

Ecological Correlates and Conservation Implications of Overestimating Species Geographic Ranges

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Abstract: *Species range maps based on extents of occurrence (EOO maps) have become the basis for many analyses in broad-scale ecology and conservation. Nevertheless, EOO maps are usually highly interpolated and overestimate small-scale occurrence, which may bias research outcomes. We evaluated geographical range overestimation and its potential ecological causes for 1158 bird species by quantifying EOO map occurrence across 4040 well-studied survey locations in Australia, North America, and southern Africa at the scale of 80–742 km². Most species occurred in only 40–70% of the range indicated by their EOO maps. The observed proportional range overestimation affected the range-size frequency distribution, indicating that species are more range-restricted than suggested by EOO maps. The EOO maps most strongly overestimated the distribution of narrow-ranging species and ecological specialists with narrow diet and habitat breadth. These relationships support basic ecological predictions about the relationship between niche breadth and the fine-scale occurrence of species. Consequently, at-risk species were subject to particularly high proportional range overestimation, on average 62% compared with 37% of nontthreatened species. These trends affect broad-scale ecological analyses and species conservation assessments, which will benefit from a careful consideration of potential biases introduced by range overestimation.*

Keywords: biodiversity, biogeography, macroecology, ornithology, range occupancy, species richness

Correlaciones Ecológicas e Implicaciones para la Conservación de la Sobrestimación de los Rangos Geográficos de Especies

Resumen: *Los mapas de rango de especies con base en la extensión de ocurrencia (mapas EDO) se han vuelto la base para muchos análisis en ecología de escala amplia y en conservación. Sin embargo, los mapas EDO usualmente están muy interpolados y sobrestiman la ocurrencia a pequeña escala, lo cual puede sesgar los resultados de investigaciones. Evaluamos la sobrestimación de rango proporcional y sus potenciales causas ecológicas para 1158 especies de aves mediante la cuantificación de la ocurrencia en mapas EDO en 4040 localidades bien estudiadas en Australia, Norte América y el sur de África, a la escala de 80–742 km². La mayoría de las especies sólo ocurrieron en 40–70% del rango indicado por sus mapas EDO. La sobrestimación de rango proporcional observada afectó la distribución de frecuencias de extensión de rango, lo que indica que una el rango de las especies está más restringido que lo sugerido por los mapas EDO. Los mapas EDO principalmente sobrestimaron la distribución de especies de rango angosto y a especialistas ecológicos con reducida amplitud de dietas y de hábitat. Estas relaciones sustentan a predicciones ecológicas básicas sobre la relación entre la amplitud de nicho y la ocurrencia de especies a escala fina. Consecuentemente, las especies en riesgo estaban sujetas a una sobrestimación de rango particularmente alta, en promedio 62% en comparación con 37% de las especies no amenazadas. Estas tendencias afectan a los análisis ecológicos de escala amplia y*

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las evaluaciones de la conservación de especies, que se beneficiarán de una cuidadosa consideración de los sesgos potenciales introducidos por la sobrestimación de rangos.

Palabras Clave: rango de ocupación, riqueza de especies.

Introduction

For lack of better alternatives, range maps (and estimates of species geographic ranges based on them) have become the baseline data for many broad-scale analyses in conservation and ecology (e.g., Balmford et al. 2001; Jetz & Rahbek 2002; Ceballos et al. 2005; Orme et al. 2005; Jetz et al. 2007). Extent-of-occurrence (EOO) maps are the most frequently used type of range map. They show “the minimum convex polygon drawn to encompass all the known, inferred, or projected sites of present occurrence of a taxon, excluding cases of vagrancy” (IUCN 2001). An EOO map is typically hand drawn by experts on the basis of original records or their own knowledge of the putative boundaries of a species distribution (Gaston 1994, 1996; Brown & Lomolino 1998; Hawkins et al. 2003; Hannah et al. 2005). Consequently, EOO maps are scale-dependent “abstracts” of the actual occurrence of a species (Hartley & Kunin 2003; Wilson et al. 2004; Graham & Hijmans 2006; Russell et al. 2006; Hurlbert & Jetz 2007).

Extent of occurrence maps can overestimate species actual distributions and geographic range sizes and may thereby distort perceived, broad-scale ecological patterns and their correlates (Hurlbert & White 2005; Graham & Hijmans 2006; McPherson & Jetz 2007b) (but see Mathias et al. 2004). Overestimation may affect estimates of rarity and threat that depend heavily on range size (Gaston 1994; Hartley & Kunin 2003; Wilson et al. 2004; Goehring et al. 2007). Here we define *proportional range overestimation* as the fraction of sites inside the geographic range in which a species is actually absent, or $1 - \text{proportional “range occupancy”}$ (Hurlbert & White 2005). Proportional range occupancy is the proportion of range that is covered by actual range, and by definition varies between 0 and 1.

