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A stochastic model for integrating changes in species richness and community similarity across spatial scales

Phillip Cassey, Tim M. Blackburn, Julie L. Lockwood and Dov F. Sax

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Human activities have elevated the extinction of natural populations as well as the invasion of new areas by non-native species. These dual processes of invasion and extinction may change the richness and similarity of communities, but the form these changes take is likely to depend on the manner in which invasions and extinctions occur and the spatial scale at which the changes are measured. Here, we explore the influence of differing patterns of extinction and invasion on the similarity and richness of a meta-community. In particular, we model simple stochastic processes analogous to realistic modes of human-mediated introduction of non-native species and range expansion by native species. We show that different modes of invasion and extinction can produce very different changes in diversity, and that the relative magnitude of these changes depends both on where in the meta-community diversity is measured and the degree of initial species aggregation. At any spatial scale of measurement, changes in the richness and similarity of communities following invasion and extinction are not necessarily strongly coupled: relatively large increases in richness may or may not also be associated with relatively large increases in similarity among communities. Thus, in real systems, the influence of human-induced invasions and extinctions on diversity will depend on both the precise mode of these processes (especially invasion), and how species populations are distributed across space.

P. Cassey (p.cassey@bham.ac.uk) and T. M. Blackburn, School of Biosciences, Birmingham Univ., Edgbaston, Birmingham, UK, B15 2TT. – J. L. Lockwood, Ecology, Evolution & Natural Resources, Rutgers Univ., USA. – D. F. Sax, Inst. of Ecology, Univ. of Georgia, GA, USA.

It is widely acknowledged that processes associated with human actions will leave a long-lasting imprint on geographic patterns of biodiversity (Elton 1958, Flannery 1994, Diamond 1998, Cassey et al. 2005). Nevertheless, the exact nature of this legacy is hotly debated. A frequent assumption is that human-induced environmental changes will always lead to decreases in biodiversity, whether measured using diversity indices or as numbers of biodiversity 'units' lost (e.g. genes, populations, species; Soulé 1987). However, this is not necessarily true. Many processes in ecology and evolution are scale dependent, varying in their effect with changes in both spatial and temporal extent. Depending on the scale considered, and the relative influence of different processes, it is conceivable that human activities have in fact resulted in increases in biodiversity (Sax and Gaines 2003, Brown and Sax 2004). Here we explore a stochastic model of invasion and extinction played out across multiple spatial scales that illustrates the complex outcomes associated with human impacts on biodiversity at sub-global scales (Sax and Gaines 2003).

The number of species in an area (for any higher taxon) changes in composition via human actions through the dual processes of extinction and invasions,

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and so transformations of biodiversity patterns may be acute in regions that are simultaneously extinction and invasion hotspots (i.e. double-hotspots sensu Lockwood 2006). Extinction always leads to a reduction in biodiversity at the global scale as the extinction of any species necessarily results in a decrease in global species diversity. At all scales less than global, however, net increases in species richness are possible whenever the number of species extinctions is exceeded by the number of non-native species invasions. For example, in New Zealand more than 2000 non-native plant species have established self-sustaining populations, while fewer than 10 native plant species have gone extinct – resulting in a large net increase in plant species richness across the islands of New Zealand (Duncan and Williams 2002). Nevertheless, net species richness can also decrease at local or regional scales. For example, the islands of Hawaii lost at least 74 endemic bird species to extinction following human colonisation, but have gained only 51 bird species through non-native bird introductions (Scott et al. 2001). However, within the archipelago, some islands (e.g. Kauai, Oahu, Lanai and Hawaii) have gained more bird species than they have lost (Blackburn et al. 2004). Thus, Hawaiian bird extinctions have lead to decreases in avian diversity at the global and archipelago scales, but have in some cases been more than offset by introductions leading to increases in avian species richness at the scale of individual islands (Lockwood 2006).

Such increases or decreases in species richness (i.e. changes in alpha or gamma diversity) are not the sole product of human-induced invasions and extinctions. Changes in biodiversity may also be accompanied by increases in species similarity between locations (i.e. decrease in beta diversity). The extinction of unique native populations and the introduction of widespread non-native species can decrease the distinctiveness of biotas at a range of spatial scales, a process termed taxonomic homogenization (McKinney and Lockwood 1999, Olden and Rooney 2006). However, it is equally plausible that the extinction of local populations of ubiquitous species and the establishment of non-native species within only one or a few localities can increase the distinctiveness of biotas at a range of spatial scales, termed taxonomic differentiation (Olden and Poff 2003, Marchetti et al. 2006, Olden and Rooney 2006).

The extent to which both richness and similarity increase or decrease as a result of human activities may also depend on the manner in which invasion occurs. Human activities have given rise to a variety of ways in which species may be introduced to non-native locals. Species may be introduced deliberately for the purposes of agriculture, hunting or aesthetic appeal; the last as promoted by various acclimatisation societies (Lever 1992). However, accidental introductions may also occur. For example, a diverse assemblage of marine organisms has been transported across and between ocean basins in the ballast tank water of ships. Such tanks may hold several thousand tons of water, potentially resulting in large unintentional introduction events (Wonham et al. 2000, Drake and Lodge 2004). Clearly, the characteristics of deliberate and accidental introduction events, and of the species spreading via them, are likely to be quite different from those introduced intentionally. Moreover, human activities may promote range expansion by some species without direct human intervention (e.g. in response to urbanization or climate change), for which invasions may have different characteristics again.

