

Toward a Mechanistic Understanding and Prediction of Biotic Homogenization

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ABSTRACT: The widespread replacement of native species with cosmopolitan, nonnative species is homogenizing the global fauna and flora. While the empirical study of biotic homogenization is substantial and growing, theoretical aspects have yet to be explored. Consequently, the breadth of possible ecological mechanisms that can shape current and future patterns and rates of homogenization remain largely unknown. Here, we develop a conceptual model that describes 14 potential scenarios by which species invasions and/or extinctions can lead to various trajectories of biotic homogenization (increased community similarity) or differentiation (decreased community similarity); we then use a simulation approach to explore the model's predictions. We found changes in community similarity to vary with the type and number of nonnative and native species, the historical degree of similarity among the communities, and, to a lesser degree, the richness of the recipient communities. Homogenization is greatest when similar species invade communities, causing either no extinction or differential extinction of native species. The model predictions are consistent with current empirical data for fish, bird, and plant communities and therefore may represent the dominant mechanisms of contemporary homogenization. We present a unifying model illustrating how the balance between invading and extinct species dictates the outcome of biotic homogenization. We conclude by discussing a number of critical but largely unrecognized issues that bear on the empirical study of biotic homogenization, including the importance of spatial scale, temporal scale, and data resolution. We argue that the study of biotic homogenization needs to be placed in a more mechanistic and predictive framework in order for studies to provide adequate guidance in conservation efforts to maintain regional distinctness of the global biota.

Keywords: invasion, extinction, biodiversity, native, nonnative, habitat loss.

Human-assisted dispersal of nonnative species and the modification of natural habitats have sparked widespread changes in the global distribution of organisms. Geographic modifications in patterns of species occurrences have been predominantly in two directions: the range expansion of cosmopolitan, nonnative species and the range contraction of rare, often endemic, native species. The gradual transition to nonnative-dominated communities has resulted in increased spatial and temporal similarity in the taxonomic characteristics of once-disparate biotas, a phenomenon termed "biotic homogenization" (Vitousek et al. 1996, 1997; Bright 1998; Lockwood and McKinney 2001).

While of great contemporary concern, biotic homogenization is not a new phenomenon in the earth's history. The paleontological record is replete with examples of episodic mixing of biotas that were historically isolated, such as the Great American Interchange resulting from the formation of the Panama Isthmian land bridge and the opening of transpolar interchange between the Pacific and Atlantic oceans (Vermeij 1991). Recognition of faunal mixing traces back at least to Charles Elton (1958), who discussed the breakdown of Wallace's Faunal Realms by global commerce. Even more recently, humans have greatly accelerated the mixing process through activities such as canal building (Por 1978), international commerce (Carlton and Gellar 1993), recreation (Fuller et al. 1999), aquaculture (Naylor et al. 2001), and horticulture (Reichard and White 2001). As a result, humans have helped dissolve natural biogeographic barriers that once separated indigenous populations, causing the homogenization of the earth's biota to an extent unseen by any previous natural episodes. Consequently, we are now entering a period characterized by an unprecedented rate of biotic homogenization, appropriately dubbed the "Homocene," in a place appropriately called the "New Pangaea" (Rosenzweig 2001).

In the wake of continued human enhancement of species invasions and extinctions, the study of biotic homogenization is a rapidly emerging area in biology. For example, in the preface of a recent synthesis, McKinney and

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Lockwood (2001) emphasize the importance of identifying and understanding present-day patterns of homogenization that may lead to proactive conservation goals aimed at reducing biotic mixing. Almost all research to date has focused on documenting patterns of homogenization for particular taxonomic groups such as plants (McKinney and Lockwood 2001), trees (Rooney et al. 2001), birds (Lockwood et al. 2000), insects (Blair 2001), fish (Radomski and Goeman 1995; Rahel 2000; Marchetti et al. 2001; Scott and Helfman 2001), reptiles and mammals (Wilson 1997), mussels and amphibians (Duncan and Lockwood 2001b), snails (Cowie 2001), and marine algae and invertebrates (Carlton 1996). Of this research, quantitative estimates of biotic homogenization have been mainly limited to freshwater faunas (Rahel 2002).

In contrast to empirical advances, the invasion and extinction mechanisms underlying biotic homogenization have yet to be explored, as have the more subtle ecological and evolutionary consequences of homogenization (J. D. Olden, unpublished manuscript). Because a narrow focus on patterns of biodiversity loss may shed little insight into the potential consequences of biotic homogenization (Collins et al. 2002), a premium should be placed on understanding how the processes of species invasion and extinction contribute to the homogenization process. A necessary first step in understanding biotic homogenization and its ecological consequences is the development of theory that identifies the breadth of possible mechanisms that may drive current and future patterns and rates of homogenization. Ultimately, a sound theoretical foundation to the study of biotic homogenization is needed to assist in the development of future studies as well as to aid in the analysis and interpretation of existing data.

Driven by the need for theory, our primary goal in this article is to develop a theoretical framework that provides a mechanistic basis for understanding current and predicting future patterns of biotic homogenization. We propose a conceptual model that describes 14 unique scenarios through which different combinations of species invasions and extinctions can drive the homogenization process. These scenarios reflect the possible ecological outcomes resulting from interactions among nonnative species, native species, and habitat loss and fragmentation. Using a simulation approach, we apply the conceptual model to generate predictions of homogenization for each scenario as a function of differential patterns and numbers of nonnative species invasions and native species extinctions, the historical degree of compositional similarity among the communities, and the species richness of the communities. Based on the simulation results, we present a unifying model for biotic homogenization that provides explanatory and predictive insight into the relative roles of different invasion and extinction processes that may be

shaping currently observed patterns of homogenization in aquatic and terrestrial ecosystems. We conclude by discussing a number of important topics that require careful consideration in future studies of biotic homogenization, including issues associated with the influence of spatial and temporal scales on the investigation of homogenization, the importance of data resolution and the various approaches to quantifying homogenization, and the potential influence of species richness on observed patterns of homogenization. Our overarching goal is to provide a coherent and robust theoretical basis for the study of biotic homogenization. We hope this framework will help guide the collection, analysis, and interpretation of empirical data as well as ultimately enhance our understanding and prediction of future losses of regional distinctiveness in both space and time.

Mechanisms Driving Biotic Homogenization: 14 Scenarios of Species Invasions and Extinctions

Conceptual Model of Biotic Homogenization

Biotic homogenization, defined as an increase in species similarity among a set of communities through time, is quantified simply as the change in the pairwise community similarity between two time periods. Homogenization can arise through many ecological mechanisms that represent specific and often quite different interactions among native species, nonnative species, and the environment. Two distinct processes drive biotic homogenization: extinction of resident species (referred to as the losing species) and invasion of species (referred to as the winning species) into new areas (McKinney and Lockwood 1999; Lockwood and McKinney 2001). Here, we use the term extinction to denote the local loss (i.e., extirpation) of a species from a community. While it is true that invasion and extinction are required to fuel biotic homogenization, it is not generally appreciated that the magnitude and even the direction of change in community similarity can vary greatly depending on (1) the relative numbers and taxonomic identities of the winning and losing species (defined by the differential impacts of nonnative species on the recipient communities and the differential response of native and nonnative species to habitat degradation), (2) the historical compositional similarity among the communities, and (3) the species richness of the communities. Variation in these factors can result in very different magnitudes of increased community similarity (biotic homogenization) or even decreased community similarity (which we will refer to as biotic differentiation).

Below, we propose 14 scenarios that depict different pathways or mechanisms by which species invasions and extinctions can drive biotic homogenization and differ-

entiation (illustrated in fig. 1 and summarized in table 1). We quantitatively illustrate patterns of community change associated with each of these scenarios by using two hypothetical communities (referred to as sites 1 and 2) with an initial community similarity of 50% based on an initial pool of four species (a, b, c, and d) and using Jaccard's coefficient to quantify changes in community similarity (fig. 1). This example is only illustrative. Later, we expand this example to consider how patterns in homogenization change when the numbers of winning and losing species are varied, when initial community similarity is varied, and when the assumption of fixed species richness is relaxed.

The 14 scenarios are divided into three groups depending on whether the process is driven by only species invasions (scenarios I1, I2), only species extinctions (scenarios E1–E4), or both invasions and extinctions (scenarios IE1–IE8). Because changes in community similarity are assessed in a pairwise manner between two biological communities, we can derive each of the 14 scenarios from the combination of answers to the following dichotomous questions (represented as splits in fig. 1): (1) Do nonnative species invade and successfully establish in both recipient communities? (2) If nonnative species integration occurs, do the same or different invasive species establish in the recipient communities? (3) In addition to the invasion, does the extinction of a native species in the recipient communities occur? (4) If extinction occurs, is it bilateral (i.e., occurring in both sites) or unilateral? (5) If bilateral extinction occurs, do the same or different native taxa become extinct? (6) If unilateral extinction occurs, does a shared (i.e., originally occurring in both sites) or an unshared native species (i.e., originally occurring in only one site) become extinct? (7) Conversely to questions 2–6, in the absence of a species invasion, does unilateral/bilateral extinction of the same/different or shared/unshared native species occur? It is important to note that the invasion and extinction events in questions 2–6 do not necessarily imply that the invading species causes the extinction of the native species. Rather, these situations can equally arise from the introduction and extinction events being independently facilitated by anthropogenic disturbances such as habitat loss or fragmentation. In summary, the questions above reflect the possible ecological outcomes resulting from the interactions between invading species, the resident species of the native communities, and environmental conditions. Although these scenarios are not completely exhaustive, they represent a broad array of possible outcomes associated with species invasions and extinctions, and the scenarios are well supported by empirical evidence. Each of these scenarios is discussed below with reference to general and specific examples from the aquatic and terrestrial literature.

