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# Sequences of patch disturbance in a spatial eco-evolutionary model

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*Keywords:* Eco-evolutionary model; Spatial model; Meta-community; Invasions

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## Abstract

An eco-evolutionary food web model assembles two heterogeneous meta-communities on a $6 \times 6$ spatial network, which are subjected to a series of patch disturbances that either kill or evict the local population. If patch destruction is permanent, displacement of affected populations is as severe as eliminating them. If re-colonisation of cleared patches is permitted, the meta-community can endure repeated displacement indefinitely but with limited biodiversity. Whether repeated elimination of local populations can be endured depends on the rules governing migration. In meta-communities composed of rare, low-range species, displacing the inhabitants of low-diversity individual patches can be more damaging to global biodiversity than eliminating them, demonstrating the destructive potential of small invasions and the need for careful efforts when relocating endangered populations.

## 1. Introduction

Anthropological causes of habitat destruction including deforestation, urbanisation and climate change are a widely-recognised modern concern for global biodiversity [1]. An increasingly powerful means of predicting the effects of such damage to an ecosystem is through mathematical and computational models of abstract ecological communities on spatial networks. Using model meta-communities as the basis for dynamic perturbation and conservation experiments, researchers may try to determine principles such as the properties of the most vulnerable species or the most important habitats to protect, guiding the steps that could be taken to mitigate the danger posed by habitat destruction.

These investigations are a natural extension to a spatial dimension of theoretical ecology's large body of research on the stability of model food webs. Food web stability has many interpretations, including species deletion stability (the fraction of species who can be individually deleted without incurring further losses to the ecosystem), community robustness (the fraction of species who must be manually deleted in order to cause a loss of at least 50% of diversity), and persistence in the sense of asking which species can survive until the end of the experiment, with Pascual and Dunne's chapter providing a helpful overview of this topic [2]. Tests of stability typically concern the response of a single closed community to a perturbation in the form of species loss [3, 4] due to external effects provoking an unexpected extinction, or of an invasion by non-native species [5]. Scaling a food web model up to a meta-community model, in a similar manner we may simulate the effects of habitat destruction in a spatial network composed not just of many species, but also of many patches. Instead of asking which species are the most important to maintain the food web, we can ask which patches are the most devastating when destroyed. Whilst food web stability has been a topic of interest in theoretical ecology since May's work in the 1970's [6, 7], studying the meta-stability of meta-communities has the potential to yield results that can be more easily translated into actionable and urgent environmental-protection policy. For example, there are theoretical applications of spatial models to the optimal size and geographic placement of nature reserves [8, 9]. For an overview of the discussions surrounding the stability-complexity relationship, with a particular focus on conservation, see the review by McCann [10].

Emerging studies of meta-community theory [11, 12, 13] look set to make a particular contribution to the stability-complexity problem, with multiple studies employing different meta-population models and definitions of stability finding that spatial effects either increase stability of the meta-community or result in a positive stability-complexity relationship within the individual food webs [14, 15, 16, 17, 18, 19]. However, the greatest benefits are consistently observed when there is in some sense an intermediate strength of coupling between patches [20, 11, 21, 17], as if the coupling is too strong the meta-community model effectively reduces to a single large, well-mixed habitat and the benefits of spatial segregation (such as refuges for prey, or geographic separation between competitors allowing the emergence

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of new ecological niches) become lost. Other principles that have been elucidated include the benefits of omnivory [11, 22, 23] and generalist predators [24] for meta-foodweb stability. Many of these studies do not explicitly simulate the impact of habitat destruction, but by considering the aspects important for stability of the meta-communities they can make inferences on the outcome of the diversity reduction, displacement of species, habitat fragmentation, and loss of spatial complexity that would result.

Previous studies have modelled the impact of either patch removal or patch fragmentation (separating previously connected local habitats) in spatially-explicit ecological models [25], considering two competing species [26, 27], species with differing degrees of specialisation [28], a single predator and a prey species [29], or a three-species web [22]. Other approaches do not use explicit population dynamics [30]. Empirical studies, for example of populations in harvested woodlands [31] or reclaimed estuaries [32], provide a useful comparison, and can test some of the recommendations for conserving species in managed habitats. However, most of the existing work explicitly concerning habitat destruction in meta-community models only use small food webs in each patch, or simpler dynamics, or do not take into account the role of significant processes that shape food web structure. Recently, Ryser et al [33] employed a model with sophisticated allometric population dynamics to study the role of patch connectivity and the results of fragmentation in a meta-community, although the large food webs (of 40 species) were generated using a statistical rather than an evolutionary process. Moreover, the complex interactions of meta-community features and their combined implications for ecosystem functioning and stability has led to a recognition of the need for models that account for some or all of them simultaneously in sufficiently-large food webs [34, 35, 11, 36, 22, 23].

An alternative approach to applying meta-community models to habitat destruction arises out of recent work on eco-evolutionary food web models. These models emphasise large-scale community ecosystems that incorporate both predator-prey and competitive population dynamics and the possibility of speciation through small mutations and evolutionary pressures. In such models the food web structure, and the traits of those species who persist, emerge dynamically as a result of the ecological and evolutionary mechanisms driving the model rather than being specified beforehand. By simulating these processes of food web construction and maintenance, they can assemble realistic model communities that respond sensibly to perturbation. A useful summary of the research in this field until 2012, including earlier model design philosophies, can be found in the review by Brännström et al [37]. Some eco-evolutionary models have begun to be extended to incorporate spatial effects [18, 38], but so far these efforts have been primarily concerned with the initial dispersal of species across the meta-network and not with subsequent response of the established meta-community to perturbations such as habitat fragmentation.

