

Notes and Comments

Occupancy Is Nine-Tenths of the Law: Occupancy Rates Determine the Homogenizing and Differentiating Effects of Exotic Species

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ABSTRACT: Biotic homogenization, the loss of local biotic distinctiveness among locations (beta diversity), is a form of global change that can result from the widespread introduction of nonnative species. Here, we model this process using only species' occupancy rates—the proportion of sites they occupy—without reference to their spatial arrangement. The nonspatial model unifies many empirical results and reliably explains >90% of the variance in species' effects on beta diversity. It also provides new intuitions and principles, including the conditions under which species' appearance, spread, or extirpation will homogenize or differentiate landscapes. Specifically, the addition or spread of exotic species that are more common than the native background rate (effective occupancy) homogenizes landscapes, while driving such species to extinction regionally or introducing rarer species differentiates them. Given the primacy of occupancy and our model's ability to explain its role, homogenization research can now focus on other factors.

Keywords: biotic homogenization, species invasions, beta diversity, biotic similarity, approximation.

Introduction

The recent unprecedented interchange of organisms among previously distinct biotas has eroded local biotic distinctiveness (beta diversity) in an important form of global change known as biotic homogenization (McKinney and Lockwood 1999; Ricciardi 2007; McKinney 2008). Biotic homogenization, or increases in the similarity of biotas among locations, can occur in several ways (Olden and Poff 2003; Olden and Rooney 2006), but one of the best studied is when exotic species become established across a region (e.g., McKinney 2004a; Leprieur et al. 2008). Be-

cause diversity among communities reflects how local ecological interactions translate into diversity at regional scales, biotic homogenization can alter the structure, function, and biogeography of whole regions (Olden 2006; Olden and Rooney 2006). In many systems, species additions via biotic interchanges are more common than species losses via extinction (Sax and Gaines 2008). Thus, a general understanding of how exotic and invasive species contribute to the homogeneity of landscapes is a critical aspect of the study of conservation biogeography and global change (Olden and Poff 2003; Smith et al. 2009).

Much of what is currently known about homogenization is based on case studies, with limited theoretical exploration and few general principles (reviewed in McKinney 2004a, 2008; Olden 2006; but see Olden and Poff 2003). In the absence of a theoretical framework, it has been difficult to predict the effects of exotic species or to explain why different taxa and landscapes show homogenization versus differentiation (McKinney 2004a, 2008; Rooney et al. 2007). In particular, few studies have addressed the need to distinguish the simple numerical effects of species presence and occupancy per se from the effects driven by novel species interactions, such as facilitation and competition (reviewed in Olden and Rooney 2006; but see Leprieur et al. 2008; Smith et al. 2009). The ability to distinguish these two forms of homogenization (i.e., numerical effects of species presence and occupancy vs. ecological effects) has been hindered in part by the computational difficulty of performing millions of comparisons among sites across thousands of simulated landscapes (e.g., Leprieur et al. 2008) and of analyzing them while taking into account that the comparisons are not statistically independent (Olden et al. 2008).

Here, we attempt to address these limitations by developing a nonspatial analytical approximation of mean similarity and homogenization (as well as a free software package for comparing the approximation with observed results). This approximation makes it possible to accu-

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rately estimate biotic homogenization of nontrivial landscapes for the first time and can provide ecologists with relevant parameters and summary statistics that will help them focus on the most important aspects of those landscapes. We assessed the robustness of these estimates and summaries by comparing approximate predictions with observations from 47 real data sets and a range of simulated landscapes.

Importantly, the analytical approximation yields a model that makes several intuitive and novel predictions about homogenization. For instance, though it has long been understood that cosmopolitan species homogenize landscapes while rare and endemic species differentiate them (McKinney and Lockwood 1999; Rooney et al. 2007), the full relationship between occupancy rates and similarity has not been characterized. Our simplifying assumptions allow us to do so, uniting previously disconnected observations and hypotheses about homogenization into a single framework.

The Model

We begin with a widely used measure of compositional similarity, Jaccard's index (Magurran 1988; Gotelli and Ellison 2004). Jaccard's index is calculated as the proportion of species shared between site i and site j , that is, S_{ij}/T_{ij} , where S_{ij} is the number of species that occur in both sites and T_{ij} is the total number of unique species in the two sites combined (fig. 1A). Jaccard's index ranges from 0 (no species shared) to 1 (all species shared) and is sometimes preferred over other occupancy-based similarity measures, such as Sørensen's index, because its complement (dissimilarity) behaves more like Euclidean distance (Gotelli and Ellison 2004). Approximations could also be constructed for many other similarity indices (including Sørensen's) using similar methods, with broadly similar results.

