

Amphibian and reptile communities and functional groups over a land-use gradient in a coastal tropical forest landscape of high richness and endemism

Morgan J. Trimble and Rudi J. van Aarde¹

Conservation Ecology Research Unit, Department of Zoology & Entomology, University of Pretoria, South Africa

Corresponding authors: R.J. van Aarde or M.J. Trimble, Conservation Ecology Research Unit, Department of Zoology & Entomology, University of Pretoria, Private Bag X20, Hatfield Pretoria 0028, South Africa, Telephone: +27 12 420-2753, Fax: +27 12 420-4523, email: rjvaarde@zoology.up.ac.za or morgantrimble@gmail.com

ABSTRACT

Information on the response of herpetofauna to different land uses is limited though important for land-use planning to support conservation in human-modified landscapes. Though transformation is dogmatically associated with extinction, species respond idiosyncratically to land-use change, and persistence of species in habitat fragments may depend on careful management of the human-modified matrix. We sampled herpetofauna over a vegetation-type gradient representative of regional land uses (old-growth forest, degraded forest, acacia woodland (i.e. new-growth forest), eucalyptus plantation, and sugar cane cultivation) in the forest belt skirting the southeastern coast of Africa, part of a biodiversity hotspot hosting many endemic herpetofaunal species in a highly transformed landscape. We categorized species into

¹ Author Contributions: MJT and RJvA designed the study. MJT carried out the project, analyzed the data, and wrote the manuscript with input from RJvA, who supervised the study.

trait-derived functional groups, and assessed abundance and richness of groups and compared community metrics along the gradient. We further assessed the capacity of environmental variables to predict richness and abundance. Overall, old-growth forest harbored the highest richness and abundance, and frogs and reptiles responded similarly to the gradient. Richness was low in cultivation and, surprisingly, in degraded forest but substantial in acacia woodland and plantation. Composition differed between natural vegetation types (forest, degraded forest) and anthropogenic types (plantation, cultivation), while acacia woodland grouped with the latter for frogs and the former for reptiles. Functional group richness eroded along the gradient, a pattern driven by sensitivity of fossorial/ground-dependent frogs (F2) and reptiles (R2) and vegetation-dwelling frogs (F4) to habitat change. Variables describing temperature, cover, and soil were good predictors of frog abundance, particularly of functional groups, but not for reptiles. Conserving forest and preventing degradation is important for forest herpetofaunal conservation, restoration and plantations have intermediate value, and cultivation is least beneficial. Our study demonstrates the utility of function-related assessments, beyond traditional metrics alone, for understanding community responses to transformation. Particularly, fossorial/ground-dependent frogs and reptiles and vegetation-dwelling frogs should be closely monitored.

Key-words: acacia woodland; amphibia; anura; cultivation; functional diversity; human-modified landscape; plantation; Maputaland

INTRODUCTION

Increasingly, scientists study biodiversity in human-modified landscapes to augment conservation efforts in protected areas with appropriate management beyond them (Daily, 1999; Trimble & van Aarde, 2012). This is a salient issue in the biologically rich and unique coastal forest belt skirting Africa's southeastern coast, part of the Maputaland Center of endemism (van Wyk, 1996) and the Maputaland-Pondoland-Albany biodiversity hotspot (Küper *et al.*, 2004; Perera, Ratnayake-Perera & Proches, 2011). Mining, tourism, agriculture, and subsistence communities have contributed to substantial forest loss and degradation (Kyle, 2004). An estimated 82% of coastal forest in KwaZulu-Natal has been destroyed, jeopardizing ecological integrity and species persistence (Olivier, van Aarde & Lombard, 2013; Trimble & van Aarde, 2011). However, some species may occur or persist in certain land-use types within the matrix. Determining the amenability of different land uses to forest species based on species-specific responses could contribute to evidence-based policy that could mitigate some effects of fragmentation (see O'Connor & Kuyler, 2009; Sutherland, 2004).

Herpetofauna are specialized in habitat requirements (Botts, Erasmus & Alexander, 2013; Kanowski *et al.*, 2006), are sensitive to habitat modification, and face global extinction crises (Böhm *et al.*, 2013; Gibbons *et al.*, 2000; Stuart *et al.*, 2008). While herpetofauna are important components of ecosystems (e.g. Beard, Vogt & Kulmatiski, 2002; Whiles *et al.*, 2006), they are little studied (Trimble & van Aarde, 2010), particularly in human-modified landscapes (Trimble & van Aarde, 2012), and especially in Africa (Gardner, Barlow & Peres, 2007a). Herpetofauna do occur in human-modified landscapes, so encouraging appropriate matrix land uses could contribute to their conservation (Anand *et al.*, 2010; Sodhi *et al.*, 2010). Habitat modification is a non-random filter for species; thus, identifying characteristics of species that are sensitive to

land-use change (see Suazo-Ortuno, Alvarado-Diaz & Martinez-Ramos, 2008) could provide insight into taxonomic and functional homogenization to inform conservation strategies (Cadotte, Carscadden & Mirochnick, 2011; Mouillot *et al.*, 2013; Smart *et al.*, 2006). However, function-related responses to habitat change are poorly understood for herpetofauna (Gardner *et al.*, 2007a).

To clarify the effects of forest transformation and inform land-use planning, we sought to document the response of herpetofaunal communities to a gradient of land uses characteristic of the coastal forest region, which is rich in herpetofauna and harbors many endemic and threatened species (Armstrong, 2001; Branch, 1998; du Preez & Carruthers, 2009; IUCN, 2012; Measey, 2011; Perera *et al.*, 2011; Stuart *et al.*, 2008). We sampled terrestrial herpetofaunal communities of five vegetation types, subjectively ranked by structural similarity to old-growth forest: forest, degraded forest, acacia woodland (a seral stage of forest regeneration (van Aarde *et al.*, 1996)), eucalyptus plantation, and sugar cane cultivation. We focused on three aims: 1) to test how abundance, richness, diversity, and composition of frog and reptile communities change along the gradient, 2) to assign species to functional groups, sets of species with similar ecological roles, and assess changes in relative and proportional abundance of groups and group richness along the gradient, and 3) to quantify potential ecological drivers of community change by relating environmental variables to overall richness and abundance of frogs and reptiles and to abundance of functional groups.

METHODS

Study Area

We sampled terrestrial herpetofauna along 25kms of coastline across a land-use gradient southwest of Richards Bay, KwaZulu-Natal, South Africa, from 4km north of the Umlalazi River mouth to just south of the Richards Bay harbor, up to 2.3km inland (Fig. 1). The region falls within the southern end of the East African Tropical Coastal Forest (see van Aarde, Guldmond & Olivier, 2013).

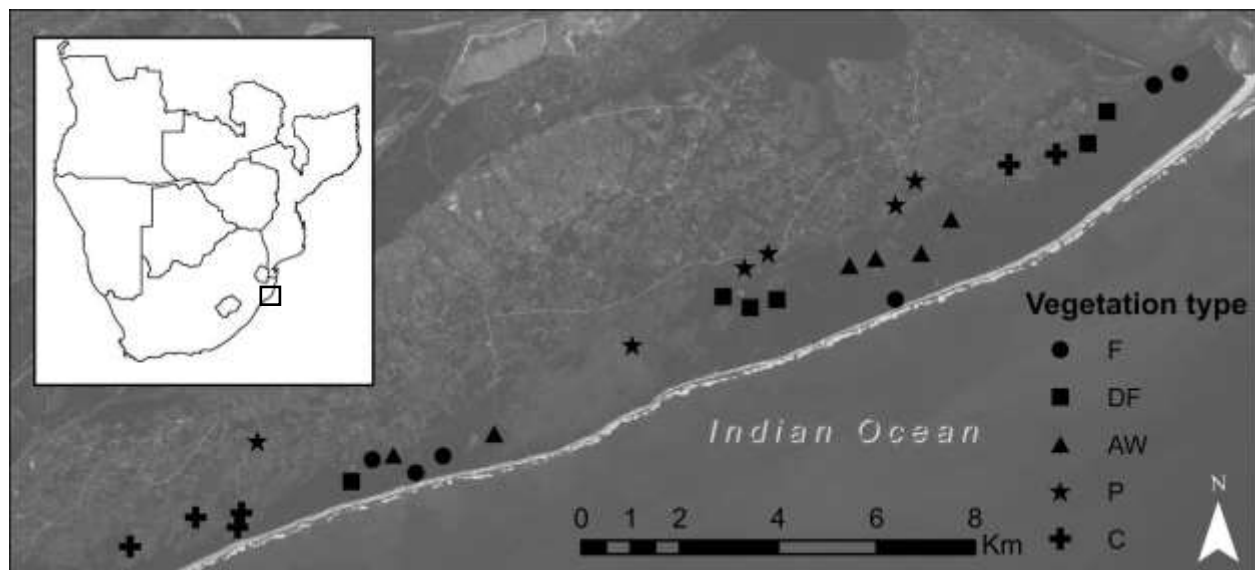


Figure 1. Study area map indicating location of trapping arrays in five vegetation types (F = forest, DF = degraded forest, AW = acacia woodland, P = plantation, C = cultivation); inset shows study area location in southern Africa.

