

RESEARCH
PAPER



The role of transitional areas as avian biodiversity centres

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ABSTRACT

Aim With the ever-increasing threats to biodiversity, efforts are being directed towards identifying hotspots of special importance for conservation. In particular, there has been an effort to identify irreplaceable regions that are especially rich in rare species. Areas of transition between ecological systems in which multiple species coincide are expected, almost by definition, to be species-rich. Here, we examine whether this is simply a result of an overlap between two communities in boundary regions, or whether boundary areas also hold concentrations of rare (e.g. range-limited) species. We ask whether an analysis that includes areas of transition may be a useful contribution to the identification of biodiversity centres.

Location and methods To address these questions, we examined the relationship between passeriform richness and range size rarity of approximately 2300 bird species in 4889 1° New World grid cells, and the distance of the cells to boundaries between adjacent plant-based ecoregions.

Results Areas nearer to boundary regions between ecoregions not only had more bird species, but also scored more highly in terms of species rarity. The range centres of the rarest 10% of species were distributed significantly closer to boundaries between ecoregions than were species in general. This pattern persisted for rarity when we divided the New World into three latitudinal belts and analysed each separately, and when we excluded the Andes. It also persisted when compared with randomly generated ecoregion polygons.

Main conclusions The findings of this work suggest that transitional environments harbour many rare species, in addition to high richness. Consequently areas of biotic transition should be highly valued as biodiversity centres and need to be included in future global conservation analyses and decisions.

Keywords

Biodiversity, birds, boundaries, conservation, ecoregions, ecotones, New World, passeriforms, range-size rarity, transitional areas.

INTRODUCTION

In our continuing quest to identify areas in which rare species (defined here in terms of restricted range) are concentrated, research has often focused on pre-defined ecosystems, ecoregions or other distinct landscape units. Recent studies at the global scale have attempted to rank levels of species richness and rarity across such area units in order to assign our conservation and financial efforts more effectively (Myers *et al.*, 2000). This approach has led to the exclusion of areas of transition where these units intergrade (also termed ecotones) from many conservation

programmes (Smith *et al.*, 2001a; Kark & van Rensburg, 2006), especially at the global scale. For example, one of the important recent initiatives to conserve the Earth's richest biodiversity hotspots is based on identifying regions with exceptional (mainly plant-based) concentrations of rare species, wherein each area features a 'separate biota or community of species that fits together as a biogeographical unit' (Myers *et al.*, 2000). Thus, current studies often exclude areas of transition from large-scale analyses; however, such areas have been proposed as possible centres for important ecological and evolutionary processes such as speciation (Schilthuizen, 2000). Do we find higher

concentrations of species, and especially of rare species, as we approach transitional areas? At regional and even at global scales spatial co-occurrence of especially high richness and rarity seems to be limited to unique areas. For example, for birds at a global scale, only a few areas show congruence between hotspots of richness and of rarity (narrow endemism) (Orme *et al.*, 2005). A recent quantitative analysis has shown that centres of endemism for African birds cannot be explained by environmental, stochastic or geometric constraints or sampling effects alone (Jetz *et al.*, 2004). Other, namely historical, factors seem to be responsible for the spatial co-occurrence of richness and rarity (range restriction). Here, we aim to examine whether areas of transition serve as such convergent centres, in which both richness and rarity are high. We ask whether an analysis that includes areas of transition may be a useful contribution to the identification of biodiversity hotspots. While sharing attributes of two or more environments that coincide in ecotonal areas, there is evidence that these regions also offer unique transitional habitats (Holland *et al.*, 1991; Risser, 1995). As such, they have the potential to maintain unique biodiversity. Here, we test two hypotheses: (1) species richness will increase with proximity to transition zones at a continental scale and (2) transition zones will tend to harbour a higher number of rare (range-limited) species than expected by chance.

MATERIALS AND METHODS

To test our hypotheses we examined the relationship between native species richness of New World passeriform birds measured in 4889 1° × 1° latitude–longitude grid cells, and their distance to the nearest ecoregion boundary (a map of distances with reference to richness and rarity patterns is shown in Fig. 1). The same was done for range size rarity instead of richness. We repeated this for the mean distance of each cell to up to the five nearest boundaries in order to examine the effect of multiple boundaries (see below).

Our data base included 2279 passeriform bird species native and restricted to the Americas for which distribution data were available. More details on the data set can be found in Manne *et al.* (1999). A 1° grid was chosen to avoid digitizing the data from range maps at a finer scale than the maps warranted. Alien bird species (e.g. *Passer domesticus*, *Sturnus vulgaris*) were not included in our analyses. Birds that are mostly Russian in distribution, and barely make it into northern or eastern Alaska (three species of *Plectrophenax*) were also excluded.

