

A Continent-Scale Test of Multiple Hypotheses on the Abundances of Neotropical Birds

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<p>Note: The following files were submitted by the author for peer review, but cannot be converted to PDF. You must view these files (e.g. movies) online.</p>	
DataA1.csv	

Neotropical Bird Abundance

1 A Continent-Scale Test of Multiple Hypotheses on the Abundances of Neotropical Birds

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*Neotropical Bird Abundance*28 **Abstract**

29 Explaining variation in the abundance of species remains a challenge in ecology. We sought to
30 explain variation in abundance of Neotropical forest birds using a dataset of population densities
31 of 596 species. We tested *a priori* hypotheses for the roles of species traits, environmental
32 factors, and species interactions. Specifically, we focused on four factors: 1) body mass (trait); 2)
33 habitat type (environmental factor), 3) net primary productivity (NPP; environmental factor); and
34 4) species richness of competitors (species interaction). Body size explained much variation in
35 density, although only when analyzed at higher taxonomic levels. Habitat type was a strong
36 predictor of density. The relationship between density and productivity was weak. Densities were
37 related negatively to the species richness of heterospecifics, however – this trend was particularly
38 strong within closely related groups. Our results show that the influence of energetic factors such
39 as body size and productivity depends on phylogeny, and they act through indirect relations with
40 other variables; alternative ecological factors such as habitat structure and species interactions
41 play a more direct and stronger role in determining abundance than previously thought.

*Neotropical Bird Abundance*42 **Introduction**

43 A fundamental question in ecology is how the abundance of species is governed (McGill 2008,
44 Storch et al. 2018), which is central to numerous ecological and evolutionary processes (e.g.
45 Gotelli 1995, Charlesworth 2009). Many factors may influence abundance, including
46 environmental variables (Damuth 1981, Srivastava and Lawton 1998, Kaspari et al. 2000, Brown
47 et al. 2004), species traits (Rosenzweig and Lomolino 1997, Murray et al. 2002, McGill et al.
48 2006, Umaña et al. 2015), and interactions with other species (MacArthur et al. 1972, Hudson et
49 al. 1992, Robertson 1996, Berger and Gese 2007). Despite much investigation, no single factor
50 appears sufficient to explain variation in species abundance (no. individuals/species; Murray et
51 al. 2002, Hurlbert 2004, McGill 2008). Instead, we must examine trends across environmental
52 gradients (McGill et al. 2006), taking into account the separate contribution of abiotic and biotic
53 factors (Warton et al. 2015), while at the same time controlling for correlations between
54 predictor variables (Dormann et al. 2013).

55 Some elements that are hypothesized to be most important for controlling abundance are
56 energy, species interactions, and spatial variation. These broad categories are often broken down
57 into more specific factors. For example, the influence of energy can be broken down into its
58 availability, i.e. productivity, or its use, with limitations imposed by metabolic rates (Brown et al.
59 2004). Below, we describe mechanisms by which some of these factors are hypothesized to
60 function, and connect them with particular predictions. We considered four more specific factors
61 for explaining variation in abundance, and tailored our reasoning to build predictions about how
62 they would influence the population densities of Neotropical forest birds. Bird populations in the
63 Neotropics are poorly studied in comparison with Nearctic ones or those of large mammals. This

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64 makes them an ideal study group to broaden our understanding of general principles that govern
65 variation in animal populations.

66 The first factor that we selected was body size, which is one of the traits most commonly
67 used to model abundance (McGill et al. 2006), and is often found to have explanatory power
68 (White et al. 2007). This relationship is predicted to occur if population sizes scale according to
69 the energy requirements of individuals (Brown 1995, Brown et al. 2004). Formalized as the
70 energetic equivalence rule, the number of animals that can be supported by a given amount of
71 energy is determined by $N \propto M^{-3/4}$, where N is the number of individuals of a species, M is their
72 average body mass, and the value of the exponent describes the relationship between body mass
73 and metabolic rate (Damuth 1981). This predicts that local abundance will decrease with body
74 size. Empirically, the relationship between body size and abundance in bird species is tenuous
75 (Brown and Maurer 1987, Russo et al. 2003); however, greater success has been had in
76 connecting body size to bird abundance at higher taxonomic levels (McGill 2008). Based on
77 these previous results, we hypothesized that body size would best explain variation in species
78 abundance in the Neotropics at higher taxonomic levels (Hurlbert and White 2007, McGill
79 2008).

80 A second factor predicted to govern abundance is the productivity of a locality (Srivastava
81 and Lawton 1998, Kaspari et al. 2000, Hurlbert 2004, Storch et al. 2018). The relationship
82 between productivity and the number of individuals in a community is unresolved (reviewed in
83 Storch et al. 2018). At the very least, however, most theoretical frameworks agree that
84 productivity can place an upper bound on abundance. This could produce a positive correlation
85 between productivity and abundance across localities. We then asked on what scale it makes
86 sense to seek such a correlation. Much variation in species abundance will result from changes in

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87 habitat type, as some species will be adapted to high-productivity habitats (e.g. rainforest) and
88 others to low-productivity habitats (e.g. dry forest). Therefore, hypothesizing that energy
89 availability regulates species abundance makes most sense for comparisons within habitat types.
90 We call this the productivity hypothesis, which predicts a positive correlation between
91 productivity and species abundance, once the correlation between productivity and habitat has
92 been taken into account.