Sampling Methods

We used a stratified random sample design of 30 trap arrays divided evenly among 5 vegetation types: forest, degraded forest (determined by presence of invasive plants *Lantana camara* and/or *Chromolaena odorata*), acacia woodland (new-growth forest dominated by *Acacia karroo*),

eucalyptus plantation, and sugar cane cultivation. Trap arrays were installed in three periods, two arrays per vegetation type per period, between February 19 and March 13, 2012. We checked arrays daily for five days, identified species captured, and released them $\geq 50\text{m}$ away (to minimize recapture). Each array was operational for $120 \pm 1\text{hrs}$. Arrays were separated from each other by $\geq 500\text{m}$ and from known water bodies by $\geq 300\text{m}$ (Fig. 1).

Each array employed seven complementary sampling techniques, detailed in Appendix S1, to represent as many species as possible while maintaining a standardized effort (Ribeiro-Júnior, Gardner & Ávila-Pires, 2008). Arrays consisted of three 15m arms of 0.5m-tall black plastic drift fence, dug 0.1m into the ground, spaced at 120° , and connected at a central pitfall bucket. Arms featured pitfall buckets at 7.5 and 15m from the center bucket, and a funnel trap on either side between the outer two pitfalls. The fence guided frogs and reptiles into pitfalls and funnel traps. Four polyvinyl chloride (PVC) pipe traps (see Trimble & van Aarde, 2013) and four wooden cover boards were installed 10m beyond the northern-pointing fence arm and checked on days two, four, and five. An active search was performed and audio recordings were made in the vicinity of each array, and species found when installing or removing traps were recorded. We measured eight environmental variables at each array and assessed the distribution of array points along southwest—northeast and coastal distance geographic gradients, see Appendix S1.

Analyses

We assessed sampling saturation overall and per vegetation type, separately for amphibians and reptiles, with sample-based accumulation curves calculated in EstimateS 8.2.0 (Colwell, 2009; Gotelli & Colwell, 2001). We assessed whether vegetation type affected observed richness (species per array) and abundance (individuals per array) with Poisson generalized linear

modeling (GLM) and analysis of deviance based on the X^2 distribution (or quasi-Poisson GLM and F -tests to account for overdispersion) (Zuur *et al.*, 2009).

We estimated richness of frogs and reptiles per vegetation type with non-parametric richness estimators calculated in EstimateS: four abundance-based (Chao1, ACE, Jack1, and Jack2) and two incidence-based that included frog species identified from audio recordings (Chao2 and ICE). We calculated the range of the proportion of estimated richness that we actually observed based on the lowest and highest of the six estimators. We used the asymmetrical 95% CI of Chao1 and Chao2 to assess whether richness differed between vegetation types (Colwell, 2009).

We calculated Shannon diversity overall and per vegetation type based on abundance data for frogs and reptiles and explored differences in evenness and diversity with Rényi diversity profiles calculated in BiodiversityR (Kindt & Coe, 2005).

To assess composition, we calculated pairwise Bray-Curtis similarity on raw frog and reptile abundance, square-root-transformed abundance (to decrease the influence of abundant species), and frog incidence data including species identified in audio recordings (here, Bray-Curtis simplified to Sorenson similarity) (Anderson *et al.*, 2011; Clarke & Gorley, 2006). We used Primer 6's (Clarke & Gorley, 2006) analysis of similarity (ANOSIM) to compare community composition among vegetation types and visualized differences with non-metric multidimensional scaling (NMDS).

We assigned species to functional groups based on functional traits from published information (Branch, 1998; du Preez & Carruthers, 2009; Pla, Casanoves & Di Rienzo, 2012). Frogs traits comprised maximum snout-urostyle length, primary stratum of activity (fossorial, on ground, or in vegetation), where eggs are laid (ground, water, or vegetation), and where tadpoles

develop (water or underground). Reptiles traits comprised maximum snout-ventral length, mean clutch size, active stratum (allowing multiple options of burrowing/fossorial, ground-active, or climbing on vegetation/rocks), reproductive strategy (viviparous or egg-laying), locomotion (legs or legless), and feeding style (venomous, constrictor, or ambush). We defined functional groups in InfoStat (Di Rienzo *et al.*, 2011); following Pla *et al.* (2012), we transformed categorical variables into a set of quantitative principal coordinates with multidimensional scaling and retained a set of axes that explained $\geq 85\%$ of variation, then used Euclidian distances and the Ward linkage algorithm to create dendrograms for frogs and reptiles separately. We retained four functional groups each for frogs and reptiles and used MANOVA with Hotelling post-test and Bonferroni adjustment to assess grouping significance.

We modeled abundance of functional groups on vegetation type with Poisson GLM and compared to the null model with analysis of deviance based on the X^2 distribution (or quasi-Poisson GLM and F -tests to account for overdispersion) (Zuur *et al.* 2009). Similarly we compared proportional abundance of each functional group across vegetation types with binomial GLM (or quasi-binomial to account for overdispersion) (Zuur *et al.*, 2009). We also tallied the number of functional groups represented per vegetation type.

We compared environmental variables among vegetation types with ANOVA. We dropped canopy cover and height from further analyses because they were significantly collinear with each other and with temperature range, herb cover, and litter depth with correlation coefficient magnitude ≥ 0.6 (Zuur *et al.*, 2009); we retained the latter variables plus litter cover, soil pH, and mean temperature. We used Poisson GLM to assess the relationships between environmental variables and frog and reptile richness and abundance and the abundance of functional groups. For each case, we parameterized the model set of all single-order

combinations of six environmental variables and a null model. We used AICc to compare models and performed multi-model averaging across models with AICc differences (Δ_i) < 4 (Grueber *et al.*, 2011). Where overdispersion was present, we used quasi-Poisson GLMs and quasi-AICc (QAICc) (Zuur *et al.*, 2009).

RESULTS

We captured 436 individuals representing 17 frog and 20 reptile species (Table 1). Nine frog species were recorded with audio recorders (three that were not captured in arrays), bringing the number of species recorded to 40. Many calls carried further than the 50m estimated by Hilje and Mitchell Aide (2012); thus, we excluded five species recorded in audio recordings that are only known to call from water bodies (Channing, 2001; du Preez & Carruthers, 2009), resulting in 38 species considered in further analyses (Table 1). Only *Amietophrynus gutturalis* (Table 1 provides common names) was recorded in every vegetation type.

Richness, abundance, and diversity

Sampling approached but did not reach an asymptote for frogs or reptiles overall or any vegetation type, and 95% CI for frog and reptile abundances overlapped among vegetation types (Fig. S1). The proportion of expected species that we observed was 71-93% for frogs and 63-84% for reptiles and differed by vegetation type (Table 2). Richness estimators varied but were similar within groups, except for reptiles in forest (Table 2). Incidence-based estimators were higher than abundance-based estimators for frogs because they included auditory records (Table 2).