We applied the terrestrial ecoregions and biomes of the New World, as classified by WWF (Figs 1 and 2 in Olson *et al.*, 2001 and <http://www.worldwildlife.org/science/data/terreco.cfm>). Ecoregions are based primarily on biogeographical units containing a distinct assemblage of native species and communities (mostly plant communities) (Olson *et al.*, 2001). Each ecoregion is also classified into one of 14 biomes, which are coarse, globally distributed major habitat types (Olson *et al.*, 2001). We examined the relationship between bird species richness and rarity in each of the 4889 cells and the mean distance from its centre to the nearest boundary between ecoregions, as well as the distance to multiple boundaries, which was taken as the mean distance from

the cell centre to the nearest two and up to five different boundaries. This was repeated for biomes. This was also repeated after excluding islands of all sizes and cells for which full environmental data were unavailable ($n = 4075$). Distance calculations were performed using an extension for ArcView GIS 3.X named Nearest Features, with Distances and Bearings (v. 3.5). We included only inland ecoregion boundaries (excluding coastlines as boundaries). Range size rarity was estimated as the sum of the inverse of the range sizes of the species occurring in each cell (estimated as the number of cells in which the species occurs) *sensu* Williams (1996, 2000). As no single projection provides true distance across such a large latitudinal span, each cell centre was re-projected to an azimuthal-equidistant projection centred on that point, providing true distances from that point to any other. Results using the corrected and the simple map-projection calculations were, however, very similar. To check the effect of the removal of small ecoregion patches on these results, we then excluded from the analysis those cells located in the smallest ecoregion patches (for two ecoregion size categories: < 10,000 m² and < 100,000 m²).

To study the effect of potentially confounding variables we examined the standardized partial correlation coefficient (β) (Sokal & Rohlf, 1995) between species richness in a cell, as well as its rarity score and its distance to the nearest boundary (or multiple two to five boundaries) while controlling for area of the ecoregion or biome patch in which the cell occurs (as well as total area size of all patches of that community over the study area), and for latitude and longitude for both ecoregions and biomes. To control further for the effect of latitude, a major factor shaping global richness and rarity patterns, we examined the relationship between distance to the nearest ecotone (and mean distance to the nearest two to five boundaries) and the residuals from a regression between log richness and latitude. The same was done for log range size rarity. We re-ran all analyses separately for each of three New World latitudinal sub-bands from (1) 90° N to 30° N (the northernmost cell with richness > 1 was at 82.5° N), (2) 30° N to 30° S, and (3) 30° S to 90° S (the southernmost cell with richness > 1 was at 68.5° S).

We then tested whether the rarest 10% of bird species in our data set are more closely associated with boundaries than would be expected by chance. We did this by comparing the observed mean distances to boundaries for the 10% of species occupying the fewest cells with the distribution of distances expected if the same number of species were drawn at random from among all species 1000 times. If the observed distance was less than the expected distance bounding the lower 5% tail of the distribution, then the null hypothesis that the two are the same was rejected at the 0.05 level of probability. This was done using Worldmap software (available at <http://www.nhm.ac.uk/science/projects/worldmap/>). The analysis was repeated after excluding all islands, because even the largest islands (e.g. Cuba) had no more than six ecoregions.

In addition, we ran a multiple regression model separately for log richness and for log range size rarity as the dependent variables and the following predictors: latitude (absolute values); longitude (to control for the effect of north–south mountain