The 14 Scenarios of Species Invasions and Extinctions

Species Invasion Only (Scenarios I1, I2). Numerous studies in the literature have suggested that species invasions are often not accompanied by local extinction of native species (e.g., Simberloff 1981; Ebenhard 1988; Williamson 1996). In an extensive review, Simberloff (1981) reported that in 79% of studies (examining a large number of vertebrate and invertebrate species), the introduced species caused no extinction of native species. Consequently, species invasions may result in community augmentation where species are added to rather than subtracted from the communities. This may be especially true for plant communities where large numbers of native and nonnative species coexist at landscape scales (Stohlgren et al. 1999, 2003) and where the number of invasions have been shown to exceed extinctions on islands across the globe (Sax et al. 2002). In aquatic ecosystems, the introduction of small-bodied fish species via bait-bucket releases provides good support for scenario I1 driving homogenization (i.e., same species invade; fig. 1). In North America, particular fish species are used preferentially for bait (Litvak and Mandrak 1993), and given that repeated introductions generally increase the probability of successful establishment (e.g., Forsyth and Duncan 2001) and bait fishes are small and nonpiscivorous, we might expect that bait-bucket releases will result in the introduction of the same species across the landscape without the extinction of resident fish species. In contrast, the intentional release of aquarium fish (Courtenay and Stauffer 1990) supports the importance of scenario IB for driving differentiation (i.e., different species invade; fig. 1). In this case, many different species are introduced to multiple sites (likely because of the large pool of fish species common in the aquarium trade), again with no or little associated extinction pressure on the resident species.

Species Extinction Only (Scenarios E1–E4). Species extinctions without associated species invasions can play a large role in homogenization and differentiation and may arise from at least three processes. First, increased modification and fragmentation of natural habitats have increased the rates of imperilment and extinction of many taxa (Saunders et al. 1991; Kerr and Currie 1995). Second, nonnative species may drive native species to extinction when invading a community, even when the nonnative species ultimately fail to successfully establish themselves. For example, while attempting to establish itself, an invasive species could reduce the abundance of a particular resident species (e.g., prey species) and drive the resident to extinction, thereby contributing to its own eventual disappearance from the community because of lack of sufficient resources. This has been termed “indirect failure” by Case

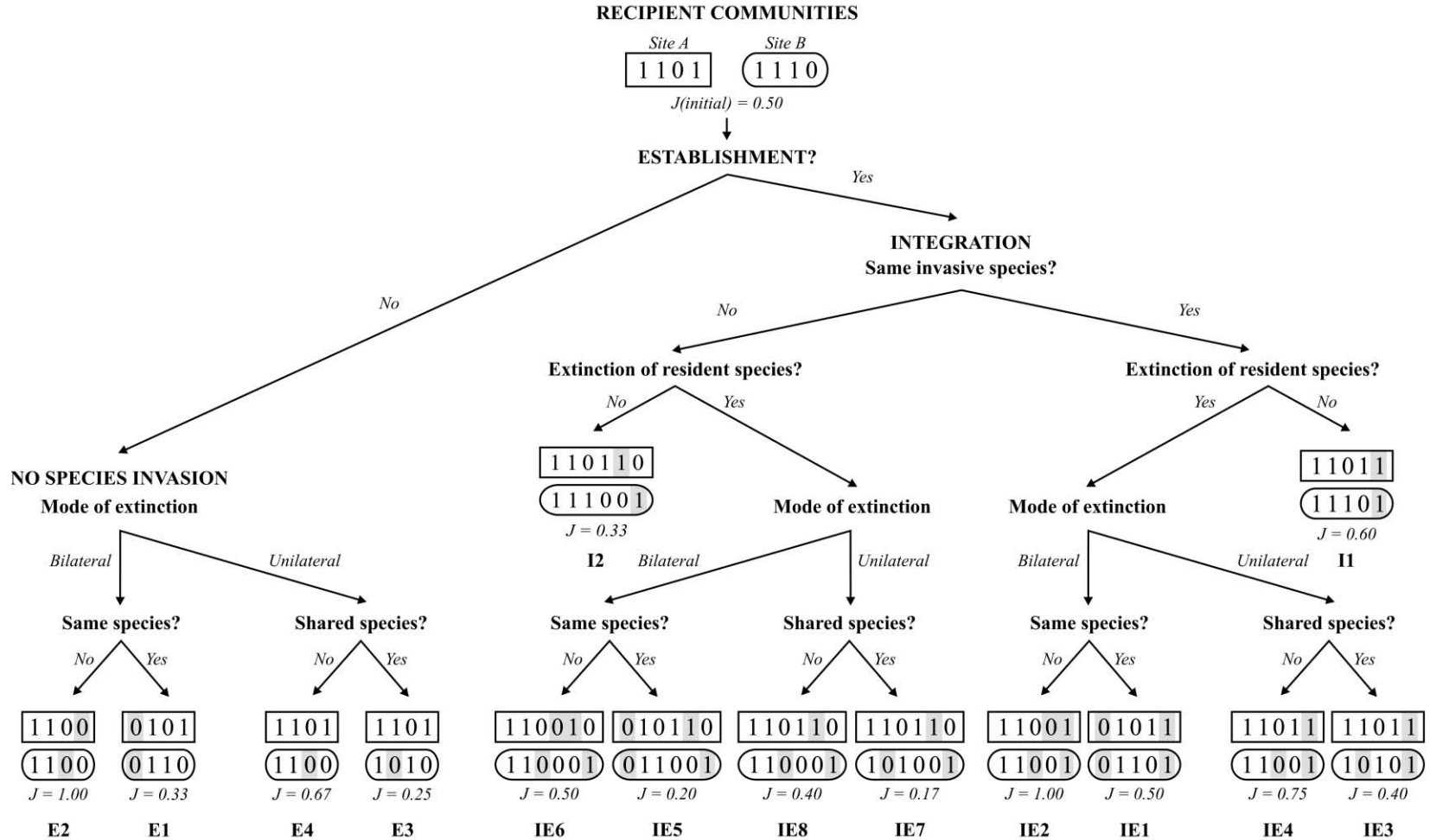


Figure 1: A conceptual model depicting 14 scenarios representing different pathways or mechanisms by which species invasions and extinctions can drive biotic homogenization (increased community similarity) and differentiation (decreased community similarity). The 14 scenarios are divided into three groups, depending on whether the process is driven by only species invasions (scenarios I1, I2), only species extinctions (scenarios E1–E4), or both invasions and extinctions (scenarios IE1–IE8) and are derived from the combination of answers to a series of dichotomous questions represented as splits in the figure (discussed in the text). We quantitatively illustrate patterns of community change associated with each of these scenarios using two recipient communities (sites 1 and 2) with an initial community similarity of 50% ($J_{\text{initial}} = 0.50$), based on an initial pool of four species (a, b, c , and d) and using Jaccard's coefficient to quantify changes in community similarity. Species occurrence is coded 0 or 1, and highlighted species represent changes in community membership because of a species invasion (represented by 1) or species extinction (represented by 0). Under scenario IE4, for example, species e becomes established in sites 1 and 2, and species c (which was originally unshared by the communities) goes extinct in site 2, causing the Jaccard's coefficient to increase from 0.50 to 0.75 (i.e., 25% homogenization). Conversely, under scenario E3, no species invade, and species b (which was originally shared by the communities) becomes extinct in site 2, causing the Jaccard's coefficient to decrease from 0.50 to 0.25 (i.e., 25% differentiation).

Table 1: Summary of the 14 invasion-extinction scenarios used in the conceptual model for biotic homogenization (fig. 1)

Scenario	Description
Invasion only:	
I1	Same species invade, no extinction of resident species
I2	Different species invade, no extinction of resident species
Extinction only:	
E1	No species invasion, extinctions in both communities involve same species
E2	No species invasion, extinctions in both communities involve different species
E3	No species invasion, extinction in one community of a species that was originally shared by both communities
E4	No species invasion, extinction in one community of a species that was originally not shared by both communities
Invasion and extinction:	
IE1	Same species invade, extinctions in both communities involve same species
IE2	Same species invade, extinctions in both communities involve different species
IE3	Same species invade, extinction in one community of a species that was originally shared by both communities
IE4	Same species invade, extinction in one community of a species that was originally not shared by both communities
IE5	Different species invade, extinctions in both communities involve same species
IE6	Different species invade, extinctions in both communities involve different species
IE7	Different species invade, extinction in one community of a species that was originally shared by both communities
IE8	Different species invade, extinction in one community of a species that was originally not shared by both communities

Note: The scenarios are divided into three groups, depending on whether changes in community similarity are driven only by species invasions (I1, I2), only by species extinctions (E1–E4), or by both species invasions and extinctions (IE1–IE8).

