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

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Abstract

Information on the response of herpetofauna to different land uses is limited although important for land-use planning to support conservation in human-modified landscapes. Although 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 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 amphibians 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 amphibians and the former for reptiles. Functional group richness eroded along the gradient, a pattern driven by the sensitivity of fossorial/ground-dependent amphibians (A2) and reptiles (R2) and vegetation-dwelling amphibians (A4) to habitat change. Variables describing temperature, cover and soil were good predictors of amphibian 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 amphibians and reptiles, and vegetation-dwelling amphibians should be closely monitored.

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 (Trimble & van Aarde, 2011; Olivier, van Aarde & Lombard, 2013). 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 Sutherland, 2004; O'Connor & Kuyler, 2009).

Herpetofauna are specialized in habitat requirements (Kanowski *et al*., 2006; Botts, Erasmus & Alexander, 2013), are sensitive to habitat modification and face global extinction crises (Gibbons *et al*., 2000; Stuart *et al*., 2008; Böhm *et al*., 2013). 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, 2007*a*). 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 (Smart *et al*., 2006; Cadotte, Carscadden & Mirotchnick, 2011; Mouillot *et al*., 2013). However, function-related responses to habitat change are poorly understood for herpetofauna (Gardner *et al*., 2007*a*).

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 (Branch, 1998; Armstrong, 2001; Stuart *et al*., 2008; du Preez & Carruthers, 2009; Measey, 2011; Perera *et al*., 2011; IUCN, 2012). 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: (a) to test how abundance, richness, diversity, and composition of amphibian and reptile communities change along the gradient; (b) 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 (c) to quantify potential ecological drivers of community change by relating environmental variables to overall richness and abundance of amphibians and reptiles and to abundance of functional groups.

Methods

Study area

We sampled terrestrial herpetofauna along 25 km of coastline across a land-use gradient southwest of Richards Bay, KwaZulu-Natal, South Africa, from 4 km north of the Umlalazi River mouth to just south of the Richards Bay harbor, up to 2.3 km inland (Fig. 1). The region falls within the southern end of the East African Tropical Coastal Forest (see van Aarde, Guldemond & Olivier, 2014).

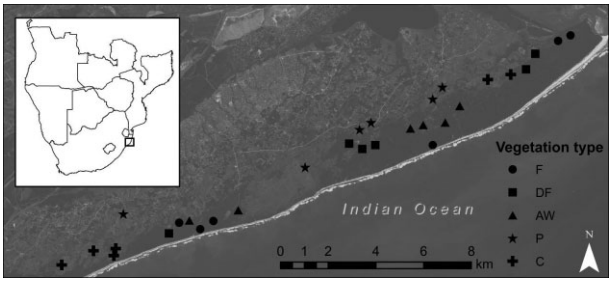

Figure 1 Study area map indicating location of trapping arrays in five vegetation types (F, forest; DF, degraded forest; AW, acacia woodland; P, plantation; C, cultivation); inset shows study area location in southern Africa.

Sampling methods

We used a stratified random sample design of 30 trap arrays divided evenly among five 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 5 days, identified species captured and released them ≥ 50 m away (to minimize recapture). Each array was operational for 120 ± 1 h. Arrays were separated from each other by ≥ 500 m and from known water bodies by ≥ 300 m (Fig. 1).

Each array employed seven complementary sampling techniques, detailed in Supporting Information Appendix S1, to represent as many species as possible while maintaining a standardized effort (Ribeiro-Júnior, Gardner & Ávila-Pires, 2008). Arrays consisted of three 15-m arms of 0.5-m tall black plastic drift fence, dug 0.1 m into the ground, spaced at 120°, and connected at a central pitfall bucket. Arms featured pitfall buckets at 7.5 and 15 m from the center bucket, and a funnel trap on either side between the outer two pitfalls. The fence guided amphibians and reptiles into pitfalls and funnel traps. Four polyvinyl chloride pipe traps (see Trimble & van Aarde, 2013) and four wooden cover boards were installed 10 m beyond the northern-pointing fence arm and checked on days 2, 4 and 5. 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 Supporting Information 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 (Gotelli & Colwell, 2001; Colwell, 2009). 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 χ^2 distribution (or quasi-Poisson GLM and *F*-tests to account for overdispersion; Zuur *et al*., 2009).

