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Research paper

Empirical evidence for the scale-dependence of biotic interactions

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Scaling of biotic interactions

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Abstract.

Aim. While it is recognized that ecological patterns are scale-dependent, the exact scales over which specific ecological processes operate is still under intense controversy. In particular, understanding the scales over which biotic interactions operate is critical for predicting species distributional changes in the face of the ongoing biodiversity crisis. It has been hypothesized that biotic interactions operate predominately at fine grains, yet this conjecture has received relatively little empirical scrutiny. We use United States woodpeckers as a model system to assess the relative importance of biotic interactions, environmental suitability, and geographic proximity to other intraspecific occurrence sites, across scales.

Location. Conterminous United States.

Methods. We combined species occurrence data from the North American Breeding Bird Survey (BBS) with a large pair-wise interaction matrix describing known interactions among woodpeckers and other bird species. We then established the relative importance of biotic interactions as predictors of woodpecker occurrences in relation to environment and geographic proximity to intraspecific occurrence sites using a logistic mixed modeling framework.

Results. We found that geographic proximity becomes a stronger predictor of woodpecker occurrence as grain becomes coarser, while environment is grain-invariant. As opposed to environment and geographic proximity, we found that when the focal species experienced positive biotic interactions, interaction importance decreased with increased grain. However, positive interactions remained important up to a grain size of entire BBS routes (~40km), which is much coarser than the grain size used by most species distribution models. In contrast, when the focal species experienced negative interactions we did not find clear grain-dependence.

Scaling of biotic interactions

Main conclusions. Biotic interactions (both positive and negative) are important predictors of species occurrences. While these interactions are strongest at fine grains, they can remain important even at coarse grains and are thus critical for predicting distributional changes in the face of the ongoing biodiversity crisis.

Keywords. Species distribution models; Biotic interactions; Breeding Bird Survey; Scale; Grain; Extent; Co-occurrence

INTRODUCTION

It is widely acknowledged that ecological processes are scale dependent (Levin, 1992; Schneider, 2001; Maurer & Taper, 2002; McGill, 2010; Belmaker & Jetz, 2011). However, the exact scales over which specific ecological processes operate are still under intense controversy. The current paradigm states that biotic interactions, such as competition, predation and facilitation, are important determinants of species distributions only at small spatial scales (i.e., fine grains) where direct interspecific interactions occur (Shmida & Wilson, 1985; Whittaker *et al.*, 2001; Cavender-Bares *et al.*, 2009; McGill, 2010). At coarser grains, other processes such as dispersal and environmental associations are believed to gain prominence. Empirical evidence for the importance of biotic interactions in shaping species distributions has largely come from studies at local scales due to the difficulty in performing landscape-scale experiments and measuring the effects of biotic interactions at coarse scales. Thus, it has been a challenge to obtain data on the scale-dependence of biotic interactions relative to other processes affecting species distributions.

Establishing the scale-dependence of biotic interactions goes beyond pure interest in understanding the processes structuring natural assemblages. The grain size at which the influence of an interaction can no longer be detected is critical for predicting species-specific distributional changes in the face of the ongoing biodiversity crisis. If biotic interactions are only important at very fine grains, we may only need species-specific attributes, such as habitat suitability or dispersal ability, to predict broad-scale distributional changes. If, however, biotic interactions remain important across grain sizes, changes in one species may initiate cascading effects on many other species (Van der Putten *et al.*, 2010; Kissling *et al.*, 2012; Zarnetske *et al.*, 2012; Tuanmu *et al.*, 2013; Wisz *et al.*, 2013). This knowledge gap is profoundly impacting the

Scaling of biotic interactions

field of species distribution modeling (Guisan & Thuiller, 2005), which is now faced with uncertainty regarding how significantly biotic interactions could alter predictions and model accuracy (Elith & Leathwick, 2009; Godsoe & Harmon, 2012; Record *et al.*, 2013).

Evidence for the importance of biotic interactions at coarse grains has been accumulating (Gotelli *et al.*, 2010, Afkhami *et al.*, 2014, Araujo & Rozenfeld, 2014, de Araujo *et al.*, 2014). A study on Danish birds found signals of competition at grid resolutions of 5 and 10 km (Gotelli *et al.*, 2010). Predictions of butterfly occurrences at a resolution of 50 km were improved by incorporating the distribution of host plants (Araujo & Luoto, 2007) and predictions of owl distributions were improved by incorporating positive interactions with woodpeckers within 10 km and, to a lesser extent, 40 km (Heikkinen *et al.*, 2007). At even coarser grains the dispersal abilities of frugivores may affect the distributions of the tree species they disperse (Johnson & Webb, 1989; Beaudrot *et al.*, 2013) and over evolutionary time biotic interactions may even constrain range overlap between species (Pigot & Tobias, 2013). A recent simulation study (Araujo & Rozenfeld, 2014), showed that the scale at which biotic interactions remain important is dependent on the type of interaction under study. While positive interactions such as mutualism may remain important across grains, negative interactions such as competition were discerned only at fine grains (Araujo & Rozenfeld, 2014). Nevertheless, empirical analyses to date have been restricted to one or very few spatial scales which prevents a complete evaluation of scale-response curves.

In this study, we combined species occurrence data from the North American Breeding Bird Survey (BBS) with independently collected data on species interactions (e.g., competition, commensalism, predation). We focused on woodpeckers, a guild of birds in which most species excavate nesting cavities in dead or dying trees, because these species are known to interact in

Scaling of biotic interactions

both positive and negative ways with each other and other bird species. We created a large pairwise interaction matrix describing known interactions among woodpeckers in the United States and their interacting bird species. We then quantified the importance of positive and negative biotic interactions as predictors of species occurrences. Biotic interactions were contrasted with predictors that are typically thought to affect species distributions at broader spatial scales, including environment and geographic proximity to other intraspecific occurrences. This framework allowed us to assess how the relative importance of biotic interactions, environmental effects and geographic proximity changes across scales.

