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Ecological Correlates of Geographic Range Occupancy in North American Birds

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6 **Ecological correlates of geographic range occupancy**
7 **in North American birds**
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35 **ABSTRACT**

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

41 **Location** North America.

42 **Methods** We used survey data from 1993-2002 from the North American Breeding Bird
43 Survey along with digital range maps produced by NatureServe to calculate range occupancy for
44 298 species of terrestrial birds. We tested whether species traits explained variation in range
45 occupancy values using linear regression techniques.

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

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

54 **Introduction**

55 Studies of the distribution of species are typically conducted at two distinct spatial scales. At
56 broad scales, many biogeographic and macroecological analyses utilize polygonal range maps as
57 the fundamental unit of analysis (Brown 1995; Brown *et al.* 1996; Gaston 2003). For taxa that
58 are well known, these range maps may represent fairly detailed knowledge of species'
59 distributions, while for more obscure or cryptic groups range maps are more likely to be blob-
60 like approximations. Range maps have been used to explore environmental factors that may limit
61 species distributions over broad spatial scales (e.g., Root 1988b; Thompson *et al.* 1999), and to
62 infer future distributions under climate change (Shafer *et al.* 2001; Beaumont *et al.* 2005). At
63 finer scales, field studies often examine the distribution and abundance of species in local areas
64 that are typically much smaller than the entire species range. Such local studies provide more
65 detailed information about the climatic conditions, habitats, and biotic contexts under which a
66 given species occurs and is most abundant (e.g., Van Buskirk 2005; Illera *et al.* 2006).

67 In recent years, survey- and atlas-based distributional data have become available at
68 continental extents for a number of taxa, and the pairing of survey and range map data has led to
69 novel analyses and insights (Hurlbert & White 2005; Murphy *et al.* 2006; Symonds & Johnson
70 2006; Walter Jetz, James Watson & Cagan Sekercioglu unpublished manuscript). With regard
71 to species' distributions, the combination of these two data types allows for an analysis of the
72 internal structure of geographic ranges, as opposed to the examination of distributional limits *per*
73 *se*. In his seminal work on geographic ranges, Rapoport (1982) noted that species ranges are
74 often discontinuously occupied, making the comparison to a slice of Swiss cheese. Studies
75 explicitly looking at abundance surfaces across the range have also documented regions of zero
76 abundance inside the range boundaries (Root 1988a; Price *et al.* 1995). While a number of

77 metrics exist for characterizing the spatial distribution of individuals or occupied sites within a
78 range (see for example Pocock *et al.* 2006), perhaps the simplest to interpret is ‘proportional
79 range occupancy’ (*sensu* Hurlbert and White 2005), or the proportion of surveyed sites inside the
80 range boundaries at which a species is observed to occur. Species with high values of range
81 occupancy are found uniformly and reliably across their range, while species with low values
82 tend to occur more patchily (Fig. 1).

83 Proportional range occupancy differs substantially from other measures of the geographic
84 distribution of species (Fig. 1). The two most prominent measures of distribution, extent of
85 occurrence (the area within the geographic range boundary) and area of occupancy (the area over
86 which the species actually occurs) (Gaston 1991, 1994), are effectively coarse and fine
87 approximations of geographic range size. In contrast, range occupancy is a measure of the
88 porosity of a species range, and can be thought of as the ratio of area of occupancy to extent of
89 occurrence. As such it is logically independent of range size *per se* and therefore potentially
90 orthogonal to these more traditional measures of distribution. Thus, a species might have a small
91 area of occupancy (as measured by the total number of sites or quadrats it occupies), and yet a
92 high value of range occupancy if those sites where it occurred represent the majority of sites
93 spanned by its geographic range (Fig. 1). Conversely, a species with a relatively large area of
94 occupancy may have a low value of range occupancy.

95 Range occupancy also differs in important ways from the ‘occupancy’ of most
96 occupancy-abundance relationships. For such relationships examined over broad (e.g.
97 continental) extents, occupancy is synonymous with ‘area of occupancy’ (see discussion above).
98 However, as noted by Gaston (1996), the vast majority of abundance-occupancy relationships are
99 examined over some limited extent (e.g. the Siskiyou Mountains, or Great Britain) much smaller

100 than the geographic ranges of the species being examined. In this case, occupancy is a measure
101 of space-filling in the same way as range occupancy. The crucial difference is that the former
102 measure represents the level of space-filling over some limited extent that is identical for all
103 species, while the latter measures average space-filling of each species across its entire
104 geographic range (Fig. 1). Thus, range occupancy reveals an intrinsic property of a species, while
105 inference based on ‘occupancy’ alone will be limited to the interaction between species and a
106 particular regional extent.

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

117

118 **Potential Correlates of Range Occupancy**

119 1. *Abundance*. Many studies have reported a positive relationship between average local
120 abundance and aspects of distribution such as overall range size (Bock & Ricklefs 1983; Brown
121 & Maurer 1987; Gaston & Blackburn 1996; Murray *et al.* 1998) or regional occupancy (Hanski
122 1982; Brown 1984; Gaston 1996). We expect that species with higher mean densities may also

123 have higher range occupancy because they will tend to have lower local extinction rates and
124 higher rates of colonization of unoccupied regions within the range due to metapopulation
125 dynamics (Hanski 1991). It has been noted that positive abundance-occupancy relationships can
126 result simply by the random placement of individuals within the domain (Wright 1991). For
127 determining range occupancy, the relevant domain is different for each species, dependent on
128 both the size and position of that species' geographic range. As such, there is no simple null
129 relationship that can be predicted between average abundance and range occupancy based on the
130 random placement of individuals without incorporating additional species-specific information.

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

140 Alternatively, given that larger-bodied species typically have large ranges while smaller-bodied
141 species may have large or small ranges (Brown 1995), we might expect a positive relationship
142 between body size and range occupancy if range size and occupancy are correlated as described
143 below.