Covariation of range overestimation with species ecological attributes may introduce substantial biases in conservation assessments or ecological analyses based on EOO maps. The World Conservation Union (IUCN) Red List of Threatened Species assigns species to extinction risk categories on the basis of criteria that combine indicators of population size, temporal population trends, and geographic range size (IUCN 2001; Lamoreux et al. 2003; Butchart et al. 2004). One important criterion uses estimates of species range size in combination with measures of population fragmentation, decline, or fluctuation to assign threat categories (criterion B, IUCN 2001). The

IUCN Red List measures range size either in the form of EOO to evaluate the spatial spread of extinction risk (Criterion B1) or in the form of area of occupancy (Criterion B2), which measures actual range size and is more closely linked to population size (IUCN 2006). Species may qualify as at-risk under either criterion.

Crucially, the critical range-size threshold applied when using EOO is invariant across all species. For example, either an EOO of 20,000 km² (criterion B1) or an area of occupancy of 2,000 km² (criterion B2) potentially qualifies a species as vulnerable (IUCN 2001). The assumption here is that the level of extinction risk faced by a species meeting the range-size threshold of a particular threat category under the B criterion is broadly the same for the B1 or the B2 criterion. Extending this assumption beyond the way the criterion is actually used by IUCN, one could argue that behind it potentially lies the expectation of a roughly constant proportional range overestimation of $(20,000 - 2,000 \text{ km}^2) / 20,000 \text{ km}^2$ (i.e., 90% across species). If observed proportional range overestimation is in fact larger, then species that should be listed as threatened according to criterion B2 would not qualify under criterion B1, which suggests that B1 may be too restrictive. If overestimation is smaller, criterion B1 may be too inclusive.

According to the IUCN guidelines, the two B criteria are targeted toward separate sets of species (IUCN 2006), and temporal and spatial criteria are applied carefully and jointly (Akçakaya et al. 2006). Yet, across species with similar temporal population trends, interspecific variation in proportional range overestimation may lead to an associated variation in probability of being considered threatened. Although careful attempts have been made to refine EOO maps for some past (e.g. Stattersfield et al. 2000) and current assessments, it is not possible in all cases (e.g., reptiles, invertebrates) to achieve fully satisfactory refinement. We determined whether empirical levels of proportional range overestimation may cause potential conservation biases, even in a well-studied group like birds. Our study provides general advice to conservation planners about what sort of species may potentially be misrepresented in range-based threat assessments.

Ecological observations of and theory on the ecological niches of species provide some insights and predictions as to how range overestimation may vary across species (Grinnell 1917; Colwell & Futuyma 1971; Brown 1995; Holt 2003; McPherson & Jetz 2007a). Generalist species with broad dietary and habitat requirements are

expected to occupy more habitats and sites within a geographic range than those species with narrower preferences. Ecological specialists may therefore be subject to particularly strong range overestimation. Furthermore, species with broad geographic ranges are often characterized as having relatively broad environmental tolerances. Broad geographic ranges in turn imply that species are likely to occupy a wider range of environmental conditions and habitats within their range. Therefore, from an environmental niche perspective, the distributions of wide-ranging species are expected to be captured more accurately by EOO maps than those of narrow-ranging taxa (Wilson et al. 2004). Nevertheless, mapping methodologies offer an opposite prediction. Because map sizes in publications are often standardized to an absolute size that is not scaled with the species range extents, wide-ranging species are often mapped with much less detail and at coarser resolution than species with small ranges. If this shortcoming is the dominant determinant of EOO map accuracy, proportional range overestimation should increase with increasing range size.

We sought to quantify the prevalence of and variation in proportional range overestimation across a broad spectrum of bird species and to identify potential causes and correlates of overestimation. Our findings can guide scientists in separating methodological from biological trends in their data and aid the objective assessment of species under threat. We assessed range overestimation by scrutinizing EOO map occurrences of species across well-surveyed locations on three continents. Specifically, we asked (1) What is the magnitude of proportional range overestimation and how does it vary across regions? (2) What are the methodological and ecological correlates of proportional range overestimation that may bias studies in conservation and ecology? (3) Are the ranges of threatened and range-restricted species in particular strongly overestimated? (4) What effect does proportional range overestimation have on the core macroecological pattern of range-size frequency distribution?

