapsite day/nights, comprising of 70,470 individual trap nights.
2. Nocturnal censuses, 20-minutes duration, were undertaken by four authors (GG, SH, JS and AUH) using head torches within a 20 m radius of each pitfall trap. Searches were undertaken between 1830 and 2200 h. Nocturnal censuses were undertaken at least once during each year that each site was sampled except 2005, totalling 404 nocturnal censuses.
3. During 2001 and 2002, diurnal surveys of 60 minutes duration, were undertaken by GG and SH within a 20 m radius of each pitfall trap. Visual scans and active searches under rocks, logs, and within litter and debris were undertaken; however, this method was unproductive (see Gillespie et al. 2005). Subsequently visual scans were undertaken daily within 20 m of the pitfall site, on approaching and leaving during daily checking (GG, SH, JS and AUH).

2.3. Anthropogenic disturbance and habitat structure

We used distance from the road and distance to the nearest village from our sampling sites as proxies for human disturbance. Previous studies have demonstrated that anthropogenic disturbance levels in tropical forests are strongly related to distance from roads (Trombulak and Frissell, 1999; Laurance et al. 2009; Hoang et al. 2011) and distance from villages (Karanth et al. 2006; Bhat et al. 2011; Allnutt et al. 2013; Kodandapani et al. 2014). We also observed at our study sites that local people accessed the forest for harvesting of various forest resources via walking trails originating from the road or nearby villages. Hence greater levels of disturbance were expected at locations proximal to the road or nearby villages. The four villages in proximity to sample

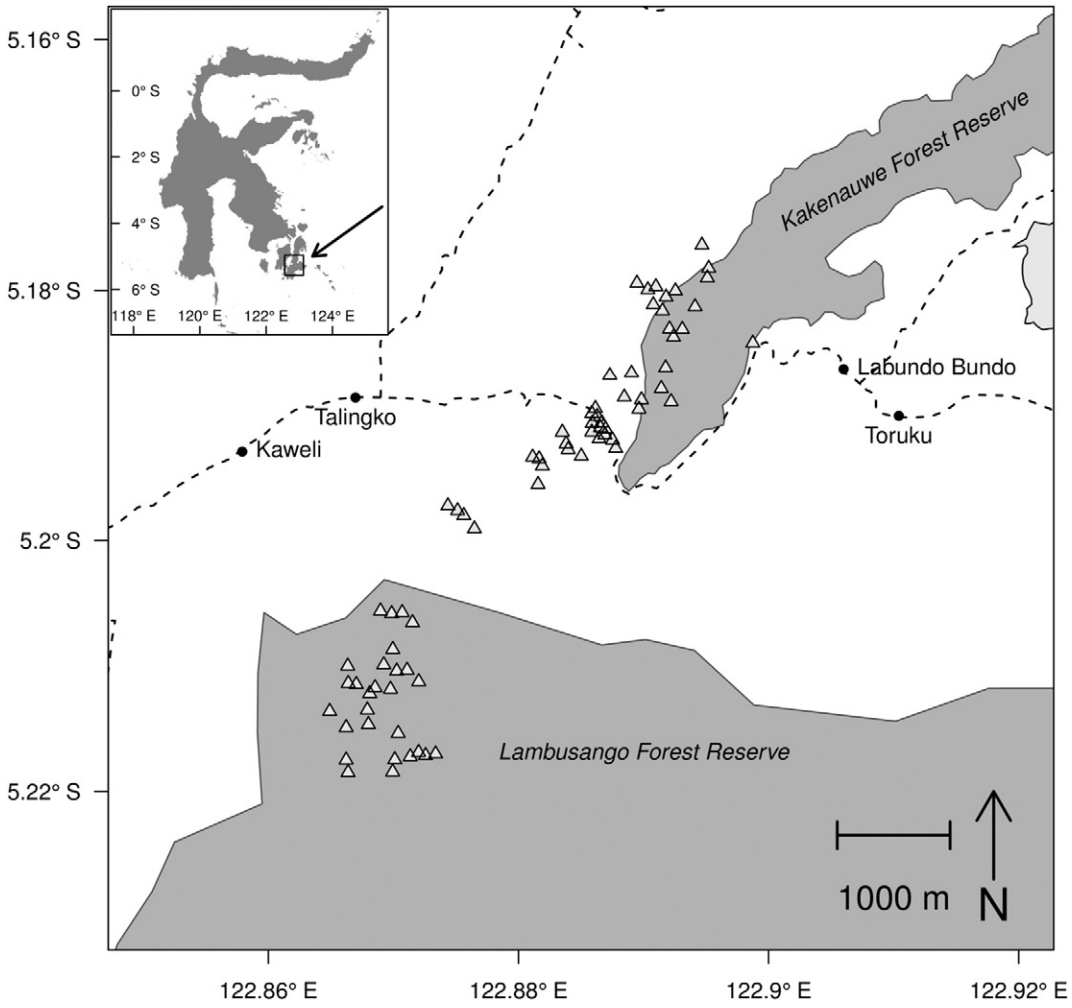

Fig. 1. Study are on Buton Island with Sulawesi in-set. Shaded areas — official protected areas; triangles — sample sites. Dotted line — roads; solid circles — villages.

sites varied in size from 25 to 40 houses and were assumed to have similar types of impacts on nearby forest areas.

GPS data for roads and villages and sample sites were imported into *R* (R Core Team, 2013) to calculate the distance of each site from the road and villages, using the *R* package *rgeos* (Bivand and Rundel, 2013). These distances were used in analyses of site-to-site variation in herpetofaunal community composition.

Habitat structural measurements previously identified as important influences on tropical reptile and amphibian distribution and abundance were recorded at each site, encompassing the canopy, mid-strata, understorey and forest floor (Table 1). Means and variances were calculated for the various measurements within each site and amongst years of sampling.

2.4. Statistical analyses

Trap and sample data were pooled for all statistical analyses.

2.4.1. Species composition

Pairwise dissimilarities between herpetofaunal assemblages of sites were computed using Jaccard's distance measure for presence/absence data. We did not use metrics of abundance of species in analyses

Table 1
Selected habitat variables used, and rationale underpinning each of their inclusion.

Variable	Rationale	References
Litter depth	Litter depth influences species diversity.	Scott (1976), Heinen (1992), Whitfield and Pierce (2005), Gardner et al. (2007a,b), Wanger et al. (2009).
Tree diameter (DBH)	High DBH values indicate relatively large, old trees. The presence of large old trees is indicative of low levels of logging.	Pawar et al. (2004), Whitfield and Pierce (2005).
Number of buttresses	Important shelter and foraging microhabitats for herpetofauna, and contribute to habitat complexity.	Heyer and Berven (1973), Scott (1976), Voris (1977).
Canopy cover	High canopy cover, with few large canopy gaps is indicative of undisturbed forest. Conversely, heliothermic species may prefer lower canopy cover.	Heinen (1992), Vitt et al. (1998).
Number of logs >30 cm	Logs are used for shelter/basking. Logs are rich in arthropods, which are important food for many reptiles and amphibians. Availability of logs influences species richness.	Whitfield and Pierce (2005), Wanger et al. (2009), Hu et al. (2013)
Number of vines	Lianas are a significant component of the vertical structural complexity of tropical forests	Gardner et al. (2007a)
Distance to road	Surrogate for anthropogenic disturbance – villagers access forest from roads for hunting, timber and rattan harvesting.	Fretes (1992), Mohd Azlan (2006), Sodhi et al. (2010).
Elevation	Herpetofauna species richness generally declines, and species composition shifts, with elevation	McCain (2010).

because these assume, unjustifiably, that individual encounter rates are indicative of true species abundances, and do not account for differing detection probabilities between species and amongst sample sites (Kéry and Royle, 2008; Guillera-Arroita et al. 2014). The matrix of dissimilarities was then used to construct a two-dimensional ordination of herpetofaunal species composition, using non-metric multidimensional scaling (NMDS). In an NMDS ordination, multivariate data are projected into a space with a smaller number of dimensions. They are arranged in space such that the sites that are most similar are close together, whilst sites that are more different are further apart. The axes themselves are arbitrary, and don't represent any particular quantity — the configuration of points in the space can be rotated or reflected without changing the underlying ordination, as long as the pair-wise distance between sites are not altered.