144 3. *Range size*. Species with large ranges must be able to persist under a wide variety of
145 climatic and/or habitat conditions, all else being equal. Therefore, large ranges are expected to

146 have fewer internal discontinuities because the individuals of the species are more likely to be
147 able to tolerate the conditions encountered throughout the range, and we expect a positive
148 relationship between range size and range occupancy. Range size has also been shown to be
149 positively correlated with abundance (e.g., Blackburn *et al.* 1997; Harte *et al.* 2001) and
150 therefore it may also be correlated indirectly with range occupancy through Relationship 1.

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

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

166 6. *Habitat heterogeneity.* If the landscape is homogeneous and suitable, then both
167 generalists and specialists are expected to have high levels of range occupancy. However, if the
168 area over which a species occurs is heterogeneous, then specialists are only expected to occur

169 where their diet/habitat/climatic needs are met, while generalists are still expected to occur
170 nearly everywhere. Thus, range occupancy should be determined by an interaction between the
171 niche breadth of a species and the habitat heterogeneity encompassed by its geographic range.

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

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

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

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

188

189 **Methods**

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

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

201 We also gathered or calculated data on a number of species-level traits that might explain
202 variation in range occupancy. Mean species body mass was obtained from Dunning's (1993)
203 Handbook of Avian Body Masses. Mean abundance on BBS surveys where a species is present
204 was calculated for the period 1993-2002. Data on survey-wide population trends for each
205 species, measured in percent per year over the period 1966-2004, were obtained from Sauer et al.
206 (2005) for 278 of the 298 species. Population trend estimates were not used if data for that
207 species were considered to have an 'important deficiency' (Sauer *et al.* 2005). Area of the
208 breeding range ('range size') was calculated from the digital range maps using a geographic
209 information system. Species were categorized as belonging to different foraging guilds (aerial
210 forager, bark gleaner, foliage gleaner, ground gleaner, hawkler, and hover/gleaner) and trophic
211 groups (granivores, nectarivores, omnivores, omnivorous insectivores, and strict insectivores)
212 according to Ehrlich et al. (1988). Herbivores (primarily grouse and ptarmigan species) were not
213 included because they are few in number and often not well surveyed by BBS routes. Species

214 were also categorized as being year-round residents, short distance migrants, or Neotropical
215 migrants.

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

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

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

267 We modeled range occupancy as a function of predictor variables using linear multiple
268 regression. Because range occupancy values range from 0 to 1 and therefore non-linear
269 relationships are expected, we modeled occupancy using a logit transformation. We examined
270 models using all variables for the 278 species for which all data were available, and we also
271 examined models excluding population trend for all 298 species. In addition, we examined a
272 smaller model of what appeared to be core predictor variables. One consideration for
273 comparative analyses of this sort is that species traits are often considered not to be
274 phylogenetically independent (Harvey & Pagel 1991). We conducted a nested analysis of
275 variance on each of our dependent and independent variables in order to partition the variance
276 explained at the class, family, genus, and species levels (Fig. 3). We found that aside from body
277 size (see Smith *et al.* 2004), all variables including range occupancy, exhibited very little
278 evidence of phylogenetic conservatism with most of the variation in traits being explained at the
279 species level. As such, we conducted simple cross-species analyses using ordinary least squares
280 regression rather than employing any phylogenetic regression methods (see Pocock *et al.* 2006
281 for discussion and justification). Some variables were log-transformed to satisfy statistical
282 assumptions (see Tables 1 and 2).

283

284 **Results**

285 The correlation matrix of independent variables and range occupancy is shown in Table 1.

286 Among independent variables, moderately strong positive correlations existed among the number
287 of biomes, biome diversity, range size, and regional niche breadth. Range size was negatively
288 correlated with niche position as expected.

289 The strongest univariate correlates of range occupancy were positive relationships with
290 mean abundance and local niche breadth, and a negative relationship with niche position (Table
291 1, Fig. 4). Range occupancy was more weakly correlated with range size, the number of biomes,
292 and regional niche breadth, and showed little evidence of correlation with body mass, biome
293 diversity, or population trend.

294 A full multiple regression model including all variables as well as an interaction term
295 between regional niche breadth and biome diversity explained 55% of the variation in range
296 occupancy across 278 bird species (Table 2a). The model identified a positive interaction
297 between biome diversity and regional niche breadth rather than the negative interaction predicted
298 (other combinations of niche breadth measures and biome diversity measures produced similar
299 results). Nearly all of the explained variation was derived from only three core variables: mean
300 local abundance, local aggregation, and regional niche position (Fig. 5). For the 278 species data
301 subset, these variables explained 52% of the variation in range occupancy (not shown), and for
302 the complete dataset they explained 54% of the variation (Table 2b). We used Akaike's
303 Information Criterion to compare this core model to other three-predictor models made up of
304 other potentially strong predictors based on Table 1. The core model was identified as superior

305 with the next best model having a delta AIC value of 138. Delta AIC values >10 are considered
306 to represent almost no support for the competing models (Burnham & Anderson 2002).

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

310

311 **Discussion**

312 Our study highlights previously unexamined connections between the ecology of species and
313 their geographical distributions. For 298 species of North American birds, we calculated range
314 occupancy, a simple measure of the degree to which species occupy sites within their geographic
315 range. While many species are distributed quite continuously across the entire range, other
316 species' ranges are better likened to slices of Swiss cheese with numerous discontinuities in
317 species presence.

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

328 We found the majority of the variation in range occupancy to be explained by three
329 relatively independent ecological traits. First, we identified a positive relationship between mean
330 local abundance and range occupancy. While, to our knowledge, this is the first study to assess
331 correlates of range occupancy, the observed relationship is consistent with the commonly
332 observed interspecific abundance-occupancy relationship described for a variety of taxa (Gaston
333 1996; Gaston *et al.* 2000). Combined with correlations between abundance and range size this
334 suggests that species that are more locally abundant tend to be both more widespread with
335 respect to the extent of their range (Blackburn *et al.* 1997; Harte *et al.* 2001), and more
336 widespread within their range.

