

Research

A continent-scale test of multiple hypotheses on the abundances of Neotropical birds

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Oikos

128: 235–244, 2019

doi: 10.1111/oik.05625

Subject Editor: Jiri Reif
Editor-in-Chief: Dries Bonte
Accepted 14 August 2018

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

Keywords: bird abundance, energy limitation, species interaction, Andes, Amazon, density compensation

Introduction

A fundamental question in ecology is how the abundance of species is governed (McGill 2008, Storch et al. 2018), which is central to numerous ecological and evolutionary processes (Gotelli 1995, Charlesworth 2009). Many factors may influence abundance, including environmental variables (Damuth 1981, Srivastava and Lawton 1998, Kaspari et al. 2000, Brown et al. 2004), species traits (Rosenzweig and Lomolino 1997, Murray et al. 2002, McGill et al. 2006, Umaña et al. 2015), and interactions with other species (MacArthur et al. 1972, Hudson et al. 1992, Robertson 1996, Berger and Gese 2007). Despite much investigation, no single factor appears sufficient to explain variation in species abundance (number of individuals/species; Murray et al. 2002, Hurlbert 2004, McGill 2008). Instead, we must examine trends across environmental gradients (McGill et al. 2006), taking into account the separate contribution

of abiotic and biotic factors (Warton et al. 2015), while at the same time controlling for correlations between predictor variables (Dormann et al. 2013).

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

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

A second factor predicted to govern abundance is the productivity of a locality (Srivastava and Lawton 1998, Kaspari et al. 2000, Hurlbert 2004, Storch et al. 2018). The relationship between productivity and the number of individuals in a community is unresolved (Storch et al. 2018). At the very least, however, most theoretical frameworks agree that productivity can place an upper bound on abundance. This could produce a positive correlation between productivity and abundance across localities. We then asked on what scale it makes sense to seek such a correlation. Much variation in species abundance will result from changes in habitat type, as some species will be adapted to high-productivity habitats (e.g. rainforest) and others to low-productivity habitats (e.g. dry forest). Therefore, hypothesizing that energy availability regulates species abundance makes most sense for comparisons within habitat types. We call this the productivity hypothesis,

which predicts a positive correlation between productivity and species abundance, once the correlation between productivity and habitat has been taken into account.

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

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

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

Methods

The dataset

Many of the Neotropical studies measuring bird abundances were known to us at the outset of this project. Searching through them, and works citing them, provided the backbone

of our database. We supplemented our knowledge by searching Google Scholar, JSTOR, and Wiley using the terms ‘bird density’ combined with the names of Neotropical countries and zones in English, Spanish, and Portuguese, as the local abundance of bird species is generally reported as a population density estimate. We read the introduction and methods sections of each paper to see if it met our criteria for estimating population density accurately. All papers we included used one or more of three methods to estimate population densities: spot mapping, point counts, and transect counts. All of the studies that used point counts and some studies that used transect counts also used the software Distance to correct for the probability of detecting the animals as a function of perpendicular distance away from the transect (Buckland et al. 2015).

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

To clean our dataset, we first excluded aquatic and riparian taxa, because their populations are difficult to census and the energy available in aquatic ecosystems was not addressed by our metric of Net primary productivity (NPP). Second, we excluded fragmented habitats because we wished to examine ecological processes unaffected by anthropogenic confounding factors such as edge effects (Murcia 1995). Third, we decided to focus on forest habitats because relationships between productivity and abundance are expected to be monotonic within forests; the relationship may reverse in grasslands (Hurlbert 2004). Fourth, we excluded migrants. Fifth, we excluded taxa considered *incertae sedis* because we were not able to account for the influence of their taxonomic affiliation on population density. In the final dataset that we used for analysis, we retained 1331 records from 47 studies (see Fig. 1 for locations and relative number of species measured at each study site). This included 596 species from 310

genera in 54 families spread among 21 orders. This dataset is described in Supplementary material Appendix 1 Table A1. Associated references are provided in Supplementary material Appendix 1 Metadata A1, and visualizations of the dataset are given in Fig. 2.

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

To provide a measure of energy availability, we used a geographical information systems (GIS) layer for NPP at 1 km resolution (Zhao et al. 2005). The layer uses the MOD17 algorithm to estimate NPP averaged across the years 2000–2013 in each cell. We did not have NPP data from outside this time window, yet some of the measurements of population density were recorded outside of it. They are from protected areas, however, so we made the assumption that the mean NPP values across 2000–2013 would be an adequate approximation of their NPP at the time of observation.