We estimated the richness of amphibians and reptiles per vegetation type with non-parametric richness estimators calculated in EstimateS: four abundance-based [Chao1, abundance-based coverage estimator (ACE), Jack1, and Jack2] and two incidence-based that included amphibian species identified from audio recordings [Chao2 and incidence-based coverage estimator (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% confidence interval (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 amphibians 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 amphibian and reptile abundance, square–root-transformed abundance (to decrease the influence of abundant species), and amphibian incidence data including species identified in audio recordings (here, Bray–Curtis simplified to Sorenson similarity; Clarke & Gorley, 2006; Anderson *et al*., 2011). 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). Amphibian 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). Reptile 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 ≥ 85% of variation, then used Euclidian distances and the Ward linkage algorithm to create dendrograms for amphibians and reptiles separately. We retained four functional groups each for amphibians and reptiles, and used multivariate analysis of variance 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 with the null model with analysis of deviance based on the χ^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 analysis of variance. 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, amphibian 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 Akaike's corrected information criterion (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 amphibian and 20 reptile species (Table 1). Nine amphibian species were recorded with audio recorders (three that were not captured in arrays), bringing the total number of species recorded to 40. Many calls carried further than the 50 m estimated by Hilje & 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 herptofaunal 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 amphibians or reptiles overall or any vegetation type, and 95% CI for amphibian and reptile abundances overlapped among vegetation types (Supporting Information Fig. S1). The proportion of expected species that we observed was 71–93% for amphibians 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 amphibians because they included auditory records (Table 2).

While species and individuals recorded per array did not differ significantly between vegetation types (Fig. 2), 95% CI

Table 1 Abundance of amphibian and reptile species captured in trapping arrays (where *indicates confirmation of amphibian species by audio recording[a]) across vegetation types, 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
Amphibian							
Amietophrynus gutturalis, guttural toad	41	44	16	27	33	161	A3
Arthroleptis wahlbergi, bush squeaker	89	51	10	5	0	155	A2
Phrynobatrachus natalensis, snoring puddle frog	0	0*	0*	0	10	10*	A1
Breviceps sopranus, whistling rain frog[c]	3	2	2	0	2	9	A2
Phrynobatrachus mababiensis, dwarf puddle frog	6	0	0	2	0	8	A1
Afrixalus spinifrons (spinifrons), Natal leaf-folding frog	2	2	0	0	0	4	A4
Amietophrynus rangeri, raucous toad	1	2	0	1	0	4	A3
Breviceps mossambicus, Mozambique rain frog[c]	0	0	0	3	0	3	A2
Phrynobatrachus acridoides, East African puddle frog	0	0	0	0	3	3	A1
Afrixalus fornasinii, greater leaf-folding frog	2	0	0	0	0	2	A4
Hyperolius pusillus, water lily frog	0	0	1	0	1	2	A1
Kassina senegalensis, bubbling kassina	1*	0	0	1*	0	2*	A1
Leptopelis natalensis, Natal tree frog	1	1*	0	0	0*	2*	A2
Amietophrynus garmani, eastern olive toad	0	0	1	0	0	1	A3
Hemisus guttatus, spotted shovel-nosed frog	0	0	0	1	0	1	A2
Hyperolius tuberilinguis, tinker reed frog	0	0	1	0	0	1	A4
Strongylopus fasciatus, striped stream frog	0	0	0	1	0	1	A2
Ptychadena oxyrhynchus, sharp-nosed grass frog	0	0*	0*	0*	0*	0*	A3
Reptiles							
Scelotes mossambicus, Mozambique dwarf burrowing skink	6	5	2	0	0	13	R2
Panaspis wahlbergii, Wahlberg's snake-eyed skink	0	0	1	3	3	7	R3
Mabuya varia, variable skink	0	1	6	0	0	7	R3
Lygodactylus capensis (capensis), Cape dwarf gecko	0	0	0	1	3	4	R3
Zygaspis vandami (arenicola), Van Dam's round-headed worm lizard	1	0	3	0	0	4	R2
Mabuya striata (striata), striped skink	0	0	0	0	3	3	R3
Hemidactylus mabouia, Moreau's tropical house gecko	1	0	0	1	0	2	R3
Acontias plumbeus, giant legless skink	2	0	0	0	0	2	R2
Gerrhosaurus flavigularis, yellow-throated plated lizard	0	0	0	0	1	1	R3
Psammophis brevirostris (brevirostris), short-snouted grass snake	0	0	0	1	3	4	R4
Leptotyphlops sp., thread snakes[d]	0	0	0	4	0	4	R2
Crotaphopeltis hotamboeia, herald snake	0	1	0	2	0	3	R4
Psammophis mossambicus, olive grass snake	0	0	1	2	0	3	R4
Aparallactus capensis, Cape centipede eater	1	0	0	2	0	3	R2
Causus rhombeatus, rhombic night adder	1	0	1	0	0	2	R4
Lamprophis fuliginosus, brown house snake	0	0	0	1	0	1	R1
Philothamnus natalensis (natalensis), eastern green snake	1	0	0	0	0	1	R1
Mehelya nyassae, black file snake	1	0	0	0	0	1	R1
Thelotornis capensis (capensis), vine snake	0	0	1	0	0	1	R4
Philothamnus hoplogaster, 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*, tinker 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 & 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).
AW, acacia woodland; C, cultivation; DF, degraded forest; F, forest; P, plantation.