METHODS

Bird occurrence data

We used the North American Breeding Bird Survey (BBS) (USGS, 2012) to obtain breeding bird counts and locations across forested regions of the conterminous United States for the year 2006, to assure temporal alignment with the environmental data. We focused on woodpeckers for which there is relatively good knowledge on biotic interactions. The BBS consists of point counts during the breeding season (May and June) at 50 stops, spaced approximately every 800 m along approximately 39-km routes. At each of the 50 stops per route, observers record the number of individuals of all species seen or heard within a 400-m radius during a 3 minute period. Some 4,000 routes are repeated each year by trained volunteers, generating a unique systematic sampling of breeding birds across a broad spatial extent.

The vast majority of analyses on the BBS data are performed at the route level. However, in order to assess the influence of different predictors (e.g., biotic interactions, environment) on the occurrence of species, we included the finest stop level resolution. Stop-level geographic

Scaling of biotic interactions

locations are not published for all BBS routes, yet route locations are known, and point locations exist for the first stop of each route. For routes between 29 and 49 km in length, we used ArcGIS and Python to generate likely locations for the remaining 49 stops, spaced equidistant along each route, beginning at the known start point. Routes that appeared interrupted or contained sections that crossed were removed manually upon visual inspection.

We restricted the BBS location data to only those stops with <10% land cover change from 1992-2006 to minimize the effects of land cover change on our results. To determine this selection, we first generated buffers centered on each stop location that measured 400 m on either side of the BBS route, and 800 m along the BBS route. The 400 m buffer represents the maximum distance at which BBS observers record birds (Meehan *et al.*, 2010), while the larger 800 m distance along the route represents the potential for misplacing the location of each stop point. Within each 400 m by 800 m buffer, we summed the 30-m National Land Cover Database (NLCD; Fry *et al.*, 2011) pixels for which land cover had changed from 1992 to 2006 within each buffered stop, and only kept stops whose buffers contained less than 10% land cover change pixels over this timeframe. After filtering for land cover change, the total number of BBS routes used in the analyses was 3,126.

Altering grain and extent

We varied grain and extent as follows:

(1) We changed grain by aggregating stop-data within each BBS route. Grain varied by aggregating different numbers of stops, with 1 stop being no aggregation, then 2, 5, 10, 25, and 50 stops (all stops within each route are used). We refer to a site as the aggregated stops within a route. A species was deemed present in a site if it was seen at least once within the stops considered and absent if it did not occur at all within the stops considered. Environmental data

Scaling of biotic interactions

(see below) were averaged across stops within a site. Two variations of changing grain size were examined. In the first, multiple data points were used within each route (e.g., for a grain size of 25, we used 2 sites within a route). This resulted in sites within routes being very close and typically having similar environmental conditions, which may be regarded as a form of pseudoreplication. It additionally meant that sample size was smaller when aggregating the data more (e.g., for a grain size of 1 we had 50 stops within a route while for a grain size of 50 we had only 1 stop). In the second version, we always used the first site within a route, regardless of the aggregation level, thus maintaining sample size across grains but necessarily excluding a large proportion of the data.

(2) We varied extent by altering the spatial area considered with diameters ranging from 500 km through 1,000, 2,000 up to 4000 km. This was done by choosing a random route and only including routes that fell within the above distances to it. Sample size always increased with increased extent.

Biotic interactions estimates

We completed an extensive literature review to capture the interactions other bird species may have with woodpeckers (table 1). For example, primary cavity-nesting woodpeckers can facilitate secondary cavity nesters (Martin & Eadie, 1999; Aitken & Martin, 2007). In addition, woodpeckers interact with other birds via competition, predator-prey relationships, kleptoparasitism, and brood parasitism. To identify these interactions, we searched the Birds of North America Online (Poole, 2005) for each woodpecker species in the dataset. The Birds of North America is a comprehensive online resource providing life-history information, including specific sections on behavior and interspecific interactions. Account contents are updated

Scaling of biotic interactions

regularly and reference peer-reviewed journal articles. For each woodpecker, we recorded all reported interactions with any other bird species as identified by the articles containing mention of the woodpecker species. We did not include interactions that occur at bird feeders because these can represent unnatural situations, and we also did not include interactions related to interspecific flocking behavior.

It is likely that not all interactions were reported for each species. This can lead to several types of biases. First, it is possible more interactions are reported for the most common species, leading to rare species being underrepresented in the interaction matrix. However, we do not find such a pattern as the correlation between species abundance and the total number of interactions observed for a species was low ($r = 0.41$). Second, it is highly probable that rare interactions between species were not observed nor reported. However, this should not influence our results as rare interactions should not strongly influence species occupancy. Finally, there might be geographic biases in reporting, based on more in-depth studies in certain locations. Although this type of bias is hard to correct, in our case we repeated our analyses across different extents and locations across the conterminous United States. Thus, geographic biases will increase the variability in our results but should not alter the major patterns. Despite these potential biases, the Birds of North America is still the most comprehensive resource for North American breeding birds (Poole, 2005) and thus provided the best collection of interaction information for North American woodpeckers as a whole.

We separated the positive and negative interactions exerted on each species. For each interaction type we summed the number of positive and negative interactions experienced by each focal woodpecker species from all co-occurring species at a site to produce an estimate of total positive and total negative interactions.