93 The role of competition in determining macroecological patterns is contentious (Connor and
94 Simberloff 1979, Diamond and Gilpin 1982, Harmon and Harrison 2015, Rabosky and Hurlbert
95 2015). Indeed, null model analyses of species co-occurrence and abundance matrices suggest that
96 certain species may be excluded by direct competitors (Gotelli and McCabe 2002, Ulrich and
97 Gotelli 2010). Whether or not diffuse competition between many species influences abundance
98 across communities at a continental scale is unknown. When more species compete for
99 resources, they may force one another to utilize narrower niches than in the absence of
100 competition (Hutchinson 1957). Conversely, when they experience competitive release, such as
101 after colonizing an island, populations may undergo what has been called density compensation
102 (Crowell 1962, MacArthur et al. 1972, Nilsson 1977, Wright 1980). Fewer competing species
103 could lead to higher population densities if decreased competition allows residents to exploit a
104 wider range of available resources. We call this process the interspecific competitors hypothesis
105 (also called the “Density Compensation Hypothesis”; Ferenc et al. 2016). Above, in the
106 productivity hypothesis, we explain the necessity of controlling for habitat type before
107 examining the effects of productivity on abundance. Therefore, the interspecific competitors
108 hypothesis must also take this into account: its critical prediction is that, after controlling for

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109 variation in productivity within habitat types, birds living in areas with lower species richness
110 will have higher population densities.

111 Finally, habitat type itself may affect abundance. Different habitat structures can partition
112 available energy into more or fewer niches (MacArthur 1957, Willson 1974), affecting which
113 species can live there and their population abundances. If habitats make resources available to
114 consumers in different ways, then species abundance may best be predicted by variation in
115 habitat rather than directly through productivity. We do not have strong *a priori* hypotheses
116 about how habitat should affect abundance, except that some functional guilds may have higher
117 densities in montane forest than in lowland rainforest (Kattan and Beltran 2002, Ding et al. 2005,
118 Kikuchi 2009, Ferenc et al. 2016).

119 Here, we build models using regression methods to control for correlations between predictor
120 variables. We use them to examine the relative importance of energy, species traits, and species
121 interactions in governing the local abundance of species across a biogeographic region.

122

123 Methods*124 The Dataset*

125 Many of the Neotropical studies measuring bird abundances were known to us at the outset of
126 this project. Searching through them, and works citing them, provided the backbone of our
127 database. We supplemented our knowledge by searching Google Scholar, JSTOR, and Wiley
128 using the terms “bird density” combined with the names of Neotropical countries and zones in
129 English, Spanish, and Portuguese, as the local abundance of bird species is generally reported as
130 a population density estimate. We read the Introduction and Methods sections of each paper to
131 see if it met our criteria for estimating population density accurately. All papers we included

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132 used one or more of three methods to estimate population densities: spot mapping, point counts,
133 and transect counts. All of the studies that used point counts and some studies that used transect
134 counts also used the software Distance to correct for the probability of detecting the animals as a
135 function of perpendicular distance away from the transect (Buckland et al. 2015).

136 For each species in each study, we extracted population density estimates and converted them
137 into individuals km⁻². In all analyses reported below, when studies reported multiple estimates
138 for the same species at the same site, we used the median value of those estimates. When
139 different densities were reported for a species within sub-areas of a study site, we registered them
140 as separate observations. For all population density measurements except for one, these sub-areas
141 were far enough apart to register in separate 10 km-resolution grid cells, giving them unique
142 values for the ecological variables we included in the analysis (below); most of the taxa in
143 studies using sub-areas were from the families Cracidae, Strigidae, and Psittacidae. In addition,
144 we recorded the following information for each entry: species taxonomic affiliation (from
145 Cornell's Neotropical Birds Online; Schulenberg 2016), mean body mass (from Handbook of
146 Birds of the World [del Hoyo et al. 2016] and Cornell's Neotropical Birds), its migratory status
147 in the Neotropics, whether it is primarily terrestrial or aquatic, the habitat in which it was
148 documented (Amazonian forest, Atlantic forest, cerrado, chaco, coniferous forest, dry forest,
149 non-Amazonian humid forest, mangrove, mountain forest, open area, paramo, riparian forest, salt
150 marsh, shrubland, tree plantation), whether or not populations were in a continuous tract of forest
151 or a fragmented one, the protection status of the study area, the method of census used, the date
152 of the observation, and the latitude & longitude of the locality.

153 To clean our dataset, we first excluded aquatic and riparian taxa, because their populations
154 are difficult to census and the energy available in aquatic ecosystems was not addressed by our

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155 metric of Net Primary Productivity (NPP). Second, we excluded fragmented habitats because we
156 wished to examine ecological processes unaffected by anthropogenic confounding factors such
157 as edge effects (Murcia 1995). Third, we decided to focus on forest habitats because
158 relationships between productivity and abundance are expected to be monotonic within forests;
159 the relationship may reverse in grasslands (Hurlbert 2004). Fourth, we excluded migrants. Fifth,
160 we excluded taxa considered *incertae sedis* because we were not able to account for the
161 influence of their taxonomic affiliation on population density. In the final dataset that we used
162 for analysis, we retained 1331 records from 47 studies (see Figure 1 for locations and relative
163 number of species measured at each study site). This included 596 species from 310 genera in 54
164 families spread among 21 orders. This dataset is described in Supplementary material Appendix
165 A, Table A1. Associated references are provided in Supplementary material Appendix A,
166 Metadata A1, and visualizations of the dataset are given in Figure 2.

