

Spatial congruence between ecotones and range-restricted species: implications for conservation biogeography at the sub-continental scale

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ABSTRACT

Aim To examine whether at a sub-continental scale range-limited species tend to occur close to areas of transition between vegetation boundaries more often than expected by chance.

Location South Africa and Lesotho.

Methods We examined the relationship between the distance of a grid square to ecological transition areas between vegetation types and both avian and frog range-limited species richness in the quadrat. We used quadrats at a spatial resolution of quarter degree ($15' \times 15' \approx 676 \text{ km}^2$). Spatial congruence between areas representing range-restricted species and those representing ecological transition zones was assessed using a random draw technique.

Results Species richness and range size rarity are generally negatively correlated with distance to transition areas between vegetation communities when analysed for the whole region for both groups. Although this relationship becomes weaker after controlling for environmental energy and topographical heterogeneity, the explanatory power of distance to transition areas remains significant, and compared to the different biomes examined, accounts for most of the variation in bird richness (20%), frog richness (18%), range-restricted bird species (17%) and range-restricted frog species (16%) in the savanna biome. The random draw technique indicated that areas representing range-restricted species were situated significantly closer in space to those areas representing transition areas between vegetation communities than expected by chance.

Main conclusions We find that at the sub-continental scale, when examined for South Africa, areas of transition between vegetation communities hold concentrations of range-limited species in both birds and frogs. We find that South African endemic/range-limited birds and frogs are located closer to ecological transition zones than endemics and non-endemics combined. This has important implications for ongoing conservation planning in a biogeographical context.

Keywords

Areas of transition, biome, birds, complementary, country scale, energy availability, frogs, range-limited species, topographical heterogeneity.

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INTRODUCTION

Studies, with a focus mainly on the local and continental scales, have shown that boundary regions between ecological communities, for terrestrial and marine systems, can be highly diverse. Such diversity can be found at both the within-species level (e.g. having unique alleles, peak genetic diversity (Barton, 2001;

Bowie *et al.*, 2004; Fjelds  *et al.*, 2007; Kark *et al.*, 2008) and high morphological divergence (Smith *et al.*, 1997)) as well as at the community level (e.g. due to edge or mass effects and unique ecotonal species; Shmida & Wilson, 1985; Spector, 2002).

Because ecotones, areas with relatively sharp environmental gradients (Risser, 1995), are often congruent in space with peripheral populations of species (see review by Kark & van Rensburg,

2006), biologist on the one hand have argued that such diversity can lead to high speciation rates in these areas (Mayr, 1970; Schneider *et al.*, 1999; Schilthuizen, 2000) and to these communities being more resistant to the effects of environmental changes (e.g. changes in climate and competing land uses; Parmesan, 2006). This is due to their historical genetic structure, occurrence of unique alleles and exposure to multiple selection pressures (e.g. Schilthuizen, 2000; Moritz, 2002). Such ecotone significance is evident especially in topographically well-structured parts of the world, and notably where abiotic factors, such as sea currents and wind systems, interact with topography and are coupled with low seasonality (see, e.g. Jetz *et al.*, 2004). Such environmental conditions often lead to high lineage persistence and thus high degrees of genetic divergence of local populations (i.e. speciation) (Jetz *et al.*, 2004; see also Fjelds  *et al.*, 2007).

On the other hand, other scientists have argued that peripheral populations, often found in areas of transition, are associated with the small-population and declining-species paradigms (Hedrick *et al.*, 1996; Vucetich & Waide, 2003; Brooks *et al.*, 2006, but see also Sagarin & Gaines, 2002; Samis & Eckert, 2007). Such populations show relatively small species ranges, which relate strongly with their probability of extinction (Lande, 1998). Furthermore, based on Southern African birds, Gaston *et al.* (2001) showed that minimum complementary sets of sites, often used as the starting point for regional conservation programs (Margules & Pressey, 2000), may be a questionable strategy because these sites tend to select peripheral populations, where abundances are expected to be lower compared to the core.

Clearly, despite the existence of several studies that have examined these issues at multiple spatial scales (Bestelmeyer & Wiens, 2001; Brooks *et al.*, 2001; Smith *et al.*, 2001; Moritz, 2002; Kark & van Rensburg, 2006), there is little consensus among conservation biologists on how best to embrace the challenges of a non-static temporal and spatial (e.g. landscape heterogeneity) environment when prioritizing conservation areas, especially when evaluating the conservation value of peripheral populations often found in ecotones (see review by Eckert *et al.*, 2008). Debate has been polarized around two recent papers. In the first, Smith *et al.* (2001) argues that in addition to the more conventional approach of ranking levels of species richness and rarity across ecological regions predefined for use as planning units in conservation prioritization processes (e.g. Myers *et al.*, 2000), conservation efforts should also focus on the ecotones associated with these units to retain as much of the ecological and evolutionary processes as possible.

In contrast, Brooks *et al.* (2001) argue that in order to have any chance in succeeding with a global conservation vision to include all of biodiversity at a global scale, conservation priority should be given to biodiversity hotspots as opposed to their associated transitional zones as the latter areas are mostly characterized by widespread species whose ranges simply meet at ecotones or by peripheral populations with low persistence. In this context, some authors have suggested that transitional areas may not be the most efficient areas in ensuring the maintenance of species in the long term (Brown *et al.*, 1995; Gaston *et al.*, 2001; but see also Ara jo & Williams, 2001).