For testing the interspecific competitors hypothesis, we required a measure of species richness. We used a 10 km

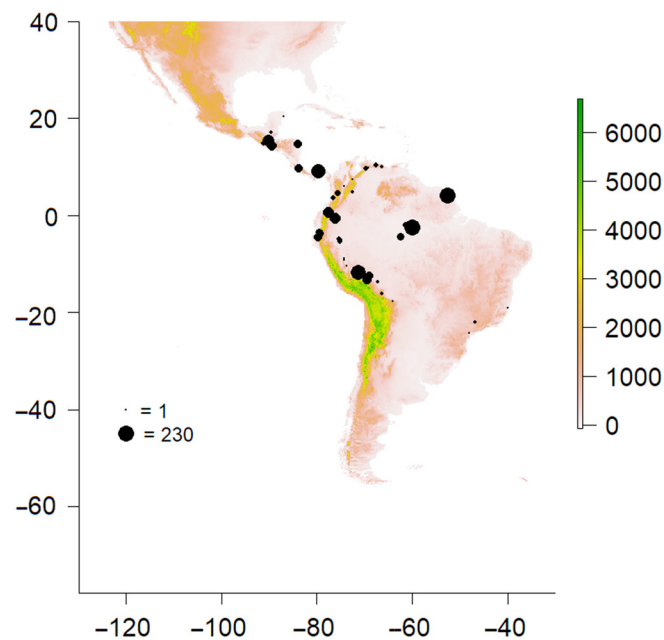


Figure 1. Locations of study sites (black dots) in final dataset of population density estimates of Neotropical forest birds, superimposed on an elevational map of the Neotropics (m a.s.l. = meters above sea level). Radius of dots is related to $\log_2(\text{number of species sampled at each site})$: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

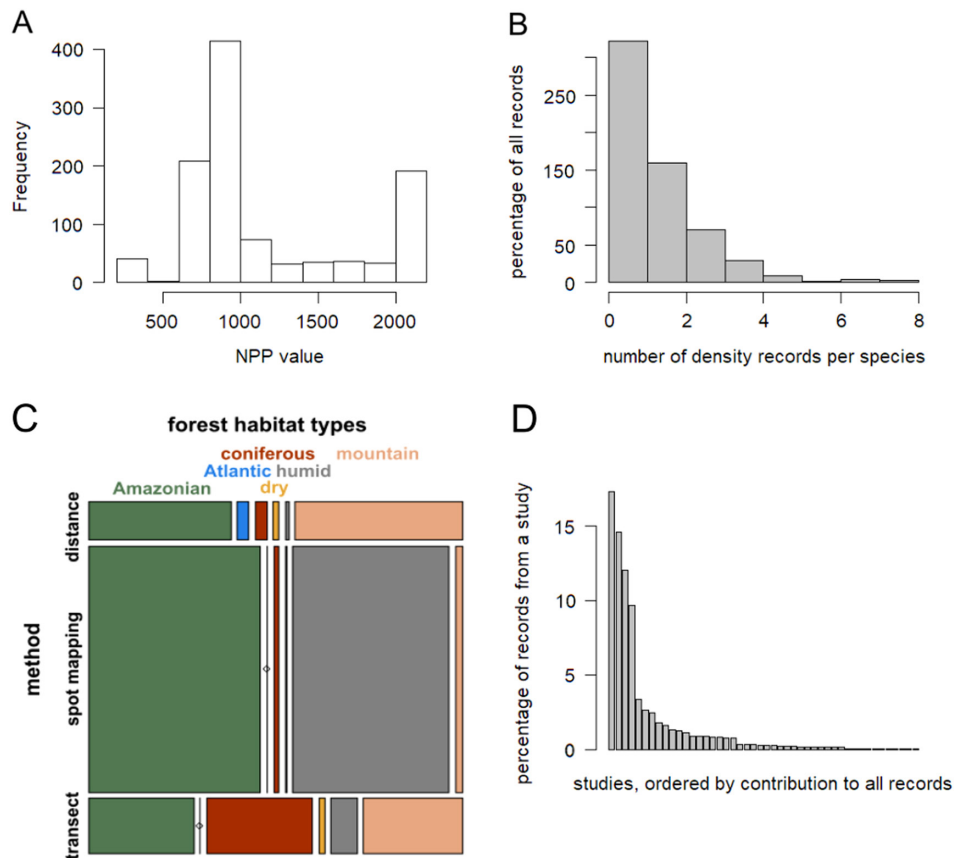


Figure 2. Metadata describing the final dataset, with median measures used for multiple observations of the same species at the same site. (A) Distribution of NPP values among records. (B) Distribution of records per species. Most Neotropical species are represented by only a single density observation.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