In their recent review of meta-community modelling approaches, Gross et al [39] highlight the role that dispersal rates (which may be influenced by allometry) play in meta-community dynamics, and the potential for interaction between evolutionary processes, dispersal, spatial topology [18] and adaptive dynamics in ultimately shaping the features of meta-communities. As network structure plays an important role in influencing population dynamics [40] (and spatial effects also influence population dynamics directly [41]), to simulate the response of complex meta-communities to global challenges such as climate change or deforestation there is a need for further development of models that generate spatial meta-community structures shaped by the interplay of adaptive evolutionary and ecological processes, including predation, competition, allometrically-scaled dispersal and mortality. The goal of the present work is therefore to contribute to efforts to bridge the gap between eco-evolutionary models and the large-scale spatial meta-community models that have been applied to habitat destruction but usually have simpler ecological dynamics and no evolutionary component. We study the impact of patch disturbance in a pair of model meta-communities consisting of several hundred species assembled from first species by an allometric eco-evolutionary model. The patches each possess unique environmental conditions, and distinct local arrangements of species emerge due to the combination of ecological, evolutionary and migration rules. When the meta-community is subjected to habitat disruption, the ecological mechanisms of the model will determine the impact of the patch loss on the remaining local populations.

## 2. Allometric spatial eco-evolutionary model

Webworld is an eco-evolutionary food web model, with the standard implementation laid down by Drossel et al in 2001 [42] following the original 1998 design [43]. Species are assigned ten discrete traits (from a set of 500) that dynamically determine the existence, strength and direction of predator-prey relationships between species and the presence of interspecific competition. The population dynamics equations are iterated, and new mutant species are periodically introduced who inherit nine of the traits of their parent species. We have studied this version further [44], and extended it to a spatially-explicit variant [45] where feeding and reproduction takes place amongst local populations in patches arranged on a two-dimensional network. Different rules can be utilised to govern the movement of populations between adjacent patches on the spatial network. Recently, we implemented allometric scaling [46], inspired by Brännström et al's version [47] of the alternative Loeuille-Loreau eco-evolutionary model [48]. This modification assigns an additional continuous bodysize trait to each species, so that they loosely prefer to feed on other species within a suitable window of smaller bodysizes. This results in the emergence of a more structured community with increased feeding links and proportions of basal species, it reduces the prevalence of omnivory to permit the existence of top predators, and it has been demonstrated to increase stability in the form of community robustness. The version of the model implemented in this work is comprehensively described in that article along with a schematic of the three nested loops, but we outline the key processes and the rules governing population movement below.

### 2.1. Description of the model

A single simulation consists of three nested stages: the evolutionary, ecological, and foraging loops.

### 2.1.1. Evolutionary timestep

At the outermost layer is the evolutionary loop. At each timestep in this loop, one parent species is selected and a child species is introduced in one the patches where the parent is present. The child retains nine of its parents' ten traits, with the other being replaced at random by a trait that it does not already possess, and its bodysize is drawn from a uniform distribution in the window $[0.8s, 1.2s]$ where $s$ is the bodysize of the parent.

### 2.1.2. Ecological timestep

Between each evolutionary event, the following ecological timestep is iterated until either 100,000 iterations expire or an equilibrium for all local populations is roughly achieved.

At the $t^{th}$ ecological timestep, local populations $N_i$ of species $i$ in each patch are iterated once with terms accounting for natural mortality, gains due to feeding and reproduction, and losses to predation by other species in the same patch. This is given by the following formula, derived from a balance ODE using the Euler method with step size $\Delta = 0.1$:

$$N^t_{i,x,y} \mapsto N^t_{i,x,y} + \Delta\Bigg( - d_0 \exp\big( - qr_i\big) N^t_{i,x,y} + \lambda s_i^{-1} N^t_{i,x,y} \sum_{j=0}^{n} g_{i,j} s_j - \sum_{k=1}^{n} N^t_{k,x,y} g_{k,i} \Bigg) \tag{1}$$

where the first term within the bracket determines loss due to natural mortality, and $r_i = \ln(s_i)$ converts bodysize to a logarithmic scale. We set $q = 0.25$ following [47] and [49] to implement allometric scaling of mortality rates, and choose $d_0 = 2$ to place the mortality rate of the initial species on the same order as in the earlier non-allometric versions of the model.

The second term calculates the the population gains for species $i$ through predation. The functional response $g_{i,j}$ is the number of prey of species $j$ that are killed by member of species $i$. This is scaled by the body-size $s_j$ of the prey and summed over all prey species, to obtain the total biomass gained per member of $i$. This is then multiplied by the population of $N_i$ to obtain the overall biomass consumed by the local population of species $i$. Next, the ecological efficiency $0 < \lambda < 1$ controls the efficiency of energy transfer between the trophic levels. It is set at 0.3 as in previous investigations with this model variant [46], but a higher or lower value would result in longer or shorter food chains and thus higher or lower maximum trophic levels, respectively. Finally, the available new biomass is divided by body-size $s_i$ to yield the number of new members of the population of species $i$ that result.

The third term describes the overall loss of members of the population $N_i$ due to predation by other species.