Kark *et al.* (2007) found that, based on richness patterns for passeriform species mapped at a one-degree grid resolution, transitional environments across the New World hold concentrations of range-restricted species (i.e. species spanning small range sizes), in addition to high overall richness. As for previous studies asking similar questions (e.g. Orme *et al.*, 2005), the pattern reported for the New World birds is, however, associated with a large spatial extent (continental) and analysed at a coarse spatial resolution (one degree). While local and continental scale decisions are important, many conservation actions are more likely to be implemented at the national and regional scale (Mooers, 2007), which is also a representative scale for many ecological processes generating richness patterns (see, e.g. Lombard, 1995; Van Jaarsveld *et al.*, 1998). Moreover, the extent to which transitional areas may hold concentrations of species and rare species may change significantly at smaller spatial extents, thus providing different outcomes to those studies undertaken over larger areas, making the generalization of such patterns difficult. Similarly, should these patterns not be scale dependant, then such a novel answer in itself should further, for example, the Smith *et al.* (2001) versus Brooks *et al.* (2001) discussion about the importance of ecotones for conservation.

We are unaware of any empirical studies that have examined whether ecological transitional areas are areas with high richness and rarity at a sub-continental or country level scale examining an array of different environments, ecoregions and energy levels using (1) fine resolution data, and (2) data for more than one taxon.

South Africa spans from subtropical to Mediterranean and arid climate regions over several latitudinal belts, and is known for its high plant and animal diversity and high levels of endemism (Huntley, 1984; Cowling *et al.*, 1997; Harrison *et al.*, 1997). This enables us to compare the patterns for the whole region and also across different biomes to examine the generality of the regional patterns. South Africa also has an excellent history of high quality data collection for various taxa (e.g. birds – Harrison *et al.*, 1997 and frogs – Minter *et al.*, 2004). As such, it provides us with a unique opportunity to test, at the country scale, the relationship between species richness, species range size rarity, environmental energy and ecotones across the landscape using the data resolution employed for local conservation (i.e. at a quarter-degree resolution; Lombard, 1995; Anonymous, 1997).

Here, we examine the hypothesis, as suggested by Odum (1953, chapter 8) that areas of transition between vegetation communities hold concentrations of bird and frog species and range-limited species. We test this while taking into account the extent to which these relationships are being affected by environmental variables, specifically available environmental energy and topographical heterogeneity. It is well known that energy either has a primary role in generating spatial variation in species richness or is an important modulating factor (Currie, 1991; O'Brien, 1998; Morin, 2000). Also, topographical heterogeneity has often been identified as an important explanatory variable for speciation rates (Fjelds  *et al.*, 2007) and species richness patterns (Owen, 1990; Allan *et al.*, 1997; Patterson *et al.*, 1998; Rahbek & Graves, 2001), especially for the geographical location of centres of endemism (Jetz *et al.*, 2004). More specifically, we

ask whether these patterns differ among the major ecoregions (plant biomes) in South Africa and between the two taxa examined. Compared to frogs, birds are a more mobile group and therefore expected to be more likely to reject the hypothesis of showing high range-limited species richness values in ecotonal areas.

METHODS

Data

Data on South African bird ($n = 1858$ cells) and frog ($n = 1632$ cells) distributions were obtained at a quarter-degree grid cell resolution ($15' \times 15' \approx 676 \text{ km}^2$) from Harrison *et al.* (1997) and Minter *et al.* (2004) (see Appendix S1 in Supporting Information for more information on these data sets and on how undersampling was taken into account).

Southern Africa is characterized by a marked east–west (longitudinal) aridity gradient that is thought to have a significant effect on vegetation heterogeneity in South Africa (O'Brien, 1998). This gradient is responsible for considerable transitions in vegetation and climate that are well captured by Low & Rebelo's (1996) classification system of 68 vegetation types for the region (see Appendix S2). Using ArcView GIS, we plotted these vegetation types in order to identify the spatial position of the edge of each vegetation type, which was then defined as the transitional area between these vegetation communities. Based on an approach of vegetation type richness, Gaston *et al.* (2001) and Van Rensburg *et al.* (2004) have also used this classification system in order to identify biome edges and transition between different vegetation compositions. We performed calculations of the distance to the nearest transition areas between vegetation communities using an extension for ArcView GIS 3.X named Nearest Features, with Distance and Bearings (version 3.5) (Jenness, 2001). Coastlines were not included as a boundary. We used Albers equal area map-projection following Kark *et al.* (2007).

Although more comprehensive and updated than the Low & Rebelo (1996) vegetation map, we opted not to use the Mucina & Rutherford (2006) classification system of 435 vegetation types for the region due to the spatial resolution of this classification being too fine relative to the coarse quarter-degree grid cell resolution of the biological data (i.e. bird and frog richness data). For example, using the same bird data as for our study, van Rensburg *et al.* (2004) suggested that the resolution of the bird data could be too coarse to reveal fine-scale effects. Considering this limitation of the biological data, and given that this is the best national scale data currently available for both groups, a coarser vegetation classification, even though not as accurate, is more appropriate to address the broader regional scale aims of this study.

