Ecological correlates of geographical range occupancy in North American birds

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ABSTRACT

Aim The degree to which a species is predictably encountered within its range varies tremendously across species. Understanding why some species occur less frequently within their range than others has important consequences for conservation and for analyses of ecological patterns based on range maps. We examined whether patterns in geographical range occupancy can be explained by species-level traits.

Location North America.

Methods We used survey data from 1993 to 2002 from the North American Breeding Bird Survey along with digital range maps produced by NatureServe to calculate range occupancy for 298 species of terrestrial birds. We tested whether species traits explained variation in range occupancy values using linear regression techniques.

Results We found three species traits that together explained more than half of the variation in range occupancy. Population density and niche breadth were positively correlated with occupancy, while niche position was negatively correlated with occupancy.

Main conclusions Our results suggest that high range occupancy will occur in species that are common at sites on which they occur, that tolerate a relatively wide range of ecological conditions and that tend to have ranges centred on areas with common environmental conditions. Furthermore, it appears that niche-based characteristics may explain patterns of distribution and abundance from local habitats up to the scale of geographical ranges.

Keywords

Abundance, birds, density, geographical range, macroecology, niche breadth, range maps, occupancy, species range.

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INTRODUCTION

Studies of the distribution of species are typically conducted at two distinct spatial scales. At broad scales, many biogeographical and macroecological analyses utilize polygonal range maps as the fundamental unit of analysis (Brown, 1995; Brown *et al.*, 1996; Gaston, 2003). For taxa that are well known, these range maps may represent fairly detailed knowledge of species distributions, while for more obscure or cryptic groups range maps are more likely to be blob-like approximations. Range maps have been used to explore environmental factors that may limit species distributions over broad spatial scales (e.g. Root, 1988b; Thompson *et al.*, 1999) and to infer future distributions under climate change (Shafer *et al.*, 2001; Beaumont *et al.*, 2005). At finer scales, field studies often examine the distribution and abundance of species in local areas that are typically much smaller than the entire species range. Such local studies provide more detailed information about the climatic conditions, habitats and biotic contexts under which a given species occurs and is most abundant (e.g. Van Buskirk, 2005; Illera *et al.*, 2006).
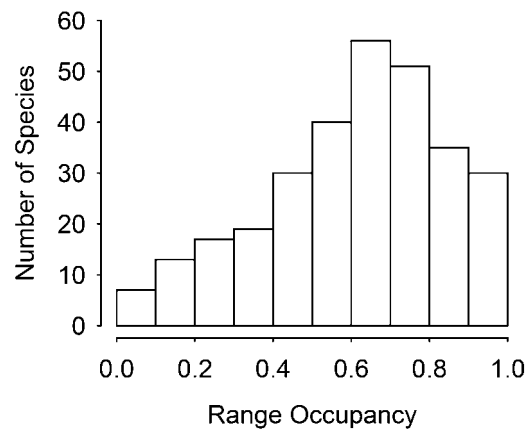
In recent years, survey- and atlas-based distributional data have become available at continental extents for a number of taxa, and the pairing of survey and range map data has led to novel analyses and insights (Hurlbert & White, 2005; Murphy *et al.*, 2006; Symonds & Johnson, 2006; W. Jetz, J. Watson & C. Sekerciouglu, unpublished). With regard to species distributions, the combination of these two data types allows for an analysis of the internal structure of geographical ranges, as opposed to the examination of distributional limits *per se*. In his seminal work on geographical ranges, Rapoport (1982) noted that species ranges are often discontinuously occupied, making the comparison to a slice of Swiss cheese. Studies explicitly looking at abundance
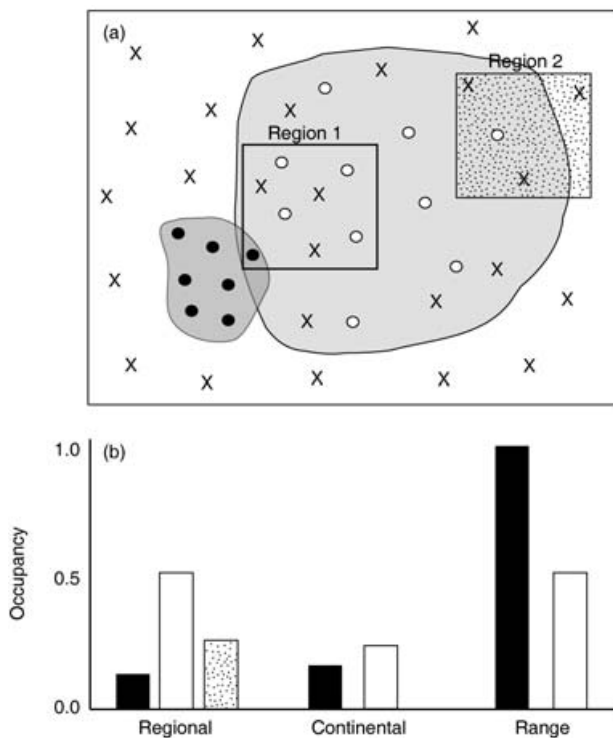
Figure 1 (a) Map showing two hypothetical species ranges (irregular polygons) across a 'continent' (the outer box). Squares represent two regions over which regional occupancy may be calculated. Symbols indicate the location of field surveys, with X denoting the absence of either focal species, and filled and hollow circles indicating the respective species' presence. (b) Three measures of occupancy calculated for each of the two species in (a). Regional occupancy for the light species is shown for both regions 1 and 2 as denoted by the stippling.

