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Herpetofaunal responses to anthropogenic habitat change within a small forest reserve in Eastern Ecuador

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One of the key drivers of worldwide species loss is habitat change, defined as habitat deforestation, fragmentation and deterioration. We studied the effects of structural habitat change on herpetological richness and diversity in the Yachana Reserve, Amazonian Ecuador, using pitfall traps and visual encounter surveys between 2009 and 2010, recording 1551 amphibians of 37 different species and 234 reptiles of 27 species. Estimated species richness and diversity was less in pastureland and plantation habitats. Abandoned plantations supported relatively high abundances of individuals, but were markedly depauperate in species richness and diversity. Abandoned pastureland showed the opposite trend, retaining higher species richness and diversity than abandoned plantation sites, but in significantly lower relative abundances. We emphasize the importance of small reserves with a matrix of anthropogenic disturbance in preserving areas of primary habitat and providing areas of secondary regeneration. Such reserves can aid in the identification of the factors that underlie inter-specific variation in response to habitat change at the species level.

Key words: amphibians, cacao plantation, habitat change, habitat structure, herpetofauna, regenerating tropical forest, reptiles

INTRODUCTION

One of the key drivers of worldwide species loss is habitat change, defined as habitat deforestation, fragmentation and deterioration (Urbina-Cardona et al., 2006; Urbina-Cardona, 2008; Gardner, 2010). The rapid rate of forest conversion in the neotropics has presented a large-scale expansion of secondary forest, plantation and pastureland (Wright, 2005; Gardner et al., 2007c). Despite the increasingly dominant role of these degraded habitats within tropical landscapes, there is little consensus within the scientific community about the extent of their conservation value for herpetofaunal communities (Faria et al., 2007; Ficetola et al., 2007; Gardner et al., 2007c). Wright and Mulller-Landau (2006) predicted that the future loss of primary forest will be counterbalanced by regenerating secondary forest and that the predicted loss of species due to habitat change may not occur. Several studies have acknowledged that richness values are often unaltered and on some occasions slightly increased within secondary forest (Fredericksen & Fredericksen, 2002; 2004), whilst Gillespie et al. (2012) highlight the potential disaster in converting secondary forests to plantations. The study of habitat change is of major importance and deserves more attention, particularly within plantations and regenerating secondary habitats.

Amphibians and reptiles are important primary, mid-level and top consumers in neotropical ecosystems; therefore it is important to understand the specific responses of these organisms to structural habitat change (Bell & Donnelly, 2006). Amphibians and reptiles are also considered to be the most threatened groups of terrestrial vertebrates (Gardner et al., 2007c; Böhm et al., 2013). This is especially true in the neotropics which, despite an estimated 89% of threatened species being affected by habitat loss, have been the subject of just 10% of the world's herpetological studies (Gardner et al., 2007a). There is a general consensus amongst herpetologists that information about the effect of structural habitat change on determining amphibian and reptile distributions is limited and should be addressed in current research (Pearman, 1997; Krishnamurthy, 2003; Urbina-Cardona et al., 2006).

Leaf-litter and low strata herpetofauna lend themselves well to biological conservation studies as they are abundant in neotropical forests and are easy to sample (albeit requiring more survey effort than temperate regions). The structural habitat changes associated with secondary and plantation forests cause microhabitat

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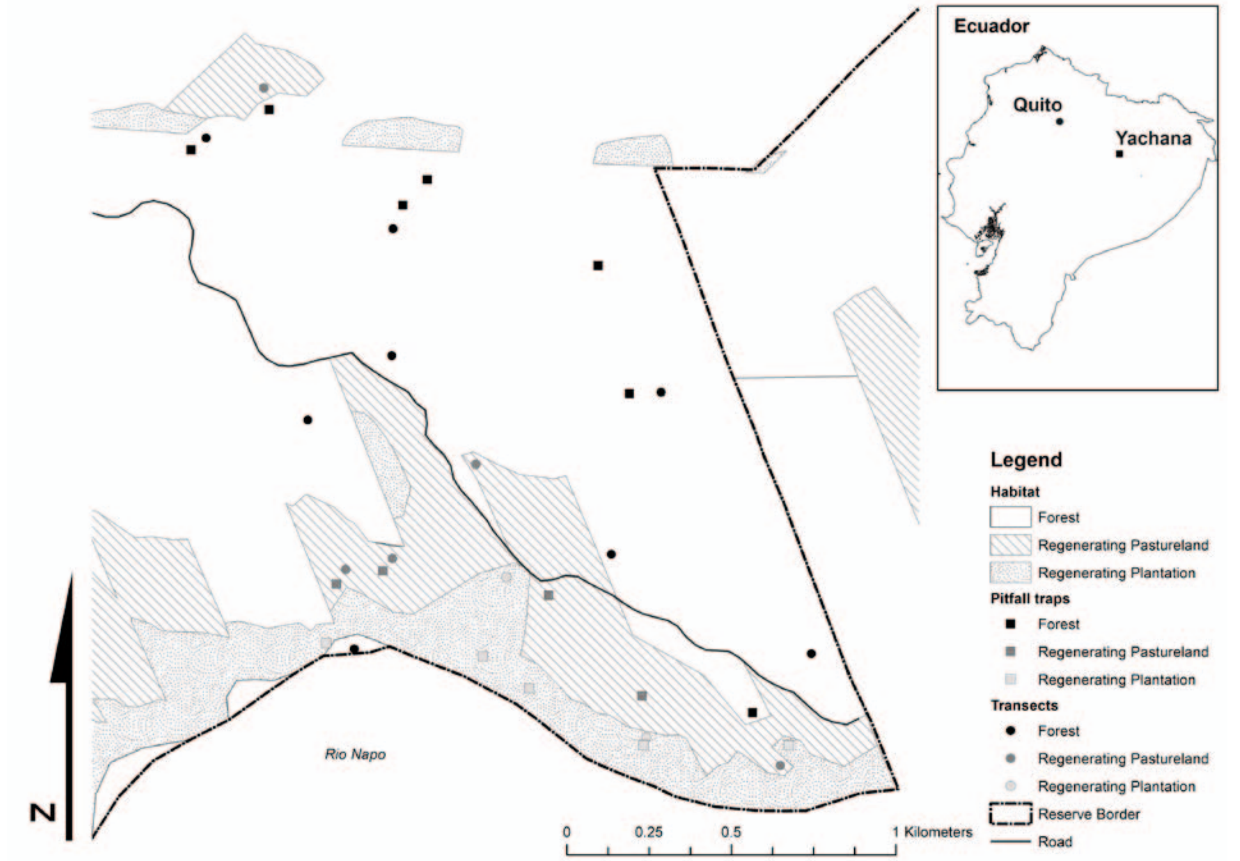

Fig. 1. Situation of the Yachana Reserve within Amazonian Ecuador and the location of the survey sites across different habitats. Each survey site was also habitat feature mapped.

changes through both environmental factors (i.e. incident light, temperature and relative humidity), and interspecific interactions (i.e. predation, parasitism and competition). To date, loss of reproductive sites, loss of genetic diversity, changes in home ranges, population isolation due to the incapacity to cross anthropogenic matrix habitats, changes in individual growth rates and activity patterns, and changes in microhabitat use have been documented (Gibbons et al., 2000; Gardner et al., 2007a; Urbina-Cardona, 2008; Dixo et al., 2009). Despite these alterations, two recent studies report that the variety of microhabitats provided by shaded plantations and degraded forest edges are sufficient to maintain up to 80% of primary forest leaf-litter herpetofauna diversity (Faria et al., 2007; Dixo & Martins, 2008). However, active plantations appear to be more detrimental to lizard richness than abandoned ex-plantation sites (Glor et al., 2001). Other research suggests that the management of cacao agroforestry for example will enhance the richness and abundance of disturbance-tolerant species but native forests remain vital for rare, more specialized species (Wanger et al., 2009). Recent work has demonstrated that species-specific responses to these environmental and inter-specific factors can vary (Oldekop et al., 2012). Despite the fact that some researchers find stable or increasing richness values following structural changes (Fredericksen & Fredericksen, 2002; 2004), community structure will frequently be disrupted and distinct from that of original forest, usually containing a large abundance of generalist species and a loss of primary forest specialized species in altered landscapes (Heinen, 1992; Furlani et al., 2009). Widespread, abundant, habitat generalists might dominate similarity analyses even when relatively rare specialists are present. Additional species-level analyses of habitat specialization will be needed before the conservation value of tropical secondary regenerating forest is fully understood (Dent & Wright, 2009).