We used for analyses the two main forms of environmental energy namely, productive energy availability (amount of resources available for consumers to turn into biomass) and solar energy (amount of solar radiation reaching the earth's surface) (Evans *et al.*, 2005). We used the mean January normalized difference vegetation index (NDVI; Tucker, 1979; Hurlbert & Haskell, 2003) values as estimates of available environmental energy, and data on minimum temperature ($^{\circ}\text{C}$) as a surrogate for solar

energy (see Appendix S1 for more information on these data sets). Primary productivity (measured using NDVI) and precipitation are often highly correlated; especially in semiarid areas such as parts of South Africa, where precipitation sets the limits to available environmental energy (Van Rensburg *et al.*, 2002). Therefore, we did not include both variables in our analyses, but rather chose to use NDVI. To estimate topographical heterogeneity we included altitudinal range (maximum height above sea level minus minimum height above sea level, in metres – DEM, following Jetz *et al.*, 2004) derived from standard 1 : 250,000 topographical map information for South Africa (South African Surveyor General, 2004).

To control for the effect of human-related land transformation, a major factor shaping species richness and rarity patterns (Sala *et al.*, 2000), we conducted our analyses using (1) all grid cells, (2) only those cells with 50% or less land transformation (birds: $n = 1603$; frogs: $n = 1382$), and (3) only those cells with 25% or less land transformation (birds: $n = 1281$; frogs: $n = 1067$) (see Appendix S1 for more information on related calculations). Results using these three data sets were qualitatively similar and therefore we present only those from analyses that used the entire data set.

The analyses of overall species richness estimates were based on 650 bird species and 110 frog species (marine, vagrant, marginal, exotic, and escaped species were excluded from analysis) that occur in South Africa. Species range-size rarity estimates were based on a smaller subset of 55 endemic bird species (with > 90% of their distributions within South Africa and for which no taxonomic uncertainties exist; Hockey *et al.*, 2005), and on 62 frog species endemic to South Africa (Minter *et al.*, 2004) (see Appendix S3 for a detailed list of the species). The species considered for range-size rarity estimates can therefore be treated as globally range restricted, making the question of whether vegetation transitions, per se, are important for range-restricted species a relevant question with important implications for conservation. We estimated species range-size rarity as the sum of the inverse of the range sizes of the species occurring in each cell (estimated as the number of cells that each of the endemic species occurring in each cell occupies) *sensu* Williams (2000).

To determine the effect of variation in spatial extent and levels of environmental energy and topographical variation on the extent to which species richness and range size rarity is related to distance to transition areas between vegetation communities, we conducted analyses at two spatial scales, including the whole South Africa (hereafter referred to as 'regional scale') and the biome scale. The latter includes the savanna, forest (including the thicket biome), grassland, fynbos, Nama karoo and succulent karoo biomes (see Appendix S1 for more information on the biome data set and Appendix S4 for biome map).

Analyses

The effects of possible collinearity between the different predictor variables (i.e. NDVI, minimum temperature, DEM and distance to nearest transition area between vegetation communities) were first taken into account before multiple regression modelling was

performed. This is important when applying explanatory models where collinear variables in the logistic function each have its own explanation rationale. To detect collinearity, the tolerance value for each predictor variable was examined. Tolerance, as defined by Neter *et al.* (1996), is 1 minus the squared multiple correlation of a predictor variable with all other independent variables in the regression equation (Statsoft Inc., 1999); the lower the tolerance of a given variable, the stronger the correlation between the variable in question and one or more of the other predictors (Quinn & Keough, 2002). Following Quinn & Keough (2002), those variables with tolerance values < 0.1 were eliminated from subsequent analyses. The explanatory variables showed weak signs of collinearity with tolerance values varying between 0.72 and 0.86. None of the explanatory variables were therefore found to be redundant at the 0.1 tolerance level and all were included in the subsequent analyses. Square terms of all predictor variables were included to detect simple non-linear relationships. To reduce heteroscedasticity in our response variables, species richness and range size rarity values for both birds and frogs were logarithmically transformed to base 10.

To examine whether distance to nearest transition area between vegetation communities is also a significant explanatory variable of spatial variation in species richness and range size rarity patterns, when important environmental variables, including NDVI, minimum temperature values and DEM are part of the model; we investigated the relationship between (1) species richness and (2) range size rarity, for frogs and birds, respectively, in each of the quarter-degree grid cells and the distance of the grid centre to the nearest transition area between vegetation communities, both with and without taking spatial variation in the environmental variables into account.

To determine how well distance to the nearest vegetation boundary explains variation in richness and range size rarity values, and the form this relationship takes, models with all combinations of the three environmental predictors (NDVI, minimum temperature and DEM), boundary distance and their squared terms were constructed. We made use of the PROC MIXED procedure using SAS version 9.1 (SAS Institute Inc., Cary, USA). This procedure takes spatial autocorrelation into account (see Littell *et al.*, 1996 for more information on how this procedure fits a spatial covariance matrix to the data). Model fit was determined using the Akaike's Information Criterion (Burnham & Anderson, 1998; model with the lowest value was reported) and Akaike weights (Westphal *et al.*, 2003; all models with a weight value > 2 were reported). In addition, the PROC GLM (assuming independent errors) procedure to implement general linear models was constructed. Although this procedure does not take spatial autocorrelation into account, it is important to note that coefficients of determination cannot be calculated for spatial PROC MIXED models. Calculating the coefficients of determination values with the PROC GLM procedure will assist us to examine the extent to which the partial boundary distance term loses its explanatory power after the inclusion of the environmental predictors to the model as explanatory variables.