Figure 2 Range occupancy values for 298 species of North American land birds.

surfaces across the range have also documented regions of zero abundance inside the range boundaries (Root, 1988a; Price *et al.*, 1995). While a number of metrics exist for characterizing the spatial distribution of individuals or occupied sites within a range (see for example Pocock *et al.*, 2006), perhaps the simplest to interpret is 'proportional range occupancy' (*sensu* Hurlbert & White, 2005), or the proportion of surveyed sites inside the range boundaries at which a species is observed to occur. Species with high values of range occupancy are found uniformly and reliably across their range, while species with low values tend to occur more patchily (Fig. 1).

Proportional range occupancy differs substantially from other measures of the geographical distribution of species (Fig. 1). The two most prominent measures of distribution — extent of occurrence (the area within the geographical range boundary) and area of occupancy (the area over which the species actually occurs) (Gaston, 1991, 1994) — are effectively coarse and fine approximations of geographical range size. In contrast, range occupancy is a measure of the porosity of a species' range, and can be thought of as the ratio of area of occupancy to extent of occurrence. As such it is logically independent of range size *per se* and therefore potentially orthogonal to these more traditional

measures of distribution. Thus, a species might have a small area of occupancy (as measured by the total number of sites or quadrats it occupies), and yet a high value of range occupancy if those sites where it occurred represent the majority of sites spanned by its geographical range (Fig. 1). Conversely, a species with a relatively large area of occupancy may have a low value of range occupancy.

Range occupancy also differs in important ways from the 'occupancy' of most occupancy–abundance relationships. For such relationships examined over broad (e.g. continental) extents, occupancy is synonymous with 'area of occupancy' (see discussion above). However, as noted by Gaston (1996), the vast majority of abundance–occupancy relationships are examined over some limited extent (e.g. the Siskiyou Mountains, or Great Britain) much smaller than the geographical ranges of the species being examined. In this case, occupancy is a measure of space-filling in the same way as range occupancy. The crucial difference is that the former measure represents the level of space-filling over some limited extent that is identical for all species, while the latter measures average space-filling of each species across its entire geographical range (Fig. 1). Thus, range occupancy reveals an intrinsic property of a species, while inference based on 'occupancy' alone will be limited to the interaction between species and a particular regional extent.

In a previous study (Hurlbert & White, 2005), we found that range occupancy values varied tremendously for North American bird species (Fig. 2). Since range occupancy represents an under-explored characteristic of species distributions, it is important to understand why some species occur uniformly across their ranges while others are present over only small fractions of their total geographical extent. Here we undertake an exploratory analysis to determine how much of the variation in range occupancy can be explained by ecologically important species-level traits. A species trait is here defined loosely as any property that can be used to summarize characteristics of a species' distribution, morphology or ecology. We begin by discussing the species traits in our analysis and how each might affect range occupancy based on other macroecological relationships.

Potential correlates of range occupancy

(1) *Abundance.* Many studies have reported a positive relationship between average local abundance and aspects of distribution such as overall range size (Bock & Ricklefs, 1983; Brown & Maurer, 1987; Gaston & Blackburn, 1996; Murray *et al.*, 1998) or regional occupancy (Hanski, 1982; Brown, 1984; Gaston, 1996). We expect that species with higher mean densities may also have higher range occupancy because they will tend to have lower local extinction rates and higher rates of colonization of unoccupied regions within the range due to metapopulation dynamics (Hanski, 1991). It has been noted that positive abundance–occupancy relationships can result simply from the random placement of individuals within the domain (Wright, 1991). For the determination of range occupancy, the relevant domain is different for each species, dependent on both the size and position of that species' geographical range. As such, there is no simple null relationship that can be predicted between average abundance and range occupancy based on the random placement of individuals without incorporating additional species-specific information.