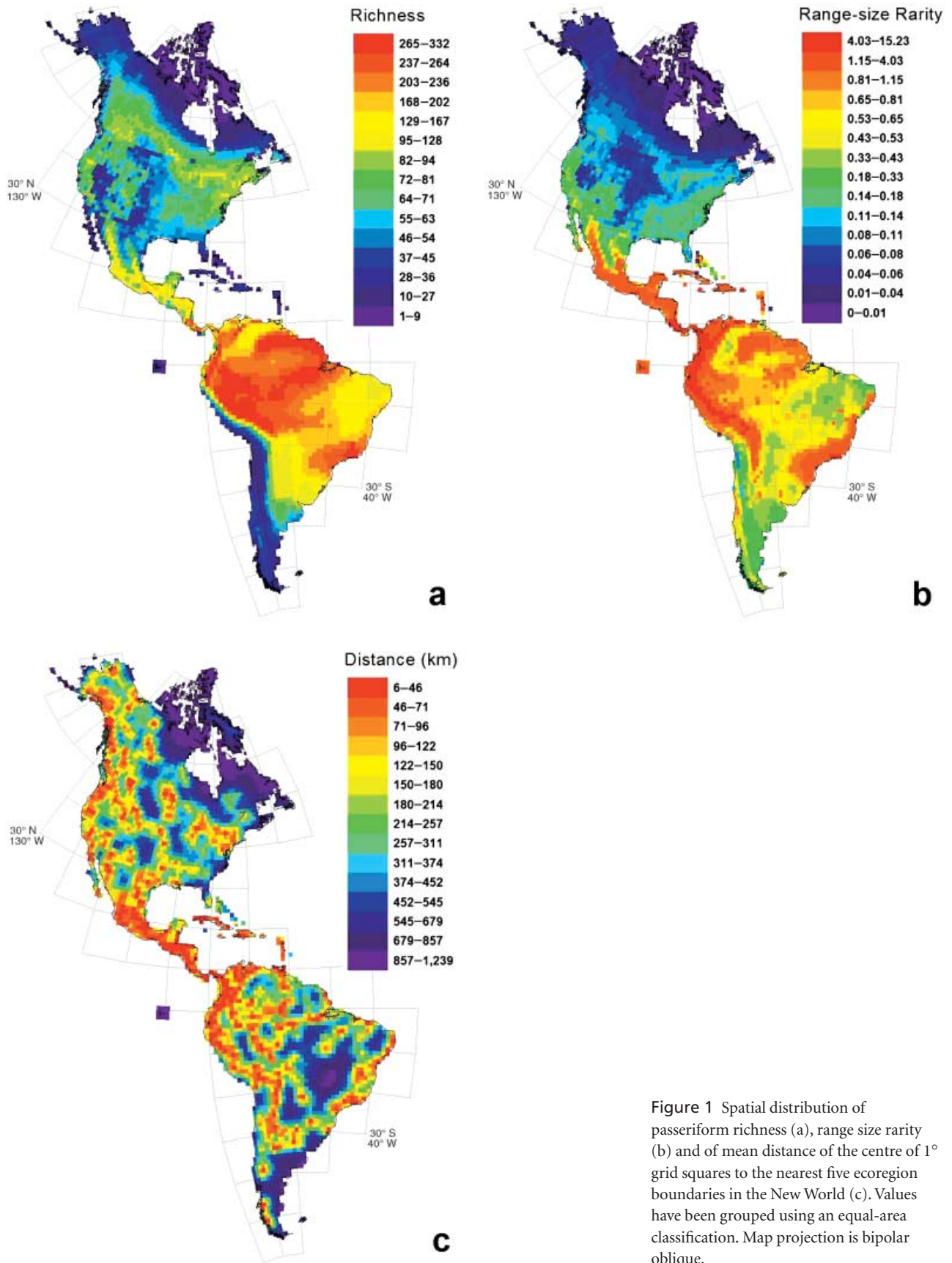


Figure 1 Spatial distribution of passeriform richness (a), range size rarity (b) and of mean distance of the centre of 1° grid squares to the nearest five ecoregion boundaries in the New World (c). Values have been grouped using an equal-area classification. Map projection is bipolar oblique.

ranges such as the Rockies, Sierras and Andes); size of ecoregion in which grid cell was located; and the distance of the grid centre to the nearest ecoregion boundary. This calculation was repeated for the mean distance to the nearest multiple boundaries (up to five). To test for collinearity, we used the variance inflation estimator (VIF) estimate for collinearity, which represents $1/(1 - r_i^2)$, or the amount that the variance of the *i*th regression coefficient is inflated due to collinearity (Philippi, 1993), as calculated by JMPIN 5.1 (SAS Institute, 2003). We made sure that the VIF was low for all variables in the model. When collinear variables showed values of VIF higher than 10, we saved only one in the model, following Philippi (1993).

Environmental variables

We then ran the model again including environmental variables instead of latitude and longitude. After degrading the resolution to 1° to fit that of the bird data base, we included the following environmental variables: (1) rainfall: mean annual rainfall between the years 1961 and 1990 based on Leemans (1999) and <http://www.fao.org/sd/EIdirect/climate/EIsp0002.htm>; (2) temperature: minimum monthly temperature, maximum monthly temperature, mean monthly temperature between the years 1961 and 1990 based on Leemans (1999) and <http://www.fao.org/sd/EIdirect/climate/EIsp0002.htm>; (3) net primary productivity (NPP): mean value for the years 1982–98 based on Potter (1999), Potter *et al.* (2003) and http://gcmd.nasa.gov/records/GCMD_NASA_AMES_GLEMIS.html; (4) elevation: (a) mean elevation in a 1° grid cell resolution based on the USGS EROS Data Center (EDC) GTOPO30 global digital elevation model data base (<http://www1.gsi.go.jp/geowww/globalmap-gsi/gtopo30/gtopo30.html>) and (b) elevation range (maximum minus minimum elevation in a 1° grid cell) based on the same sources. We also examined the effect of the size of the grid square, which decreases with increasing latitude due to the projection used. Naturally, this variable is highly correlated with latitude.