337 A number of explanations have been put forward to explain positive abundance-
338 occupancy relationships (see Introduction for distinctions between these patterns). Brown (1984)
339 suggested that a positive relationship between abundance and occupancy results from the
340 positive dependence of each variable on niche breadth. However, our data on breeding birds
341 show only a weak correlation between local density and niche breadth. Other hypotheses have
342 focused on the role of metapopulation dynamics (Hanski 1991) or vital rates (Holt *et al.* 1997;
343 Freckleton *et al.* 2006) in generating abundance-occupancy relationships, but we are unable to
344 definitively evaluate them with the present data. However, we did observe a tendency toward
345 higher variance in range occupancy at lower densities consistent with a recent formalization of
346 the vital rates hypothesis (Freckleton *et al.* 2006). The idea that species occurring at higher
347 densities have lower local extinction rates as well as increased occupancy of less favorable
348 habitat via mass effects (Shmida & Wilson 1985) is an intuitive explanation for the observed
349 correlation and deserves further examination.

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

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

373 Finally, niche position had a strong negative effect on range occupancy. Recall that niche
374 position reflects how similar the average environmental conditions across a species' range are to
375 the average environmental conditions across the entire sample space (i.e., North America).
376 Species that occur solely in rare habitats have higher values of niche position and tend to have
377 lower values of range occupancy. Niche position is naturally confounded with range size because
378 the average environmental conditions across extremely large ranges will tend to be similar to the
379 average conditions across the continent. Range occupancy did increase with range size,
380 consistent with a niche breadth-based explanation as described above. However, the fact that
381 niche position is a better predictor of range occupancy than range size suggests that the average
382 conditions over which a species occurs is at least as important as the range of conditions for
383 determining how uniformly a species is found across its range. Other studies have similarly
384 documented a negative relationship between niche position and various measures of abundance
385 or distribution in British birds (Gregory & Gaston 2000), freshwater fish (Tales *et al.* 2004), and
386 aquatic invertebrates (Heino 2005).

387 Our results highlighted a number of variables that are notably uncorrelated with range
388 occupancy. Body size, despite its relevance to various life history traits and to individual
389 resource requirements (Peters 1983; Calder 1984), explained almost none of the variation in
390 range occupancy. This is perhaps not surprising given that population density, the intermediate
391 variable hypothesized to link body size and range occupancy, itself shows only a very weak
392 correlation with body size in birds (Brown & Maurer 1987). It is also possible that the body size-
393 range size relationship might act to cancel out any body size-density effects. Population trend
394 over the past forty years was a similarly weak predictor of range occupancy. We also found little
395 evidence for differences in range occupancy among different trophic levels, foraging strategies,

396 or migratory groups. This last result is in contrast to an earlier study that described the ranges of
397 migrants as being more highly fragmented than those of residents (Linder *et al.* 2000).

398 In her canonical work on commonness and rarity, Rabinowitz (1981) identified three axes
399 along which species could be described as rare: range size, average population size, and habitat
400 specificity. A growing body of literature describes the complex interrelations among these
401 variables, suggesting that they are far from orthogonal (e.g., Brown 1995; Gregory & Gaston
402 2000; Gaston 2003; McGill & Collins 2003; Heino 2005; Murphy *et al.* 2006; Pocock *et al.*
403 2006). Here, we have analyzed a distinctly different measure of distribution, range occupancy,
404 and found it to be strongly tied to these others. In fact, range occupancy was the strongest
405 correlate of both abundance and local niche breadth among all of the ecological variables
406 examined despite the fact that niche breadth and abundance were only weakly correlated with
407 each other. This suggests that range occupancy may represent an unappreciated link between
408 different characterizations of species' distributions.

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

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

434 Finally, we have recently shown major differences in the results of ecological analyses
435 generated using range map and survey based data (Hurlbert and White 2005). The characteristic
436 porosity of species ranges implies that range map based analyses represent distribution at an
437 inherently coarser spatial grain relative to survey data. Since much of ecology is interested in
438 processes that are operating at local spatial scales it is important to be able to infer processes at
439 those scales (McPherson *et al.* 2006). Unfortunately geographic scale survey data are extremely
440 rare making range map based analyses much more tractable. By developing models of range
441 occupancy based on species-level characteristics, and environmental correlates (Hurlbert &

442 White 2005; McPherson *et al.* 2006), it may eventually be possible to estimate the composition
443 and diversity of local assemblages using range map data.

444

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458 **References**

- 459 Beaumont L.J., Hughes L. & Poulsen M. (2005) Predicting species distributions: use of climatic
460 parameters in BIOCLIM and its impact on predictions of species' current and future
461 distributions. *Ecological Modelling*, **186**, 250-269.
- 462 Blackburn T.M., Gaston K.J., Quinn R.M., Arnold H. & Gregory R.D. (1997) Of mice and
463 wrens: The relation between abundance and geographic range size in British mammals
464 and birds. *Philosophical Transactions Of The Royal Society Of London Series B-*
465 *Biological Sciences*, **352**, 419-427.
- 466 Bock C.E. & Ricklefs R.E. (1983) Range size and local abundance of some North American
467 songbirds: a positive correlation. *American Naturalist*, **122**, 295-299.
- 468 Box E.O., Holben B.N. & Kalb V. (1989) Accuracy of the AVHRR vegetation index as a
469 predictor of biomass, primary productivity and net CO₂ flux. *Vegetatio*, **80**, 71-89.
- 470 Brown J.H. (1984) On the relationship between abundance and distribution of species. *American*
471 *Naturalist*, **124**, 255-279.
- 472 Brown J.H. (1995) *Macroecology*. University of Chicago Press, Chicago.
- 473 Brown J.H. & Maurer B.A. (1987) Evolution of species assemblages: effects of energetic
474 constraints and species dynamics on the diversification of the North American avifauna.
475 *American Naturalist*, **130**, 1-17.
- 476 Brown J.H., Stevens G.C. & Kaufman D.M. (1996) The geographic range: size, shape,
477 boundaries, and internal structure. *Annual Review of Ecology and Systematics*, **27**, 597-
478 623.
- 479 Burnham K.P. & Anderson D.R. (2002) *Model selection and multi-model inference: A practical*
480 *information-theoretic approach*. Springer, New York.