Recently, Olden and Poff (2003, 2004) presented a mechanistic investigation of how communities may homogenize or differentiate given particular species pools of native and non-native species. They presented 14 different scenarios for the effects of invasion and extinction on the similarity of a simple two-habitat model. These scenarios differed in whether the same or different (or no) species invaded the two habitats, or whether the same or different (or no) species went extinct from them. There has been a rapid growth in interest in homogenization since the publication of McKinney and Lockwood (1999), but as Olden and Poff (2003) pointed out, there has been remarkably little progress in building a theoretical framework that can describe the full set of expectations given various invasion and extinction scenarios. Though their model was quite simple, these authors showed that predictions from it could be used to draw conclusions about patterns in taxonomic homogenization and extrapolate to real data (Olden and Poff 2004, Olden et al. 2006).

Here we employ a stochastic modelling approach to explore the influence of different processes by which extinction and invasion occur on changes in both species richness and community similarity at different spatial scales. As the number of case studies in homogenization increases, there is a growing recognition of the importance of spatial scale in determining how diversity is modified by extinctions and invasions (Marchetti et al. 2001, McKinney 2005, Olden and Rooney 2006). Thus, we expand the model universe of Olden and Poff from just two interacting habitats to include a series of nested ‘patches’, or a meta-community (Leibold et al. 2004). As a consequence of envisioning the model universe as a meta-community we can also explicitly treat the various modes of invasion seen in the real world (as described above) and thus determine the relative effects of each of these modes on homogenization patterns as suggested by Lockwood (2004). We show that different mechanisms of species gain and loss give qualitatively different patterns of change in species richness at different spatial scales, which with appropriate data allows us to draw inferences about the action of these processes in real ecological systems. We also relate these changes in richness to changes in community similarity and show that these two metrics of biodiversity (Olden and Rooney 2006) have a complex relationship that varies between scales.

A simulation model of population extinction and habitat invasion

Our simulation model is a population-based spatially explicit model of extinction and invasion that follows the work of Olden and Poff (2003). All species are considered equivalent, there are no trophic interactions, and we include no intra- or inter-specific population dynamics. We extend previous models by directly incorporating spatial scale whereby habitats are nested within 'islands' and islands are nested within 'archipelagos' (Fig. 1). This is an idealized scenario that can produce a set of 'null' expectations in terms of the effects of invasions and extinctions on diversity patterns. It can be easily extended with more complex dynamics typical of meta-community models in future versions (Discussion).

Our model universe is composed of nested landscapes of j habitat patches with variable capacities (i.e. potential species richness) and n species, where the number of species, n, is equal to the number of habitats, j. A single habitat patch is the smallest spatial level and x habitat patches are nested within an 'island', x islands are nested within an 'archipelago', and x archipelagos are nested globally (Fig. 1). Thus, the number of habitat patches per level increments by a single power q (where if $q = 0, \ldots, 3$ then x^0 = a single habitat patch, x^1 = the number of habitat patches per island, x^2 = the number of habitat patches per archipelago, and $x^3 = j$ = the total number of habitat patches). Although any number of nested spatial levels and populations per patch are possible, for brevity we present results for the situation where $q = 0, \ldots, 3$ and $x = 5$, and hence j and n both equal 125. Results for the range of $x = 2, \ldots, 10$ are simple to compute and consistent with all the findings we present here.

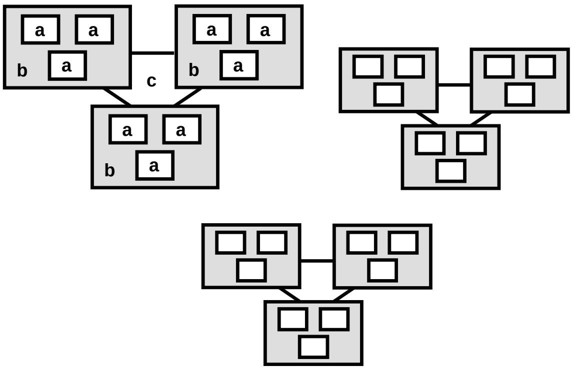

Fig. 1. A diagram of our meta-community including habitats (a) small hollow rectangles; within islands (b) larger grey rectangles; and islands within archipelagos (c) joined by solid lines, for the situation where $x = 3$. All species in our meta-community are considered trophic equivalents. Extinction and invasion are stochastic and are not influenced by inter- or intra-specific interactions. We model thirteen extinction and invasion scenarios between the elements of our meta-community to determine their associated effect on species richness and community similarity.

By spatially extending the simple two-habitat model of Olden and Poff (2003), we had to confront the question of how initially to distribute 'native' species' populations across the various meta-community levels. We set our rules for 'seeding' the various habitats such that they reflect observed species' population distributions. First, the number of populations allocated to each species followed a log-series distribution, such that the total number of populations was constant for any given species,

$$S_i = 0.5n - \left(\frac{0.5n - 1}{\ln(n)}\right)\ln(i) \qquad (1)$$

where S_i is a whole (absolute) number of populations for the ith species and S_i is always less than j/2. The log-series was chosen as a reasonable description of the distribution of populations amongst species in many natural assemblages (Hubbell 2001).