After controlling for collinearity we were left with two final models, one of which included latitude and the other that included the environmental variables that are often used as surrogates for latitude. The two models were run for both log richness and log range size rarity.

Model 1 included these predictors: latitude (absolute values), area size of the ecoregion in which the grid cell was located, and the distance of the grid centre to the nearest ecoregion boundary. Model 2 included these predictors: mean annual rainfall, minimum and maximum mean annual temperature, NPP, mean elevation and the range of elevations in the grid cell, area size of the ecoregion in which the grid cell was located, and the distance of the grid centre to the nearest ecoregion boundary.

Random ecoregions

To test whether our findings could be related to some bias caused by the distance calculations or geometrical constraints, we created 10 sets of randomized New World ecoregions. We then recalculated the relationship between richness and rarity in each

grid cell and their mean distances to the nearest one to five randomly generated ecoregion boundaries. The randomization was done using Idrisi 32.2 GIS software macros (Clark Laboratories, 2002) with a Lambert azimuthal equal area projection at a spatial resolution of 10 km in the following sequence: (1) We created a random distribution of more than 300 points (about the number of original ecoregions) falling within the continental area. From these, we generated Thiessen polygons (Aurenhammer, 1991). The point with the smallest Thiessen polygon area was assigned such that it received the smallest original ecoregion area, and so on, in an increasing order. (2) The random polygons were generated sequentially using cost surface modelling (Aurenhammer, 1991). This approach enabled us to exclude cells with infinite cost from the analysis at each step, applying the Idrisi COSTGROW algorithm. This was done until the largest polygon (based on the size distribution of the real ecoregions) was reached. (3) Neighbouring pixels (including diagonals) that remained unassigned to a polygon were given a unique ID. (4) The resulting map was projected to the Geographic Projection at a spatial resolution of 1/15-by-1/15 degrees (4').

Altogether we created 10 sets of *c.* 300 random ecoregions for the Americas (the range was between 308 and 327). The main difference between the random ecoregions generated using the above approach and the real ecoregions is that some of the real ones are separated into more small patches. The random ecoregion boundaries were converted from raster to vector and were exported to ArcView 3.2 GIS. To estimate the possible effect of the vector to raster and raster to vector conversions, as well as that of the specific spatial resolutions that we used and the mode filter, we also applied these manipulations on the original ecoregion polygons, thus creating an additional set for which we performed the distance calculations, here termed the rasterized ecoregions.

Spatial autocorrelation

Spatial autocorrelation can influence the null distribution of Pearson's *r*, leading to overestimating the number of degrees of freedom, and may therefore elevate the probability of a Type I error (Clifford *et al.*, 1989). Yet if one of the two variables in a correlation shows no significant spatial autocorrelation this problem does not persist (Clifford *et al.*, 1989). The Mantel test, which examines the relationship between two square matrices (often distance matrices), was calculated using the `PASSAGE` software (available at <http://www.passagesoftware.net/>). Spatial autocorrelation was relatively low for distance to nearest boundary ($r < 0.12$ in all cases), yet the variables showed significant spatial autocorrelation. Therefore, we used the `PASSAGE` software to run the modified *t*-test for correlation, which calculates Pearson's product-moment correlation between two variables and tests its significance following Clifford *et al.* (1989). All results hold after this corrected test, with highly significant values.

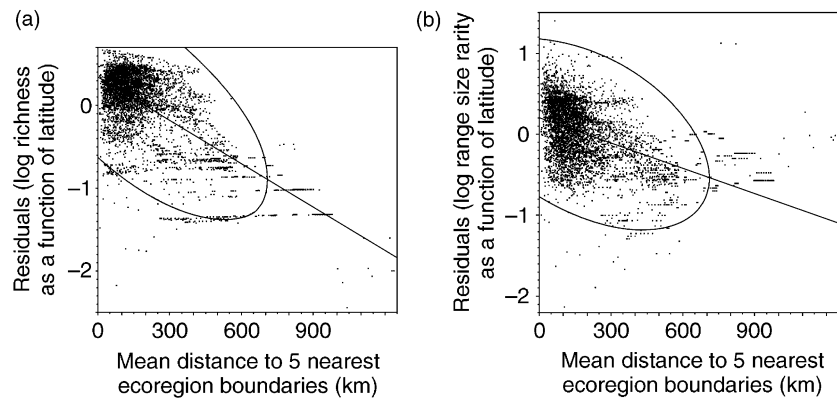
The boundaries between ecoregions (and biomes) used here have been determined independently of this study for different conservation-related purposes. Yet, it is clear to us that in nature, environmental gradients and areas of environmental transition