(2) *Body size.* Body size might affect range occupancy in three ways. First, body size is usually correlated negatively with population density (Damuth, 1981; Peters, 1983), and thus we expect a negative relationship between body size and range occupancy if abundance and occupancy are correlated as described above. For birds, the body size–density relationship is not particularly strong (Brown & Maurer, 1987), and thus the hypothesized relationship may be weak compared with other groups. Second, if larger-bodied species require larger contiguous areas of suitable habitat to meet home range or resource requirements (McNab, 1963; Peters, 1983; Haskell *et al.*, 2002), then they may be absent from more sites within their range compared with smaller-bodied species for which a greater proportion of the landscape might be habitable. Third, given that larger-bodied species typically have large ranges while smaller-bodied species may have large or small ranges (Brown, 1995), we might expect a positive relationship between body size and range occupancy if range size and occupancy are correlated as described below.

(3) *Range size.* Species with large ranges must be able to persist under a wide variety of climatic and/or habitat conditions, all else being equal. Therefore, large ranges are expected to have fewer internal discontinuities because the individuals of the species are more likely to be able to tolerate the conditions encountered throughout the range, and we expect a positive relationship between range size and range occupancy. Range size has also been shown to be positively correlated with abundance (e.g. Blackburn *et al.*, 1997; Harte *et al.*, 2001) and therefore it may also be correlated indirectly with range occupancy through relationship (1).

(4) *Niche breadth.* Related to relationship (3), species that are more catholic in their diet or habitat preferences (regardless of whether this generalism occurs within or between individuals) should be able to occupy their range more fully, while specialist species are expected to be absent from the portions of their range that do not meet their special requirements. Thus, we predict a positive relationship between niche breadth and range occupancy.

(5) *Niche position.* Niche position measures the degree to which the habitat or environmental conditions over which a species occurs reflects the average habitat conditions found across the entire study area (Dolédec *et al.*, 2000; Gregory & Gaston, 2000). Species with niches close to the average environmental conditions (i.e. those with low values for niche position) are likely to have high values of range occupancy for two reasons. First, such species occur over the most typical habitats and conditions in the study area, and may thus be expected to achieve higher densities (Gregory & Gaston, 2000; Heino, 2005). Second, niche position should be negatively correlated with range size (see relationship (3)) because the mean conditions over which a species occurs will tend to approach the mean environmental conditions (and thus niche position will approach zero) as range size approaches the size of the entire study area.

(6) *Habitat heterogeneity.* If the landscape is homogeneous and suitable, then both generalists and specialists are expected to have high levels of range occupancy. However, if the area over which a species occurs is heterogeneous, then specialists are only expected to occur where their diet/habitat/climatic needs are met, while generalists are still expected to occur nearly everywhere. Thus, range occupancy should be determined by an interaction between the niche breadth of a species and the habitat heterogeneity encompassed by its geographical range.

(7) *Population trend.* A species that has been undergoing steady population decline and/or range contraction may have a low value of range occupancy because the range map is an overestimate of its current distribution. Conversely, if a species has been steadily increasing in global abundance, then portions of the range that were previously unoccupied are more likely to become colonized. Therefore, we expect a positive relationship between population trend and range occupancy. This relationship is analogous to the intraspecific abundance–occupancy relationship shown over more limited extents (Gaston *et al.*, 2000).

(8) *Migratory status.* Permanent residents must tolerate a wider spectrum of environmental variation than migrants, and therefore should be able to occupy their range more fully.

(9) *Trophic and foraging groups.* Although we had no a priori expectations, we also compared range occupancy values among groups that have been compared in other types of occupancy–abundance relationships. We tested for differences in range occupancy between different trophic levels and foraging strategies (Holt & Gaston, 2003).

While this is not an exhaustive list of all the species traits that could potentially influence range occupancy, it contains many ecologically relevant traits to aspects of distribution and therefore represents a good starting point for understanding observed variability across species.

METHODS

We calculated data on range occupancy for 298 North American land bird species as described in Hurlbert & White (2005). Range occupancy represents the ratio of the number of surveys on

which a species was observed within its range to the number of surveys on which it was expected to occur (i.e. the total number of surveys within its range). We used digital range maps of breeding distributions from Ridgely *et al.* (2003), and survey data from the North American Breeding Bird Survey (BBS; Sauer *et al.*, 2005). Each BBS survey consists of 50 point counts evenly spaced along a 40-km route. At each point along the route, a 3-min count of all birds seen or heard within 400 m is conducted. A species was counted as present at a site if it was observed at least once over the 10-year period from 1993 to 2002. This temporal window minimizes the number of false absences where species present in a given year were simply too rare to be observed.