Second, populations of species had to be distributed among habitat patches so that initial levels of 'native' richness and endemism were biologically reasonable. Initially, we aggregated all the populations of a species as much as possible (aggregated model). Thus, one habitat was randomly selected for each species, and remaining populations of the species were added to habitats on this island until either all populations of the species were allocated or all habitats of an island were full. In the latter case, we allocated any remaining populations to a second island in the same archipelago, and so on until either we allocated all populations of the species to a habitat or all habitats in the archipelago were full. In this latter case, we choose another archipelago at random and the process was repeated. In this model, any species with a range size (number of populations) less than the number of habitats on an island is a single island endemic. Under this aggregated model of initial species distribution, average species richness was 12.4 for habitats, 14.4 for islands and 28.5 for archipelagos.

In reality, for most taxa the true level of richness may be higher and endemism lower than in the above aggregated model. Thus we constructed a second model of initial species distribution (clustered model) aiming to produce a low-endemism, high richness 'bracket' to the aggregated model such that the two distribution models together would capture most realistic species' distributions. In the clustered model, we chose a random habitat and we assigned a species' first population to this habitat. We arbitrarily numbered habitats within an island k_1 to k_x. We allocated subsequent populations of this species to higher numbered habitats on this island (e.g. following the assignment of habitat k_i, we assigned subsequent populations to habitats k_i to k_x only) until either we allocated all populations of the species to a habitat or all available habitat patches were occupied. In the latter case, we allocated remaining populations to a second island, with the same allocation rule for habitats within the island, and with the probability that this second island is in the same archipelago as the first set to be 0.5. We repeated this process until all populations of all species were allocated to a habitat patch. Under this model, average species richness was 12.9 for habitats, 21.6 for islands and 56.5 for archipelagos.

The aggregated and clustered models both produced levels of endemism that are comparable to known empirical data. Under the aggregated model, 33% of species are, on average, restricted to a single island, and 86% to a single archipelago. These values fall to 22% and 36% for the clustered model. These values compare to 52% of native species found only on one island and 74% in one archipelago for the data on real island bird distributions compiled by Blackburn et al. (2004). Blackburn and colleagues' data are likely an over-estimate of single island endemism as presence on only one island in their dataset does not exclude a species presence elsewhere (as their database does not include all islands globally). Nevertheless, the clustered and aggregated models do not differ hugely from these observed levels of endemism for birds, suggesting that they may reasonably reflect real-world distribution patterns.

Thirteen scenarios of species invasions and extinctions

For both initial distribution methods, we modelled a series of simple modes (13 scenarios) of extinction and invasion (Fig. 2). We first describe each mode separately, and then how we combine them to model changes in species richness and across-community similarity. In each case we are interested only in the relative change in species richness or similarity. We therefore assume an ecological state where species or population identity is fixed and each series of extinction and invasion transitions occur only once.

Population extinction (1)

p populations are randomly chosen for extinction from the n species. By chance, common species are more likely to lose populations (since they have a greater total number of populations) and only very rare species are likely to become 'globally' extinct (since only species represented by a very small total number of populations are likely to lose all those populations 'randomly' in a single time step). This scenario of population extinction is consistent with empirically observed progression of a widespread species moving towards extinction, in which populations are systematically lost well before entire species become extinct (Hobbs and Mooney 1998), and with extinction in highly endemic species in which the loss of a population equates directly with the loss of the entire species (e.g. single island endemic).

Widespread invasion (2)

P species are randomly chosen to be invasive. In this model, a species doubles its original number of populations S_i by invading S_i randomly chosen novel habitats from where it was previously absent. We constructed this invasion scenario to portray the effects of a few species being introduced successfully worldwide, as is the case with species used in agriculture and aquaculture. This scenario could also reflect instances where a single species has been successfully introduced worldwide due

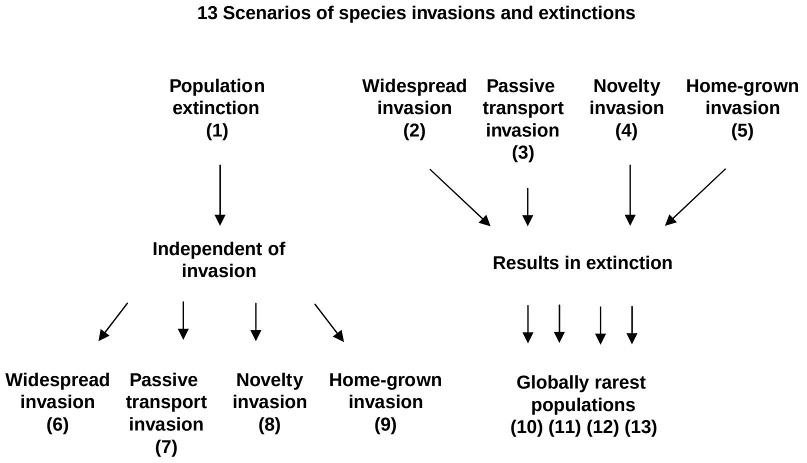

Fig. 2. Summary of the 13 invasion and/or extinction scenarios modelled. Initially, we model extinction (scenario 1) and invasion (scenario 2–5) as separate processes. We then model population extinction subsequently followed by each of the four invasion modes (scenario 6–9). Conversely, each of the four invasion modes may lead to extinction of the globally rarest population in the invaded habitat (scenario 10–13).

to its widespread appeal as a game or pet species. For example, goldfish *Carassius auratus*, rainbow trout *Oncorhynchus mykiss* and the mallard *Anas platyrhynchos* are all distributed worldwide due to the frequency and consistency that they have been introduced given human preferences for pets and game (Fuller et al. 1999, Lockwood 1999).