- 481 Calder W.A. (1984) *Size, function, and life history*. Harvard University Press, Cambridge.
- 482 Cardillo M., Mace G.M., Jones K.E., Bielby J., Bininda-Emonds O.R.P., Sechrest W., Orme
483 C.D.L. & Purvis A. (2005) Multiple causes of high extinction risk in large mammal
484 species. *Science*, **309**, 1239-1241.
- 485 Collins S.L. & Glenn S.M. (1990) A hierarchical analysis of species' abundance patterns in
486 grassland vegetation. *American Naturalist*, **135**, 633-648.
- 487 Damuth J. (1981) Population density and body size in mammals. *Nature*, **290**, 699-700.
- 488 Doleddec S., Chessel D. & Gimaret-Carpentier C. (2000) Niche separation in community analysis:
489 a new method. *Ecology*, **81**, 2914-2927.
- 490 Dunning J.B. (1993) *Handbook of avian body masses*. CRC Press, Boca Raton.
- 491 Ehrlich P.R., Dobkin D.S. & Wheye D. (1988) *The Birder's Handbook: A field guide to the*
492 *natural history of North American birds*. Simon & Schuster, New York.
- 493 Freckleton R.P., Noble D. & Webb T.J. (2006) Distributions of habitat suitability and the
494 abundance-occupancy relationship. *American Naturalist*, **167**, 260-275.
- 495 Gaston K.J. (1991) How large is a species' geographic range? *Oikos*, **61**, 434-438.
- 496 Gaston K.J. (1994) Measuring geographic range sizes. *Ecography*, **17**, 198-205.
- 497 Gaston K.J. (1996) The multiple forms of the interspecific abundance-distribution relationship.
498 *Oikos*, **75**, 211-220.
- 499 Gaston K.J. (2003) *The structure and dynamics of geographic ranges*. Oxford University Press,
500 Oxford.
- 501 Gaston K.J. & Blackburn T.M. (1996) Global scale macroecology: interactions between
502 population size, geographic range size and body size in the Anseriformes. *Journal of*
503 *Animal Ecology*, **65**, 701-714.

- 504 Gaston K.J., Blackburn T.M., Greenwood J.J.D., Gregory R.D., Quinn R.M. & Lawton J.H.
505 (2000) Abundance-occupancy relationships. *Journal of Applied Ecology*, **37** (Suppl. 1),
506 39-59.
- 507 Gregory R.D. & Gaston K.J. (2000) Explanations of commonness and rarity in British breeding
508 birds: separating resource use and resource availability. *Oikos*, **88**, 515-526.
- 509 Hanski I. (1982) Dynamics of regional distribution: the core and satellite species hypothesis.
510 *Oikos*, **38**, 210-221.
- 511 Hanski I. (1991) Single species metapopulation dynamics: concepts, models and observations.
512 *Biological Journal of the Linnean Society*, **42**, 17-38.
- 513 Harte J., Blackburn T. & Ostling A. (2001) Self-similarity and the relationship between
514 abundance and range size. *American Naturalist*, **157**, 374-386.
- 515 Harte J., Kinzig A.P. & Green J. (1999) Self-similarity in the distribution and abundance of
516 species. *Science*, **284**, 334-336.
- 517 Hartley S., Kunin W.E., Lennon J.J. & Pocock M.J.O. (2004) Coherence and discontinuity in the
518 scaling of species' distribution patterns. *Proceedings of the Royal Society B-Biological*
519 *Sciences*, **271**, 81-88.
- 520 Harvey P.H. & Pagel M.D. (1991) *The comparative method in evolutionary biology*. Oxford
521 University Press, Oxford.
- 522 Haskell J.P., Ritchie M.E. & Olf H. (2002) Fractal geometry predicts varying body size scaling
523 relationships for mammal and bird home ranges. *Nature*, **418**, 527-530.
- 524 Heino J. (2005) Positive relationship between regional distribution and local abundance in
525 stream insects: a consequence of niche breadth or niche position. *Ecography*, **28**, 345-
526 354.

- 527 Holt A.R. & Gaston K.J. (2003) Interspecific abundance-occupancy relationships of British
528 mammals and birds: is it possible to explain the residual variation? *Global Ecology and*
529 *Biogeography*, **12**, 37-46.
- 530 Holt R.D., Lawton J.H., Gaston K.J. & Blackburn T.M. (1997) On the relationship between
531 range size and local abundance: back to basics. *Oikos*, **78**, 183-190.
- 532 Hurlbert A.H. & White E.P. (2005) Disparity between range map- and survey-based analyses of
533 species richness: patterns, processes and implications. *Ecology Letters*, **8**, 319-327.
- 534 Hurlbert S.H. (1990) Spatial distribution of the montane unicorn. *Oikos*, **58**, 257-271.
- 535 Illera J.C., Diaz M. & Nogales M. (2006) Ecological traits influence the current distribution and
536 range of an island endemic bird. *Journal of Biogeography*, **33**, 1192-1201.
- 537 IUCN (2001) *IUCN Red List Categories and Criteria: Version 3.1*. IUCN Species Survival
538 Commission, Gland, Switzerland.
- 539 Kolb A., Barsch F. & Diekmann M. (2006) Determinants of local abundance and range size in
540 forest vascular plants. *Global Ecology and Biogeography*, **15**, 237-247.
- 541 Kunin W.E. (1998) Extrapolating species abundance across spatial scales. *Science*, **281**, 1513-
542 1515.
- 543 Linder E.T., Villard M.A., Maurer B.A. & Schmidt E.V. (2000) Geographic range structure in
544 North American landbirds: variation with migratory strategy ; trophic level ; and breeding
545 habitat. *Ecography*, **23**, 678-686.
- 546 Maurer B.A. & Nott M.P. (1998) Geographic range fragmentation and the evolution of
547 biological diversity. In: *Biodiversity Dynamics: Turnover of Populations, Taxa, and*
548 *Communities* (eds. McKinney ML & Drake JA), pp. 31-50. Columbia University Press,
549 New York.