In order to avoid possible local minima and unstable solutions in the NMDS ordination, the final selected NMDS solution was the best configuration found amongst 20 independent runs of the fitting algorithm with 20 different random starting configurations. Relationships between species assemblage structure, environmental variables and disturbance proxies were explored by fitting linear vectors to the NMDS ordination space, using the function *envfit* within the *vegan* package of *R* (Oksanen et al., 2013). Statistical significance of the environmental vectors was assessed using a permutation test with 1000 random permutations of the covariate data. Separate NMDS plots were generated to compare relationships amongst taxonomic groups (frogs, lizards and snakes) and arboreal versus leaf litter species.

2.4.2. Species richness

Species richness of each of the sample sites was estimated using jackknife and bootstrap non-parametric species richness estimators from the survey data (see Colwell and Coddington, 1994). These estimates were compared to observed species richness by Spearman's rank correlation (r_s) to assess the adequacy of sampling, and the extent to which the number of species actually encountered accorded with the likely true numbers of species present at each site. High correlations were found between observed species richness and both estimates (jackknife $r_s = 0.85$; bootstrap $r_s = 0.99$), so for simplicity, observed species richness was used for subsequent analyses.

Generalized additive models (GAM; Hastie and Tibshirani, 1990; Wood, 2006) with Poisson error structure and logarithmic link-functions were used to examine relationships between species richness and distance to road, and a selection of habitat variables, for which there were reasons to expect influences on species richness (Table 1). All habitat and disturbance proxy variables were checked for multicollinearity; correlations between the variables used in the GAM analyses were no more than 0.46 (Appendix 1).

A series of GAMs were fitted using the *R* package *mgcv* (Wood, 2006). We initially fitted a full model with smooth-terms for all of the selected covariates. On initial fitting, some covariates were found to be best-fitted by smooth-terms with effective degrees of freedom (edf) equal to one, implying simple linear effects. Accordingly, these terms were simplified to linear terms. Subsequently, the least significant terms in the models were successively dropped until the Akaike's Information Criterion (AIC) no longer improved (Burnham and Anderson, 2002), leading to a final selected model for habitat effects on species richness. Partial effects of each habitat term were plotted, to reveal the shape of the response curve associated with each selected habitat variable.

Using the same procedure, separate analyses of species richness-habitat relationships were undertaken on snakes, lizards and frogs. Arboreal and leaf litter species are potentially more sensitive to disturbance (Vitt et al. 1998; Gardner et al. 2007a), therefore we also examined the influence of habitat variables on species richness within these guilds separately.

3. Results

We recorded 8562 individuals of 49 species (10 frogs, 18 lizards, 20 snakes, and 1 freshwater turtle; Table 2). The most frequently encountered species were small (<30 g), predominantly terrestrial,

Table 2
Taxa detected during the study, showing those identified as predominantly arboreal or litter-dwelling.

Taxon and abbreviation		Habitat association
Bufonidae		
Ingerophrynus cf. *celebensis*	Ic	Litter
Microhylidae		
Kaloula cf. *baleata*	Kb	Litter
Oreophryne sp. *nov.*	O	Litter
Dicroglossidae		
Fejervarya cancrivora	Fc	
Limnonectes sp. *1*	Li	
Limnonectes sp. *G2*	Lg	
Ranidae		
Hylarana mocquardi	Hm	Arboreal
Rhacophoridae		
Polypedates iskandari	Pi	Arboreal
Rhacophorus georgii	Rg	Arboreal
Rhacophorus cf. *edentulus*	Re	Arboreal
Agamidae		
Bronchocela celebensis	Bc	Arboreal
Draco beccarii	Db	Arboreal
Dibamidae		
Dibamus sp. *nov.*	D	Litter
Gekkonidae		
Cyrtodactylus jellesmae	Cj	
Gehyra mutilata[a]	Gm	Arboreal
Gehyra cf. *oceanica*	Go	Arboreal
Ptycozoon cf. *kuhli*[a]	Pk	Arboreal
Scincidae		
Eutropis grandis	Eg	
Eutropis multifasciata	Em	
Eutropis rudis	Er	
Lamprolepis smaragdinum	Ls	Arboreal
Lipina infralineolata	Li	Arboreal
Sphenomorphus cf. *sarasinorum*	Ss	Arboreal
Tytthoscincus sp. *nov* 1	T1	Litter
Tytthoscincus sp. *nov* 2	T2	Litter
Sphenomorphus tropidonotus	St	Arboreal
Sphenomorphus cf. *variagatum*	Sv	
Varanidae		
Varanus salvator	Vs	
Colubridae		
Ahaetulla prasina	Ap	Arboreal
Amphiesma celebica	Ac	Litter
Boiga irregularis[a]	Be	Arboreal
Calamaria cf. *brongersmai*	Cb	Litter
Calamaria butonensis	Bu	Litter
Calamaria longirostris	Cl	Litter
Calamaria cf. *nuchalis*	Cn	Litter
Coelognathus erythrurus celebensis[a]	Ce	
Dendrolaphis marenae	Dm	Arboreal
Oligodon waandersi	Ow	Litter
Psammodynastes pulverulentus	Pp	
Rhabdophis callistus	Rc	
Xenochrophis trianguligera	S	
Crotalidae		
Tropidolaemus subannulatus	Ts	Arboreal
Cylindrophidae		
Cylindrophis melanotus	Cm	Litter
Elapidae		
Ophiophagus hannah[a]	Oh	
Typhlopidae		
Cyclotyphlops deharvengi	Cd	Litter
Ramphotyphlops braminus	Rb	Litter
Ramphotyphlops olivaceus	Ro	Litter
Xenopeltidae		
Xenopeltis unicolor	X	
Geoemydidae		
Cuora amboinensis	Ca	

[a] Species recorded only once.

litter-dwelling lizards, snakes and frogs, and comprised almost 98% of all detections. Arboreal and/or large species (>100 g) were much less frequently encountered (Fig. 2).

3.1. Habitat structure and disturbance

Vector fitting indicated that eight parameters describing habitat structure, along with elevation, distance to road and distance to nearest village explained most of the variation in herpetofaunal assemblage structure amongst sampling sites (Table 3; Fig. 3A). Most variation was evident along an axis correlated with the number of buttresses per tree, distance to road, mid-storey tree density and maximum vine diameter. Mid-storey tree density and number of large trees varied inversely with lower understorey density; several measures of vine size and abundance varied positively with elevation, but negatively with mean number of buttresses per tree. Road distance varied with village distance. Neither elevation nor any of the habitat parameters were strongly related to road or village distance; however mean diameter at breast height (DBH) was partially correlated with village distance, and understorey vegetation density and mid-storey tree density varied partially with road distance.

3.2. Species composition

Overall herpetofaunal species composition varied mostly in relation to large tree density, maximum vine diameter, number of buttresses per tree and understorey vegetation density (Axis 1; Fig. 3A & B), followed by distances to road and villages (Axis 2). However, the relatively larger amount of variation along Axis 1 resulted from four species that were detected on only single occasions (Table 2; Fig. 2).

No clear differences in species composition were observed amongst guilds with respect to any specific habitat variables (Fig. 3C); however, occurrences of litter-dwelling species were less variable on either axis than arboreal species. Amphibians tended to occur at sites further from roads with less dense understorey vegetation than lizards (Fig. 3D), which tended to occur at sites with high densities of large trees and large vines. Most species with strong associations to road and villages were arboreal lizards, whilst species with strong negative associations with these parameters were arboreal frogs, the single turtle species, and snakes.

Table 3
Habitat variables measured at each site and results of fitting habitat vectors to NMDS ordination of herpetofaunal assemblage similarity. For each vector, r^2 is a measure of goodness of fit of the habitat variable to the ordination space; p-value (significant values in bold) is based on a randomization test, with 1000 random permutations of the habitat variable. DBH — diameter at breast height, measured at 1.5 m above ground.

Environmental parameters	NMDS1	NMDS2	r^2	P
Mid-storey tree density	0.995	−0.104	0.224	**0.001**
Maximum vine diameter	0.934	0.358	0.248	**0.001**
Mean number of buttresses per tree	−0.954	−0.301	0.267	**0.001**
Road distance	−0.603	0.798	0.204	**0.001**
Lower under storey density	−0.959	0.284	0.135	**0.003**
Vine density	0.762	0.647	0.137	**0.003**
Canopy tree density	0.992	0.129	0.139	**0.004**
Elevation	0.648	0.762	0.132	**0.005**
Mean vine diameter	0.873	0.488	0.139	**0.007**
Nearest village distance	−0.099	0.995	0.132	**0.010**
Mean DBH of canopy trees	−0.643	−0.766	0.099	**0.028**
Canopy cover variance	−0.753	0.658	0.058	0.131
Largest tree DBH	−0.377	−0.926	0.054	0.133
Number of large logs	−0.877	−0.480	0.050	0.165
Mean litter depth	0.182	−0.983	0.048	0.167
Litter depth variance	−0.407	−0.913	0.032	0.316
Mean canopy cover	0.115	0.993	0.021	0.448
Maximum number of buttresses	−0.472	−0.882	0.020	0.495
Total buttress number	−0.868	0.497	0.014	0.615
Mean log diameter	−0.463	−0.886	0.003	0.906
Maximum log diameter	−0.995	0.099	0.000	0.992

Bold font indicates significance of $p < 0.05$.