Jaccard's index is a pairwise similarity measure, so when the number of pairs is large, researchers often average these pairwise similarities to obtain a single value for the landscape. We call this value \bar{J} (fig. 1B, 1C):

$$\bar{J} = \text{mean}\left(\frac{S_{ij}}{T_{ij}}\right). \quad (1)$$

While calculating \bar{J} may require comparisons among thousands of pairs of sites, $\text{mean}(S_{ij})$ and $\text{mean}(T_{ij})$ can each be calculated independently of species' spatial arrangement, based solely on how many sites they occupy (app. A). We can then approximate the average ratio of shared to total species (\bar{J}) as the ratio of their averages (Turelli et al. 1982). We call this approximation J^* (fig. 1B, 1C):

$$J^* = \frac{\text{mean}(S_{ij})}{\text{mean}(T_{ij})} = \sum_k \binom{p_k n}{2} \bigg/ \sum_k \left[\binom{n}{2} - \binom{(1-p_k)n}{2} \right]. \quad (2)$$

Here, n is the number of sites in the landscape, p_k is the proportion of those sites occupied by species k , and the notation

$$\binom{x}{2}$$

denotes the number of different pairs that can be chosen from a set of x items, $x(x-1)/2$. Note that unlike equation (1), which averages across actual pairs of sites, equation (2) has no information about species' spatial arrangement. This means that the approximation is blind to any effects of spatial associations or dissociations among species on mean similarity. If these associations are particularly strong, substantial disagreement between the approximation and \bar{J} can result (fig. 1C; Chase 2007). Fortunately, the analyses in appendix B suggest that this disagreement will typically be small.

To simplify further, we consolidate the p_k terms in equation (2) into a shared, "effective" occupancy rate p^* . In population genetics, effective population size is the number of individuals that would produce the observed patterns of inbreeding or drift in an idealized population. Likewise, we define the effective occupancy rate as the value of p_k that would produce the observed value of J^* in an idealized landscape where all species had the same occupancy rate. After simplification, this yields

$$p^* = \frac{J^*(2n-1) + 1}{(J^* + 1)n}. \quad (3)$$

When species do not vary in their occupancy rates, p^* is simply the occupancy rate that they share; otherwise, the more common species play a disproportionate role in determining p^* because they appear in a greater number of pairwise comparisons.

Importantly, equations (2) and (3) are relatively insensitive to the number of sites (n): with greater than 10 sites, $n > 10$, $J^* \approx p^*/(2-p^*)$ and $p^* \approx 2J^*/(1+J^*)$. These simplifications provide the most basic relationships between occupancy and similarity.

Equation (2) allows us to model how changes in occupancy affect mean similarity, simply by taking the difference in J^* values. The parameter p^* has a very important role in these predictions (fig. 1D). If an exotic species' occupancy in equation (2) is manipulated while all other species' occupancy rates are held constant, it can be shown that the exotic species has a net differentiating effect (low-