Table 1 The relationship between native passeriform richness and range size rarity in each of 4889 $1^\circ \times 1^\circ$ latitude–longitude grid squares of the New World and the mean distance of the cell centre to the nearest one to five boundaries between ecoregions. Pearson's r is shown. In all cases $P < 0.01$ (after correcting for the effect of spatial autocorrelation using the modified t -test, see text; significance values appear in the table). The full data set had a sample size of $n = 4889$. Results for a subset of the data set excluding islands of all sizes and cells for which full environmental data were unavailable with a sample size of $n = 4075$ are also presented. Richness and rarity were log-transformed to approximate normality. Results were generally similar when we used the non-parametric Spearman's r (Rho). Results were very similar when biomes were used instead of ecoregions

		Mean distance to the nearest one to five boundaries				
	Sample size	Nearest boundary	Nearest two boundaries	Nearest three boundaries	Nearest four boundaries	Nearest five boundaries
Richness	$n = 4889$	-0.34***	-0.61***	-0.65***	-0.68***	-0.71***
	$n = 4075$	-0.26**	-0.36**	-0.42**	-0.44**	-0.45**
Rarity	$n = 4889$	-0.29**	-0.54**	-0.59**	-0.62**	-0.65**
	$n = 4075$	-0.28**	-0.38**	-0.43**	-0.46**	-0.48**

** $P < 0.01$; *** $P < 0.001$.

Figure 2 Relationship between the mean distance of each of 4889 grid square centres to the nearest five ecoregion boundaries (x -axis) and the residuals from a regression between the absolute value of latitude and log species richness (a) or log range size rarity (b) (y -axis). This presentation shows the effect of distance to boundary on richness or rarity after removing the effect of latitude. A linear regression line and a bivariate normal ellipse are shown. This ellipse contains the specified mass of points as determined by a 99% probability. Figures for the one to four nearest boundaries generally show similar relationships.



can rarely be delimited by a fine line (e.g. see maps of varying transition-zone breadth in Williams *et al.*, 1999). Although the line used to mark the transition is somewhat subjective, we expect, based on the spatial resolution used in this study, that the range of inaccuracy around the location of the line (which ideally should have been in that area where the environmental change is steepest) to be much smaller than the mean distance to the nearest boundary, and the error around the location of this line should not greatly influence the relationships observed.

RESULTS

Our results support both of our hypotheses. First, bird richness significantly increases with decreasing distance to the nearest boundary for both ecoregions and biomes at the continental scale for New World birds (Table 1). The negative relationship is also maintained in a residual analysis controlling for latitude (Fig. 2). Second, rarity increases with proximity to boundaries between ecoregions (Table 1). When we examine the rarity patterns on a species basis we find that the rarest 10% of species are located significantly ($P < 0.05$) closer to boundary regions between ecoregions when compared with a random draw of the

same sample size from among all species. The above trends become stronger in areas where multiple ecoregions meet, resulting in an increasing effect of multiple boundaries (Table 1). Much of the increase in the correlation values occurs between the nearest one and two boundaries. Although r values are somewhat lower, the above patterns are generally maintained and are significant after excluding islands (Table 1).

The multiple regression (Model 1) described above showed that longitude does not have a significant effect, and it was dropped from the final model. Latitude (absolute values), area size and the distance of the grid centre to the nearest five ecoregion boundaries (Model 1) were significant, and together had an adjusted r^2 of 0.74 (Table 2a). The results persisted and became stronger when distance to multiple boundaries was calculated. All VIF values were less than or equal to 1.5. Results were generally similar when variables were log transformed (for range of elevations and distance to nearest boundary) or square root transformed (for richness, range size rarity, rainfall and area size of ecoregion) to approach normality.

Similar findings were obtained for log range size rarity, where relationships were stronger and the adjusted r^2 was 0.85 (Table 2b). When log richness was included in Model 1, with

Table 2 Results of a multiple regression model for log richness (a) and log range size rarity (b) as the dependent variables (Model 1, see text). Independent variables include the absolute value of latitude, size of ecoregion (1000 × km²) and mean distance to the five nearest ecoregion boundaries (km). VIF = variance inflation estimator, see text for details

(a) Response log richness: summary of fit

R^2 adjusted	0.738				
Observations (sum weights)	4889				
Parameter estimates					
Term	Estimate	Std error	<i>t</i> ratio	Prob > <i>t</i>	VIF
Intercept	2.5317	0.0097	260.1	< 0.0001	
Latitude	-0.0141	0.0002	-65.6	< 0.0001	1.330
Ecoregion area size	8×10^{-5}	1×10^{-5}	6.7	< 0.0001	1.145
Mean distance to five nearest boundaries	-0.0016	3×10^{-5}	-50.4	< 0.0001	1.496
Effect tests					
Source	Nparm	DF	Sum of squares	<i>F</i> ratio	Prob > <i>F</i>
Latitude	1	1	382.5	4307.3	< 0.0001
Ecoregion area size	1	1	4.0	44.5	< 0.0001
Mean distance to five nearest boundaries	1	1	225.7	2541.3	< 0.0001