We also gathered or calculated data on a number of species-level traits that might explain variation in range occupancy. Mean species body mass was obtained from Dunning's (1993) *Handbook of Avian Body Masses*. Mean abundance on BBS surveys where a species is present was calculated for the period 1993 to 2002. Data on survey-wide population trends for each species, measured in per cent per year over the period 1966 to 2004, were obtained from Sauer *et al.* (2005) for 278 of the 298 species. Population trend estimates were not used if data for that species were considered to have an 'important deficiency' (Sauer *et al.*, 2005). The area of the breeding range ('range size') was calculated from the digital range maps using a geographical information system. Species were categorized as belonging to different foraging guilds (aerial forager, bark gleaner, foliage gleaner, ground gleaner, hawker and hover/gleaner) and trophic groups (granivores, nectarivores, omnivores, omnivorous insectivores and strict insectivores) according to Ehrlich *et al.* (1988). Herbivores (primarily grouse and ptarmigan species) were not included because they are few in number and often not well surveyed by BBS routes. Species were also categorized as being year-round residents, short-distance migrants or Neotropical migrants.

We calculated a regional measure of niche breadth, as well as niche position, for each species using a multivariate principal components-based approach (the 'outlying mean index') described by Dolédec *et al.* (2000; see also Heino, 2005). Each BBS route was characterized by the following environmental variables within a 40-km radius (the length of a BBS route) of the survey's starting coordinates: mean summer temperature (June–August), mean winter temperature (December–February), mean summer normalized difference vegetation index (NDVI), mean winter NDVI, annual precipitation, mean elevation and elevational range. Temperature and precipitation data are mean values from 1961 to 1990 from the Climatic Research Unit (http://www.cru.uea.ac.uk/cru/data/tmc.htm) and have a 10′ base resolution. The NDVI is a remotely sensed index of greenness related to productivity (Box *et al.*, 1989; Paruelo *et al.*, 1997), and data represent mean values of the index from 1982 to 2000, excluding 1994, at a resolution of 0.1°. Elevational data are from a 30″ digital elevational model made available by the US Geological Survey (http://edc.usgs.gov/products/elevation/gtopo30.html). The measure of niche position ('marginality') described by Dolédec *et al.* (2000) characterizes the abundance weighted deviation of a species distribution (based on BBS data) from the overall mean habitat conditions of all surveys in North America based on the above environmental variables. The corresponding measure of niche breadth ('tolerance') captures variation in those environmental variables encompassed by the species' observed distribution. This niche breadth measure has the advantage of being explicitly linked to environmental conditions and is thus less susceptible to the inclusion of aggregation behaviour due to non-niche-based characteristics (see below).

A species' niche breadth may also be reflected in the aggregation of individuals across the landscape. While generalists might potentially occur uniformly over an area, specialist species are expected to be restricted to pockets of suitable habitat. Therefore, we also calculated an index of local aggregation that ranks how spatially aggregated or clumped individuals of a species tend to be along a BBS survey route relative to the other species occurring on that route. We grouped the 50 point counts into five groups of ten consecutive point counts to avoid problems related to estimating aggregation when the number of individuals is much smaller than the number of spatial bins. However, the results were similar to those obtained by examining aggregation across the 50 individual point counts (correlation coefficient for the two methods = 0.88). For each survey, we ranked species according to their Morisita index of aggregation (Morisita, 1959), a measure essentially independent of population density (Hurlbert, 1990). This ranking was then standardized by the total number of species observed on the survey. This results in each species having a value between 0 and 1, indicating how spatially aggregated it is relative to the other species found on that survey. This ranking and standardization controls for differences in the average habitat heterogeneity and other factors across the sites at which a species occurs. The rank-standardized measure of aggregation was averaged over a 3-year period (2003–2005) for each species on each route and these values were then averaged over all of the surveys on which a species occurred, yielding a measure of mean relative local aggregation at the scale of a local BBS survey. This measure has the potential advantage of allowing the data to tell us how the species view the environment as opposed to the regional measure where the niche axes of relevance must be determined a priori and are often constrained by the availability of data. However, it has the disadvantage that factors other than niche breadth (e.g. social behaviour, territoriality) may contribute to patterns of spatial aggregation.

Lastly, we characterized the habitat heterogeneity encompassed by a species' range using a digital version of Reichenbacher *et al.*'s (1998) map of *North American Biotic Communities*. Habitat heterogeneity was measured both as the total number of distinct biome types encountered within a species' breeding range, as well as a Shannon–Wiener index of biome diversity based on the areal representation of each biome type within the range. Note that in addition to providing a characterization of the landscape occupied by each species, these metrics could also be viewed as alternative measures of niche breadth.