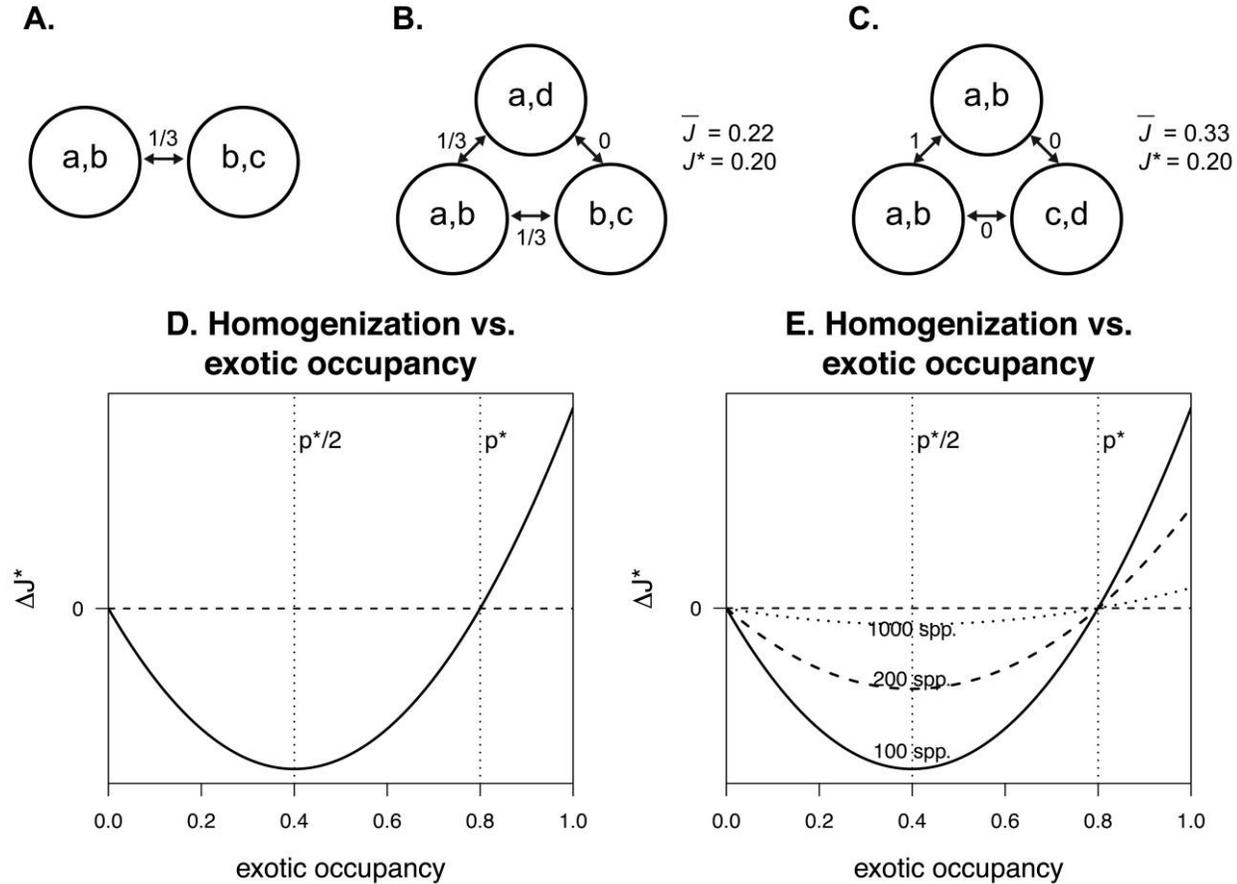


Figure 1: Calculation of observed and predicted biotic similarity based on Jaccard's index. *A*, Single pair of sites, each with two species. One species (*b*) of three total species (*a–c*) is shared, yielding a Jaccard similarity of $1/3$. *B*, When there are multiple comparisons, their similarity values can be averaged to find \bar{J} . Mean similarity can be approximated as J^* from the species' occupancy rates. *C*, Changing the locations of species relative to *B* without changing their occupancy rates can change \bar{J} but not J^* . The strong spatial association between species *a* and species *b* and their dissociation from species *c* and *d*, combined with the small number of species on the landscape, prevent a good fit between \bar{J} and J^* . *D*, Predicted effects of exotic species with varying occupancy rates invading a landscape with $p^* = 0.8$. As nonnative species' occupancy increases, the effect on biotic similarity of each individual nonnative species changes from differentiation (negative values) to homogenization (positive values). The intersection of the line with the horizontal axis is at p^* , while the lowest point on the curve is at about half that value. *E*, With more native species (numbers near lines), individual exotic species have less of an effect on J^* . Richness does not affect the qualitative patterns, however (e.g., the locations of the critical points at p^* and $p^*/2$).

ers J^*) whenever its occupancy is less than p^* and a net homogenizing effect (raises J^*) whenever its occupancy exceeds that value. It can also be shown that the point where differentiation is maximized converges to half of p^* . In other words, if we follow an exotic, biologically inert species (a weak invader *sensu* Ortega and Pearson 2005) from the moment it first appears on a landscape until it has spread to every site, it will start off too rare to significantly alter similarity but will increasingly differentiate the landscape as its occupancy increases until it reaches about half the background occupancy rate of the other species in the landscape. Further increases in occupancy

will reverse these changes, until occupancy exceeds p^* and net homogenization begins. Though several authors have intuited aspects of this relationship between occupancy and similarity (e.g., McKinney 2004a; Rooney et al. 2007; La Sorte et al. 2008), the full relationship has not been formalized until now, and the critical values had not been found.