Passive transport invasion (3)

p populations are randomly chosen to invade a random novel habitat. In each iteration of this scenario p is calculated as ΣS_i from the P species chosen in the previous model. By chance, common species are more likely to have an invasive population than are rare species. We constructed this invasion scenario to represent the passive or unintentional transport of non-native species. These species are typically randomly entrained within ballast water or cargo holds, or they hitchhike on other species, as a simple function of their ubiquity in their native range.

Novelty invasion (4)

R species are randomly chosen (with replacement from p populations) to invade a random new habitat. This model assumes that invasiveness is not related to population abundance and, by chance, rare species therefore expand their distribution (proportionally) more than common species (since rare species have smaller geographical ranges and any expansion of that range is likely to increase total range size more than for a common species). This scenario differs from species invasion (scenario 2) in that each time a species is randomly selected its S_i increases by 1, rather than doubling, and each species can be randomly chosen multiple times. We constructed this scenario to represent the many thousands of species that are moved into a non-native locale because of their aesthetic appeal to people, which is often idiosyncratic, and not necessarily repeatable from place to place. In some years such species may be introduced to many locations (i.e. a burst of introduction activity following fashion trends), and in some years they may be introduced to only a few. Examples of novelty invasions include the many finches that have established on Hawaii, Tahiti and Puerto Rico due to the efforts of acclimatization societies (Long 1981); the various non-native freshwater fishes established within California watersheds due to game, pet, and bait releases (Marchetti et al. 2006); or the many different plant species introduced through time to the Czech Republic following various connections to other countries and changing human perceptions of the utility of plants (Pyšek 2003).

Home-grown invasion (5)

p populations are randomly chosen to invade the ‘closest’ novel habitat within the same island or the same archipelago. In this model if the species already occurs within all habitats of an archipelago a random novel habitat is then chosen outside the archipelago. Cox (1999) labelled species that expand their ranges within their native continent or island due to the environmental changes wrought by human actions as “home-grown exotics”. Interest in these species has increased recently as they are often considered nuisance species, and they may play a large role in the homogenization of local biological communities (McKinney 2005).

For the above modes of extinction and invasion, we considered the following processes of taxonomic homogenization. We first examined the influence of extinction and invasion as separate processes (Fig. 2; model 1 to 5). This scenario represents a baseline run where we can deduce the effects of invasions and extinctions on biodiversity patterns independently of one another. Second, we treated population extinction and invasion as sequential independent processes where population extinction is subsequently followed by the invasion of novel habitats (Fig. 2; model 6 to 9). This scenario matches the suggestions of Gurevitch and Padilla (2004), Davis (2003) and others who marshal evidence that invasions often do not directly cause extinctions. Instead, invasions follow the extinction of native species because they are both the by-products of human actions that drastically alter biological conditions. Nevertheless, there are clearly instances when invasive species may have harmful impacts on natives often to the point of driving populations of native species extinct (Cox 1999). If enough populations of negatively impacted, or the native species is globally rare, the invader can drive a native species extinct. Thus, in our third scenario, we considered the case where invasion explicitly caused the extinction of the globally rarest populations (Fig. 2; model 10 to 13).

Measuring average changes in species richness and across-community similarity

Each iteration of the model included all 13 extinction and invasions scenarios starting with the same initial spatial distribution of populations, and with a constant number of species P, chosen as invaders. Each simulation consisted of 1000 iterations. From each iteration, we chose a single random habitat and the average change in species richness and similarity was calculated (below) for each scenario across the 1000 iterations. Average changes in species richness and similarity were also calculated for the island and the archipelago that contained the random habitat, and the global change in species richness.

The change in species richness at a given scale (habitat, island, archipelago, global) was estimated as the average proportional change in number of species between the null state (pre invasion and/or extinction) and the transition state (post invasion and/or extinction), expressed as $(S_{TR}\text{-}S_{NULL})/\ S_{NULL}$.

The change in community similarity (presence or absence of a species within a community) at a given scale (habitat, island, archipelago) was estimated as the average ΔCS (change in community similarity). The average ΔCS was calculated as the difference in Bray-Curtis similarity coefficients between the transition state and the null state. The Bray-Curtis similarity coefficient was calculated as:

$$S_{jk} = 100\left[1 - \frac{\sum_{i=1}^{p} |y_{ij} - y_{ik}|}{\sum_{i=1}^{p} |(y_{ij} + y_{ik})|}\right] \tag{2}$$

where S_{jk} is the similarity coefficient, y_{ij} is the presence of the ith species in the jth location and y_{ik} is the presence of the same species (ith) in the kth location. The similarity coefficient (S_{jk}) ranges from 0, in the case where no species are in common between localities, to 100, in the case where two localities are identical in composition (Legendre and Legendre 1998). Similarity coefficients were calculated between a locale and all other locales for each of the three scales (habitat, island, archipelago). ΔCS were then calculated between the transition state and the null state and these scores (representing the change in Bray-Curtis coefficients between the null and transition states for each pairwise locale comparison) were averaged for each habitat, island, and archipelago. If the average ΔCS is positive, the locale has (on average) become more similar to the other locales after invasion and extinction. If the average ΔCS is negative, the locale has (on average) become less similar to the other locales.