Following this iteration for all species in all patches, movement of individuals between vertically or horizontally adjacent patches may occur (diagonally-adjacent patches are not considered to be connected), and the local population of species $i$ in patch $(x, y)$ is updated according to:

$$N^t_{i,x,y} \mapsto N^t_{i,x,y} + \sum_{j=1}^{x_{max}} \sum_{k=1}^{y_{max}} \delta_{j,k,x,y} \mu_{i,j,k,x,y} N^t_{i,j,k} - \sum_{j=1}^{x_{max}} \sum_{k=1}^{y_{max}} \delta_{x,y,j,k} \mu_{i,x,y,j,k} N^t_{i,x,y} \tag{2}$$

where $\delta_{j,k,x,y} = 1$ if the patches $(j, k)$ and $(x, y)$ are connected and distinct, and zero otherwise. $\mu_{i,j,k,x,y}$ denotes the fraction of the local population of species $i$ in $(j, k)$ that migrates to $(x, y)$ if possible during this ecological time step, with a minimum of one whole individual being required for movement to occur (if $\mu_{i,j,k,x,y} N^t_{i,j,k} < 1$ then it is set to zero). There are two possible rulesets that we implement in the investigations presented here, described below.

### *2.1.3. Foraging timestep*

Between each ecological timestep, the foraging routine is iterated. This allows local populations to update their feeding efforts in response to the current conditions and the success of their previous strategy, and in turn their ratio-dependent functional responses $g_{i,j}$ for each prey species $j$ are updated based on the division of their feeding efforts and the traits possessed by each species. A full description of this mechanism is provided in [46].

### *2.1.4. Movement rules*

The choice of movement mechanism is likely to have a very strong influence on the composition of the final trophic meta-communities [39], and hence on the impact of habitat destruction. For example, if there is a high rate of constant diffusion of all populations between adjacent patches there may be very little impact of temporary habitat destruction as the co-evolved food webs will be highly synchronised across the patches and most eliminated populations can thus be immediately replenished [45]. From a practical perspective, constant diffusion of all species on a $6 \times 6$ grid slows the simulation so that an excessive runtime is required for a sufficient number of evolutionary timesteps. We have therefore selected two rulesets for migration that should both be computationally-feasible and give rise to spatially-heterogeneous distributions of species, constructing distinct local food webs even when they co-evolve from the beginning of the simulation. In both cases, movement rates are allometrically scaled so that larger species have increased mobility [49, 50].

The first is a version of diffusion with constant potential for dispersal, but with requirements for certain traits gating movement through each link between adjacent patches in the spatial meta-network. At the beginning of the simulation, a set of 100 (out of 500 possible) traits are randomly selected for each link between vertically or horizontally-adjacent patches, and a species that lacks all of these in its 10 traits will never be able to traverse the link between these two patches. The movement function of species $i$ from patch $(j, k)$ to $(x, y)$ is then given by:

$$\mu_{i,j,k,x,y} = \max\left\{1,\ \frac{\mu_0 s_i}{s_0} \times \frac{M_{j,k,x,y}(i)}{10}\right\} \times D^{-1}_{(j,k)} \tag{3}$$

Here, $s_0 = 1$ denotes the bodysize of the resources, the migration constant is taken as $\mu_0 = 0.001$, and degree $D_{(j,k)}$ is the number of other patches that $(j, k)$ is connected to, so that central patches in the grid do not experience greater emigration by default. The function $M_{j,k,x,y}(i) \in \{0, 1, \dots, 10\}$ returns the number of the traits of species $i$ that are associated with the link between patches $(x, y)$ and $(j, k)$ and so scale the total migration by how well-adapted the species is to traverse this particular link.

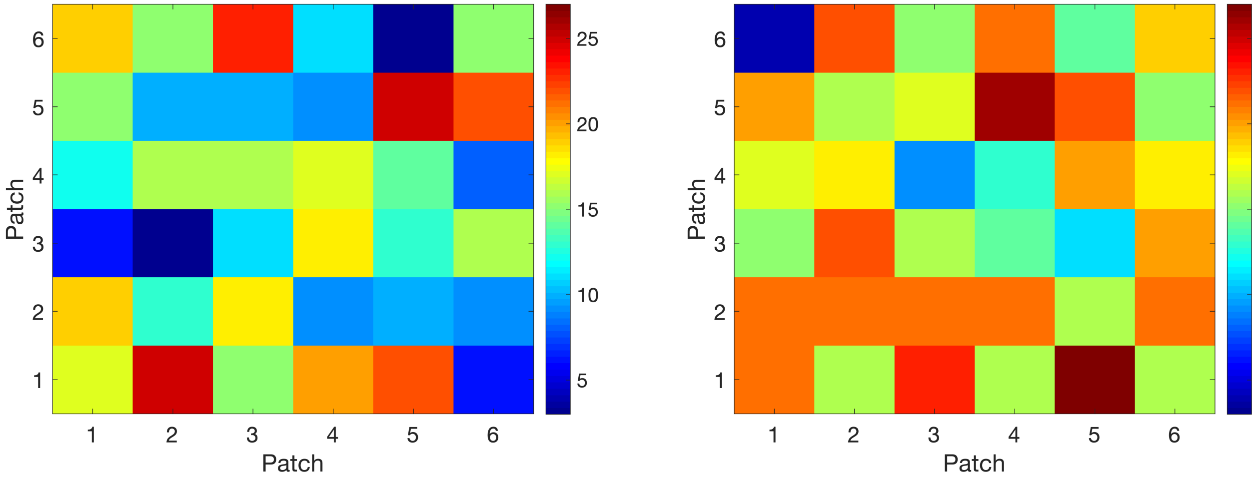
The second scheme is a form of adaptive migration, given by:

$$\mu_{i,j,k,x,y} = \begin{cases} \max\left\{1,\ \frac{\mu_1 s_i}{s_0} \times \frac{N^{t-1}_{i,j,k} - N^t_{i,j,k}}{N^{t-1}_{i,j,k}}\right\} \times D^{-1}_{(j,k)}, & \text{if } N^{t-1}_{i,j,k} > N^t_{i,j,k} \\ 0 & \text{otherwise.} \end{cases} \tag{4}$$

Here, $N^t_{i,j,k}$ denotes the population of species $i$ in cell $(j, k)$ during the $t^{th}$ ecological timestep, and the migration constant is increased to $\mu_1 = 0.03$ in order to induce a suitable amount of dispersal on the occasions that the population does travel. Under this mechanism, any species may travel between any pair of adjacent patches, but they will only elect to do so when their population experiences decline in the current local conditions. The amount of the remaining population that emigrates is proportional to the severity of the decrease since the previous ecological timestep. This scheme is an allometrically-scaled version of the adaptive migration used in our previous spatial extension of Webworld [45, 46] where it was demonstrated to construct meta-communities of highly-diverse and distinct food webs. More generally, adaptive migration has been shown to improve species persistence in other work, including recent non-evolutionary models [51].