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

All of our study areas were on the same scale as our raster files or less. We used the latitude and longitude coordinates provided in each study or georeferenced them based on their descriptions to extract values of NPP and species

richness from our GIS layers. For this we used the ‘extract’ function from the package ‘raster’ in R (<www.r-project.org>), having obtained the appropriate raster files associated with the studies that generated the data (Zhao et al. 2005, Jenkins et al. 2013).

Testing mechanisms affecting population density

We tested four hypotheses for how the population densities of Neotropical birds are governed. Before analysis, we scaled and centered all of our continuous predictor variables so that they had mean=0 and standard deviation=1. The exception to this procedure was log(body mass) (hereafter simply body mass), which was only used in initial regressions. The first hypothesis that we tested was that population density should decrease with body mass. Species-level regressions of body mass typically provide a poor fit to avian population densities (Brown and Maurer 1987, McGill 2008). This may be because body mass is a conserved trait that varies more at the level of family and order among birds (Hurlbert and White 2007, McGill 2008), while other traits (presumably also important for governing abundance) vary at lower taxonomic levels. To verify these trends among Neotropical

birds, we performed the following analyses: 1) an ordinary least-squares (OLS) regression of the population densities of each species at each site against body mass on a logarithmic scale, 2) a linear mixed model fit with maximum likelihood of $\log(\text{density})$ with no fixed effects and order/family/genus as random effects, 3) a linear mixed model of $\log(\text{mass})$ regressed without fixed effects but order/family/genus as random effects, and 4) a log-linear model of the geometric mean densities for each family against the geometric mean body masses for each family (McGill 2008). The first model reveals the inadequacy of species-level analysis. The next two models illustrate that density is explained better at higher taxonomic levels, and that this is strongly related to how variance in body mass varies at those levels. The final model examines the relationship between density and body mass at the taxonomic level where it is most appropriate – where most of the variation occurs.

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

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

Testing the fourth hypothesis, the interspecific competitors hypothesis, which predicts that population density decreases with species richness, required the creation of a second variable by way of an additional sequential regression. We regressed species richness against habitat type + residuals(NPP ~ habitat type) to create a third predictor variable, and added this to a linear mixed model of $\log(\text{density})$ with the two variables it was regressed against, with order/family/genus as random intercepts. The R pseudocode

for the model is $\log(\text{density}) \sim \text{habitat type} + \text{resid}(\text{NPP} \sim \text{habitat type}) + \text{resid}(\text{species richness} \sim \text{resid}(\text{NPP} \sim \text{habitat type})) + (1|\text{order/family/genus})$. The effect of species richness is interpreted as independent, but only after its contribution to $\log(\text{density})$ through its correlations with NPP and habitat type have been taken into account.

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

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

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

A caveat in interpreting sequential regression is that it is sensitive to the order in which orthogonal axes are created. We chose the sequence of regressions to accord with our a priori hypotheses for how variables influence one another. However, we wished to examine the robustness of our results

to a different statistical method. To do so, we also performed a linear mixed model with habitat, NPP, and regional species richness as fixed predictors of $\log(\text{density})$, and order/family/genus as random effects. This approach does not use orthogonal predictors, but does break free from some of our assumptions.

Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.k5912k6>> (Kikuchi et al. 2018).

Results

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

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

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

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

The interspecific competitors hypothesis predicts that population densities will decrease with increasing species richness. We tested this effect after taking into account the contribution that species richness made to $\log(\text{density})$ through its correlation with NPP and habitat. This prediction of the interspecific competitors hypothesis was confirmed (LRT: $\chi^2_1 = 33.2$; $p < 10^{-3}$). Its effect size was on the same order of magnitude as the largest effect sizes for different habitat levels (Table 2).