3.3. Species richness

The best supported model for the influence of environmental variables on overall species richness included the number of large logs, mean number of buttresses per tree and elevation (Table 4). Generally species richness increased as buttress and log numbers increased, and decreased with elevation (Fig. 4). Evidence for the effects of all other environmental covariates was not strong, and they were dropped from the best supported model.

The best supported model for arboreal species included terms for canopy cover (negative linear relationship), mean DBH (concave down non-linear relationship) and elevation (negative, linear) (Table 4;

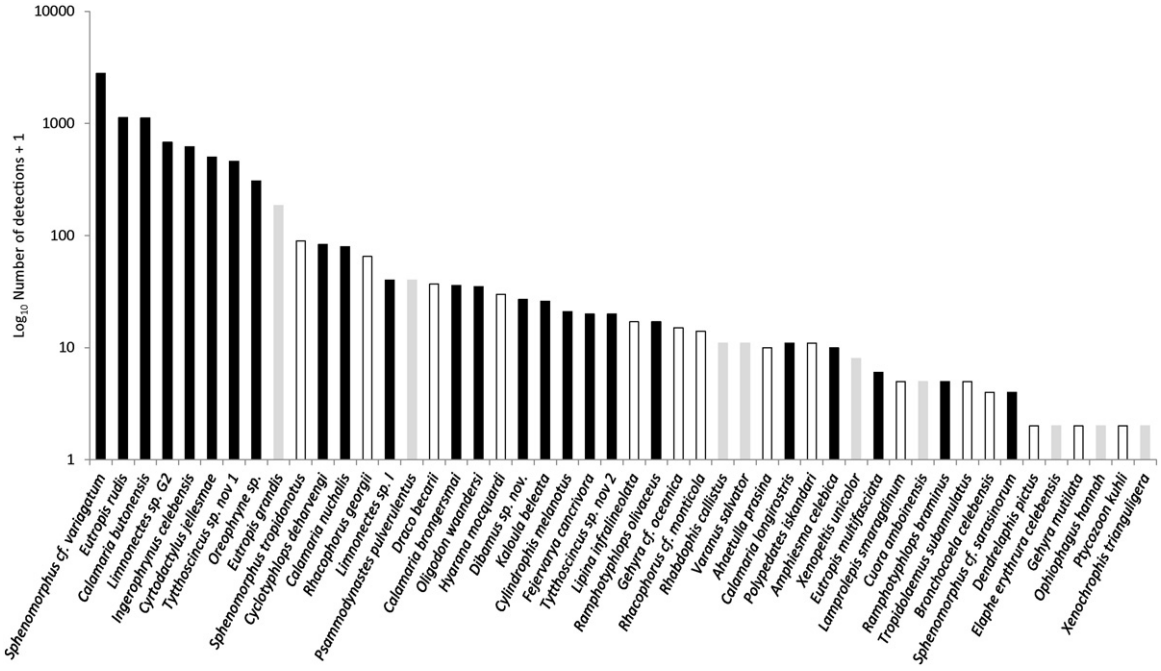

Fig. 2. Number of encounters of each species. Black bars — predominantly terrestrial <30 g; grey bars — predominantly terrestrial >30 g; open bars — predominantly arboreal species.

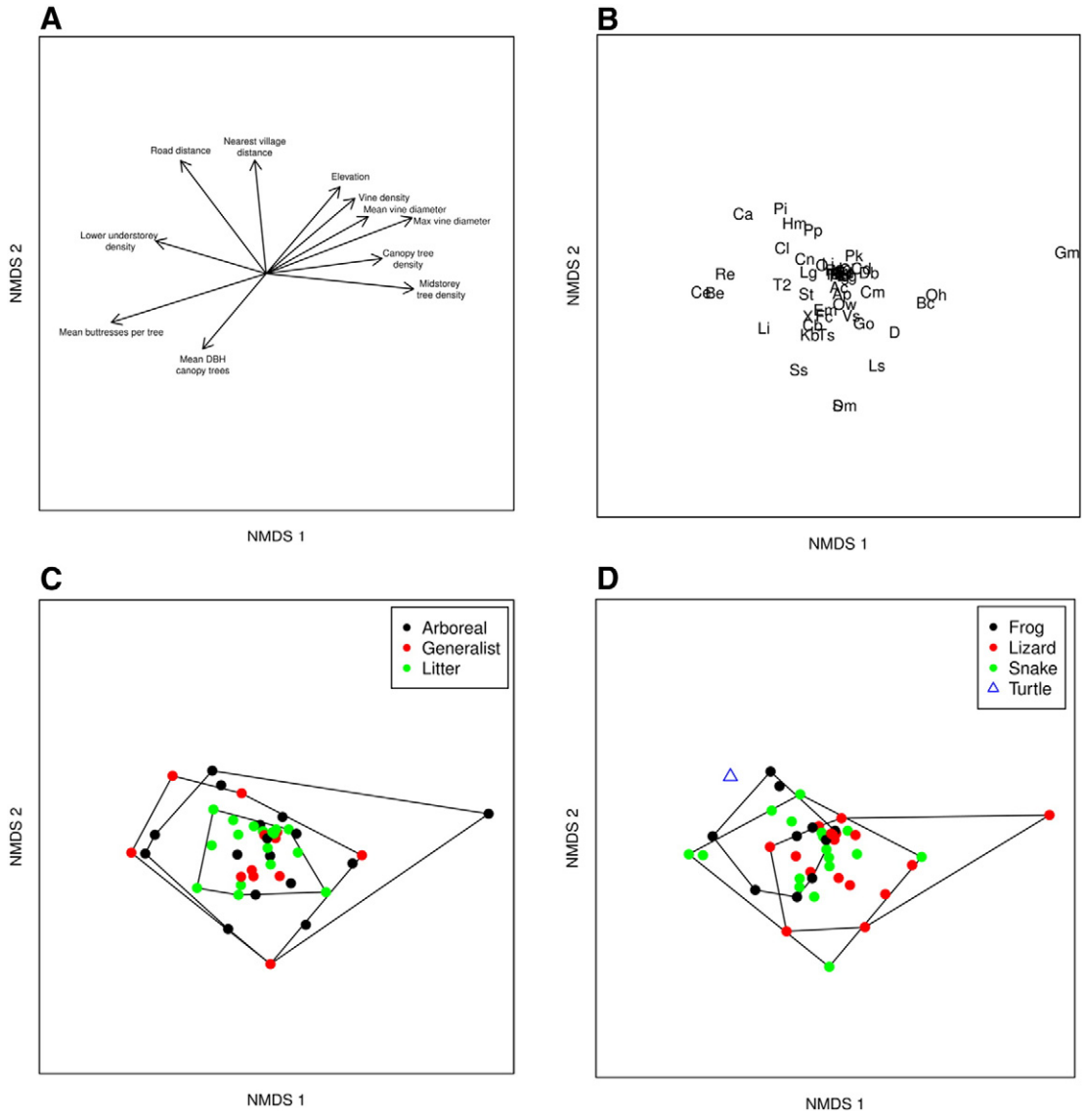

Fig. 3. NMDS ordination of habitat dissimilarity. A — direction and magnitude (encoded by vector length) of fitted linear habitat vectors in the ordination space. Only vectors where the permutation test gave $p < 0.1$ were included in the plot for clarity (see Table 3). See Table 2 for species initials and names; C— species coded by guild; D — species coded by taxonomic group.

Fig. 5). For litter species the best model included mean buttresses per tree (positive linear) (Fig. 6).

The best supported model for frog species richness included terms for mean buttresses per tree (positive linear relationship), elevation (negative linear relationship), mean litter depth (negative non-linear), and distance from road (negative binomial) (Table 5; Fig. 7). For snake species richness the best model included mean litter depth (positive linear), large log density (positive linear), mean tree DBH (convex negative non-linear) and mean number of buttresses per tree (concave positive non-linear) (Fig. 8). For lizard species richness, the null model was better supported than any model containing habitat covariates (Table 5).

