

Complex organism–environment feedbacks buffer species diversity against habitat fragmentation

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Understanding the factors that determine the extent of biodiversity loss following habitat destruction is central to ecosystem conservation and management. One potential factor is the ecological feedbacks between organisms and local environmental conditions, which can influence how species affect one another and, consequently, whether or not species persist in fragmented landscapes. We investigated this possibility using a spatially explicit individual-based model of plant communities. In this model, plant species affected their own and other species' competitiveness by modifying local environmental conditions. These plant–environment feedbacks were assumed to vary among species pairs in direction and strength to mimic complex feedbacks observed between plants and soil conditions in real communities. We found that complex feedbacks reduced the extent of diversity loss, effectively buffering species against habitat fragmentation. Our analysis suggested that this buffering effect operated via two mechanisms. First, complex feedbacks decreased the likelihood of immediate extinction by making the spatial distribution of each species less clustered and consequently less likely to be eliminated entirely by fragmentation. Second, complex feedbacks decreased the likelihood of additional extinction by generating negative density dependence among surviving species, thereby keeping low-abundance species from going extinct due to demographic stochasticity and other forces. The buffering effect was particularly strong when species dispersed locally and abiotic environmental conditions varied globally. Our findings highlight the potential importance of organism–environment feedbacks in explaining species extinction by habitat destruction.

Habitat loss and fragmentation are among the most dominant anthropogenic forces causing species extinction (Tilman et al. 1994, Brooks et al. 1999, Balmford et al. 2003, Sax and Gaines 2003, Vellend et al. 2006, Kuussaari et al. 2009, Krauss et al. 2010). Therefore, understanding the factors that determine whether species persist or go extinct following these disturbances is central to effective conservation and management of ecological communities. Building on MacArthur and Wilson's (1967) theory of island biogeography, early work identified fragment size and isolation as primary factors, although their relevance to conservation has been debated (Simberloff and Abele 1976, Wilcox and Murphy 1985, Soulé and Simberloff 1986, Lasky and Keitt 2013). More recent work applying the metacommunity concept (Leibold et al. 2004, Holyoak et al. 2005) has emphasized species' dispersal ability as a major factor. For example, dispersal-limited species may be more likely to go extinct as a result of fragmentation because of the lack of rescue effects among fragmented populations (Brown and Kodric-Brown 1977, Gonzalez et al. 1998, Eriksson et al. 2014). Studies have also suggested that the spatial scale at which species disperse relative to the scale at which environmental conditions vary mediates the effect of habitat fragmentation on species diversity (Palmer 1992, Chesson 2000, Mouquet and Loreau 2003, Mouquet et al. 2006, Lasky and Keitt 2013).

An additional factor that is not as well studied, but potentially important is the ecological feedbacks between organisms and their local environment, whereby organisms modify the environment and affect the survival and reproduction of individuals that subsequently utilize the altered environment. Well-documented examples of organism–environment feedbacks include those between plants and soil conditions (Bever et al. 2012) and metabolic cross-feeding among microbial populations (Rozen et al. 2009, Harcombe 2010). Such feedbacks have long been a subject of ecological research, and an increasing number of studies indicate that they can influence a range of ecological phenomena, including the maintenance of species diversity (Odling-Smee et al. 2003, Bever et al. 2010), the trajectory of community succession (Kardol et al. 2006, Jiang and DeAngelis 2013), the generation of priority effects (Kardol et al. 2007), the spread of invasive species (Levine et al. 2006, Eppstein and Molofsky 2007), and the emergence of long-term transient community states (Fukami and Nakajima 2011, 2013). However, the role of organism–environment feedbacks is poorly understood in the context of habitat loss and fragmentation.

In this paper, we use a spatially explicit individual-based model of plant communities to ask the following three questions. First, how do organism–environment feedbacks influence the extent of diversity loss following habitat

fragmentation? In addressing this question, we focus on what we refer to as complex feedbacks, in which species affect some of the other species positively and others negatively, with varying magnitudes, via environmental modification. Such variation in the direction and strength of feedbacks has been observed in plant–soil feedbacks (Kulmatiski et al. 2008, van de Voorde et al. 2011, van der Putten et al. 2013). Second, how does the spatial scale of dispersal relative to the scale at which abiotic environmental conditions vary modulate the effect of complex feedbacks on diversity loss? We ask this question because previous work suggests that the effect of organism–environment feedbacks on species diversity may depend on both dispersal range (Bever et al. 1997, Eppstein and Molofsky 2007, Mack 2012) and environmental heterogeneity (Reynolds et al. 1997, Brandt et al. 2013). Third, how do the effects of complex feedbacks on diversity loss differ in fragmented landscapes compared to landscapes with habitat loss, but no fragmentation? This question was motivated by the interest in quantifying the effects of habitat fragmentation per se separate from those of habitat loss (Fahrig 2003, Ewers and Didham 2006).

Methods

Simulation model

Overview

We constructed a model following the methods developed by Mouquet et al. (2002) and modified by Fukami and Nakajima (2011, 2013) for simulating establishment, reproduction, and death of sessile organisms competing for local resources. In our model, individuals represented terrestrial plants, but the model should be applicable to other taxa characterized by dispersing propagules (seeds or larvae) and sessile adults that modify local environmental conditions in ways that alter species competitiveness. In the model, seedlings competed for establishment at local sites, where competitive outcomes (e.g. light availability, soil nutrient availability, ambient temperature and moisture) and by species-specific effects of previously established plants on local environmental conditions. Once established, all plants produced seeds at each time step. Seeds were dispersed across the landscape, but with a limited dispersal range (see Dispersal range below). Established individuals of all species each had a fecundity of 10 seeds each time step. Each time step, established individuals died with a fixed probability of 0.4, vacating the site they occupied for establishment of a new individual during the following time step. If no seeds landed at a vacant site, it remained unoccupied until future establishment. Time steps in our model are equivalent to years, and our plant species approximate perennial life histories. All simulation runs were performed in MATLAB (The MathWorks 2012), and subsequently analyzed and visualized in R (R Core Team).