Methods

Extent of Occurrence Map Data

We extracted EOO maps of bird ranges from the best available regional sources (for details see Jetz et al. 2007). Our analyses included only breeding ranges and excluded all pelagic and freshwater birds, defined as those species that feed predominantly in open water habitats. We also excluded the following groups owing to their different and variable detection probabilities in surveys: nightjars and allies (Caprimulgiformes), owls (Strigiformes), birds of prey (Falconides), and shorebirds (Charadriides). For southern African birds, we took EOO maps of nonpasserine birds from del Hoyo et al. (1992) and those of passer-

ines from Brown et al. (1992). The original digital files on which the maps in these volumes were based were kindly provided by the respective publishers. We georegistered and converted the maps to GIS format. For Australia nonpasserine distributions were compiled following del Hoyo et al. (1992). Maps for passerine species were hand-digitized from Simpson and Day (2004) to a projected map with ESRI Arcview. The different sources for passerine and nonpasserine birds did not significantly affect our analyses (effect of passerine/nonpasserine membership on proportional range overestimation; southern Africa: $F_{1,435} = 0.17$; Australia: $F_{1,392} = 0.10$). For North American birds we used EOO maps in GIS format from Ridgely et al. (2003). Originally in polygon format, the maps were resampled to 0.01° resolution in geographic projection for further analysis.

Survey Data

We used confirmed presences from survey data to estimate the proportional range overestimation incurred by EOO maps. Survey data for southern Africa were taken from the recently published bird atlases for southern Mozambique (Parker 1999), South Africa, Swaziland, Lesotho, Zimbabwe, and Namibia (Harrison et al. 1997), which georeference bird sightings to quadrats of 0.25° latitude-longitude. The area of survey quadrats used in the analyses varied from 635.90 to 742.37 km². These levels of variation in area have been recently shown to be negligible in broad-scale ecological analyses (Nogués-Bravo & Araújo 2006). The data for Australia were extracted by the Australian Atlas team across a 25×25 km (625 km²) equal-area grid (Barrett et al. 2003).

In all atlas assessments of this type, survey effort varies across survey locations, which can lead to a significant bias. In our data an approximate measure of observer effort was given by the number of surveys (i.e., visits) as indicated by the number of filled-in survey cards per quadrat. Quadrats that are surveyed poorly are likely to display more false absences than those that are well studied. Interspecific differences in detectability and their potential ecological correlates (Jetz & Bezzel 1993; Bibby 2000) may affect perceived correlates of proportional range overestimation. To overcome this potential bias, we conducted a combination of species-accumulation and rarefaction analyses to ascertain appropriate numbers of surveys per atlas quadrat. In both regions visual inspection indicated that species accumulation and rarefaction curves start to plateau after approximately 30 surveys (only summer and spring surveys were counted in the case of southern Africa). To verify this result we conducted a pairwise analysis of neighboring quadrats and assessed how survey effort of the less-sampled quadrat affected the similarity in species. Species similarity across quadrat pairs increased with increasing minimum survey effort, but plateaued above 30 surveys in the less-sampled

quadrat. We therefore limited our subsequent analyses to survey quadrats with ≥ 30 surveys conducted in them and accordingly used 1546 (of 7088) survey quadrats in Australia and 935 (of 2717) in southern Africa. To evaluate the potential sensitivity of our results to this threshold, we repeated our analyses with ≥ 50 surveys as a cutoff point and a limited set of 1048 and 751 quadrats, respectively. Across all 832 species with survey records, all evaluated trends retained the same direction and similar statistical strength (see Supplementary Material).

For North America survey-based species presences were obtained from the Breeding Bird Survey, years 1996 to 2004. Only routes with 8 or 9 years of data were included ($n = 1559$), close to the 10 years that were demonstrated to achieve good survey effort (see Hurlbert & White 2005 for a comparison of observed range occupancies across 1, 5, and 10 years of surveys). The BBS routes are approximately 40 km long, and their geographic position was available in GIS format. We buffered routes by 1 km on each side along the route to account for potential georeferencing errors, which resulted in polygons approximately 40 km long and 2 km wide (total area: ca. 80 km²). Survey quadrats and polygons from all three regions were then resampled to 0.01° resolution in geographic projection for further analysis.

Ecological Traits

We extracted information on body mass, diet, and habitat preferences from the literature listed in Sekercioglu et al. (2004) and Sibley and Monroe (1991) and assigned species to 120 core habitat and 9 core diet categories. We used the count of different categories recorded for each species as measures of dietary and habitat niche breadth. To test for differences across diet types, we condensed the 9 diet categories into 5 (vertebrates, invertebrates, fruits or nectar, other plant material or seeds, mixed). We used the predominant habitats known for each species to attribute a habitat openness score by ranking habitats from 1, maximally open (e.g., desert, savannah), to 4, maximally closed (closed forests). Body mass values came from Dunning (1993) and del Hoyo et al. (1992). Regional geographic range sizes were defined as the proportion of a study region occupied (varying from 0 to 1) and were estimated from the same EOO maps described in "Extent of Occurrence Map Data." Global geographic range sizes were measured in square kilometers. For the study regions they were derived from the same data sources described above. For the area beyond the study regions, sources and methodology used for calculation of range sizes followed Jetz et al. (2007). Finally to test for a potential relationship between proportional range overestimation and threat levels, we extracted the threat categorization of all species in the analysis from the IUCN Red List (IUCN 2004).