## 3. Base datasets

The basis for our patch disturbance experiments are two meta-communities assembled on a 6 × 6 spatial grid. Each simulation begins with 36 static resources (one located in each patch, so that the environments are spatially-heterogeneous) and a single non-resource species with bodysize $e$ and its traits selected so that it can successfully feed on the resource in patch $(1, 1)$ where it starts with an initial population of 1. After 10,000 evolutionary timesteps, the meta-communities constructed using the diffusion and adaptive movement rulesets contain 494 and 577 unique species (458 and 541 non-resource species) respectively. The local diversity of these arrangements are shown in Figure 1, while the full set of local food webs in the two meta-communities are illustrated in Figure 2. In the case of trait-gated diffusive movement, the final non-resource species have the capability of traversing 80.0% - 98.3% of links to some extent (some routes potentially much more so than others), with a mean of 89.8%.



(a) Diffusive migration

(b) Adaptive migration

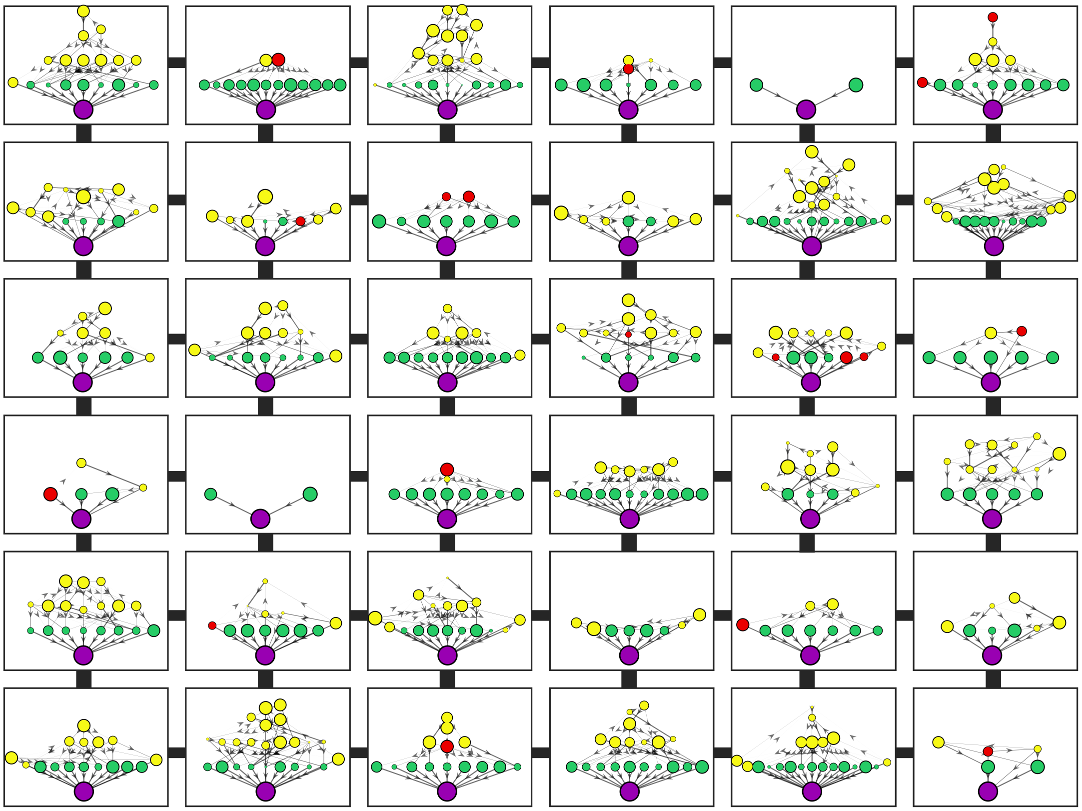
Figure 1: Initial local biodiversity after 10,000 evolutionary timesteps.

Properties of the two evolved meta-communities are given in Table 1. Global diversity refers to the total number of unique species present in the ecosystem, the link density of each local food web is the ratio of the number of feeding relationships to the number of species, while connectance is the fraction of all possibly feeding links that are realised. The shortest-chain trophic level (SCTL) of a species is the length of its shortest path to the resource. Range describes the number of patches where the species has a local population, and evolutionary lifespan is the number of evolutionary timesteps from the creation of a species to its extinction or the end of the simulation.