Landscapes and species

Each replicate landscape contained 1024 sites (Fig. 1a) in one-dimensional, circular array. Each site could support only one adult individual at a time. The abiotic environmental condition of each site k was defined by a single value, H_k ,

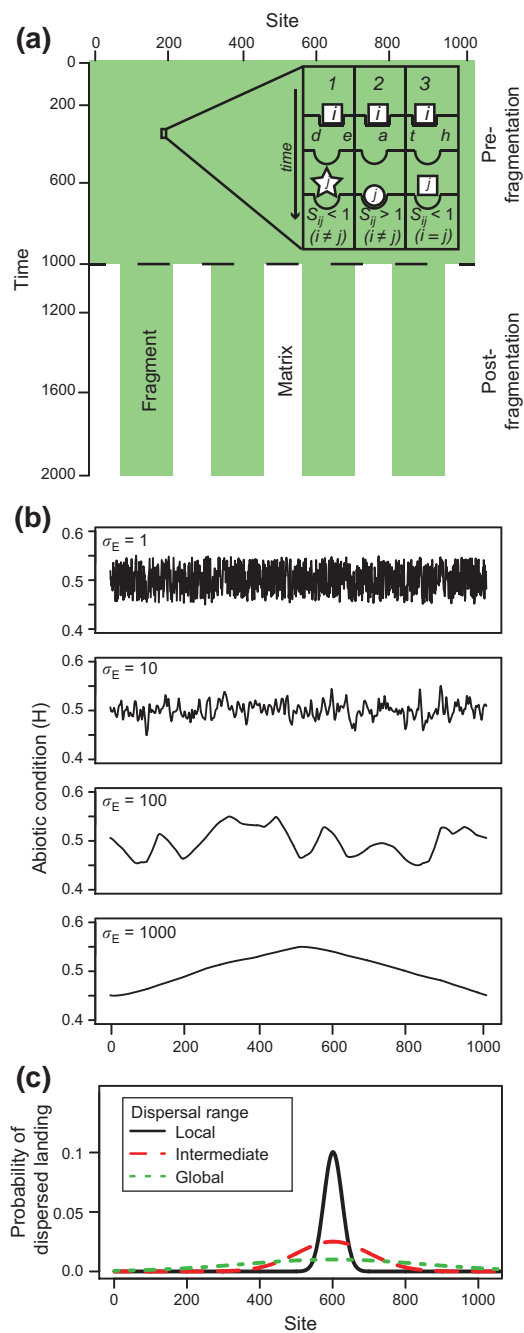


Figure 1. Schematic description of the simulation model. (a) Simulated landscape, in which green areas represent where organisms are viable, and white represents the uninhabitable matrix after habitat fragmentation. Time moves from top to bottom. Each fragment is of equal size. Inset: diagram of how positive and negative S_{ij} values can change the competitiveness of species at vacant sites, by altering the environmental conditions (i.e. the shape of vacant site). Column 1 shows negative feedback between the ‘square’ species and the ‘star’ species; column 2 shows a positive feedback between the ‘square’ species and the ‘circle’ species and column 3 shows a negative intraspecific feedback between two individuals of the ‘square’ species. (b) Spatial distribution of abiotic environment assumed in the simulation. Each panel shows the abiotic condition values for the entire landscape with a specific σ_E value (shown in upper left of each panel). (c) Gaussian dispersal probabilities for local (solid, black), intermediate (dashed, red), and global (dotted, green) dispersal. All functions shown are for a focal individual at site 600. The x-axes of (a–c) all are shared, representing sites.

drawn randomly from a uniform distribution $U(0.45, 0.55)$. To generate landscapes with varying abiotic spatial structure, we used wavelet transformations to adjust the degree of spatial autocorrelation in H_k values among sites (Keitt 2000). The spatial scale of environmental variation was determined by σ_E , following the wavelet model, i.e. $\text{Var}(w; \sigma_E) \propto \exp(-2 \sigma_E^2 f^2)$, where w represented wavelet coefficients and f was the inverse scale of analysis (Keitt 2009, Lasky and Keitt 2013), using the ‘waveslim’ package in R (Whitcher 2012). This approach allowed us to keep the same set of H_k values among replicated landscapes, while modifying the spatial scale at which environmental conditions varied in the landscape. We varied the spatial scale of abiotic environmental variation (σ_E) over the range $\sigma_E = \{1, 10, 100, 1000\}$. Lower σ_E values translate to low amounts of abiotic autocorrelation among sites, whereas high σ_E values indicate high autocorrelation (Fig. 1b).

We initiated simulation runs by randomly occupying all 1024 sites in the landscape with approximately equal proportions of 100 species, whose trait values were each defined by a single value, Z_i , randomly drawn from a uniform distribution $U(0,1)$ for each species i . From this initial community, we ran the simulation for 1000 time steps to allow the landscape to approach equilibrium. At $t=1000$, we disturbed the landscape. At the time of this disturbance, 50% of the habitat was lost, and the remaining habitat was divided into four habitat fragments of equal size (Fig. 1a). The fragments were evenly distributed in space, and the interspersed portions of the landscape were immediately converted to an uninhabitable matrix. After fragmentation, the simulation continued following the same rules of individual establishment, reproduction, and death for 1000 additional time steps. In total, each simulation run lasted a total of 2000 time steps.

Individual establishments

When two or more seeds simultaneously landed at a vacant site, the individual with the highest value of competitiveness, C_{ijk} , established, and all other individuals that landed at the site were removed from the landscape. As in Fukami and Nakajima (2013), C_{ijk} of species i at site k was defined as $C_{ijk} = (1 - |H_k - Z_i|)S_{ij}$, where j indicates the species of the individual that vacated the site during the preceding time step by dying. The parenthetical term measures the relative fit of the species to the local environment, and the S_{ij} term modulates this fit, as determined by the previous occupant of the site, as detailed in the next section. Once established, a plant persisted until its stochastic death, regardless of whether more competitive seeds arrived at its site. As all species had identical fecundities and mortality rates, when species had the same C_{ijk} values, they were ecologically neutral.