Scaling of biotic interactions

Simulation studies suggest that the scale-dependence of biotic interactions may change according to interaction type (Araujo & Rozenfeld, 2014). We thus also split the effect of the interactions on the focal species into the following categories:

- (1) Positive effect on the focal species and negative effect on the interacting species. This category includes focal species that interact by being a brood parasite (brood parasitism), steal food from the interacting species (kleptoparasitism), or are predators (predator-prey).
- (2) Negative effect on the focal species and positive effect on the interacting species. This category includes focal species that are the victim of food theft (kleptoparasitism), are hosts to brood parasites (brood parasitism), or are prey species (predator-prey).
- (3) Positive effect on the focal species and no effect on the interacting species. This category includes focal species that benefit from commensalism (e.g. secondary cavity nesters).
- (4) Negative effect on the focal species and negative effect on the interacting species. This includes species that have competitive interactions.

Other interactions, such as amensalism and mutualism, were too rare or nonexistent in our literature review to be analyzed. A list of the total number of interactions documented for each species can be found in table 1.

Environmental suitability

We chose a suite of environmental variables to use as predictors that are relevant to the distributions of breeding birds in North America (Meehan *et al.*, 2010; Rittenhouse *et al.*, 2010; Matthews *et al.*, 2011; Barbet-Massin & Jetz, 2014). These included climatic variables generated from PRISM (PRISM, 2010) monthly datasets (4 km resolution), intersected at each stop point. With these data, we used the “biovars” command in the R package “dismo” to generate 19

Scaling of biotic interactions

bioclimatic predictors. For each buffered stop area, we also calculated the proportion of land cover types in 2006 from the NLCD land cover dataset (Fry *et al.*, 2011). Based on the 30-m National Biomass and Carbon Dataset for the year 2000 (NBCD2000; Kellndorfer *et al.*, 2012) we calculated the average basal area-weighted canopy height for each buffered stop area. To reflect productivity of vegetation, we obtained the 95th percentile of the Enhanced Vegetation Index (EVI) from a 2005-2007 time series of a 250-m 16-day MODIS composite (MOD13Q1) for each 250-m pixel. We then calculated the area-weighted average for each buffer area. We used the 95th percentile over the three years to capture the EVI at the peak of a growing season, but to avoid including spuriously high values. The use of the three-year time series increases the number of valid EVI values for the calculation and minimizes the effect of potential land cover change. A full list of variables is presented in table A1.

For each species we estimated the probability of a site being within the suitable environment using bioclimatic envelope models, implemented through the function ‘bioclim’ in the R package ‘dismo’ (Hijmans *et al.*, 2013). The models were based on the first ten axes of a principal component analysis (PCA) among all of the above-mentioned environmental variables, which jointly explained > 99.9% of the total variance in environmental data. Within each grain or extent (see above) we randomly selected 80% of the BBS routes to serve as training data while the remaining 20% of the routes served as test data. The training data were used to generate environmental-suitability predictions for each of the test data points for each species. The predictions for the test data points only were used in the final analyses (logistic mixed-effects models, see below).

Geographic proximity

Scaling of biotic interactions

We performed spatial interpolation to estimate the contribution of geographic proximity to other occupied sites to species occurrence probability, independent of environmental suitability (Bahn & McGill, 2007). We used Gaussian kernel density smoothers to calculate the density of occurrence for each site based on the geographic location of sites. We controlled for variation in sampling effort by dividing observed occurrence density by the density of sampling stops (Broennimann *et al.*, 2012). This ensures that sparsely sampled regions do not receive exceptionally low densities. For each species, we applied a kernel density smoother to the training data and generated predictions for the test data. This resulted in an occurrence probability for each species and testing site based on geographic proximity to other known occurrences of that species.

Analyses

We performed a logistic mixed-effects model analysis for all woodpeckers across all testing sites, using the species- and site-specific estimates obtained from the environmental suitability and geographic proximity analyses (figure 1). We ran a single model across all woodpecker species observed at a given grain and extent. Thus, the presence or absence of species at each site was the binary response variable with four fixed effects: (1) Environmental suitability - environmental suitability according to the bioclimatic envelope model; (2) Geographic proximity - occurrence probability according to the Gaussian kernel density smoother; (3) Positive biotic interactions - summed interactions of all co-occurring species that exert a positive effect on the focal species; and (4) Negative biotic interactions - similar to positive biotic interactions, but including only species that exert a negative effect on the focal species. Heterogeneity among species and sites was accounted for by incorporating species- and site-specific random-effect intercepts. We compared models with random intercepts only to those with random intercepts

Scaling of biotic interactions

and slopes. We found that for 80% and 58% of the models (for positive and negative interactions, respectively) random intercept only models were superior (in terms of AIC) to random-slope models. The percentage of models for which random slope models were not statistically superior to random intercept models (AIC differences < 2) was even higher (89% and 69% of the models respectively). Consequently, we retained only the simpler random-intercept models throughout the study. A species was included in the models only when it had more than three presences within the sites investigated to remove rare species for which the random-effect could not be estimated. Environmental suitability and geographic proximity were logit transformed and standardized (to a mean of zero and a standard deviation of one) to allow for comparison of fixed effect estimates. Over local extents some analyses contained few routes, and these were excluded when the number of routes fell below 50.

We extracted parameter estimates and unconditional standard errors from the models. For each fixed effect, importance was calculated as the Akaike weight of the full model relative to the model excluding that predictor. We assessed the goodness of fit by calculating marginal and conditional R^2 (R^2_M and R^2_C , respectively), which are measures of the variance explained by the fixed effects and fixed and random effects, respectively (Nakagawa & Schielzeth, 2013). All analyses were conducted in R Version 2.15.0 (R development core team, 2012).