(1991), and although we are unaware of a published study documenting this phenomenon (likely because of our limited ability to observe this event), it has clear implications for community stability (Case 1995). Third, species invasions outside the focal taxonomic group can have significant impacts on native species in the communities in which homogenization is being studied and quantified. Examples include (but are not limited to) the extinction of native bird species by the Australian brown tree snake (Savidge 1987) and extinction of island reptiles by a variety of mammalian predators (Case and Bolger 1991), the loss of amphibian populations by fish introductions (Blaustein and Wake 1990), the effects of riparian plant invasions on aquatic macroinvertebrate biodiversity (Bailey et al. 2001), and the effects of browsing herbivores on native avifauna by modifying native habitats and consuming native plants (Diamond and Veitch 1981).

Of the three processes discussed above, the conversion of natural habitat into land dominated by agriculture and other anthropogenic activities is likely the primary mechanism causing species extinctions. The vulnerability of a species to extinction is primarily defined by the interaction of intrinsic individual characteristics, which determine survival and reproduction, and the degree of habitat modification (Pimm et al. 1988). Therefore, spatial patterns in

species extinctions are expected to depend on species-specific vulnerability to different sources of habitat modification (influencing whether the same or different species become extinct in scenarios E1 and E2) and on the distribution of the species across the landscape and the spatial configuration and magnitude of habitat loss and fragmentation (influencing whether the extinction species was originally shared or unshared between the communities in scenarios E3 and E4).

Species Invasion and Extinction (Scenarios IE1–IE8). Invasive species may cause local extinctions of resident populations or even cause global extinction of spatially restricted fauna via direct (e.g., predation, grazing, competition, habitat alteration) and indirect pathways (e.g., alteration to fire regimes, nutrient cycling, hydrology, energy budgets; Mack et al. 2000). Extreme examples include (but are not limited to) the ecological effects of the Argentine ant (Holway et al. 2002), rosy wolfsnail (Hadfield 1986), African crystalline ice plant (Vivrette and Muller 1977), spiny South American shrub (Braithwaite et al. 1989), Nile perch (Witte et al. 1992), and zebra mussel (Ricciardi et al. 1998). The probability of species extinction is expected to depend on the extinction vulnerability of the native species to species invasions (e.g., birds: Owens

and Bennett 2000; plants: Lonsdale 1999) and the environmental template upon which these biotic interactions occur.

In addition to the potential biotic mechanisms driving species extinctions in these scenarios, both invasions and extinctions can be independently facilitated by natural and human-induced alteration to native habitats. For example, the modification of natural stream flow and thermal regimes in riverine ecosystems throughout the United States presumably has resulted in both the invasion of numerous exotic fish species and the loss of native fish species (Richter et al. 1997). Similarly, alterations to forest ecosystems have independently and interactively led to the successful invasion and extinction of bird species around the globe (Case 1996). As such, although it is useful to examine the conceptual model in figure 1 in a causal manner, we emphasize that scenarios IE1–IE8 do not necessarily imply a direct mechanistic link between species invasion and extinction in recipient communities. The empirical literature amply shows that habitat modification independently facilitates species invasions and extinctions (Elton 1958); however, for the purposes of this article, we restrict our focus to highlighting the empirical evidence supporting the scenarios where species invasions result directly in the extinction(s) of native species.

Scenarios IE1 and IE2. There are many instances where ubiquitous introductions of species (i.e., the same species invading many sites) result in significant local extinctions (see references above). Whether the same species (scenario IE1, fig. 1) or different species (scenario IE2, fig. 1) are driven to extinction by the invader will depend primarily on the extinction vulnerability of the native species and the species-specific impacts (e.g., prey selectivity, competitive dominance) of the invader(s). High prey selectivity will likely result in the extinction of the same species across sites (scenario IE1) because the invader will selectively target particular native species, as in the case of a species-specific pathogen or predator. In contrast, low prey selectivity has a greater chance of causing the extinction of different native species across sites (scenario IE2). The probability that the same invasive species will be established and that the same native species will become extinct in multiple sites (i.e., scenario IE1) is supported by the fact that winning and losing species involved in the homogenization process are not randomly distributed among taxonomic categories (McKinney 1997; Russell et al. 1998; McKinney and Lockwood 1999). Furthermore, evidence is accumulating to support the notion that invasion- and extinction-prone species traits are phylogenetically constrained, including among birds (Lockwood et al. 2000), fish (Duncan and Lockwood 2001a), mammals (Russell et al. 1998), and plants (Pyšek 1998).

Scenarios IE3 and IE4. The introduction of the same

species into multiple sites may lead to unilateral patterns of species extinctions, resulting in either the loss of a shared species (i.e., originally occurring in both sites; scenario IE3, fig. 1) or an unshared species (i.e., originally occurring in only one site; scenario IE4, fig. 1). Unilateral extinction could occur when species only become extinct at sites lacking potential source populations to support rescue effects (*sensu* Brown and Kodric-Brown 1977) or lacking refugia from predation (Huffaker 1958). Similarly, species invasions associated with habitat disturbance may lead to greater chances of extinction compared to sites that are not subjected to this additional environmental stress (e.g., Ruiz et al. 1999). For instance, Moyle (1986) contended that for the eastern United States, the local fish faunas appear to have adjusted to nonnative invasions without much loss of native species, whereas for more environmentally disturbed ecosystems in the western United States and Florida, introduced species appear to have greater negative impacts on native communities. Unilateral extinction, coupled with the fact that species invasions may occur in communities that initially exhibit varying degrees of similarity in their species composition, supports the notion that an invading species may cause the extinction of a shared (scenario IE3) or an unshared (scenario IE4) species.

Scenarios IE5 and IE6. The invasion and establishment of different nonnative species across sites can influence community similarity by causing the bilateral extinction of the same (scenario IE5, fig. 1) or different species (scenario IE6, fig. 1). The global transport of nonindigenous marine organisms in ship ballast waters provides a powerful example where a large number of different species can be introduced into a region (Carlton and Geller 1993). After establishment, we might expect different invaders to cause the bilateral extinction of the same native species if, for example, they exhibit similar species-specific impacts (e.g., same prey preference and/or feeding mode, scenario IE5) or the extinction of different native species if they have dissimilar impacts (scenario IE6).

Scenarios IE7 and IE8. Similar to scenarios IE3 and IE4, species invasions may result in the loss of a native species in one site but not another, an outcome that is again dependent on the occurrence of source populations to support recolonization events and the availability of refugia from predation. Different invaders can cause unilateral extinction (i.e., one invasive species causes an extinction, whereas the other species does not) via differential predation or competition pressures on the native species of the recipient communities. Moreover, given differences in the initial species compositions of the recipient communities, it is possible that the species driven to extinction may (scenario IE7, fig. 1) or may not (scenario IE8, fig. 1) be originally shared by the communities.

Simulation Experiments: Exploring Biotic Homogenization under the 14 Scenarios of Species Invasions and Extinctions

Biotic homogenization is quantified by comparing the degree of similarity in community composition between two sites based on two points in time. Concordance in community composition across space can be quantified using any one of a suite of similarity indices, cluster analyses, or ordination approaches (see Rahel 2002). Jaccard's coefficient of similarity (Jaccard 1900) is one of the most commonly used methods in ecology for quantifying community similarity and is employed almost exclusively in homogenization studies (e.g., Radomski and Goeman 1995; Rahel 2000; Marchetti et al. 2001; Rahel 2002). We used Jaccard's coefficient to measure similarity and to estimate the degree of biotic homogenization and differentiation in our simulated communities. Jaccard's coefficient ranges from 0 (no species in common) to 1 (identical species composition) and is calculated simply as

$$J(x_1, x_2) = \frac{a}{a + b + c}, \quad (1)$$

where x_1 and x_2 represent two sites, a is the total number of species present in both x_1 and x_2 , b is the number of species present in x_1 and absent in x_2 , and c is the number of species absent in x_1 and present in x_2 .

A deterministic simulation approach was used to examine how changes in community similarity differed among the 14 invasion-extinction scenarios. We restricted our simulations to reflect deterministic events because we wished to pursue a systematic exploration of the expected range of potential trajectories of biotic homogenization and differentiation resulting from interactions between native species, nonnative species, and environmental change. While stochastic dynamics are likely to be important in nature, they are difficult to infer from the "snapshot" data presented in the literature. Moreover, the ecological processes we simulate are common in nature and can be argued to have strong deterministic elements, and therefore, our simulation approach is informative.

