



## Lizard diversity in response to human-induced disturbance in Andean Ecuador

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The cloud-forests of the Western Ecuadorean Andes are highly diverse and under threat from anthropogenic habitat disturbance. Reptiles are sensitive to habitat change and are therefore useful indicators of ecosystem state. Overall diversity has been shown to be highest in old-growth (primary) forest, although older secondary forests can recover to near pre-disturbance levels. We systematically surveyed leaf-litter lizard diversity along a gradient of disturbance in a montane cloud-forest fragment whilst controlling for the potentially confounding effect of elevation. We deployed 21 pitfall trap-lines equally between primary forest, secondary forest of mid-age (18–30 years), and agroforestry, between three altitudinal bands for ten days each over a period of three years. We investigated diversity patterns using Chao 1 and 2 indices (estimated richness), effective species number (ESN), relative abundance of individual species, relative abundance of pooled species, and observed species richness. We also conducted an opportunistic inventory of reptile species. We recorded 7 species of leaf-litter lizards and 15 other species of squamate, the majority of which are rare, recently described and/or of restricted distribution. Elevation was strongly negatively correlated with diversity. Richness and most indices of diversity were higher in primary forest but abundance was similar in primary forest and agroforestry. ESN followed a negative linear response to disturbance but for all other measures agroforestry supported diversity that was either higher than or equal to secondary forest. We conclude that, particularly at high elevations, mid-aged secondary forest is depauperate of leaf-litter lizards but agroforestry potentially supports relatively large populations of generalist species.

*Key words:* Andes, cloud-forest, disturbance, Ecuador, lizard

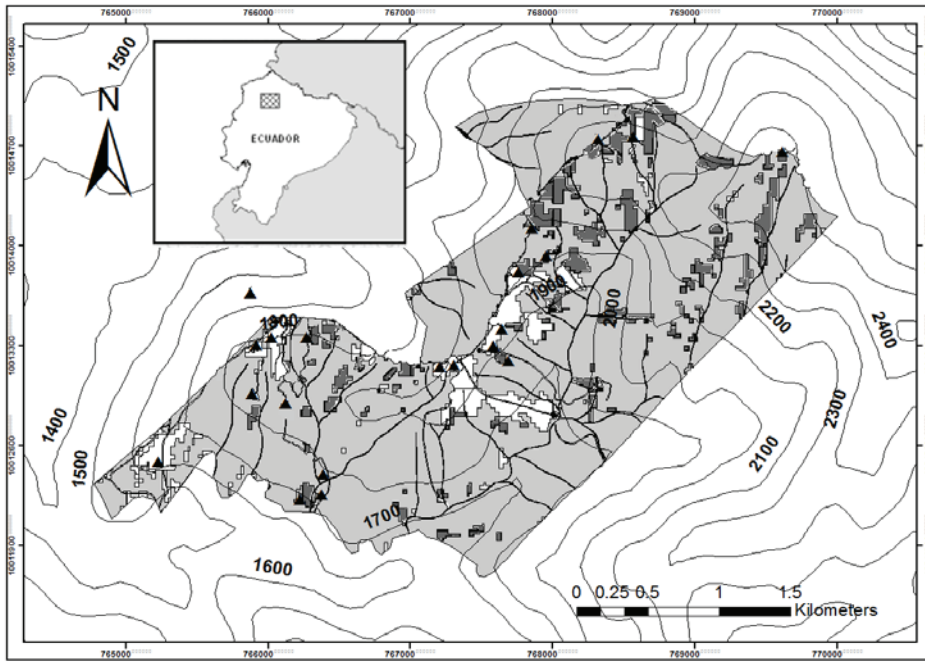
### INTRODUCTION

Ecuador is subject to the greatest annual loss of tropical forest in South America (FAO, 2010) and Western Ecuador is greatly threatened by habitat loss and fragmentation (Cisneros-Heredia, 2006). Located within the Tropical Andes Biodiversity hotspot (CEPF, 2014), the Ecuadorean Andes constitute one of the most biologically diverse areas on earth, but are increasingly under threat from agricultural encroachment, road building and timber extraction (Ortega-Andrade et al., 2010).