To assure that the results found for biotic interactions were not an artifact related to species richness (e.g. species experience more positive interactions simply because of higher species richness), or related to reporting bias of the biotic interactions, we compared the observed patterns with a null model and calculated Effect Sizes (ES) as standardized deviation from the null. The null expectations were generated from 100 runs of the model. To generate the null models, we randomly shuffled interactions such that the interactions experienced by each

Scaling of biotic interactions

focal species were assigned to random interacting species. For example, for a woodpecker with five interacting bird species at a site, we sampled interactions from the complete species list and randomly assigned them to one of the five interacting species. Thus, this null model did not alter the identity of co-occurring species or the total number of interactions experienced by the focal species.

BBS route identity varied across model runs, even for the same grain and extent, both because different regions were selected and because different sites were randomly designated for training and testing. We thus performed 100 runs in each grain (aggregation of 1, 2, 5, 10, 25 and 50 stops) and extent (diameters of 500, 1000, 2000 and 4,000 km) combination resulting in a total of 2,000 mixed-effect models.

RESULTS

Environmental suitability and geographic proximity had strong effects on woodpecker occurrence. This was seen both in the positive coefficient estimates and high variable importance (figure 2). This meant that there was a higher chance of seeing a specific woodpecker species at a site if: (1) the environment was more suitable; and (2) the site was closer to other sites in which the same species was seen. Geographic proximity showed strong grain-dependence where increasing grain size resulted in increased coefficient estimates. Environment did not show similar patterns and its effect was relatively constant across grains. Generally similar results were found when only the first site within each route was included to maintain sample size across grains (figure S1). However, these results were more variable, reflecting the high uncertainty associated with each particular observation.

Scaling of biotic interactions

Increasing spatial extent caused a substantial increase in the variance explained by the models (figure S2). This result reflects the larger number of BBS routes sampled at broader extents and the associated larger environmental gradients. However, for most predictors the effect of extent on coefficient estimates was minor. Thus, when the analyses were conducted at local extents (such as extents of 500 and 1000 km) predictors maintained overall positive coefficients but with larger variability (table A2, figure S3). The only predictor to show clear extent-dependence was geographic proximity for which the estimated coefficient increased dramatically as extent broadened (figure S2).

Both positive and negative interactions displayed positive coefficients across scales meaning that occurrence probability of a focal species is higher when other species, which are known to interact with it, were recorded at the site (figure 2). Positive coefficients for negatively interacting species were surprising, but can happen when the species being considered had similar habitat requirements, not captured by the environmental model, leading to net positive co-occurrence. However, at all grains and extents the coefficients for positive interactions were higher than those for negative interactions, suggesting the presence of signal of biotic interactions beyond XXXX. As opposed to environment and geography, positive biotic interactions showed a clear decrease in coefficient estimates with increased grain (figure 2). In contrast, negative interactions do not show any clear grain-dependence.

To control for potential biases related to the distribution of the number of total biotic interactions across richness gradients, we calculated standardized deviations from null models as effect sizes (ES). Positive and negative interactions had the expected positive and negative ES (respectively), attesting to the importance of taking into account the null distribution. We found that positive interaction ES had similar patterns to the raw coefficients and were generally

Scaling of biotic interactions

positive but decreased in strength with increasing grain (figure 3). Nevertheless, even at the coarsest grains, ES for biotic interactions were significant for a substantially higher proportion of the models than predicted by chance alone (e.g., at a grain size of 50 and extent of 2000km, 14% of the models are significant versus the expected 2.5%). For negative interactions we found negative ES, which declined in strength with increasing grain size (figure 3). However, here the ES remained non-significant across grains.

When parceling out the biotic interactions to different interaction types we generally found few ES that were significant, likely due to the low power of the analyses. Nevertheless, we found evidence for grain-dependence when the focal species experienced a positive effect and the interacting species experienced a negative effect (figure 4). There was no clear grain dependence with other types of interactions.

DISCUSSION

Species are altering their distributions in response to environmental changes and anthropogenic impacts. The prevailing paradigm states that at coarse grains understanding and predicting these distributional changes does not require accounting for biotic interactions among species.

However, some evidence suggests that biotic interactions may be important even at coarse grains (Gotelli *et al.*, 2010; Araujo & Rozenfeld, 2014; Kissling & Schleuning, 2014). Nevertheless, we still have a poor understanding of: (1) how important biotic interactions are relative to other processes; and (2) at what grain biotic interactions are too important to be ignored, e.g., in the context of predicting future distributional changes. In this study, we used detailed interaction information for North American woodpeckers and their interacting avian species to show that: (1) biotic interactions (both positive and negative) are important predictors of species

Scaling of biotic interactions

occurrences, although typically less important than environmental variables or geographic proximity, and (2) biotic interactions remain important even at coarse grains.

We found that all three types of predictors (i.e., biotic interactions, environment and geographic proximity) were important for understanding woodpecker occurrences across scales. However, the relative importance of these predictors changed with the grain and, to a lesser degree, the extent considered. For positive interactions, although increasing grain size resulted in reduced coefficient estimates and variable importance, interactions remained substantial even at coarse grains of entire BBS routes (~ 40km). The significance of positive interactions was evident by the positive coefficients, high importance and generally positive effect sizes. These results show, for the first time, that biotic interactions influence species occurrence across different scales. We suggest that fine grain analyses can always benefit from the explicit incorporation of biotic interactions, but that their importance diminishes, at least for North American woodpeckers, at grain sizes coarser than ~40km (the length of a BBS route). As roughly half of species distribution models use grains of up to 100km² (Record *et al.*, unpublished data), incorporating biotic interactions across scales will be key to improving predictive performance for many different species.