Analysis

For survey data no information about species distributions below the scale of the survey quadrats and polygons was available. The EOO maps, at least technically, had information about putative occurrence below this resolution, and it was necessary to choose a minimum area that would qualify as EOO map presence within a survey polygon. We used the pixel size of EOO and survey data (0.01°, ca. 0.9–1.2 km²) as minimum overlap requirement: when a species EOO map overlapped with a survey polygon by at least one 0.01° pixel it was considered an EOO map presence for this species and survey location. We deemed this as most appropriate because equally just one survey observation (representing at most one 0.01° pixel) was enough to yield a species presence for the whole survey polygon. The nature of our data did not allow scrutiny of range overestimation below the scale of survey quadrats and polygons. Accounting for the fact that EOO ranges sometimes only cover parts of a presence survey polygon would decrease measured range overestimation; survey-based knowledge about actual absences within presence survey quadrats and polygons would increase measured range overestimation. Given the blob-like nature of EOO maps compared with often fractal-like actual species distributions (Hartley et al. 2004), one would expect range overestimation to increase toward finer scales (Graham & Hijmans 2006; Hurlbert & Jetz 2007).

The resulting data we used for analysis was a list of survey and EOO map presence records across survey quadrats and polygons for each species. We calculated proportional range overestimation for each species as the fraction of occupied EOO map polygon records for which surveys failed to confirm presence. This measure is equal to $1 - \text{proportional range occupancy}$ (Hurlbert & White 2005). We used single and multipredictor general linear models on this response variable to evaluate the effect of ecological variables on proportional range overestimation. Diagnostic plots indicated that model assumptions were met, and repeated analyses alternatively conducted with log-transformed response data or a logistic regression yielded qualitatively identical results.

Counting just one 0.01° pixel as EOO map presence across a whole survey quadrat (southern Africa, Australia) or polygon (North America) potentially underestimates actual range overestimation because the EOO pixels within the survey polygon may not actually overlap with the exact survey record. Nevertheless, visual inspection indicated that almost all survey grids or polygons were included fully within the EOO range map, so the effect of the small overlap threshold of 0.01° for assessing agreement between EOO range maps and survey grids or polygons would have limited effect on our results. To further quantify this, we calculated for each Australian bird species in the analysis proportional range overestimation

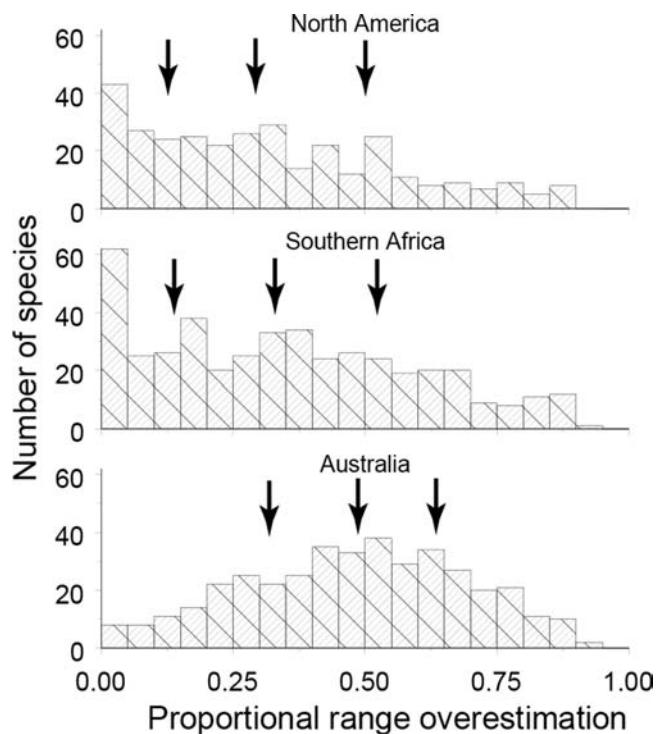


Figure 1. Frequency distribution of proportional range overestimation across all species in the analysis ($n = 1158$). Proportional range overestimation is calculated across 4040 intensely studied survey quadrats and polygons in North American, South American, and Australia and is defined as the proportion of extent-of-occurrence map presence records in which surveys indicated absence. Arrows indicate 25th, 50th, and 75th percentiles, respectively.

at the scale of 0.01° pixel rather than that of survey quadrats and polygons. We counted the 0.01° pixels of the EOO range that were inside survey quadrats and polygons and set these in relation to the sum of 0.01° pixels of all quadrats and polygons with survey records. Both

estimates of range overestimation differed on average by only 0.01 and were highly correlated with each other ($r_{\text{Pearson}} = 0.98$, $n = 393$), suggesting that the effect of a different overlap threshold on our results was negligible.