Organism–environment feedbacks

Organism–environment feedbacks occurred when a species that previously occupied a local site altered the abiotic environment for subsequent species. We incorporated organism–environment interactions into our model primarily with plant–soil feedbacks in mind, as in Fukami and Nakajima (2011, 2013). The strength and direction of feedbacks between a pair of species was measured by the value of S_{ij} , which was assumed constant for a given pair of

species i and j . When $S_{ij} > 1$, there was positive feedback, in which the previous occupation of a site by species j increased the competitiveness of species i at that site during the next time step. When $S_{ij} < 1$, there was negative feedback. When $S_{ij} = 1$, there was no feedback. We used what we refer to as the ‘complex feedback’ regime, where S_{ij} values were drawn randomly from a uniform distribution $U(0.5, 1.5)$ for interspecific (i.e. $i \neq j$) feedbacks, and from $U(0.5, 1)$ for intraspecific (i.e. $i = j$) feedbacks. This assignment of S_{ij} values results in complex (i.e. varying in both sign and magnitude among species pairs) heterospecific feedbacks ($i \neq j$) and negative conspecific feedbacks ($i = j$), consistent with some empirical observations (Kulmatiski et al. 2008, van de Voorde et al. 2011, van der Putten et al. 2013). For each pair of species, the two S_{ij} values were assigned independently. We compared results from simulations with this complex feedback regime to simulations with no feedbacks (i.e. all $S_{ij} = 1$, for both $i = j$ and $i \neq j$) in order to assess the effect of complex feedbacks on diversity loss (see Data analysis below). A schematic description of how positive and negative feedbacks alter species competitiveness is inset in Fig. 1a.

Dispersal range

Dispersal distances of seeds from each individual were drawn from a Gaussian distribution with a mean at the location of the focal individual and a variance, σ_D , which determined how far seeds dispersed. The dispersal distance of each seed from an individual was drawn independently. We used $\sigma_D = \{25, 100, 250\}$, which we refer to as ‘local’, ‘intermediate’, and ‘global’ dispersal (Fig. 1c). After fragmentation, seeds that landed in the uninhabitable matrix perished. Depending on the spatial scale of dispersal, habitat fragments may act as local species pools for other fragments in the landscape following fragmentation, with global dispersal treatments having the highest likelihood for among-fragment dispersal.

Treatments and replication

For all 24 parameter combinations (= 4 abiotic spatial structures, $\sigma_E \times 3$ dispersal ranges, $\sigma_D \times 2$ feedback regimes, i.e. with or without complex feedbacks), we ran 50 replicates, totaling 1200 simulations.

To examine if the results of the above simulations are robust to assumptions regarding the distribution of H_k and Z_i values, we also ran supplementary simulations using different ranges of abiotic environmental conditions (H_k values) and species trait values (Z_i values) that represented greater differences in competitiveness among species or more competitively neutral conditions than were assumed in our primary simulation. Specifically, in addition to our primary simulation where $H_k = \{0.45-0.55\}$ and $Z_i = \{0-1\}$, we analyzed the following five parameter combinations: 1) $H_k = \{0.45-0.55\}$ and $Z_i = \{0.45-0.55\}$, simulating reduced niche differentiation; 2) $H_k = \{0.45-0.55\}$ and all $Z_i = 0.5$, simulating competitive neutrality; 3) $H_k = \{0-1\}$ and $Z_i = \{0-1\}$, simulating large niche differentiation on a highly heterogeneous landscape; 4) $H_k = \{0-1\}$ and $Z_i = \{0.45-0.55\}$, simulating relatively small niche differentiation on a highly heterogeneous landscape; and 5) $H_k = \{0-1\}$ and all $Z_i = 0.5$, simulating competitive neutrality on a highly heterogeneous landscape.

Data analysis

Extent of diversity loss

To quantify the extent of species diversity loss caused by habitat fragmentation, we calculated the difference between the number of species present in the landscape immediately before fragmentation and the total number of species present at the end of the simulation, in both the absolute number of species lost and the proportion of the pre-fragmentation diversity lost. The latter implicitly captures the number of species maintained in the community. To account for random variation, the pre- and post-fragmentation numbers of species were computed as time-averaged species richness values over 50 time steps (i.e. $t = 950\text{--}1000$ and $t = 1950\text{--}2000$), respectively. Over both of these time ranges, the communities appeared to have reached an equilibrium number of species (Fig. 2).

Spatial clustering of conspecific individuals

In order to understand the mechanisms by which complex feedbacks affected the extent of diversity loss, we performed four additional analyses. First, since whether or not species go extinct due to fragmentation depends in part on how broadly they are spatially distributed across the landscape prior to fragmentation, we quantified the spatial scale over which conspecific individuals were clustered. To this end, for each simulation, we randomly drew 1000 pairs of individuals immediately before fragmentation occurred, and generated histograms of the number of conspecific and heterospecific pairs with respect to distance between the pair of individuals on the landscape (Fig. 3a). We then calculated the D statistic from the

Kolmogorov–Smirnov test, which quantified the difference between the cumulative distribution functions of the number of conspecific and heterospecific pairs for given distances along the landscape (Fig. 3b). Larger D values correspond to more clustering of conspecifics, where species occur in more local aggregates and are thus more prone to extinction by fragmentation (Fig. 3b). Smaller D values correspond to a greater chance of species being close to heterospecifics.