indicated Chao1 for amphibians was significantly higher in forest, acacia woodland and plantation than in degraded forest or cultivation. Chao2 for amphibians 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

Table 2 Observed species richness (Species obs., where numbers in parentheses include auditory records) and abundance (Ind. obs.), abundance- and incidence-based richness estimators, percentage of predicted richness actually observed, and Shannon diversity of amphibians and reptiles across five vegetation types

			Abundance-based estimators				Incidence-based estimators		Percentage observed	Shannon
	Species obs.	Ind. obs.	Chao 1 (95% CI)	ACE	Jack1	Jack 2	Chao 2 (95% CI)	ICE	(range)	diversity
Amphibian										
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

ACE, abundance-based coverage estimator; AW, acacia woodland; C, cultivation; CI, confidence interval; DF, degraded forest; F, forest; ICE, incidence-based coverage estimator; P, plantation.

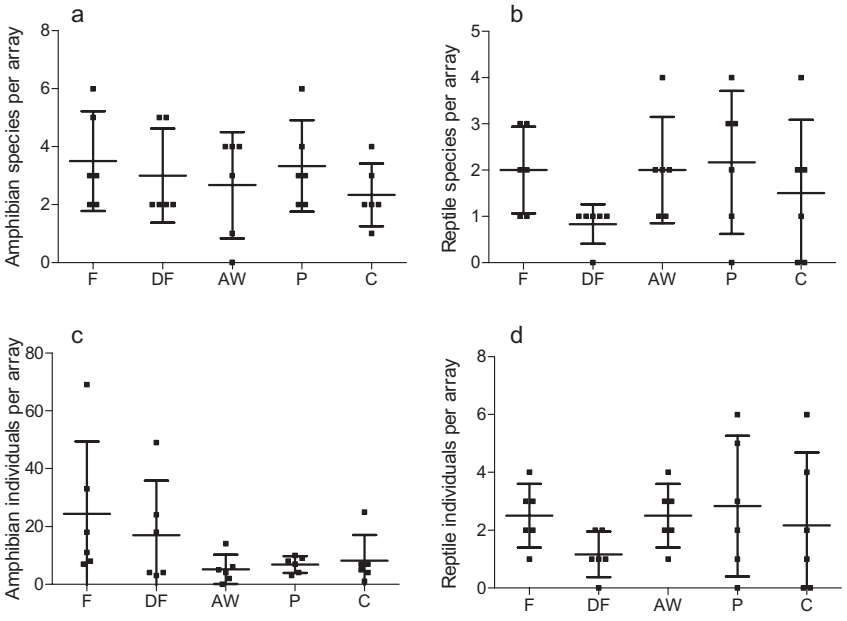

Figure 2 Vegetation type (F, forest; DF, degraded forest; AW, acacia woodland; P, plantation; C, cultivation) was not a significant predictor in Poisson or quasi-Poisson generalized linear modeling for species observed per array for (a) amphibians [$\chi^2 = 1.87$, degrees of freedom (d.f.) = 4, $P = 0.76$] and (b) reptiles ($\chi^2 = 4.73$, d.f. = 4, $P = 0.32$) or individuals recorded per array for (c) amphibians ($\Phi = 11.40$, $F_{4,25} = 2.70$, $P = 0.05$) and (d) reptiles ($\Phi = 1.18$, $F_{4,25} = 1.05$, $P = 0.40$). Graphs illustrate mean and 95% confidence interval.