In this study we focused on an Ecuadorian lowland rainforest and aimed to answer the following questions: (i) What are the effects of structural habitat change of tropical lowland rainforest on herpetological richness and diversity? (ii) How does structural habitat change influence community composition? (iii) Are there species-specific variations in responses to habitat modification?

METHODS

Study Site

The research was conducted in the Yachana Reserve (Fig. 1) between April 2009 and December 2010. The reserve is situated within the Napo province in the Amazonian region of Ecuador (77°13'43.9"W, 0°50'45.281"S; 300–350m altitude). The Yachana Reserve is a legally-designated Bosque Protector (Protected Forest), consisting of approximately 1000 ha of predominantly primary lowland rainforest, as well as abandoned regenerating plantations (generally cacao, *Theobroma cacao*), small abandoned pastureland patches, riparian forest and a road. The reserve is surrounded by large areas of pastureland, small active cacao farms and forest. The abandoned pastureland and plantation sites within the study are generally <3 ha in size and are interspersed within patches of forest on the south side of the road. The largest part of contiguous forest is found on the northern side of the road: the majority of forest sites were located here. The abandoned pastureland and plantations had been untouched by farmers and their cattle for around 10 years at the time of sampling (information obtained through the Yachana Foundation and local landowners). The regenerating plantation sites contained a mix of native shrubs and trees, now beginning to succeed the plantation trees, some of which still remained, whilst the pastureland was still heavily dominated by grass, with little succession from other plants.

Site locations and sampling methodology

Surveying was conducted through both wet and dry seasons (November to March is generally considered the wet season and April to October the drier season), in order to obtain an annual representation of community structures. Pitfall traps (PFT) and nocturnal visual encounter surveys (VES) were conducted simultaneously in order to avoid any bias in capturing temporally different fauna due to the trapping method used at any particular time. Where possible, sites were placed within a given habitat at least 70 m from a clear habitat edge or stream/water body to reduce the influence of edge effects following Demaynadier & Hunter (1998). Due to the steep and locally dense nature of the terrain, sample sites were placed in areas that were accessible yet away from existing trails within the reserve. Locating sampling sites off the trails avoided known detection biases (Von May & Donnelly, 2009).

Fifteen PFT arrays were established throughout the reserve: seven within primary forest, four within abandoned pastureland and four within regenerating plantation. The 25 m long arrays consisted of four 25-litre buckets connected by 8 m lengths of drift fence that were 40 cm in height. Pitfall traps were opened for a period of 10 days in each trapping session. Seven trapping sessions were conducted throughout the study period resulting in 70 days of pitfall trapping per site. Open PFTs were checked once daily between 0630 and 1300 hours. Lids were placed 10 cm above the buckets to prevent flooding during prolonged periods of rain during the trapping periods and then closed tight between sessions.

VES were used to complement the pitfall data due to their known effectiveness in sampling tropical herpetofauna (Bell & Donnelly, 2006) and their higher yields per unit effort than other sampling methods (Rödel & Ernst, 2004; Bell & Donnelly, 2006). Fifteen 75 x 6 m (450 m^2) VES transects were established throughout the reserve: eight within primary forest, five within abandoned pastureland and two within regenerating plantation. All transects were surveyed at night, commencing at 2015 hours ±15 mins. Transects were surveyed by five searchers over a period of 90 mins up to 2 m in height. Search teams consisted of one experienced herpetologist and four trained international conservation volunteers. Each transect was searched every three months for the duration of the study period (*n*=10), with the exception of five transects which were added during the study period and were thus searched on fewer occasions. We ensured that these five additional transects were studied throughout both dry and wet seasons, as with all other transect sites. The order in which transects were searched within each of the three month periods was randomized to avoid systematic sampling bias. Diurnal VES transects were not performed, as nocturnal VES sampling has previously been shown to be the most efficient method in herpetological inventorying and still allows to detect resting diurnal species (Doan, 2003).

All amphibians and reptiles encountered were identified in the field where possible (see Beirne & Whitworth, 2011; Whitworth & Beirne, 2011 for full indentification criteria and a complete list of identification resources used throughout the project). For PFTs, individuals were released approximately 40 m away from the trap site to reduce the probability of recapture. Individuals captured during VES were released behind the searchers, so that the same individual could not be encountered twice within a survey. Unidentifiable individuals were anaesthetized with Lidocaine and fixed with 10% formalin then subsequently identified and stored at the Ecuadorian Natural Science Museum (MECN) in Quito.

Owing to the previous detection of a single case of chytridiomycosis within the study site (Global Vision International, unpublished) codes of good practice were strictly adhered to. This was achieved by the systematic cleaning of tools and equipment. Sterile bags were used when handling amphibians and small reptiles.

Habitat Classification

In order to confirm that each sampling site was appropriately assigned as forest, plantation or pasture habitat, each visual encounter survey and pitfall site was subjected to vegetation mapping on one occasion following the guidelines outlined by the Ecuadorian Natural Science Museum (MECN), Quito. All sites were mapped between June and December 2009. The following parameters were estimated: Upper canopy and mid canopy cover (% estimate only, conducted by two trained observers to the nearest 5%); height of both upper and mid canopy using clinometers to measure base height of the canopy (m); shrub and herb coverage using a modified Braun-Blanquet scale (Hurst & Allen, 2007); vine, palm, epiphyte, fern, grass and plantation coverage by using the DAFOR scale (5=dominant, 4=abundant, 3=frequent, 2=occasional, 1=rare); and leaf litter depth measured to the nearest 0.5 cm, using a marked dowel to the top of the leaf litter.

PFTs had three vegetation mapping plot points consisting of a 10 x 10 m grid, one situated at the midpoint of the pitfall array and one at each end. VES had the same grid plots conducted along the transect line, one at each end and then two further plots along the transect line. The data gathered from the plots were then averaged to provide a representative set of values for each survey site. In order to compare structural features between habitat classifications, average values for each structural habitat parameter were calculated per site (Online Appendix 1). A factor analysis was then performed using Minitab v.14.12 in order to detect the separation of sites by their specific habitat variables. Factor scores were sorted and rotated with an Equamax rotation in order to provide the most logical representation of the data visually.

The influence of structural habitat change on species richness and diversity

In order to determine the influence of structural habitat change on herpetofaunal assemblage richness and diversity we first determined the effectiveness of the sampling techniques. Captures from both PFT and VES were then combined in order to provide as near to "true" representation of herpetofaunal assemblages as possible (Gardner et al., 2007c). Reptiles and amphibians were analyzed separately to reflect differences in life histories (Gardner et al., 2007b). In order to control for differences in sampling efforts, species accumulation curves were calculated using the Rich package (Rossi, 2011) and plotted using R (R Core Team, 2012). Species richness was defined as the mean of two non-parametric richness estimators – Chao1 and jack1. Species diversity was defined using the Shannon diversity index. Repeating the analyses using Fisher's Alpha and Simpson diversity indices did not change the results and as such are not presented. All richness and diversity estimators were calculated in Estimate S (Colwell, 2006).

In order to confirm the association between structural habitat parameters and site level species richness and diversity, a series of general linear models (GLMs) were applied (Minitab v.14.12). The three site specific habitat structure factor scores generated from the factor analysis that had eigenvalues >1 were used as explanatory variables to determine their influence on estimated richness and Shannon diversity index values as dependent variables.