- 550 McGill B. & Collins C. (2003) A unified theory for macroecology based on spatial patterns of
551 abundance. *Evolutionary Ecology Research*, **5**, 469-492.
- 552 McNab B.K. (1963) Bioenergetics and the determination of home range size. *American*
553 *Naturalist*, **97**, 133-140.
- 554 McPherson J.M., Jetz W. & Rogers D.J. (2006) Using coarse-grained occurrence data to predict
555 species distributions at finer spatial resolutions--possibilities and limitations. *Ecological*
556 *Modelling*, **192**, 499-522.
- 557 Morisita M. (1959) Measuring of dispersion of individuals and analysis of the distributional
558 patterns. *Memoirs of Faculty of Science, Kyushu University Series E* **3**
- 559 Murphy H.T., VanDerWal J. & Lovett-Doust J. (2006) Distribution of abundance across the
560 range in eastern North American trees. *Global Ecology and Biogeography*, **15**, 63-71.
- 561 Murray B.R., Fonseca C.R. & Westoby M. (1998) The macroecology of Australian frogs.
562 *Journal of Animal Ecology*, **67**, 567-579.
- 563 Paruelo J.M., Epstein H.E., Lauenroth W.K. & Burke I.C. (1997) ANPP estimates from NDVI
564 for the Central Grassland Region of the United States. *Ecology*, **78**, 953-958.
- 565 Peters R.H. (1983) *The ecological implications of body size*. Cambridge University Press,
566 Cambridge.
- 567 Pocock M.J.O., Hartley S., Telfer M.G., Preston C.D. & Kunin W.E. (2006) Ecological
568 correlates of range structure in rare and scarce British plants. *Journal of Ecology*, **94**,
569 581-596.
- 570 Price J., Droege S. & Price A. (1995) *The summer atlas of North American birds*. Harcourt Brace
571 and Company, London.
- 572 Purvis A., Jones K.E. & Mace G.M. (2000) Extinction. *Bioessays*, **22**, 1123-1133.

- 573 Rabinowitz D. (1981) Seven forms of rarity. In: *The Biological Aspects of Rare Plant*
574 *Conservation* (ed. Synge H). Wiley, Chichester.
- 575 Rapoport E.H. (1982) *Areography: geographical strategies of species*. Pergamon Press, Oxford.
- 576 Reichenbacher F., Franson S.E. & Brown D.E. (1998) *North American Biotic Communities*.
577 University of Utah Press, Salt Lake City.
- 578 Ridgely R.S., Allnutt T.F., Brooks T., McNicol D.K., Mehlman D.W., Young B.E. & Zook J.R.
579 (2003) *Digital Distribution Maps of the Birds of the Western Hemisphere, version 1.0*.
580 NatureServe, Arlington, Virginia, USA.
- 581 Root T. (1988a) *Atlas of Wintering North American Birds: An Analysis of Christmas Bird Count*
582 *Data*. University of Chicago Press, Chicago.
- 583 Root T. (1988b) Environmental factors associated with avian distributional boundaries. *Journal*
584 *of Biogeography*, **15**, 489-505.
- 585 Sauer J.R., Hines J.E. & Fallon J. (2005) The North American Breeding Bird Survey, Results
586 and Analysis 1966 - 2004. Version 2005.2. In. USGS Patuxent Wildlife Research Center,
587 Laurel, MD
- 588 Shafer S.L., Bartlein P.J. & Thompson R.S. (2001) Potential changes in the distributions of
589 western North America tree and shrub taxa under future climate scenarios. *Ecosystems*, **4**,
590 200-215.
- 591 Shmida A. & Wilson M.V. (1985) Biological determinants of species diversity. *Journal of*
592 *Biogeography*, **12**, 1-20.
- 593 Smith F.A., Brown J.H., Haskell J.P., Lyons S.K., Alroy J., Charnov E.L., Dayan T., Enquist
594 B.J., Ernest S.K.M., Hadly E.A., Jones K.E., Kaufman D.M., Marquet P.A., Maurer B.A.,

- 595 Niklas K.J., Porter W.P., Tiffney B. & Willig M.R. (2004) Mammalian body size across
596 space and time. *American Naturalist*, **163**, 672-691.
- 597 Symonds M.R.E. & Johnson C.N. (2006) Determinants of local abundance in a major radiation
598 of Australian passerines (Aves: Meliphagoidea). *Journal of Biogeography*, **33**, 794-802.
- 599 Tales E., Keith P. & Oberdorff T. (2004) Density-range size relationship in French riverine
600 fishes. *Oecologia*, **138**, 360-370.
- 601 Thompson R.S., Anderson K.H. & Bartlein P.J. (1999) Atlas of relations between climatic
602 parameters and distributions of important trees and shrubs in North America. In: *U.S.*
603 *Geological Survey Professional Paper 1650 A&B*. U.S. Geological Survey Press, Denver.
- 604 Van Buskirk J. (2005) Local and landscape influence on amphibian occurrence and abundance.
605 *Ecology*, **86**, 1936-1947.
- 606 Wright D.H. (1991) Correlations between incidence and abundance are expected by chance.
607 *Journal of Biogeography*, **18**, 463-466.
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- 610

611 **Table 1.** Correlation matrix of species traits and range occupancy. Traits are abbreviated as
 612 follows: logN - \log_{10} of the geometric mean of abundance on survey routes where a
 613 species is present, logM – \log_{10} body mass, logRS - \log_{10} range size, BiomeH – biome
 614 diversity (Shannon-Wiener) within the range, Biomes – number of biomes within the
 615 range, RegNB – regional niche breadth, logNP - \log_{10} niche position, LocAgg – local
 616 aggregation, PopTrend – population trend over 1966-2004, RO – range occupancy, logit
 617 transformed. Correlation coefficients are based on data for 298 land bird species, with the
 618 exception of correlation coefficients for population trend which are based on a subset of
 619 278 species. Absolute values of $r > 0.18$ are significant at $P < 0.001$. Absolute values $>$
 620 0.4 are in bold for visual purposes.