and plantation than in cultivation, while Chao2 was significantly higher in forest than in 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 amphibians 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, that is, Rényi profiles intersected (Kindt & Coe, 2005; Supporting Information Fig. S2).

Composition

ANOSIM of square–root-transformed data indicated significant difference in composition among vegetation types (Table 3). Amphibian 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

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

	Amphibian (global $R = 0.174$, $P < 0.01$)		Reptiles (global $R = 0.194$, $P < 0.001$)	
Vegetation type comparison	R statistic[a]	P[b]	R statistic[a]	P[b]
Forest–degraded forest	–0.02	0.52	–0.05	1.00
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 $*P \leq 0.05$, $**P \leq 0.01$, $***P \leq 0.001$.

Table 4 Functional group descriptions (A*x* are amphibian groups, R*x* 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) generalized linear modeling, 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
A1	Small, ground-dwelling frogs (except water lily frog) that lay eggs in water	5	$\Phi = 2.05$, $F_{4,25} = 1.93$, $P = 0.14$	$\chi^2 = 27.05$, d.f. = 4, $P < 0.001$
A2	Fossorial or ground-dwelling species (except Natal tree frog) that lay eggs in the ground, that is, ground-dependent species. Tadpoles of three species develop in the ground	6	$\Phi = 7.32$, $F_{4,25} = 5.89$, $P < 0.01$	$\Phi = 1.62$, $F_{4,24} = 11.60$, $P < 0.001$
A3	Large, ground-dwelling frogs that lay eggs in water	4	$\Phi = 4.82$, $F_{4,25} = 0.79$, $P = 0.54$	$\Phi = 1.25$, $F_{4,24} = 7.93$, $P < 0.001$
A4	Small, vegetation-dwelling frogs that lay eggs in vegetation	3	$\chi^2 = 9.15$, d.f. = 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	$\chi^2 = 8.38$, d.f. = 4, $P = 0.08$	$\chi^2 = 7.69$, d.f. = 4, $P = 0.10$
R2	Legless, burrowing species, tend toward small clutch size	5	$\chi^2 = 14.01$, d.f. = 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	$\Phi = 1.03$, $F_{4,25} = 1.07$, $P = 0.39$	$\Phi = 1.17$, $F_{4,21} = 0.68$, $P = 0.61$

d.f., degrees of freedom.

patterns (Supporting Information Fig. S3). Results based on raw abundance and amphibian incidence data were similar (Supporting Information Fig. S3, Supporting Information Table S1).

Functional groups

Group size was similar, and species groupings seemed ecologically relevant (Tables 1 and 4). Traits differed between functional groups for amphibians (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.

Vegetation type was a significant predictor of abundance for functional groups A2 and R2, and of proportional abundance for A1, A2, A3 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).

Environmental predictors

Environmental variables differed significantly among vegetation types (Fig. 4). They were variably effective at predicting amphibian 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 A2 (Supporting Information Table S2). Generally, models performed better for amphibians than for reptiles, and for functional group abundance than for overall richness and abundance (Supporting Information