The influence of structural habitat change on community composition

Community compositions and structures were compared by producing dominance-diversity (Whittaker) plots using the vegan package (Oksanen et al., 2011) in program R (R Core Team, 2012). Such plots compare the evenness of a community, whereby shallow curves represent a community of many species of similar abundance whereas steep curves represent a skewed assemblage with one or more species in substantially higher relative abundance than others. Significant differences in slope, and therefore significant differences in community evenness, were assessed through the use of a linear model with log relative abundance as the response term and an interaction between species rank and habitat type as continuous and categorical fixed effects, respectively. Results are reported as ΔG which corresponds to absolute change in gradient between forest and the modified habitats, whereby more negative values denote steeper curves and thus less even assemblages.

The influence of habitat change on species specific relative abundance

In order to determine if herpetofaunal responses to structural habitat change were species specific, we determined the relationship between habitat structure parameters and species specific relative abundances using a series of GLMs (Minitab v.14.12). Relative abundance values were calculated for both VES and PFT methods. VES-based abundances were calculated as numbers of individuals encountered within 450 m^2 of the transect area, and PFT abundances were defined as the number of individuals encountered at an individual trap array based on 70 nights of trapping. Where a sufficient number of individuals had been encountered (n>10), significant differences in relative abundances across habitats were determined using the Kruskall-Wallis test (also conducted on overall relative abundance levels for amphibians and reptiles).

RESULTS

Habitat classifications

The factor analysis resulted in the original 13 habitat structure variables producing three factors with an eigenvalue>1. These three factors represent 65.8% of variation in the original dataset (factors 1, 2 and 3 contained 31%, 19.3% and 15.5% of the variation respectively). Factor 1 loaded positively with increasing upper canopy height, upper canopy coverage and fern, epiphyte and vine coverage, and negatively with the presence of grass (Fig. 2). Factor 2 loaded positively with increasing plantation plant coverage, mid canopy coverage and shrub layer, and negatively with mid canopy height. Factor 3 loaded with increasing mid canopy height, shrub coverage and the palms abundance (Online Appendix 2). The first factor separates sites by the structure of the

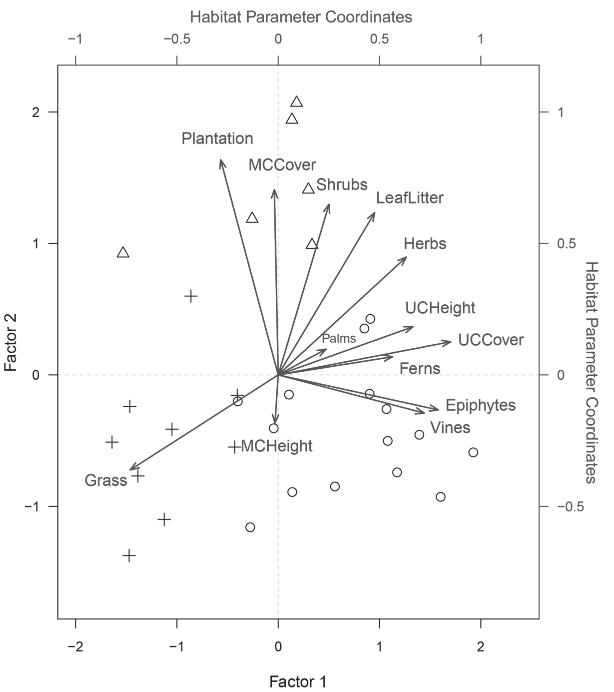

Fig. 2. Habitat variable loadings for factor 1 vs. factor 2 (Equamax rotation). The arrows demonstrate the direction and strength of each variable and C stands for canopy. Site specific scores plotted against one another for factor 1 (primary forest vs. grass) and factor 2 (mid canopy structure). O=forest, +=pasture and Δ= plantation.

Table 1. Capture frequency, actual and estimated species richness and sample completeness per habitat classification. Where: [a]Number of individuals encountered, [b]Number of species observed, [c]Mean estimated species richness (Chao 1 and jack 1) *'s denote bias corrected Chao1 estimates, [d]Sampling coverage defined as: b/c*100, [e]Number of species found exclusively within the given habitat, [f]Number of species observed as a percentage of combined species across all habitats.

	Habitat class	*n*[a]	Species[b]	Estimated Richness[c]	Coverage (%)[d]	Exclusive Species[e]	Completeness (%)[f]
Amphibians	Forest	1028	36	42.6	84.5	18	97.30
	Plantation	355	14	17.4*	80.3	0	37.84
	Pasture	168	13	16.9*	76.7	1	35.14
	Total	1551	37	-	-		-
Reptiles	Forest	137	24	29.0	82.8	10	88.88
	Plantation	63	14	17.0	82.4	2	51.85
	Pasture	34	12	21.5*	55.7	1	44.44
	Total	234	27	-	-	-	-

higher canopy and presence of primary forest features. The second factor represents features related to the mid-forest structure. Factors 1 and 2 were plotted against each other in order to demonstrate the validity of our habitat classifications (Fig. 2). The pastureland and forest sites clearly separated along factor 1 (primary forest features vs. grass) whilst the plantation areas separated from both forest and pastureland sites on factor 2 (mid canopy features).

The influence of structural habitat change on species richness and diversity

In total, 1551 amphibians of 37 different species and 234 reptiles of 27 species were recorded (Table 1). Survey coverage across all habitats was over 75%, with the exception of reptiles within pastureland habitat with coverage of just 55.7% of estimated species richness. Forest harboured the highest frequency of exclusive amphibian species (18) and the highest proportions of total species for both amphibians and reptiles (97.3% and 88.9% respectively). Examination of the individual rarefaction curves 95% confidence intervals suggests that, for amphibians, forest habitat supports more species than abandoned plantation and pasture (Fig. 3). Reptiles show a less defined pattern, with only the number of species recorded in plantations through VES being lower than in the forest. The forest habitat was the most diverse, followed by pasture and plantation for both amphibians and reptiles (Shannon estimates, Fig. 4). The same trend was found for other diversity estimators: Simpson and Fisher's alpha (data not shown).

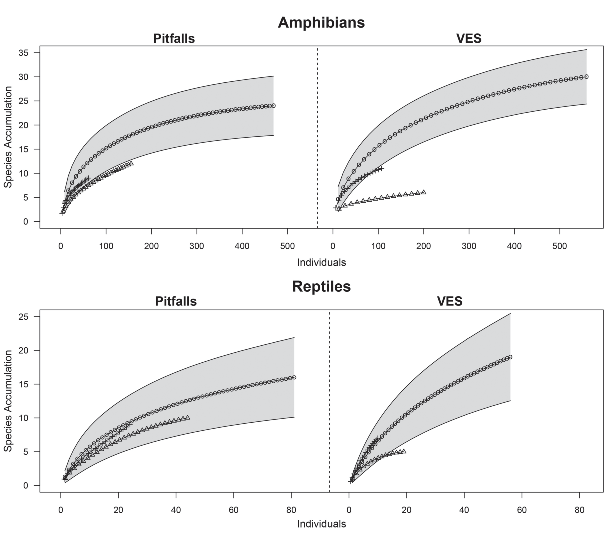

Fig. 3. Individual rarefaction curves for both amphibians and reptiles between the three habitats for both pitfall trapping and visual encounter surveys. The gray areas represent the 95% confidence intervals for primary habitat. Mean species accumulation lines falling outside of this envelope are deemed statistically significant. O= forest, +=pasture and Δ=plantation.

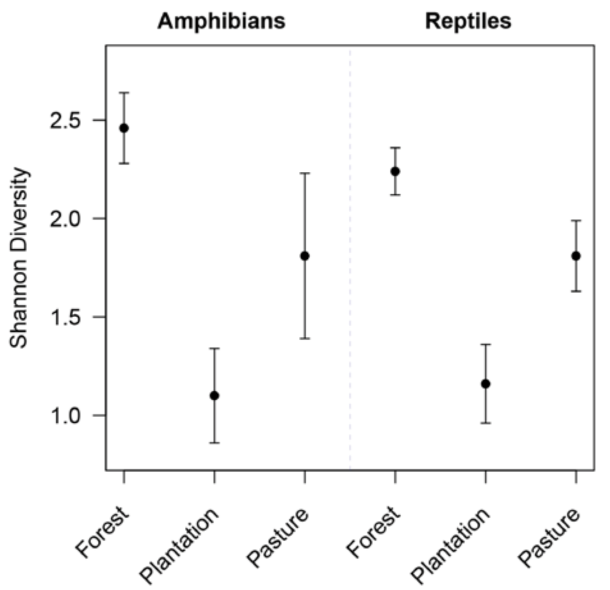

Fig. 4. Shannon species diversity estimates with 95% confidence intervals for amphibians and reptiles between the three habitat types.