To further test our hypothesis of whether areas located near ecological transition zones are particularly rich in range-limited

bird and frog species, respectively, we tested at the regional scale whether the subset of endemic species to the study region occur more closely to transition areas than would be expected for non-range-limited species (i.e. non-endemics). We did this by comparing the observed mean distances to the vegetation community boundaries for the endemic species with the distribution of distances expected if the same number of species were drawn from among all (650 bird and 110 frog) species 10,000 times. The observed sample cells representing the distribution ranges of the endemic species were not spatially aggregated and are therefore expected to be well replicated in the randomization, which will be heterogeneously spread over the study area.

Finally, to understand better the topographical heterogeneity in each biome examined, the mean altitudinal range was compared among the different biomes using analysis of variance and Tukey's honestly significantly different test.

RESULTS

Species richness and range size rarity were negatively correlated with distance to the nearest transition between vegetation communities before taking the spatial variation in environmental variables into account (Table 1). The shape of this relationship was that of a decelerating decrease of range size rarity and species richness with an increase in boundary distance (Fig. 1). No indication of a humped-shaped relationship is evident from the relationship patterns. This result is supported by the square term of boundary distance being mainly non-significant, and therefore not contributing to the explanatory power of the models showed in Table 1. If there was some evidence of these relationships being humped-shaped, then such a result would suggest that the hypothesis predicting a peak in species richness and in range-restricted species nearest to boundaries would not necessarily be true, even though the overall relationship is negative.

Comparing the explanatory power of only distance of each quadrat to the nearest boundary between vegetation communities over all the ecoregions, after controlling for environmental energy and topographical heterogeneity, transition areas showed the highest explanatory power for variation in both bird and frog richness and range size rarity in the savanna biome. This pattern was followed by the whole South African (i.e. regional) scale for rarity, the succulent karoo biome for frog richness, although significance was not reached here, and the fynbos biome for avian richness (Table 1). In general, the highest explanatory powers of these interactions at the biome scale were double the power of those found at the regional scale.

After taking environmental energy and topographical variation into account, although the statistical power of boundary distance in explaining the variation in richness and range size rarity values (indicated in bold in Table 1) remained significant, their explanatory powers were largely reduced. That is, boundary distance as the partial term explained between 9% and 20% of the variation in richness and range size rarity values compared to the power of the full models including both boundary distance and environmental variables which explained between 28% and 72% of the variation (Table 1).

Table 1 Coefficients of determination (R^2) and significant levels associated with F ratios for the relationships between distance to the nearest boundary between vegetation communities and avian/anuran species richness and range size rarity. This was calculated without taking spatial variation in environmental energy availability into account using multiple regression models. Response variables were logarithmically transformed prior to analysis to achieve normality. Models in bold indicates those partial R^2 boundary distance terms with the highest and second highest explanatory power for each response variable compared across all the major ecoregions examined.