4. Discussion

4.1. Habitat structure and disturbance

Many key structural components of habitat varied independently of our disturbance proxies, suggesting that inherent heterogeneity in these parameters, due to topography and natural disturbance regimes, was high relative to the effects of anthropogenic disturbance. Understorey vegetation density and mid-storey tree density increased with greater proximity to human access, consistent with effects of selective logging, a key anthropogenic disturbance process in the region. Selective logging removes large, mature trees, along with associated vines; creates canopy gaps, and increases light penetration to the forest floor, resulting in increased density of undergrowth (Fimbel et al. 2001). The density of smaller mid-storey trees also increases as saplings grow to fill canopy gaps. The lack of relationship between human disturbance proxies and metrics of tree size, such as mean DBH, may be indicative of loggers targeting preferred tree species, rather than the largest trees. Alternatively, topography may have a stronger influence on relative tree size; a strong inverse relationship was apparent between elevation and tree size, consistent with well-drained ridge-tops with skeletal karst soils supporting smaller statured trees, compared with gullies with deeper soils and greater moisture retention.

4.2. Community composition

Species composition was influenced by a range of habitat characteristics (Table 3; Fig. 3A & B), all of which were expected to affect habitat suitability for various forest species differently (see Heyer and Berven, 1973; Voris, 1977; Pawar et al., 2004). Composition varied on a gradient from

Table 4
Summary statistics for GAMs for overall species richness relationships, and litter and arboreal species, with selected habitat variables. edf — effective degrees of freedom for model smooth terms.

All species	Estimate	SE	Z	p
Parametric coefficients:				
Intercept	2.992	0.238	12.58	<0.001
Number logs > 30 cm	0.042	0.023	1.840	0.066
Elevation	−0.001	0.0009	−1.517	0.129
Smooth terms	edf	df	Chi sq	p
s (mean buttress number)	1.190	1.345	5.508	0.032
Adjusted R^2 of model	0.200			
Litter species				
Parametric coefficients:				
Intercept	1.917	0.113	16.996	<0.001
Mean buttress number	0.072	0.030	2.358	0.018
Smooth terms	edf	df	Chi sq	p
–	–	–	–	–
Adjusted R^2 of model	0.135			
Arboreal species				
Parametric coefficients:	Estimate	SE	Z	p
Intercept	0.764	0.082	9.337	<0.001
Smooth terms	edf	df	Chi sq	p
s (mean DBH)	1.868	1.982	7.180	0.027
s (mean canopy cover)	1.254	1.444	3.594	0.097
s (elevation)	1.671	1.891	7.560	0.021
Adjusted R^2 of model	0.188			

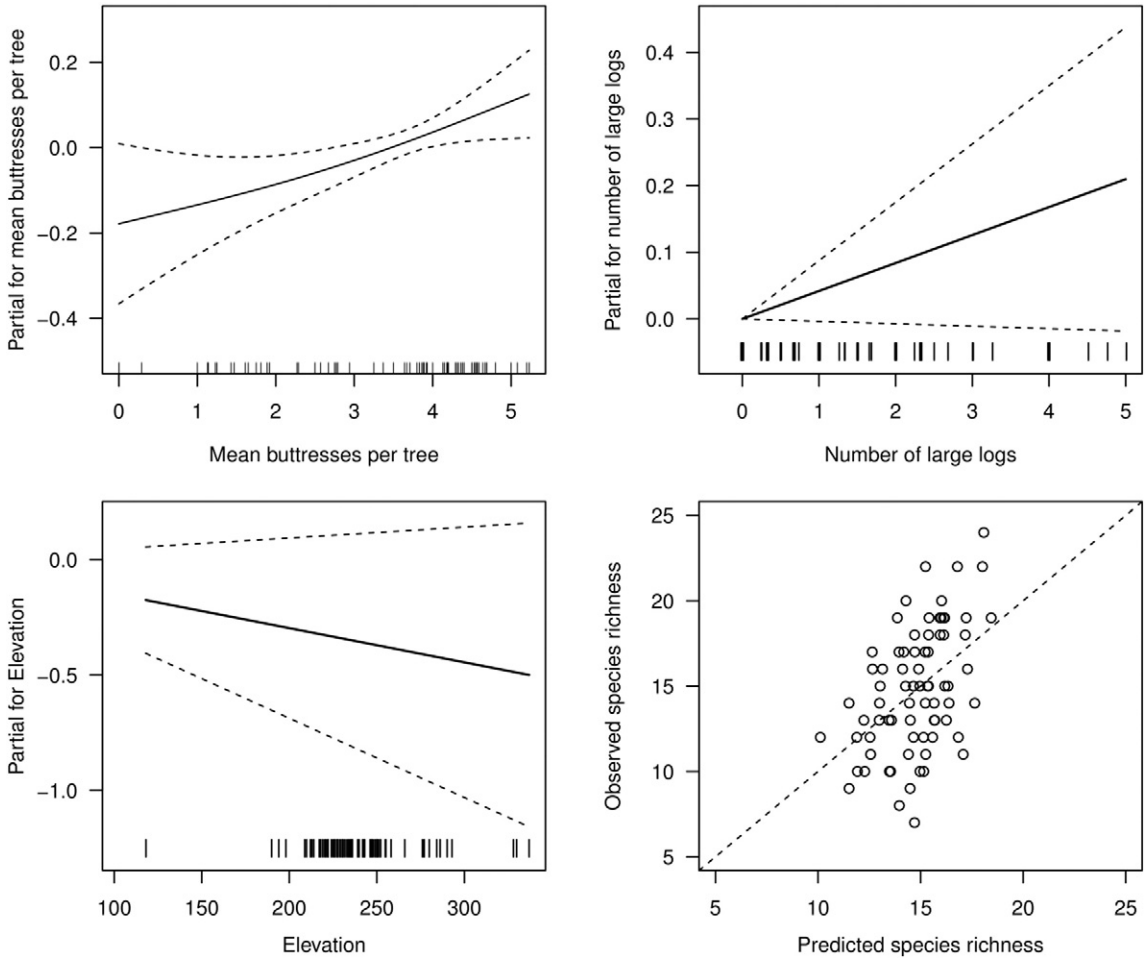

Fig. 4. Partial effects of variables in the GAM model for estimated overall species richness. Bottom right panel shows relationship between observed and predicted species richness. Dashed lines are ±2 standard errors.