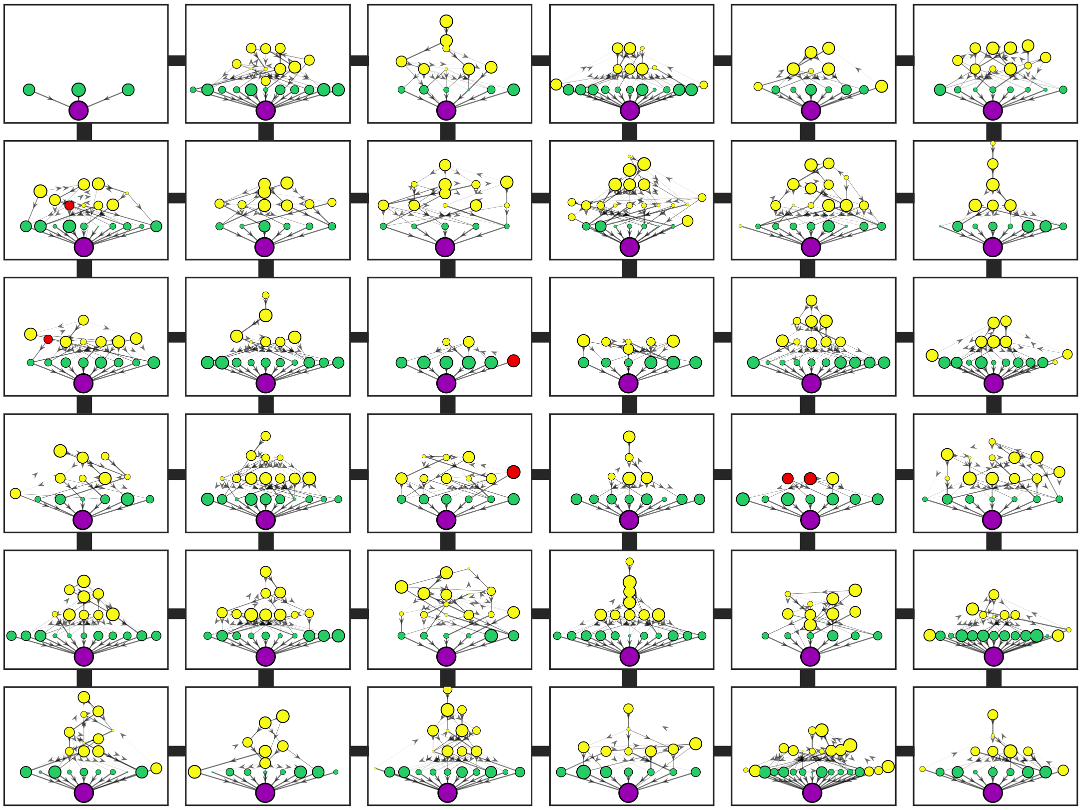
| **Property** | **Diffusive** | **Adaptive** |
|---|---|---|
| Global diversity | 494 | 577 |
| Mean link density of local food webs | 2.021 | 2.101 |
| Mean connectance of local food webs | 0.357 | 0.262 |
| Mean mean SCTL of local food webs | 1.310 | 1.577 |
| Mean maximum SCTL of local food webs | 2.278 | 3.111 |
| Mean bodysize of species | 3.534 | 3.733 |
| Mean range of species | 1.125 | 1.309 |
| Mean evolutionary lifespan of all species | 660.7 | 920.8 |

Table 1: Properties of the meta-communities after 10,000 evolutionary timesteps.

Adaptive migration of this form has allowed faster growth in biodiversity and species that can persist for nearly 50% more evolutionary timesteps, and helps to form significantly more complex food webs with higher trophic levels, whilst permitting slightly greater overlap of species between different patches. However, in both scenarios the rules for population dispersal has resulted in a meta-community of local food webs that are very distinct, consisting of highly-specialised species that are adapted to the specific local ecosystem, and few species occupying more than one patch. This feature may not be a realistic abstraction of most real spatially-structured ecosystems, although it possibly could represent the competitive and trophic interactions between unique, sedentary endangered species on an archipelago of loosely connected islands with strongly divergent local environmental conditions. Nonetheless, it is important to experiment with all types of systems to facilitate future comparisons between models, and it will be interesting to see what impact this choice about species behaviour has had on the overall response of the evolved meta-community to various forms of perturbation. For example, as a consequence of the frequency of unique species in each patch we might expect to see a significant impact on global biodiversity from deleting the inhabitants of even a single local habitat.



(a) Diffusive migration



(b) Adaptive migration

Figure 2: Initial meta-communities after 10,000 evolutionary timesteps. Purple denotes the resource, green a basal species (feeds only upon the resource), red a top predator, and yellow otherwise. Line thickness is proportional to feeding effort, with arrows from predator to prey, and vertical height corresponds to trophic level. Node radius is proportional to population size on a log scale.

## 4. Patch disturbance events

With no further mutation events, both meta-communities are subjected to experiments to test the impact of several different varieties of habitat destruction events, both individual and sequential. In each case patches are selected from the 36, and the local populations of all non-resource species present in the patch will be affected in one of two ways: either they will all be immediately killed ("elimination") or they will be evenly dispersed amongst all connected neighbouring patches ("displacement"). In the latter case, when utilising a trait-gated diffusive model of migration, this dispersal is not prevented or scaled by the traits associated with the patch links, thus representing a potentially abnormal displacement of species such as deliberate relocation by human conservation efforts or a pathway (such as a road in previously dense swampland) that is created by the destructive activity itself. Regardless of movement scheme, if there are no adjacent patches available to migrate to (that have not been permanently destroyed), then the populations will simply perish.