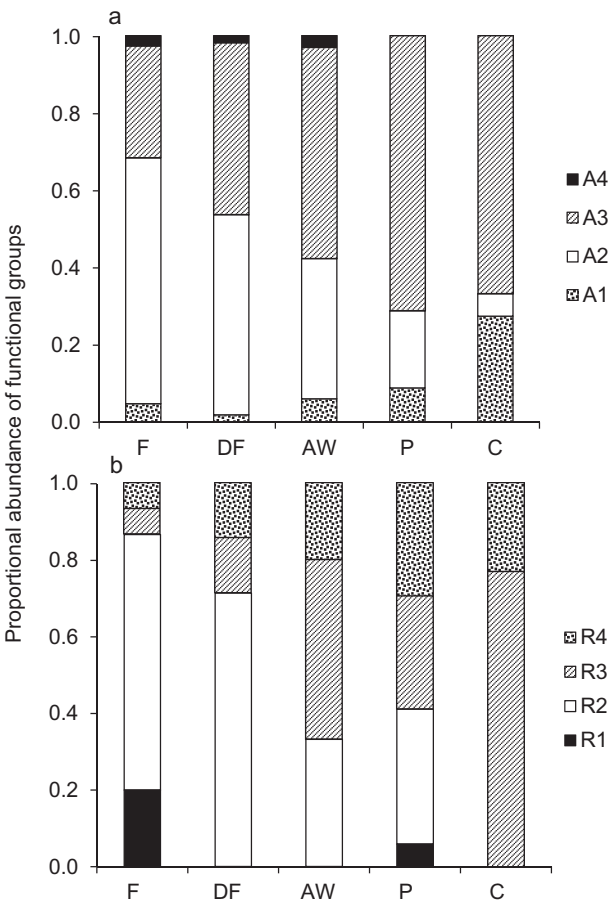

Figure 3 Proportional abundance of functional groups for (a) amphibians and (b) reptiles for each vegetation type (F, forest; DF, degraded forest; AW, acacia woodland; P, plantation; C, cultivation).

Tables S2, S3). The importance and effect of environmental variables differed among dependent variables (Supporting Information 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 (Stuart *et al*., 2008; Böhm *et al*., 2013).

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 amphibians.

Degraded forest hosted an impoverished version of the forest assemblage for both amphibians 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, for example, 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*., 2007*a*). However, in West African forests, Hillers, Veith & Rodel (2008) found that degradation, represented by structural measures, was associated with reduced richness and altered community composition of leaf-litter amphibians, 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 (van Aarde *et al*., 1996; Grainger & van Aarde, 2012), is expected to support lower richness than old-growth forest (Wassenaar *et al*., 2005). Our results are similar to other studies' (Gardner *et al*., 2007*a*; Wanger *et al*., 2010; Hilje & Mitchell Aide, 2012), which 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 amphibians hints at barriers to amphibian recolonization of new-growth forest.

Plantations of exotic trees hosted structurally distinct amphibian and reptile communities compared with forest, but a high richness and diversity, in agreement with other studies (Vonesh, 2001; Gardner *et al*., 2007*a*). 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 & Downs (2012) found few amphibian 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, for example, 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, for example *Psammophis brevirostris*, but they were