Habitat heterogeneity and human disturbance are consistently documented to affect community structure of reptiles (Luja et al., 2008). Inevitably these effects will vary according to numerous factors, including taxon studied, biogeographical region, microhabitat structure, area and disturbance history. A meta-analysis of the literature on the effects of structural habitat change

on reptile communities universally documents fewer species in regenerating/secondary forest (defined as forests between 15 and 35 years old) than in primary (undisturbed) forest (Gardner et al., 2007a). However, studies comparing lizard diversity and community structure along a disturbance gradient that additionally includes recently cleared or managed forest (e.g., induced grassland, plantations and agro-forestry) have produced more equivocal results. Higher richness of semi-fossorial 'leaf-litter' lizards has been documented in primary relative to both secondary and recently cleared forests, with no difference between the latter two categories (Gardner et al., 2007b; Luja et al., 2008). However, lower abundance of leaf-litter lizards has also been reported in both primary and secondary forest relative to plantations (Gardner et al., 2007b). Furthermore, there is evidence that, under specific environmental conditions and over extended timescales, secondary forests can support species richness similar to that of pre-disturbance levels

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**Fig. 1.** Map of Santa Lucía Cloud-forest Reserve (SLCR) and location in North-Western Ecuador, showing contours (m.a.s.l.), the major habitat types and other features, and the locations of the 21 lizard trap-lines (including one located in secondary forest just outside the reserve boundaries). Black triangles=trap-lines; pale grey shading=primary forest; dark grey shading=secondary forest; white shading=silvopasture; solid black lines=watercourse; stippled black and white lines=trails.

(20–40 years for ants and birds: Dunn, 2004; 30 years for frogs and lizards: Panwar et al., 2004).

The responses of small vertebrates such as reptiles to habitat change are particularly complex in mountain environments where diversity is further stratified by elevation (Peck et al., 2014). Patterns of reptile diversity along elevational gradients may follow a range of distinct forms, including negative associations, mid-elevation peaks and low elevation plateaus (McCain & Sanders, 2010). However, in general, reptile populations are under-represented at higher elevations. We studied patterns in leaf-litter lizard diversity along a full gradient of disturbance within Andean cloud-forest in north-western Ecuador. Using various measures of diversity, our objective was to test for differences in leaf-litter lizard communities between primary forest, secondary forest and agroforestry, whilst controlling for the effects of elevation. Biodiversity in the area is incompletely described, with the majority of taxa being data deficient. We therefore additionally conducted a general inventory of reptile species.

## MATERIALS AND METHODS

### Study site

Santa Lucía Cloud-forest Reserve (hereafter referred to as SLCR) is located at 00.11429°N, 078.57075°W (WGS 84) (Fig. 1) within the southern section of the Chocó-Andean conservation corridor in Pichincha province, North-Western Ecuador (Rainforest Concern, 2008), a priority region designated by Ecuador's National Biodiversity Strategy (NBS) under the Convention for Biological Diversity (CBD). SLCR encompasses 730 ha of tropical montane forest ranging in altitude from 1400–2560 masl. Approximately 80% of the reserve is covered by unexploited old-growth primary forest, with the remaining area constituting around 15% secondary regrowth forest (selectively felled in the 1990s) and 5% cattle

pasture (cleared between 2000 and 2002) regenerated as an agroforestry system termed silvopasture. Secondary forest was therefore 18–30 years old, and silvopasture 6–10 years old, at the time of study.