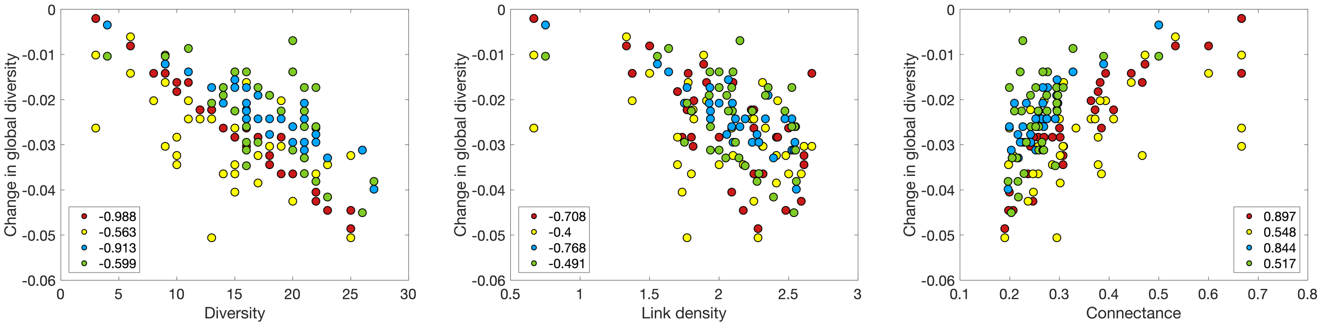
Section 5 will contrast the outcome of individually selecting each patch in the two meta-communities for both elimination and displacement-style perturbations. Then in Section 6 we will consider sequences of the same type of habitat destruction events. This requires two additional choices. First, whether the destruction event is "permanent", meaning that once chosen, the patch is removed from the meta-community so that it may not be chosen again for perturbation and other patches are no longer considered to be adjacent to it. Henceforth during that particular experiment, no populations will be able to re-enter that patch. Alternatively, the event may be "temporary", and local populations in neighbouring patches will immediately have the ability to move into and re-colonise it as usual. The second additional decision is how the sequence of patches to be deleted should be chosen. We shall compare the selection of ten random sequences with a dynamic targeted sequence where the patch that currently possesses the highest local diversity is selected for the next habitat destruction event. A summary of these options is shown in Table 2.

| **Effect on population** | **Nature of event** | **Sequence** |
|---|---|---|
| Elimination | Permanent | Random |
| Displacement | Temporary | Targeted |

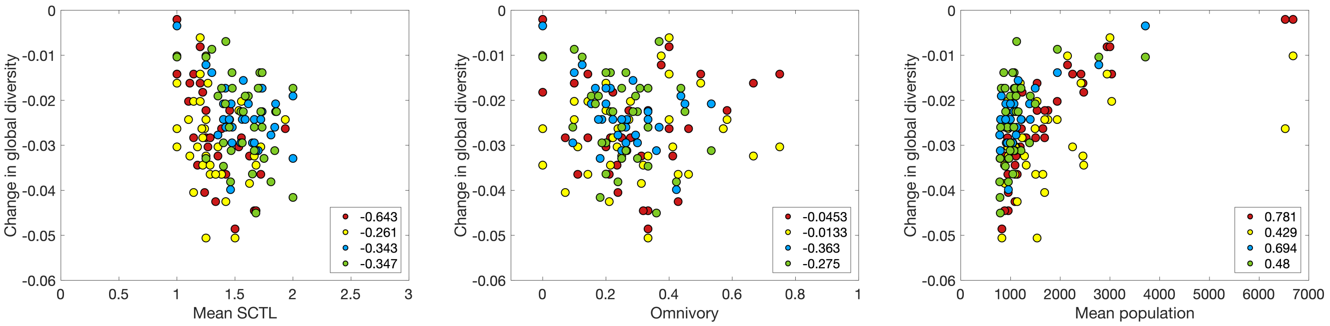
Table 2: Variants of the habitat destruction event

## 5. Correlation between patch properties and diversity loss

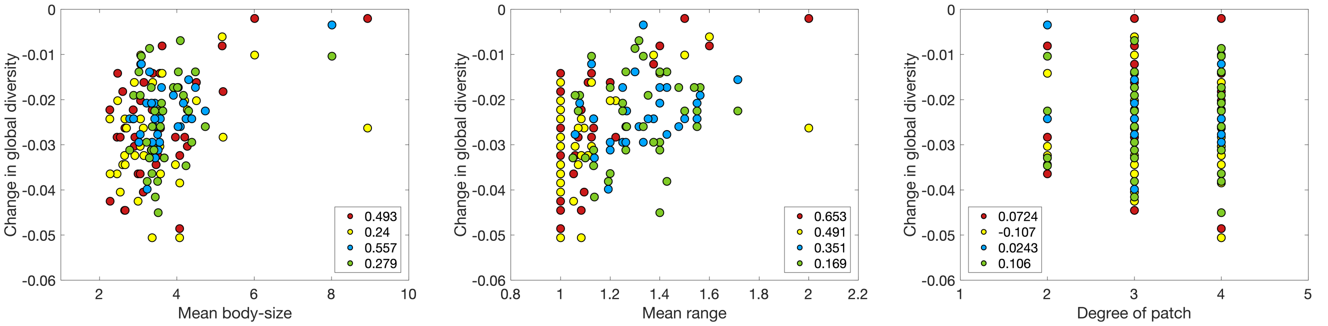
To begin, we examined the impact of removing each patch in isolation. For each of the 36 patches, we deleted it and iterated the ecological loop once, allowing the remaining populations an opportunity to re-colonise the perturbed patch, and replenishing the local resource. The resulting change in global diversity was recorded as a fraction of the initial global diversity (Figure 3). The whole system was then restored before deleting the subsequent patch. In each case, we calculate the correlation coefficient of the effect on diversity with several standard properties of the removed patch prior to its deletion (e.g. diversity, feeding link density, fraction of omnivorous species). These results are determined separately according to the meta-community and the type of habitat destruction event - whether the local populations in the removed patch were eliminated or displaced to surrounding habitats.