167 In our final dataset, we tested whether different survey methods produced consistent density
168 estimates. Another study has shown that they do so for cracids (Kattan et al. 2016), but cracids
169 are relatively large and easy to survey. Although our dataset is not designed to cross-validate
170 different methods, we wished to obtain some sense of their comparability. To see if densities
171 differed among sampling methods, we used a linear mixed model explaining $\log(\text{density})$ with a
172 fixed effect “method,” which had three levels: spot mapping, studies that used the software
173 Distance to correct their estimates, and uncorrected transect counts. We included site as a
174 random intercept because records were unevenly distributed among sites.

175 To provide a measure of energy availability, we used a geographical information systems
176 (GIS) layer for NPP at 1 km resolution (Zhao et al. 2005). The layer uses the MOD17 algorithm
177 to estimate NPP averaged across the years 2000-2013 in each cell. We did not have NPP data

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178 from outside this time window, yet some of the measurements of population density were
179 recorded outside of it. They are from protected areas, however, so we made the assumption that
180 the mean NPP values across 2000-2013 would be an adequate approximation of their NPP at the
181 time of observation.

182 For testing the interspecific competitors hypothesis, we required a measure of species
183 richness. We used a 10 km resolution layer that represents regional species richness at a
184 landscape scale (100 km²), calculated as the number of overlapping species ranges in each cell
185 (obtained from Birdlife International; Jenkins et al. 2013, Pimm et al. 2014). Ideally, we would
186 have used alpha diversity at each study locality, because competitive interactions such as
187 exploitation, interference, and territoriality take place at a local scale (Kaspari et al. 2000,
188 Jankowski et al. 2012). Complete data on local species richness were not available for many of
189 the study sites in our dataset; however, local species richness is a subset of regional species
190 richness, and the two numbers are highly correlated, although the correlation is moderated by
191 NPP to some degree (White and Hurlbert 2010). We only used the regional richness layer after
192 we controlled for NPP (below), and therefore consider it an adequate proxy for local richness.
193 Furthermore, layers describing the species richness of the clades Psittaciformes, Trochilidae,
194 other non-Passeriformes, Tyranni, and Passeri are provided, which we used to test the
195 interspecific competitors hypothesis within these groups.

196 All of our study areas were on the same scale as our raster files or less. We used the latitude
197 and longitude coordinates provided in each study or georeferenced them based on their
198 descriptions to extract values of NPP and species richness from our GIS layers. For this we used
199 the “extract” function from the package “raster” in R 3.4.4, having obtained the appropriate

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200 raster files associated with the studies that generated the data (Zhao et al. 2005, Jenkins et al.
201 2013).

202

203 Testing mechanisms affecting population density

204 We tested four hypotheses for how the population densities of Neotropical birds are governed.
205 Before analysis, we scaled and centered all of our continuous predictor variables so that they had
206 mean = 0 and standard deviation = 1. The exception to this procedure was log(body mass)
207 (hereafter simply body mass), which was only used in initial regressions. The first hypothesis
208 that we tested was that population density should decrease with body mass. Species-level
209 regressions of body mass typically provide a poor fit to avian population densities (Brown and
210 Maurer 1987; McGill 2008). This may be because body mass is a conserved trait that varies
211 more at the level of family and order among birds (Hurlbert and White 2007; McGill 2008),
212 while other traits (presumably also important for governing abundance) vary at lower taxonomic
213 levels. To verify these trends among Neotropical birds, we performed the following analyses: 1)
214 an ordinary least-squares (OLS) regression of the population densities of each species at each site
215 against body mass on a logarithmic scale; 2) a linear mixed model fit with maximum likelihood
216 of log(density) with no fixed effects, and order/family/genus as random effects; 3) a linear mixed
217 model of log(mass) regressed without fixed effects, but order/family/genus as random effects;
218 and 4) a log-linear model of the geometric mean densities for each family against the geometric
219 mean body masses for each family (McGill 2008). The first model reveals the inadequacy of
220 species-level analysis. The next two models illustrate that density is explained better at higher
221 taxonomic levels, and that this is strongly related to how variance in body mass varies at those

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222 levels. The final model examines the relationship between density and body mass at the
223 taxonomic level where it is most appropriate – where most of the variation occurs.

224 The second hypothesis we tested was the habitat hypothesis. We used a linear mixed model
225 of $\log(\text{density})$ against habitat type, with order/family/genus as random effects to control for
226 effects of body size (see Results). This also controls for other phylogenetically conserved traits,
227 potentially including but not limited to trophic level, territorial behavior, nest site preferences,
228 mating system, and life history.

229 The third hypothesis focuses on productivity and predicts that population density increases
230 with NPP, after the correlation between NPP and habitat has been taken into account. We chose
231 sequential regression to control for the correlation between these variables because it creates
232 orthogonal predictor variables while preserving interpretability (Graham 2003, Dormann et al.
233 2013). This method is distinct from regression of residuals, which is not recommended
234 (Freckleton 2002). In sequential regression, one predictor is regressed against another predictor
235 and the residuals of this regression are used as a new predictor. Thus, the new predictor has the
236 desirable property of being orthogonal to the other predictor variable. Therefore, it may be
237 somewhat conservative in estimating the effects of the second variable that is regressed upon the
238 first. We regressed NPP upon habitat type, then used residuals($\text{NPP} \sim \text{habitat type}$) as a new
239 predictor variable. Habitat type and this new predictor variable were fixed effects in a linear
240 mixed effects model of $\log(\text{density})$ with order/family/genus as random effects. The new
241 predictor can only be interpreted as having an effect after its correlation with the other predictor
242 has been taken into account. In our model testing the productivity hypothesis, one finds the effect
243 of NPP on $\log(\text{density})$, independent of its contribution already made through its correlation with
244 habitat type.