Equation (2) also indicates that if native richness is high relative to exotic richness, then similarity will depend primarily on native occupancy rates because most comparisons will involve native species. We refer to this effect as the native landscape's "inertia." Conversely, the greater the

proportion of exotic species, the stronger their ability to overcome this inertia and either increase or decrease mean similarity, as shown in figure 1E. Changes in richness per se, however, do not influence the other parameters discussed above, including J^* or the threshold between homogenization and differentiation. In other words, after controlling for occupancy, richness does not affect the direction of exotic species' effects on J^* , only the magnitude.

Methods

Here, we compare the model predictions to observed \bar{J} values in both real and simulated landscapes using *blender*, a free, open-source software package written by D. J. Harris in R (ver. 2.11.1; R Development Core Team 2010). The package can be downloaded from within R using the command `install.packages("blender")` or from the Comprehensive R Archive Network (<http://cran.r-project.org/web/packages/blender/index.html>). For efficiency, some of *blender*'s calculations rely on the *vegan* R package, which is also available from CRAN (Oksanen et al. 2010).

It is important to note that *blender* calculates homogenization as the difference in mean similarity between the full landscape and the landscape with exotic species removed. Calculating homogenization this way is not ideal because the full effect of exotic species cannot be assessed without time series (Olden and Rooney 2006). However, in part because time series data on species invasions are rare, this method remains common (e.g., references in Olden and Rooney 2006; Smith 2006; Castro and Jaksic 2008; Leprieur et al. 2008; Olden et al. 2008; but see Rahel 2000). Because ascribing particular colonization and extirpation events to a given biotic or abiotic factor such as an invasive species is complex and outside the scope of the model, we have chosen to follow this convention and ignore any changes in the native community for these analyses. We discuss the implications of this choice for interpreting our results below.

Comparison with Data

We began by extracting county-level floristic inventories of plants for the contiguous United States (excluding Maryland) from the USDA PLANTS database (USDA, NRCS 2010). Because of the scope of the database, sampling is necessarily uneven across taxa, counties, and states, so we do not necessarily expect the values we estimate for individual states to be meaningful. Despite these limitations, the database gives us a rare opportunity to assess the model's accuracy on 47 U.S. state landscapes of various sizes, biogeographies, richnesses, and similarities, providing a wide-ranging examination of the approximation's robustness. Importantly, plant species in the database vary

in occupancy from <0.01 to 1, allowing us to explore how occupancy affects the homogenizing or differentiating effect of nonnative species across the entire parameter space. The portion of the PLANTS database that we used has been included with *blender*.

Next, we used *blender* to assess the model's ability to predict native \bar{J} and changes in \bar{J} associated with the addition of entire exotic biotas and of individual exotic species. From the individual species results, *blender* evaluated the correspondence between the "true" critical values (estimated by smoothing the data with R's loess function for locally weighted regression) and those predicted by the model (i.e., p^* and $p^*/2$). The data for Delaware could not be smoothed because of an insufficient range of exotic occupancy rates, so critical values were not estimated for that state. For each analysis, correspondence was calculated as the proportion of the observed variance that could be explained by the model (R^2).

Simulations

Precisely identifying the causes of error introduced by our approximation is difficult (Welsh et al. 1988), but the analyses in appendix B suggest that richness plays a major role in ameliorating it. We assessed this by comparing \bar{J} and J^* values calculated for landscapes based on the Colorado, Michigan, Minnesota, and Rhode Island native occupancy matrices but with a range of reduced richness values. For each of these landscapes, we performed the following steps.

For each power of 2 between 16 and the total number of species in the original landscape, *blender* created 1,000 reduced-richness landscapes by randomly selecting subsets of the species in the original landscape. *Blender* then calculated \bar{J} and J^* for each of these reduced landscapes, and we found 95% confidence intervals of the discrepancies between these two values for each level of simulated richness.