We used AIC to compare the fit of all of the models that we fit for $\log(\text{density})$. This provided an alternative to the likelihood ratio test to see if there was an improvement in model fit when each predictor was added to the model. We found that the addition of each predictor resulted in an

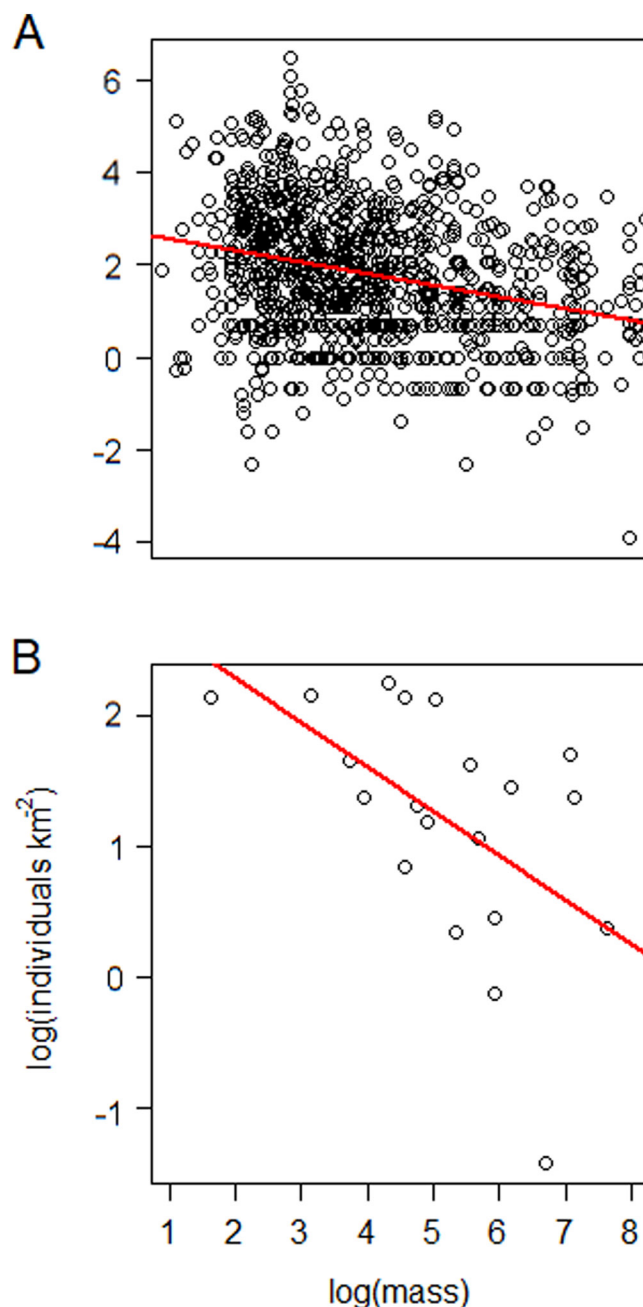


Figure 3. (A) Population densities of Neotropical forest bird species regressed against body mass on a log-log scale. (B) Geometric mean population densities of Neotropical forest bird families regressed against $\log(\text{geometric mean body mass})$ on a log-log scale.

improvement in model fit by at least 2 points, with the exception of productivity (Table 1). The ΔAIC separating the best-fit model from others was 30.5, indicating almost no support for any of the simpler models, and therefore arguing that the residuals of species richness are indispensable as a predictor of $\log(\text{density})$.

Within taxonomic groups, species richness was an inconsistent predictor of population density. Although in all cases the estimated relationship was negative, in the non-Passeriformes

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

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

(excluding Psittaciformes and Trochilidae) and the Passeri, species richness of each group was not a significant predictor of population density (Table 3). By contrast, in the Psittaciformes, Trochilidae, and Tyranni, it was (Table 3).

Results from a linear mixed model with predictors included simultaneously were largely in agreement with those of sequential regressions (Table 4). In this model, NPP was a significant predictor of population density in the predicted direction (LRT: $\chi^2_1 = 16.9$; $p < 10^{-3}$), although the magnitude of its effect remained small compared with those of species richness and different levels of habitat. Habitat (LRT: $\chi^2_1 = 39.5$; $p < 10^{-3}$) and species richness (LRT: $\chi^2_1 = 33.2$; $p < 10^{-3}$) remained significant predictors of log(density).