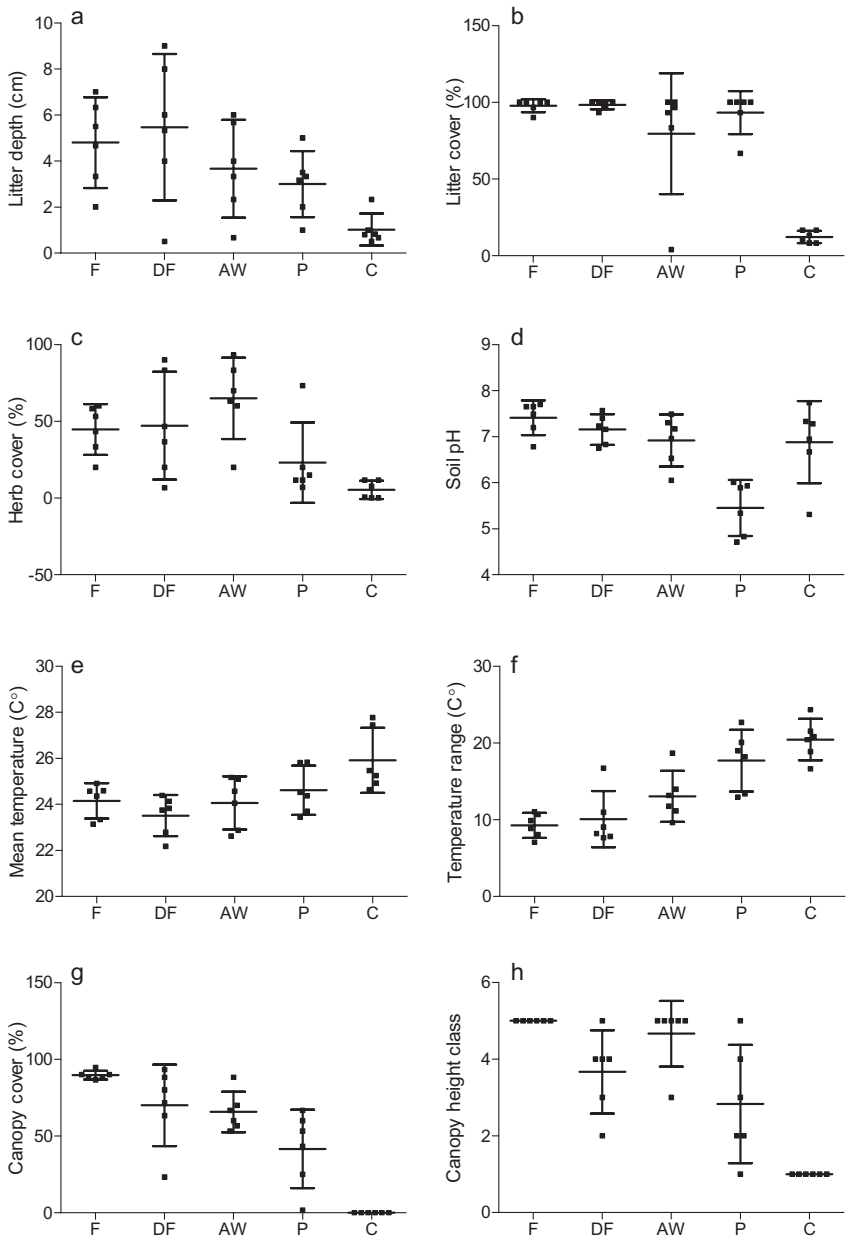

Figure 4 Environmental variables differed significantly among vegetation types (F, forest; DF, degraded forest; AW, acacia woodland; P, plantation; C, cultivation) for (a) litter depth ($F_{4,25}$ = 4.69, P < 0.01); (b) litter cover ($F_{4,25}$ = 24.70, P < 0.001); (c) herb cover ($F_{4,25}$ = 6.02, 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% confidence interval.

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; for example small-bodied amphibians and those that lay eggs in soil are thought to be more disturbance-sensitive than large-bodied amphibians and those that lay eggs in water (Suazo-Ortuno *et al.*, 2008). In our study, fossorial/ground-dependent amphibians (A2) and reptiles (R3) decreased along the gradient in abundance and proportional abundance. Vegetation-dwelling amphibians (A4) 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*., 2007*a*). Pineda *et al*. (2005) found reduced amphibian guild richness in coffee plantations compared with forest. Our results agree with, and extend to plantations and cultivation, the observation that amphibian 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 (Braiser & Lockwood, 2011), and has consequences for ecosystem function (e.g. Tilman *et al*., 2001; O'Connor & Crowe, 2005).

Environmental predictors

Environmental variables were good predictors of abundance of amphibian functional groups, probably because functional groups combine species that are similarly dependent on particular resources and conditions. A1, A2 and A3 all showed a significant negative relationship with herb cover and mean temperature, while soil pH and litter cover had positive effects. Abundance of A4 was positively related to litter depth, which conceivably reflects dependence of vegetation-dwelling amphibians on increased canopy cover or vegetation density rather than litter depth *per se* (canopy cover was correlated with litter depth). The relationship between amphibian abundance and environmental variables suggests that amphibians respond to the vegetation-type gradient because of 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 amphibians (Wyman, 1988; Suazo-Ortuno *et al*., 2008).