The analyses in appendix B also indicated that J^* tends to most closely approximate \bar{J} when species distributions are uncorrelated (see also fig. 1B, 1C). To verify this, we took the simulated landscapes described above and removed any such correlations by randomly reshuffling each species' locations in the landscape. This reshuffling held species occupancy rates constant but allowed local richness to vary among simulation runs; in Gotelli's (2000) terms, *blender* holds row sums fixed while columns are equiprobable (SIM2). We concluded by finding 95% confidence intervals for model error for each level of richness in these reduced and reshuffled landscapes.

Because \bar{J} is not defined for pairs of landscapes that each have zero richness, simulated landscapes with empty sites were discarded. Confidence intervals were calculated for a given level of richness only if at least 100 reduced land-

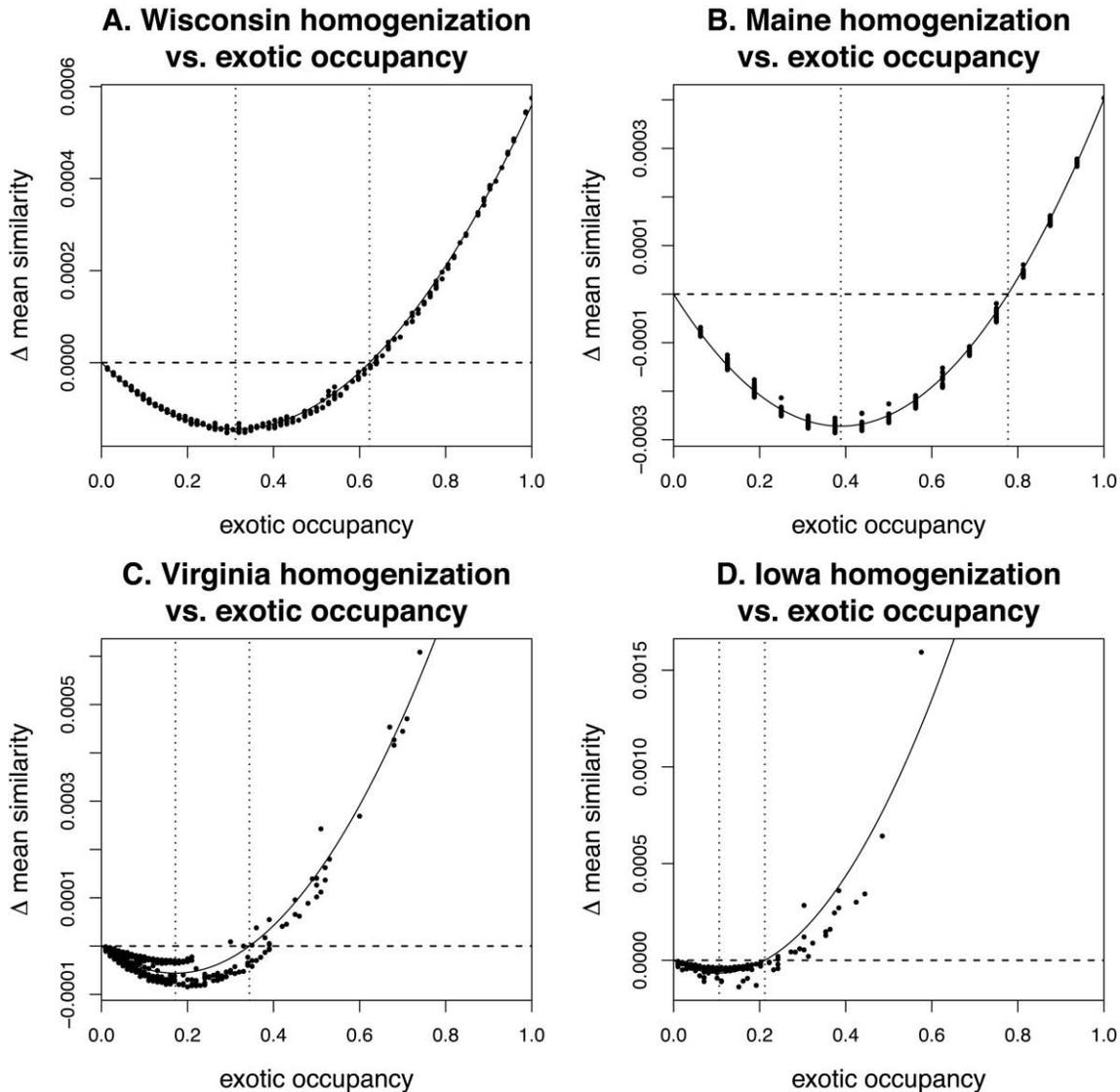


Figure 2: Predicted and observed changes in mean similarity for two of the best-fit states (A: Wisconsin, $R^2 = 0.998$; B: Maine, $R^2 = 0.998$) and two of the worst-fit states (C: Virginia, $R^2 = 0.915$; D: Iowa, $R^2 = 0.861$). Each point is a single pairwise comparison of average floristic similarity among counties, with a different exotic species added to the landscape for each point to produce a change in \bar{J} .

scapes and their shuffled counterparts remained after this step.