The simulation experiments involved generating 25 pairs of communities representing different levels of initial species richness ($s = 4$ to 100 species, increasing by increments of four species) for each of three different historical or initial community similarities ($J_{\text{initial}} = 0.25, 0.50, \text{ and } 0.75$). The species composition of each pair was simulated to ensure the initial community similarity by increasing the value of a by $s \times J_{\text{initial}}$ and the sum of b and c by $s \times (1 - J_{\text{initial}})$ in equation (1) for each incremental increase of four species in the recipient community; for example, $J_{\text{initial}} = 0.25$, species richness = 4 ($a = 1$,

$b + c = 3$); $J_{\text{initial}} = 0.25$, species richness = 8 ($a = 2$, $b + c = 6$); $J_{\text{initial}} = 0.50$, species richness = 4 ($a = 2$, $b + c = 2$); $J_{\text{initial}} = 0.50$, species richness = 8 ($a = 4$, $b + c = 4$). Simulations were started at a species richness of four because this is the lowest value at which community similarity could be set to the J_{initial} and also change via species extinction(s) or invasion(s). The simulation protocol predicted percent community similarity for each of the 75 simulated communities (i.e., 25 different initial levels of species richness and three different initial community similarities) following the mechanisms defined by each of the 14 scenarios for all possible combinations of the number of winners and losers. For all simulations, the number of winners ranged from 0 (i.e., scenarios E1–E4) to s (i.e., all other scenarios), whereas the possible number of losers was constrained by the number of species that the communities shared or did not share and the number of species that were available to become extinct and therefore varied depending on the initial community similarity and particular scenario. In total, the simulations were completely exhaustive in that they generated predictions of community similarity under each invasion-extinction scenario for a range of species richness, initial community similarity, and numbers of winners and losers.

Percent change in community similarity (hereafter referred to as Δ_j) was calculated as the change in Jaccard's coefficient (expressed as a percent) between the predicted community similarity (generated from the simulation experiment) and the initial community similarity, that is, predicted similarity minus the initial similarity of the communities. A positive Δ_j represents biotic homogenization, and a negative Δ_j represents the biotic differentiation. All simulations were conducted using computer macros in the MatLab R programming language written by J. D. Olden.

Predictions of Biotic Homogenization: The Influence of Species Richness, Initial Community Similarity, and Species Invasions and Extinctions

The results from the simulations show that patterns in Δ_j are a function of the species richness of the recipient communities being invaded, the initial degree of compositional similarity among the communities, the type of invasion-extinction scenarios, and the ratio of winning (invasive) to losing (extinct) species.

We examined the relationship between species richness of the recipient communities and Δ_j for each of the 14 invasion-extinction scenarios and for the three levels of initial community similarity (averaged across all combinations of the numbers of winners and losers). Relationships were consistent among the different levels of initial community similarity, and therefore, for the sake of brevity, we present only the results for $J_{\text{initial}} = 0.50$ (fig. 2).

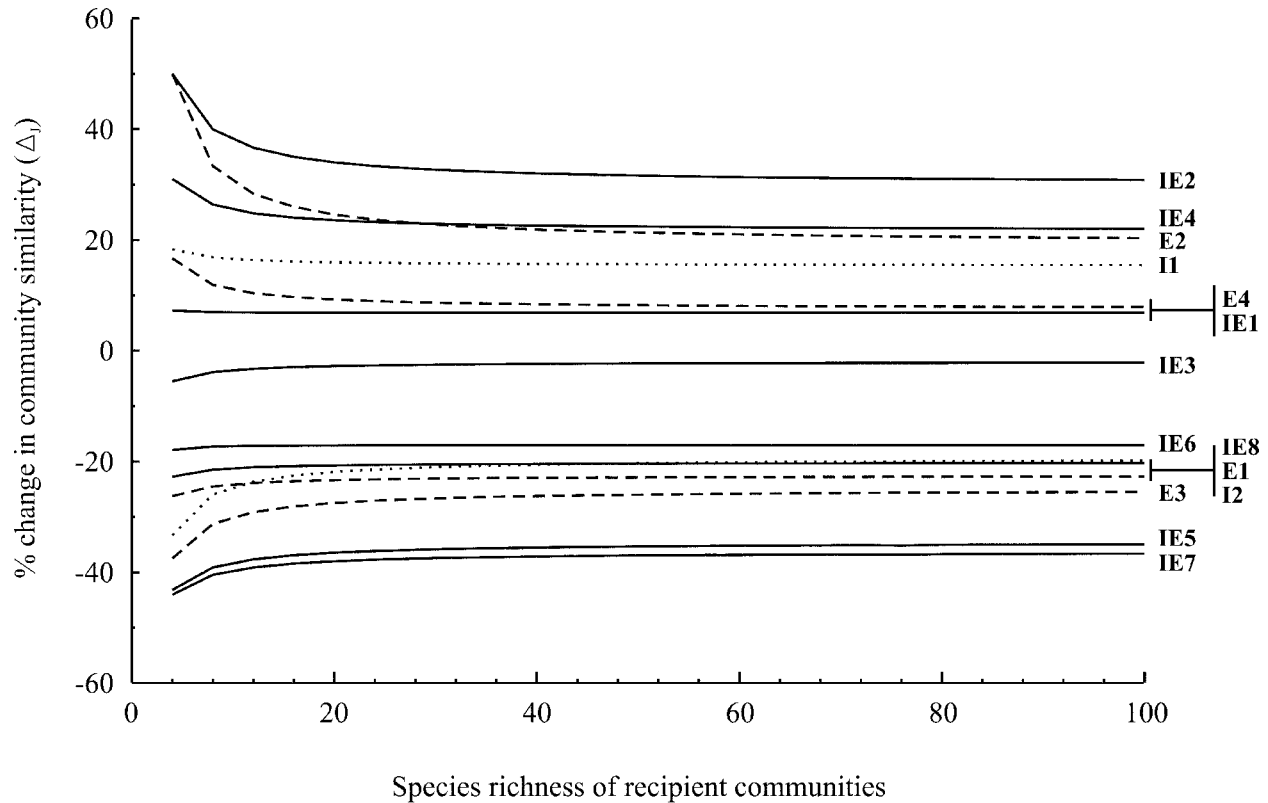


Figure 2: Patterns of community similarity change as a function of species richness for an initial community similarity of 50% ($J_{\text{initial}} = 0.50$) under the 14 invasion-extinction scenarios. Results are averaged across over all combinations of the number of winners and losers. Positive percentage change in community similarity indicates homogenization, whereas negative percentage change in community similarity indicates differentiation. Dotted lines represent scenarios I1, I2; dashed lines represent scenarios E1–E4; and solid lines represent scenarios IE1–IE8. Curves are based on simulation results from species richness values from 4 to 100 (by increments of four), and data points were removed for clarity. Relationships were similar for $J_{\text{initial}} = 0.25$ and $J_{\text{initial}} = 0.75$.

The effects of species richness on Δ_j for all scenarios were greatest at low species richness, but beyond a species richness of 20, patterns of community similarity became independent of richness. Although extinction-only scenarios (E1–E4) showed the strongest relationships with richness, in general, the predicted Δ_j for all scenarios was insensitive to species richness. Further, this general pattern did not change in response to varying ratios of winners to losers (results not shown). Based on these findings, all subsequent examinations of changes in community similarity were averaged across all levels of species richness.

For all combinations of the number of winners and losers, relative patterns of Δ_j across the scenarios were similar but not identical for the three different initial community similarities (fig. 3). It is important to emphasize that, even though the range of possible values of Δ_j is the same for the three initial community similarities, the critical upper and lower bounds differ ($J_{\text{initial}} = 0.25$: –25% to 75%; $J_{\text{initial}} = 0.50$: –50% to 50%; $J_{\text{initial}} = 0.75$: –75%

to 25%). Regardless of the initial community similarity and the number of winners or losers, scenarios I1, E2, E4, IE2, and IE4 always caused an increase in community similarity (i.e., biotic homogenization), whereas scenarios I2, E1, E3, IE5, and IE7 always caused a decrease in community similarity (i.e., biotic differentiation). The remaining four scenarios (IE1, IE3, IE6, IE8) resulted in both positive and negative Δ_j for all initial community similarities, although the median Δ_j for these scenarios was consistently either positive or negative across the gradient of initial community similarities. The one exception, however, was scenario IE3, which predicted a positive median Δ_j for $J_{\text{initial}} = 0.25$, no median change in compositional similarity for $J_{\text{initial}} = 0.50$, and a negative median Δ_j for $J_{\text{initial}} = 0.75$ (fig. 3). In summary, measures of central tendency and dispersion were found to vary with initial community similarities (fig. 3). Median Δ_j either increased (e.g., E4), decreased (e.g., I1, I2, E3, IE1–IE8) or showed no relationship (e.g., E1, E2) with increasing initial com-