(a) Diversity (b) Link density (c) Connectance



(d) Mean SCTL (e) Omnivory (f) Mean population



(g) Mean bodysize (h) Mean range (i) Patch degree

Figure 3: Correlation coefficients of prior local properties and resulting fractional global extinctions. Legend:
Red = diffusive movement and elimination;
Yellow = diffusive movement and displacement;
Blue = adaptive movement and elimination;
Green = adaptive movement and displacement;

In the case of elimination, there is unsurprisingly a strong negative correlation between the diversity of the deleted patch and the resulting change in global diversity (Figure 3(a), red and blue) regardless of movement scheme. This should be expected, as both versions of the model construct networks where on average species reside in only 1-2 patches (Table 1, range). As adaptive migration results in slightly greater average range, high-diversity patches are more likely to include some species that persist in other regions and thus the loss of a local population may not be so devastating.

If local populations are merely displaced, there are still always negative consequences for the biodiversity of the meta-community, but the magnitude of the effects are not as clearly correlated with the local diversity of the removed patch (Figure 3(a), yellow and green). Under adaptive migration, for many patches displacement results in less damage than elimination. However, displacing small amounts of species in the diffusive migration model can actually cause much *greater* relative damage to the global ecosystem than eliminating them (Figure 3(a), yellow - consider how far below the diagonal these points lie) although this is never more than 6% of the pre-existing total global biodiversity. If we measure this strength of change in global biodiversity relative to the size of the community in the perturbed patch, this effect is more clearly revealed. Here, the pattern for diffusive migration with displacement (Figure 4, yellow) is strongly impacted by a single patch (6,5) on the edge of the spatial network. This patch (see the top-right of Figure 1(a) and Figure 2(a)) hosted only two non-resource species, but their eviction to the three neighbouring patches (including patch (5,5) which is home to 24 species) resulted in thirteen extinctions. On the other hand, outright killing these two local populations results in only a single permanent extinction as both species were also present in precisely one other patch. However, when the inhabitants of (5,5) are killed, all 24 species are removed as they all only existed in this patch, but displacing them into the four neighbouring patches only results in one additional extinction. Thus, the reversed direction of the correlation between the number of evictions and the relative change in the global community (Figure 4, correlation coefficients in the insert) can be explained: displacing smaller groups into the often larger, stable neighbouring arrangements of species causes disproportionate levels of disruption and extinctions, and conversely if very large co-adapted ecosystems are forcibly displaced, they typically invade smaller communities and thus cannot cause as much damage relative to the number of species displaced. In this way, these simulations have organically demonstrated the destructive potential of introducing just one or two invasive species into a large, naturally-isolated ecosystem - even if it was conducted or permitted for the purposes of environmental conservation. In this case, the utilitarian approach might have been to allow (or even to ensure) the population of patch (6,5) to be eliminated, unless it were possible to transport them to more suitable distant habitats.

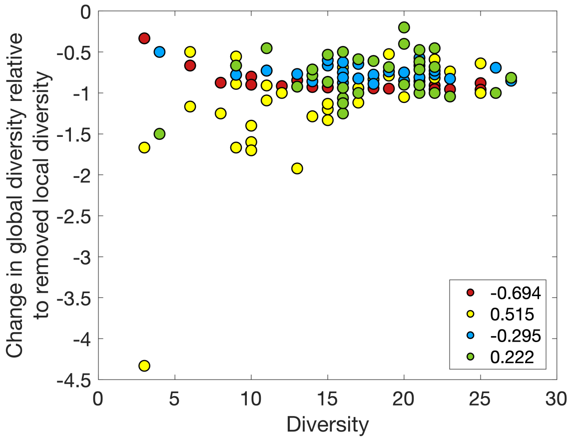


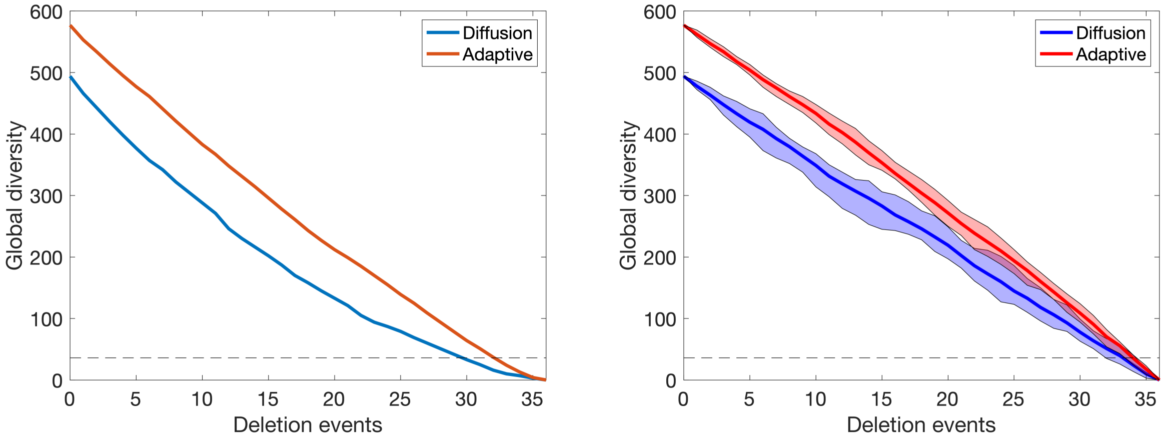
Figure 4: Correlation coefficients of local diversity and resulting fractional global extinctions relative to prior local diversity. Legend as for Figure 3.