Ecoregions and response variables	d.f.	BD	BD ²	MIN	MIN ²	NDVI	NDVI ²	DEM	DEM ²	Model R^2 (%)	Partial R^2 boundary distance term (%)
South Africa											
Avian richness	1, 1849	–	– n.s.	–	+ n.s.	++++	– – – –	+++	– – – –	54.0	9.0
Avian rarity	1, 1800	– –	+ n.s.	– n.s.	– –	++++	++++	++++	– – – –	47.2	11.0
Anuran richness	1, 1623	– –	+ n.s.	– n.s.	++++	++++	–	++	– n.s.	57.4	8.0
Anuran rarity	1, 1135	– – – –	++	– n.s.	+	+ n.s.	+ n.s.	+ n.s.	++++	29.1	8.7
Grassland											
Avian richness	1, 474	– n.s.	+ n.s.	– n.s.	+ n.s.	– n.s.	+ n.s.	– – – –	++++	33.2	1.3
Avian rarity	1, 474	– n.s.	+ n.s.	– – –	+ n.s.	++++	++++	++++	– – – –	55.4	6.8
Anuran richness	1, 472	– n.s.	– n.s.	+ n.s.	+ n.s.	+ n.s.	+ n.s.	– n.s.	+	37.0	5.0
Anuran rarity	1, 375	+ n.s.	– n.s.	– –	+++	++++	++++	+ n.s.	++	52.2	2.4
Succulent karoo											
Avian richness	1, 122	– n.s.	+ n.s.	– n.s.	+ n.s.	– n.s.	+	– n.s.	+ n.s.	24.0	1.5
Avian rarity	1, 122	+ n.s.	– n.s.	+ n.s.	– n.s.	+++	++	– n.s.	+ n.s.	41.0	1.0
Anuran richness	1, 111	– n.s.	– n.s.	+ n.s.	– n.s.	– n.s.	+ n.s.	+ n.s.	+ n.s.	28.0	9.3
Anuran rarity	1, 99	– n.s.	+ n.s.	+ n.s.	– n.s.	– n.s.	– n.s.	– n.s.	+ n.s.	29.0	0.1
Nama karoo											
Avian richness	1, 448	– n.s.	+ n.s.	+ n.s.	– n.s.	+ n.s.	+ n.s.	++++	– –	44.0	4.5
Avian rarity	1, 448	– n.s.	+	+	– –	++++	++++	++++	– –	33.2	4.2
Anuran richness	1, 331	+ n.s.	+ n.s.	– n.s.	+ n.s.	– n.s.	+++	++	– –	25.1	1.6
Anuran rarity	1, 215	– n.s.	+ n.s.	– n.s.	+ n.s.	– n.s.	– n.s.	+ n.s.	+ n.s.	6.0	2.0
Savanna											
Avian richness	1, 616	–	– n.s.	– n.s.	+	++++	– – – –	– n.s.	+ n.s.	72.1	20.0
Avian rarity	1, 567	–	+ n.s.	– – – –	++++	++++	+++	+ n.s.	+ n.s.	50.0	17.1
Anuran richness	1, 521	–	– n.s.	– n.s.	+ n.s.	++++	– – – –	–	+ n.s.	71.0	18.1
Anuran rarity	1, 260	– – – –	++++	– n.s.	+	++	++	– n.s.	+ n.s.	34.0	16.1
Forest											
Avian richness	1, 37	– n.s.	+ n.s.	– n.s.	– n.s.	+ n.s.	+ n.s.	– n.s.	+ n.s.	25.2	0.4
Avian rarity	1, 37	– n.s.	+ n.s.	– n.s.	+ n.s.	+ n.s.	+ n.s.	– n.s.	+ n.s.	14.4	1.3
Anuran richness	1, 37	– n.s.	+ n.s.	+ n.s.	– n.s.	++++	– n.s.	– n.s.	+ n.s.	62.3	5.6
Anuran rarity	1, 36	+ n.s.	– n.s.	– n.s.	+ n.s.	+ n.s.	+ n.s.	– –	++	50.4	1.4
Fynbos											
Avian richness	1, 107	– –	+	– n.s.	+ n.s.	++++	– – –	– n.s.	+ n.s.	61.3	11.0
Avian rarity	1, 107	– n.s.	+ n.s.	+ n.s.	– n.s.	– n.s.	– –	+ n.s.	– n.s.	54.0	4.6
Anuran richness	1, 106	– n.s.	+ n.s.	– n.s.	+ n.s.	++	– n.s.	+ n.s.	– n.s.	51.0	1.6
Anuran rarity	1, 105	– n.s.	+ n.s.	– n.s.	+ n.s.	+ n.s.	+ n.s.	+ n.s.	+ n.s.	35.0	4.1

d.f., degrees of freedom; BD, boundary distance; MIN, average monthly minimum temperatures ($^{\circ}$ C); NDVI, normalized difference vegetation index; DEM, altitudinal range. Significance levels: positive effects + n.s., + $P < 0.05$, ++ $P < 0.01$, +++ $P < 0.001$, ++++ $P < 0.0001$; negative effects – n.s., – $P < 0.05$, – – $P < 0.01$, – – – $P < 0.001$, – – – – $P < 0.0001$; n.s. = not significant.

After taking both environmental variables (energy and topography) and the spatially structured component of the variation in the environmental variables (i.e. spatial autocorrelation) into account, distance to transition areas between vegetation communities was not included in any of the spatial models as an explanatory variable for variation in species

richness and range size rarity values (results for this are therefore not presented here).

When analysed for range-restricted species alone, the mean distance to the nearest transition area between vegetation communities was significantly lower ($P < 0.001$; 10,000 permutations) than expected by chance. In other words, at the regional scale,