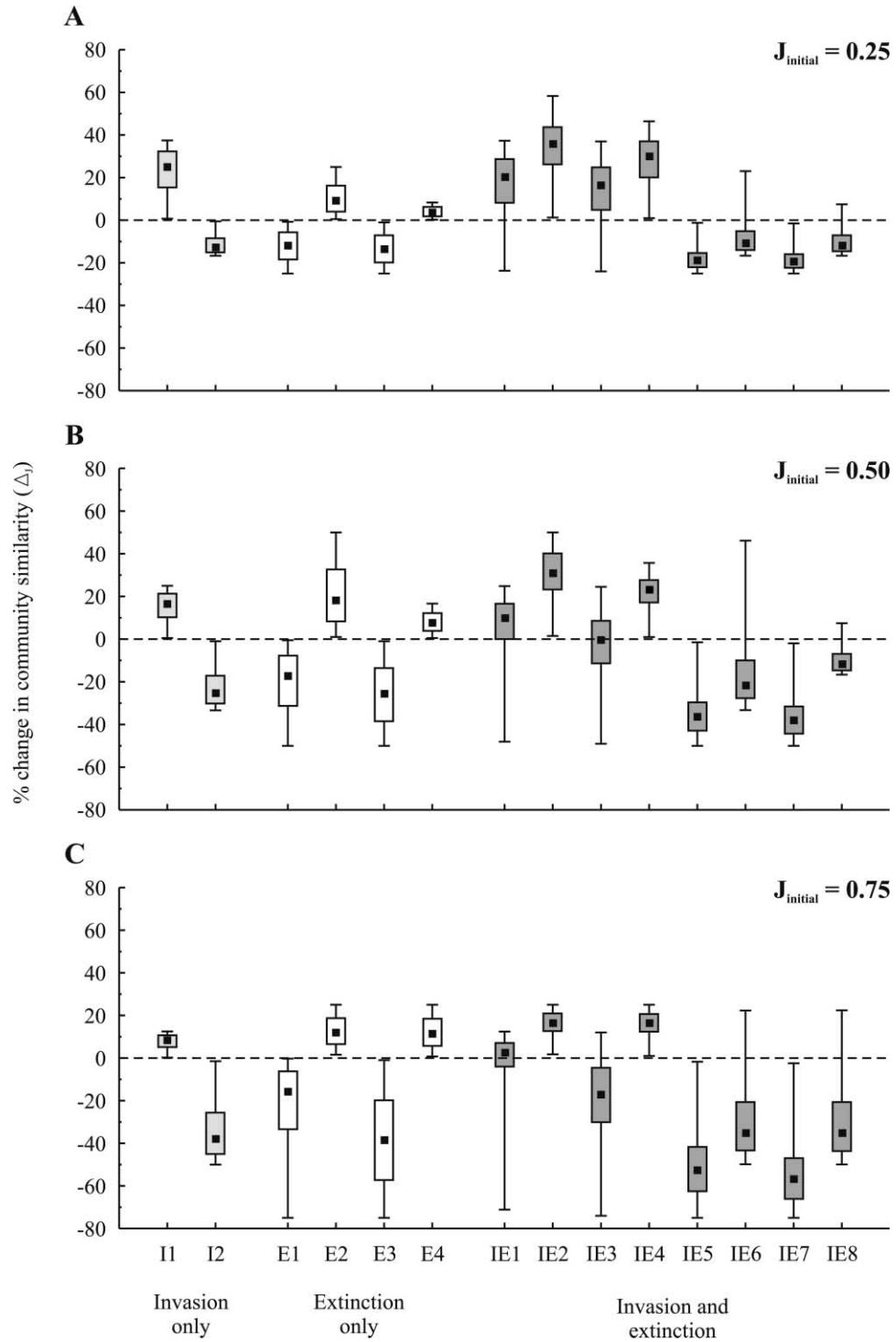


Figure 3: Patterns of community similarity change under the 14 invasion-extinction scenarios for three levels of initial community similarity ($J_{\text{initial}} = 0.25, 0.50$, and 0.75). Results are for all combinations of numbers of winners and losers (averaged over all levels of species richness [see fig. 2]). Square symbol is the median, boxes represent interquartile ranges, and whiskers represent the minimum and maximum values. Dashed line demarcates homogenization (positive community similarity) from differentiation (negative community similarity).

munity similarity (fig. 3), and variation in Δ_j either increased (e.g., I2, E1, E3, E4, IE1, IE3, IE5–IE8), decreased (e.g., I1, IE2, IE4), or showed no relationship (e.g., E2) along the same gradient.

To gain a finer understanding of the influence of numbers of winners and losers on the homogenization process, and thus to provide insight into the sources of variation in predicted levels of Δ_j in figure 3, we examined three different ratios of losers to winners (hereafter denoted by $L:W$). Increasing $L:W$ ratios represent increasing levels of extinction pressure associated with an invasion or proportionally greater effects of environmental alteration on rates of extinction compared with rates of invasions. The three levels examined were low ($0 < L:W \leq 1$), intermediate ($1 < L:W \leq 2$), and high ($L:W > 2$). We found that variation in Δ_j to be a function of the $L:W$ ratio (table 2). Regardless of the initial community similarity, increasing $L:W$ led to increasing Δ_j under scenarios IE6 and IE8, decreasing Δ_j under scenarios IE1, IE3, and IE4, and no effect under scenario IE5 and IE7. Interestingly, the relationship between Δ_j and $L:W$ for scenario IE2 depends on the level of initial community similarity. The varying effects of $L:W$ on Δ_j shown in table 2 provide insight into why particular scenarios (i.e., IE1, IE3, IE6, and IE8) show both positive and negative Δ_j in figure 3.

These results show that predicted patterns of Δ_j can exhibit a positive, negative, or no relationship with increasing numbers of losers relative to winners and that the direction of change does not generally vary as a function of initial similarity (table 2; fig. 3). Consequently, we explore in greater detail the effects of varying contributions of winners and losers on predicted levels of Δ_j for $J_{\text{initial}} = 0.50$ (again averaging across all values of species richness) because the results from these simulations were generally intermediate in magnitude. Figure 4 shows that scenarios I1, E2, and E4 always resulted in positive Δ_j , whereas scenarios I2, E1, and E3 always resulted in negative Δ_j . Patterns of homogenization and differentiation were more complex for the remaining scenarios. For example, community similarity increased with increasing numbers of the same winners and either increasing numbers of different or unshared losers (scenarios IE2 and IE4; fig. 4D, 4F) or decreasing numbers of the same or shared losers (scenarios IE1 and IE3; fig. 4C, 4E). In contrast, community similarity decreased with increasing numbers of different winners and either increasing numbers of different or unshared losers (scenarios IE6 and IE8; fig. 4H, 4J) or decreasing numbers of the same or shared losers (scenarios IE5 and IE7; fig. 4G, 4I). The relative influence of $L:W$ to observed patterns in Δ_j depended on the particular invasion-extinction scenario and on the numbers of winners and losers involved in the interaction. The number of winners exhibited the greatest influence on Δ_j

under scenarios IE1, IE3, IE6, and IE8 when the number of losers is large, whereas the number of losers showed the greatest effects in scenarios IE2, IE4, IE5, and IE7 when the number of winners is small.

Figure 5 illustrates patterns of average Δ_j (averaged across all species richness and for $J_{\text{initial}} = 0.50$) for each invasion-extinction scenario under different $L:W$. Community similarity is predicted to increase when same species establishment is accompanied with no extinction (I1), extinction of different species (IE2), unilateral extinction of an unshared species (IE4), or when only extinction of different (E2) or unshared species (E4) occurs. In contrast, community similarity is predicted to decrease when different species establishment is accompanied with no extinction (I2), extinction of the same species (IE7), unilateral extinction of a shared species (scenario IE5), or when only extinction of the same (E1) or shared species (E3) occurs. For the remaining scenarios, the expected Δ_j is a function of $L:W$. When the number of losers is less than the number of winners, Δ_j is dependent solely on the specific taxonomic identities of the winning species but not the identities of the losing species (fig. 5B). Consequently, invasion of the same species resulted on average in positive Δ_j , whereas the invasion of different species produced negative Δ_j . However, when there was a greater number of losers than winners, the direction and magnitude of Δ_j depended on both the number and identity of the winning and losing species (fig. 5C, 5D).

Discussion

We have shown that patterns of biotic homogenization and differentiation are a function of the type and number of winning and losing species, the historical degree of similarity among the communities, and to a lesser degree, the richness of the recipient communities. Figure 6 provides a unifying model for homogenization and highlights the deterministic relationships between the invasion-extinction scenarios, the number of winners and losers, and patterns in biotic homogenization. The two-dimensional space in figure 6 indicates the scenarios that are expected to cause homogenization given different combinations of numbers of winners and losers (i.e., $L:W$), which are independent of species richness and the level of initial community similarity. Scenarios I1, E2 and E4, and IE2 and IE4 will always result in homogenization independent of the number of winners, losers, and the ratio of the two. Scenario IE1 only results in homogenization when the number of winners is greater than the number of losers, whereas the opposite is true for scenario IE6. Homogenization will occur via scenario IE3 only when the number of losers is half that of the number of winners and via scenario IE8 only when the number of losers is twice the number of winners. The var-

Table 2: Patterns of community similarity change as a function of three levels of initial community similarity under the 14 invasion-extinction scenarios