(b) Response log range size rarity: summary of fit

R^2 adjusted	0.848				
Observations (sum weights)	4889				
Parameter Estimates					
Term	Estimate	Std error	<i>t</i> ratio	Prob > <i>t</i>	VIF
Intercept	0.519	0.011	49.2	< 0.0001	
Latitude	-0.027	0.0002	-117.5	< 0.0001	1.330
Ecoregion area size	-0.0002	1×10^{-5}	-17.4	< 0.0001	1.145
Mean distance to five nearest boundaries	-0.001	3×10^{-5}	-35.1	< 0.0001	1.496
Effect tests					
Source	Nparm	DF	Sum of squares	<i>F</i> ratio	Prob > <i>F</i>
Latitude	1	1	1440.1	13810.8	< 0.0001
Ecoregion area size	1	1	31.5	302.4	< 0.0001
Mean distance to five nearest boundaries	1	1	128.4	1231.1	< 0.0001

range size rarity as the dependent variable, the r^2 increased to 0.9 (with the VIF estimate for richness collinearity being 2.9). When we excluded all islands and cells that did not have full environmental data, and included in the model absolute latitude, log area size of the ecoregion in which the cell is found and the cell distance to nearest five boundaries, r^2 for richness was 0.65 and for range size rarity was 0.81.

Similar results were found for Model 2, which included the environmental variables mean rainfall, minimum and maximum mean temperature, NPP, mean elevation and range of elevations, with all VIF values being under 5, usually closer to 1. The model showed for log richness an r^2 of 0.82 and for log range size rarity an r^2 of 0.83. Similar results were seen when we used mean monthly temperature and range of temperatures instead of minimum and maximum temperatures. When the size of the grid cell was included in the model, r^2 values increased to 0.83 for log richness and 0.88 for log endemism. When islands and grid cells with incomplete data were excluded, the model explained 77% of the variance for richness, and 85% for rarity (all VIF

values were under 7.5). The model explained 78% and 84% of the variance in log richness and log rarity, respectively, when mean temperature was used rather than minimum and maximum temperatures (all VIF values were under 5).

A model that examined the relationship between the residuals from a regression between log richness and log range size rarity and the independent variables mean distance from the nearest five boundaries, log area size of ecoregion in which grid square is located, and latitude (real values) explained 52% of the variance, suggesting that the effect seen earlier for range size rarity does not result from the relationships obtained for richness alone. Similar results ($r^2 = 0.55$) were found for Model 2. When the size of the grid cell was included in the model, r^2 values increased to 0.62.

To examine further whether the findings of our study result mainly from an effect caused by the accumulation of many rare species in the Andes, where many ecoregion boundaries are concentrated in a relatively small area, we divided the New World into three latitudinal sub-bands and repeated the analyses separately for each. The relationship between both richness and

rarity and the mean distance to the nearest ecoregion boundaries (one to five) generally persisted for all three latitudinal bands for rarity and, for the northern belt (30° and above), also for richness, and was especially strong in the arctic region. It is interesting that when broken down to three sub-regions, the negative relationship between distance to boundary and range size rarity are stronger than those for richness. Additionally, the significant difference between the distance of the rarest 10% of species and a random draw (of the same number of species) is maintained in all 15 cases (three latitudinal sub-belts, each of five nearest boundaries) but one. The negative relationships between species richness in a cell, as well as its rarity, and its distance to the nearest boundary (or multiple boundaries) are generally maintained in all cases when we control, within each of the sub-bands, for latitude, longitude and the area size of the ecoregion or biome patch in which the grid cell occurs (as well as total area size of all patches of that ecoregion over the whole study area). The standardized partial correlation coefficient (β) remains negative in all cases (one to five nearest boundaries) for both richness and rarity in both ecoregions and biomes. A path analysis for log richness (or log rarity) as the dependent variable and distance to nearest ecoregion boundary, area size (of patch in which cell is found) and absolute value of latitude shows a negative and highly significant path coefficient (P) in all cases. Our results remained significant when we excluded the smallest ecoregions, as explained in the Methods. The negative significant relationship was also maintained in all cases when we removed islands from the analysis to control for a possible effect of exceptionally large distances of islands to the nearest ecoregions on the mainland.

Our results hold for another scale of analysis: species richness and rarity increased with proximity to biome (a coarser classification of ecological regions) boundaries as well. Distance to biome boundary was a good predictor for passeriform richness and rarity. In addition, the rarest 10% of species tend to occur significantly closer to biome boundaries than do other species. This is also true for the three latitudinal belts we analysed for biomes, though for the southern belt the result is significant only for the first boundary. We also found that our results persist when we partly control for ecoregions and community type by examining the relationship between richness and the mean distance to the nearest one to five boundaries separately for each of the largest sampled ecoregions (many of which are outside the Andes).