### Field data collection

Data collection took place during five field expeditions over three years from 2008 to 2010: 25 July–1 September 2008, 24 June–22 July; 23 August–25 September 2009, 5–15 March; 25 June–14 July 2010. We systematically sampled leaf-litter species where trail access allowed surveys of representative areas by deploying pitfall traps with drift-fence arrays at 21 locations (hereafter referred to as trap-lines; Corn, 1994). Trap-lines were equally distributed between the three habitat disturbance categories (Fig. 1) and further stratified by elevation so that between 4 and 6 trap-lines per habitat were located in each of 3 elevation bands: 1400–1700, 1700–2000, and 2000–2300 masl. Steep gradients prevented placement of trap-lines at the highest elevations.

Trap-lines were spaced at least 200 m apart to avoid spatial pseudo-replication, based on the maximum circular home range for similar sized lizards (5–10 g) that occupy apparently similar ecological niches (see Verwaijen & Van Damme, 2008). Whenever possible, trap-lines were also spaced 500 m from the border of each habitat patch to reduce the impact of edge effects (see Gardner et al., 2007b). Trap-line establishment required a flat or gently sloping area of approximately 30 m<sup>2</sup>. Each trap-line measured 5 m by 5 m constructed in a 'T' shape. Five plastic buckets of 25 L volume were dug into the ground, flush with the surface, along each drift fence at intervals of 2.5 m. Five drainage holes were drilled into the bottom of each bucket to drain water from rainfall. Twigs, leaves or stones were placed in the buckets to provide cover to protect captured reptiles against predation. The drift fence was constructed from WeedBlock weed control and landscape fabric (Easy

**Table 1.** Reptile species list for Santa Lucía cloud-forest reserve (SLCR).

Lizards	Green copper lizard	<i>Alopoglossus viridiceps</i>
	Rainbow langelot	<i>Cercosaura vertebralis</i>
	Blunt-headed hedgehog lizard	<i>Echinosaura brachycephala</i>
	Spiky lirecko	<i>Lepidoblepharis conolepis</i>
	Tropical lightbulb lizard	<i>Riama oculata</i>
	Drab lightbulb lizard	<i>Riama unicolor</i>
	Yumbo lightbulb lizard	<i>Riama yumborum</i>
	O'Shaughnessys' dwarf iguana	<i>Enyalioides oshaughnessyi</i>
	Whorltail iguana	<i>Stenocercus varius</i>
	Gem anole	<i>Anolis gemmosus</i>
	Frasers' anole	<i>Anolis fraseri</i>
	Equatorial anole	<i>Anolis aequatorialis</i>
Snakes	Dunn's ground snake	<i>Atractus dunni</i>
	Giant ground snake	<i>Atractus gigas</i>
	Ground snake sp.	<i>Atractus sp.</i>
	Mountain sipo	<i>Chironius monticola</i>
	Yellow-bellied snake	<i>Coniophanes fissidens</i>
	Olive forest racer	<i>Dendrophidion dendrophis</i>
	Peters' forest racer	<i>Dendrophidion nuchale</i>
	Ecuador snail-eater	<i>Dipsas oreas</i>
	Black-headed snake	<i>Tantilla melanocephala</i>
	Eyelash viper	<i>Bothriechis schlegelii</i>

Gardener UK Limited, London) cut to a width of 50 cm and buried 5cm below ground. This prevented reptiles from passing beneath, and resulted in a functional fence height of 45 cm. Fence structure was maintained by wooden poles attached to the fabric with cable ties, at intervals of ~1 m. Trap-lines were left in situ for between 7 and 14 days and were checked once daily during the dry season (July–September) and twice daily during the rainy season (March–June); the latter to avoid excessive rain filling the traps.

Diurnal and nocturnal opportunistic direct searches for all reptiles (visual encounter surveys; Crump & Scott, 1994) were also conducted throughout all field expeditions. Where species could not be identified by sight and for arboreal and fast-moving terrestrial lizards and snakes, we used additional collection methods (pole and noose trapping, capture by hand and excavation). Materials and methods used for pole and noose trapping followed those described by Blomberg & Shine (2006). If field identification of captured reptiles to species level was not possible, specimens were euthanised with 2% roxicain injected directly into the heart and tissue samples were taken and stored in 95% ethanol for subsequent

DNA analysis. Specimens were fixed with 10% formalin before being stored in 75% ethanol and deposited at Museo de Zoología QCAZ, Pontificia Universidad Católica del Ecuador. A full list of voucher specimens can be found in Appendix 1.