Probability of eventual extinction

The clustering of conspecific individuals along the landscape can explain the extent of the immediate loss of species from habitat fragmentation, but it may not fully explain patterns of subsequent species extinction. Therefore, in our second additional analysis, we sought to determine whether complex feedbacks increased the likelihood of species persistence after the landscape was fragmented. We hypothesized that species with low abundance after fragmentation would be generally more likely to go extinct due to demographic stochasticity (Shaffer 1981, Lande et al. 2003), but that complex feedbacks would alleviate the effect of low abundance on the likelihood of species going extinct. To evaluate this hypothesis, for each parameter combination, we pooled abundance and extinction data from all 50 replicates of each treatment group. We then performed logistic regressions for each treatment combination predicting the probability of eventual extinction given post-fragmentation population size. For a given post-fragmentation population size, we used the difference between the two fitted curves (i.e. the curve for replicates with complex feedbacks and the curve for those with no feedbacks) to quantify the effect of feedbacks

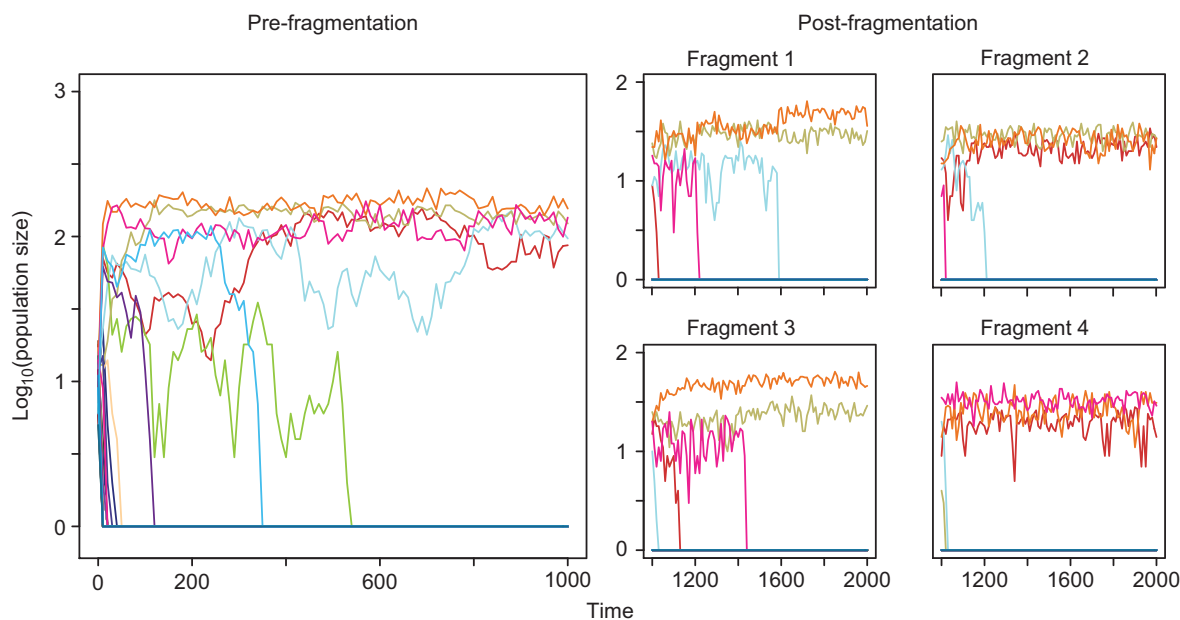


Figure 2. Representative example of temporal changes in species abundances. Each line represents a species. Abundances are shown on a logarithmic scale for a replicate simulation run with complex feedbacks, intermediate dispersal range, and $\sigma_E = 10$. The large panel shows abundances before fragmentation, in which species composition changed little 1000 time steps after the simulation started, with five species eventually coexisting in this example. The four small panels show post-fragmentation abundances within the four fragments, with different sets of species going extinct in different fragments as a result of fragmentation. Colors indicating different species are consistent with those in the large panel.