We modelled range occupancy as a function of predictor variables using linear multiple regression. Because range occupancy values range from 0 to 1, and therefore nonlinear relationships are expected, we modelled occupancy using a logit transformation.
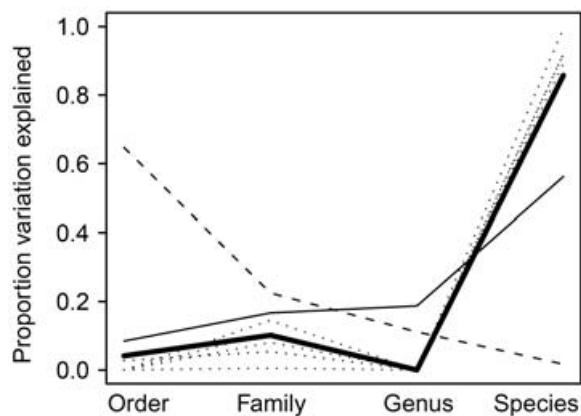
Figure 3 Proportion of variation explained at different taxonomic levels for range occupancy values (bold line) and eight other variables (see Table 1) used to predict range occupancy. Note that body mass (dashed line) is the only variable to show strong phylogenetic conservatism. The majority of the variation in all other variables occurs at the species level. The solid line is average abundance. Variance components were estimated using a nested ANOVA.

We examined models using all variables for the 278 species for which all data were available, and we also examined models excluding population trend for all 298 species. In addition, we examined a smaller model of what appeared to be core predictor variables. One consideration for comparative analyses of this sort is that species traits are often considered not to be phylogenetically independent (Harvey & Pagel, 1991). We conducted a nested analysis of variance on each of our dependent and independent variables in order to partition the variance explained at the class, family, genus and species levels (Fig. 3). We found that apart from body size (see Smith *et al.*, 2004), all variables, including range occupancy, exhibited very little evidence of phylogenetic conservatism, with most of the variation in traits being explained at the species level. As such, we conducted simple cross-species analyses using ordinary least squares regression rather than

employing any phylogenetic regression methods (see Pocock *et al.*, 2006, for discussion and justification). Some variables were log-transformed to satisfy statistical assumptions (see Tables 1 and 2).

RESULTS

The correlation matrix of independent variables and range occupancy is shown in Table 1. Among independent variables, moderately strong positive correlations existed among the number of biomes, biome diversity, range size, and regional niche breadth. Range size was negatively correlated with niche position as expected.

The strongest univariate correlates of range occupancy were positive relationships with mean abundance and local niche breadth, and a negative relationship with niche position (Table 1, Fig. 4). Range occupancy was more weakly correlated with range size, the number of biomes and regional niche breadth, and showed little evidence of correlation with body mass, biome diversity or population trend.

A full multiple regression model including all variables as well as an interaction term between regional niche breadth and biome diversity explained 55% of the variation in range occupancy across 278 bird species (Table 2a). The model identified a positive interaction between biome diversity and regional niche breadth rather than the negative interaction predicted (other combinations of niche breadth measures and biome diversity measures produced similar results). Nearly all of the explained variation was derived from only three core variables: mean local abundance, local aggregation and regional niche position (Fig. 5). For the 278 species data subset, these variables explained 52% of the variation in range occupancy (not shown), and for the complete data set they explained 54% of the variation (Table 2b). We used Akaike's information criterion (AIC) to compare this core model with other three-predictor models made up of other potentially strong predictors based on Table 1. The core model was identified as superior with the next best model having a ΔAIC value of 138. ΔAIC values >10 are considered to represent

Table 1 Correlation matrix of species traits and range occupancy. Traits are abbreviated as follows: logN, $\log_{10}$ of the geometric mean of abundance on survey routes where a species is present; logM, $\log_{10}$ body mass; logRS, $\log_{10}$ range size; BiomeH, biome diversity (Shannon–Wiener) within the range; Biomes, number of biomes within the range; RegNB, regional niche breadth; logNP, $\log_{10}$ niche position; LocAgg, local aggregation; PopTrend, population trend over 1966–2004; RO, range occupancy, logit transformed. Correlation coefficients are based on data for 298 land bird species, with the exception of correlation coefficients for population trend, which are based on a subset of 278 species. Absolute values of $r > 0.18$ are significant at $P < 0.001$. Absolute values > 0.4 are shown in bold.