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245 Testing the fourth hypothesis, the interspecific competitors hypothesis, which predicts that
246 population density decreases with species richness, required the creation of a second variable by
247 way of an additional sequential regression. We regressed species richness against habitat type +
248 residuals(NPP ~ habitat type) to create a third predictor variable, and added this to a linear mixed
249 model of log(density) with the two variables it was regressed against, with order/family/genus as
250 random intercepts. The R pseudocode for the model is log(density) ~ habitat type + resid(NPP ~
251 habitat type) + resid(species richness ~resid(NPP ~ habitat type)) + (1|order/family/genus). The
252 effect of species richness is interpreted as independent, but only after its contribution to
253 log(density) through its correlations with NPP and habitat type have been taken into account.

254 The richness of all species is an imperfect proxy for the number of competing species. Not all
255 species compete with one another to an equal degree. Furthermore some may participate in other
256 interactions such as predation or mutualism. Generally, it is assumed that the more closely
257 related species are, the more strongly they compete (Losos 2008). Consequently, the test we
258 performed above using the richness of all species is conservative with respect to our hypothesis,
259 because distantly-related species should contribute noise to the signal. However, it is also
260 possible that any result we observe from that test will be driven by another, unmeasured
261 confounding variable that is 1) uncorrelated with habitat or productivity, and 2) drives
262 underlying patterns of species richness *and* abundance. Therefore, we tested the additional
263 prediction that species within closely related groups should have a stronger effect on each other's
264 densities, compared to the effect that species within more distantly related groups have on each
265 other's densities.

266 We used linear mixed models to test the relationship between log(density) and species
267 richness *within* the following clades: non-Passeriformes (excluding Psittaciformes and

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268 Trochilidae), Psittaciformes, Trochilidae, Tyranni, and Passeri. We used the sequential
269 regression framework described above, but instead of using the richness of all species, we
270 created new predictors using the richness of each group. Assuming that more closely related
271 species compete more strongly, if the interspecific competitors hypothesis is supported, we
272 should see a stronger relationship between $\log(\text{density})$ and clade-specific species richness
273 within closely-related groups such as the Psittaciformes, Trochilidae, Tyranni, and Passeri
274 compared to the diffuse non-Passeriformes, which includes birds from tinamous to vultures.
275 Each group was analyzed using a separate model that included lower-level taxa as random
276 effects, and the significance of group-specific richness was assessed using the likelihood ratio
277 test.

278 The sequential regressions that we used were nested within one another, such that the simpler
279 models were subsets of more complex ones. This was advantageous because it allowed us to see
280 whether adding each new variable that corresponded to an additional hypothesis made a
281 significant improvement in model fit by using both the likelihood ratio test (LRT) and the
282 Akaike Information Criterion (AIC; Akaike 1974, Burnham and Anderson 2004, Bolker 2008).
283 Furthermore, the most complex model makes it possible to assess at a glance the relative
284 contributions of each predictor to explaining the variance.

285 A caveat in interpreting sequential regression is that it is sensitive to the order in which
286 orthogonal axes are created. We chose the sequence of regressions to accord with our *a priori*
287 hypotheses for how variables influence one another. However, we wished to examine the
288 robustness of our results to a different statistical method. To do so, we also performed a linear
289 mixed model with habitat, NPP, and regional species richness as fixed predictors of $\log(\text{density})$,

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290 and order/family/genus as random effects. This approach does not use orthogonal predictors, but
291 does break free from some of our assumptions.

292

293 Results

294 We found no evidence that survey methods yielded significantly different density estimates
295 (likelihood ratio test (LRT); $\chi^2_2 = 0.49$; $p = 0.78$).

296 The linear regression of $\log(\text{density})$ against $\log(\text{body mass})$ was statistically significant
297 (OLS regression, $r^2 = 0.08$, $F_{1,1063} = 93.23$, $p < 10^{-3}$; Figure 3A). However, its fit to the data was
298 poor compared with a model that had no fixed effects, but included order, family, and genus as
299 random effects (Table 1). This occurred because the largest proportion of variance in body size
300 was explained at the levels of genus (0.14), family (0.18) and order (0.65), whereas the variance
301 by species and site (combined in the residuals; 0.03) was low. The OLS regression of geometric
302 mean density of families against their geometric mean body mass had a better fit than the
303 regression on the species level (OLS regression, $r^2 = 0.29$, $F_{1,18} = 7.21$, $p = 0.015$; Figure 3B).

304 Habitat type made a strong contribution to model fit (Table 1; LRT: $\chi^2_5 = 121.55$; $p < 10^{-3}$).
305 Relative to Amazonian forests, Atlantic and coniferous forests were estimated to have lower
306 population densities, while dry, humid, and montane forests were estimated to have higher
307 densities (Table 2).

308 The productivity hypothesis predicts that species abundances are positively correlated with
309 NPP, once the contribution of NPP due to its correlation with habitat structure is taken into
310 account. This prediction was not confirmed (LRT: $\chi^2_1 = 1.29$; $p = 0.26$), although the estimated
311 coefficient was in the predicted direction (Table 2).

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312 The interspecific competitors hypothesis predicts that population densities will decrease with
313 increasing species richness. We tested this effect after taking into account the contribution that
314 species richness made to $\log(\text{density})$ through its correlation with NPP and habitat. This
315 prediction of the interspecific competitors hypothesis was confirmed (LRT: $\chi_1^2 = 33.2$; $p < 10^{-3}$).
316 Its effect size was on the same order of magnitude as the largest effect sizes for different habitat
317 levels (Table 2).