Together, these analyses allowed us to track the range of model error across four landscapes as a function of richness and of whether we retained landscape information beyond occupancy that could interfere with our predictions.

Results and Discussion

Comparison with Data and Simulations

The model explained 99.8% of the variation in observed mean similarity (\bar{J}) of native species across states as well

as 99.4% of the differences in floristic similarity owing to the inclusion of all nonnative species as a group. Changes in mean similarity owing to the inclusion of individual species followed the expected “scoop” shape almost exactly when we added exotic species one at a time (mean $R^2 = 0.980$, SD = 0.029; fig. 2). In particular, the thresholds between homogenization and differentiation occurred very close to p^* ($R^2 = 0.995$), and the minima occurred very close to $p^*/2$ ($R^2 = 0.980$). In other words, the model’s central qualitative predictions held in real landscapes: in general, the inclusion of individual nonnative

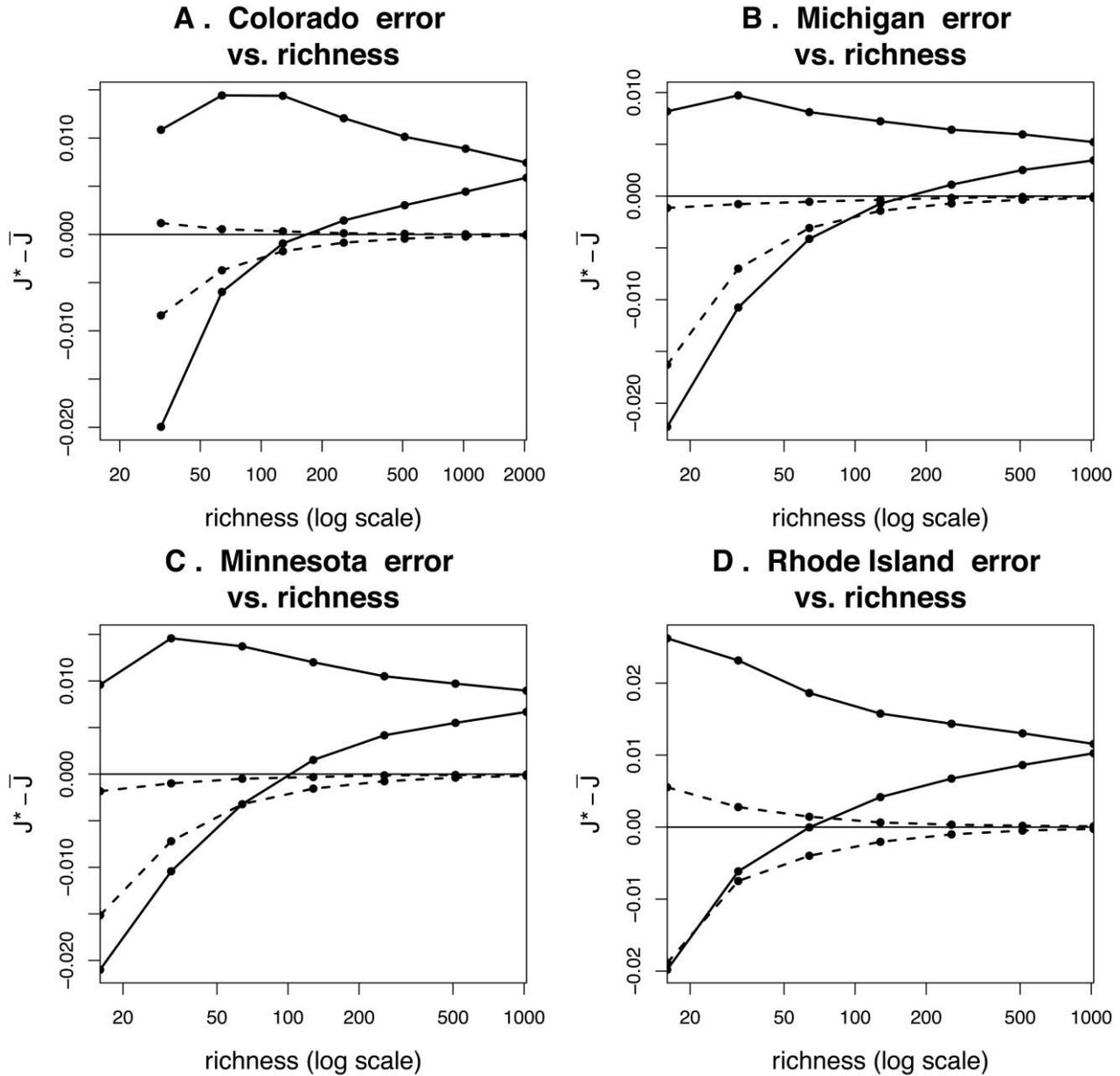


Figure 3: 95% confidence intervals showing the range of disagreement between predicted and observed mean similarity for a subsample of four states: Colorado (A), Michigan (B), Minnesota (C), and Rhode Island (D). The results bounded by solid lines include the nonrandom associations between species that structured the landscapes, which increases the level of error relative to randomized landscapes' results, bounded by dashed lines.

species increases mean similarity if and only if they occupy more sites than their native counterparts (as defined by p^*), while differentiation is maximized when exotic occupancy is about half that value. These rules formalize previous empirical observations, which stated only that common species homogenize and rare ones differentiate

(Olden and Poff 2003; McKinney 2004a; Clavero and García-Berthou 2006; La Sorte and McKinney 2006; Rooney et al. 2007; La Sorte et al. 2008).

As discussed in appendix B and by Turelli et al. (1982), the approximation we used is most accurate when species distributions are independent of one another and the

number of species is greater than about 20. Our simulations with randomly arranged species confirmed this result (fig. 3, *dashed lines*). Adding the nonindependence among species' spatial distributions as found in real landscapes substantially slowed convergence and added some systematic error (fig. 3, *solid lines*), but the fit was usually very good even when richness was heavily reduced.

Integrating Model Predictions with Previous Results