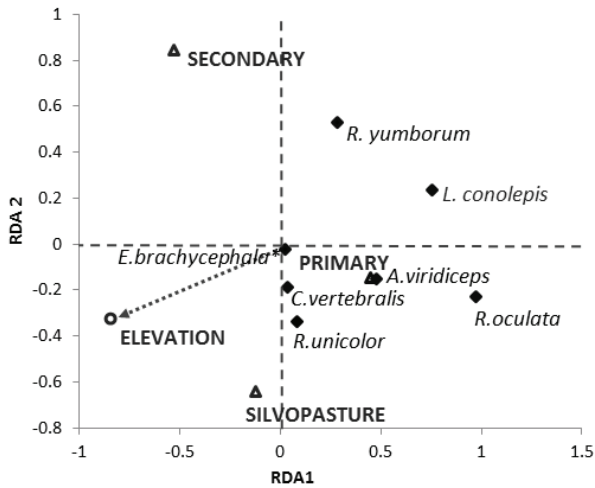
#### Data analysis

Statistical analyses of pitfall trap-line data were computed using R v. 2.13 (R Core Team, 2014) and EstimateS (Colwell, 2009). Redundancy Analysis (RDA) was used to explore patterns within the dataset, which comprised three variables: relative abundance (hereafter referred to as 'abundance') of individual species, habitat disturbance, and elevation. We derived estimates of total species richness using the Chao 1 and Chao 2 indices (Chao, 2005) and species diversity using effective species number (ESN) (Jost et al., 2010) in EstimateS. We then compared all three indices across habitats and elevational bands.

Finally, observed species richness and abundance (pooled across species) were regressed against habitat disturbance and elevation, using generalised linear modelling (GLM) with a Poisson error distribution and

**Table 2.** Sample sizes, diversity indices and estimated species richness for primary and secondary forest and silvopasture in Santa Lucía cloud-forest reserve (SLCR).

	Primary	Secondary	Silvopasture
Total number of trap-lines	7	7	7
Total number of lizards captured	32	14	18
Mean number of lizards captured per trap-line	4.6	2	2.6
Chao 1 index (mean and 95% CIs)	9.0 (7.2–29.1)	3.5 (3.0–11.4)	5.0 (5.0–5.9)
Chao 2 index (mean and 95% CIs)	8.0 (7.1–18.1)	5.0 (3.2–25.1)	5.2 (5.0–9.7)
Effective Species Number (mean and 95% CI)	4.9±0.1	2.6±0.3	1.5±0.1



**Fig. 2.** Redundancy Analysis (RDA) biplot for the 7 species of leaf-litter lizards. RDA 1 and 2 combined account for 94.7% of the variance in the dataset. \*one individual only.

logit link function. Number of days sampled was entered into each model as a log-transformed offset. A backwards stepwise model selection procedure was used where the two main effects and the interaction term between them were initially entered together before sequential removal of variables that were non-significant at the 95% level, based on lowest deviance values. Model fits were then compared using AIC (Akaike's Information Criterion) and percentage deviance, and a Minimum Adequate Model (MAM) selected. Statistical comparison between the MAM and the next-best-fit model was conducted using one-way analysis of variance (ANOVA).

## RESULTS

We captured a total of 64 individuals from 7 species of leaf-litter lizards in pitfall trap-lines, and 109 individuals of 22 species of squamate (12 lizards and 10 snakes) using opportunistic direct searches (Table 1; Table 2). No genus dominated, with a maximum of three species for each of the genera *Anolis*, *Riama* and *Atractus*. *Riama oculata* was the most commonly encountered lizard species and *Tantilla melanocephala* the most common snake, recorded in all habitat types and elevation bands.