Table 1. Abundance of frog and reptile species captured in trapping arrays (where * indicates confirmation of frog species by audio recording^a) across vegetation types (F = forest, DF = degraded forest, AW = acacia woodland, P = plantation, C = cultivation), and functional group to which species are assigned based on functional traits.

Scientific name, common name ^b	F	DF	AW	P	C	Total	Functional group
Frogs							
<i>Amietophrynus gutturalis</i> , guttural toad	41	44	16	27	33	161	F3
<i>Arthroleptis wahlbergi</i> , bush squeaker	89	51	10	5	0	155	F2
<i>Phrynobatrachus natalensis</i> , snoring puddle frog	0	0*	0*	0	10	10*	F1
<i>Breviceps sopranus</i> , whistling rain frog ^c	3	2	2	0	2	9	F2
<i>Phrynobatrachus mababiensis</i> , dwarf puddle frog	6	0	0	2	0	8	F1
<i>Afrixalus spinifrons</i> (<i>spinifrons</i>), Natal leaf-folding frog	2	2	0	0	0	4	F4
<i>Amietophrynus rangeri</i> , raucous toad	1	2	0	1	0	4	F3
<i>Breviceps mossambicus</i> , Mozambique rain frog ^c	0	0	0	3	0	3	F2
<i>Phrynobatrachus acridoides</i> , East African puddle frog	0	0	0	0	3	3	F1
<i>Afrixalus fornasinii</i> , greater leaf-folding frog	2	0	0	0	0	2	F4
<i>Hyperolius pusillus</i> , water lily frog	0	0	1	0	1	2	F1
<i>Kassina senegalensis</i> , bubbling kassina	1*	0	0	1*	0	2*	F1
<i>Leptopelis natalensis</i> , Natal tree frog	1	1*	0	0	0*	2*	F2
<i>Amietophrynus garmani</i> , eastern olive toad	0	0	1	0	0	1	F3
<i>Hemisis guttatus</i> , spotted shovel-nosed frog	0	0	0	1	0	1	F2
<i>Hyperolius tuberilinguis</i> , tinker reed frog	0	0	1	0	0	1	F4
<i>Strongylopus fasciatus</i> , striped stream frog	0	0	0	1	0	1	F2
<i>Ptychadena oxyrhynchus</i> , sharp-nosed grass frog	0	0*	0*	0*	0*	0*	F3
Reptiles							
<i>Scelotes mossambicus</i> , Mozambique dwarf burrowing skink	6	5	2	0	0	13	R2
<i>Panaspis wahlbergii</i> , Wahlberg's snake-eyed skink	0	0	1	3	3	7	R3
<i>Mabuya varia</i> , variable skink	0	1	6	0	0	7	R3
<i>Lygodactylus capensis</i> (<i>capensis</i>), Cape dwarf gecko	0	0	0	1	3	4	R3
<i>Zygaspis vandami</i> (<i>arenicola</i>), Van Dam's round-headed worm lizard	1	0	3	0	0	4	R2

<i>Mabuya striata (striata)</i> , striped skink	0	0	0	0	3	3	R3
<i>Hemidactylus mabouia</i> , Moreau's tropical house gecko	1	0	0	1	0	2	R3
<i>Acontias plumbeus</i> , giant legless skink	2	0	0	0	0	2	R2
<i>Gerrhosaurus flavigularis</i> , yellow-throated plated lizard	0	0	0	0	1	1	R3
<i>Psammophis brevirostris (brevirostris)</i> , short-snouted grass snake	0	0	0	1	3	4	R4
<i>Leptotyphlops sp.</i> , thread snakes ^d	0	0	0	4	0	4	R2
<i>Crotaphopeltis hotamboeia</i> , herald snake	0	1	0	2	0	3	R4
<i>Psammophis mossambicus</i> , olive grass snake	0	0	1	2	0	3	R4
<i>Aparallactus capensis</i> , Cape centipede eater	1	0	0	2	0	3	R2
<i>Causus rhombeatus</i> , rhombic night adder	1	0	1	0	0	2	R4
<i>Lamprophis fuliginosus</i> , brown house snake	0	0	0	1	0	1	R1
<i>Philothamnus natalensis (natalensis)</i> , eastern green snake	1	0	0	0	0	1	R1
<i>Mehelya nyassae</i> , black file snake	1	0	0	0	0	1	R1
<i>Thelotornis capensis (capensis)</i> , vine snake	0	0	1	0	0	1	R4
<i>Philothamnus hoplogaster</i> , green water snake	1	0	0	0	0	1	R1
Total individuals observed	161	109	46	58	62	436	
Total species observed (including audio recordings)	18	9(11)	13(15)	17(18)	10(12)	37(38)	

^a Audio records of guttural toad *Amietophrynu gutturalis*, water lily frog *Hyperolius pusillus*, tinkler reed frog *Hyperolius tuberilinguis*, painted reed frog *Hyperolius marmoratus*, and red-legged kassina *Kassina maculata* were excluded because they only call from water bodies.

^b Scientific and common names follow nomenclature in du Preez and Carruthers (2009) and Branch (1998).

^c These *Breviceps* species are cryptic (Minter, 2003), and while species identification was confirmed by expert examination of photographs, only genetic identification would provide certainty; these results should be interpreted with caution.

^d We did not identify *leptotyphlops* to species level because they are cryptic, and the complex is under further revision. Currently, four species are known from the region of our study (Branch, 1998).

Table 2. Observed species richness and abundance, abundance- and incidence-based richness estimators, percent of predicted richness actually observed, and Shannon diversity of frogs and reptiles across five vegetation types (F = forest, DF = degraded forest, AW = acacia woodland, P = plantation, C = cultivation).

	Species obs.	Ind. obs.	Abundance-based estimators				Incidence-based estimators		Percent observed (range)	Shannon diversity
			Chao 1 (95% CI)	ACE	Jack1	Jack 2	Chao 2 (95% CI)	ICE		
Frogs										
Total	17 (18)	369	18.2 (17.1-27.4)	20.6	22.8	23.9	22.8 (18.9-46.9)	22.9	71-93%	1.35
F	9	146	10.0 (9.1-19.7)	12.2	12.3	13.4	10.3 (9.1-19.8)	14.6	62-90%	1.09
DF	6 (8)	102	6.0 (6.0-6.0)	6.7	8.5	10.0	9.7 (8.2-21.7)	14.2	56-100%	0.99
AW	6 (8)	31	7.5 (6.2-21.1)	12.0	8.5	10.0	12.2 (8.6-35.2)	18.4	43-80%	1.22
P	8 (9)	41	11.0 (8.4-31.0)	10.8	12.2	14.4	10.3 (9.1-19.8)	13.7	56-87%	1.23
C	5 (7)	49	5.0 (5.0-5.0)	5.6	6.7	6.9	8.7 (7.2-20.7)	15.6	45-100%	0.97
Reptiles										
Total	20	67	23.8 (20.6-42.0)	23.8	27.7	31.6	25.4 (21.1-46.3)	28.5	63-84%	2.71
F	9	15	19.5 (11.0-63.2)	37.5	15.7	21.0	32.3 (15.2-96.6)	67.8	13-57%	1.9
DF	3	7	4.0 (3.1-15.9)	7.0	4.7	6.0	3.8 (3.06-14)	6.7	43-79%	0.8
AW	7	15	10.0 (7.4-30.0)	13.5	10.3	12.5	9.5 (7.3-26.6)	11.9	52-74%	1.68
P	9	17	10.5 (9.2-21.5)	12.0	13.2	14.4	10.7 (9.2-21.1)	14.6	62-86%	2.07
C	5	13	5.0 (5.0-6.6)	5.4	6.7	6.9	5.3 (5.0-10.2)	6.6	72-100%	1.55

While species and individuals recorded per array did not differ significantly between vegetation types (Fig. 2), 95%CI indicated Chao1 for frogs was significantly higher in forest,