Scenario	$J_{\text{initial}} = 0.25$			$J_{\text{initial}} = 0.50$			$J_{\text{initial}} = 0.75$		
Invasion only:									
I1	25.2 (.7–37.5)			16.8 (.5–25.0)			8.4 (.3–12.5)		
I2	–12.6 (–16.7–[–.5])			–25.1 (–33.3–[–1.0])			–37.7 (–50.0–[–1.5])		
Extinction only:									
E1	–11.7 (–25.0–.8)			–17.1 (–50.0–[–.5])			–15.6 (–75.0–[–.3])		
E2	9.2 (.5–25.0)			18.4 (1.0–50.0)			12.2 (1.5–25.0)		
E3	–13.5 (–25.0–[–1.0])			–25.6 (–50.0–[–1.0])			–38.5 (–75.0–[–1.0])		
E4	3.9 (.3–8.3)			7.8 (.5–16.7)			11.7 (.8–25.0)		
Invasion and extinction:	Low	Intermediate	High	Low	Intermediate	High	Low	Intermediate	High
IE1	22.7 (.0–37.3)	–3.4 (–10.7–[–.8])	–11.4 (–23.7–[–1.5])	13.5 (.0–24.9)	–4.3 (–16.7–[–.5])	–17.1 (–48.0–[–1.0])	6.0 (.0–12.4)	–3.3 (–15.0–[–.3])	–15.2 (–71.2–[–.5])
IE2	37.6 (1.3–58.3)	25.0 (1.8–41.2)	19.2 (2.4–34.7)	31.0 (1.5–50.0)	32.8 (2.6–50.0)	31.7 (3.7–50.0)	16.6 (1.8–25.0)	17.8 (3.4–25.0)	18.3 (5.0–25.0)
IE3	18.7 (–5.0–37.0)	–6.8 (–13.9–[–1.2])	–13.9 (–24.0–[–2.2])	3.9 (–16.7–24.5)	–17.2 (–30.0–[–1.5])	–28.4 (–49.0–[–2.5])	–8.0 (–32.1–12.0)	–30.7 (–47.7–[–1.7])	–43.8 (–74.0–[–2.7])
IE4	31.9 (1.0–46.4)	15.0 (1.3–24.5)	9.2 (1.5–17.5)	24.3 (1.0–35.7)	16.7 (1.5–24.7)	13.7 (2.0–21.3)	16.3 (1.0–25.0)	18.1 (1.8–25.0)	17.9 (2.6–25.0)
IE5	–18.8 (–25.0–[–1.2])	–18.9 (–25.0–[–2.0])	–18.2 (–25.0–[–2.8])	–36.2 (–50.0–[–1.5])	–38.1 (–50.0–[–2.0])	–33.3 (–50.0–[–2.5])	–52.4 (–75.0–[–1.7])	–58.0 (–75.0–[–2.0])	–45.7 (–75.0–[–2.3])
IE6	–11.6 (–16.6–.0)	2.4 (.5–8.3)	8.9 (1.0–23.1)	–23.2 (–33.2–.0)	4.8 (1.0–16.7)	17.9 (2.1–46.2)	–36.2 (–49.8–.0)	3.9 (1.5–1.7)	11.8 (3.1–22.3)
IE7	–19.1 (–25.0–[–1.5])	–19.8 (–25.0–[–2.5])	–19.4 (–25.0–[–3.4])	–37.5 (–50.0–[–2.0])	–40.9 (–50.0–[–2.9])	–38.6 (–50.0–[–3.9])	–54.9 (–75.0–[–2.5])	–63.1 (–75.0–[–3.4])	–58.6 (–75.0–[–4.4])
IE8	–12.5 (–16.6–[–.2])	–1.5 (–4.7–.0)	2.1 (.3–7.5)	–25.0 (–33.3–[–.5])	–3.1 (–9.3–.0)	4.1 (.5–14.9)	–37.5 (–49.9–[–.7])	–4.6 (–14.0–.0)	6.2 (.8–22.4)

Note: Reported values are medians and ranges (in parentheses) across all levels of species richness. The low, intermediate, and high categories describe different relative numbers of losing species to winning species (for invasion and extinction scenarios only). Low $L : W$, $0 < L : W \leq 1$; intermediate $L : W$, $1 < L : W \leq 2$; high $L : W$, $L : W > 2$.

ying effects of the number of winners and losers on levels of homogenization account for the fact that scenarios IE1, IE3, IE6, and IE8 can result in both homogenization and differentiation (fig. 3). Finally, scenarios I2, E1, E3, IE5, and IE7 always result in biotic differentiation regardless of the numbers of winners and losers. For scenarios that involve both species invasions and extinctions, figure 6 shows that, based on the relative number of winners and losers, the potential for scenarios IE2 and IE4 to drive biotic homogenization is four times greater than scenarios IE3 and IE8 and two times greater than scenarios IE1 and IE6.

Our proposed conceptual model and its predictions can be used to provide important mechanistic insight into the invasion and extinction processes that are likely responsible for current patterns in biotic homogenization. For all levels of initial community similarity, predicted levels of homogenization were highest for scenarios involving the invasion of similar species and either no extinction or the differential extinction of native species across communities. These scenarios are in agreement with current empirical evidence that supports the occurrence of widespread introductions of cosmopolitan, nonnative species and the limited extirpation of native species in fish (Rahel 2000), bird (Case 1996), and plant communities (Lonsdale 1999; Sax et al. 2002) and therefore may represent the dominant mechanisms driving the homogenization of these groups. Future studies should involve the statistical validation of the conceptual model by comparing predicted changes in community similarity under the different invasion-extinction scenarios with empirical estimates of biotic homogenization reported in the literature. For example, the elimination of the regional distinctiveness of fish faunas across the United States is perhaps the best documented example (in terms of quantifying changes in community similarity) of biotic homogenization to date (e.g., Radomski and Goeman 1995; Rahel 2000; Duncan and Lockwood 2001*b*; Marchetti et al. 2001; Scott and Helfman 2001; Rahel 2002) and thus provides a good opportunity to validate the conceptual model. Furthermore, for taxonomic groups currently lacking quantitative estimates of biotic homogenization (e.g., birds, plants), the conceptual model may potentially be used to provide insight into the most likely processes operating to produce contemporary patterns in biotic homogenization. The model may also offer a framework for predicting future patterns of homogenization based on estimated invasion and extinction rates of species of known taxonomic identities. Clearly, a prerequisite to generating reliable predictions of future homogenization is validation of the conceptual model using existing empirical data, an exercise that can be done for some aquatic and terrestrial taxonomic groups (J. D. Olden, unpublished manuscript).

Important Issues Relevant to the Study of Biotic Homogenization

Understanding and predicting patterns of biotic homogenization (e.g., resulting from the conceptual model presented here) may be influenced by a number of largely unrecognized constraints that warrant explicit discussion. Among these are the influence of spatial and temporal scales on the investigation of homogenization, the importance of data resolution and the various approaches to quantifying homogenization, and the potential influence of species richness on observed patterns of homogenization. Here, we briefly discuss these with the hope they will receive greater attention by researchers in the future.

Biotic homogenization is a scale-dependent phenomenon in that the observed number of winners and losers between any two time steps will be a function of the spatial extent over which the number of species is tabulated and the length of time during which species have the opportunity to invade or become extinct. In the spatial sense, increasing the extent of an analysis will increase the probability of recording species invasions because a greater number of communities and diversity of habitats are sampled. Additionally, the probability of recording an extinction event will decline because a greater diversity of habitats in the larger sampling area will promote the continued existence of populations and increase the probability of sampling relic populations. Therefore, at the regional scale, we would expect lower $L:W$, leading to the apparently greater relative roles of particular invasion-extinction scenarios (i.e., IE1 and IE3) in the homogenization process. As the spatial extent decreases, we would expect an increase in the probability of observing the introduction of different species and extinction of different or unshared species because the finer sampling resolution accentuates among-site habitat differences. Accordingly, at the local scale we would expect biotic differentiation via scenarios involving the establishment of different species and differential patterns of extinctions (i.e., IE6 and IE8). The spatial dependency of the biotic interactions driving homogenization may explain why Marchetti et al. (2001) found differentiation among fish communities in individual California watersheds but homogenization in zoogeographic provinces.