318 We used AIC to compare the fit of all of the models that we fit for $\log(\text{density})$. This
319 provided an alternative to the likelihood ratio test to see if there was an improvement in model fit
320 when each predictor was added to the model. We found that the addition of each predictor
321 resulted in an improvement in model fit by at least 2 points, with the exception of productivity
322 (Table 1). The ΔAIC separating the best-fit model from others was 30.5, indicating almost no
323 support for any of the simpler models, and therefore arguing that the residuals of species richness
324 are indispensable as a predictor of $\log(\text{density})$.

325 Within taxonomic groups, species richness was an inconsistent predictor of population
326 density. Although in all cases the estimated relationship was negative, in the non-Passeriformes
327 (excluding Psittaciformes and Trochilidae) and the Passeri, species richness of each group was
328 not a significant predictor of population density (Table 3). By contrast, in the Psittaciformes,
329 Trochilidae, and Tyranni, it was (Table 3).

330 Results from a linear mixed model with predictors included simultaneously were largely in
331 agreement with those of sequential regressions (Table 4). In this model, NPP was a significant
332 predictor of population density in the predicted direction (LRT: $\chi_1^2 = 16.9$; $p < 10^{-3}$), although
333 the magnitude of its effect remained small compared with those of species richness and different

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334 levels of habitat. Habitat (LRT: $\chi_1^2 = 39.5$; $p < 10^{-3}$) and species richness (LRT: $\chi_1^2 = 33.2$; $p <$
335 10^{-3}) remained significant predictors of $\log(\text{density})$.

336

337 Discussion

338 To understand causes of variation in population abundance at a continental scale, we took data
339 on densities of Neotropical forest bird species and tested four hypotheses based on body mass,
340 productivity, interspecific competitors, and habitat. We used sequential regression to construct
341 the most likely series of relationships between these explanatory variables. First, we took into
342 account effects of body mass. Then, we postulated that habitat would have an independent
343 influence on abundance, and that within habitats, productivity could modify abundances. Finally,
344 we hypothesized that the richness of competing species should determine the way that species
345 divide up the available productivity within habitats. Using this approach, we found support for
346 the importance of all the explanatory variables except for productivity in predicting abundances.
347 Multiple regression largely agreed with the results of sequential regression, although NPP had a
348 small yet significant effect in the predicted direction.

349 Body mass explains relatively little variance when it is a fixed effect used to model
350 abundance on the species level, but on the family level this variable explains much more
351 variation in abundance. Other authors have also noted this relationship between body size and
352 taxonomic level, and the ability to predict abundance (Hurlbert and White 2007; McGill 2008).

353 Of all of the variables we examined, habitat type appeared to have the greatest effect on the
354 population abundance of birds (Table 2; Table 4). Montane forests have previously been found to
355 host higher avian population densities (Kattan and Beltran 2002, Ding et al. 2005, Kikuchi 2009,
356 Ferenc et al. 2016). Why should species of birds in humid forest, montane forest, and dry forest

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357 have higher densities than those found in Amazonian, Atlantic, or coniferous forest? One
358 possibility is that available energy is divided among fewer niches in some habitats. A potential
359 mechanism by which this might come about is through a decrease in the ratio of forest
360 height:productivity. Avian niches are often circumscribed by foliage height diversity and volume
361 (Willson 1974). If foliage height diversity changes more rapidly than productivity between two
362 habitats, there may be fewer niches among which productivity is distributed. For example, if two
363 species divide their foraging among canopy and understory in one habitat, but those two layers
364 are combined in another habitat, one species may be competitively excluded by the
365 disappearance of its niche. Additionally, high rates of topsoil turnover in regions prone to
366 landslides and earthquakes could elevate the available nutrients. Another possibility is that
367 density compensation may occur in some bird communities (Ferenc et al. 2016). Although we
368 found an independent effect of species richness on abundance, even after its correlation with
369 habitat had been taken into account (in our combined model), some of the variance in these two
370 predictors was inextricably confounded, potentially reducing the apparent effects of competitive
371 release. Finally, the metapopulation dynamics of lowland forests (i.e. Amazonian and Atlantic
372 forests) and other forests could be different. In the lowlands, groups that fare poorly at some sites
373 may nevertheless be more easily rescued by immigration through the matrix of forest; in other
374 areas such as montane forest, maintenance of low-density populations in areas to which they are
375 poorly adapted may be impossible because of geographical barriers.

376 The interspecific competitors hypothesis is supported. Particularly, the effect of species
377 richness was strongest within the hummingbirds (Table 3), which feed within the same trophic
378 level and display signatures of competition in the distribution of traits among their assemblages
379 (Graham et al. 2012, Maglianesi et al. 2014). Competition may also be fierce in the Tyranni,

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380 which often specialize in the interiors of forests (Ricklefs 2002). Studies that have found
381 correlations between density, species richness, and mean territory size have to a large degree
382 focused on this group, in the forest interior (Kikuchi 2009). The negative relationship between
383 density and species richness in the Psittaciformes also accords with the predictions of the
384 interspecific competitors hypothesis, although we do not have a particular explanation as to why
385 besides their shared evolutionary history. The Passeri may suffer less from competition than
386 other monophyletic groups, having recently invaded South America where they typically inhabit
387 the canopy and feed on a greater diversity of carbohydrate foods (Ricklefs 2002). Finally, the
388 lack of a relationship between density and species richness in non-Passerines (excluding
389 Psittaciformes and Trochilidae) is wholly in agreement with the predictions of the interspecific
390 competitors hypothesis, as this group is paraphyletic, with miscellaneous trophic ecologies,
391 microhabitat preferences, and life history strategies.