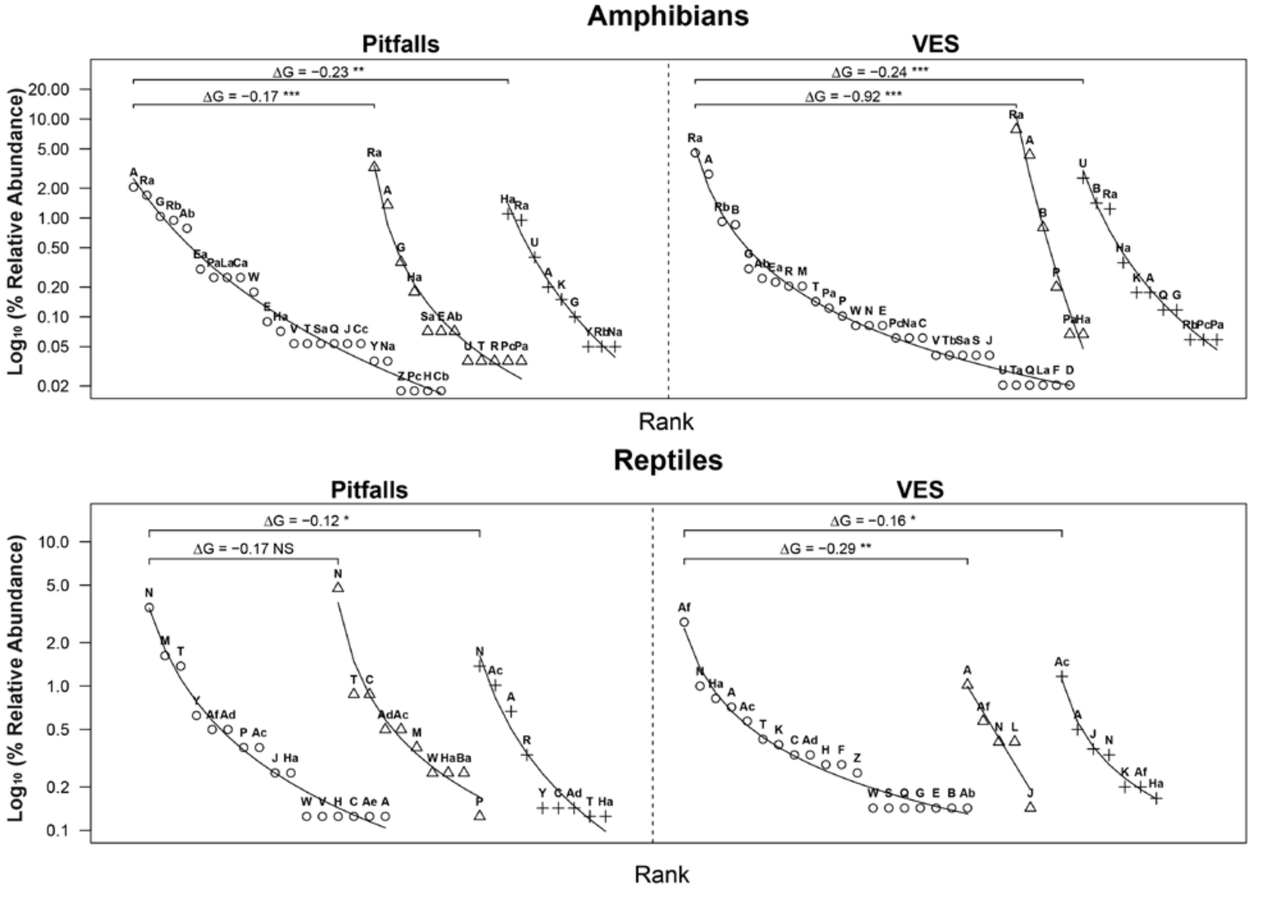

Fig. 5. Dominance-diversity (Whittaker) plots for amphibians and reptiles. Each set displays plots for both PFT and VES. Species represented by points are labelled with a code provided in Tables 2 and 3 for amphibians and Tables 4 and 5 for reptiles. For each habitat the relative abundance of each species (*ni*/*n*) was plotted on a logarithmic scale against the species rank ordered from most to least abundant. O=forest, +=pasture and Δ=plantation. Linear models were used to determine if the slopes of plantation and grassland were significantly different to forest where ΔG denotes an absolute change in gradient from the forest habitats predicted line and the symbol denote the level of significance of the deviation where ***=0.001, **=0.01,*=0.05 and NS=not significant.

We found strong evidence that anthropogenic habitat change, particularly the introduction of grassland and plantation, increasing density of the mid canopy and shrub layers with a concurrent reduction in mid-canopy height, were detrimental to overall amphibian richness and diversity. Increasing upper canopy height, upper canopy coverage and fern, epiphyte and vine coverage and the decrease of grass coverage (factor 1 loading parameters) were associated with increased estimated richness and Shannon diversity of amphibian assemblages (GLM: p=0.01 for estimated richness and p=<0.01 for Shannon diversity), whereas increasing plantation coverage, mid canopy coverage and shrub layer and decreasing mid-canopy height (habitat parameters loaded onto factor 2) are associated with decreases (GLM: p=0.01 for estimated richness and p=<0.01 for Shannon diversity). Factor 3 showed no significant association with amphibian richness or diversity (p=0.46 for estimated richness and p=0.42 for Shannon diversity). No evidence was found for associations between habitat parameters and reptile estimated richness or diversity (Online Appendix 5).

The influence of structural habitat change on community composition

Dominance-diversity plots demonstrate that, for both amphibians and reptiles, forest habitat supports a significantly more even assemblage (regular intervals between species) and more rare species (increased tail length) than both plantation and pasture (Fig. 5). All plantation and pasture assemblage comparisons to the primary forest were significantly more skewed at the 95% level, except for reptiles in plantation habitat using the pitfall methodology which was marginal (0.058). For amphibians, the plantation habitat assemblage is particularly skewed, with *Pristimantis kichwarum* (Ra) and *Ameerega bilinguis* (A) being substantially more abundant than accompanying species. For reptiles, the plots highlight differences in detectability between the two methods employed (VES and PFT): *Leposoma parietale* (N) dominating PFT sites across all habitats and for VES sites *Anolis trachyderma* (Af), *A. fuscaratus* (A) and *A. nitens scypheus* (Ac) dominating forest, plantation and pasture habitats respectively.

The influence of habitat change on species specific relative abundance

When including only species observed in all three habitats, strong evidence of species-specific affinities for different habitat types, regardless of the genus to which amphibians belong was found (Table 2). Three species (*Allobates zaparo*, *Engystomops petersi* and *Pristimantis lanthanites*) were more abundant in forest and one species (*P. kichwarum*) was more abundant in plantation habitat across both methodologies. A further two species were found to be more abundant in forest habitat (*Hypodactylus nigrovittatus* and *P. altamazonicus*), one species was more abundant in plantation habitat (*Ameerega bilinguis*) and one species was more abundant in pasture habitat (*Leptodactylus andreae*) in one of PFT or VES. There was no clear trend for overall amphibian abundance regardless of species. The relative abundance of individuals was higher in forest habitat using PFT and in plantation habitat using VES. The lack of overall trend in total abundance is likely driven by species specific variation in detectability dependant on the sampling methodology employed.

No evidence was found for individual-specific habitat affinities (Table 3) in reptiles. Considering overall abundance of reptiles, only species in plantations recorded with VES were significantly more abundant than in other habitats. The lack of significant associations could reflect reptiles as being robust to anthropogenic habitat change within small reserves, or could be due to lower detection probability and therefore decreased sample size.