The results of comparative analyses across species may be affected by phylogenetic nonindependence of model residuals (Martins & Hansen 1997; Freckleton et al. 2002). In our data set, congeners often showed vastly different levels of proportional range overestimation, and occurrence was recognized as having very low phylogenetic dependence (Freckleton et al. 2006). To confirm this we performed a preliminary analysis of the potential effect of phylogeny on proportional range overestimation. We used a simple phylogenetic classification following Sibley and Ahlquist (1990) and nested analysis of variance with different taxonomic levels fitted as random effects. Variation in proportional range overestimation occurred almost exclusively below the family level, indicating negligible phylogenetic effects.

Results

Across all 1158 bird species, proportional range overestimation varied between 0% and 91%. On average, a species was not present in 39 of 100 survey locations within its EOO range. These values differed between regions and corresponding EOO map source types (Fig. 1; Table 1). Average proportional range overestimation was 32% in North America ($n = 326$ species), 33% in southern Africa ($n = 437$ species), and 48% in Australia ($n = 395$). North America and southern Africa differed from Australia in that they had many species with relatively little proportional range overestimation (lowest quartile ca. 15%). In Australia the lower quartile was at 32% proportional range overestimation (Fig. 1).

Across all three regions, range overestimation for species decreased with increasing geographic range size (Table 1; Fig. 2). Although global range size was a significant predictor, the effect of regional range size (the

Table 1. Ecological correlates of overestimation of species ranges^a in 4040 intensely studied survey quadrats and polygons in Australia, North America, and southern Africa.

	Model							
	one predictor					multipredictor ^b		
	df	b	F	P	r ²	B	F	p
Region	2,1154		49.94	0.00	0.08		42.75	0.00
Global range size (log)	1,1156	-0.09	96.63	0.00	0.08			
Regional range size	1,1156	-0.29	134.8	0.00	0.10	-0.26	105.40	0.00
Diet breadth	1,1123	-0.04	40.29	0.00	0.03	-0.03	19.59	0.00
Habitat width	1,1148	-0.03	41.77	0.00	0.04	-0.02	17.74	0.00
Diet	4,1152		4.24	0.03	0.01			
Habitat openness	1,1067	-0.02	5.19	0.02	0.01			
Body size	1,1030	0.00	0.39	0.57	0.00			

^aThe overestimation of species ranges is the proportion of extent of occurrence map presence records in which surveys indicated absence.

^bCombines the four strongest single predictors. Global range size was excluded in favor of the highly collinear regional range size.

proportion of the study region occupied by the species) was stronger, highlighting the importance of the distribution as it pertains to the study region rather than beyond. Two ecological determinants of proportional range overestimation were diet breadth and habitat width (Table 1; Fig. 2). The ranges of species with broad dietary and habitat niches were overestimated much less than those of more specialist taxa. Actual diet type and an index of habitat openness had weak effects. Proportional range overestimation was slightly higher in invertebrate feeders and species inhabiting closed habitats such as woodlands and forests. The latter effect was not significant when region was accounted for ($F_{1,1065} = 0.67$). Finally, there was no effect of body size (Table 1).

Because the three important traits were weakly correlated with each other (r [regional range size – diet breadth] = 0.08, r [regional range size – habitat breadth] = 0.13, r [diet breadth – habitat breadth] = 0.12), we included all three predictors in a multipredictor model to account for collinearity (Table 1). Region, geographic range size, and both measures of niche breadth emerged as core predictors, and all four explained separate parts of the variation in the response variable. Specialist species with narrow ranges emerged as most susceptible to range overestimation. Nevertheless, much unexplained scatter in range overestimation remained. Although the ecological trends were strong and highly significant, the multipredictor model accounted for only 21.2% of the variation ($F_{5,1114} = 59.96$, $r^2 = 0.212$). Analyses excluding North America and using a more restrictive survey threshold confirm these overall results (Table S1, S2).

Ecological specialization and restricted distribution often characterize species of greatest conservation concern, suggesting that the ranges of threatened species may be subject to particularly large proportional range overestimation (Fig. 3). Mean proportional range overestimation was 37% (SE 1%) for species classified as non-threatened (least concern, $n = 1088$) and 62% (SE 3%) for at-risk species (near-threatened or worse $n = 69$), a 25% difference ($F_{1,1155} = 72.59$, $p < 0.001$). This significant difference remained when region was controlled for ($F_{1,1153} = 70.02$, $p < 0.001$).