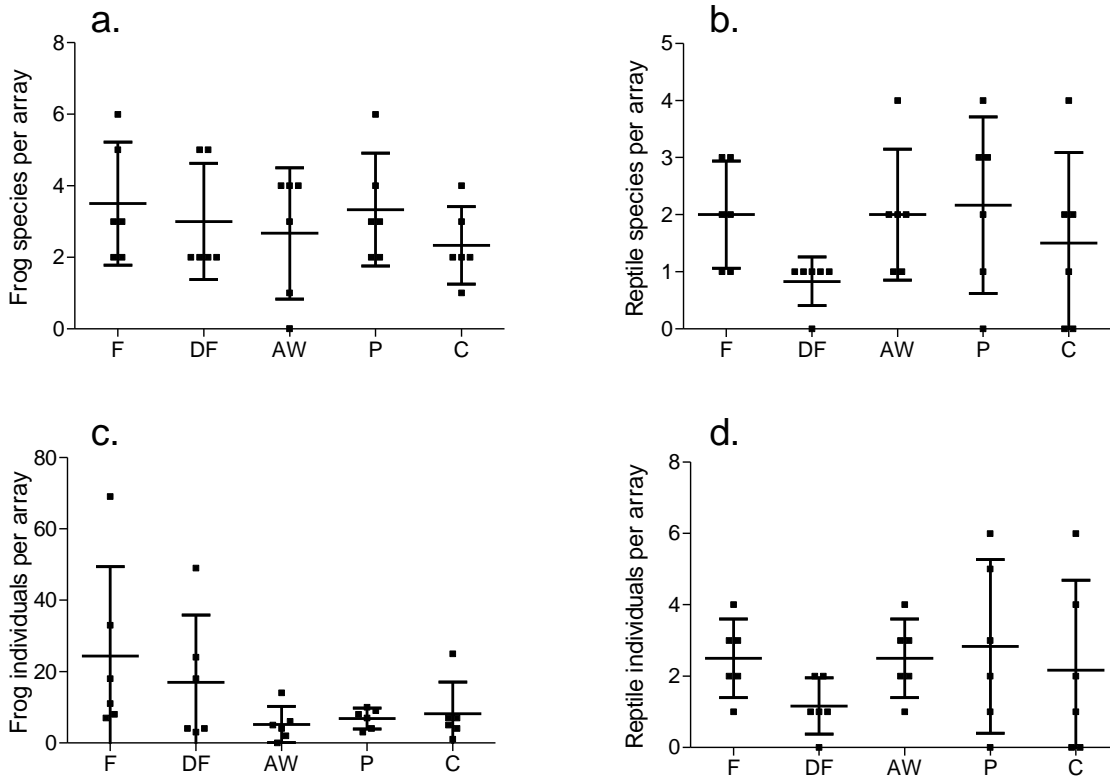


Figure 2. Vegetation type (F = forest, DF = degraded forest, AW = acacia woodland, P = plantation, C = cultivation) was not a significant predictor in Poisson or quasi-Poisson GLM for species observed per array for (a) frogs ($X^2 = 1.87$, $df = 4$, $p = 0.76$) and (b) reptiles ($X^2 = 4.73$, $df = 4$, $p = 0.32$) or individuals recorded per array for (c) frogs ($\Phi = 11.40$, $F_{4,25} = 2.70$, $p = 0.05$) and (d) reptiles ($\Phi = 1.18$, $F_{4,25} = 1.05$, $p = 0.40$). Graphs illustrate mean and 95% CI.

acacia woodland, and plantation than in degraded forest or cultivation. Chao2 for frogs did not differ significantly among vegetation types. Other estimators ranked vegetation types variably but suggested higher richness in forest, acacia woodland, and plantation and lower richness in

degraded forest and cultivation (Table 2). Reptile Chao1 was significantly higher in forest, acacia woodland, and plantation than in cultivation, while Chao2 was significantly higher in forest than degraded forest and cultivation (Table 2). Other estimators consistently ranked reptile richness highest in forest; intermediate in acacia woodland and plantation; and lowest in degraded forest and cultivation.

For both frogs and reptiles, Shannon diversity was highest in plantation and lowest in cultivation and degraded forest (Table 2). Rényi profiles confirmed these rankings and showed diversity rankings of other vegetation types depended on the influence of evenness, i.e. Rényi profiles intersected (Kindt & Coe, 2005) (Fig. S2).

Composition

ANOSIM of square-root-transformed data indicated significant difference in composition among vegetation types (Table 3). Frog community structure in forest differed significantly from that in acacia woodland, plantation, and cultivation, while degraded forest differed from cultivation. Reptile community structure differed significantly between natural vegetation types (forest, degraded forest, or acacia woodland) and anthropogenic types (cultivation or plantation), except degraded forest did not differ significantly from plantation. NMDS ordination illustrated these patterns (Fig. S3). Results based on raw abundance and frog incidence data were similar (Fig. S3, Table S1).

Functional groups

Group size was similar, and species groupings seemed ecologically relevant (Tables 1 & 4). Traits differed between functional groups for frogs (Wilks' $\lambda=1.6 \times 10^{-4}$, $F_{12,29}=64.82$, $p<0.001$) and reptiles (Wilks' $\lambda=2.4 \times 10^{-5}$, $F_{24,27}=42.63$, $p<0.001$), and Hotelling post-tests indicated these differences were significant among all functional groups.

Table 3. Analysis of similarity (ANOSIM) results comparing frog and reptile community composition among vegetation types based on Bray-Curtis similarity of square-root-transformed abundance data.

Vegetation type comparison	Frogs (Global R=0.174, p<0.01)		Reptiles (Global R=0.194, p<0.001)	
	R statistic ^a	p ^b	R statistic ^a	p ^b
	Forest–degraded forest	-0.02	0.52	-0.05
Forest–acacia woodland	0.22	<0.05*	0.15	0.08
Forest–plantation	0.24	<0.05*	0.25	<0.05*
Forest–cultivation	0.79	<0.01**	0.38	<0.001***
Degraded forest–acacia woodland	0.00	0.40	0.09	0.2
Degraded forest–plantation	-0.01	0.47	0.18	0.06
Degraded forest–cultivation	0.27	<0.05*	0.28	<0.05*
Acacia woodland–plantation	0.05	0.20	0.30	<0.01**
Acacia woodland–cultivation	0.16	0.07	0.35	<0.01**
Plantation–cultivation	0.11	0.10	0.09	0.17

^a ANOSIM generates an R statistic ranging from -1 (where similarities across different vegetation types are higher than within types) to 1 (where similarities within types are higher than between types) (Clarke & Gorley, 2001).

^b Significance of each comparison is indicated by * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

Vegetation type was a significant predictor of abundance for functional groups F2 and R2 and of proportional abundance for F1, F2, F3, and R2 (Table 4). Proportional abundance of several functional groups changed directionally along the gradient from forest to cultivation, while number of groups represented decreased (Fig. 3).

Table 4. Functional group descriptions (Fx are frog groups, Rx are reptile groups), number of species per group, and statistics describing significance of vegetation type as a predictor of abundance and proportional abundance of each functional group in Poisson (or quasi-Poisson) and binomial (or quasi-binomial) GLMs respectively (see Table 1 for species composition of groups).