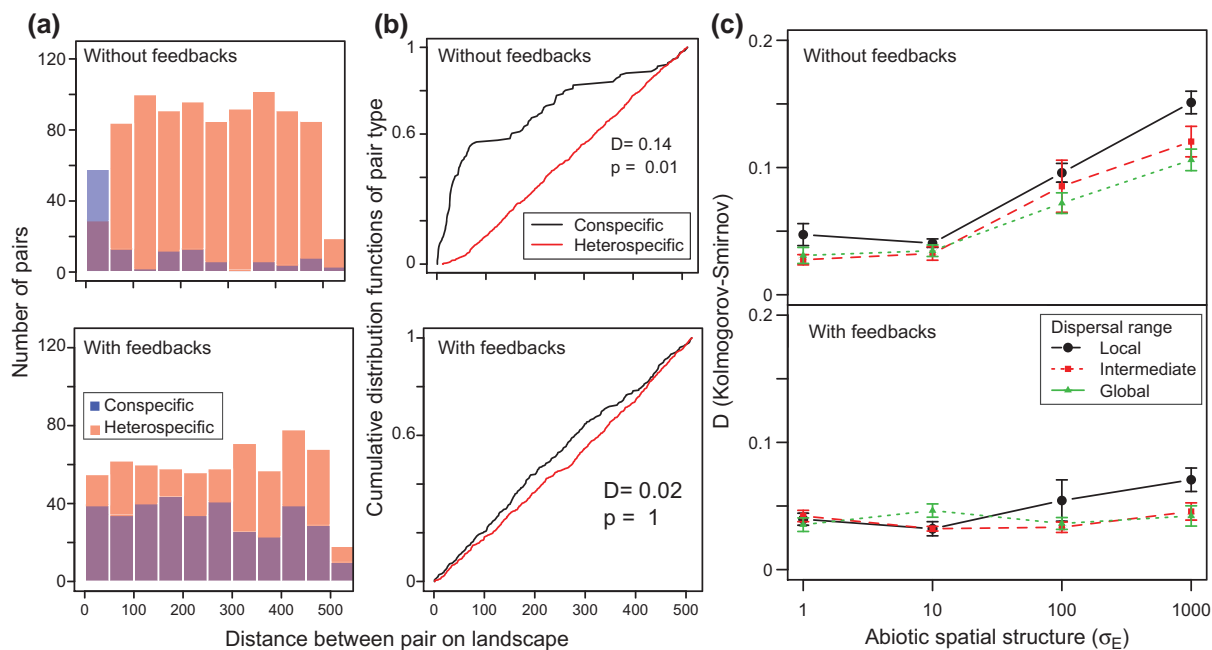


Figure 3. Complex organism–environment feedbacks reduce clustering of conspecific individuals. (a) Two contrasting examples, in the absence (upper panel) and presence (lower panel) of feedbacks, of the histograms summarizing 1000 randomly chosen pairs of individuals, separated as conspecific (blue) or heterospecific (red), as a function of physical distance on the landscape. In both panels, dispersal is local and $\sigma_E = 1000$. In the upper example, conspecific individuals are more spatially clustered. By contrast, in the lower example, conspecific individuals are distributed more evenly across the landscape. (b) Cumulative distribution functions of the number of random conspecific and heterospecific pairs ('pair-type') with physical distance for the two examples shown in (a). The distance between the two curves correlates with, and can therefore be summarized by, the Kolmogorov–Smirnov statistic (D statistic), with larger D values indicating more clustering of conspecific individuals. (c) Mean D statistic values for different dispersal ranges and σ_E values. The D statistic is smaller in the presence of feedbacks (bottom) than in their absence (top), indicating that complex feedbacks reduce clustering of conspecifics. This effect is particularly strong when σ_E is large. Error bars show standard errors.

on the probability of eventual extinction. In addition, to investigate the effect of the complex feedback regime (i.e. negative intraspecific feedback and both negative and positive interspecific feedbacks) further, we compared results for replicates with complex feedbacks to those for replicates with 'mixed feedbacks', where both intra- and interspecific feedbacks could vary in both negative and positive directions. This comparison allowed us to isolate the effects of the strictly negative intraspecific feedbacks on the probability of eventual extinction.

Feedback strength values for surviving and extinct species

In our third additional analysis, we measured how the distributions of intraspecific (S_{ij} where $i = j$) and interspecific (S_{ij} where $i \neq j$) feedback strength values differed among surviving species and those that went extinct. We pooled data from all replicates for each treatment and generated separate histograms of intraspecific and interspecific feedback strength values separately for surviving and extinct species. Similar to the analysis of spatial clustering above, we calculated the D statistic from the Kolmogorov–Smirnov to quantify the differences between surviving and extinct species in the distribution of feedback strength values.

Effect of fragmentation per se vs effect of habitat loss

In this study, we were interested in the effect of habitat fragmentation on extinction, but the effect of habitat fragmentation can be confounded with that of habitat loss (Fahrig

2003, 2013, Ewers and Didham 2006, Didham et al. 2012). Thus, in our fourth additional analysis, we sought to evaluate the effect of habitat fragmentation per se by using results of additional simulation runs in which landscapes lost an equivalent amount of habitat (50%), but in a single, contiguous area (i.e. without fragmentation). In these simulation runs, 50% of the habitat was lost, but the remaining habitat was a single contiguous patch, rather than 4 separate fragments distributed across the landscape.

Results

Extent of diversity loss

In all simulation runs, most of the initial 100 species quickly went extinct, with a mean of 4.37 species (standard deviation = 1.75 species) coexisting before the fragmentation event. Following fragmentation, landscapes with complex organism–environment feedbacks tended to suffer less extinction than those without feedbacks, a pattern we refer to as the buffering effect ($p < 0.002$; Fig. 4a; see also Supplementary material Appendix 1, Fig. A1). The scale of dispersal (σ_D) and abiotic variation (σ_E) jointly affected the magnitude of the buffering effect, particularly when measured by the absolute difference in diversity loss (Fig. 4b). The scale of abiotic variation (σ_E) had little effect on the strength of the buffering effect when dispersal occurred globally ($\sigma_D = 250$,

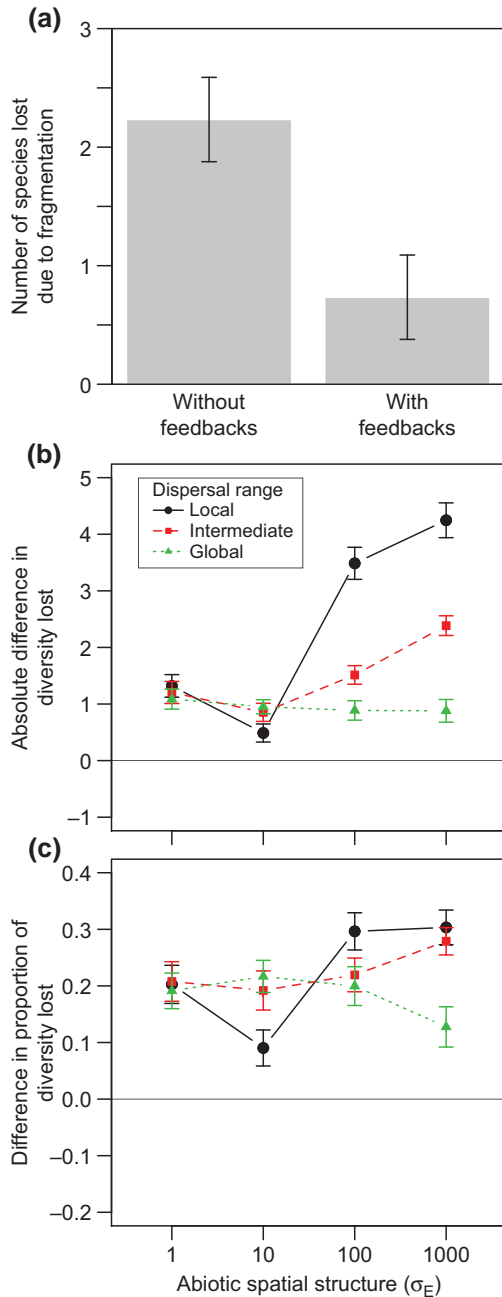


Figure 4. Complex organism–environment feedbacks buffer species diversity against habitat fragmentation. (a) Averaged across all treatment combinations, more species went extinct due to fragmentation in the absence of feedbacks than in their presence (t -test, $p = 0.001$). (b, c) The buffering effect (as measured by the number of species lost due to fragmentation when feedbacks are present vs. when they are absent) was always significant in both the absolute number of species (b) and the proportion of species (c), but the strength of the buffering effect depended on dispersal distance and abiotic spatial structure. Absolute difference in diversity lost was calculated as diversity without feedbacks minus diversity with feedbacks. Proportional difference in diversity lost was measured as the proportion of diversity lost without feedbacks minus the proportion of diversity lost with feedbacks. Error bars show standard errors. Values on y -axis are on a linear (non-logarithmic) scale.

mean = 0.95 species, green triangles in Fig. 4b). By contrast, the buffering effect was strongest under higher values of σ_E and when dispersal was more local ($\sigma_D = 100$, mean = 2.39 species, red squares; $\sigma_D = 25$, mean = 4.25 species, black circles, respectively in Fig. 4b).