Proportional range overestimation had a particularly severe effect on range-restricted or endemic species and thus affected the shape of the range-size frequency distribution. For all species, we estimated a ‘corrected’ global range size by multiplying a species EOO range size with that species proportional range occupancy based on surveys (i.e., $1 - \text{proportional range overestimation}$). According to the original EOO maps in the analysis, 36 species had range sizes of 50,000 km² or less (a commonly used threshold to identify narrow-ranged and thus potentially threatened species; Stattersfield et al. 1998). Applying the proportional range-overestimation correction yielded a count of 84 in this category. The corrected range-size frequency distribution further illustrates the

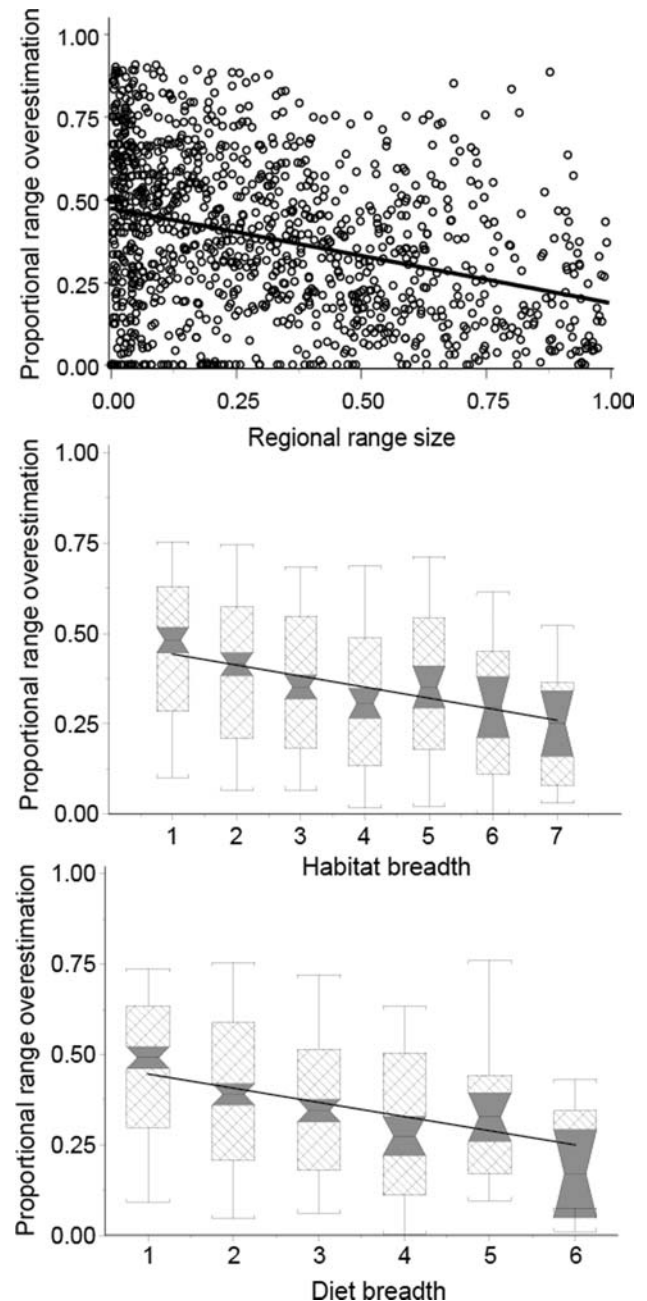


Figure 2. Effects of regional range size (proportion of region occupied by a species, $n = 1158$ species), diet breadth (number of broad diet types a species consumes; $n = 1150$ species), and habitat width (number of broad habitat categories over which a species occurs, $n = 1149$ species) on the proportion of extent of occurrence-map presence records in which surveys indicated absence (i.e., proportional range overestimation). Illustrated are independent, single-predictor relationships. Line is least-squares regression on individual species data points (see Table 1). Box plots show 10th and 90th percentile, quartiles, and 95% CI (notches).

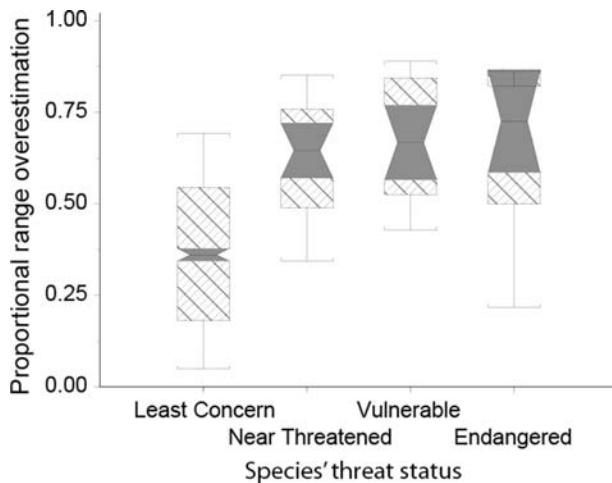


Figure 3. The variation of proportional range overestimation across species threat levels. Least concern species ($n = 1086$) are those not considered at risk (near threatened, $n = 32$; vulnerable, $n = 24$; endangered, $n = 13$ [category includes one species classified as critically endangered]). For box plot details see legend of Fig. 2.