We found little grain-dependence in the magnitude of environmental coefficients. This is in contrast to several studies that found strong grain-dependence in the strength of environment as a predictor of species distribution and richness (Guisan *et al.*, 2007; Randin *et al.*, 2009; Belmaker & Jetz, 2011). This grain-independence of environmental predictors reflects our use of a large suite of environmental predictors that include climate and detailed land cover information. Whereas climate may be important at coarse grains (Whittaker *et al.*, 2001;

Scaling of biotic interactions

Belmaker & Jetz, 2011), land cover may be more influential at fine grains resulting in overall grain-invariance.

In contrast to environment, geographic proximity was markedly scale-dependent. The coefficients for geographic proximity became larger as grain became coarser and as extent broadened. Thus, at grain sizes approaching entire BBS routes and extent approaching the entire continent, the presence of a species was strongly dependent on the presence of conspecifics in adjacent routes (Bahn & McGill, 2007). This pattern likely reflects the cohesiveness of species' ranges at coarse grains and broad extents. With finer grain, species presence becomes more patchy, reflecting the underlying heterogeneity in the environmental and biotic landscape. As a result, the statistical contribution of geographic proximity decreases.

Our approach to quantify the importance of biotic interactions relies on observational data. Thus, when multiple species respond positively to an environmental resource we may find positive co-occurrence even if the underlying interactions between the species are negative. Indeed, the coefficients for negative interactions were positive, although we would expect to observe negative coefficients as the presence of interacting species should reduce probability of occurrence. However, the coefficients for positive interactions were always higher than the coefficients for negative interactions. If the effects of biotic interactions were entirely due to shared environmental preference we would expect to find no difference between the coefficients for positive and negative interactions. Thus, the difference between positive and negative coefficients represents the net influence of biotic interactions after accounting for shared environmental preferences of co-occurring species.

Biotic interactions exhibited mixed grain dependence. For positive interactions, both the coefficients and effect sizes (ES) were high at fine grains and decreased with increased grain, but

Scaling of biotic interactions

remained positive overall (figure 3). However, ES for negative interactions were slightly negative at fine grains only, and were not significant across all grains (figure 3). These patterns reinforce the simulation results of Araujo & Rozenfeld (2014), who found positive interactions, such as mutualism, to be important across grains but competition only important at fine grains. When separating the interactions into categories, we found that grain dependence was particularly apparent when the focal species benefited and the interacting species suffered (figure 4). In woodpeckers, such interactions mainly include kleptoparasitism, in which a woodpecker species gains or steals food originally obtained by another species and rare cases of woodpecker predation on other species. In contrast, it appears that competition (negative-negative) was generally weak and did not exhibit clear grain dependence. Together these findings suggest that emphasis should shift from focusing on competition as the prime biotic determinant of species geographical distributions to a full range of interactions types (e.g., predator-prey relationships, facilitation).

We would like to emphasize that the only way to truly estimate interaction strength is to perform manipulative experiments. Observational studies can never completely disentangle shared or divergent environmental preferences versus true biotic interactions. For example, the apparent importance of interactions at macroecological scales will be contingent on environmental data resolution. Coarse habitat designations will tend to equate negative co-occurrence patterns with competition while at fine enough resolutions we may detect habitat partitioning as the underlying cause. Thus, the apparent importance of biotic interaction should be considered in light of the data used. For the commonly-used environmental predictors used in these analyses, it appears that incorporating species interactions improves species occupancy

Scaling of biotic interactions

predictions. However, a similar model using better resolved environmental data may find a demised signal of such biotic interactions.

Our results have important implications for applied research on species distribution models and community assembly theory. First, we show that information on biotic interactions will likely improve species distribution models by demonstrating that qualitative data gleaned from the literature or expert knowledge provide valuable information for predicting species occurrences. Second, we find that contrary to the present ecological paradigm, biotic interactions remain important even at coarse grains. This finding shows that the inclusion or exclusion of biotic interactions should be based on ecological knowledge and cannot simply be dismissed using the coarse grain or extent of the models as a justification.

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Table A1: Environmental predictors used in the analyses.

Table A2: Summary statistics for the linear mixed effect models.

Figure S1. Same as figure 1, but only taking the first (aggregated) stop within each route.

Figure S2: Changes across extent.

Figure S3. Same as figure 1, but using an extent of 1,000 km.

Biosketch.

The authors are a working group initiated at the Ecological Society of America workshop: "Scaling UP: Population and Community Ecology. A Workshop for Early Career Scientists".

The workshop focused on identifying key questions in population and community ecology that can or should be addressed at continental scales, assessing the status of existing analytical, physical, and software tools needed to address these questions, and identifying needs and capabilities for developing new tools to address continental-scale questions.

Scaling of biotic interactions

TABLES

Table 1: The total number of bird-bird interactions experienced by woodpecker species in the conterminous United States, when the woodpecker is the focal species. Interaction counts in the table are split by biotic interaction types, where the first interaction represents the effect on the focal species. For example, Positive - Negative interactions indicate interactions where the focal woodpecker species has a negative effect on the interacting species, and the interacting species has a positive effect on the focal woodpecker. Negative-Null and Positive-Positive interactions were not found and are therefore not included. Null-Positive interactions exist but were not used in this study.