The additional simulations suggested that our qualitative result of complex feedbacks buffering communities against species loss following habitat fragmentation was robust (Supplementary material Appendix 1). However, a few differences were observed. For example, in simulations where competitive differences among species were widened, the magnitude of the buffering effect was relatively high (Supplementary material Appendix 1, Fig. A2–A3) because a greater number of species were able to coexist prior to fragmentation in these scenarios (Supplementary material Appendix 1, Fig. A4). In simulations representing ecological neutrality, the buffering effect was strongest when dispersal was local. In neutral simulations, there was little effect of the scale of abiotic heterogeneity on the strength of the buffering effect (Supplementary material Appendix 1, Fig. A5–A6). (In Supplementary material Appendix 2, Fig. A7–A9, we discuss results from the parameter combination that did not qualitatively match our main findings.)

Spatial clustering of conspecific individuals

In the absence of feedbacks, the likelihood that a random pair of individuals were conspecifics was higher when they located closer to each other on the landscape, particularly under large σ_E values (Fig. 3c, upper panel). By contrast, in simulations with complex feedbacks, the probability that a pair of individuals were conspecifics depended only modestly on their physical proximity (Fig. 3c, lower panel). Across dispersal treatments, the mean D value was higher for simulations without feedbacks (mean $D = 0.07$) than for those with complex feedbacks (mean $D = 0.04$; t -test, $p < 0.02$), indicating that complex feedbacks reduced clustering of species across the landscape, effectively making it more likely that any species would be neighboring a heterospecific individual. In other words, for a given species, conspecific individuals tended to be distributed more evenly across the landscape in the presence of complex feedbacks than in their absence.

Probability of eventual extinction

Although extinction rate approached to zero over time in all treatments, it was consistently higher in communities without complex feedbacks (Supplementary material Appendix 1, Fig. A12, black curves). Complex feedbacks tended to decrease the probability of eventual extinction, particularly under local ($\sigma_D = 25$; mean probability of extinction decreased by 17%, across all scales of abiotic variation) and intermediate dispersal range ($\sigma_D = 100$; mean probability of extinction decreased by 9%, across all scales of abiotic variation) and under larger-scale abiotic variation ($\sigma_E = 100$ and 1000) (Fig. 5; also see Supplementary material Appendix 1, Fig. A11 for representative examples of individual logistic regressions).