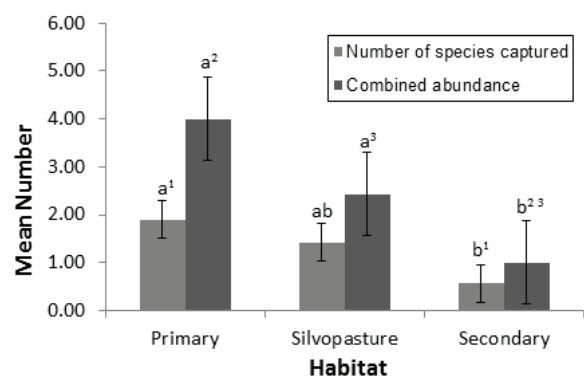
### Leaf-litter lizard diversity patterns

The Chao 1 richness estimator identified a threshold pattern in estimated species richness between disturbance categories, with primary forest supporting the most species and secondary forest the least (Table 2;  $p < 0.05$  for all pairwise combinations). However, Chao 2 failed to identify any differences ( $p > 0.05$  for all pairwise combinations). Diversity (ESN) followed a negative linear relationship with disturbance, with the highest value in primary forest and the lowest in silvopasture (Table 2). A negative linear correlation was also detected between diversity and elevation, with an ESN of 4.70 at the lowest band of 1400–1700; 4.53 at mid-elevations of 1700–2000; and 1.00 at 2000–2300 masl ( $p < 0.05$  for all pairwise combinations). Estimated richness did not differ between bands ( $p$  always  $> 0.05$ ).

Abundance of all 7 species was strongly linked to lower elevations with elevation orientated towards the first axis (Monte Carlo permutation test, eigenvalue RDA 1=0.845, variance explained by RDA 1=72.4%, Fig. 2). Abundance of all species was closely correlated with primary forest, except for *R. yumborum*, which was linked to secondary forest. Habitat disturbance category was orientated towards the second axis (Monte Carlo permutation test, eigenvalue RDA 2=0.256, variance explained by RDA 2=22.3%, Fig. 2).

For GLMs, the best-fit minimum adequate model (MAM) predicting abundance (pooled across species) differed significantly from the next best fit model (ANOVA, Likelihood Ratio  $\chi^2=7.552$ ,  $df=1$ ,  $p < 0.05$ ) and retained elevation and habitat (disturbance) as main effects, with elevation accounting for a greater proportion of the variance in the response (Appendix 2, Table 1). The interaction term did not reach convergence and was therefore excluded. Abundance was negatively correlated with elevation (GLM, Maximum Likelihood Parameter Estimate (MLPE)=-0.004,  $z=-3.343$ ,  $df=1$ ,  $p < 0.001$ ) and showed a threshold response to habitat disturbance, with higher numbers in both primary forest and silvopasture relative to secondary forest, and no difference between primary forest and silvopasture (Fig. 3).

The MAM predicting observed species richness was significantly different to the next best fit model (ANOVA,  $\Delta$  Deviance=-5.162,  $df=1$ ,  $p < 0.05$ ), and again retained elevation and disturbance as main effects, with a greater influence of elevation (Appendix 2, Table 2). The interaction term did not reach convergence. Observed species richness was negatively linearly correlated with elevation (GLM, MLPE=-0.002,  $z=-2.127$ ,  $df=1$ ,  $p < 0.05$ ) and was higher in primary than secondary forest but no different between silvopasture and the other forest types (Fig. 3).