392 Competition may be a pervasive force in determining bird species abundance across the
393 Neotropics. Some continental localities may have lower equilibrium species richness than others
394 of equivalent productivity if they are more difficult to colonize, or subject to more frequent local
395 extinction (*sensu* Hanski 1982). This may be the case in montane communities because of area
396 effects along elevational belts (Kattan and Franco 2004), or environmental filtering (e. g.,
397 temperature or precipitation effects; Graham et al. 2012). If depauperate communities exhibit
398 density compensation, then they may host avifauna occupying larger realized niches than those
399 in lowland forests; it would be fascinating to know if this is the case, and whether individuals
400 have broader niches, or populations are composed of more variable individuals (Van Valen 1965,
401 Bolnick et al. 2015).

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402 Productivity itself was a poor predictor of species abundance, explaining negligible variance
403 (Table 1), although whether or not it was a significant predictor depended on the statistical
404 method used (Table 2 vs. Table 4). This result is perhaps unsurprising, as productivity has the
405 most scope to explain total abundance of *all* individuals summed across species, and moreover
406 *between* large (e.g. continental) regions (Storch et al. 2018). Willson (1974) and Hurlbert (2004)
407 also found that productivity was a poor predictor of the abundance of forest birds. Hurlbert
408 (2004) suspected a bias in the Breeding Bird Survey data that he used. Any such bias in our
409 study would be far less, however, due to the exhaustive methods of many studies that we
410 included in our database (hours of sampling effort for each transect of the BBS, versus months of
411 for the plots in the studies used here).

412 After using either sequential or multiple regression, much unexplained variance remains.
413 This variance may be attributed to other variables that we did not include in this study, but which
414 are correlated with the ones that we used; however, *a priori* hypothesis testing through sequential
415 regression is the best precaution we could take against this possibility, balancing thoroughness
416 against the inevitable improvement in model fit that more predictors bring. Specific traits that are
417 less phylogenetically conserved than body mass may improve estimates of species abundance.
418 Traits that reflect ecological specialization such as foraging substrate and method, circadian and
419 seasonal activity patterns, and aspects of morphology related to foraging and movement may be
420 worthwhile avenues of investigation (Pigot et al. 2016). The data structure required to explain
421 how traits influence species abundance may be complex, however (Warton et al. 2015).
422 Furthermore, better validation of methods used to measure avian densities in tropical habitats
423 may reduce noise in estimates.

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424 It is possible to count on one hand the number of studies that have completely described the
425 abundance of breeding birds in Neotropical avian communities (Terborgh et al. 1990, Thiollay
426 1994, Robinson et al. 2000, Johnson et al. 2011). All are from lowland rainforest. Other studies
427 in other habitats have described subsets of communities, often delimited by functional guilds
428 (Kattan and Beltran 2002, Stouffer 2007, Kikuchi 2009). The data coverage of some areas,
429 especially Atlantic forest, Andean forests south of Ecuador, and many drier biomes such as
430 Cerrado, Chaco, and Caatinga, is exceptionally sparse. Given that many fundamental questions
431 in ecology and evolution require being able to calculate abundances and biomass, the importance
432 of gathering abundance data from complete avian communities in a variety of Neotropical
433 habitats cannot be overstated. Future work on the community structure should measure both
434 population densities and species richness, particularly at multiple sites across ecological
435 gradients.

436 The pith of our study reveals that hypotheses that attempt to connect the abundance of
437 species to energy, whether via body mass (as energy consumption) or via productivity (as energy
438 availability), fall short unless certain caveats are observed. In the case of body mass, the caveat is
439 statistical: population density is better explained at higher taxonomic levels. In the case of
440 productivity, perhaps its effect on abundances depends on the way available energy is partitioned
441 according to habitat structure. Ecologically oriented hypotheses such as the type of forest habitat
442 and the number of potential competitors are better predictors of species abundances. However,
443 ultimately habitat type and the number of competitors reflect patterns of energy distribution
444 among consumers in complex environments, so for predictive purposes these two variables may
445 be more important, but mechanistically the abundance structure of communities is probably
446 dependent on energy fluxes (McGill et al. 2007).

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450

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453

454 **Data**

455 All data used in the analyses performed in this study are available as online supplements

456

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598 Table 1. Factors affecting population densities of Neotropical forest birds. The table shows all of
 599 the species-level models of log(density) fitted in the study, with their number of parameters k ,
 600 AIC scores, and Δ AIC scores separating them from the best-fit model.

601

Fixed effects	Random effects	k	AIC	Δ AIC
~ habitat + resid(NPP ~ habitat) + resid(species richness ~ resid(NPP ~ habitat))	order/family/genus	12	3474	0
~ habitat + NPP + species richness	order/family/genus	12	3474	0
~ habitat	order/family/genus	11	3504	30.5
~ habitat + resid(NPP ~ habitat)	order/family/genus	10	3505	31.2
~ 1	order/family/genus	5	3615	142
~ log(body mass)	none	3	3653	180

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612 Table 2. Summary of results of the most complex sequential regression model explaining
 613 population density of Neotropical forest birds as a function of habitat type, net primary
 614 productivity and species richness. Forest habitat (factor) and the residuals of NPP (continuous)
 615 and residuals of species richness (continuous) were predictors.