Functional Group	General description	Number of species	Vegetation type as predictor of abundance	Vegetation type as predictor of proportional abundance
F1	Small, ground-dwelling frogs (except water lily frog) that lay eggs in water	5	$\Phi = 2.05, F_{4,25} = 1.93, p = 0.14$	$\chi^2 = 27.05, df = 4, p < 0.001$
F2	Fossorial or ground-dwelling species (except Natal tree frog) that lay eggs in the ground, i.e. ground dependent. Tadpoles of three species develop in the ground	6	$\Phi = 7.32, F_{4,25} = 5.89, p < 0.01$	$\Phi = 1.62, F_{4,24} = 11.60, p < 0.001$
F3	Large, ground-dwelling frogs that lay eggs in water	4	$\Phi = 4.82, F_{4,25} = 0.79, p = 0.54$	$\Phi = 1.25, F_{4,24} = 7.93, p < 0.001$
F4	Small, vegetation-dwelling frogs that lay eggs in vegetation	3	$\chi^2 = 9.15, df = 4, p = 0.06$	$\Phi = 3.78, F_{4,24} = 0.29, p = 0.88$
R1	Snakes that attack by constricting or ambush, tend to be shorter than R4	4	$\chi^2 = 8.38, df = 4, p = 0.08$	$\chi^2 = 7.69, df = 4, p = 0.10$
R2	Legless, burrowing species, tend towards small clutch size	5	$\chi^2 = 14.01, df = 4, p < 0.01$	$\Phi = 1.69, F_{4,21} = 3.09, p < 0.05$
R3	Ground-active and climbing lizards, locomotion with legs, hunt by ambush	6	$\Phi = 1.64, F_{4,25} = 2.15, p = 0.10$	$\Phi = 1.84, F_{4,21} = 2.56, p = 0.07$
R4	Venomous snakes, tend to be longer than R1	5	$\Phi = 1.03, F_{4,25} = 1.07, p = 0.39$	$\Phi = 1.17, F_{4,21} = 0.68, p = 0.61$

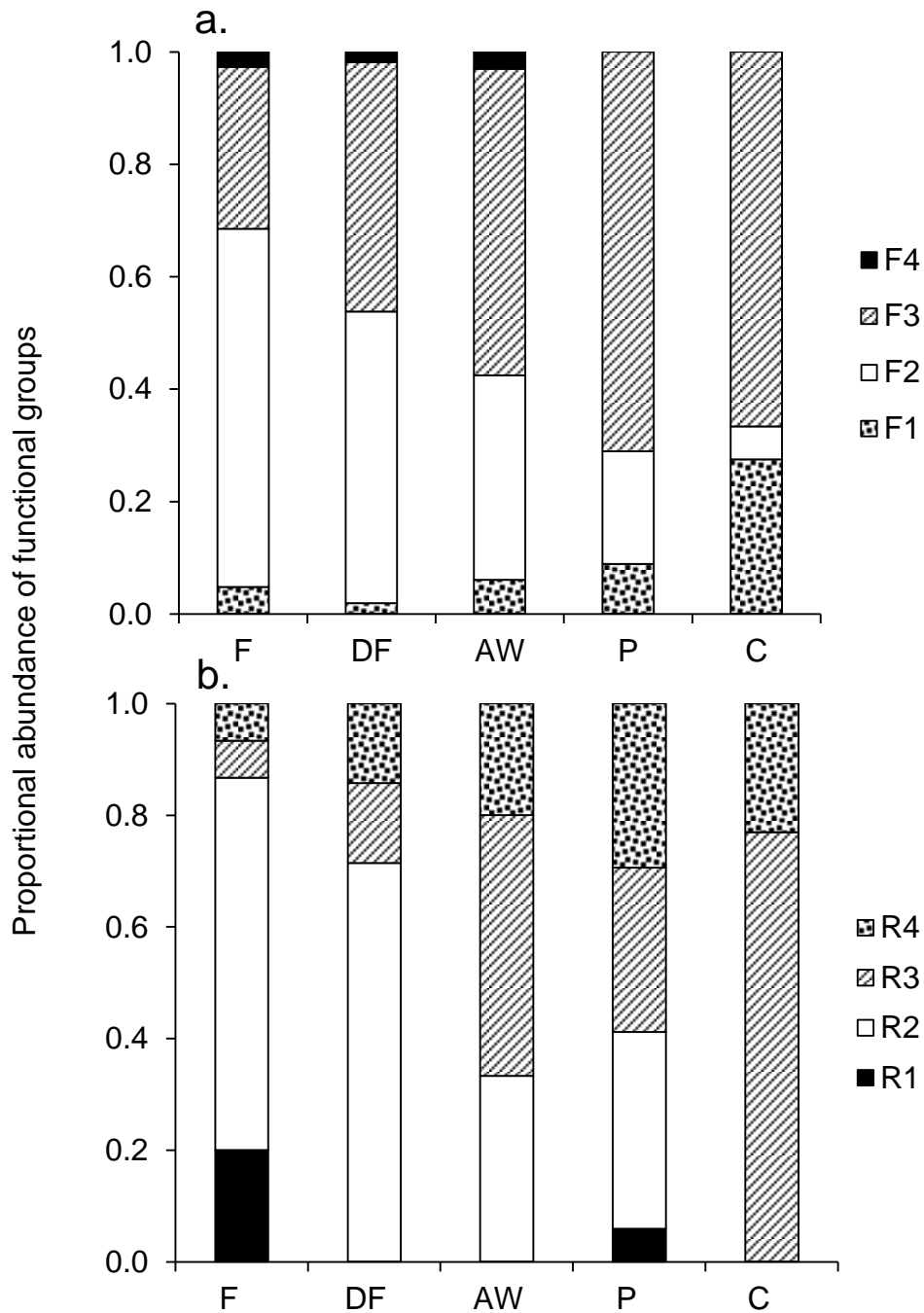


Figure 3. Proportional abundance of functional groups for (a) frogs and (b) reptiles for each vegetation type (F = forest, DF = degraded forest, AW = acacia woodland, P = plantation, C = cultivation).

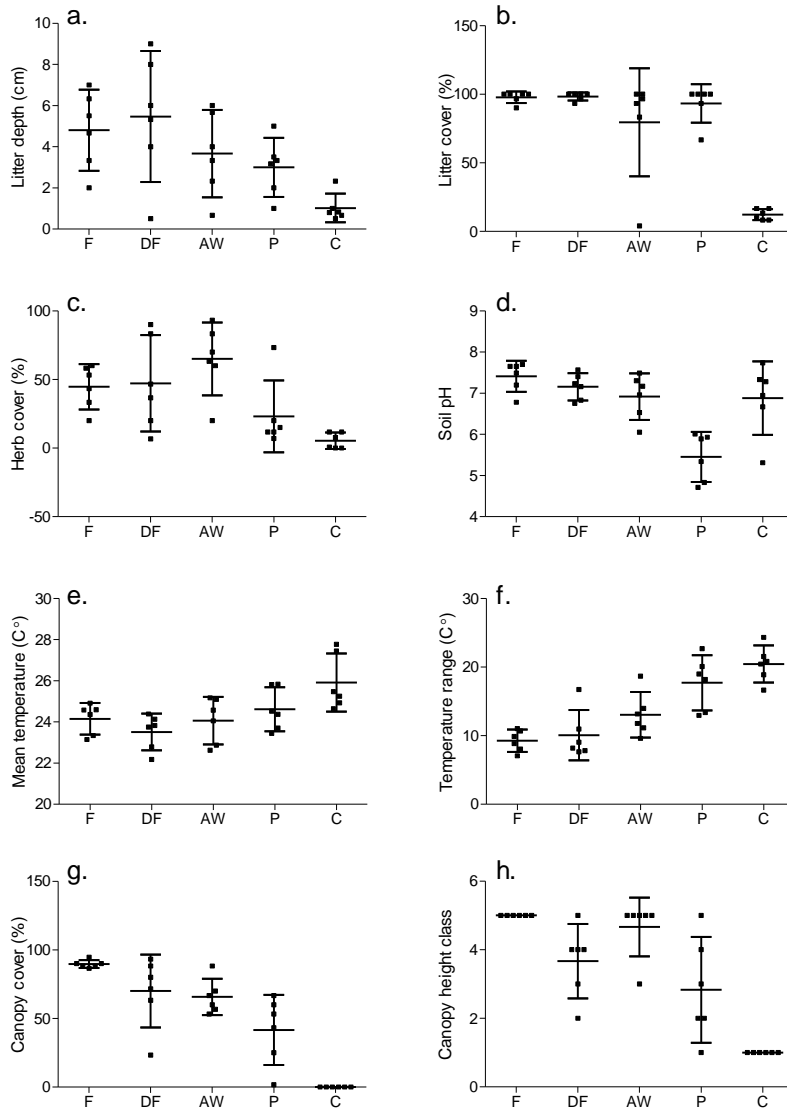


Figure 4. Environmental variables differed significantly among vegetation types (F = forest, DF = degraded forest, AW = acacia woodland, P = plantation, C = cultivation) for, (a) litter depth ($F_{4,25} = 4.69$, $p < 0.01$), (b) litter cover ($F_{4,25} = 24.70$, $p < 0.001$), (c) herb cover ($F_{4,25} = 6.02$, $p < 0.01$), (d) soil pH ($F_{4,25} = 11.08$, $p < 0.001$), (e) mean temperature ($F_{4,25} = 4.66$, $p < 0.01$), (f) temperature range ($F_{4,25} = 15.38$, $p < 0.001$), (g) canopy cover ($F_{4,25} = 25.29$, $p < 0.001$), and (h) canopy height (in classes: 1 = 0-2 m, 2 = >2-4 m, 3 = >4-6 m, 4 = >6-8 m, and 5 = >8 m) ($F_{4,25} = 19.83$, $p < 0.001$). We illustrate means and 95% CI.