Discussion

To understand causes of variation in population abundance at a continental scale, we took data on densities of Neotropical forest bird species and tested four hypotheses based on body mass, productivity, interspecific competitors, and habitat. We used sequential regression to construct the most likely series of relationships between these explanatory variables. First, we took into account effects of body mass. Then, we postulated that habitat would have an independent influence on abundance, and that within habitats, productivity could modify abundances. Finally, we hypothesized that the richness of

competing species should determine the way that species divide up the available productivity within habitats. Using this approach, we found support for the importance of all the explanatory variables except for productivity in predicting abundances. Multiple regressions largely agreed with the results of sequential regression, although NPP had a small yet significant effect in the predicted direction.

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

Of all of the variables we examined, habitat type appeared to have the greatest effect on the population abundance of birds (Table 2, 4). Montane forests have previously been found to host higher avian population densities (Kattan and Beltran 2002, Ding et al. 2005, Kikuchi 2009, Ferenc et al. 2016). Why should species of birds in humid forest, montane forest, and dry forest have higher densities than those found in Amazonian, Atlantic, or coniferous forest? One possibility is that available energy is divided among fewer niches in some habitats. A potential mechanism by which this might come about is through a decrease in the ratio of forest height:productivity. Avian niches are often circumscribed by foliage height diversity and volume (Willson 1974). If foliage height diversity changes more rapidly than productivity between two habitats, there may be fewer niches among which productivity is distributed. For example, if two species divide their foraging among canopy and understory in one habitat, but those two layers are combined in another habitat, one species may be competitively excluded by the disappearance of its niche. Additionally, high rates of topsoil turnover in regions prone to landslides and earthquakes could elevate the available nutrients. Another possibility is that density compensation may occur in some bird communities (Ferenc et al. 2016). Although we found an independent effect of species richness on abundance, even after its correlation with habitat had been taken into account (in our combined model), some of the variance in these two predictors was inextricably confounded, potentially reducing the apparent effects of competitive release. Finally, the metapopulation dynamics of lowland forests (i.e. Amazonian and Atlantic forests) and other forests could be different. In the lowlands, groups that fare poorly at some sites may nevertheless be more

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

Effect	Estimate	SE
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

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

Group	χ^2_1 (LRT)	p-value	Effect size	SE
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

easily rescued by immigration through the matrix of forest; in other areas such as montane forest, maintenance of low-density populations in areas to which they are poorly adapted may be impossible because of geographical barriers.

The interspecific competitors hypothesis is supported. Particularly, the effect of species richness was strongest within the hummingbirds (Table 3), which feed within the same trophic level and display signatures of competition in the distribution of traits among their assemblages (Graham et al. 2012, Maglianesi et al. 2014). Competition may also be fierce in the Tyranni, which often specialize in the interiors of forests (Ricklefs 2002). Studies that have found correlations between density, species richness, and mean territory size have to a large degree focused on this group, in the forest interior (Kikuchi 2009). The negative relationship between density and species richness in the Psittaciformes also accords with the predictions of the interspecific competitors hypothesis, although we do not have a particular explanation as to why besides their shared evolutionary history. The Passeri may suffer less from competition than other monophyletic groups, having recently invaded South America where they typically inhabit the canopy and feed on a greater diversity of carbohydrate foods (Ricklefs 2002). Finally, the lack of a relationship between density and species richness in non-Passerines (excluding Psittaciformes and Trochilidae) is wholly in agreement with the predictions of the interspecific competitors hypothesis, as this group is paraphyletic, with miscellaneous trophic ecologies, microhabitat preferences and life history strategies.

Competition may be a pervasive force in determining bird species abundance across the Neotropics. Some continental localities may have lower equilibrium species richness than

others of equivalent productivity if they are more difficult to colonize, or subject to more frequent local extinction (Hanski 1982). This may be the case in montane communities because of area effects along elevational belts (Kattan and Franco 2004), or environmental filtering (e.g. temperature or precipitation effects; Graham et al. 2012). If depauperate communities exhibit density compensation, then they may host avifauna occupying larger realized niches than those in lowland forests; it would be fascinating to know if this is the case, and whether individuals have broader niches, or populations are composed of more variable individuals (Van Valen 1965, Bolnick et al. 2015).

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

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

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

Effect	Estimate	SE
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

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

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

Acknowledgments – We thank Allen Hurlbert for helpful comments.
Funding – DWK was supported by NIH-2K12GM000708-18.

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Supplementary material (available online as Appendix oik-05625 at <www.oikosjournal.org/appendix/oik-5625>). Appendix 1–2.