Common name	Latin name	Positive - Negative	Negative - Positive	Positive - Null	Negative - Negative	Total
Acorn Woodpecker	<i>Melanerpes formicivorus</i>	2	5	0	8	15
American Three-toed Woodpecker	<i>Picoides dorsalis</i>	0	0	1	3	4
Arizona Woodpecker	<i>Picoides arizonae</i>	0	0	0	7	7
Black-backed Woodpecker	<i>Picoides arcticus</i>	0	1	0	6	7
Downy Woodpecker	<i>Picoides pubescens</i>	1	5	1	22	29
Gila Woodpecker	<i>Melanerpes uropygialis</i>	4	1	0	4	9
Gilded Flicker	<i>Colaptes chrysoides</i>	0	10	0	6	16
Golden-fronted Woodpecker	<i>Melanerpes aurifrons</i>	3	1	0	3	7
Hairy Woodpecker	<i>Picoides villosus</i>	0	8	1	18	27
Ladder-backed Woodpecker	<i>Picoides scalaris</i>	0	0	0	2	2
Lewis's Woodpecker	<i>Melanerpes lewis</i>	1	5	6	11	23
Northern Flicker	<i>Colaptes auratus</i>	25	68	0	30	123
Nuttall's Woodpecker	<i>Picoides nuttallii</i>	0	1	1	12	14
Pileated Woodpecker	<i>Dryocopus pileatus</i>	1	6	0	13	20
Red-bellied Woodpecker	<i>Melanerpes carolinus</i>	10	3	0	14	27
Red-breasted Sapsucker	<i>Sphyrapicus ruber</i>	0	4	0	1	5
Red-cockaded Woodpecker	<i>Picoides borealis</i>	0	4	0	11	15
Red-headed Woodpecker	<i>Melanerpes erythrocephalus</i>	9	3	1	16	29
Red-naped Sapsucker	<i>Sphyrapicus nuchalis</i>	0	4	0	2	6
White-headed Woodpecker	<i>Picoides albolarvatus</i>	0	2	0	8	10
Williamson's Sapsucker	<i>Sphyrapicus thyroideus</i>	2	2	1	9	14
Yellow-bellied Sapsucker	<i>Sphyrapicus varius</i>	0	2	1	4	7
Total interactions		58	135	13	210	416

Scaling of biotic interactions

FIGURE LEGENDS

Figure 1. Schematic diagram presenting the major steps in our analyses. For each site (aggregated stops) within the BBS routes, we calculated species-specific probability of occurrence estimated from bioclimatic envelope models (environmental suitability) and geographic proximity (kernel density smoothers). We additionally calculated for each species at each site the summed number of positive and negative interactions. At the second step, these variables were combined within a mixed-effect model across woodpecker species. Bird line drawings by J. Woerner, K. Kraeer, L. Van Essen and T. Saxby, IAN image library (ian.umces.edu/imagelibrary/).

Figure 2. Violin plots depicting the scaling of the three ecological predictors (biotic interactions, environment and geographic proximity) examined across different grain sizes, measured as the level of aggregation of stops within BBS routes. (a) Variable coefficient; (b) importance of the variables within a full model relative to a model excluding that variable. Biotic interactions (left panels) are separated into positive (grey) and negative (black) interactions experienced by the focal species. The tick marks represent the results from each of the 100 mixed-effect models, each containing several species across all testing sites. Solid lines represent median values at each grain. The shaded area represent the result of a Gaussian kernel density smoother. Results are based on analyses from an extent of 2,000 km.

Figure 3: Violin plots depicting: (a) scaling of biotic interaction coefficients, and (b) effect sizes (ES; standardized deviation from null). Dashed lines in (b) represent ES of ± 1.96 , beyond which they are statistically significant. The tick marks represent the results from each of the 100 mixed-

Scaling of biotic interactions

effect models. Solid lines represent median values at each grain. The shaded area represent the result of a Gaussian kernel density smoother. Results are based on 2,000 km extent.

Figure 4: Violin plots depicting changes in effect sizes (ES; standardized deviation from null) across grains for different types of biotic interactions. Dashed lines represent ES of ± 1.96 , beyond which ES are statistically significant. Solid lines represent median values at each grain. The shaded area represent the result of a Gaussian kernel density smoother. Results are based on analyses from an extent of 2,000 km.