621

	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

622

623

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

Variable	Estimate	SE	<i>t</i>	<i>P</i>
(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

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629

630 **Figure Legends**

631

632 **Figure 1** (a) Map showing two hypothetical species ranges (irregular polygons) across a
633 'continent' (the outer box). Squares represent two regions over which regional occupancy may
634 be calculated. Symbols indicate the location of field surveys, with X's denoting the absence of
635 either focal species, and filled and hollow circles indicating the respective species' presence. (b)
636 Three measures of occupancy calculated for each of the two species in (a). Regional occupancy
637 for the light species is shown for both Regions 1 and 2 as denoted by the stippling.

638

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

640

641 **Figure 3** Proportion of variation explained at different taxonomic levels for range occupancy
642 values (bold line) and eight other variables used to predict range occupancy. Note that body mass
643 (dashed line) is the only variable to show strong phylogenetic conservatism. The majority of the
644 variation in all other variables occurs at the species level. The solid line is average abundance.
645 Variance components were estimated using a nested ANOVA.

646

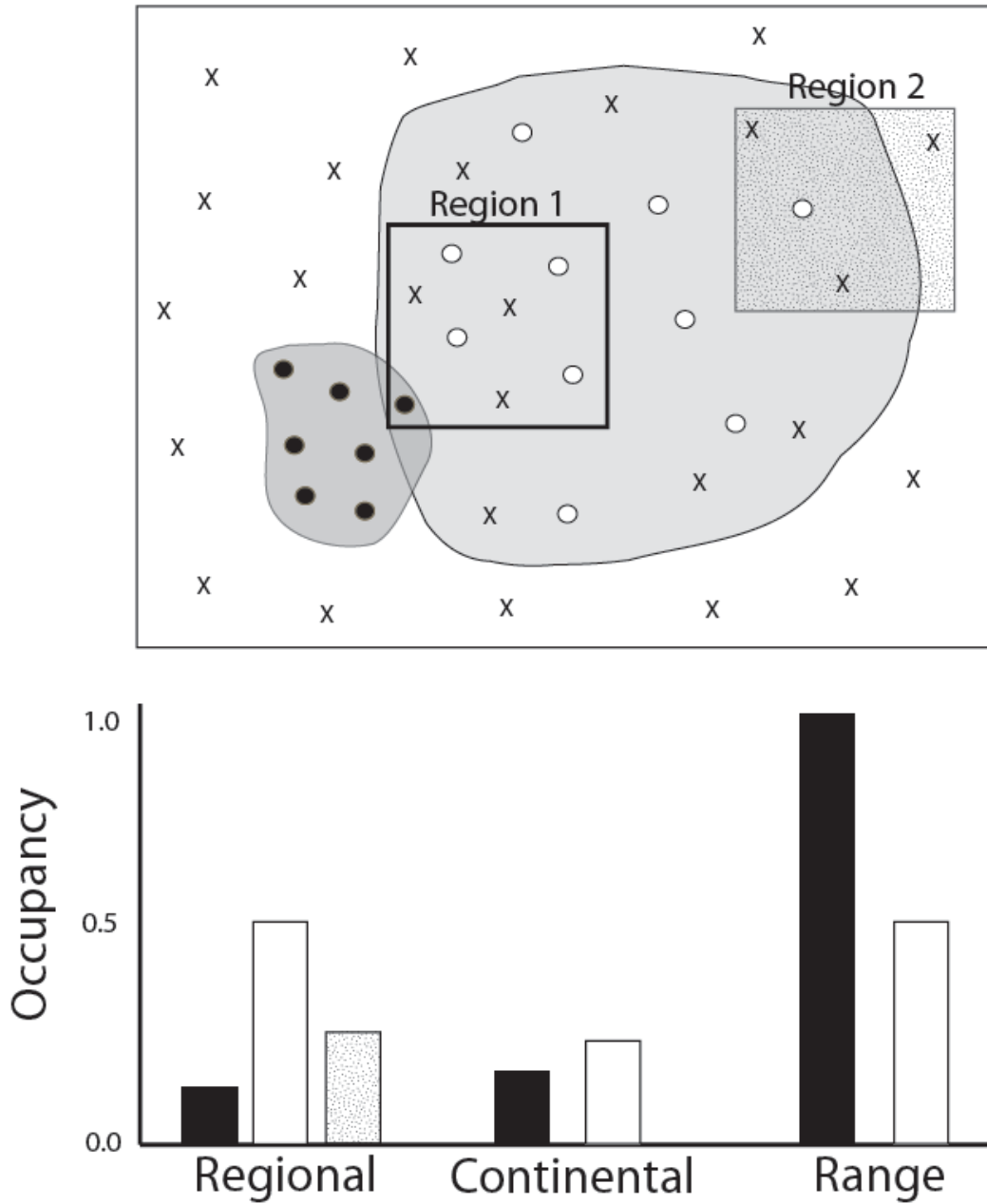
647 **Figure 4** Major univariate relationships between range occupancy (logit transformed) and four
648 predictor variables across 298 North American bird species. Lines represent ordinary least
649 squares regressions.