Perceived patterns of biotic homogenization can also be influenced by the length of time over which homogenization is being examined. Longer periods increase the probability of observing species invasions and extinctions, leading to higher expected rates of homogenization or differentiation (assuming no temporal trends in native species turnover). This temporal dependence complicates comparisons of homogenization rates across different regions. For example, community similarity increased by 9% in

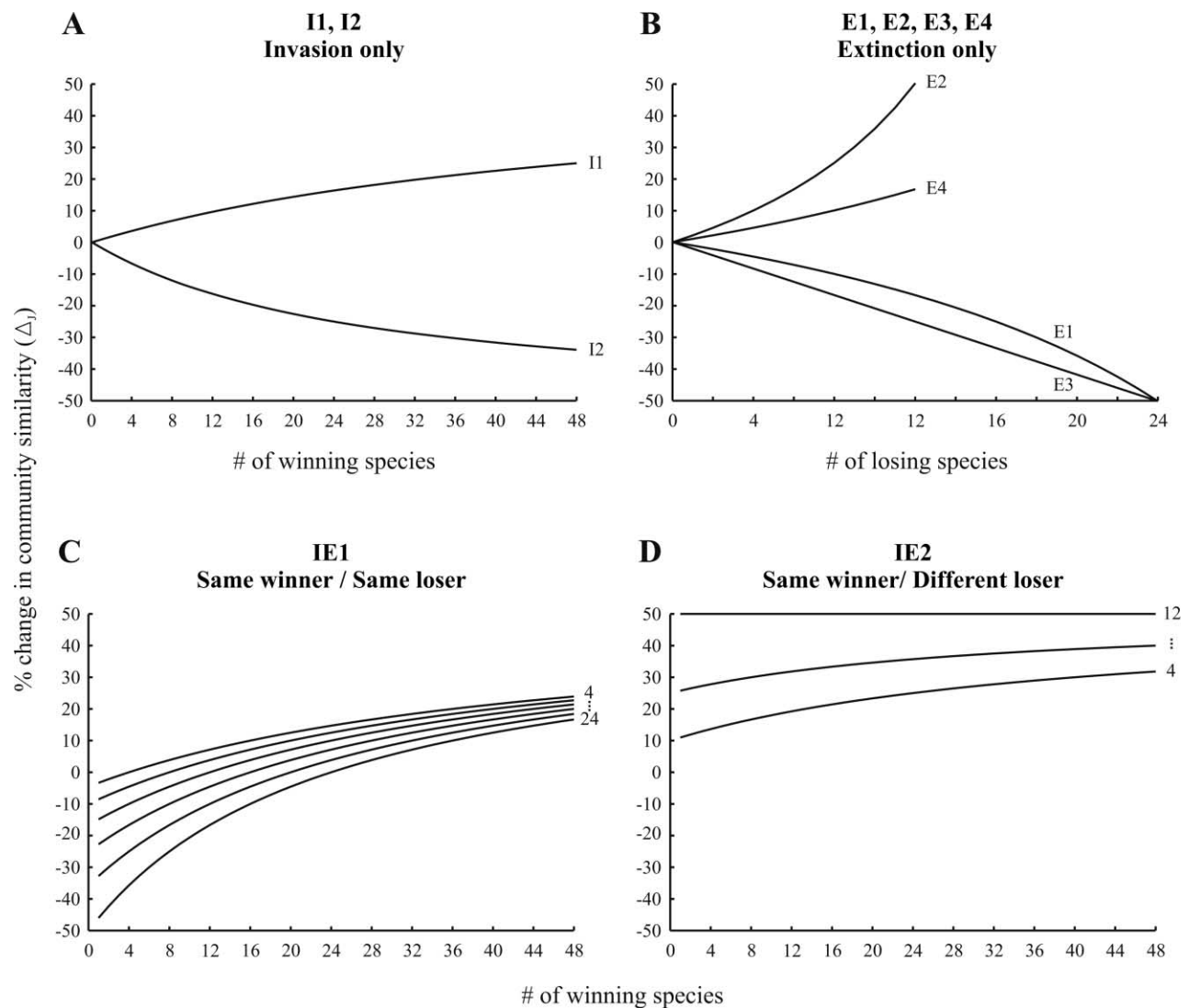


Figure 4: Patterns of community similarity change under the 14 invasion-extinction scenarios, based on $J_{\text{initial}} = 0.50$, as a function of varying numbers of winning species (i.e., number of nonnative species established in the recipient communities) and losing species (i.e., number of native species gone extinct in the recipient communities). For all simulations, the number of winners ranged from 0 (i.e., scenarios E1–E4) to s (i.e., all other scenarios), whereas the possible number of losers was constrained by the number of species that the communities shared or did not share and the number of species that were available to become extinct; the number of losers, therefore, varied depending on the initial community similarity and particular scenario. The number of losing species for scenarios IE1–IE8 is represented by sets of curves reported in intervals of four, from four to 24 for scenarios IE1, IE3, IE5, and IE7, and from four to 12 for scenarios IE2, IE4, IE6, and IE8. Curves in panels C–J do not originate at the Y-axis because scenarios IE1–IE8 always involve at least one winner.

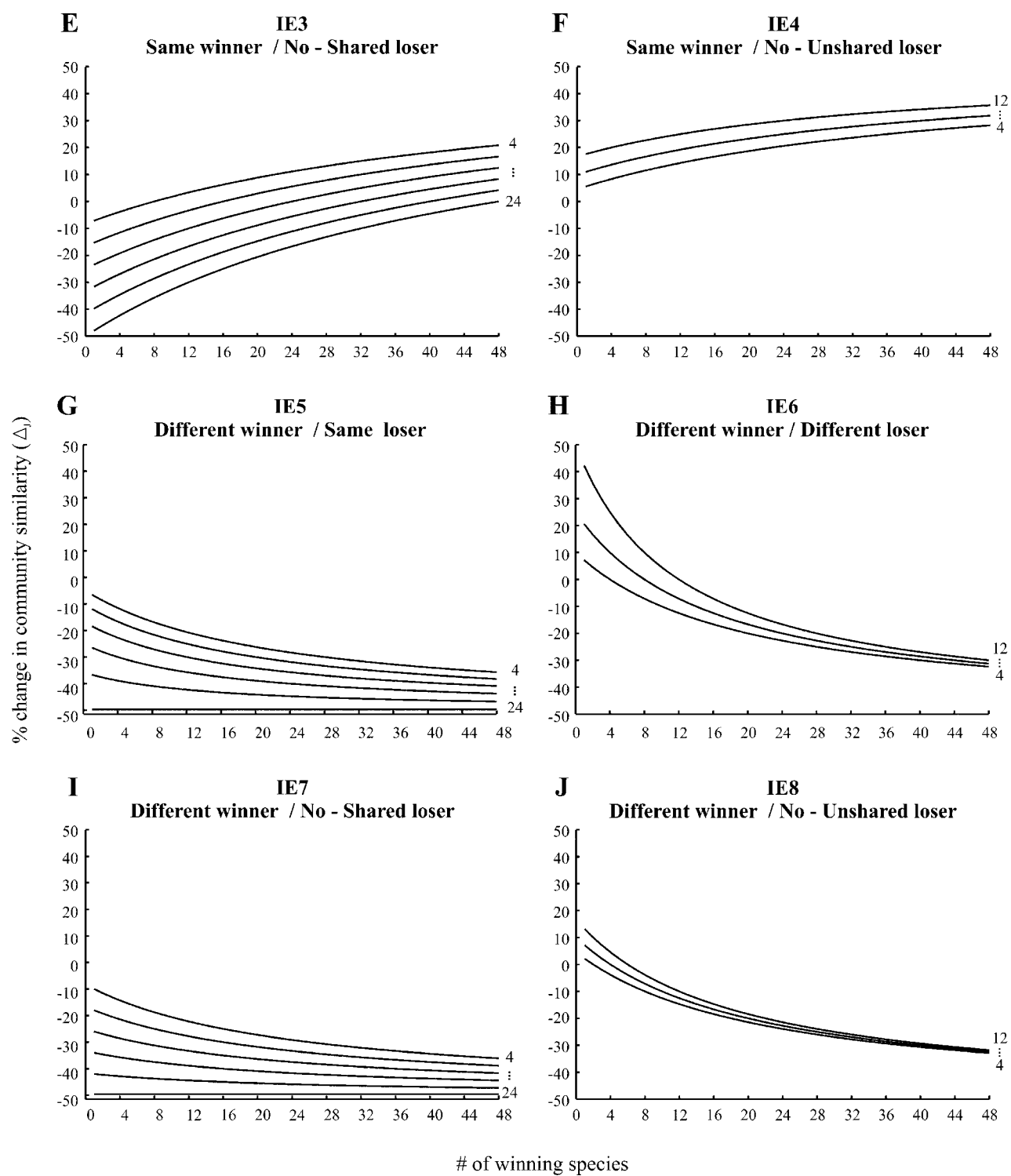


Figure 4 (continued)