Scaling of biotic interactions

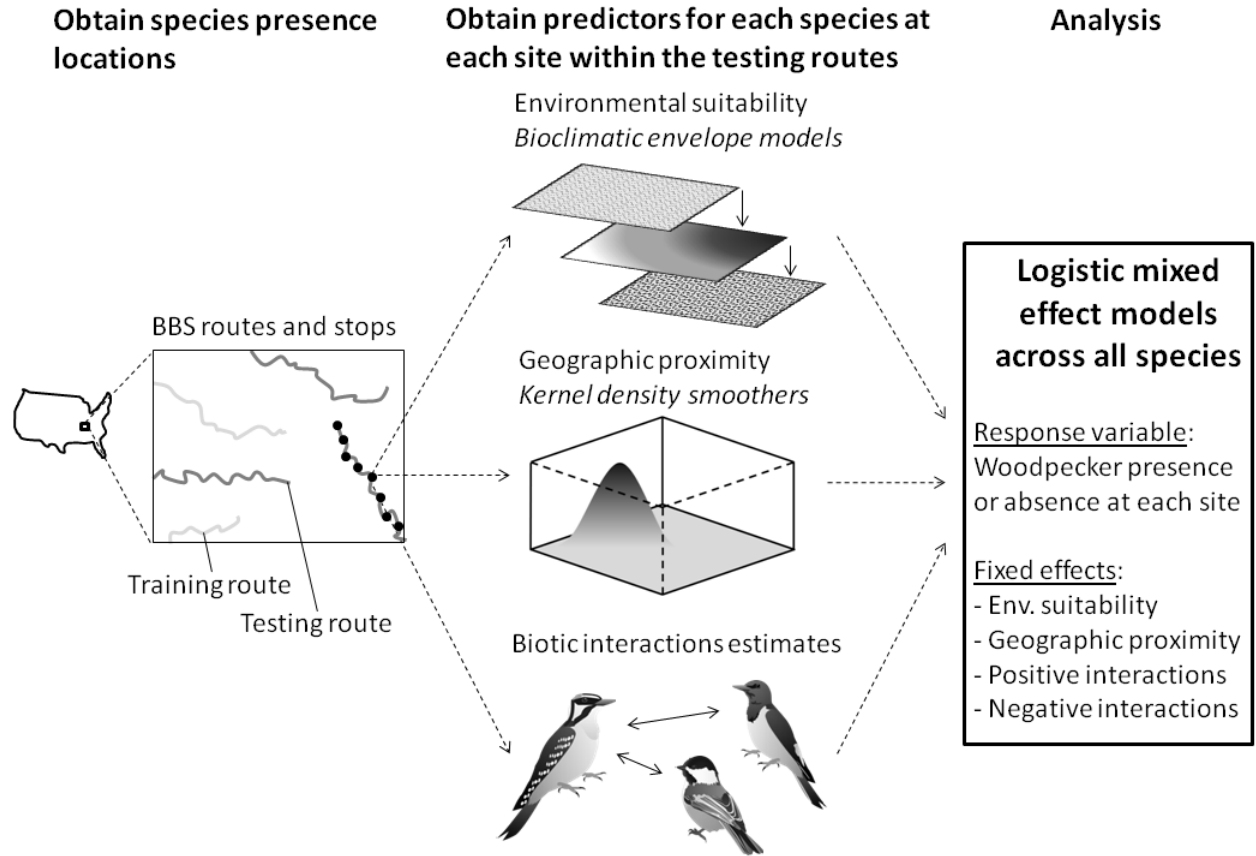


Figure 1.

Scaling of biotic interactions

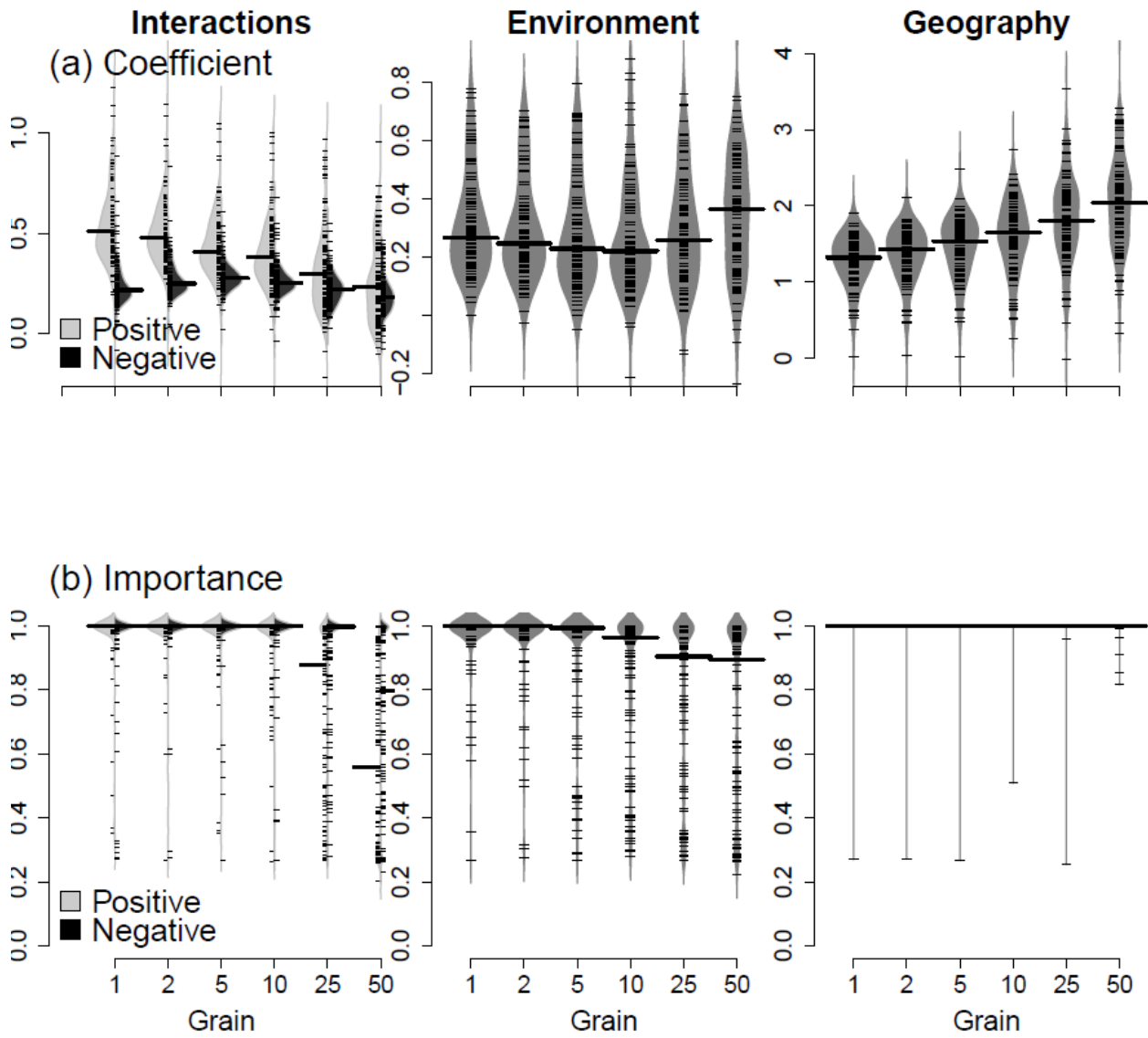


Figure 2.