The explanatory power of our model demonstrates the central role for occupancy—and especially effective occupancy (p^*)—in understanding biotic distinctiveness and (nontemporal measures of) biotic homogenization. With p^* , an ecologist can quickly estimate average similarity or differences in similarity without the need for spatially explicit data or simulations. Importantly, p^* also unites many previously disconnected results. For instance, why do older invaders increase similarity more than recent ones (Clavero and García-Berthou 2006; Kühn and Klotz 2006; La Sorte et al. 2007)? And why are local range expansions associated with greater homogenization than invasions from other continents (McKinney 2005; La Sorte and McKinney 2006; Leprieur et al. 2008; Spear and Chown 2008)? In both cases, the answer can be boiled down to occupancy. Species that have had longer to spread or whose local occupancy rates did not start at zero will have higher occupancy rates and are therefore more likely to contribute to increased similarity.

The model also clarifies how a landscape's richness-based inertia operates during invasions, unifying several additional previously observed patterns in homogenization research. For instance, both the reduced homogenizing effect of nonnative species in species-rich landscapes (Olden and Rooney 2006) and the stronger effects observed in opposite directions as nonnative richness increases (McKinney 2004a, 2004b) are consistent with the model's prediction that, all else equal, the degree of homogenization or differentiation caused by exotic species will increase with increasing exotic richness and decrease with increasing native richness. Inertia also explains the small size of the effects demonstrated in figure 2; a single exotic species can do very little to overcome the inertia of hundreds or thousands of native species. When multiple exotic species were added simultaneously, the effects were often orders of magnitude larger.

Our results differ substantially from those of Smith et al. (2009), who used time series data and found large discrepancies between observed patterns and those expected by changes in occupancy alone. The most important reason we did not find such discrepancies in the USDA PLANTS data is that our widely used method for calculating "changes" in similarity (i.e., simply comparing land-

scapes with and without exotic species) does not allow exotic species to affect their native counterparts' occupancy rates, richness, or spatial distributions (reviewed in Olden and Rooney 2006). For this reason, any attempt to attribute ecological mechanisms to the results of static studies of biotic homogenization such as ours should be approached with caution.