**Fig. 3.** Mean observed species richness and pooled relative abundance per trap-line for leaf-litter lizards across habitat types. Letters and numbers denote *post-hoc* comparisons using GLM z-tests. Bars with different letters denote significant pairwise differences at the 95% level. <sup>1</sup>primary versus secondary for richness (MLPE=1.415,  $z=2.730$ ); <sup>2</sup>primary versus secondary for abundance (MLPE=1.226,  $z=2.213$ ) <sup>3</sup>silvopasture versus secondary for abundance (MLPE=1.108,  $z=2.012$ ). \* $p < 0.05$ ; \*\* $p < 0.01$ .

## DISCUSSION

In our study, secondary forest that was between 18 and 30 years old universally harboured a depauperate leaf-litter lizard fauna. Therefore, our results do not support the hypothesis that secondary forests can regenerate to near pre-disturbance levels in a relatively short time scale (e.g., Dunn, 2004; Pawar et al., 2004). The presence of a plateau effect for some measures of species richness is consistent with Gardner et al. (2007b) and Luja et al. (2008) and further supports this assertion. For leaf-litter lizards, forests that were cleared or selectively logged 30 years ago are not richer than those that were cleared a decade ago. Stand age has been demonstrated to be correlated with species richness of reptiles (Gardner et al., 2007a), but recovery of secondary forests may take hundreds of years (Wright & Muller-Landau, 2006), a timescale beyond most monitoring programmes.

Abundance followed a threshold effect along the disturbance gradient, suggesting that increased time post-disturbance does not increase overall numbers but may actually hinder the recovery of populations. However, this pattern does not persist when overall measures of diversity are used. Silvopasture may therefore support relatively large numbers of a few, more generalist species. Basic ecological information such as life-history strategy is lacking for the semi-fossorial gymnophthalmids that comprised our lizard captures, particularly for the genus *Riama* (Reyes-Puig et al., 2008; Maddock et al., 2011a; b). However, features of a more open habitat structure relating to light, temperature and moisture, which generally affect reptile populations via thermoregulatory effects (see Pringle et al., 2003), are likely to have an impact.

Feeding guild and degree of mobility are important predictors of vertebrate sensitivity to habitat change. For example, Vetter et al. (2011) demonstrated that non-volant insectivores, a group which includes the majority of lizard species (see Celedón-Neghme et al., 2005) tend to be more sensitive to disturbance than highly mobile nectarivores and frugivores. The effect of reduced micro-habitat complexity, which is associated with conversion from primary to secondary forest (e.g., Luja et al., 2008), may thus be amplified in leaf-litter lizards, which have poor dispersal abilities and occupy a dietary niche at higher trophic levels.

As expected, all measures of diversity increased with decreasing elevation consistent with what was previously reported in the literature (e.g., McCain, 2010). Negative correlations between elevation and reptile species richness are driven by temperature at potentially multiple ontogenetic stages (Navas, 2003; McCain, 2010). However, a linear relationship between temperature-dependent metabolic kinetics and elevational patterns of diversity has not been detected thus far (McCain & Sanders, 2010).

Although pitfall traps are widely considered to be effective at capturing ground-dwelling fauna (Ribeiro-Junior et al., 2008), inherent biases are associated with their use (e.g., Gardner et al., 2007b). Hence we recommend further systematic studies of leaf-litter lizards

that incorporate complementary methods such as time-constrained line transect searches. The use of relative rather than absolute abundance in our study also limits the extent to which we can draw robust conclusions. Furthermore, our inventory methods were not optimal for capturing arboreal species and we recommend that further studies employ glue or funnel traps, or artificial refugia to maximise capture success of reptiles occupying arboreal niches (e.g., Bauer & Sadlier, 1992).