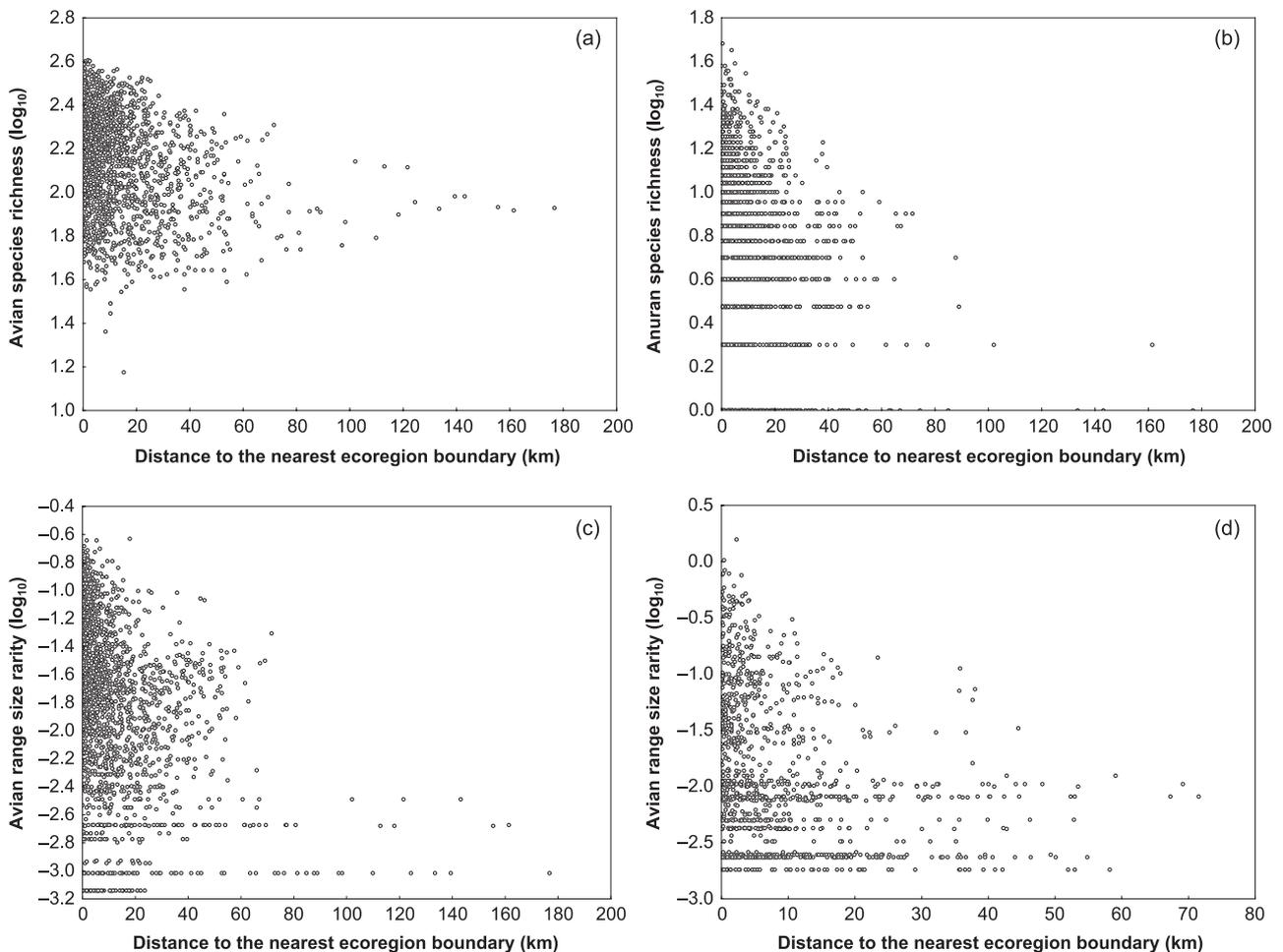


Figure 1 Relationships at the regional scale between avian and anuran species richness and range size rarity and distance to the nearest transition area between vegetation communities. (a) Log avian species richness = $2.1934 - 0.0036 \times$ distance to the nearest vegetation boundary; $r = -0.30$; $P < 0.0001$; d.f. = 1, 1856. (b) Log anuran species richness = $0.85405 - 0.0067 \times$ distance to the nearest vegetation boundary; $r = -0.31$; $P < 0.0001$; d.f. = 1, 1630. (c) Log avian range size rarity = $-1.682 - 0.0104 \times$ distance to the nearest vegetation boundary; $r = -0.32$; $P < 0.0001$; d.f. = 1, 1807. (d) Log anuran range size rarity = $-1.778 - 0.0155 \times$ distance to the nearest vegetation boundary; $r = -0.26$; $P < 0.0001$; d.f. = 1, 1142. Range size rarity is estimated as the sum of the inverse of the number of quadrats that each of the endemic species occurring in each quadrat occupies *sensu* Williams (2000).

endemic bird and frog species are located significantly ($P < 0.05$) closer to those areas representing transition areas between vegetation communities compared to a randomly selected pool of endemic and non-endemic species considered.

Finally, differences in the mean altitudinal range among the biomes examined can be seen in Appendix S5.

DISCUSSION

Despite their differences in ecological requirements, life histories and mobility, both birds and frogs at the regional scale support the ecotone hypothesis originally suggested by Odum (1953). In both groups, richness and rarity increase towards areas of transition between vegetation communities. Therefore, ecotonal areas in

South Africa tend to hold concentrations of birds and frogs, as well as range-limited species of these groups.

In contrast to Brooks *et al.*'s (2001) argument that transitional areas are characterized mostly by widespread species and therefore do not warrant high conservation priority, our findings indicate that areas of transition between vegetation communities in many cases do hold outstanding concentrations of range-limited species. We argue that these areas constitute a high conservation priority in a biogeographical context (both ecological and historical). Our findings were at the regional spatial extent and resolution, where conservation actions are most likely to be implemented (Mace, 2000). Araújo & Williams (2001), based on terrestrial vertebrates in Europe, found that modern day extinctions are determined mainly by extrinsic factors compared to demographic

factors. However, extrinsic factors have less of an impact on peripheral compared to central populations (Araújo & Williams, 2001). Thus, species with restricted range sizes will especially benefit from conservation approaches with a bias towards marginal populations (Araújo & Williams, 2001), the latter populations often found in ecological transition zones (Kark & van Rensburg, 2006). We therefore recommend that conservation planning programs at regional scales be adopted to include regions of ecological transition, and that our research agendas to step beyond the lines and boundaries that demark distinct ecological communities and that lead us to ignore the areas where they coincide.