616

Effect	Estimate	Std. error
Amazonian Forest (reference)	1.41	0.15
Atlantic Forest	-0.65	0.62
Coniferous Forest	-0.49	0.24
Dry Forest	0.21	0.50
Humid Forest	0.22	0.09
Mountain Forest	0.24	0.25
resid(NPP ~ habitat)	0.04	0.04
resid(species richness ~ resid (NPP ~ habitat))	-0.56	0.10

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620 Table 3. The effects of the species richness of groups on the population densities of their
 621 members, including the significance of resid(species richness ~ resid(NPP ~ habitat type) as
 622 assessed by the likelihood ratio test, and estimated effect sizes and standard errors.

623

Group	χ_1^2 (LRT)	p-value	Effect size	Standard error
non-Passeriformes (excluding Psittaciformes and Trochilidae)	0.29	0.59	-0.09	0.16
Psittaciformes	12.47	$< 10^{-3}$	-0.75	0.20
Trochilidae	14.58	$< 10^{-3}$	-1.34	0.31
Tyranni (suboscines)	20.2	$< 10^{-3}$	-0.61	0.13
Passeri (oscines)	0.82	0.36	-0.08	0.09

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625 Table 4. Summary of results of the linear mixed model where predictors were fit simultaneously,
 626 for comparison with the sequential regressions. Forest habitat (factor), NPP (continuous), and
 627 species richness (continuous) were predictors.

628

Effect	Estimate	Std. error
Amazonian Forest (reference)	1.48	0.16
Atlantic Forest	-0.66	0.62
Coniferous Forest	-0.36	0.23
Dry Forest	0.33	0.50
Humid Forest	0.42	0.09
Mountain Forest	0.46	0.23
NPP	0.19	0.05
Species Richness	-0.56	0.09

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633 FIGURE LEGENDS

634

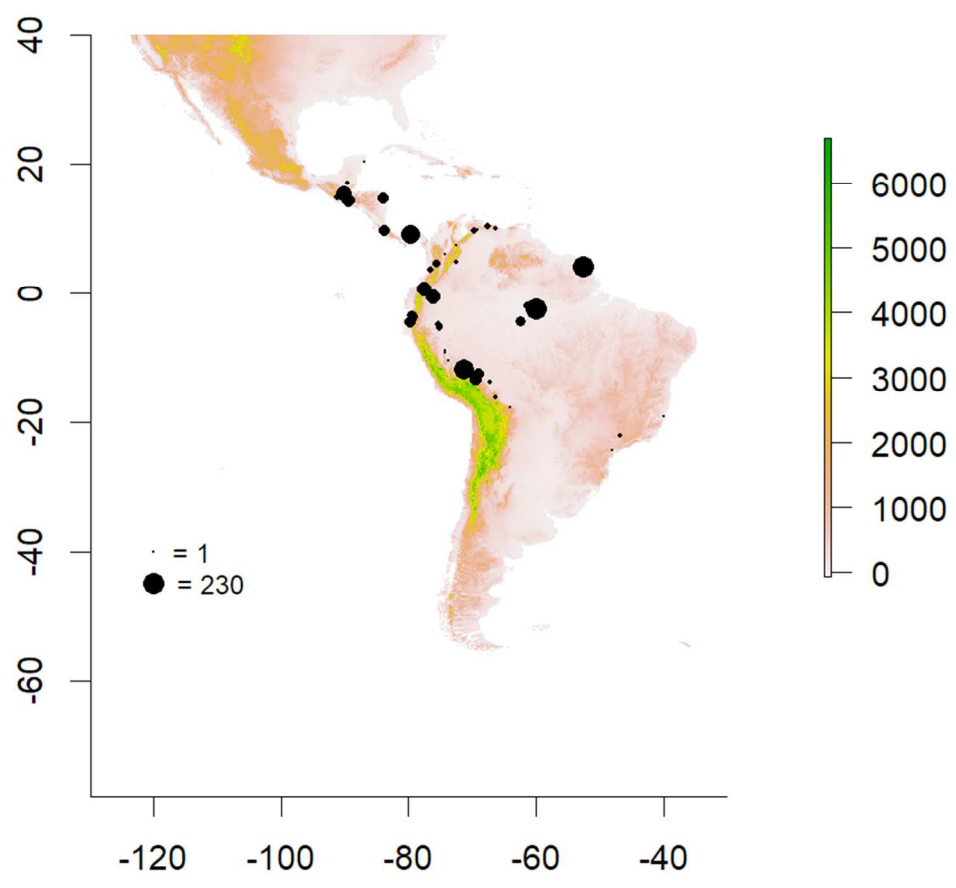
635 Figure 1. Locations of study sites (black dots) in final dataset of population density estimates of
636 Neotropical forest birds, superimposed on an elevational map of the Neotropics (m asl = meters
637 above sea level). Radius of dots is related to $\log_2(\text{number of species sampled at each site})$:
638 minimum records = 1; maximum records = 230.