DISCUSSION

The analyses presented here highlight the same general trend: anthropogenic disturbance, in the form of pastureland and plantation, was detrimental to herpetofauna communities even after 10 years of regeneration. In general, abandoned plantations supported comparable relative abundances of individuals to forest, but was depauperate in species diversity. Abandoned pastureland supported higher species diversity estimates than plantation sites, with lower relative abundances. Species-specific analyses demonstrated that such trends were driven by idiosyncratic responses to disturbance. Whilst the majority of species declined in abundance, some species increased. The degree to which the herpetofauna is affected by disturbance and our ability to detect responses is dependent on the nature of the disturbance, the sum of the species specific responses to habitat disturbance within each study site and the methodology employed.

Amphibians

Despite encouraging estimates of richness and diversity elsewhere (Ewers & Didham, 2006; Faria et al., 2007), our comparison of estimated species richness, individual based rarefaction analysis and diversity indices demonstrate that regenerating pastureland and regenerating plantation did not support comparable levels of amphibian species richness and diversity to forest habitat. In real terms, regenerating pasture and plantation areas were characterized by as much as a 60% decrease in estimated species richness. Although

Table 2. Details the mean relative abundances for amphibians at each site within the three habitat types. Where: F=Forest, Pl=Plantation and Pa=Pasture. PFT relative abundances represent the number of individuals encountered per 70 trapping days at a given site; VES relative abundances represent the number of individuals encountered within 450 m^2 of transect**.** *n*=frequency of individuals encountered across all habitats**;** *p*= *p*-value for Kruskall-Wallis analysis of variance (only conducted in species with *n*>10). Codes given next to species name relate to those given in Fig. 5. Survey effort is given in trapping nights for PFT and observer hours for VES. For complete tables see Online Appendices 3A and 3B. Significant values in *italics*.

Species	Pitfalls					VES				
	F	Pl	Pa	*n*	*p*	F	Pl	Pa	*n*	*p*
A. zaparo (Ab)	5.5	0.5	0	46	*0.01*	0.2	0	0	12	*0.01*
A. bilinguis (A)	14.4	9.5	1.2	157	0.11	2.8	4.3	0.1	204	*0.01*
B. peruviana (B)	-	-	-	-	-	0.9	0.8	1.1	78	0.55
C. insperatus (Ca)	1.8	0	0	14	0.25	-	-	-	-	-
E. petersi (Ea)	2.1	0	0	17	*0.02*	0.2	0	0	11	*0.02*
H. nigrovittatus (G)	7.3	2.5	0.6	70	*0.03*	0.3	0	0.1	17	0.12
L. andreae (Ha)	0.5	1.3	6.4	31	*0.01*	-	-	-	-	-
L. rhodomystax (La)	1.8	0	0	14	0.53	-	-	-	-	-
P. altamazonicus (Pa)	1.8	0.3	0	15	*0.01*	-	-	-	-	-
P. kichwarum (Ra)	11.9	22.8	5.5	205	*0.03*	4.6	7.9	1	362	*0.01*
P. lanthanites (Rb)	6.6	0	0.3	54	*0.01*	0.9	0	0.1	46	*0.01*
P. varabilis (U)	-	-	-	-	-	0	0	2.1	44	0.09
All Species	58.6	38.8	17.8	685	*0.03*	11.4	13.3	5.1	866	*0.04*
Survey effort	560	280	280			490	150	170		

Table 3. The mean relative abundances for reptiles at each site within the three habitat types, where: F=Forest, Pl=Plantation and Pa=Pasture. PFT relative abundances represent the number of individuals encountered per 70 trapping days at a given site; VES relative abundances represent the number of individuals encountered within 450 m^2 of transect. *n*=frequency of individuals encountered across all habitats**;** *p*=*p*-value for Kruskall-Wallis analysis of variance (only conducted in species with *n*>10). Codes given next to species name relate to those given in Fig. 5. Survey effort is given in trapping nights for PFT and observer hours for VES. For full table output see Online Appendices 4A and 4B. Significant values in *italics*.

Species	Pitfalls					VES				
	F	Pl	Pa	*n*	*p*	F	Pl	Pa	*n*	*p*
A. fuscoauratus (A)	-	-	-	-	-	0.2	1.2	0.2	15	0.21
A. nitens scypheus (Ac)	0.5	0.7	2.5	11	0.13	-	-	-	-	-
A. trachyderma (Af)	-	-	-	-	-	0.7	0.6	0.1	21	0.14
K. pelviceps (M)	2.3	0.7	0.0	15	0.06	-	-	-	-	-
L. parietale (N)	5.0	8.6	4.2	62	0.15	0.3	0.4	0.1	11	0.41
P. guianensis (T)	2.0	1.4	0.4	16	0.39	-	-	-	-	-
All Species	14.5	15.7	10.0	149	0.51	2.5	*2.8*	1.1	85	*0.03*
Survey effort	560	280	280			490	150	170		

relative abundance was maintained in plantation habitat, it decreased between 30–45% within regenerating pastureland areas in comparison to forest habitat. The habitat structure analysis indicates that the patterns in richness and abundance are driven by the physical structure and abundance of vegetation. Primary forest characteristics, such as a high and dense upper canopy and increasing abundances of ferns, epiphytes and vines were correlated with increased richness and diversity. Disturbed forest characteristics such as the presence of grassland, plantation trees and increasing mid canopy density were found to be detrimental.

In agreement with recent multiple taxon assessments regarding the impact of habitat change (Dent & Wright, 2009; Pardini et al., 2009) we found species-specific responses to anthropogenic disturbance. For example, *A. bilinguis* and *A. zaparo* are sympatric fossorial amphibians with similar life histories and size. Despite this, no statistically significant decrease in *A. bilinguis* relative abundance was detected outside of primary forest, whereas the abundance of *A. zaparo* was found to be reduced by as much as 90%.

Of the eight species-specific responses detected, only one and two species were found in significantly increased relative abundance in pasture and plantation habitats, respectively. The high abundance of amphibians within plantation habitat was driven almost exclusively by the increased abundance of the generalist species *P. kichwarum.* Such generalists have broad habitat and dietary requirements which can render them either insensitive to or benefiters of structural habitat change (Dent & Wright, 2009). This is supported by the fact that the relative abundance of *P. kichwarum* correlates positively with disturbed habitat characteristics across both methodologies. Species specific associations with habitat parameters such as canopy height, plantation presence and epiphyte abundance on the relative abundances were detected for seven further species. Oldekop et al. (2012) have also demonstrated that distribution patterns of leaf-litter frogs were correlated with habitat characteristics (epiphytic ferns) across environmental gradients. Such species-specific associations with habitat features highlight the potential driving factors behind community level changes, and may inform future management strategies. Failure to detect species which were not influenced by habitat structure suggests the influence of factors not measured here such as, food availability, underlying physiology, predation and inter-specific competition.

Reptiles

Diversity indices, estimated richness and individual-based rarefaction curves suggest that forest habitat sustains higher reptile richness, diversity and a more even species composition. However, the responses are not as clear as for amphibians. No overall differences in relative abundance between habitat types were detected using PFTs. However, a significant increase in relative abundance in plantation habitat was detected using VES. The overall richness, diversity and abundance trends observed were not associated with structural habitat features. Despite reptile assemblages in the anthropogenically modified habitats being less even than in forest, no species-specific habitat affinities or associations with structural habitat characteristics were detected. These results may suggest that reptiles are generally more resilient to habitat disturbance than amphibians; however, the sample size for reptiles was considerably lower than for amphibians. These results highlight the difficulty of understanding reptile distributions specifically, as they are generally wider ranging and often less frequently encountered.