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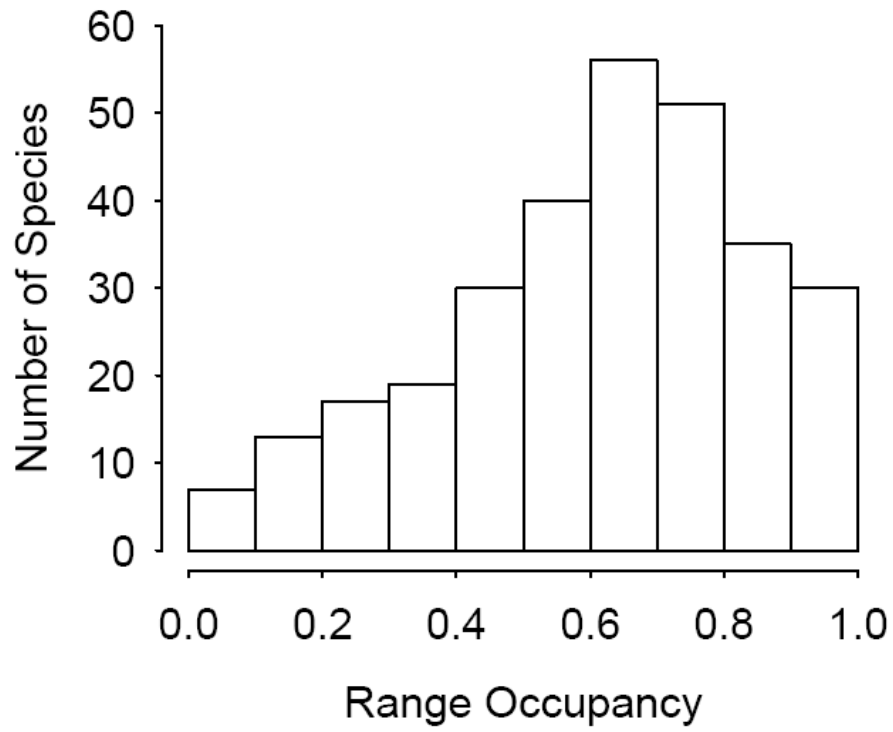
651 **Figure 5** The maximum proportion of variance explained (adjusted R^2) by models predicting
652 range occupancy as a function of the number of predictors included in the model.

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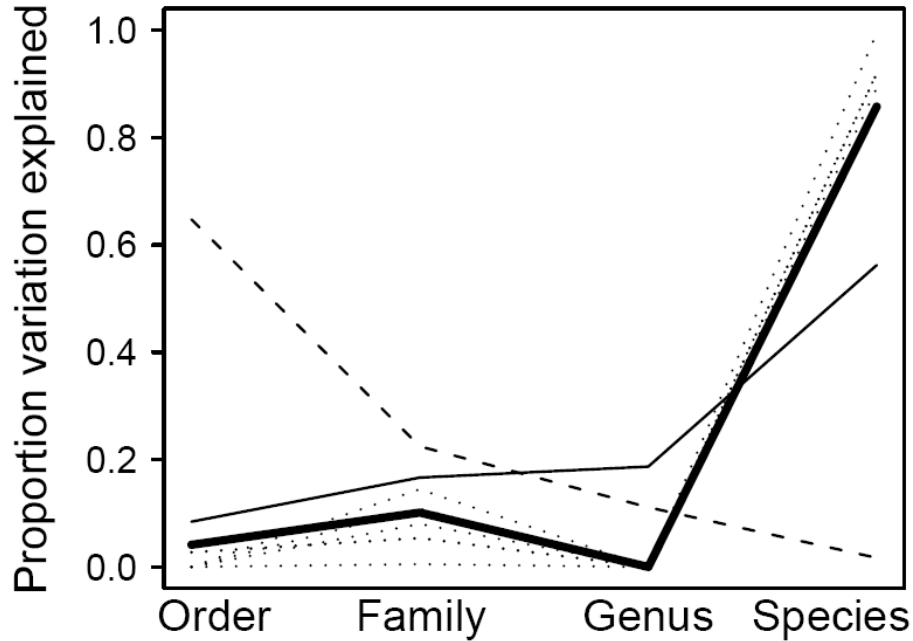


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 659 Three measures of occupancy calculated for each of the two species in (a). Regional occupancy
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661

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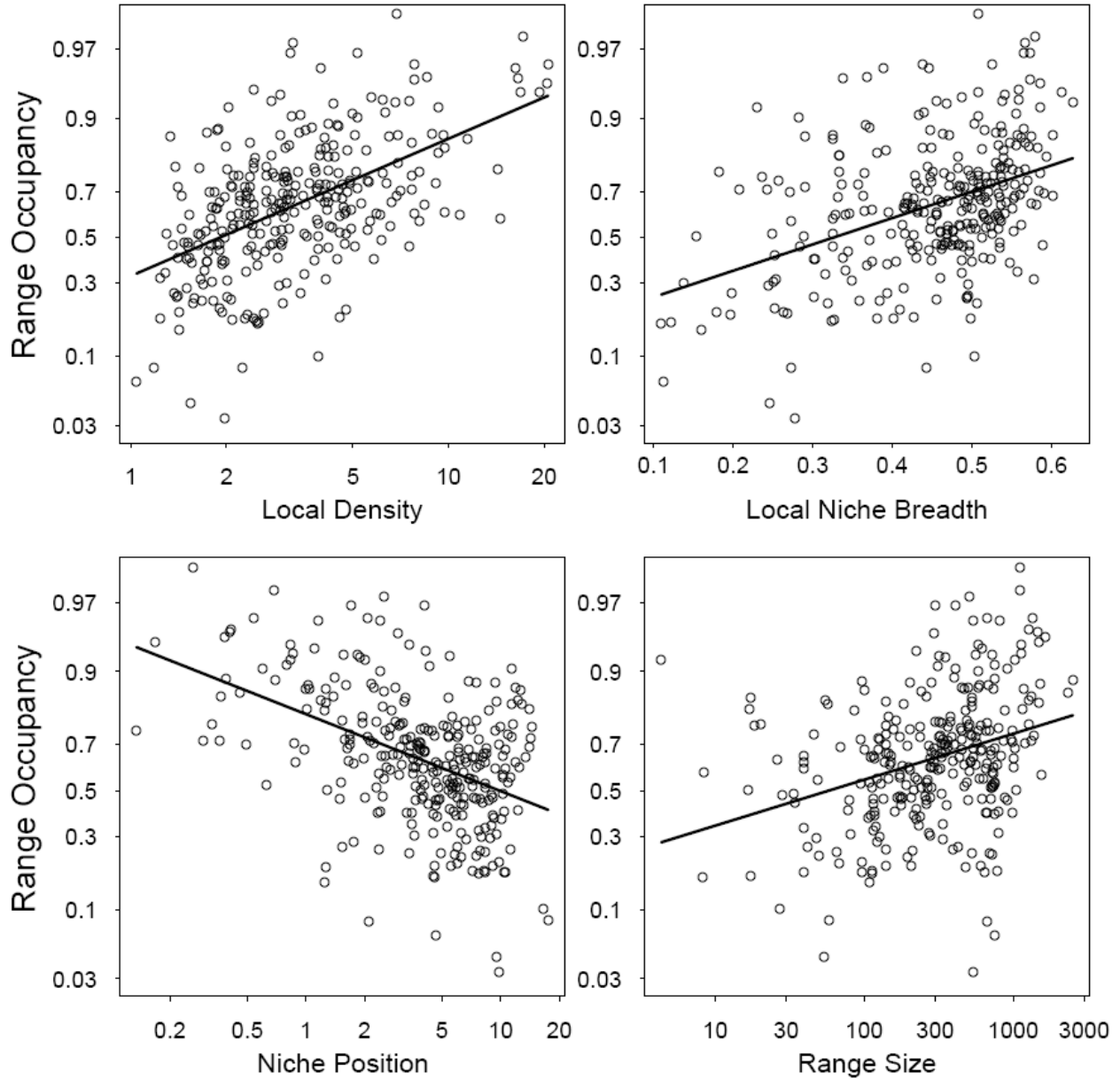