Outcomes of simulation models

The results of our simulation model show that different distributions of populations across habitats, as well as different modes of extinction and invasion all have strong influences on changes in species richness and across-community similarity at different spatial scales. Depending on the combination of these scenarios a wide range of outcomes are possible. Relationships are plotted as the average of 1000 model iterations within Fig. 3. In all cases, measures of error are too small to be visually informative and are thus not represented in these figures. Thus, all lines in Fig. 3 are non-overlapping and represent distinct outcomes from stochastic extinction and invasion across scales.

The influence of invasion and extinction on species richness

For scenarios where extinction and invasion occur as separate processes (scenarios 1–5), changes in richness are primarily positive for invasion and negative for extinction (Fig. 3a, 3d). Population extinction removes, on average, 10% of species only at the habitat scale. The lower rates of extinction at larger scales result because the extinction of a population from a habitat on an island does not necessarily mean the extinction of that species from that island (or if it does cause extinction from the island, not necessarily from the archipelago or globally). The more spatially aggregated the populations, the less population extinction decreases richness at the larger scales (Fig. 3a, cf. 3d). Aggregation ensures that the extinction of a population from an island or archipelago is less likely to lower island or archipelago richness because other populations of the species are more likely to survive (an "insurance effect").

All modes of invasion increase average richness at the habitat scale by 10% when their effects are considered separately (Fig. 3a, 3d). This is expected since, on average, $\Sigma S_i = 10\%$ of all populations are invasive. Global richness is unaffected by invasion alone (Fig. 3a, 3d). Of all invasion scenarios, novelty invasion results in the greatest increases in average richness at the island and archipelago scales. Since species are chosen for novelty invasion independently of their population number, this invasion mode confers a relatively high opportunity for rare species to expand their range, which as a result leads to increases in richness at island and archipelago scales. In contrast, home-grown invasion produces the smallest increases in average richness at the island and archipelago scales because the nearest available habitat is invaded, which is often on the same island as the original 'native' population. Widespread and passive transport invasions produce changes in richness at both the island and archipelago scales intermediate to the other two modes, with greater increases due to passive transport invasion. Relative to widespread invasion, passive transport invasion is likely to favour the spread of more widespread species, because populations of such species are more likely to be chosen for invasion. However, passive transport invasion also resulted in invasion by 60% of species, on average (cf. only 10% of species spread by widespread invasion), and so has a slightly greater positive effect on richness at intermediate scales as more species reach new islands and archipelagos as compared to widespread invasion.