Spatial caveat

Our findings concur with those found by Gardner et al. (2007a) who report the value of primary forest and the substantially lower estimates of neighbouring regenerating plantation forests with regards to diversity and abundances. The restricted spatial extent precludes discerning the permanent presence of a species from transient movement out of more suitable primary habitat. Such individuals could falsely bias the estimates of species richness and diversity, especially since the methods employed (PFT and VES without marking of individuals) cannot distinguish between an individual temporarily occupying an unsuitable habitat from one which permanently occupies it. This is not an issue within studies utilizing spatially independent study sites, and consequently the importance of defining the spatial scale of degraded forests cannot be overestimated. This study nevertheless robustly demonstrates that at local scales within small heterogeneous forest reserves, regenerating plantation and pastureland generally support lower herpetofaunal richness and diversity than forest habitats and that idiosyncratic species specific responses to structural habitat features underpin such differences.

The Yachana Reserve

Over six years of research at the Yachana Reserve (2005–2010) a species list was compiled by field staff from Global Vision International, which consists of 71 amphibian and 72 reptile species. These numbers are considerably higher than the figures stated within this study as we only used two main methods focused towards terrestrial leaf-litter herpetofauna, avoiding habitats such as swamps, streams and high canopy. Vigle (2008) found similar numbers at the Biological Research station of Jatun Sacha, also based in the lowlands of Ecuador. De la Torre & Reck (2003) however, working from the Tiputini research station in the Biosphere Reserve of Yasuni, also situated in lowland Ecuador, used six survey methods over four years and produced a species list containing 105 amphibians and 80 reptiles. This suggests that their large areas of contiguous primary forest contain up to ~30% more amphibian species but not a great deal more reptiles. This is likely due to the higher sensitivity of amphibians to disturbance regimes. What these inventorying figures show is that despite utilizing different survey methods and effort, a small private reserve in areas of past disturbance history can sustain relatively high levels of herpetological diversity and are most certainly worth protecting for future land management plans to assist in providing areas of regeneration and connectivity between protected areas.

Conclusions

We find that structural habitat change, in this case cacao plantation and pastureland are generally detrimental to herpetofaunal richness, diversity and relative abundance in comparison to forest habitat despite 10 years of regeneration. Where relative abundance of amphibians is increased, the responses are driven by a small number of generalist species responding positively to disturbance, skewing community assemblages through their dominance. Habitat characteristics were found to correlate with diversity, richness and species specific abundances, elucidating potential drivers of the observed trends. Further species specific investigations are recommended in order to elucidate why particular species display different responses to habitat change. Such information will be critical in determining the potential of different types of regenerating forest to sustain natural levels of diversity. Understanding such variation in responses can aid in the conservation of future herpetological communities as agricultural practices increase, causing further habitat change to tropical forests.

We emphasize the value of small reserves with a matrix of anthropogenic disturbance, such as the Yachana Reserve, in preserving areas of forest habitat and encouraging secondary regeneration. Such reserves are well suited to the identification of the factors that underlie inter-specific variation in responses to habitat change at the species level. Such research is vital for the production of sustainable management guidelines for future agricultural land use changes in tropical ecosystems. We firmly support that herpetofaunal conservation priorities and land management strategies should focus on the preservation of primary forest as advocated by Gardner et al. (2008) and further suggest that expanding reserves by protecting surrounding secondary areas and providing a timescale of regeneration, it may be possible to partially retain primary forest richness and diversity levels.

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ONLINE APPENDIX

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Appendix 1. Raw data for habitat profiling: Regenerating pastureland; rows 1–9, regenerating plantation; rows 10–15, primary; rows 16–30.

Site	Upper C height	Upper C cov	Mid C height	Mid C cov	Herbs	Shrubs	Vines	Palms	Epiphytes	Ferns	Grass	Plantation	Leaf Litter
PFN4	0	0	7.89	39.375	1	1.75	0	0.25	0	0.25	3.75	1.75	0
S5	0	0	8.65	18.8125	1	1.375	0.125	0	0	0	3.75	0.875	0
BV	20.2	4.12125	10.23	61.2625	1	1.625	0	0.125	0	0	3.625	1.25	0
Front	0	0	9.96	50.8	2.25	2.375	0.625	0	0.5	0.5	2.875	0.5	0
PFN5	25.07	6.1375	7.75	40	1.75	2	0.25	0	0.75	0.5	2.5	1	0
Spf5	0	0	8.27	32.25	1.25	1	0	0	0	0	2.5	0	21.21764706
Spf3	0	0	9.42	38.13	1.25	1.25	0	0.75	0	0	2.5	0	31.1875
S1	20.47	14.0625	11.25	64.46875	1.875	2.25	0	0	0	0.125	1	1.125	32.40645161
S6	17.12	10.9375	10.685	18.3125	3.625	3.25	1.375	0.875	0	1.375	1.5	1.625	0
Spf6	16.89	9.9575	7.15	69.625	2.75	1	0.5	0	0	1	0	4	22.7625
PFN1	20	20.625	8	69.895	3	3.75	1	1.5	0	1.25	0	3.75	65.26666667
PFN2	25	39.6875	9	60.73	2.75	2.5	0.25	0.25	0.25	0.5	0	3.75	92.56666667
S3	14.485	27.75	5.625	66.09375	3	3.125	1	0	0.25	0	0	3.625	50.7
PFN3	19.54	32.25	10.8	43.5	2.75	4	0.25	0.5	2	0.5	0	2.5	78.4
S2	0	0	13.555	59.75	2.625	2.375	0	0	0	0.25	0	2.375	24.08787879
Ppf6	17.71	18.81	14.36	41.88	1.25	1	1.25	1	0.25	1	0	0	15.13125
Ppf1	19.66	61.875	10.24	29.6875	3.5	1.5	1	0	1	1.5	0	0	18.7625
Ppf5	15.96	10.44	10.78	23.75	2.5	2	1.25	0	0.25	1	0	0	22.04375
Ppf3	23.53	21.56	10.59	40	2	1.75	1.25	0	1.25	0	0	0	22.9125
P1	23.4725	40.30625	10.03	48.75	2.125	1.625	1.5	1.875	2	1.25	0	0	26.0125
Ppf4	26.68	20	9.57	49.69	2.5	1.75	0	0	0.75	0	0	0	26.0875
Ppf2	18.39	44.6875	8.09	45.9375	2.25	1.75	1	0.25	1.25	0.25	0	0	32.925
P2	25.34	15.25	12.56	34.3125	2.625	2.25	0.5	0.75	1.125	0.25	0	0	33.0125
P4	21.14	47.08125	10.18	39.57375	3.625	2.5	2.25	0.5	2.25	0.875	0	0	35.41875
P3	20.1	28.9525	11.34	58.735	2.5	2.5	1.5	1.125	2	1.25	0	0	37.365625
Spf2	32	20.88	16.6	34.25	2.5	2.75	1	2.25	0.75	0.75	0	0	42.28125
P5	28.86	31.7625	11.995	55.46875	2.375	2.375	2	0.25	1.375	0.625	0	0	43.53125
P6	21.82	23.65625	8.875	54.21875	3.75	2.625	1	1.375	1.625	1.375	0	0	53.1
S4	31.995	19.3225	10.525	35.3125	2.625	2.25	1.375	1.375	2.375	2.375	0	0	63.36666667
Rip (T01)	25.27	19.475	7.885	42.1875	2.5	2.875	0.5	0	1	1.875	0	0	73.37

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Appendix 2. Habitat Variable Rotated Factor Loadings and Communalities. Equamax Rotation Sorted Rotated Factor Loadings and Communalities.

Variable	Factor1	Factor2	Factor3	Communality
Upper C cov	0.846	0	0	0.743
Epiphytes	0.817	0	0	0.719
Vines	0.743	0	0	0.641
Grass	-0.723	0	0	0.72
Upper C height	0.673	0	0	0.592
Herbs	0.602	0.466	0	0.644
Ferns	0.588	0	0	0.475
Plantation	0	0.814	0	0.812
Mid C cov	0	0.711	0	0.538
Shrubs	0	0.656	0.424	0.657
Leaf Litter	0.46	0.625	0	0.611
Mid C height	0	0	0.805	0.702
Palms	0	0	0.798	0.704
Variance	4.0333	2.5101	2.0152	8.5587
% Var	0.31	0.193	0.155	0.658

Appendix 3A. Relative abundances for amphibian pitfall trapping. Pitfall values represent the estimated number of individuals encountered per 70 trapping days. RA is the mean relative abundance for each site within a given habitat. NE is the number of individuals encountered within that habitat type across all sites for a given habitat. The given *p*-value corresponds to a Kruskall-Wallis analysis of variance in order to analyze the mean relative abundance across habitats (analyses were only conducted in species with an encounter rate greater than 10 individuals - NE>10, where * represents a statistically significant difference, F=highest RA in Forest, Pl=highest RA in plantation, Pa=highest RA in pastureland). Codes given next to species name relate to those given in Fig. 5A and 5B.