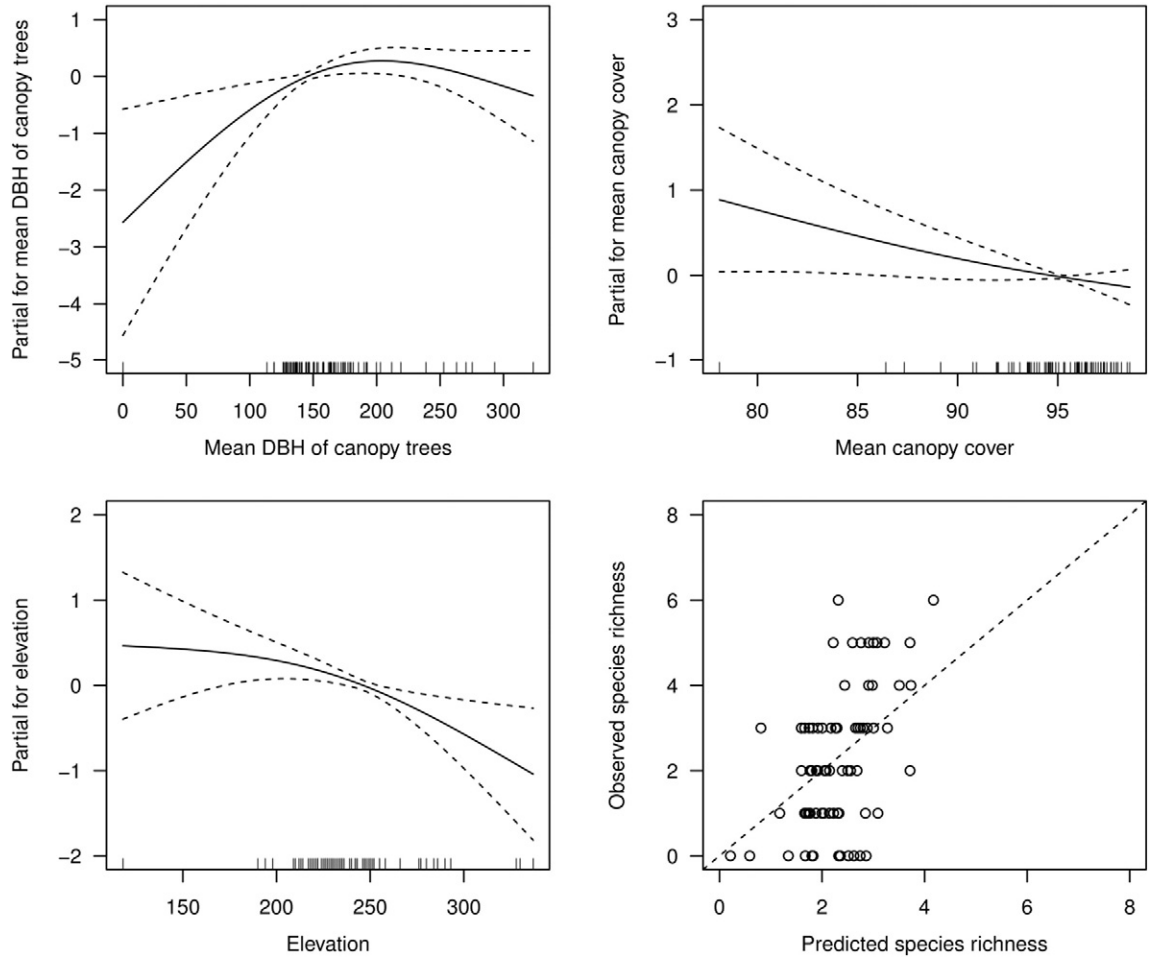

Fig. 5. Partial effects of terms in the GAM for observed species richness for frog species only. The bottom panel shows the relationship between observed and predicted species richness. Dashed lines are ±2 standard errors.

large trees with a simple understorey and mid storey structure, to smaller trees with a dense and complex understorey of saplings and lianas. Much of this variation was independent of proximity to human access. In contrast to previous tropical forest disturbance studies (Table 1) variation in litter and canopy cover did not influence species composition significantly. The relatively low variability in these parameters relative to others, including our disturbance proxies of village and road distance, suggests that anthropogenic disturbance regimes have not been severe enough to alter these characteristics enough to influence community composition beyond levels of inherent natural variation.

All taxonomic groups and guilds varied in species composition in relation to human access (Fig. 3C & D). The compositional changes related to human disturbance differed from those associated with inherent habitat variability (Fig. 3A), suggesting subtle ecological effects of

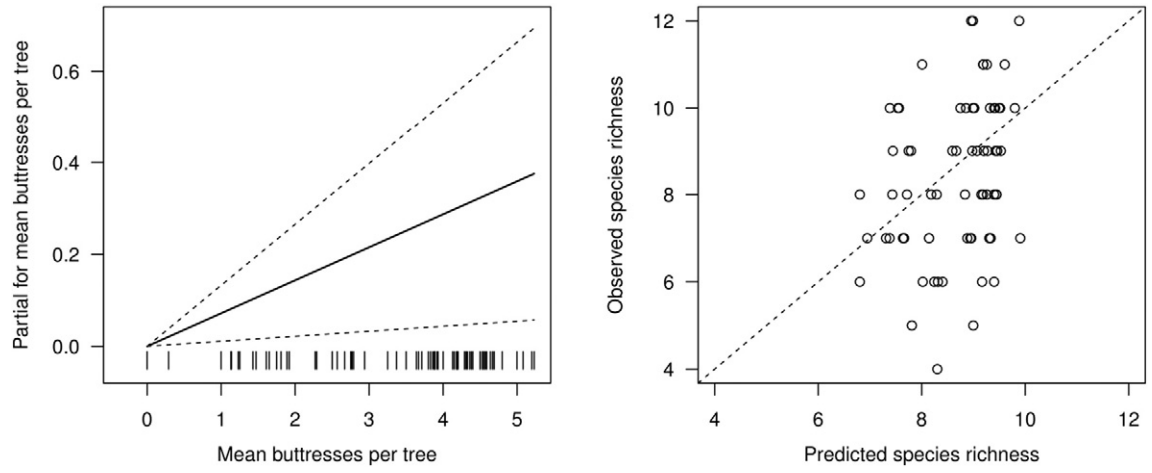

Fig. 6. Partial effects of each of the terms in the GAM for observed species richness of litter species only. The bottom panel shows the relationship between observed and predicted species richness. Dashed lines are ±2 standard errors.

Table 5
Summary statistics for the GAMs for species richness relationships with selected habitat variables for frogs, lizards and snakes. edf — effective degrees of freedom for the smooth terms in the models.

Frogs	Estimate	SE	Z	p
Parametric coefficients:				
Intercept	1.976	0.589	3.342	<0.001
Mean buttresses	0.112	0.056	1.990	0.047
Elevation	−0.004	0.002	−2.010	0.044
Smooth terms	edf	df	Chi sq	p
s (mean litter depth)	1.561	1.807	4.316	0.096
s (road distance)	1.774	1.949	3.077	0.205
Adjusted R^2 of model	0.294			
Lizards				
Parametric coefficients:				
Intercept	1.907	0.045	42.860	<0.001
Smooth terms	edf	df	Chi sq	p
–	–	–	–	–
Adjusted R^2 of model	0			
Snakes				
Parametric coefficients:				
Intercept	0.979	0.216	4.533	<0.001
Mean litter depth	0.008	0.005	1.615	0.106
Number logs > 30 cm	0.083	0.045	1.830	0.067
Smooth terms	edf	df	Chi sq	p
s (mean DBH)	1.681	1.894	1.866	0.363
s (mean buttress number)	1.839	1.970	4.862	0.0855
Adjusted R^2 of model	0.197			

anthropogenic disturbance on herpetofaunal diversity not directly associated with the habitat parameters we measured. Furthermore, these anthropogenic influences had variable effects on different guilds, with more frog species showing negative, and more lizard species showing positive responses. These findings are consistent with those of some other studies (e.g. Vallan, 2002; Burivalova et al. 2014) but not by others (e.g. Crump, 1971; Gardner et al. 2007b; Wanger et al. 2010). Community responses to forest disturbance may depend on the type of disturbance and the ecological characteristics of the constituent species (Gardner et al. 2007b). However our study examined patterns of community change under much more moderate intensities of disturbance compared to the above-mentioned studies. Our findings indicate that anthropogenic disturbance thresholds for maintaining herpetofaunal community composition of tropical forests may be much higher than previously indicated (Gardner et al. 2007b; Gibson et al. 2011), but also that 'natural' habitat variation reflecting abiotic conditions (hydrology, topography, soil etc.) or disturbances (e.g. natural tree falls) may have equally strong effects.

4.3. Species richness

We found little evidence of any relationship between species richness and human disturbance proxies. Species richness was generally related to availability of buttresses, canopy tree size, litter depth, availability of large logs, and elevation; all of which are known to influence herpetofaunal diversity (Table 1). Only frog species richness showed any relationship with a disturbance proxy, with species richness peaking at intermediate distances from the road. Inherent habitat heterogeneity of these forests seemingly had a larger influence on species richness than variation in levels of human disturbance.

Reductions in herpetofaunal species richness in response to disturbances have been largely explained in other studies by reduced forest leaf litter or decreasing canopy cover (Whitfield and Pierce, 2005; Faria et al. 2007; Gardner et al. 2007b; Whitfield et al. 2007; Wanger et al. 2009). Whilst litter and canopy cover were positively associated with species richness, there was minimal variation in these parameters across the disturbance gradient (Table 3; Fig. 3A). Previous studies investigating herpetofaunal diversity and tropical forest disturbance have typically examined more intensive disturbance regimes, such as secondary forest regeneration from commercial logging or abandoned agriculture, plantations or other non-forest habitats (e.g. Gardner et al. 2007b; Wanger et al. 2009, 2010; Burivalova et al. 2014). Gillespie et al. (2005) also found marked changes in both species richness across similarly wide environmental gradients in the vicinity of our study site. Our findings suggest that, in contrast to wholesale forest conversion, low-level selective logging and other subsistence disturbance processes in this region do not alter these habitat attributes beyond thresholds that grossly affect species richness.