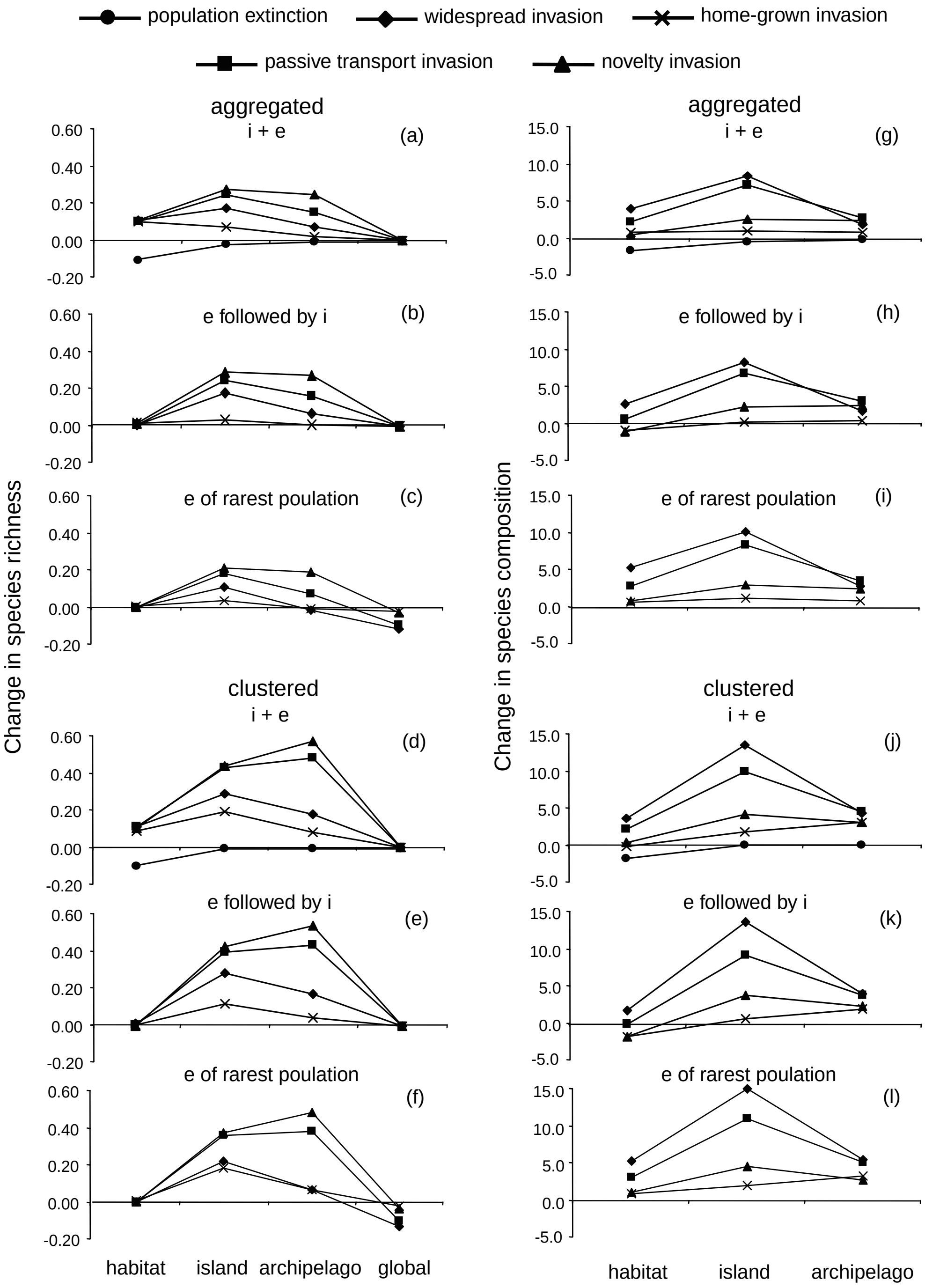

Fig. 3. Average changes in diversity (species richness) and community similarity for 1000 model iterations at different spatial scales for different invasion (i) and extinction (e) modes and different spatial distributions of native populations. Note that standard errors are too small to plot on these graphs. Average changes in diversity when native populations are (a) aggregated and invasion and extinction are independent; (b) aggregated and population extinction is followed by subsequent invasion; (c) aggregated and invasion results in extinction of the rarest population; (d) clustered and invasion and extinction are independent; (e) clustered and population extinction is followed by subsequent invasion; (f) clustered and invasion results in extinction of the rarest population. Average changes in community similarity when native populations are (g) aggregated and invasion and extinction are independent; (h) aggregated and population extinction is followed by subsequent invasion; (i) aggregated and invasion results in extinction of the rarest population; (j) clustered and invasion and extinction are independent; (k) clustered and population extinction is followed by subsequent invasion; (l) clustered and invasion results in extinction of the rarest population. See the text for details on how the spatial distributions of native populations are determined in the aggregated and clustered models.

Passive transport invasion leads to lower increases in archipelago richness than novelty invasion because the latter tends to favour the spread of rare species.

Increasing the initial spatial aggregation of species' populations increases the effect of invasion on richness at island and archipelago scales (Fig. 3a, cf. 3d). This is due to the greater aggregation of populations decreasing the number of islands and archipelagos on which any given species occurs, and consequently increasing the probability that invasion will place a species on an island or archipelago on which it did not previously occur. Aggregation also lowers the average richness of islands (clustered = 21; aggregated = 15) and archipelagos (clustered = 58; aggregated = 29), and hence a given number of new species invading will lead to a greater percentage increase in richness by default.

All invasion processes lead to diversity increases at the island and archipelago scale when population extinction is followed by subsequent habitat invasion (scenario 6–9; Fig. 3b, 3e). Home-grown invasion leads to the lowest increases in diversity at the island and archipelago scales because most invaders are already present in another habitat on any given island. Novelty invasion tends to lead to the greatest diversity increases on islands and archipelagos because it favours the spread of rare species more than the other invasion modes. Widespread invasion involves fewer species than passive transport invasion (10% vs an average of 60%), hence leading to the lower increases in diversity at the island and archipelago scale for widespread invasion. Diversity is more likely to increase at island and archipelago scales the more aggregated are a species' populations. Aggregation increases both the probability that invasion will place a species on an island or archipelago on which it did not previously occur and the probability that the insurance effect will prevent island- or archipelago-wide extinction.

Clearly, invasion cannot compensate for extinction at the global scale, and so global richness always declines when both extinction and invasion are coupled together. However, these declines tend to be very slight at both levels of population aggregation when the population going extinct from each habitat is chosen at random with respect to the species' global abundance (model 6–9; Fig. 3b, 3e). This is because populations of common species are more likely to be selected for extinction, and hence very few species go globally extinct in these models. The outcome is somewhat different if invasion of a habitat causes the extinction of the globally rarest species in that habitat (scenario 10–13). The deletion of rare species from habitats leads ultimately to global extinction for some. Nevertheless, all modes of invasion lead to increases in richness at the island and archipelago scales (Fig. 3c, 3f) as population aggregation guarantees that extinction is reduced by the insurance effect while invasion still generally takes species to islands they did not previously occupy.

The influence of invasion and extinction on between-community similarity

For the scenario where extinction and invasion are separate processes, all invasion modes lead to increases in community similarity (homogenization) at all scales as species are spread to habitats, islands and archipelagos they did not previously occupy. Invasions necessarily increase habitat-level richness by a constant amount, but they vary in the extent to which they homogenize communities at this scale. Passive transport and widespread invasion processes tend to lead to the greatest homogenization at all scales (Fig. 3g, 3j), as common species or a restricted set of species, respectively, are spread across the model universe. Home-grown invasion leads to small changes in CS at the island and archipelago scales. At the habitat scale, home-grown invasion leads to homogenization as it redistributes species within islands rather than across them. This effect also serves to limit the extent to which home-grown invasion leads to habitat homogenization across the entire model universe. Novelty invasion also leads to relatively small increases in CS, as it tends to favour the movement of rare species. Thus, the degree of homogenization that is expected via (any) invasion is offset by the distinctiveness of the non-native species being gained, which in turn tends to moderate increases in CS. Increasing population aggregation increases the homogenizing effect of the various invasion processes (Fig. 3g, 3j). Clearly, the more aggregated populations are initially, the more dissimilar habitats, islands and archipelagos are likely to be on average, and so the greater the increase in CS that results from invasion.