	logM	logRS	BiomeH	Biomes	RegNB	logNP	LocAgg	PopTrend	RO
logN	0.11	0.17	0.20	0.25	0.10	−0.18	0.14	−0.08	**0.53**
logM		−0.01	0.08	0.09	0.07	−0.02	−0.31	0.09	0.01
logRS			0.27	**0.60**	**0.47**	**−0.56**	0.15	0.02	0.32
BiomeH				**0.83**	**0.47**	−0.01	0.10	0.07	0.09
Biomes					**0.60**	−0.36	0.06	0.07	0.21
RegNB						−0.25	0.05	0.11	0.19
logNP							−0.06	−0.08	**−0.45**
LocAgg								0.09	**0.42**
PopTrend									0.11
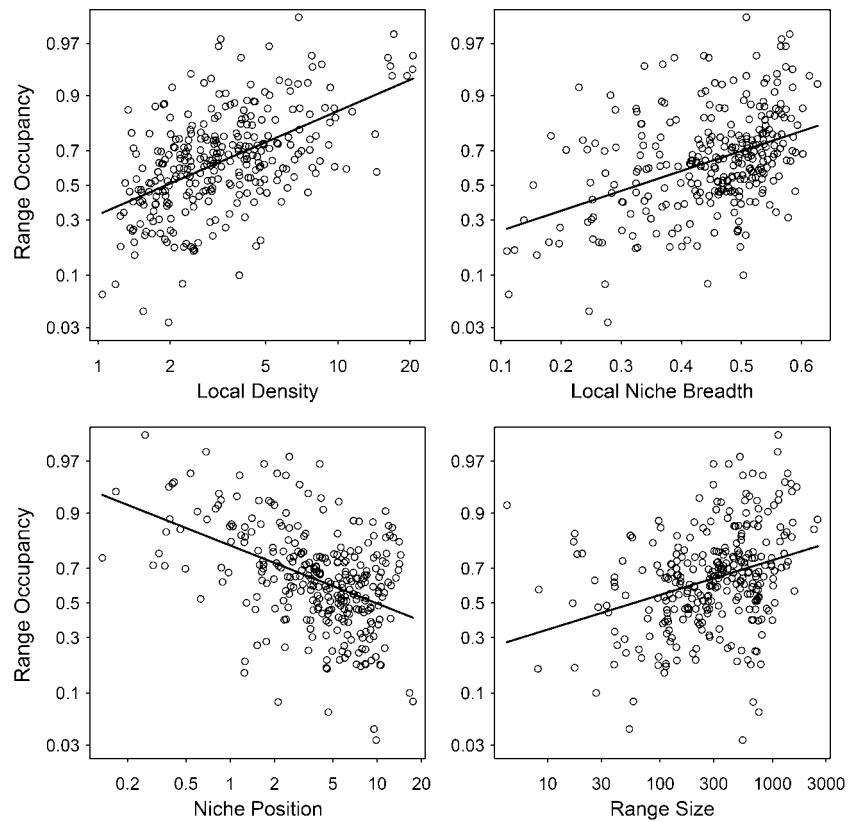
Figure 4 Major univariate relationships between range occupancy (logit transformed) and four predictor variables across 298 North American bird species. Lines represent ordinary least squares regressions.

Table 2 (a) Full regression model explaining range occupancy (logit transformed) as a function of species traits for the 278 land bird species for which population trend data are available. (b) The core regression model explaining range occupancy as a function of the three best predictor variables for all 298 species.

Variable	Estimate	SE	t	P
(a) Full model: $F_{10,267} = 35.21$, adjusted $R^2 = 0.55$				
Intercept	−1.01	1.07	−0.94	0.35
Log abundance	1.86	0.19	9.73	<0.0001
Log body mass	0.12	0.09	1.31	0.19
Log range size	−0.17	0.17	−1.00	0.32
Population trend	0.03	0.02	1.50	0.14
Log niche position	−1.27	0.17	−7.60	<0.0001
Local aggregation	3.84	0.48	7.94	<0.0001
Regional niche breadth	1.73	0.40	4.32	<0.0001
Number of biomes	−0.002	0.014	−0.12	0.91
Biome diversity	0.30	0.20	1.47	0.14
Regional niche breadth × biome diversity	−0.77	0.19	−4.08	<0.0001
(b) Core model: $F_{3,293} = 114.7$, adjusted $R^2 = 0.54$				
Intercept	−1.62	0.24	−6.75	<0.0001
Log abundance	2.01	0.19	10.39	<0.0001
Local aggregation	4.12	0.46	8.95	<0.0001
Log niche position	−1.15	0.13	−9.10	<0.0001

almost no support for the competing models (Burnham & Anderson, 2002).

Finally, no biologically meaningful differences in range occupancy were identified based on migratory class ($F_{2,295} = 0.13$, $P = 0.88$), foraging strategy ($F_{6,291} = 0.31$, $P = 0.93$) or trophic level ($F_{5,285} = 0.54$, $P = 0.74$).