Environmental variables were generally poor predictors of reptile functional group abundance, perhaps because of un-modeled factors or a lesser dependence on specific microhabitat conditions. Compared with reptiles, amphibians 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 amphibians (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*., 2007*a*; 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 because of true rarity and furtive habits of many species. For example, predominantly arboreal species would likely have been under-sampled compared with ground-active species, potentially biasing richness estimates. Additional trapping arrays were not feasible because of cost (~32 person-hours per array), seasonal effects (e.g. Gardner *et al*., 2007*b*) and the 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 with other studies (e.g. Bell & Donnelly, 2006; Gardner *et al*., 2007*c*; Suazo-Ortuno *et al*., 2008). Clearly, failure to detect a species does not imply absence, nor does presence imply persistence (Gardner *et al*., 2007*a*). 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*., 2007*a*). Our functional group approach goes some way toward 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 amphibians in the region have undergone range contractions over the past century, likely because of 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, for example *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 amphibians should also be monitored.

Maintaining old-growth forest is important for conserving herpetofauna. However, other vegetation types did support the 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 (van Aarde *et al*., 2014; Olivier *et al*., 2013). Degraded forest harbored particularly low richness and diversity, so degradation must be prevented. Forest degradation is a concern even within protected areas, many of which 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 because of their diverse combination of forest and open-habitat species including species of

conservation concern, for example, *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.

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Methodological details of sampling.
Figure S1. Species accumulation curves for (a) the total frog dataset; (b) frog samples grouped by vegetation type; (c) the total reptile dataset; and (d) reptile samples grouped by vegetation type. Error bars represent 95% confidence intervals (CIs) and in (b) and (d) are shown only for forest.
Figure S2. Rényi diversity profiles for (a) frogs and (b) reptiles in different vegetation types [dark blue is forest (F); green is degraded forest (DF); black is acacia woodland (AW), light blue is plantation (P), red is cultivation (C)]. Rényi diversity profiles are calculated with the formula $H_a = \ln\left(\sum p_i^a\right)/(1-\alpha)$, where H_α is the diversity value; p_i values are the proportions of each species (which are taken to the exponent α and summed for all species recorded); and α is a parameter taken from 0 to infinity to generate the profile (Kindt & Coe, 2005). Values of H_α reflect species richness at $\alpha = 0$, are equivalent to the Shannon diversity index at $\alpha = 1$, and yield the logarithm of the reciprocal Simpson diversity index at $\alpha = 2$. Profiles indicate that frog diversity is lowest in cultivation, and reptile diversity is lowest in degraded forest and highest in plantation. The remaining vegetation types cannot be ranked definitively as their Rényi diversity profiles overlap.
Figure S3. Non-metric multidimensional scaling ordination of Bray–Curtis similarities based on square–root-transformed (a) frog and (b) reptile abundance data, and (c) raw frog abundance, (d) frog incidence, and (e) raw reptile abundance data. Symbols represent samples taken at 30 trapping array sites across five vegetation types (F, forest; DF, degraded forest; AW, acacia woodland; P, plantation; C, cultivation), and clustering indicates similar community composition among sites. One array site for frogs and four array sites for reptiles were not plotted because they were outliers with zero captures.
Table S1. Analysis of similarity (ANOSIM) results comparing amphibian and reptile community composition among vegetation types based on Bray–Curtis similarity of raw abundance data for frogs and reptiles and incidence data for frogs including species identified from audio recordings.
Table S2. Top selected models ($\Delta_i < 4$) relating environmental variables to (a) frog species richness; (b) frog abundance; (c) reptile species richness; (d) reptile abundance; and to abundance of functional groups (e) A1; (f) A2; (g) A3; (h) A4; (i) R1; (j) R2; (k) R3; and (l) R4 (D^2, deviance explained by global models; VIF, variance inflation factor of global model; Par., number of parameters in the model; LL, log–likelihood; AICc, Akaike's corrected information criterion; QAICc, Quasi-AICc; Δi, AICc or QAICc difference from best model; wi, Akaike weights – the normalized relative likelihood of the model given the data; see Tables 1 and 4 for functional group composition and descriptions).
Table S3. Multi-model averages (see Supporting Information Table S2 for list of generalized linear models with $\Delta_i < 4$ contributing to each average model) relating environmental variables to frog species richness, frog abundance, reptile species richness, reptile abundance, and to abundance of functional groups A1, A2, A3, A4, R1, R2, R3 and R4 (see Tables 1 and 4 for functional group composition and descriptions).