Population extinction decreases CS at the habitat scale but does not change CS at larger scales, as it rarely leads to changes in species composition on islands or archipelagos. Consequently, when population extinction is subsequently followed by invasion CS tends to increase (Fig. 3h, 3k). Homogenization also results when invasion causes the extinction of the globally rarest species in the habitat (Fig. 3i, 3l). This may be because replacing the most distinctive species from a habitat has less effect on overall CS when all habitats on an island have initially similar species compositions, and so invasion is as likely to decrease overall CS as increase it. Increases in similarity are greatest at the island scale since this scale has the highest probability of receiving novel species. As aggregation increases, the degree of homogenization at the island scale also increases. This is because increasing aggregation causes islands to become relatively more dissimilar, on average, to other islands than what we see between habitats or archipelagos.

Discussion

The models we have presented here are necessarily highly simplified caricatures of the invasion and extinction processes currently altering the richness and similarity of ecological communities the world over. What does such a simplified model bring to our understanding of diversity changes in the face of human-induced extinction and invasion? Our model extends that of Olden and Poff (2003) and importantly considers the nested spatial scale of species distributions, thus providing a more complete 'bestiary' of expectations for how real world changes to diversity can be envisaged. It is thus best to view our results as a series of 'null' expectations for diversity changes that result from invasion and extinction in the absence of more complex trophic and inter-specific dynamics. For example, no attempt has been made to model differences in the probability that populations will survive the invasion process and go on to produce viable populations: it is assumed that this probability is equal for all populations (and establishment equals 100%), although setting a different constant probability would not, on average, change any of the results presented. Further, each invasion in the real world may lead to the loss of more or less than one species from the invaded habitat. However, an average loss greater (or less) than one across invaded habitats would simply serve to raise or lower the curves for changes in richness and change in community similarity we report here, rather than leading to qualitative changes in the form of those curves. Although this might lead to decreases in richness or similarity where our models show increases (or vice versa), it would not lead to differences in the rank order of the magnitude of different invasion processes (unless different invasion processes were assumed to result in different levels of extinction). Nevertheless, setting invasion and extinction rates to be proportional may not be unrealistic. Sax et al. (2002) showed that for many taxa across several locations, species richness has remained unchanged despite considerable episodes of extinctions and invasions.

We can also evaluate the influence of native species distributions across scales and show how they may react to invasion and extinction. Increasing clustering of initial species' distribution affects patterns of extinction by reducing the likelihood that the loss of a population from a habitat equates to the loss of that species from an island or archipelago. Spatial insurance effects are common features of models in ecosystem and landscape ecology (Naeem and Li 1997, Loreau et al. 2003). We note, however, that local extinction and global extinction are very different and traditionally species are most likely to be protected from extinction when their populations are more widely distributed. Clustering of initial species' distributions also affects the influence of invasion by reducing the likelihood that an invading species is already present on an island or archipelago. Therefore, overall the effect of increasing the initial spatial aggregation of species is to increase the likelihood that richness and community similarity will increase at the island and archipelago scales (Fig. 3). That is, the more distinct communities are to begin with, the greater the effect of homogenizing processes. This result has real consequences in terms of how society approaches conservation of areas with high native species richness and endemism such as can be found on remote islands (e.g. the Galapagos Islands) or within evolutionary hotspots (e.g. Isthmus of Panama). Our results suggest that these areas are especially vulnerable to the homogenizing influence of non-native species and the loss of endemics.

Whatever the initial spatial arrangement of species, however, the different processes by which we modelled invasion and extinction led to substantial quantitative differences in richness and similarity changes across spatial scales (Olden and Poff 2003). This result was expected from the growing number of case studies showing differing degrees of homogenization across observational scales (Marchetti et al. 2001, 2006, Olden and Poff 2004, McKinney 2005). However, our model provides the first full accounting of how scale effects the degree of homogenization, and how homogenization is related to changes in species richness.

In general, the least changes in richness and community similarity pertain under the model of home-grown invasion (Fig. 2, 3). The aim of this model was to mimic the natural range expansion of a species, whereby its range size increases through the dispersal of populations to nearby habitats that become 'available' via human actions. Because this type of spread relatively rarely takes a species to a new island, let alone a new archipelago, both richness and community similarity at these scales tend to remain static when invasion is considered alone. At first glance, these results contrast with McKinney's (2005) finding that species invading from nearby sources have a more homogenizing effect than species from distant sources. However, this contrast is largely due to differences in scale. McKinney compares the effects on the similarity of communities within the US of invaders from within versus outside that country, but does not consider their influence at the larger scales within which those communities are nested. Clearly, the homogenizing effect of invaders from outside the US is likely to be greater at larger spatial scales. One interesting lacuna to this model of invasion is the tendency for low levels of global extinction to occur when the globally rarest species in a habitat is driven extinct by a home-grown invader. This occurs because home-grown invasions tend to occur in a localised set of habitats. This demonstrates that the localisation of invasion to certain habitats lowers global extinction rates as a result, as most habitats (and hence species) are spared the consequences of invasion. A similar process may explain the low levels of plant species extinctions on islands, where patterns of habitat change and species extirpation have largely been concentrated in discrete (and productive) areas, leaving other areas free to support native species (and which may still provide sufficient area to support plant species that can persist at relatively low population levels).