DISCUSSION

Our study highlights previously unexamined connections between the ecology of species and their geographical distributions. For 298 species of North American birds, we calculated range occupancy, a simple measure of the degree to which species
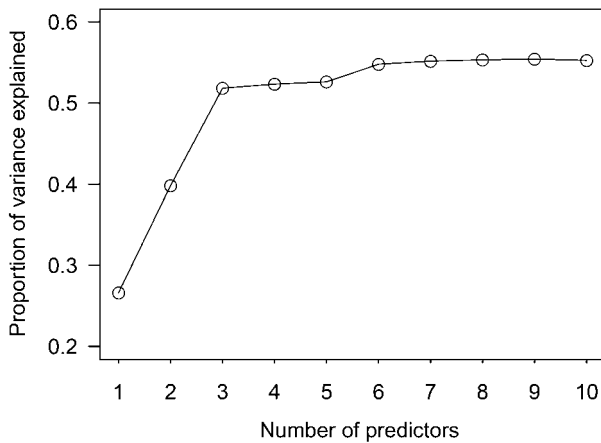
Figure 5 The maximum proportion of variance explained (adjusted R^2) by models predicting range occupancy as a function of the number of predictors included in the model.

occupy sites within their geographical range. While many species are distributed quite continuously across the entire range, other species ranges are better likened to slices of Swiss cheese, with numerous discontinuities in species presence.

The low values of range occupancy for some species may simply reflect biases in the habitats censused by the BBS. For example, most BBS routes do not survey high alpine environments, and so species characteristic of such environments [e.g. rosy finch (*Leucosticte*) and ptarmigan (*Lagopus*) species] may be undersampled. Another factor leading to low values of range occupancy could be the inaccuracy of range maps that overestimate the area of occurrence of a species. However, owing to the legions of amateur ornithologists and the ubiquity of local birding societies, knowledge of bird distributions, more so than for any other taxon, is likely to be the most complete and accurate information available on species distributions. Thus, we are confident that the variation we see in range occupancy values across species reflects real variation in the nature of species geographical distributions.

We found that the majority of the variation in range occupancy was explained by three relatively independent ecological traits. First, we identified a positive relationship between mean local abundance and range occupancy. While, to our knowledge, this is the first study to assess correlates of range occupancy, the observed relationship is consistent with the commonly observed interspecific abundance–occupancy relationship described for a variety of taxa (Gaston, 1996; Gaston *et al.*, 2000). Combined with correlations between abundance and range size this suggests that species that are more locally abundant tend to be both more widespread with respect to the extent of their range (Blackburn *et al.*, 1997; Harte *et al.*, 2001), and more widespread within their range.

A number of explanations have been put forward to explain positive abundance–occupancy relationships (see the Introduction for distinctions between these patterns). Brown (1984) suggested that a positive relationship between abundance and occupancy results from the positive dependence of each variable on niche

breadth. However, our data on breeding birds show only a weak correlation between local density and niche breadth. Other hypotheses have focused on the role of metapopulation dynamics (Hanski, 1991) or vital rates (Holt *et al.*, 1997; Freckleton *et al.*, 2006) in generating abundance–occupancy relationships, but we are unable to evaluate them definitively with the present data. However, we did observe a tendency towards higher variance in range occupancy at lower densities consistent with a recent formalization of the vital rates hypothesis (Freckleton *et al.*, 2006). The idea that species occurring at higher densities have lower local extinction rates as well as increased occupancy of less favourable habitat via mass effects (Shmida & Wilson, 1985) is an intuitive explanation for the observed correlation and deserves further examination.

The second important variable identified as a predictor of range occupancy is a measure of the spatial aggregation of individuals along each 40-km BBS route. Species with individuals that tend to occur uniformly across individual BBS routes (relative to other species) also tend to occur more uniformly throughout their geographical range. Species with relatively aggregated distributions at the local scale tend to be more patchily distributed throughout their range. A number of authors have suggested that species distributions are self-similar or nearly so across scales (Collins & Glenn, 1990; Kunin, 1998; Harte *et al.*, 1999). While our data do not bear on self-similarity *per se*, they do clearly support the idea that characteristics of the spatial distribution of species are correlated across scales.

While the relationship with local aggregation is suggestive of niche breadth as a determinant of range occupancy, it could also be due in part to social rather than niche-related aggregation of individuals. This could explain why local aggregation and regional niche breadth are only weakly correlated, though this could also be explained by an insufficiency in the variables available to characterize the niche. However, in addition to the local (aggregation-based) measure, our regional (environmentally based) measure of niche breadth was also positively related to range occupancy in both univariate and multivariate analyses, and we found a positive correlation between the number of biome types encompassed by a species range and range occupancy. Taken together, these results suggest that generalist species are more widely distributed within their ranges than specialists, and support a niche-based view of abundance and distribution (Brown, 1984, 1995; Kolb *et al.*, 2006). Further work attempting to distinguish niche-based and non-niche-based aggregation should help inform whether or not there is an additional contribution of factors such as social aggregation or dispersal abilities in determining range occupancy.