Random ecoregion runs

The distribution of the area sizes of the random ecoregions and those of the original ecoregions did not show a significant difference when a chi-square test was applied. The mean distance to the nearest one and up to the mean of the five nearest boundaries was found to be significantly different between the random ecoregions and those of the original ecoregions, including after these were rasterized (see Methods). Thus the rasterization did not bias the results. The magnitude of the differences increased with the number of ecoregion boundaries included (from one to five), and was higher for bird rarity than for bird richness. The correlation between richness and distance to boundary was

negative but low (between -0.09 and -0.13 for the 10 random ecoregion runs) and between rarity and distance was close to zero (between -0.01 and -0.03 for the 10 random ecoregion runs). This suggests that the relationships between richness or rarity and the distance to the nearest boundaries seen for the real ecoregions are not likely to be due to an artefact caused by the calculation methods or the rasterization process.

DISCUSSION

The results of this study suggest that areas located close to transitions between ecological regions, and especially those located closer to multiple boundaries, are particularly rich in bird species, as well as in range-limited species. The fact that these areas not only have high richness but also maintain more range-limited species than areas located farther from boundaries suggests that they serve as centres of unique diversity. At a 1° resolution, the finding of higher richness nearer to boundary areas and ecological gradients is not surprising. However, beyond this finding, these unique environments clearly seem to provide opportunities for rare species to persist. This supports Odum (1953), who suggested over 50 years ago that ecotonal communities should contain organisms that are restricted to the ecotone.

Why do we find higher rarity near transitions, and especially in areas where multiple boundaries coincide? The answer to this question is not trivial and deserves further attention, especially if we are to direct conservation efforts based on these findings. As a pattern, rarity scores are bound to be dependent on richness, because they have been measured as a sum of scores among the species present. As shown by Williams (2000), a dependency on richness is forced by the way each biota is a sample of the total species pool: as richness increases, so the possible range of mean range sizes among the biotas drawn from the pool is constrained to be reduced as the possible mean range sizes are forced to converge upon the overall mean. Nevertheless, unless all species from the pool are present, there is still some freedom within this constraining envelope for biological processes to operate, which could bias biotas towards more widespread or more geographically rare species. Two principle classes of processes may govern this pattern: (1) evolutionary processes, namely speciation, enhanced by ecotonal environments, and (2) ecological factors, enabling the maintenance of rare species in ecotonal areas (Kark & van Rensburg, 2006).

Evidence is accumulating to support the evolutionary scenario (Smith *et al.*, 1997; Schilthuizen, 2000). Recent studies suggest that populations occurring in transitional environments hold especially high morphological divergence and genetic diversity in the face of gene flow (Smith *et al.*, 1997; Kark *et al.*, 1999, 2002) and that they harbour rare alleles that do not occur elsewhere (Kark *et al.*, 1999). Divergent selection has been proposed to contribute to the occurrence of phenotypically unique transitional populations and forms, leading to reproductive divergence there (Schneider *et al.*, 1999). As such, transitional environments could be sources of variation and evolutionary novelty, serving as speciation pumps (Schilthuizen, 2000). If boundary regions serve as extant centres of speciation, they are expected, at least

in some cases, to contain a preponderance of recently derived species in the process of expanding their ranges (neo-endemics) (Mora *et al.*, 2003). Some studies support this idea. Fjeldså (1994) suggested that recently evolved species are concentrated in transitional ecotones surrounding the main Central African rainforest. Moritz and colleagues (Moritz *et al.*, 2000) also proposed that areas such as the Central African ecotones hold concentrations of young species and evolutionary novelty. This reasoning is congruent with the finding that ecotonal populations exhibit high morphological divergence, providing evidence that current speciation processes may be taking place in these regions (Smith *et al.*, 1997; Moritz *et al.*, 2000; Schilthuizen, 2000). Some transition areas may coincide with refugial environments, where population isolation has led to allopatric speciation (e.g. in isolated mountains). The role of refugial isolation vs. ecological gradients in shaping divergence and speciation processes has been addressed in early and recent work (see Discussion in Moritz *et al.*, 2000; Smith *et al.*, 2001b). It appears that more work is needed to assess the relationship between the two and to examine whether there are cases in which isolation and ecological gradients coincide. This may happen, for example, in mountains, and may lead to high richness and rarity in these areas.