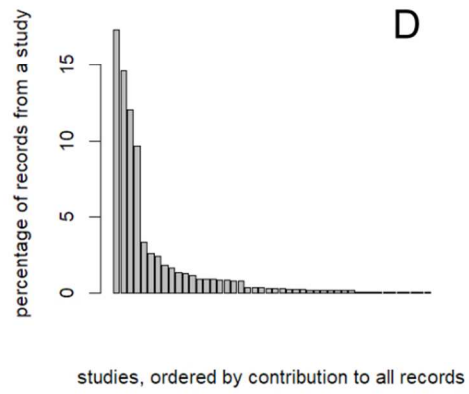
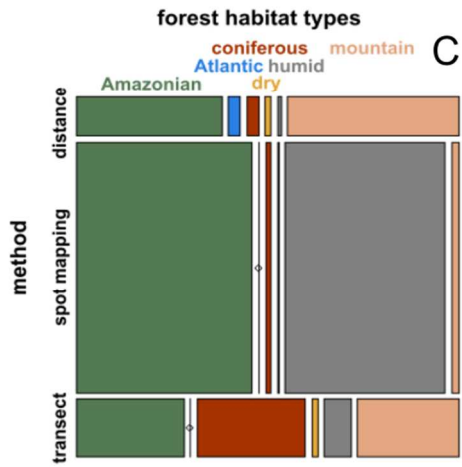
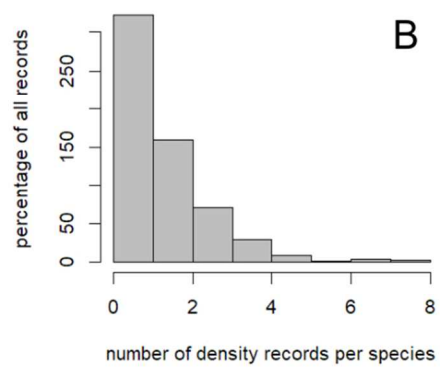
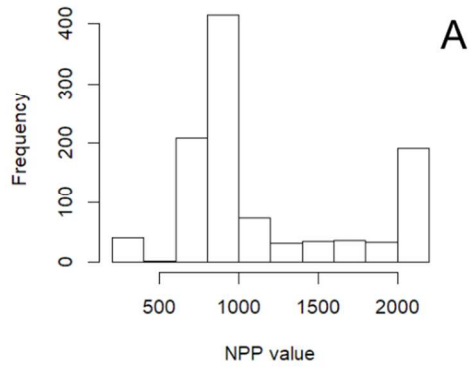
639

640 Figure 2. Metadata describing the final dataset, with median measures used for multiple
641 observations of the same species at the same site. A. Distribution of NPP values among records.
642 B. Distribution of records per species. Most Neotropical species are represented by only a single
643 density observation. C. Plot representing the number of records by habitat type and survey
644 method used. The size of the colored rectangles is proportional to the number of records. D.
645 Distribution of records from individual studies. Four major studies in lowland rainforest
646 contributed a large number of records.

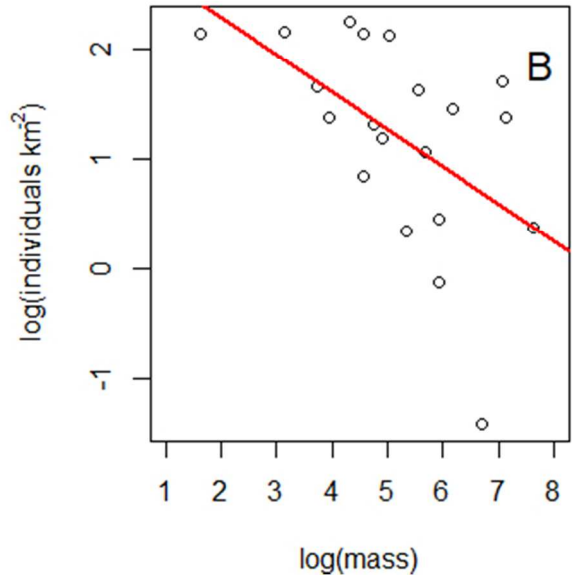
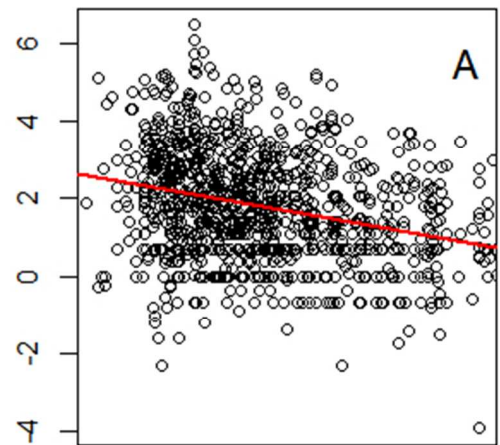
647

648 Figure 3. A) Population densities of Neotropical forest bird species regressed against body mass
649 on a log-log scale. B) Geometric mean population densities of Neotropical forest bird families
650 regressed against $\log(\text{geometric mean body mass})$ on a log-log scale.





July



Key to fields in DataA1.csv: id = an arbitrary record identification number; ords = order; family = family; genus = genus; sp = species Latin binomial; mig = migration status; study = citation from which data were retrieved (see list below); meth = survey method; lat = decimal degrees latitude; long = decimal degrees longitude; y = population density (individuals km⁻²); elev = elevation (masl); npp = net primary productivity, centered and scaled; nonPass = species richness of non-Passeriformes, centered and scaled; Psittaciformes = species richness of Psittaciformes, centered and scaled; Trochilidae = species richness of Trochilidae, centered and scaled; Tyranni = species richness of Tyranni, centered and scaled; Passeri = species richness of Passeri, centered and scaled; all = regional species richness (all birds), centered and scaled; mass = body mass of the species (g); habitat = habitat type; guild = speculation as to foraging guild (not used in analysis).

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