Despite our focus on invasion biology, our model's predictions could be adapted to other scenarios, including extirpations such as those caused by emerging diseases (Smith et al. 2009). For instance, our model predicts homogenization when species with occupancy less than p^* are extirpated and differentiation when common species' ranges shrink. Even radical changes in species composition across many sites could be modeled this way, if time series data or predictions about future occupancy rates were available.

Conclusion

By distilling the effects of nonnative species to a single parameter—their occupancy rates—and by identifying key thresholds, our model has allowed for the synthesis of several empirical observations of the process of biotic homogenization. The fact that a nonspatial model can explain so much variance in biotic similarity, as well as so many previously documented qualitative patterns, suggests that differences in mean similarity at regional scales are largely mediated by species' occupancy rates. Given that this relationship is now characterized, homogenization researchers can increase their focus on three areas: processes that determine which species spread and which species are extirpated (already of critical concern in other areas of community ecology); factors whose effect on similarity exceeds that predicted by nonspatial models; and patterns in community similarity below the regional scale, which cannot be detected by our model because of its exclusive focus on landscape-level mean similarity.

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APPENDIX A

Deriving J^*

Given a group of n sites, the number of site pairs is

$$\binom{n}{2},$$

or $n(n - 1)/2$. Thus, if p_k is the proportion of n sites occupied by species k , then the number of ways a species can appear twice (and thereby contribute to shared species [S_{ij}]) is

$$\binom{p_k n}{2}$$

out of the

$$\binom{n}{2}$$

possible comparisons. Summing across all species yields the average number of species shared in randomly chosen pairs of sites:

$$\text{mean}(S_{ij}) = \sum_k \binom{p_k n}{2} \bigg/ \binom{n}{2}. \quad (\text{A1})$$

The full distribution of S_{ij} for individual site pairs is described by Connor and Simberloff (1978) and Raup and Crick (1979). Species contribute to total species (T_{ij}) whenever they are not absent from both sites, or in

$$\binom{n}{2} - \binom{(1 - p_k)n}{2}$$

out of the

$$\binom{n}{2}$$

possible comparisons. Summing across all species yields

$$\text{mean}(T_{ij}) = \sum_k \left[\binom{n}{2} - \binom{(1 - p_k)n}{2} \right] \bigg/ \binom{n}{2}. \quad (\text{A2})$$

Dividing $\text{mean}(S_{ij})$ by $\text{mean}(T_{ij})$ yields equation (2).

APPENDIX B

Quantifying Model Error

According to Welsh et al. (1988), the full relationship between J^* and \bar{J} is given by

$$J^* = \bar{J} - \frac{\text{Cov}(T_{ij}, S_{ij}/T_{ij})}{\text{mean}(T_{ij})}. \quad (\text{B1})$$

Here, covariance should not be corrected for sample size because all possible pairs of sites are sampled. Unfortunately, as Welsh et al. (1988) acknowledge, the covariance term is always difficult to interpret, and homogenization researchers face the additional difficulty that S_{ij} and T_{ij} are aggregate properties of site pairs rather than of individual sites, which makes interpretation even harder. Still, we can draw some tentative conclusions.

First, the strong law of large numbers ensures that under a broad range of conditions, landscapes with greater average richness—specifically, greater values of $\text{mean}(T_{ij})$ —will have better agreement between J^* and \bar{J} (Turelli et al. 1982). Effectively, as the number of species increases, the effect of idiosyncrasies in their spatial positions decreases via averaging.

Second, this averaging effect works best when species distributions are independent. Specifically, when sites differ systematically along a few powerful niche axes (e.g., if species composition is largely determined by whether a specific habitat type is present), J^* will strongly overestimate \bar{J} (e.g., Chase 2007). The reason is that two sites of the same type will have the same sets of species (high similarity, low $\text{mean}(T_{ij})$), while comparisons across types will have different sets of species (low similarity, high $\text{mean}(T_{ij})$). This negative correlation makes the covariance term in equation (B1) positive and pushes \bar{J} up relative to J^* . This is the source of the large discrepancy between the two similarity measures in figure 1C. The more factors there are affecting community composition, however, and the more species there are to average across, the weaker this effect becomes and the better the approximation performs.

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