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664

665 **Figure 3** Proportion of variation explained at different taxonomic levels for range occupancy
 666 values (bold line) and eight other variables used to predict range occupancy. Note that body mass
 667 (dashed line) is the only variable to show strong phylogenetic conservatism. The majority of the
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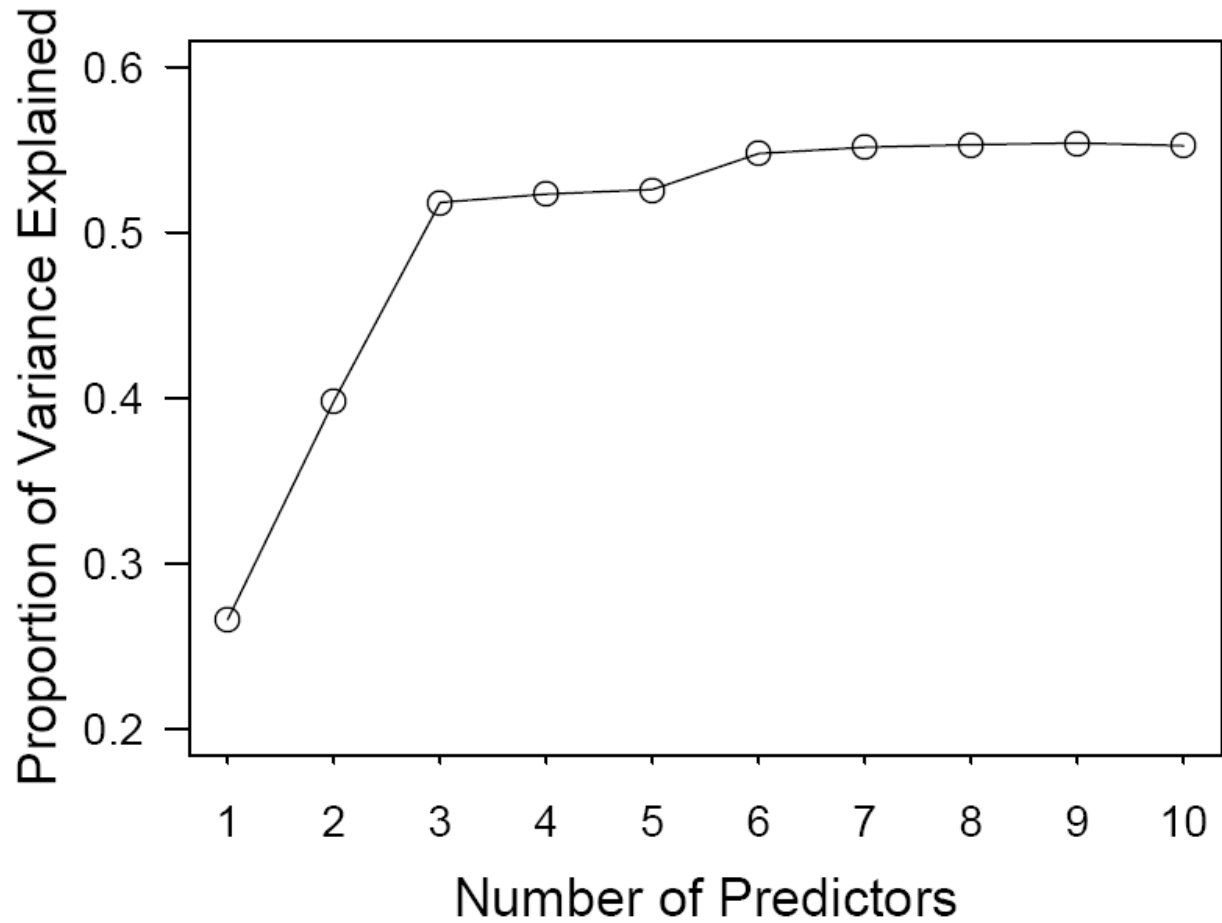
672

673 **Figure 4** Major univariate relationships between range occupancy (logit transformed) and four

674 predictor variables across 298 North American bird species. Lines represent OLS

675 regressions.

676



677

678 **Figure 5** The maximum proportion of variance explained (adjusted R^2) by models predicting

679 range occupancy as a function of the number of predictors included in the model.

680

681