Finally, niche position had a strong negative effect on range occupancy. Recall that niche position reflects how similar the average environmental conditions across a species' range are to the average environmental conditions across the entire sample space (i.e. North America). Species that occur solely in rare habitats have higher values of niche position and tend to have lower values of range occupancy. Niche position is naturally confounded with range size because the average environmental conditions across extremely large ranges will tend to be similar to

the average conditions across the continent. Range occupancy did increase with range size, consistent with a niche breadth-based explanation as described above. However, the fact that niche position is a better predictor of range occupancy than range size suggests that the average conditions over which a species occurs are at least as important as the range of conditions for determining how uniformly a species is found across its range. Other studies have similarly documented a negative relationship between niche position and various measures of abundance or distribution in British birds (Gregory & Gaston, 2000), freshwater fish (Tales *et al.*, 2004) and aquatic inverte-brates (Heino, 2005).

Our results highlighted a number of variables that are notably uncorrelated with range occupancy. Body size, despite its relevance to various life-history traits and to individual resource requirements (Peters, 1983; Calder, 1984), explained almost none of the variation in range occupancy. This is perhaps not surprising given that population density, the intermediate variable hypothesized to link body size and range occupancy, itself shows only a very weak correlation with body size in birds (Brown & Maurer, 1987). It is also possible that the body size–range size relationship might act to cancel out any body size–density effects. Population trend over the past 40 years was a similarly weak predictor of range occupancy. We also found little evidence for differences in range occupancy among different trophic levels, foraging strategies or migratory groups. This last result is in contrast to an earlier study that described the ranges of migrants as being more highly fragmented than those of residents (Linder *et al.*, 2000).

In her canonical work on commonness and rarity, Rabinowitz (1981) identified three axes along which species could be described as rare: range size, average population size and habitat specificity. A growing body of literature describes the complex interrelations among these variables, suggesting that they are far from orthogonal (e.g. Brown, 1995; Gregory & Gaston, 2000; Gaston, 2003; McGill & Collins, 2003; Heino, 2005; Murphy *et al.*, 2006; Pocock *et al.*, 2006). Here, we have analysed a distinctly different measure of distribution, namely range occupancy, and found it to be strongly tied to these others. In fact, range occupancy was the strongest correlate of both abundance and local niche breadth among all of the ecological variables examined despite the fact that niche breadth and abundance were only weakly correlated with each other. This suggests that range occupancy may represent an unappreciated link between different characterizations of species distributions.

In this study we have focused on the simplest possible characterization of range porosity. However, range occupancy provides no information regarding the spatial distribution of occupied versus unoccupied sites within the range. Metrics that capture the spatial aggregation or dispersion of these patches as in fractal analysis (e.g. Hartley *et al.*, 2004; Pocock *et al.*, 2006) are expected to be more accurate descriptors of range fragmentation and may provide additional insights into the processes underlying observed patterns of porosity. In addition, several authors have advocated the examination of abundance surfaces (e.g. Linder *et al.*, 2000; McGill & Collins, 2003). Looking at abundance as well as occupancy may reveal additional complexity in the responses of species to the environment and help to explain why some species fail to occur in certain areas within their range.

Range maps are important tools that can tell us much about the factors underlying species distributions. However, it is important to realize that another important measure of distribution is related to the internal structure of geographical ranges. North American bird species exhibit a tremendous amount of variation in the proportion of sites they occupy within their range boundaries, and the majority of this variation can be explained by species-level macroecological properties. The traits most correlated with low values of range occupancy — low population densities, small range sizes and narrow niche breadths — are also traits often associated with increased extinction risk (Purvis *et al.*, 2000; Cardillo *et al.*, 2005). Low values of range occupancy are also indicative of geographical range fragmentation, which may increase the risk of initially local, and eventually global, extinction (Maurer & Nott, 1998). Finally, for many species, conservation status is based on range size, yet our study indicates that range size alone may substantially overestimate a species' actual distribution. This suggests that threat classification as determined by the IUCN (2001) or other conservation groups should address range occupancy in addition to range size (W. Jetz, J. Watson & C. Sekerciouglu, unpublished).

Finally, we have recently shown major differences in the results of ecological analyses generated using data based on range maps and surveys (Hurlbert & White, 2005). The characteristic porosity of species ranges implies that range map-based analyses represent distribution at an inherently coarser spatial grain than survey data. Since much of ecology is interested in processes that are operating at local spatial scales it is important to be able to infer processes at those scales (McPherson *et al.*, 2006). Unfortunately geographical-scale survey data are extremely rare, making range map-based analyses much more tractable. By developing models of range occupancy based on species-level characteristics, and environmental correlates (Hurlbert & White, 2005; McPherson *et al.*, 2006), it may eventually be possible to estimate the composition and diversity of local assemblages using range map data.

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Allen Hurlbert is broadly interested in macroecology, with specific research foci including both local and global scale patterns of species richness, turnover in species composition in space and time, the structure of species geographical ranges and avian ecology.

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