The importance of proximity to ecological transition areas in harbouring concentrations of range-restricted frog species is most evident in the savanna biome, and more specifically the south-eastern part of this biome overlapping with the Maputaland anuran assemblage (Minter *et al.*, 2004). That is, 22% of all the grid cells in the greater savanna biome occupying range-restricted frog species and with distance values to the nearest vegetation transition area being less than 5 km, showed a spatial overlap with the small and restricted Maputaland frog assemblage region as defined by Minter *et al.* (2004). This result supports the pioneering work of Poynton's (1964) which, along with more recent work (e.g. Poynton, 1961, 1964; Poynton & Boycott, 1996), serves as a good foundation for understanding the amphibian biogeographical processes at work in southern Africa. Poynton described two main groups of amphibian fauna in southern Africa. First, the species-rich tropical group in the north-eastern lowlands of southern Africa that is mainly made up of the north-eastern savanna biome in South Africa, and is characterized mostly by species with large range sizes that is expected to show further range size increases as temperature rises. This biogeographical patterning of high species richness in the north-eastern lowlands of southern Africa is likely to explain the concentration of high frog richness patterns near transition areas in the savanna biome found in our study.

The second amphibian group described by Poynton (1964) is the temperate Cape group showing a significant degree of range overlap between its species and that of the tropical species leading to important allopatry speciation events (Poynton, 1964). More importantly, this area of range overlap (see Poynton, 1964, map 2) follow a close spatial overlap with the Maputaland anuran assemblage in the south-eastern part of the savanna biome in South Africa which, we in this study, identified as the biome with transitional environments harbouring many range-restricted frog species. Indeed, Poynton (1964) argues that the biogeographical patterning of frog species in southern Africa is mainly the result of recent allopatric speciation in action.

Though not significant, our study also highlighted the importance of the succulent karoo in harbouring many frog species near its ecological transition areas. That is, compared to all the ecoregions examined, the partial coefficient of determination (R^2) of the distance term (i.e. distance to the nearest transition area) in the succulent karoo showed the second highest explanatory power, next to the savanna biome, in explaining spatial variation in frog richness (Table 1). This could be due to the fact that a

large part of this biome is known to be an important transition area in seasonality of rainfall and the geographical patterning of the vegetation communities in this biome should depict this larger biome-scale transition in precipitation (Schulze, 1998). That is from a low winter rainfall in the succulent karoo to a high winter rainfall in the south moving towards the fynbos, and to summer rainfall in the east moving towards the Nama karoo. This is consistent with van Rensburg *et al.*'s (2002) study that suggested that in a semi-arid region such as South Africa, primary productivity, known to be an important driver of species richness patterns (see Evans *et al.*, 2006 for birds and frogs; Andrews & O'Brien, 2000 for mammals; O'Brien, 1998; O'Brien *et al.*, 2000; for plants), is limited mainly by rainfall (see also Chown *et al.*, 2003). Rainfall is an important factor in structuring breeding cycles, especially in amphibians, and therefore affecting their ecophysiology and thus biogeographical affinities. In this framework, Alexander *et al.* (2004) identified a significant frog assemblage known as the succulent karoo transitional assemblage.

The fact that both bird richness and concentrations of range-restricted bird species show a strong association with distance to transition areas between vegetation communities in the savanna biome is most likely a consequence of the biogeographical complexity of this biome. Within the eastern part of South Africa, the savanna biome spans an extensive latitudinal gradient which, compared to the west, has higher net primary productivity and has peak species richness areas at regional (van Rensburg *et al.*, 2002) and larger (Balmford *et al.*, 2001; De Klerk *et al.*, 2002) spatial scales. Although low in overall topographical complexity (Appendix S5), some complexity is, however, present towards the eastern parts of this biome (Mucina & Rutherford, 2006) with spatial congruence between peaks of species richness and narrow endemism (see De Klerk *et al.*, 2002). Such patterns are most likely as a result of localized climatic stability over the short-, medium-, and long-term climatic cycles (see Fjeldså, 1994; Fjeldså *et al.*, 1997, see also Jetz *et al.*, 2004 for the broader sub-Saharan Africa).

The savanna biome also spans the largest component of the distinctive east–west environmental energy gradient across South Africa known to be an important explanatory variable for avian richness patterns (van Rensburg *et al.*, 2002; see also Evans *et al.*, 2006 for frogs). A strong species–energy relationship is consistent with the well-supported species–energy theory (Morin, 2000) that suggests that areas with greater energy availability will be able to support a higher biomass and consequently enable more individual organisms to coexist, and thus higher abundances to maintain viable populations. Consequently, energy and topographical complexity, being closely related to the process of diversification and species range size dynamics (Fjeldså & Lovett, 1997; Jetz *et al.*, 2004), are stronger explanatory variables of richness patterns than distance to the nearest boundary. Also, the result of boundary distance not entering the models when controlling for the spatially structured components of the environmental variables is consistent with van Rensburg *et al.*'s (2002) conclusion that the spatially structured component of the variation in the energy variables is an important explanatory variable of the variation in species richness.