In this study we have filled a knowledge gap regarding macro-habitat and diversity patterns in the studied region, but there remains a paucity of information on the micro-habitat requirements of and threats acting on reptiles in montane fragmented cloud-forests. Several of the species we recorded were described recently, including *Riama yumborum* (Aguirre-Peñañiel et al., 2014), *Alopoglossus viridiceps* (Torres-Carvajal & Lobos, 2014), *Atractus gigas* (Myers & Schargel, 2006; Tolhurst et al., 2010) and *Echinosaura brachycephala* (Köhler et al., 2004). Some are believed to be rare, such as *A. dunni* (Cisneros-Heredia, 2005; Arteaga et al., 2013) and others e.g., *Lepidoblepharis conolepis* and *R. oculata* are reported from a limited locale (Ávila-Pires, 2001; Cisneros-Heredia, 2009). Conservation status has been assigned to only three of the species we report: *R. oculata*, *Anolis gemmosus* and *A. fraseri*. Although common in SLCR, *R. oculata* is categorised by the IUCN red list of threatened species as Endangered because its range is highly restricted: it is estimated to occur in only five localities (Cisneros-Heredia, 2009). The other species, *A. gemmosus* and *A. fraseri*, are categorised as Least Concern (Cisneros-Heredia & Mayer, 2009; Castañeda et al., 2013) as their distributions in Ecuador and Colombia are moderately large.

Taken together, our study provides evidence for threshold effects of disturbance on some aspects of diversity of neotropical leaf-litter lizards. We also show that regenerating secondary forest stands of less than 30 years of age do not support diverse communities, and that agroforestry systems have the potential to act as refugia for some species. Further studies are needed, however, to clarify patterns of diversity for a group that remains data-deficient.

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## APPENDICES

### Appendix 1.

Voucher specimens from Santa Lucía Cloud-forest Reserve (SLCR). *Anolis aequatorialis* (QCAZ 10680); *Anolis gemmosus* (QCAZ 10664); *Atractus dunnii* (QCAZ 10659, 10661, 10663, 10672, 10748); *Cercosaura vertebralis* (QCAZ 10667, 10750); *Alopoglossus viridiceps* (10666, 10670, 10671, 10753, 10821, 10826); *Echinosaura brachycephala* (QCAZ 10824); *Lepidoblepharis conolepis* (QCAZ 10660, 10662, 10665, 10669, 10674, 10823, 10828); *Riama oculata* (QCAZ 10668, 10676, 10678, 10679, 10681, 10746, 10747, 10749, 10819, 10820, 10825, 11078, 11082, 11093, 11094, 11095, 11096); *Riama yumborum* (QCAZ 10820, 10822, 10827, 11077, 11079, 11080, 11081); *Riama unicolor* (QCAZ 10673, 10675, 10677, 10745, 11083, 11084).

### Appendix 2.

**Table 1.** Model fits for predictors of and contribution of main terms to the variance in relative abundance of leaf-litter lizards. Comparisons were based on AIC and % Deviance values (Lowest AIC and highest % deviance=best-fit, minimum adequate model (MAM). MAMs and most influential terms are shown in *italic*.

MODEL FITS				
	Model terms	Model deviance	Model deviance as a % of the null	AIC
1	<i>Altitude + Habitat</i>	13.369	35.523	75.451
2	Altitude	7.208	19.152	77.612
3	Habitat	8.207	21.807	78.613
CONTRIBUTIONS OF TERMS				
terms	Model	Deviance	% of total model deviance	<i>p</i>
1	Altitude	5.162	38.612	<0.05
	<i>Habitat</i>	8.207	61.388	<0.05

**Table 2.** Model fits for predictors of and contribution of main terms to the variance in species richness of leaf-litter lizards. Comparisons were based on AIC and % Deviance values (Lowest AIC and highest % deviance=best-fit, minimum adequate model (MAM). MAMs and most influential terms are shown in *italic*.

MODEL FITS				
Model	Model terms	Model deviance	Model deviance as a % of the null	AIC
1	<i>Altitude + Habitat</i>	45.727	46.311	119.97
2	Altitude	16.499	26.226	127.94
3	Habitat	4.933	10.415	135.4
CONTRIBUTIONS OF TERMS				
terms	Model	Deviance	% of total model deviance	<i>p</i>
1	Altitude	36.183	79.128	<0.001
	Habitat	9.545	20.874	<0.01