consequences of range overestimation on a core macroecological pattern (Fig. 4). Correcting for proportional range overestimation at the analysis scale led to a shift to the left and change in the shape of the distribution for the species in the analysis. When corrected, the median range size shifted from approximately $1892 \times 10^3 \text{ km}^2$ to $1114 \times 10^3 \text{ km}^2$, the left skewness of \log_{10} -transformed

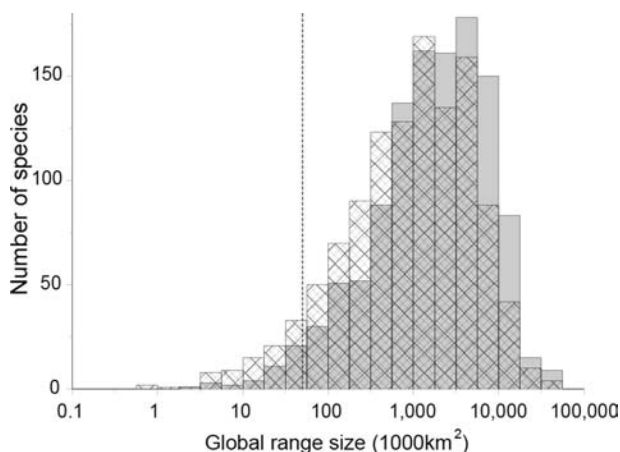


Figure 4. Frequency distribution of global range sizes of the 1158 birds in the analysis based on range maps (shaded) and corrected for overestimation (hatched, global range size range map $\times [1 - \text{proportional range overestimation}]$). Vertical dashed line indicates $50,000 \text{ km}^2$ —species to the left would likely be considered range restricted (Stattersfield et al. 1998) and potentially threatened (IUCN 2001).

range sizes decreased (skewness g_1 , from $g_1 = -0.73$ to $g_1 = -0.68$), and the distribution became slightly less leptokurtic (kurtosis g_2 , from $g_2 = 0.49$ to $g_2 = 0.44$).

Discussion

Across all three regions, proportional range overestimation consistently decreased with increasing range size, diet breadth, and habitat breadth. This confirms basic ecological predictions about the relationship between niche breadth and the fine-scale occurrence of species (Brown 1995). Owing to habitat turnover in space, high habitat specificity limits a species range occupancy in all but the most narrowly distributed species; likewise, high dietary specialization is likely to render parts of the mapped range unusable. Finally, broad ranges are indicative of generalist species that persist under a variety of environmental conditions and occupy a greater number of sites within a mapped range than more-specialized species (Stevens 1989; but see Williams et al. 2006). Even though they were weakly collinear, in our analysis the three variables explained mostly separate parts of the variation in proportional range overestimation, indicating that they played distinct roles in limiting a species fine-scale distribution. Furthermore, the negative relationship between range size and proportional range overestimation suggested that in our data ecological rather than methodological causes predominated in range overestimation.

Proportional range overestimation differed across the 3 regions even after we controlled for species ecological attributes. This may partly be due to the different environments of the regions and atlas methodologies. But these differences also served as reminders that the quality of EOO maps relied greatly on the underlying methodology and quality control applied by authors, publishers, and the digitizer, not to mention the scale of analysis. Our results confirmed that relatively species-poor North America has the most accurate EOO maps. The quality of these maps is likely partly due to the fact that the GIS-formatted EOO maps for North America had received additional quality control (Ridgely et al. 2003) and also due to the spread of surveys over at least 8 years (Hurlbert & White 2005). The Australian EOO distributions were semiautomatically or manually digitized from relatively small print maps, and as expected yielded the strongest overestimation. Smaller range overestimation was expected for EOO maps that were refined (e.g., by clipping off unsuitable elevations, habitats, Jetz et al. 2007), such as some of the maps Birdlife International produced for range-restricted species (Stattersfield et al. 2000). The aim of this study was to identify characteristic levels of range overestimation for typically used EOO maps available across broad geographic and taxonomic scales; therefore, we did not analyze any refined distribution data.

Naturally, errors of commission (false presences) are a function of spatial scale—at the scale of say Australia, both EOO maps and surveys would give the same answer about species presence (see also Graham & Hijmans 2006). At fine scale (i.e., smaller size of survey quadrats or polygons) one would expect higher errors of commission and higher range overestimation than at coarse scales (Hurlbert & Jetz 2007). Even though our study scrutinized North American EOO maps across areas about 8 times smaller than in the other two regions, they had the smallest degree of overestimation. This suggests that EOO map quality (higher in North America) outweighed the higher commission errors that one would expect given the smaller size of survey areas.