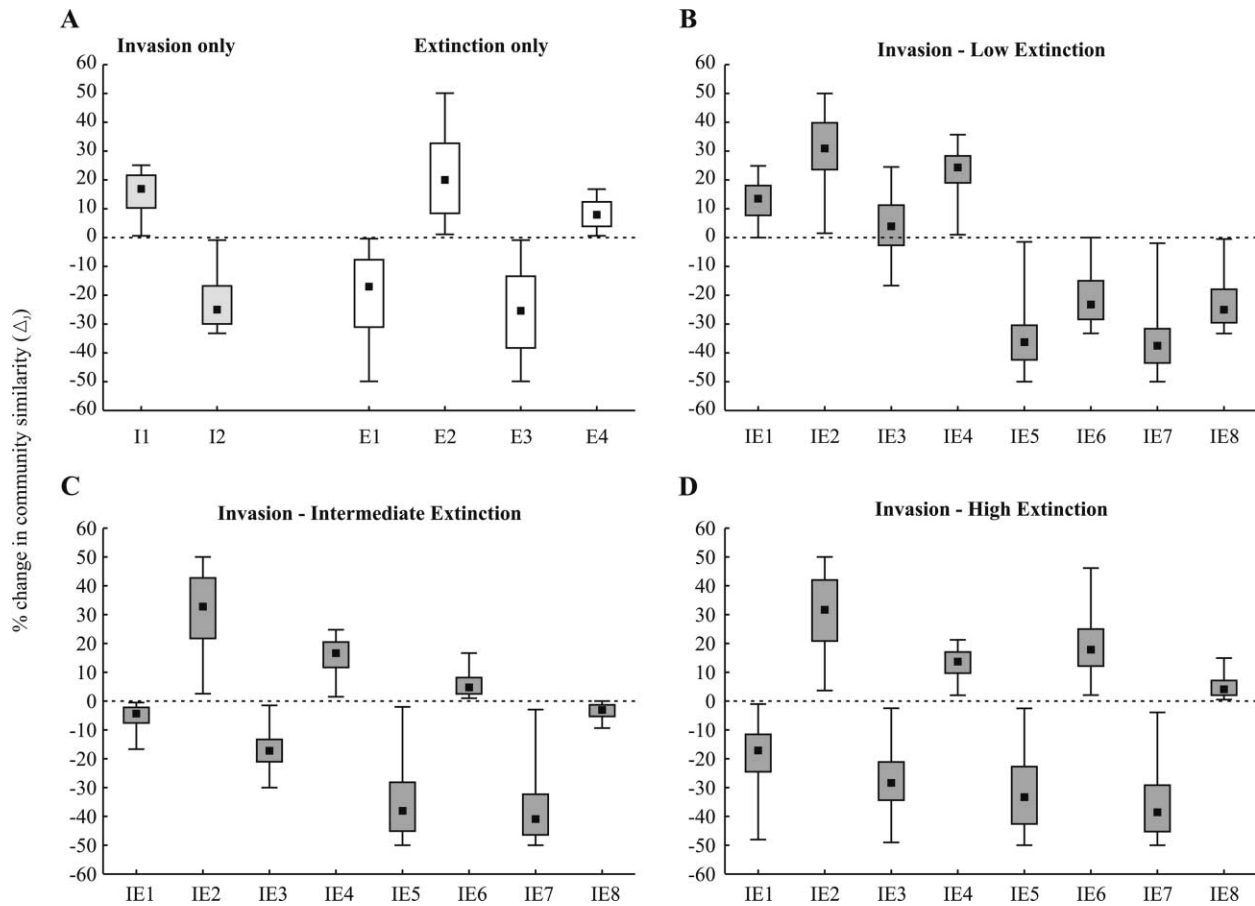


Figure 5: Patterns of community similarity change under the 14 invasion-extinction scenarios. A, Invasion-only and extinction-only events and invasion and extinction events categorized by relative number of losing to winning species ($L:W$). B, Low ($0 < L:W \leq 1$). C, Intermediate ($1 < L:W \leq 2$). D, High ($L:W > 2$). Results are for all combinations of numbers of winners and losers and are averaged over all levels of species richness and represent $f_{\text{initial}} = 0.50$. Square symbol is the median, boxes represent interquartile ranges, and whiskers represent the minimum and maximum values. Dashed line demarcates homogenization (positive community similarity) from differentiation (negative community similarity).

Minnesota lakes between 1940 and 1992 (Radomski and Goeman 1995) and by 20% in California zoogeographic provinces between pre-1850 and 2000 (Marchetti et al. 2001). It is difficult to exclude the possibility that California exhibits a greater degree of homogenization simply because of a longer data record. Future studies should account for the potential effects of scale dependence when studying biotic homogenization, and additional simulations (such as the ones presented here) could assist in assessing the sensitivity of measured biotic homogenization to variable observational time frames.

Data resolution and choice of statistical analyses can also influence perceived patterns of biotic homogenization. Typically, biotic homogenization is quantified by comparing community composition based on a particular similarity index or comparing the distance among communities in species space based on clustering or ordination

techniques (Rahel 2002). The degree to which an inference of homogenization depends on the choice of statistical approach is an important but uninvestigated issue. More fundamentally, the numeric resolution of species data strongly influences perceived community patterns (Rahel 1990); therefore, sole reliance on presence/absence data may constrain our understanding of critical mechanisms contributing to homogenization. For example, we might expect increased variation in the relative abundances of species or decreased species evenness to be indicative of biotic homogenization and its potential ecological consequences. Quantifying the homogenization of community evenness may be particularly fruitful given its importance for invasion and ecosystem processes (e.g., Wilsey and Potvin 2000). The potential influence of species abundance on predicted patterns of biotic homogenization could be accounted for by incorporating a stochastic component

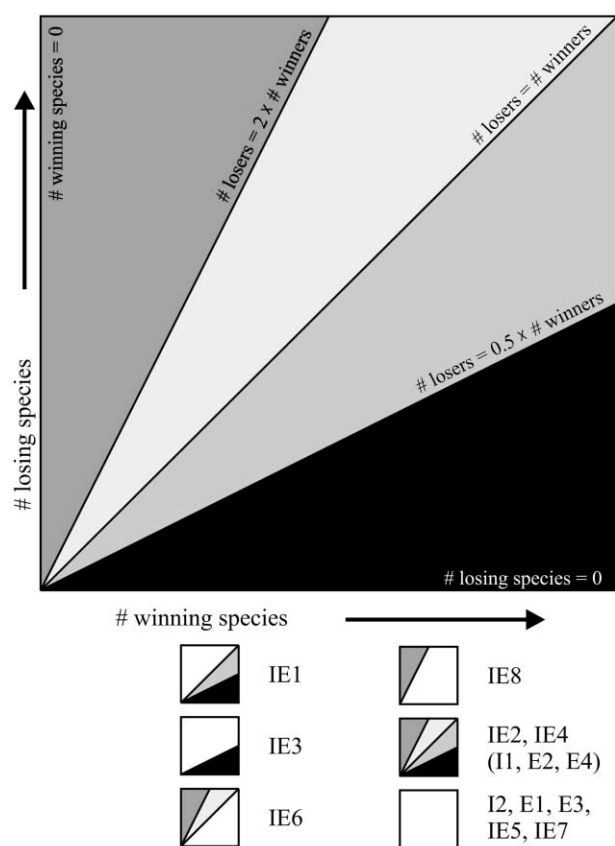


Figure 6: A proposed unifying model for biotic homogenization illustrating the conditions (i.e., relative numbers of winning and losing species) in which biotic homogenization (and not differentiation) is predicted to occur independent of both species richness and initial community similarity. Diagonal clines represent different ratios of number of winners to number of losers, and the shaded portions provide conditions where homogenization is predicted to occur for each scenario. Different degrees of shading are intended only to help differentiate among the various scenarios that lead to homogenization. For example, scenario IE1 results in homogenization only when the number of winners is greater than the number of losers, scenario IE2 always results in homogenization, and scenario I2 never results in homogenization. Note that scenarios I1, E2, and E4 always result in homogenization, but because they do not involve both winners and losers, they are represented in parentheses with IE2 and IE4.

into our conceptual model that represents the influence of species abundance on the outcome of native-nonnative species interactions.

Results from the conceptual models also suggest that species richness can have some influence on our perception of homogenization, in that we found homogenization rate (increase in community similarity per individual invasion or extinction event) to be greater at low species richness. Consequently, observed patterns of homogenization in relatively species-poor fish or bird communities

may be inflated compared to relatively speciose plant communities. Furthermore, the contribution of the different invasion-extinction scenarios to homogenization may vary globally because of geographical differences in the size of species pools. Given that species richness increases with spatial scale, we might also expect greater measured rates of homogenization at the local versus the regional scale. In addition, although we examined the influence of species richness on biotic homogenization based solely on the mathematical properties of adding or subtracting species from the recipient communities, species richness could also influence the number of winning and losing species. For example, if invasibility increases with resident species richness (see Levine and D'Antonio 1999 for a recent review), then we might expect the observed range of $L : W$ to be partially a function of species richness, which might therefore influence the relative contributions of the biological mechanisms driving homogenization.

Prospectus

Biotic homogenization is now considered one of the most prominent forms of biotic impoverishment worldwide, and it will likely continue to increase because of anthropogenic forces associated with growing human populations. So strong is this mixing force that global biotic homogenization with commensurate loss of species is argued to be the logical endpoint of the anthropogenic spread of nonnative species (Vitousek et al. 1996). To date, we have begun to better understand patterns in biotic homogenization in both aquatic (Rahel 2002) and terrestrial (Lockwood and McKinney 2001) ecosystems; however, we still lack an understanding of the mechanisms underlying current patterns and, consequently, an ability to predict future patterns of homogenization. We believe that unless study of biotic homogenization is placed in a more mechanistic and predictive framework, empirical results of homogenization studies alone will fail to provide adequate guidance in conservation efforts to maintain regional distinctness of the global biota. Accordingly, we submit that quantifying how the processes of invasion and extinction contribute to rates of biotic homogenization and understanding how levels of habitat disturbance and connectivity mediate these processes should be at the forefront of future research. Obtaining this knowledge is critical to enhancing our ability to predict which areas are most susceptible to increased homogenization and to determine which mechanisms primarily contribute to this process. Our conceptual framework, in conjunction with the collection, analysis, and interpretation of new empirical data, can contribute to an enhanced understanding and prediction of future losses of regional distinctiveness across a variety of taxa in both space and time.

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