Ecologically, areas of environmental transition provide unique environments, well beyond a simple combination of the two neighbouring regions (Holland *et al.*, 1991; Gosz, 1993; Risser, 1995). For example, habitat structure and food quality for various bird species in tropical transition zones differ dramatically from those in the adjacent rainforest (Smith *et al.*, 1997). The high spatial, and in some cases also elevated temporal, heterogeneity in transitional environments (Risser, 1995) could contribute to transitional areas having higher species richness and rarity. Various studies, mainly at local and regional scales, have shown that transitional areas indeed hold high levels of richness (alpha diversity) in different groups (e.g. Mönkkönen, 1994; Rusek, 1992; Spector, 2002). It has also been shown in various studies that beta diversity (the species turnover) increases along transitions and gradients (e.g. Able & Noon, 1976; Shmida & Wilson, 1985; van Rensburg *et al.*, 2004). However, these patterns may largely depend on the scale being used to estimate diversity. Indeed, the relationship between alpha and beta diversity is not trivial, and can vary between scales, sampling methods, groups and systems (Loreau, 2000).

The findings of this work suggest that transitional environments maintain many rare species, in addition to high richness. These two variables, richness and rarity, while they may correspond somewhat at global scales, when examined at regional scales do not necessarily coincide (see, for example, Prendergast *et al.*, 1993; Williams *et al.*, 1999; Lennon *et al.*, 2004; Vázquez, 2004). As recently suggested, based on a study of African birds (Orme *et al.*, 2005), while ecological factors have an important role in shaping wide-ranging species ranges and richness patterns, spatial patterns of endemic species richness are more likely to be a product of other processes, such as high rates of speciation or refugia remaining from past extinctions (reviewed in Haffer, 1997) or climatic changes (Jansson, 2003). Thus, both

historical and ecological factors may have shaped the high rarity found in boundary regions. It has been suggested that centres of endemism convey a strong historical signature, being concentrated in regions that offered unusually many opportunities for past speciation, combined with climatic conditions that allowed the survival of narrow endemics (Jetz *et al.*, 2004).

Although richness and rarity hotspots do not necessarily overlap, there may be exceptional areas where both high richness and high rarity coincide at regional scales due to the coincidence of historical and ecological factors, generating dual richness–rarity diversity hotspots. Areas of transition may represent such a case. For example, species-rich montane areas, which show some of the steepest environmental transitions, have also been shown to be rich in range-limited and endemic species in various cases due to a combination of historical and ecological factors (e.g. Lomolino, 2001; Knapp, 2002; Jetz *et al.*, 2004). However, our study suggests that these patterns are not limited to areas of transition that correspond with mountains but may represent a wider phenomenon.

One could argue that increasing richness and rarity with decreasing distance to ecoregion and biome boundaries found in this study may result from the fact that a rather coarse grid cell size was used here. A relatively large grid cell may capture part of one ecoregion, a transitional environment, and part of a neighbouring ecoregion, thus leading to high richness in cells that include transitions. If this were the case we would expect to see a step function in which grid squares that fall on a transition (only the very adjacent ones that contain more than two ecoregions) show higher richness and rarity, while all other cells do not show a further decline in richness and rarity with increasing distance to the boundaries. However, here we see a gradual decline in both species richness and rarity with increasing distance to areas of transition (Fig. 2), a fact that does not support the above argument. More interestingly, the continuing decline could mean that areas of transition not only maintain higher richness, rare and unique species, but may also serve as a source of this diversity via processes such as speciation, in combination with gradual range expansions beyond the original transition areas.

The findings of this study have several important practical implications. Most important, it is clear that areas holding high concentrations of rare species should be conservation priorities. Transitional zones appear to be such areas. Regions where multiple (more than two) boundaries overlap appear to be especially rich in species and particularly in rare species, and as such should receive extra conservation attention. While some authors have suggested that areas of ecological transition may coincide with locations of peripheral populations at the edge of species ranges, and therefore their conservation would be an ineffective long-term investment (Gaston *et al.*, 2001; Araújo, 2002), other studies suggest that populations in some peripheral parts of the range are those most likely to persist in the face of certain kinds of change (e.g. those involving contagious or directional processes (Channell & Lomolino, 2000a,b)). Thus, until we better understand the processes shaping the high richness and rarity in boundary areas, it may be wise to follow an approach that combines the protection of selected boundary and non-boundary

areas, enabling gene flow among them. If areas of transition, in addition to having some of the attributes of each of the adjoining regions, also in themselves provide unique habitats (Holland *et al.*, 1991; Risser, 1995) and opportunities for speciation (Schilthuizen, 2000), protecting them may enhance both the persistence of rare species for which these areas are the main option for survival as well as the maintenance of important evolutionary processes (Smith *et al.*, 2001a). Further work on multiple groups is needed to help ascertain whether transition zones are suboptimal sink areas for species that require consistent dispersal from other regions or whether these areas maintain viable populations over time that are pre-adapted to changing environments (Kark & van Rensburg, 2006).

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