Species	Forest		Plantation		Pastureland		Total Nº of Individuals	*p*-value
	RA	NE	RA	NE	RA	NE		
Allobates zaparo (Ab)	5.50	44	0.50	2	-	-	46	0.014* F
Ameerega bilinguis (A)	14.38	115	9.50	38	1.17	4	157	0.110
Bolitoglossa peruviana (B)	-	-	-	-	-	-	-	
Caecilia tentaculata (Cc)	0.38	3	-	-	-	-	3	
Chiasmocleis bassleri (C)	-	-	-	-	-	-	-	
Colostethus insperatus (Ca)	1.75	14	-	-	-	-	14	0.254
Colostethus sp (Cb)	0.13	1	-	-	-	-	1	
Edalorhina perezi (E)	0.63	5	0.50	2	-	-	7	
Engystomops petersi (Ea)	2.13	17	-	-	-	-	17	0.015* F
Hemiphractus scutatus (H)	0.13	1	-	-	-	-	1	
Hypodactylus nigrovittatus (G)	7.25	58	2.50	10	0.58	2	70	0.029* F
Hypsiboas boans (F)	-	-	-	-	-	-	-	
Leptodactylus andreae (Ha)	0.50	4	1.25	5	6.42	22	31	0.013* Pa
Leptodactylus lineatus (J)	0.38	3	-	-	-	-	3	
Leptodactylus mystaceus (K)	-	-	-	-	0.88	3	3	
Leptodactylus pentadactylus (L)	-	-	-	-	-	-	-	
Leptodactylus rhodomystax (La)	1.75	14	-	-	-	-	14	0.526
Oreobates quixensis (Na)	0.25	2	-	-	0.29	1	3	
Osteocephalus deridens (M)	-	-	-	-	-	-	-	
Osteocephalus planiceps (N)	-	-	-	-	-	-	-	
Phyllomedusa vailantii (Tb)	-	-	-	-	-	-	-	
Phyyllomedusa tomopterna (Ta)	-	-	-	-	-	-	-	
Pristimantis acuminatus (P)	-	-	-	-	-	-	-	
Pristimantis altamazonicus (Pa)	1.75	14	0.25	1	-	-	15	0.012* F
Pristimantis conspicillatus (Pc)	0.13	1	0.25	1	-	-	2	
Pristimantis delius (Q)	0.38	3	-	-	-	-	3	
Pristimantis diadematus (R)	-	-	0.25	1	-	-	1	
Pristimantis kichwarum (Ra)	11.88	95	22.75	91	5.54	19	205	0.034* Pl
Pristimantis lanthanites (Rb)	6.63	53	-	-	0.29	1	54	0.008* F
Pristimantis malkini (S)	-	-	-	-	-	-	-	
Pristimantis martiae (Sa)	0.38	3	0.50	2	-	-	5	
Pristimantis peruvianus (T)	0.38	3	0.25	1	-	-	4	
Pristimantis varabilis (U)	-	-	0.25	1	2.33	8	9	
Ranitomeya ventrimaculata (D)	-	-	-	-	-	-	-	
Rhinella dapsilis (V)	0.38	3	-	-	-	-	3	
Rhinella margaritifera (W)	1.25	10	-	-	-	-	10	
Rhinella marina (Y)	0.25	2	-	-	0.29	1	3	
Scinax ruber (Z)	0.13	1	-	-	-	-	1	
Total	58.63	469	38.75	155	17.79	61	685	0.032* F
Survey effort (trap nights)	560		280		280		1120 total	

Appendix 3B. Relative abundances for amphibian visual survey transects. Transect values represent the estimated number of individuals encountered over 450 m^2 (a single transect area). RA is the mean relative abundance for each site within a given habitat. NE is the number of individuals encountered within that habitat type across all sites for a given habitat. The given *p*-value corresponds to a Kruskall-Wallis analysis of variance in order to analyse the mean relative abundance across habitats (analyses were only conducted in species with an encounter rate greater than 10 individuals - NE>10, where * represents a statistically significant difference, F=highest RA in Forest, Pl=highest RA in plantation, Pa=highest RA in pastureland). Codes given next to species name relate to those given in Fig. 5A and 5B.

Species	Forest		Plantation		Pastureland		Total Nº of Individuals	*p*-value
	RA	NE	RA	NE	RA	NE		
Allobates zaparo (Ab)	0.24	12	-	-	-	-	12	0.007* F
Ameerega bilinguis (A)	2.78	136	4.33	65	0.14	3	204	0.009* Pl
Bolitoglossa peruviana (B)	0.86	42	0.80	12	1.14	24	78	0.553
Caecilia tentaculata (Cc)	-	-	-	-	-	-	-	
Chiasmocleis bassleri (C)	0.06	3	-	-	-	-	3	
Colostethus insperatus (Ca)	-	-	-	-	-	-	-	
Colostethus sp (Cb)	-	-	-	-	-	-	-	
Edalorhina perezi (E)	0.08	4	-	-	-	-	4	
Engystomops petersi (Ea)	0.22	11	-	-	-	-	11	0.023* F
Hemiphractus scutatus (H)	-	-	-	-	-	-	-	
Hypodactylus nigrovittatus (G)	0.31	15	-	-	0.10	2	17	0.117
Hypsiboas boans (F)	0.02	1	-	-	-	-	1	
Leptodactylus andreae (Ha)	-	-	0.07	1	0.29	6	7	
Leptodactylus lineatus (J)	0.04	2	-	-	-	-	2	
Leptodactylus mystaceus (K)	-	-	-	-	0.14	3	3	
Leptodactylus pentadactylus (L)	-	-	-	-	-	-	-	
Leptodactylus rhodomystax (La)	0.02	1	-	-	-	-	1	
Oreobates quixensis (Na)	0.06	3	-	-	-	-	3	
Osteocephalus deridens (M)	0.20	10	-	-	-	-	10	
Osteocephalus planiceps (N)	0.08	4	-	-	-	-	4	
Phyllomedusa vailantii (Tb)	0.02	2	-	-	-	-	2	
Phyyllomedusa tomopterna (Ta)	0.04	1	-	-	-	-	1	
Pristimantis acuminatus (P)	0.10	5	0.20	3	-	-	8	
Pristimantis altamazonicus (Pa)	0.12	6	0.07	1	0.05	1	8	
Pristimantis conspicillatus (Pc)	0.06	3	-	-	0.05	1	4	
Pristimantis delius (Q)	0.02	1	-	-	0.10	2	3	
Pristimantis diadematus (R)	0.20	10	-	-	-	-	10	
Pristimantis kichwarum (Ra)	4.55	223	7.87	118	1.00	21	362	0.009* Pl
Pristimantis lanthanites (Rb)	0.92	45	-	-	0.05	1	46	0.013* F
Pristimantis malkini (S)	0.04	2	-	-	-	-	2	
Pristimantis martiae (Sa)	0.04	2	-	-	-	-	2	
Pristimantis peruvianus (T)	0.14	7	-	-	-	-	7	
Pristimantis varabilis (U)	0.02	1	-	-	2.05	43	44	0.086
Ranitomeya ventrimaculata (D)	0.02	1	-	-	-	-	1	
Rhinella dapsilis (V)	0.04	2	-	-	-	-	2	
Rhinella margaritifera (W)	0.08	4	-	-	-	-	4	
Rhinella marina (Y)	-	-	-	-	-	-	-	
Scinax ruber (Z)	-	-	-	-	-	-	-	
Total	11.41	559	13.33	200	5.10	107	866	0.043* Pl
Survey effort (searcher hours)	490		150		170		810 total	

Appendix 4A. Relative abundances for reptile pitfall trapping. Pitfall values represent the estimated number of individuals encountered per 70 trapping days. RA is the mean relative abundance for each site within a given habitat. NE is the number of individuals encountered within that habitat type across all sites for a given habitat. The given *p*-value corresponds to a Kruskall-Wallis analysis of variance in order to analyse the mean relative abundance across habitats (analyses were only conducted in species with an encounter rate greater than 10 individuals, NE>10, where * represents a statistically significant difference, F=highest RA in Forest, Pl=highest RA in plantation, Pa=highest RA in pastureland). Codes given next to species name relate to those given in Fig. 5A and 5B.