4.4. Caveats

Few previous studies have robustly estimated species richness or demonstrably sampled most species in tropical herpetofaunal assemblages (e.g. Gardner et al. 2007b). We detected 90% of species known from our study area (Gillespie et al., 2005); but even so, our sampling methods were likely to have been biased towards detecting small, predominantly terrestrial, species readily located by ground-based sampling methods. The low encounter rates of arboreal species may reflect our choice of sampling methods, and is likely mirrored in most other studies (e.g. Vitt et al. 1998; Gardner et al. 2007a,b; Wanger et al. 2009, 2010), highlighting a general weakness in knowledge of this component of tropical herpetofauna.

The herpetofaunal diversity of Sulawesi is relatively depauperate compared to the adjacent Greater Sunda Shelf (Gillespie et al. 2005). The nature of the Sulawesi herpetofauna and the lineages that have successfully colonized the island from the Sunda Shelf may have resulted in a fauna that is composed of a larger fraction of disturbance-tolerant species than might be the case for other adjacent islands, e.g. Borneo. Due to these apparent founder effects, it may be conceivable that herpetofaunal communities in other regions of southeast Asia may be more sensitive to low and moderate anthropogenic disturbances.

Our study was generally uninformative about large predatory species, such as varanid lizards and large snakes, due to low encounter rates, which may have reflected low densities or low detection probabilities. For example, the reticulated python *Malayopython reticulatus* occurs at our study site (Gillespie et al. 2005) but was not detected during our sampling; the second largest reptile species, the king cobra *Ophiophagus hannah*, was only detected once. Impacts of forest disturbance on large predatory forest reptiles are a notable knowledge gap globally, as such species potentially have important top-down ecological functions (Jessop et al. 2006; Sutherland et al. 2011).

4.5. Conclusions and management implications

Low levels of anthropogenic disturbance and habitat variability influence different aspects of the herpetofauna community in different ways. We found that species composition, but not richness, varied across a gradient of low to moderate anthropogenic forest disturbance. This finding has important implications for conservation management as it could indicate the loss of disturbance-sensitive species whilst richness is maintained by the spread of disturbance-tolerant species, hence supporting the findings of Gibson et al. (2011) that maximizing tropical biodiversity conservation is dependent upon primary forest protection. Furthermore, our findings illustrate the pervasive nature of anthropogenic disturbances in tropical forests that have subtle impacts extending considerable distances into forest areas.

Conversely, high-access forests subjected to a moderately long history of anthropogenic disturbance (at least several decades), including selective logging, still retained most species associated with primary forest. Similar patterns have been found for a range of other taxa, both in this region (birds; Martin and Blackburn, 2010) and elsewhere (e.g. trees, Cannon et al., 1998; mammals and birds, Brooks et al. 1999;

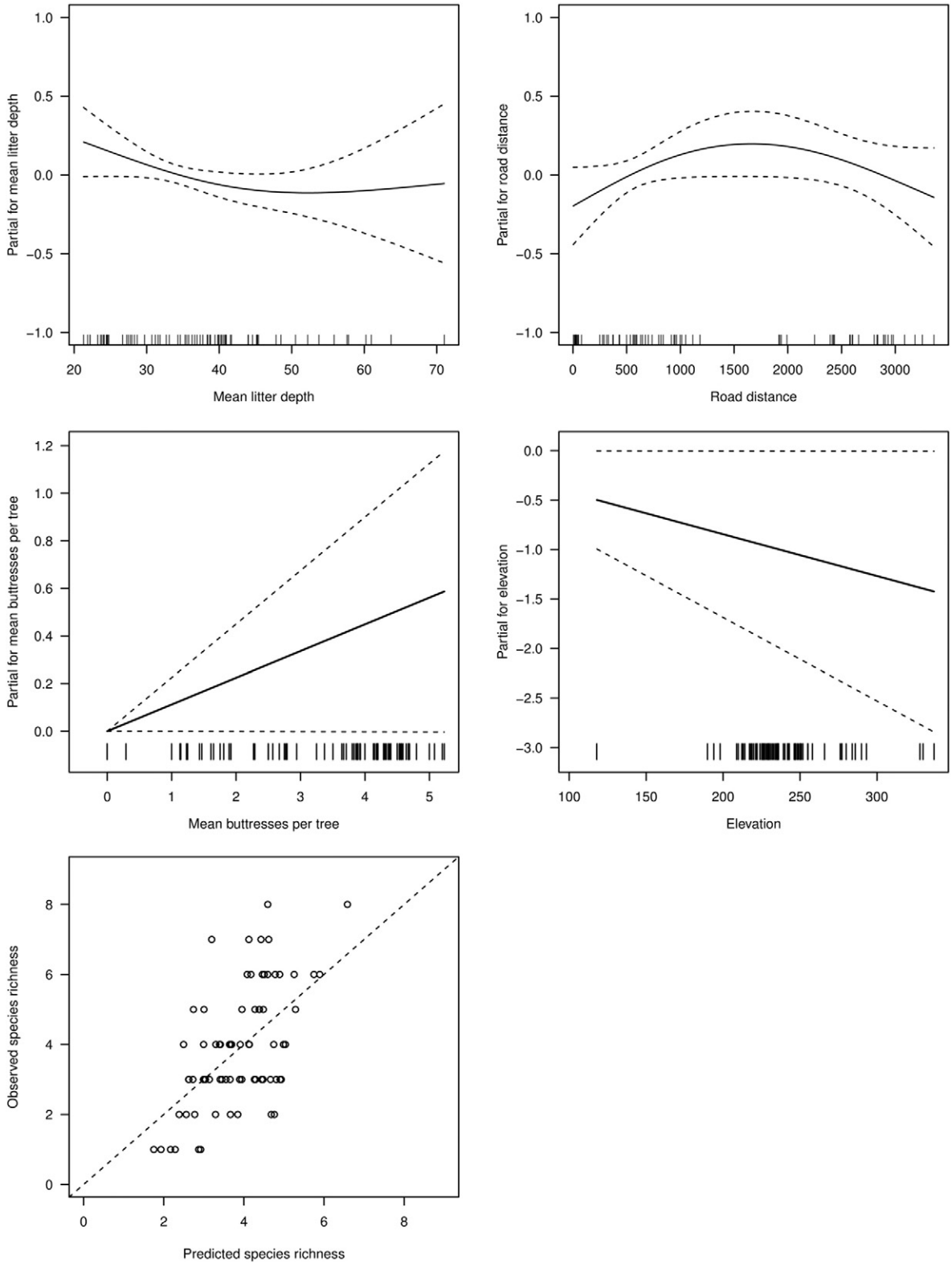

Fig. 7. Partial effects of each of the terms in the GAM for observed species richness for frog species only. The bottom panel shows the relationship between observed and predicted species richness. Dashed lines are ±2 standard errors.

bats, Peters et al. 2006; birds and ants, Berry et al. 2010). Our findings therefore suggest that tropical forests managed for multiple subsistence use contribute significantly to maintaining herpetofaunal diversity at a landscape scale.

Anthropogenically altered, multiple-use forests are now much more extensive than primary tropical forest in Southeast Asia, and constitute an important conservation resource (Edwards et al. 2011; Fisher et al. 2011). Multiple use forests can provide a