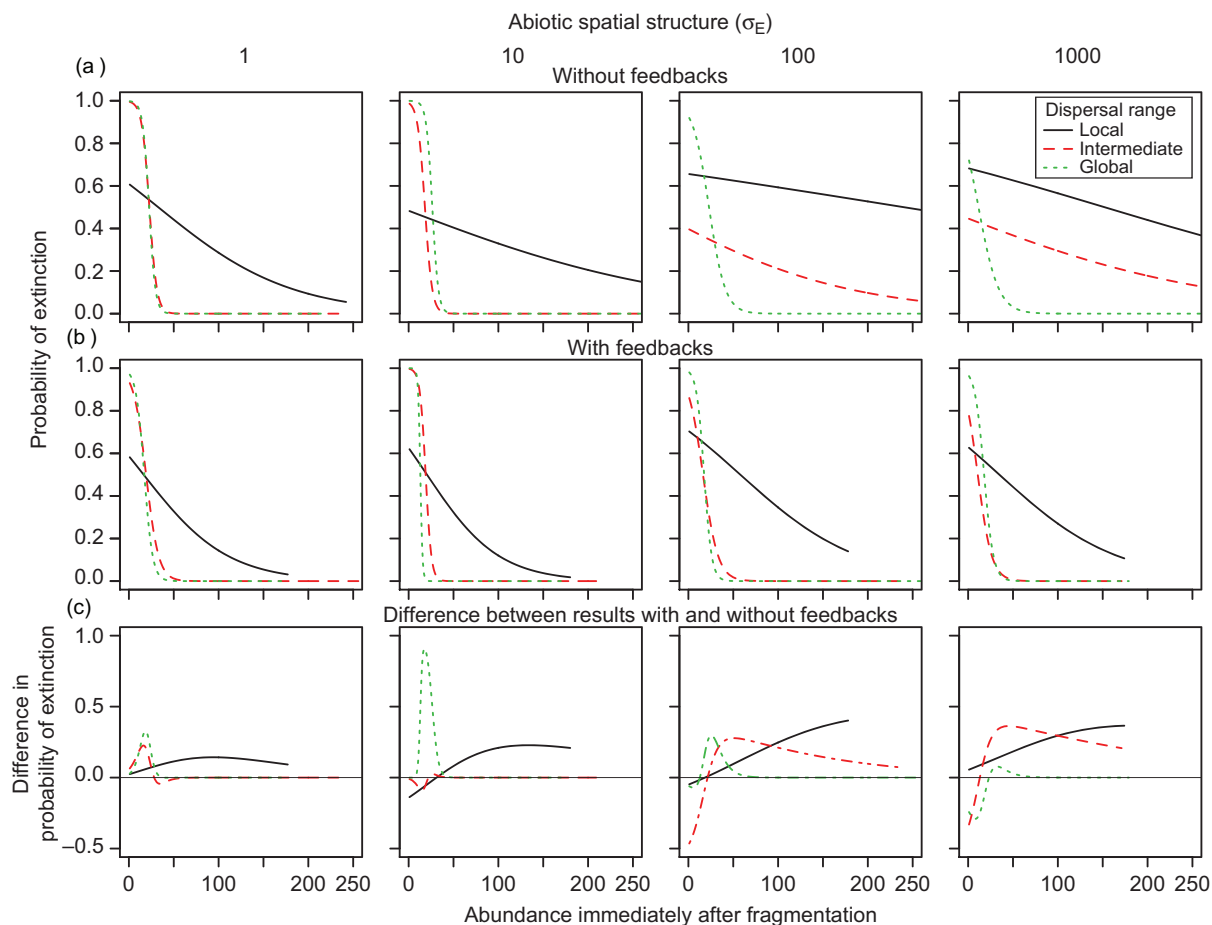


Figure 5. Probability of extinction as a function of abundance immediately after fragmentation. (a, b) Logistic fits of the probability of eventual extinction (checked 1000 time steps after fragmentation) as a function of species abundance immediately after fragmentation without feedbacks (a) and with feedbacks (b). (c) Feedbacks generally decrease the probability of extinction for a given abundance. Positive values indicate that incorporating feedbacks into the model reduced the probability of eventual extinction for a given abundance. Different line dashings and colors represent varying dispersal ranges ($\sigma_E = \{25, 100, 250\}$). Columns of panels show different values abiotic spatial structure ($\sigma_E = \{1, 10, 100, 1000\}$).

The influence of feedbacks reducing the probability of extinction was greater when intraspecific feedbacks were strictly negative (Supplementary material Appendix 1, Fig. A13). Across all treatments, the complex feedback regime resulted in a 9.3% decrease in the probability of extinction, compared to a 2.3% decrease with the mixed feedback regime.

Feedback values for surviving and extinct species

Across all parameter combinations, interspecific feedbacks became more positive for surviving species (mean change = 0.186, standard deviation = 0.003), while intraspecific feedbacks were not significantly different between surviving and extinct species (mean change = 0.004, standard deviation = 0.01) (Supplementary material Appendix 1, Fig. A10a–b). The mean value was always higher for surviving species than for extinct species (Kolmogorov–Smirnov tests, $p < 0.001$; Supplementary material Appendix 1, Fig. A10c–d). By contrast, for intraspecific feedback values, these tests did not yield significant results (Kolmogorov–

Smirnov tests, $p > 0.05$). Under the complex feedback regime, the species that remained at the time of habitat fragmentation had interspecific feedback (S_{ij} , $i \neq j$) values greater than 1, indicating that the species surviving prior to fragmentation were often mutually benefiting one another.

Effect of fragmentation per se vs effect of habitat loss

Overall, fragmented habitats lost slightly more species than non-fragmented landscapes, but feedbacks reduced the extent of diversity loss in both cases (Fig. 6a; also see Supplementary material Appendix 1, Fig. A14). In the absence of complex feedbacks, the difference in diversity loss between fragmented and non-fragmented landscapes was largest in simulations with local dispersal ($\sigma_D = 25$), and increased in more highly structured abiotic environments (mean = 2.56 species when $\sigma_E = 100$ and mean 3.84 species when $\sigma_E = 1000$) (Fig. 6b). For each scale of abiotic variation, as dispersal range was increased, the difference in diversity loss was reduced ($\sigma_D = 25$, mean difference = 2.07 species; $\sigma_D = 100$, mean

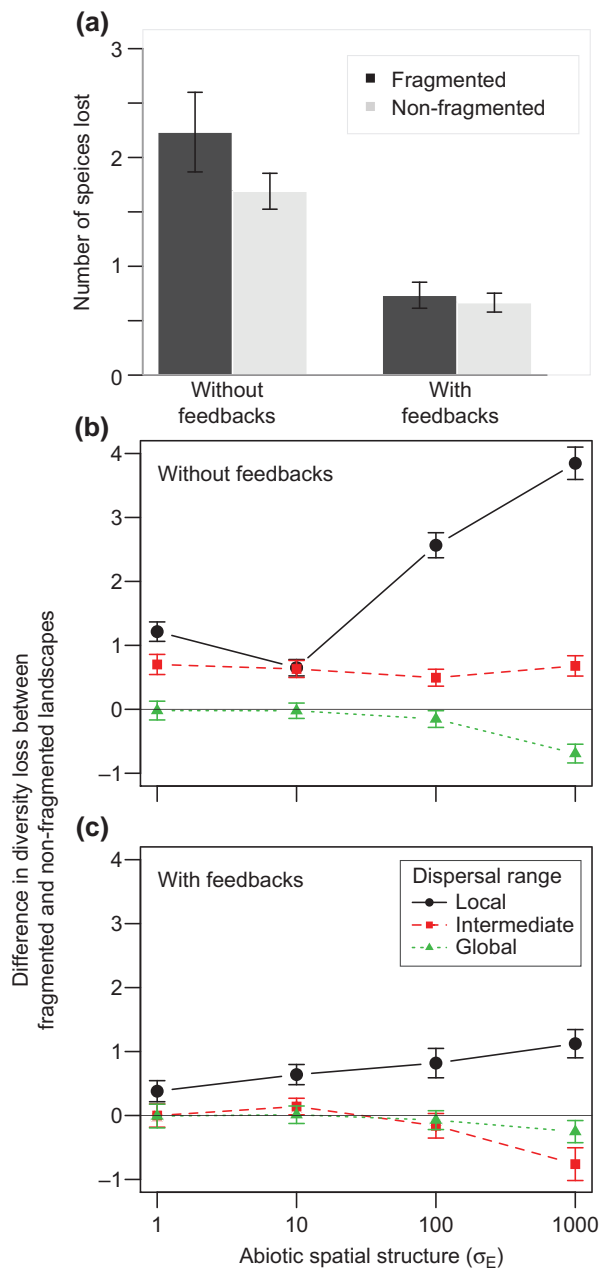


Figure 6. Difference in diversity loss between fragmented and non-fragmented landscapes. (a) Averaged across all treatment combinations, simulations on fragmented landscapes lost slightly more species than non-fragmented landscapes. Complex organism–environment feedbacks reduced diversity loss in both landscape types. (b, c) The difference in the number of species lost between fragmented and non-fragmented landscapes, without feedbacks (b) and with feedbacks (c). The difference depended on the range of dispersal and the scale of abiotic heterogeneity. Positive values indicate that the fragmented landscapes lost more species. All error bars represent standard errors.

difference = 0.62 species), and even reversed with global dispersal ($\sigma_D = 250$, mean difference = -0.22 species). With complex feedbacks, this change in sign occurred at the intermediate dispersal range ($\sigma_D = 100$) (Fig. 6c). These reversals imply that fragmented landscapes retained slightly more species than contiguous landscapes when species were dispersed globally.