In the fynbos biome, the interaction between weather systems having persisted during long geological times (e.g. stable position of the frontier between summer- and winter-rains, and the zone of mixing of cold Benguelen and warm Agulhas waters; Van Wyk & Smith, 2001; Cowling & Lombard, 2002) and physical structures of coastlines and mountain ridges may lead to the high lineage persistence and thus high degrees of speciation (see Fjelds  & Lovett, 1997; Jetz *et al.*, 2004; Forest *et al.*, 2007). This is most likely an important factor leading to increased (although not significant) richness of range-restricted bird species close to transition areas between vegetation communities in the fynbos biome. Moreau (1966) suggested that some of the endemic birds of this biome represent small clades which date back to the early/mid-Tertiary, long before the origin of the fynbos vegetation. Such spatial congruence between aggregates of palaeo- and neoenemics suggests high lineage persistence in this area that has important consequences for conservation (Jetz *et al.*, 2004). Moreover, Moreau (1952) regarded the fynbos as a distinct avifaunal district with several bird species showing small range sizes within this biome, and more recent molecular studies suggest additional bird species (phylogenetic-based) near the coast of South Africa than known by Moreau (see Dillon & Fjelds , 2005 for more details).

This pattern of high overall and range-restricted species near transition areas, however, is not seen in all ecotones in the study area. This is true at both the ecoregion and the biome scales (Table 1), and mainly includes the grassland, Nama karoo and forest biomes for both birds and frogs. This difference in the effect of ecotones among biomes is possibly as a result of varying spatial heterogeneity among regions, and especially in the steepness of the topographical and climatic changes leading to sharper or more gradual transitions (Gosz & Sharpe, 1989). Based on studies conducted by, for example Jetz *et al.* (2004) and Fjelds  *et al.* (2007), it is expected that the pattern of the relationships presented in Fig. 1 reflects, in part, the denser packing of vegetation boundaries in the topographically complex and biologically rich southern and eastern coastal zones compared with the interior regions of South Africa (see Appendix S2 for vegetation boundary arrangements).

Several reasons might be responsible for why species richness and/or range size rarity for both taxon groups did not show any significant association with transition areas between vegetation types within the grassland, Nama karoo and forest biomes. The grassland biome shows an intermediate to low level of topographical complexity, with only the savanna and Nama karoo biomes being lower (Appendix S5), coupled with mostly lower climatic stability compared to the adjacent biomes in which the two major frog biogeographical centres were identified (see Poynton, 1964, map 2; see also Jetz *et al.*, 2004 and Fjelds  *et al.*, 2007 for more information on the relationship between topographical complexity, low seasonality and species range dynamics). This may have led to a reduced effect of the boundaries, as discussed above.

For the Nama karoo, this could be as a result of the biome's overall low primary productivity, being situated in the more arid north-western part of South Africa (Appendix S4). Compared with the other biomes this region also has low topographical complexity (Appendix S5). The quarter-degree resolution of our

biological data (i.e. bird and frog richness and range size patterns) may be too coarse to reveal finer-scale effects, especially in small and highly fragmented vegetation types such as those in the forest biome (see van Rensburg *et al.*, 2004). Finally, transitional areas between vegetation types within the grassland biome may be exposed to low rates of anuran allopatric speciation, as described by Poynton (1964).

Irrespective of the different historical and ecological mechanisms that underlie the origin and maintenance of species, especially rare species, and the influential variation of these factors, our study provide partial support that areas of transition have high probability of harbouring concentrations of overall and of range-restricted species (see also Muriuki *et al.*, 1997; Seymour *et al.*, 2001; Knapp, 2002; Jetz *et al.*, 2004; Fjelds  *et al.*, 2007; for further examples of such areas). While conducted at a much smaller spatial extent and finer resolution, the present analysis compliments those findings from recent studies conducted at larger spatial scales and coarser resolution (e.g. Kark *et al.*, 2007). However, in the case of South Africa presented here, the relationship between richness and rarity and distance to vegetation boundary is weaker. Several studies conducted at the regional and continental scales (e.g. Fraser, 1998; Rahbek & Graves, 2001; van Rensburg *et al.*, 2002) have suggested that the extent to which habitat heterogeneity serves as a correlate of species range size patterns is also dependant on the spatial grain of the study, increasing in importance with a decline in spatial resolution. Our work at a regional scale enables us to start exploring the factors that may have shaped these findings and compare among the regions. The fact that some regions do not show increased richness and rarity near ecotones is especially interesting, as it enables to start untangling the factors driving this relationship found for other regions and scales.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Additional information on the biotic and abiotic data used in the Methods section.

Appendix S2 A map of Low & Rebelo's (1996) classification system of 68 vegetation types for South Africa. Each colour denotes a different vegetation type.

Appendix S3 Species list of the 55 endemic birds used for analysis (> 90% of their distribution range is within South Africa and for which no taxonomic uncertainties exist; Hockey *et al.*, 2005), and for 62 frogs endemic to South Africa (Minter *et al.*, 2004).

Appendix S4 A map of the vegetation biomes of South Africa and Lesotho based on Low & Rebelo (1996).

Appendix S5 Altitudinal range (maximum height above sea level minus minimum height above sea level, in metres) for the different South African biomes examined. Means with no letters in common denote significant differences between biomes of $P < 0.05$.

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