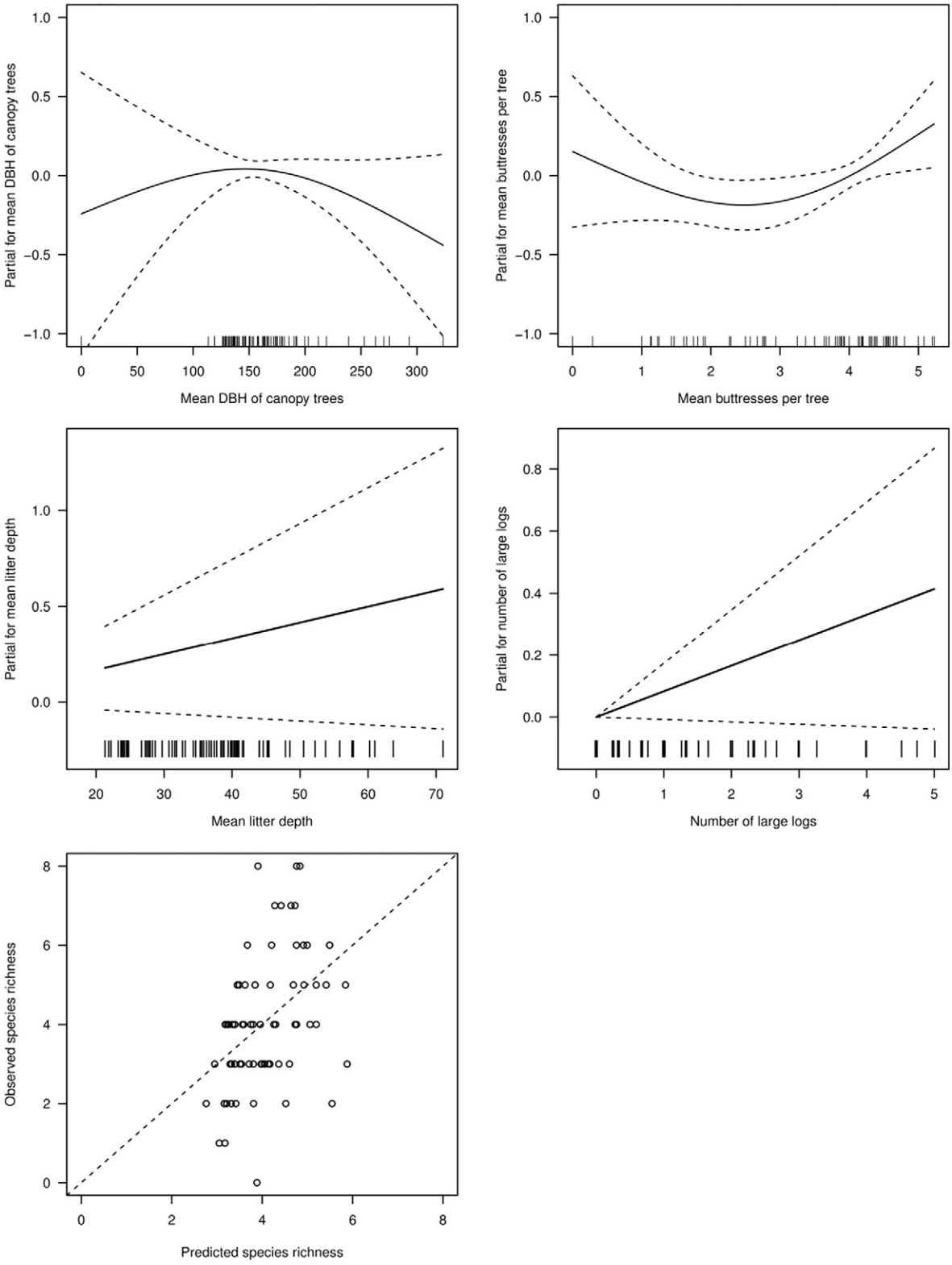

Fig. 8. Partial effects of each of the terms in the GAM for observed species richness for snake species only. The bottom panel shows the relationship between observed and predicted species richness. Dashed lines are ±2 standard errors.

geographic buffer from anthropogenic affects around core, minimally-disturbed forests, thus increasing their protection. Forest patch size, level of buffering, and connectivity may be more critical than habitat quality per se for conservation of other biota, particularly large mammals, (e.g. Kinaird and O'Brien 2006). We therefore advocate an integrated conservation approach of maintaining larger forest areas with variable disturbance and usage regimes around more remote, minimally disturbed core areas. On Buton Island, as with much of the developing world, geographic access rather than official land tenure has a far greater influence on the extent and nature of forest disturbances. Long term biodiversity conservation is therefore best maximized by minimizing human access to core

areas by limiting construction of roads through forested areas (Trombulak and Frissell, 1999; Laurance et al. 2014).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version, at http://dx.doi.org/10.1016/j.biocon.2015.08.034. These data include the Google map of the most important areas described in this article.