Environmental predictors

Environmental variables differed significantly among vegetation types (Fig. 4). They were variably effective at predicting frog and reptile richness and abundance; proportion of deviance explained by the global model ranged from 0.06 for reptile richness to 0.67 for abundance of functional group F2 (Table S2). Generally, models performed better for frogs than reptiles and for functional group abundance than overall richness and abundance (Table S2, S3). The importance and effect of environmental variables differed among dependent variables (Table S3).

DISCUSSION

We assessed how a rich herpetofaunal community responded to a land-use gradient. One-quarter of the species we encountered are endemic or near-endemic to Maputaland, a third to southern Africa, and all but one to Africa (Branch, 1998; du Preez & Carruthers, 2009). Our study falls at the juncture of three global conservation concerns: tropical forest loss (Wright & Muller-Landau, 2006), pressure on coastal habitat (Arthurton *et al.*, 2006), and herpetofaunal extinction crises (Böhm *et al.*, 2013; Stuart *et al.*, 2008).

Richness, diversity, composition

Although forest harbored the highest number of species and individuals observed, richness did not monotonically decrease along the gradient. Richness was higher in forest, acacia woodland, and plantation and lower in degraded forest and cultivation. Diversity was generally highest in plantation and lowest in degraded forest and cultivation. Community composition differed between land uses that were natural (i.e. forest, degraded forest) and anthropogenic (plantation,

cultivation), while the acacia woodland community grouped with the former for reptiles and the latter for frogs.

Degraded forest hosted an impoverished version of the forest assemblage for both frogs and reptiles. This was unexpected based on studies of herpetofaunal response to selective logging, which may be analogous to the processes that degrade forests in our study area, e.g. physical disturbance by humans and livestock and effects from neighboring transformed land. A recent review found no evidence for loss of herpetofaunal richness in selectively logged areas (Gardner *et al.*, 2007a). However, in West African forests, Hillers *et al.* (2008) found that degradation, represented by structural measures, was associated with reduced richness and altered community composition of leaf-litter frogs, possibly via changes in microclimate. In our study, degraded forest had lower mean canopy cover and height but higher ranges of these and of herb cover and litter depth than did forest. Thus, altered microclimate may drive the low abundance, richness, and diversity observed.

Acacia woodland, as a seral stage of forest succession (Grainger & van Aarde, 2012; van Aarde *et al.*, 1996), is expected to support lower richness than old-growth forest (Wassenaar *et al.*, 2005). Our results are similar to other studies' (Gardner *et al.*, 2007a; Hilje & Mitchell Aide, 2012; Wanger *et al.*, 2010) that report lower richness in new-growth but a substantial representation of old-growth species. However, that community structure in acacia woodland was similar to that of forest for reptiles but not for frogs hints at barriers to frog recolonization of new-growth forest.

Plantations of exotic trees hosted structurally distinct frog and reptile communities compared to forest but a high richness and diversity, in agreement with other studies (Gardner *et al.*, 2007a; Vonesh, 2001). Plantation communities likely combine species typical of forest with

species characteristic of open habitats and are not necessarily biodiversity deserts (see Armstrong *et al.*, 1998). Nonetheless, some studies have found plantations to be depauperate in amphibians (e.g. Kudavidanage *et al.*, 2011). Inland from our study area, Russell and Downs (2012) found few frog species in large-scale eucalyptus plantations. The plantations in our study were small-scale with vegetated understories and small, coppiced trees. Thus, the effects of plantation variables, e.g. size, age, and management, require further study.

Consistent with other studies (e.g. Russell & Downs, 2012), sugar cane cultivation had few species, few individuals, and low diversity. However, cultivation harbored species absent or rare in other vegetation types, e.g. *Psammophis brevirostris*, but they were wide-ranging, open habitat species (Branch, 1998; du Preez & Carruthers, 2009).

Functional groups

A trait- rather than species-based approach is expected to better quantify and predict the effects of disturbance on communities and the consequences for ecosystem functionality (Mouillot *et al.*, 2013). Functional groups are known to be differentially susceptible to disturbance; e.g. small-bodied frogs and those that lay eggs in soil are thought to be more disturbance-sensitive than large-bodied frogs and those that lay eggs in water (Suazo-Ortuno *et al.*, 2008). In our study, fossorial/ground-dependent frogs (F2) and reptiles (R3) decreased along the gradient in abundance and proportional abundance. Vegetation-dwelling frogs (F4) were not found in plantation or cultivation. These groups appear to be particularly challenged in human-modified habitats, likely because of changes in soil and vegetation properties, a hypothesis supported by the results of modeling functional group abundance on environmental variables.

The number of functional groups per vegetation type declined along the gradient from all eight recorded in forest to just five in cultivation, in line with the suggestion that functional

diversity declines monotonically along a disturbance gradient (Mouillot *et al.*, 2013). Few studies have investigated functional aspects of herpetofaunal response to land-use change (Gardner *et al.*, 2007a). Pineda *et al.* (2005) found reduced frog guild richness in coffee plantations compared to forest. Our results agree with, and extend to plantations and cultivation, the observation that frog functional diversity is lower in degraded forest than in primary forest (Ernst, Linsenmair & Rodel, 2006). Loss of functional groups implies increased overlap among species' trait profiles and, thus, functional homogenization (Braisner & Lockwood, 2011), and has consequences for ecosystem function (e.g. O'Connor & Crowe, 2005; Tilman *et al.*, 2001).

Environmental predictors

Environmental variables were good predictors of abundance of frog functional groups, probably because functional groups combine species that are similarly dependent on particular resources and conditions. F1, F2, and F3 all showed a significant negative relationship with herb cover and mean temperature, while soil pH and litter cover had positive effects. Abundance of F4 was positively related to litter depth, which conceivably reflects dependence of vegetation-dwelling frogs on increased canopy cover or vegetation density rather than litter depth per se (canopy cover was correlated with litter depth). The relationship between frog abundance and environmental variables suggests that frogs respond to the vegetation-type gradient due to changes in microhabitat conditions. Land uses resulting in soil acidification, reduced litter cover, or increased herb cover or mean temperature appear to be generally negative for frogs (Suazo-Ortuno *et al.*, 2008; Wyman, 1988).

Environmental variables were generally poor predictors of reptile functional group abundance, perhaps due to un-modeled factors or a lesser dependence on specific microhabitat conditions. Compared to reptiles, frogs and their eggs have more stringent moisture and

temperature requirements and are sensitive to solar radiation (Gibbons *et al.*, 2000; Suazo-Ortuno *et al.*, 2008). Furthermore, reptiles often move greater lifetime distances than do frogs (Gibbons *et al.*, 2000), so their occurrence may more often reflect mere transience.