Species	Forest		Plantation		Pastureland		Total Nº of Individuals	*p*-value
	RA	NE	RA	NE	RA	NE		
Anolis fuscoauratus (A)	0.18	1	-	-	0.83	2	3	
Anolis nitens scypheus (Ac)	0.54	3	0.71	2	2.50	6	11	0.132
Anolis trachyderma (Af)	0.71	4	-	-	-	-	4	
Arthosaura reticulata reticulate (Ad)	0.71	4	0.71	2	0.42	1	7	
Attractus major (Ab)	-	-	-	-	-	-	0	
Attractus sp (Ae)	0.18	1	-	-	-	-	1	
Bachia trisanale (Ba)	-	-	0.36	1	-	-	1	
Bothrops hyporora (B)	-	-	-		-	-	0	
Cercosaura argulus (C)	0.18	1	1.79	5	0.42	1	7	
Dendrophidion dendrophis (F)	-	-	-	-	-	-	0	
Dipsas catesbyi (E)	-	-	-	-	-	-	0	
Enyaloides laticeps (H)	0.18	1	-	-	-	-	1	
Epicrates chechria gargei (G)	-	-	-	-	-	-	0	
Gonatodes concinnatus (Ha)	0.36	2	0.71	2	0.42	1	5	
Gonatodes humeralis (J)	0.36	2	-	-	-	-	2	
Imantodes cenchoa (K)	-	-	-	-	-	-	0	
Imantodes lentiferus (L)	-	-	-	-	-	-	0	
Kentropyx pelviceps (M)	2.32	13	0.71	2	-	-	15	0.064
Leposoma parietale (N)	5.00	28	8.57	24	4.17	10	62	0.148
Neusticurus ecpleopus (P)	0.54	3	0.36	1	-	-	4	
Oxyrophus melanogenys (R)	-	-	-	-	0.42	1	1	
Pseudoboa coronate (S)	-	-	-	-	-	-	0	
Pseudogonatodes guianensis (T)	1.96	11	1.43	4	0.42	1	16	0.393
Taeniophallus brevirostris (V)	0.18	1	-	-	-	-	1	
Tropidurus plica (W)	0.18	1	0.36	1	-	-	2	
Tropidurus umbra (Y)	0.89	5	-	-	0.42	1	6	
Xenoxybelis argenteus (Z)	-	-	-	-	-	-	0	
All snakes	0.89	5	1.07	3	2.92	7	15	0.458
All lizards	13.57	76	14.64	41	7.08	17	134	0.413
Total	14.46	81	15.71	44	10.00	24	149	0.508
Survey effort (trap nights)	560		280		280		1120 total	

Appendix 4B. Relative abundances for reptiles VES. Transect values represent the estimated number of individuals encountered over 450 m^2 (a single transect area). RA is the mean relative abundance for each site within a given habitat. NE is the number of individuals encountered within that habitat type across all sites for a given habitat. The given *p*-value corresponds to a Kruskall-Wallis analysis of variance in order to analyse the mean relative abundance across habitats (analyses were only conducted in species with an encounter rate greater than 10 individuals, NE>10, where * represents a statistically significant difference, F=highest RA in Forest, Pl=highest RA in plantation, Pa=highest RA in pastureland). Codes given next to species name relate to those given in Fig. 5A and 5B.

Species	Forest		Plantation		Pastureland		Total N° of Individuals	*p*-value
	RA	NE	RA	NE	RA	NE		
Anolis fuscoauratus (A)	0.23	5	1.19	8	0.21	2	15	0.212
Anolis nitens scypheus (Ac)	0.18	4	-	-	0.21	2	6	
Anolis trachyderma (Af)	0.73	16	0.59	4	0.11	1	21	0.137
Arthosaura reticulata reticulate (Ad)	0.05	1	-	-	-	-	1	
Attractus major (Ab)	0.05	1	-	-	-	-	1	
Attractus sp (Ae)	-	-	-	-	-	-	-	
Bachia trisanale (Ba)	-	-	-	-	-	-	-	
Bothrops hyporora (B)	0.05	1	-	-	-	-	1	
Cercosaura argulus (C)	0.05	1	-	-	-	-	1	
Dendrophidion dendrophis (F)	0.09	2	-	-	-	-	2	
Dipsas catesbyi (E)	0.05	1	-	-	-	-	1	
Enyaloides laticeps (H)	0.09	2	-	-	-	-	2	
Epicrates chechria gargei (G)	0.05	1	-	-	-	-	1	
Gonatodes concinnatus (Ha)	0.23	5	-	-	0.11	1	6	
Gonatodes humeralis (J)	-		0.15	1	0.21	2	3	
Imantodes cenchoa (K)	0.09	2	-	-	0.11	1	3	
Imantodes lentiferus (L)	-		0.44	3	-	-	3	
Kentropyx pelviceps (M)	-	-	-	-	-	-	-	
Leposoma parietale (N)	0.32	7	0.44	3	0.11	1	11	0.410
Neusticurus ecpleopus (P)	-	-	-	-	-	-	-	
Oxyrophus melanogenys (R)	-	-	-	-	-	-	-	
Pseudoboa coronate (S)	0.05	1.00	-	-	-	-	1	
Pseudogonatodes guianensis (T)	0.14	3.00	-	-	-	-	3	
Taeniophallus brevirostris (V)	-	-	-	-	-	-	-	
Tropidurus plica (W)	0.05	1.00	-	-	-	-	1	
Tropidurus umbra (Y)	-	-	-	-	-	-	-	
Xenoxybelis argenteus (Z)	0.09	2.00	-	-	-	-	2	
All snakes	0.68	15	0.44	3	0.32	3	21	0.162
All lizards	1.86	41	2.37	16	0.74	7	64	0.191
Total	2.54	56	2.81	19	1.06	10	85	0.027* Pl
Survey effort (searcher hours)	490		150		170		810 total	

Appendix 5. Full GLM output table for amphibian and reptile richness and diversity indices against habitat factor scores. Where C-E=Co-efficient estimate, T=T-value, and *p*=*p*-value.

Amphibians	Estimated Richness			Alpha			Shannon			Simpson		
	C-E	T	*p*	C-E	T	*p*	C-E	T	*p*	C-E	T	*p*
Constant	11.77	8.64	>0.01	2.95	14.13	>0.01	1.41	25.13	>0.01	3.88	16.34	>0.01
Factor 1	3.89	2.74	0.01	0.73	3.34	>0.01	0.27	4.62	>0.01	0.64	2.59	0.02
Factor 2	-3.71	-2.77	0.01	-0.98	-4.76	>0.01	-0.32	-5.87	>0.01	-0.98	-4.21	>0.01
Factor 3	1	0.74	0.46	0.03	0.17	0.87	0.05	0.83	0.42	-0.13	-0.56	0.58

Reptiles	Estimated Richness			Alpha			Shannon			Simpson		
	C-E	T	*p*	C-E	T	*p*	C-E	T	*p*	C-E	T	*p*
Constant	4.47	15.34	>0.01				1.28	19.58	>0.01			
Factor 1	0.38	1.29	0.21				0.07	0.97	0.34			
Factor 2	-0.56	-2.02	0.06				-0.15	-2.37	0.03			
Factor 3	0.06	0.21	0.84				0.03	0.43	0.67			