References

Allnutt, T.F., Asner, G.P., Golden, C.D., Powell, G.V.N., 2013. Mapping recent deforestation and forest disturbance in northeastern Madagascar. Mongabay.com Open Access J. Trop. Conserv. Sci. 6, 1–15.
Berry, N.J., Phillips, O.L., Lewis, S.L., Hill, J.K., Edwards, D.P., Tawatao, N.B., Ahmad, M., Ong, R.C., Hamer, K.C., 2010. The high value of logged tropical forests: lessons from northern Borneo. Biodivers. Conserv. 19, 985–997.
Bhat, D.M., Hegde1, G.T., Shetti, D.M., Patgar, S.G., Hegde1, G.N., Furtado, R.M., Shastri, C.M., Bhat, P.R., Ravindranath, N.H., 2011. Imact of disturbance on composition, structure, and floristics of tropical moist forest in Uttara Kannada district, Western Ghats, India. Ecotropica 17, 1–14.
Bivand, R.S., Rundel, C., 2013. rgeos: interface to geometry engine — open source (GEOS). R package version 0.3–2. http://CRAN.R-project.org/package=rgeos.
Brooks, T.M., Pimm, S.L., Kapos, V., Ravilious, C., 1999. Threat from deforestation to montane and lowland birds and mammals in insular South-east Asia. J. Anim. Ecol. 68, 1061–1078.
Burivalova, Z., Sekercioglu, C.K., Koh, L.P., 2014. Thresholds of logging intensity to maintain tropical forest biodiversity. Curr. Biol. 24, 1–6.
Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer Verlag New York, USA.
Cannon, C.H., Peart, D.R., Leighton, M., 1998. Tree species diversity in commercially logged Bornean rainforest. Science 281, 1366–1368.
Colwell, R.K., Coddington, J.A., 1994. Estimating terrestrial biodiversity through extrapolation. Philos. Trans. R. Soc. B 345, 101–118.
Crump, M., 1971. Quantitative analysis of the ecological distribution of a tropical herpetofauna. Occasional Papers of the Museum of Natural History, University of Kansas 3, pp. 1–62.
De Fries, R., Hansen, A., Newton, A.C., Hansen, M.C., 2005. Increasing isolation of protected areas in tropical forests over the past twenty years. Ecol. Appl. 15, 19–26.
Edwards, D.P., Larsen, T.H., Docherty, T.D.S., Ansell, F.A., Hsu, W.W., Derhé, M.A., Hamer, K.C., Wilcove, D.S., 2011. Degraded lands worth protecting: the biological importance of Southeast Asia's repeatedly logged forests. Proc. R. Soc. B 278, 82–90.
Faria, D., Paciencia, M.L.B., Dixo, M., Laps, R.R., Baumgarten, J., 2007. Ferns, frogs, lizards, birds and bats in forest fragments and shade cacao plantations in two contrasting landscapes in the Atlantic forest, Brazil. Biodivers. Conserv. 16, 2335–2357.
Fimbel, R.A., Grajal, A., Robinson, J. (Eds.), 2001. The cutting edge: conserving wildlife in logged tropical forests. Columbia University Press, New York.
Fischer, J., Lindenmayer, D.B., Manning, A.D., 2006. Biodiversity, ecosystem function, and resilience: ten guiding principles for commodity production landscapes. Front. Ecol. Environ. 4, 80–86.
Fisher, B., Edwards, D.P., Larsen, T.H., Ansell, F.A., Hsu, W.H., Roberts, C.S., Wilcove, D.S., 2011. Cost-effective conservation: calculating biodiversity and logging trade-offs in Southeast Asia. Conserv. Lett. 4, 443–450.
Fitzherbert, E.B., Struebig, M.J., Morel, A., Danielsen, F., Brühl, C.A., Donald, P.F., Phalan, B., 2008. How will oil palm expansion affect biodiversity? Trends Ecol. Evol. 23, 538–545.
Fox, J. (Ed.), 1995. Society and Non-timber Forest Products in Tropical Asia. Honolulu, East West Center Occasional Papers No 19.
Freeman, D., 1955. Iban agriculture: a report on the shifting cultivation of hill rice by the Iban of Sarawak. HMSO, London.
Fretes, Y., 1992. Community versus company based rattan industry in Indonesia. In: Counsell, S., Rice, T. (Eds.), The Rainforest Harvest. Friends of the Earth Trust, London.
Gardner, T.A., Barlow, J., Peres, C.A., 2007a. Paradox, presumption and pitfalls in conservation biology: the importance of habitat change for amphibians and reptiles. Biol. Conserv. 138, 166–179.
Gardner, T.A., Ribeiro Jr., M.A., Barlow, J., Ávila-Pires, T.A.S., Hoogmoed, M., Peres, C.A., 2007b. The value of primary, secondary and plantation forests for a neotropical herpetofauna. Conserv. Biol. 21, 775–787.
Giam, X., Clements, G.R., Aziz, S.A., Chong, K.W., Miettinen, J., 2011a. Rethinking the 'back to wilderness' concept for Sundaland's forests. Biol. Conserv. 144, 3149–3152.
Giam, X., Scheffers, B.R., Sodhi, N.S., Wilcove, D.S., Ceballos, G., Ehrlich, P.R., 2011b. Reservoirs of richness: least disturbed tropical forests are centres of undescribed species diversity. Proc. R. Soc. B 279, 67–76.
Gibson, L., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J., Peres, C.A., Laurance, W.F., Lovejoy, T.E., Sodhi, N.S., 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. Nature 478, 378–381.
Gillespie, G.R., Howard, S., Lockie, D., Scroggie, M.P., Boeadi, 2005. Herpetofaunal richness and community structure of offshore islands of Sulawesi, Indonesia. Biotropica 37, 279–290.
Gillespie, G.R., Ahmad, E., Evans, A., Ancrenaz, M., Goossens, B., Scroggie, M., 2012. Relative value of secondary forests and non-forest habitats for amphibians in Borneo. Biol. Conserv. 152, 136–144.
Guillera-Arroita, G., Lahoz-Monfort, J.J., MacKenzie, D.I., Wintle, B.A., McCarthy, M.A., 2014. Ignoring imperfect detection in biological surveys is dangerous: a response to 'fitting and interpreting occupancy models. PLoS One 9, 1–14.
Hastie, T.J., Tibshirani, R.J., 1990. Generalized additive models. Chapman and Hall/CRC.
Heatwole, H., Taylor, J., 1987. The ecology of reptiles. Surrey Beatty and Sons, Sydney.
Heinen, J.T., 1992. Comparisons of the leaf litter herpetofauna in abandoned cacao plantations and primary rain forest in Costa Rica: some implications for faunal restoration. Biotropica 431–439.
Heyer, R.W., Berven, K.A., 1973. Species diversities of herpetofaunal samples from similar microhabitats at two tropical sites. Ecology 54, 642–645.
Hilje, B., Aide, T.M., 2011. Recovery of amphibian specie richness and composition in a chronosequence of secondary forests, northeastern Costa Rica. Biol. Conserv. 146, 170–176.
Hoang, V.S., Baas, P., Keßler, P.K.J., Slik, J.W.F., Ter Steege, H., Raes, N., 2011. Human and environmental influences on plant diversity and composition in Ben En National Park, Vietnam. J. Trop. For. Sci. 23, 328–337.
Hu, Y., Magaton, S., Gillespie, G., Jessop, T.S., 2013. Small reptile community responses to rotational logging. Biol. Conserv. 166, 76–83.
Jessop, T.S., Madsen, T., Sumner, J., Rudharto, H., Phillips, J.A., Ciofi, C., 2006. Maximum body size among insular Komodo dragon populations covaries with large prey density. Oikos 112, 422–429.
Karanth, K.K., Curran, L.M., Reuning-Scherer, J.D., 2006. Village size and forest disturbance in Bhadra Wildlife Sanctuary, Western Ghats, India. Biol. Conserv. 128, 147–157.
Kéry, M., Royle, J.A., 2008. Hierarchical Bayes estimation of species richness and occupancy in spatially replicated surveys. J. Appl. Ecol. 45, 589–598.
Kinaird, M.F., O'Brien, T.G., 2006. Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. Anim. Conserv. 6, 131–139.
Kodandapani, N., Satheesh, N., Ashutosh, S.S., Raj Kumar, K., 2014. Human dimensions of forest degradation in the Sathyamangalam landscape. Asian Nature Conservation Foundation, Sathyamangalam Forest Division, Center for Advanced Spatial and Environmental Research, Bangalore, India.
Laurance, W.F., Goosem, M., Laurance, S.G.W., 2009. Impacts of roads and linear clearings on tropical forests. Trends Ecol. Evol. 24, 659–669.
Laurance, W.F., Clements, G.R., Sloan, S., O'Donnell, C.S., Mueller, N.D., Goosem, M., Venter, O., Edwards, D.P., Phalan, B., Balmford, A., Van Der Ree, R., Arrea, I.B., 2014. A global strategy for road building. Nature 513, 229–232.
Martin, T.E., Blackburn, G.A., 2010. Impacts of tropical forest disturbance on avifauna on a small island with high endemism: implications for conservation. Conserv. Soc. 8, 127–139.
McCain, C.M., 2010. Global analysis of reptile elevational diversity. Glob. Ecol. Biogeogr. 19, 541–553.
McMorrow, J., Talip, M.A., 2001. Decline of forest area in Sabah, Malaysia: relationship to state policies, land code and land capability. Glob. Environ. Chang. 11, 217–230.
Miettinen, J., Shi, C., Liew, S.C., 2011. Deforestation rates in insular Southeast Asia between 2000 and 2010. Glob. Chang. Biol. 17, 2261–2270.
Mohd Azlan, J., 2006. Mammal diversity and conservation in a secondary forest in peninsular Malaysia. Biodivers. Conserv. 15, 1013–1025.
Oksanen, J.F., Blanchet, G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Henry, M., Stevens, H., Wagner, H., 2013. Vegan: community ecology package. R package version 2.0–10. http://CRAN.R-project.org/package=vegan.
Pawar, S.S., Rawat, G.S., Choudhury, B.C., 2004. Recovery of frog and lizard community alteration in Mizoram, Northeast India. BMC Ecol. 4, 10.
Peters, S.L., Malcolm, J.R., Zimmerman, B.L., 2006. Effects of selective logging on bat communities in the southeastern Amazon. Conserv. Biol. 20, 1410–1421.
R Core Team, 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria (URL http://www.R-project.org/).

Rodda, G.H., Perry, G., Rondeau, R.J., Lazell, J., 2001. The densest terrestrial vertebrate. J. Trop. Ecol. 17, 331–338.
Scott Jr., N.J., 1976. The abundance and diversity of herpetofaunas of tropical forest litter. Biotropica 8, 41–58.
Sodhi, N.S., 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 biodiversity in human-modified landscapes. Biol. Conserv. 143, 2375–2384.
Sutherland, D.R., Glen, A.S., de Tores, P.J., 2011. Could controlling mammalian carnivores lead to mesopredator release of carnivorous reptiles? Proc. R. Soc. B 278, 641–648.
Trombulak, S.C., Frissell, C.A., 1999. Review of ecological effects of roads on terrestrial and aquatic vertebrates. Conserv. Biol. 14, 18–30.
Vallan, D., 2002. Effects of anthropogenic environmental changes on amphibian diversity in the rain forests of eastern Madagascar. J. Trop. Ecol. 18, 725–742.
Vitt, L.J., Avila-Pires, T.C.S., Caldwell, J.P., Oliveira, V.R.L., 1998. The impact of individual tree harvesting on thermal environments of lizards in Amazonian rain forest. Conserv. Biol. 12, 654–664.
Voris, H.K., 1977. Comparison of herpetofaunal diversity in tree buttresses of evergreen tropical forests. Herpetologica 33, 375–380.
Wanger, T.C., Saro, A., Iskandar, D.T., Brook, B.W., Sodhi, N.S., Clough, Y., Tscharntke, T., 2009. Conservation value of cacao agroforestry for amphibians and reptiles in South-east Asia: combining correlative models with follow-up field experiments. J. Appl. Ecol. 46, 823–832.
Wanger, T.C., Iskandar, D.T., Motzke, I., Brook, B.W., Sohdi, N.S., Clough, Y., Tscharntke, T., 2010. Effects of land-use change on community composition of tropical amphibians and reptiles in Sulawesi, Indonesia. Conserv. Biol. 24, 795–802.
Wells, K.D., 2007. The ecology and behavior of amphibians. University of Chicago Press, Chicago.
Whitfield, S.M., Pierce, M.S.F., 2005. Tree buttress microhabitat use by a neotropical leaf-litter herpetofauna. J. Herpetol. 39, 192–198.
Whitfield, S.M., Bell, K.E., Philippi, T., Sasa, T., Bolanos, F., Chaves, G., Savage, J.M., Donnelly, M.A., 2007. Amphibian and reptile declines over 35 years at La Selva, Costa Rica. Proc. Natl. Acad. Sci. U. S. A. 104, 8352–8356.
Wood, S.N., 2006. Generalized additive models: an introduction with R. Chapman and Hall/CRC.
Wright, S.J., 2010. The future of tropical forests. Ann. N. Y. Acad. Sci. 1195, 1–27.
Zug, G.R., Vitt, L.J., Caldwell, J.P., 2001. Herpetology: an introductory biology of amphibians and reptiles. Academic Press.