Constraints and future research

Sampling efficacy is species- and habitat-dependent, and we experienced low capture success, a common challenge in herpetofaunal studies and in the tropics; these issues necessitate caution when interpreting results (Gardner *et al.*, 2007a; Ribeiro-Júnior *et al.*, 2008). We used a combination of methods emphasizing passive sampling to reduce observer bias while maintaining standardized effort across vegetation types. Still, our samples do not represent the complete community due to true rarity and furtive habits of many species. For example, predominantly arboreal species would likely have been under-sampled compared to ground-active species, potentially biasing richness estimates. Additional trapping arrays were not feasible due to cost (~32 person-hours per array), seasonal effects (e.g. Gardner *et al.*, 2007b), and impracticality of increasing the study area (coastal forest gives way to grassland and savanna inland); however, the percentage of species observed to estimated richness was comparable to other studies (e.g. Bell & Donnelly, 2006; Gardner *et al.*, 2007c; Suazo-Ortuno *et al.*, 2008). Clearly, failure to detect a species does not imply absence, nor does presence imply persistence (Gardner *et al.*, 2007a). The standardized nature of our sampling methods enables future work to build on this database by increasing the coverage extent and investigating other vegetation types and seasons.

Future research on species-specific responses to land-use change would be useful because species respond idiosyncratically (Gardner *et al.*, 2007a). Our functional group approach goes

some way towards assessing differential responses of components of the community. However, broadly defined functional groups overestimate redundancy (Cadotte *et al.*, 2011). Thus, loss of functional groups across the gradient likely underestimated true functional diversity loss (Petchey & Gaston, 2002). Further, the consequences of functional diversity loss warrant investigation.

Conservation implications

Two species in our study are of explicit conservation concern (*Afrixalus spinifrons* and *Hemisus guttatus* (IUCN, 2012)), and Botts *et al.* (2013) demonstrated that habitat specialist frogs in the region have undergone range contractions over the past century, likely due to habitat loss. Therefore, small-range, endemic species are of concern even if not formally threatened. Most reptile species in our study have not been evaluated (IUCN, 2012).

Our results highlight the sensitivity of fossorial/ground-dependent herpetofauna to forest transformation. Unfortunately, this group includes many small-range species, e.g. *Leptopelis natalensis* and *Acontias plumbeus*. Thus, although they are difficult to study (Maritz & Alexander, 2008), fossorial species warrant monitoring, especially because they are poorly known (Böhm *et al.*, 2013). Vegetation-dwelling frogs should also be monitored.

Maintaining old-growth forest is important for conserving herpetofauna. However, other vegetation types did support occurrence of some species, which should be considered in land-use planning, especially given the conservation challenges imposed by the linear nature of the coastal forest system (Olivier *et al.*, 2013; van Aarde *et al.*, 2013). Degraded forest harbored particularly low richness and diversity, so degradation must be prevented, a concern even within protected areas because many allow access to local people for wood collection and grazing or lack management altogether (Kyle, 2004). Restoration projects that generate acacia woodland could

provide habitat and increase connectivity of forest fragments. Plantations may hold some value for connecting not only forest fragments, but perhaps also savanna and grassland fragments due to their diverse combination of forest and open-habitat species including species of conservation concern, e.g. *Hemisus guttatus*. However, caution is required in extrapolating our results from small- to large-scale plantations, and hydrological impacts may negatively offset conservation value (Armstrong *et al.*, 1998). Finally, sugar cane cultivation was of little value for forest associated herpetofauna.

ACKNOWLEDGEMENTS

M.J.T. was supported by an NSF Graduate Research Fellowship. Research grants to R.J.v.A. from Richards Bay Minerals, the South African Department of Trade & Industry, and the National Research Foundation covered fieldwork expenses. A. Armstrong, B. Branch, R. Guldemon, A. Harwood, T. Lee, J. Marais, L. Minter, P. Olivier, A. Prins, L. du Preez, L. Snyman, J. Tarrant, and G. Varrie provided technical support.

REFERENCES

- Anand, M.O., Krishnaswamy, J., Kumar, A. & Bali, A. (2010). Sustaining biodiversity conservation in human-modified landscapes in the Western Ghats: Remnant forests matter. *Biol. Conserv.*, **143**: 2363-2374.
- Anderson, M.J., *et al.* (2011). Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecol. Lett.*, **14**: 19-28.
- Armstrong, A.J. (2001). Conservation status of herpetofauna endemic to KwaZulu-Natal. *Afr. J. Herpetol.*, **50**: 79-96.

- Armstrong, A.J., *et al.* (1998). Plantation forestry in South Africa and its impact on biodiversity. *S. Afr. For. J.*, **182**: 59-65.
- Arthurton, R., *et al.* (2006). Coastal and Marine Environments. In *Africa Environment Outlook 2*: 155-195. Mohamed-Katerere, J. , Sabet, M. (Eds.). Malta: Progress Print.
- Beard, K., Vogt, K. & Kulmatiski, A. (2002). Top-down effects of a terrestrial frog on forest nutrient dynamics. *Oecologia*, **133**: 583-593.
- Bell, K.E. & Donnelly, M.A. (2006). Influence of forest fragmentation on community structure of frogs and lizards in northeastern Costa Rica. *Conserv. Biol.*, **20**: 1750-1760.
- Böhm, M., *et al.* (2013). The conservation status of the world's reptiles. *Biol. Conserv.*, **157**: 372-385.
- Botts, E., Erasmus, B. & Alexander, G. (2013). Small range size and narrow niche breadth predict range contractions in South African frogs. *Global Ecol. Biogeogr.*, **22**: 567-576.
- Braiser, B. & Lockwood, J. (2011). The relationship between functional and taxonomic homogenization. *Global Ecol. Biogeogr.*, **20**: 134-144.
- Branch, B. (1998). *Field Guide to Snakes and Other Reptiles of Southern Africa*. Cape Town: Struik Publishers.
- Cadotte, M., Carscadden, K. & Mirotnick, N. (2011). Beyond species: functional diversity and the maintenance of ecological processes and services. *J. Appl. Ecol.*, **48**: 1079-1087.
- Channing, A. (2001). *Amphibians of Central and Southern Africa*. Ithaca: Cornell University Press.
- Clarke, K.R. & Gorley, R.N. (2001). *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*. Plymouth, United Kingdom: Primer-E.

- Clarke, K.R. & Gorley, R.N. (2006). *Primer v6: User Manual/Tutorial*. Plymouth, United Kingdom: Primer-E.
- Colwell, R.K. (2009). EstimateS: Statistical Estimation of Species Richness and Shared species from Samples. In: *Version 8.2. User's Guide and Application.*). Storrs, Connecticut: University of Connecticut.
- Daily, G.C. (1999). Developing a scientific basis for managing Earth's life support systems. *Conserv. Ecol.*, **3**: Art. 14.
- Di Rienzo, J.A., *et al.* (2011). InfoStat.). Córdoba: Universidad Nacional de Córdoba.
- du Preez, L.H. & Carruthers, V. (2009). *A Complete Guide to Frogs of Southern Africa*. Cape Town: Struik Nature.
- Ernst, R., Linsenmair, K. & Rodel, M. (2006). Diversity erosion beyond the species level: dramatic loss of functional diversity after selective logging in two tropical amphibian communities. *Biol. Conserv.*, **133**: 143-155.
- Gardner, T., 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., Fitzherbert, E.B., Drewes, R.C., Howell, K.M. & Caro, T. (2007b). Spatial and temporal patterns of abundance and diversity of an East African leaf litter amphibian fauna. *Biotropica*, **39**: 105-113.
- Gardner, T.A., *et al.* (2007c). The value of primary, secondary, and plantation forests for a neotropical herpetofauna. *Conserv. Biol.*, **21**: 775-787.
- Gibbons, J., *et al.* (2000). The global decline of reptiles, deja vu amphibians. *BioScience*, **50**: 653-666.