Home-grown invasion results in relatively small changes in both richness and community similarity. Observing such 'coupled' changes in these two diversity metrics was unusual in our models, however. Novelty invasion generally results in the highest increases in richness at island and archipelago scales (Fig. 3). Yet, it also tends to produce low increases in community similarity, of a similar magnitude to home-grown invasion. Both of these are a consequence of the tendency for novelty invasion to favour the spread of rare species. Rare species are less likely already to be present on any island or archipelago, and so their introduction raises richness. While invasion should also raise community similarity, the homogenizing effect of novelty introductions is mitigated when the introduced species is itself rare. Previous studies have noted that invasion can serve to differentiate communities if different species are introduced to different habitats (Marchetti et al. 2001, 2006, Olden and Poff 2003). We show that similar effects can be generated in random models when the spread of rare species is favoured.

Other modes of human-mediated invasion may depend largely on availability for transport. Examples include the spread of marine organisms via ballast water (Wonham et al. 2000, Verling et al. 2005) and the spread of plant species in ballast soil. Here, the probability that a species is introduced is likely to be largely due to its abundance in the environment from which the medium containing the propagules is removed. This is modelled by passive transport invasion, where the likelihood of spread is proportional to the number of populations each species initially possesses. Passive transport invasion tends substantially to increase the richness of islands and archipelagos (Fig. 3). The strength of this effect is related to the degree of aggregation, as initially aggregated populations are spread widely across the model universe. This process also homogenizes habitats, islands and archipelagos, as population dispersal reduces the differences between them.

Widespread invasion models a situation where a relatively small number of species are selected for introduction, but those species invade widely. As such it may mimic the spread of agricultural crops, where a limited suite of plants have become very widespread globally (Diamond 1998). This mode of invasion invariably produces the highest levels of homogenization at the different spatial scales, and especially at the island scale (Results). Simply, the same few species are spread everywhere. However, this same fact means that the resulting richness increases are relatively low.

All modes of invasion increase richness at the island and archipelago scale under realistic patterns of population aggregation, and all also increase community similarity. The spread of 10% of the populations in our model universe, and hence a 10% increase on average in the number of species in each habitat, can nonetheless lead to as much as a 50% increase in the average richness of islands, and a 60% increase in the richness of archipelagos. However, the degree of change above the habitat scale differs across the invasion processes. The changes are least for our analogue of natural colonisation. Richness increases most under the indiscriminate dispersal of passive transport invasion, and the environment is most strongly homogenized when the same few species are introduced everywhere. Yet, all modes of invasion involve the same net gain in population numbers. Thus, when considering the impacts of invasion, one cannot consider all forms of invasion as equal: how species are spread is as important as the fact that spread occurs at all. Of particular note here is that models of natural invasion (i.e. home-grown invasion) have very different, and generally lesser, effects on community richness and similarity in comparison to models that mimic human-mediated invasion modes. The fact that invasions occur naturally does not imply that the consequences of natural and human-mediated invasion are necessarily similar (Cassey et al. 2005).

The effect of coupling extinction with invasion also depends on the form that invasion takes, and the spatial structure of species' populations. The obvious exception is at the global scale, where any net change in richness is always negative. Global richness always declines when there is extinction in the system, even if that extinction affects populations at random. Increases in richness at smaller scales due to invasions do not, in the short term at least, compensate for this. At intermediate scales, extinction plus invasion can in theory increase or decrease richness, even when local richness is fixed. However, at these scales, and under realistic clustered patterns of population distribution, our models suggest that the influence of invasions on richness and community similarity tend to outweigh those of extinctions, leading to richness increases and taxonomic homogenization. Interestingly, this is true even when invasion leads to the extinction of the rarest species in any habitat, which might have been expected to drive richness down. Nevertheless, these conclusions depend on the number of extinctions per invasion. If the number of extinctions exceeds the number of invasions by a sufficient amount, decreases in richness will result. The effects on community similarity are less clear and probably non-linear. Although extinction tends to differentiate communities in our models (Fig. 3g, 3j), as the proportion of extinctions increases, it is likely that community similarity will start to increase again. Ultimately, the rarer native species will all be driven extinct, and only widespread invaders will be left.

In summary, we think that our simple models furnish three important conclusions with respect to changes in species richness and community similarity through different modes of invasion and extinction. First, the effects of invasion and extinction processes depend on the degree of spatial aggregation in native populations. Our models clearly show that the degree to which a particular taxonomic group varies in its population aggregation will influence how its richness and similarity are altered under different extinction and invasion modes. Second, the effects of invasion and extinction processes vary with scale. Although richness is constrained to stay constant on average at the habitat scale, coupling extinction and invasion can lead to substantial changes in richness and community similarity at larger spatial scales. Overall, our model universes show no net changes in population numbers, yet many species lose populations following invasion without going extinct from an island (or from an archipelago or globally), while some species are indeed driven globally extinct. Increases in richness at a given spatial scale may nevertheless belie extinction at that and/or other scales.

Third, and most importantly, different modes of invasion and extinction produce very different changes in richness. The effect is clearest for different invasion modes because we model a greater variety of these. In general, home-grown invasion leads to the lowest increases in richness, and transport invasion the highest. The greatest homogenization tends to arise through the widespread invasion model. Thus, invasion modes are not the same in terms of their effects on recipient communities. While species richness and composition at all spatial scales were altered through natural invasion processes before humans spread across the world, natural and human-mediated invasion processes may lead to very different outcomes for plant and animal communities.

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