Discussion

Taken together, our results indicate that complex feedbacks between organisms and their abiotic environment can buffer species against extinction following habitat loss and fragmentation (Fig. 4). Our results also suggest that the spatial scale of dispersal relative to the scale over which abiotic environmental conditions vary can affect the magnitude of this buffering effect, and that the buffering effect is particularly strong when dispersal occurs locally and abiotic environmental conditions vary over a large spatial scale. Qualitatively similar results were obtained across a range of parameter values, representing ecological neutrality or large competitive differences among species (Supplementary material Appendix 1, Fig. A2–A3, A4–A5; also see Supplementary material Appendix 2). The buffering effect was observed even when the loss of habitat was not in a fragmented pattern (i.e. the area of habitat loss was contiguous). However, our results also indicated that complex feedbacks allowed some additional species to persist that would be lost if the landscape was only fragmented, particularly when species could disperse only locally (Fig. 6b, c).

In the absence of complex feedbacks, our results are broadly consistent with the large body of previous research on the effects of dispersal, disturbance, and spatial environmental heterogeneity on community assembly (Drake et al. 1993, Mouquet and Loreau 2003, Jiang and Patel 2008, Fukami 2010, Gravel et al. 2010, Lasky and Keitt 2013). What is novel about this work is the focus on the role of organism–environment feedbacks in directly modifying spatial environmental heterogeneity and, in turn, indirectly altering niche differentiation and regional species coexistence. Some previous work on community assembly has considered biotically modified environmental heterogeneity (Mouquet and Loreau 2002, Shurin et al. 2004), but to our knowledge, our work is the first to consider it explicitly within the context of habitat loss and fragmentation, which led to the discovery of the buffering effect. Below, we first discuss likely mechanisms underlying the buffering effect and then identify limitations of this work to suggest future research directions.

Mechanisms of the buffering effect

Our analyses of the patterns of clustering of conspecific individuals and probabilities of eventual extinction after fragmentation suggest that the buffering effect operates via two mechanisms. First, complex feedbacks decreased the likelihood of immediate species extinction at the time of the fragmentation event by reducing the spatial clustering of conspecific individuals across the landscape, thus making species less prone to extinction when the landscape is fragmented (Fig. 3c). This effect was particularly strong when species dispersed locally because conspecifics then tended to be locally clustered unless there were complex feedbacks. Inclusion of complex feedbacks caused species to be distributed more evenly across the landscape even when dispersal was limited. Similarly, the buffering effect was particularly strong when local abiotic conditions varied over a large spatial scale. This is because species distributions closely

mirrored abiotic conditions across the landscape in the absence of complex feedbacks, resulting in immediate extinction of species whose local niche range was entirely removed when the landscape was fragmented.

The second mechanism underlying the buffering effect is that the complex feedbacks increase the probability of species persistence following fragmentation. Without complex feedbacks, species that survived the fragmentation event with relatively low abundances were at a high risk of eventual extinction (Fig. 5a), perhaps due to demographic stochasticity (Shaffer 1981, Lande et al. 2003). Complex feedbacks seem to have mitigated some of these instances of eventual extinction (Fig. 5b). The positive shift in interspecific feedback values and the lack of change in intraspecific feedback values in surviving species (Supplementary material Appendix 1, Fig. A10) underlies the negative density dependence mechanism of the buffering effect, reducing the extinction risk for small populations following fragmentation.

Limitations and future directions

Several limitations of our work point to future research directions. First, in our simulations, the feedback relationships among species (i.e. S_{ij} matrix) were invariant through time. In nature, these relationships between the species could change because of phenotypic plasticity or as an evolutionary response (Kruess and Tscharrntke 1994, Thrall et al. 2007, Schweitzer et al. 2014). How such changes may affect the extent of diversity loss by fragmentation remains unclear.

Second, habitat loss and fragmentation was instantaneous in our simulation. Although such instantaneous fragmentation is found in natural systems, for example in Hawaiian kīpuka formed by volcanic lava flows (Flaspohler et al. 2010), habitat loss and fragmentation is often a more gradual process (Skole and Tucker 1993, Ewers et al. 2013). Furthermore, the landscape matrix in our simulation suddenly became completely uninhabitable, which often does not apply in real landscapes (Cook et al. 2002, Debinski 2006). These factors should be considered in future research to understand how more realistic patterns of habitat loss and fragmentation may change our results.

Third, our model assumes that the abiotic environment is unchanging through time, an assumption we know to be violated in nature. Explicitly considering temporal variation in abiotic environmental conditions is a natural extension of our work. We expect that complex feedbacks will alter the way that communities respond to temporal environmental change. However, the precise responses are unclear as they may depend on both the feedback regime and the type of environmental change (e.g. stochastic, directional (Thompson et al. 2013)).

Finally and more generally, simple simulation models like ours are no more than heuristic tools to explore what might be plausible in real landscapes. For example, many real landscapes contain more individuals than we assumed, which may affect the importance of demographic stochasticity. It will be necessary to test the ideas developed here in models designed to simulate a specific fragmented landscape (Fagan 2002, Pütz et al. 2011) before we can fully assess the value of the ideas presented in this paper for understanding fragmentation-induced loss of diversity.

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Supplementary material (Appendix ECOG-01027 at <www.ecography.org/readers/appendix>). Appendix 1–2.