- Gotelli, N.J. & Colwell, R.K. (2001). Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.*, **4**: 379-391.
- Grainger, M.J. & van Aarde, R.J. (2012). Is succession-based management of coastal dune forest restoration valid? *Ecol. Restor.*, **30**: 200-208.
- Grueber, C.E., Nakagawa, S., Laws, R.J. & Jamieson, I.G. (2011). Multimodel inference in ecology and evolution: challenges and solutions. *J. Evol. Biol.*, **24**: 699-711.
- Hilje, B. & Mitchell Aide, T. (2012). Recovery of amphibian species richness and composition in a chronosequence of secondary forests, northeastern Costa Rica. *Biol. Conserv.*, **146**: 170-176.
- Hillers, A., Veith, M. & Rodel, M. (2008). Effects of forest fragmentation and habitat degradation on West African leaf-litter frogs. *Conserv. Biol.*, **22**: 762-772.
- IUCN (2012). IUCN Red List of Threatened Species. Version 2012.2.). Gland, Switzerland: IUCN.
- Kanowski, J.J., Reis, T.M., Catterall, C.P. & Piper, S.D. (2006). Factors affecting the use of reforested sites by reptiles in cleared rainforest landscapes in tropical and subtropical Australia. *Restor. Ecol.*, **14**: 67-76.
- Kindt, R. & Coe, R. (2005). *Tree Diversity Analysis: A manual and Software for Common Statistical Methods for Ecological and Biodiversity Studies*. Nairobi: World Agroforestry Centre.
- Kudavidanage, E., Wanger, T., de Alwis, C., Sanjeewa, S. & Kotagama, S. (2011). Amphibian and butterfly diversity across a tropical land-use gradient in Sri Lanka; implications for conservation decision making. *Anim. Conserv.*, **15**: 253-265.

- Küper, W., *et al.* (2004). Africa's hotspots of biodiversity redefined. *Ann. Mo. Bot. Gard.*, **91**: 525-535.
- Kyle, R. (2004). Resource Use in the Indigenous Forests of Maputaland. In *Indigenous Forests and Woodlands in South Africa*: 713-736. Lawes, M., *et al.* (Eds.). Scottsville, South Africa: University of KwaZulu-Natal Press.
- Maritz, B. & Alexander, G.J. (2008). Breaking ground: quantitative fossorial herpetofaunal ecology in South Africa. *Afr. J. Herpetol.*, **58**: 1-14.
- Measey, G.J. (Ed.) (2011) *Ensuring a Future for South Africa's Frogs: A Strategy for Conservation Research*, Pretoria, South African National Biodiversity Institute.
- Minter, L.R. (2003). Two new cryptic species of breviceps (Anura: Microhylidae) from Southern Africa. *Afr. J. Herpetol.*, **52**: 9-21.
- Mouillot, D., Graham, N.A.J., Villéger, S., Mason, N.W.H. & Bellwood, D.R. (2013). A functional approach reveals community responses to disturbances. *Trends Ecol. Evol.*, **28**: 167-177.
- O'Connor, N. & Crowe, T. (2005). Biodiversity loss and ecosystem functioning: distinguishing between number and identity of species. *Ecology*, **86**: 1783-1796.
- O'Connor, T.G. & Kuyler, P. (2009). Impact of land use on the biodiversity integrity of the moist sub-biome of the grassland biome, South Africa. *J. Environ. Manage.*, **90**: 384-395.
- Olivier, P., van Aarde, R. & Lombard, A. (2013). The use of habitat suitability models and species-area relationships to predict extinction debts in coastal forests, South Africa. *Divers. Distrib.*, **19**: 1353-1365.
- Perera, S.J., Ratnayake-Perera, D. & Proches, S. (2011). Vertebrate distributions indicate a greater Maputaland-Pondoland-Albany region of endemism. *S. Afr. J. Sci.*, **107**: 52-66.

- Petchey, O.L. & Gaston, K.J. (2002). Extinction and the loss of functional diversity. *Proceedings of the Royal Society B: Biological Sciences*, **269**: 1721-1727.
- Pineda, E., Moreno, C., Escobar, F. & Halfpeter, G. (2005). Frog, bat, and dung beetle diversity in the cloud forest and coffee agroecosystems of Veracruz, Mexico. *Conserv. Biol.*, **19**: 400-410.
- Pla, L., Casanoves, F. & Di Rienzo, J. (2012). *Quantifying Functional Biodiversity*. Dordrecht: Springer.
- Ribeiro-Júnior, M.A., Gardner, T.A. & Ávila-Pires, T.C.S. (2008). Evaluating the effectiveness of herpetofaunal sampling techniques across a gradient of habitat change in a tropical forest landscape. *J. Herpetol.*, **42**: 733-749.
- Russell, C. & Downs, C.T. (2012). Effect of land use on anuran species composition in north-eastern KwaZulu-Natal, South Africa. *Appl. Geogr.*, **35**: 247-256.
- Smart, S., *et al.* (2006). Biotic homogenization and changes in species diversity across human-modified ecosystems. *Proceedings of the Royal Society B: Biological Sciences*, **273**: 2659-2665.
- Sodhi, N.S., *et al.* (2010). Conserving Southeast Asian forest biodiversity in human-modified landscapes. *Biol. Conserv.*, **143**: 2375-2384.
- Stuart, S., *et al.* (Eds.) (2008) *Threatened Amphibians of the World*, Barcelona, Lynx Edicions.
- Suazo-Ortuno, I., Alvarado-Diaz, J. & Martinez-Ramos, M. (2008). Effects of conversion of dry tropical forest to agricultural mosaic on herpetofaunal assemblages. *Conserv. Biol.*, **22**: 362-374.
- Sutherland, W. (2004). The need for evidence-based conservation. *Trends Ecol. Evol.*, **19**: 305-308.

- Tilman, D., *et al.* (2001). Diversity and productivity in a long-term grassland experiment. *Science*, **294**: 843-845.
- Trimble, M.J. & van Aarde, R.J. (2010). Species inequality in scientific study. *Conserv. Biol.*, **24**: 886-890.
- Trimble, M.J. & van Aarde, R.J. (2011). Decline of birds in a human modified coastal dune forest landscape in South Africa. *PLoS ONE*, **6**: e16176.
- Trimble, M.J. & van Aarde, R.J. (2012). Geographical and taxonomic biases in research on biodiversity in human-modified landscapes. *Ecosphere*, **3**: Article 119.
- Trimble, M.J. & van Aarde, R.J. (2013). A note on polyvinyl chloride (PVC) pipe traps for sampling vegetation-dwelling frogs in South Africa. *Afr. J. Ecol.*: Early view.
- van Aarde, R.J., *et al.* (1996). An evaluation of habitat rehabilitation on coastal dune forests in northern KwaZulu-Natal South Africa. *Restor. Ecol.*, **4**: 334-345.
- van Aarde, R.J., Guldemon, R. & Olivier, P. (2013). Biodiversity Status of Dune Forests in South Africa. In *Coastal Conservation*. Lockwood, J. L., Virzi, T. , Maslo, B. (Eds.). Cambridge: Cambridge University Press.
- van Wyk, A. (1996). Biodiversity of the Maputaland Centre. In *The Biodiversity in African Savannas*: 198-207. Van Der Maesen, L., Van Der Burgt, X. , Van Medenbach De Rooy, J. (Eds.). Dordrecht: Kluwer Academic Publishers.
- Vonesh, J.R. (2001). Patterns of richness and abundance in a tropical African leaf-litter herpetofauna. *Biotropica*, **33**: 502-510.
- Wanger, T.C., *et al.* (2010). Effects of land-use change on community composition of tropical amphibians and reptiles in Sulawesi, Indonesia. *Conserv. Biol.*, **24**: 795-802.

- Wassenaar, T., van Aarde, R., Pimm, S. & Ferreira, S. (2005). Community convergence in disturbed subtropical dune forests. *Ecology*, **86**: 655-666.
- Whiles, M.R., *et al.* (2006). The effects of amphibian population declines on the structure and function of neotropical stream ecosystems. *Front. Ecol. Environ.*, **4**: 27-34.
- Wright, S.J. & Muller-Landau, H.C. (2006). The future of tropical forest species. *Biotropica*, **38**: 287-301.
- Wyman, R. (1988). Soil acidity and moisture and the distribution of amphibians in five forests of southcentral New York. *Copeia*, **1988**: 394-399.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. (2009). *Mixed effects models and extensions in ecology with R*. New York: Springer.