Scaling of biotic interactions

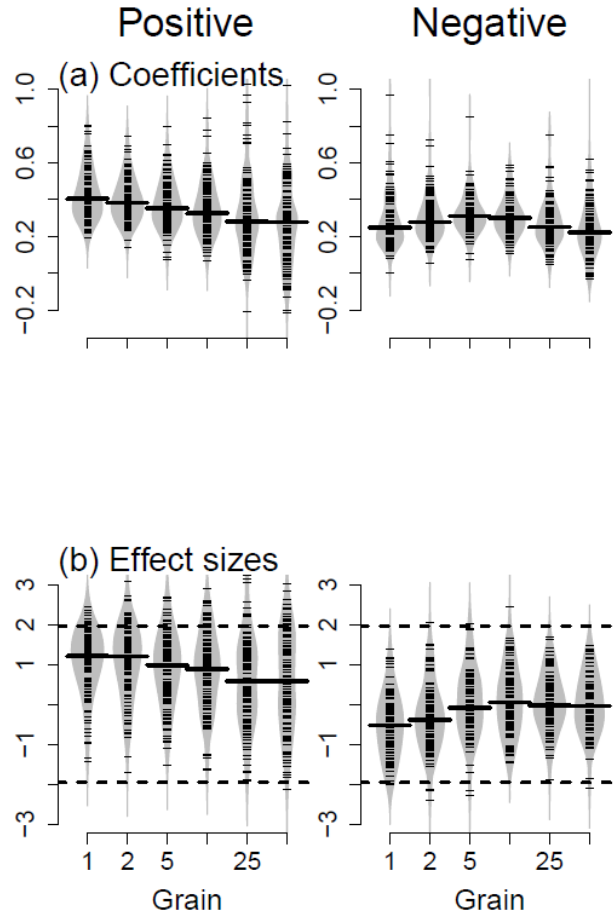


Figure 3.

Scaling of biotic interactions

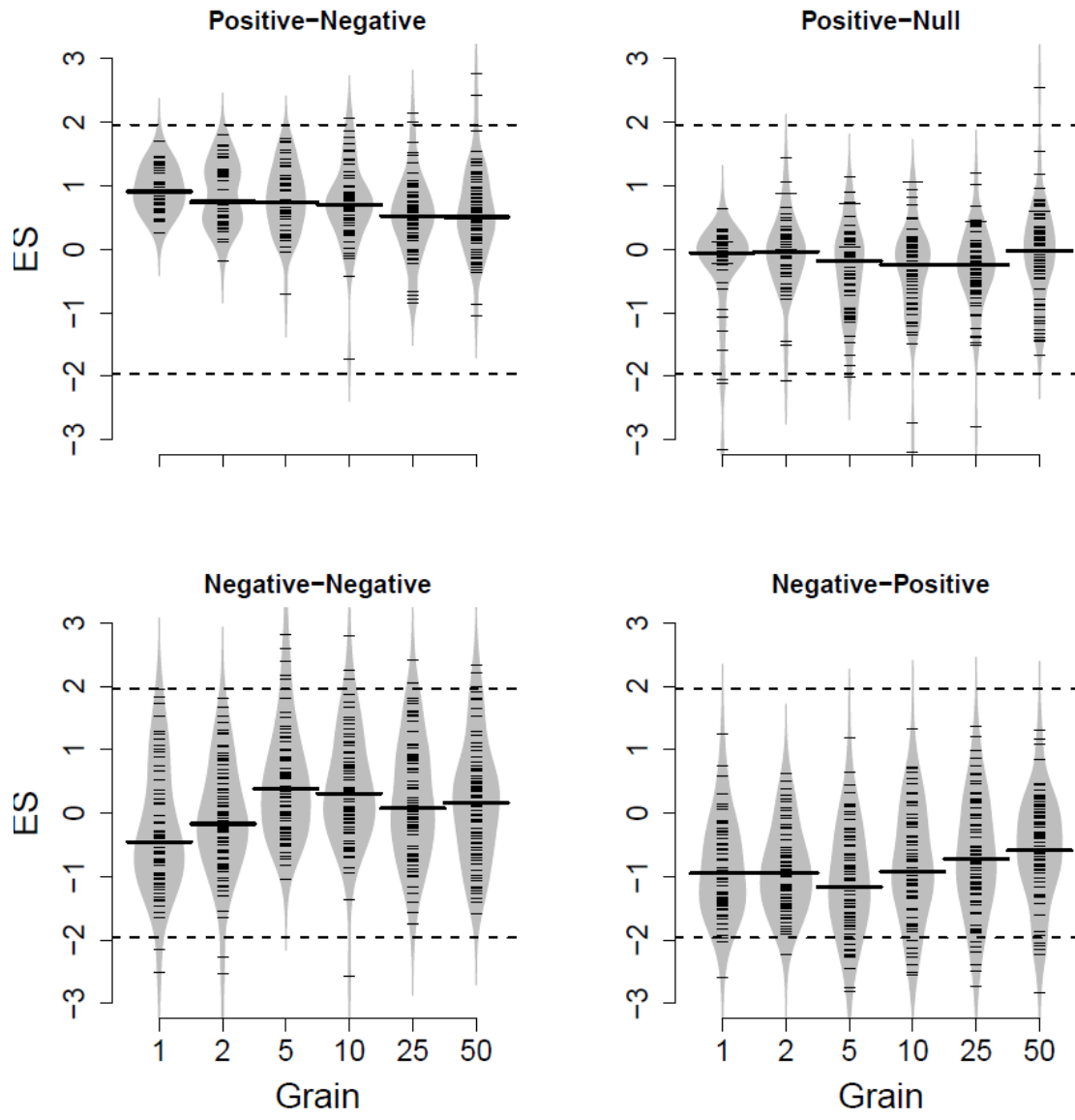


Figure 4.