Could variation in species detection by observers explain some of the patterns and ecological correlates of proportional range overestimation? One could argue that rare species are more likely to be missed than common species and these false absences can potentially inflate estimates of proportional range overestimation for rare species. Three observations of observer effort argue against this issue that affect our results in a qualitative way: (1) trends were consistent across the three regions, despite the more standardized counts in North America; (2) survey locations for which neighbor comparisons suggested missing species were excluded (see methods); (3) analyses of South African or Australian locations with ≥ 30 versus ≥ 50 surveys did not change our findings. Therefore, we believe the effect of survey omission errors on our results was negligible.

Our results demonstrate that ecological specialization and narrow geographic distribution can lead to substantial proportional range overestimation. These are the same traits that are traditionally associated with high extinction risk (Purvis et al. 2000; Sekercioglu et al. 2004; Cardillo et al. 2005). Indeed, many species listed as at risk of extinction can potentially suffer from false optimism about their distributions and range sizes. Our findings expand on those of Wilson et al. (2004). Most threatened species have declining populations and declining species often have sparse, fragmented distributions. Because they are often absent from patches of suitable, but potentially suboptimal, habitat, these species are most likely to have their ranges overestimated. On the other hand, nonthreatened, colonizing species are expected to have more aggregated distributions characteristic of range expansion, which results in greater range occupancy (Wilson et al. 2004).

In addition to the double jeopardy of rare species (Lawton 1993), namely low population densities and restricted ranges, a third factor connected to the adequate assessment of species potentially exposes rare (and usually specialized) species to high risk of extinction: range overestimation. Local population size is thought to linearly decrease with range occupancy (Freckleton et al. 2005) and any overestimation of this occupancy may therefore

have particularly severe effects on estimated total population size (which is the product of local population size and range occupancy). There is a potential danger that specialist species in decline may be falsely overlooked by species assessments because they may fail to meet the EOO threshold. The use of either range estimate for conservation assessments is inherently difficult and an issue that IUCN is in the process of reviewing and improving (S. Butchart, personal communication). The already careful and encompassing approach taken by organizations that assess species conservation status may benefit from including further ecological information. This additional data may then assist in identifying species whose range estimate requires extra consideration. Furthermore, species surveys may be designed to minimize range overestimation. For example, a hierarchical sampling regime at different nested scales to obtain measures of range occupancy at different scales (Wilson et al. 2004) allows much more accurate range interpolations.

The observed ecological trends in range overestimation may directly bias analyses of broad-scale gradients in ecology. Differences in richness–environment relationships between EOO map and survey data have been demonstrated (Hurlbert & White 2005; McPherson & Jetz 2007b). Our results indicate that, for example, geographic gradients in the specialization and range size of taxa (e.g., along latitude, Stevens 1989) may lead to associated gradients in proportional range overestimation. Therefore EOO-map-based geographic gradients (e.g., in richness) may be exaggerated; for example, at too high a resolution, peaks of richness in the tropics based on EOO maps may be somewhat inflated by the high degrees of proportional range overestimation of the often specialized and narrow-ranged species near the equator. In addition, the spatial autocorrelation of summary patterns may be artificially high and thereby favor some environmental correlates over others (McPherson & Jetz 2007b).

For this study only species-level traits for which information could be gathered from simple observations were included as predictors. This had the advantage that similar information was readily attainable for many other taxa, facilitating assessment of the sensitivity of analyses to potential biases induced by range overestimation. Although these variables are strong indicators of the ecological mechanisms at work, the degree to which they capture them in detail was imperfect and the resulting predictive ability was therefore limited. For example, counts of different food types consumed or habitats used were rather limited measures of niche breadth. In an analysis of well-studied North American birds and Breeding Bird Survey (BBS) results, Hurlbert and White (2007) used surveyed abundance and abundance-derived niche measures of niche position and breadth as predictors. These detailed variables yielded more accurate predictors of the proportion of BBS survey routes within an EOO map occupied by species. Nonetheless, close to

half the considerable variation between species remained unexplained.

It follows that no simple formula can be applied to EOO maps to compute the "correct" range size for a species at a given scale. Nevertheless, our results demonstrate that some clear ecological trends need to be considered when interpreting research based on such maps. Although EOO maps will be improved in the future, at a given scale the ecological mechanisms investigated here are likely to continue to impose systematic errors of commission. Given the prominence of broad-scale EOO maps in ecology and conservation assessments, a quantitative understanding and appreciation of their potential shortcomings will assist in putting them to their best use.

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