Patterns of link density and connectance of the local food webs, and the average population and bodysize can be related back to their diversity, as we have previously shown that larger food webs have lower connectance in the Webworld model [44], with lower mean population and higher mean bodysize, so it follows that these are also correlated with greater losses of diversity. The degree of the patch has no obvious effect, and we recall from Figure 1 that we saw no indication of either central or edge patches having notably greater biodiversity under either scheme (although constant migration without barriers can increase the diversity of central patches that have greater inflow of satellite populations [45]). Although the mean trophic level gives some moderate correlations (Figure 3(d)), we see that the range of mean SCTL is very restricted, with the only useful conclusion being that adaptive migration has helped the model to construct more complex food webs with increased average trophic levels as well as greater overall diversity.

Finally, the average range of the local species (that is, the number of patches that they occupy) has some relationship with the severity of diversity loss (Figure 3(h)). In the case of elimination, the correlation is stronger due to the intuitive reasoning that if more of the species in a patch also reside in other habitats then fewer extinctions will result from the demise of the local populations of the current patch, and therefore a stronger relationship emerges by determining the correlation coefficients between the mean range of species in the patch and the ratio of the resulting change in global biodiversity relative to the local diversity of the removed patch (0.919, -0.553, 0.799 and 0.177 for diffusion-elimination, diffusion-displacement, adaptive-elimination and adaptive-displacement respectively). As with some of the other properties, the sign of the correlation is reversed when considering displacement, but only for diffusive migration and this is again partly attributable to the influence of the two species in patch (6,5) discussed above.

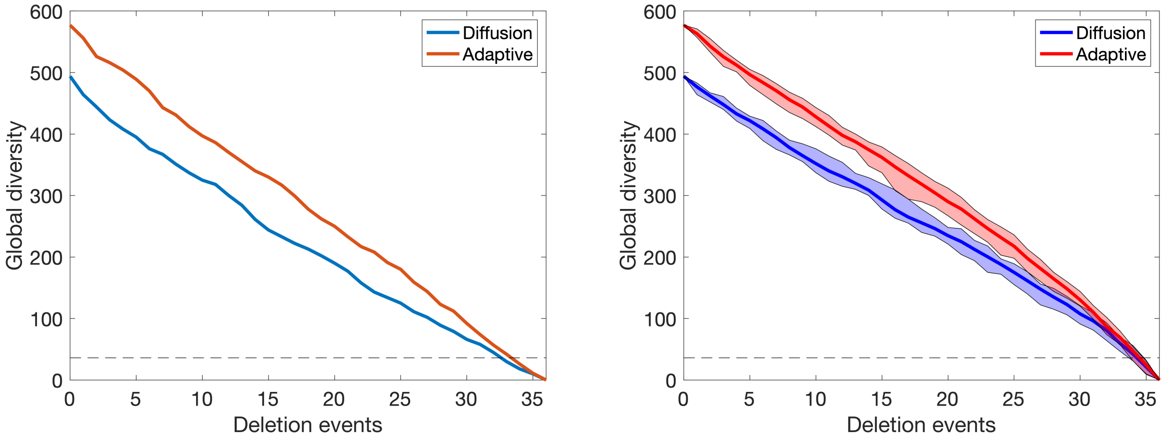
## 6. Patch disruption sequences

Next, we subjected each meta-community to sequences of repeated local habitat disruption events, with the variants summarised in Table 2. In particular, we performed sequences of 36 permanent destruction events, after which the meta-community is necessarily completely destroyed, and 1000 temporary events where re-colonisation is permitted so none of the patches are altogether removed from the spatial network. Both cases were tested using the elimination and displacement options, and for each we further compared targeting the highest-diversity patches with ten random patch deletion sequences. The impact on global diversity during these sequences for permanent and temporary removal is shown in Figure 5 and Figure 6 respectively, with the latter zoomed to the first 300 events. In the cases of randomly-ordered patch removal (Figure 5(b) and (d), Figure 6(b) and (d)), for each migration scenario the mean global diversity after that number of deletion events across all ten sequences is denoted by the central line, with the enveloping shaded area indicating the range between maximum and minimum global diversity achieved by any of the ten random sequences following that number of deletion events.



(a) Targeted-Elimination

(b) Random-Elimination

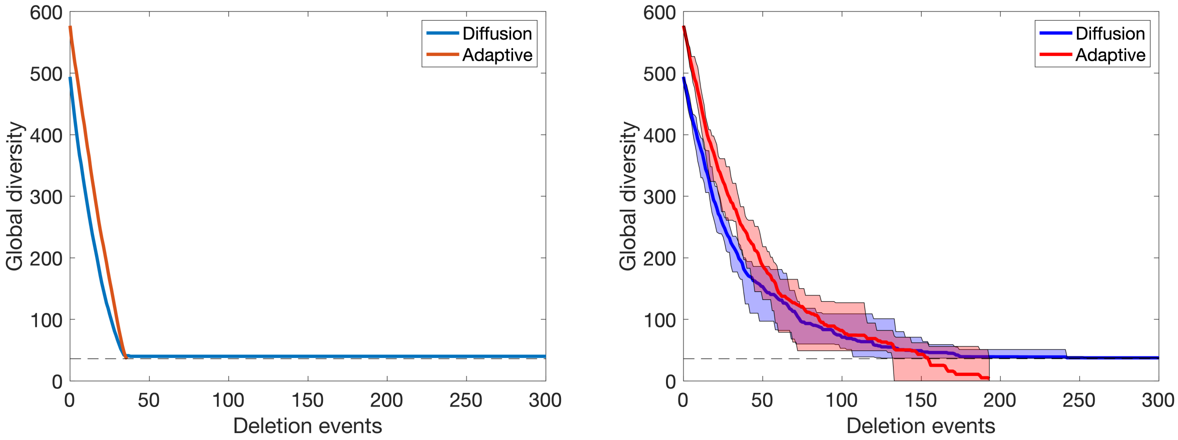


(c) Targeted-Displacement

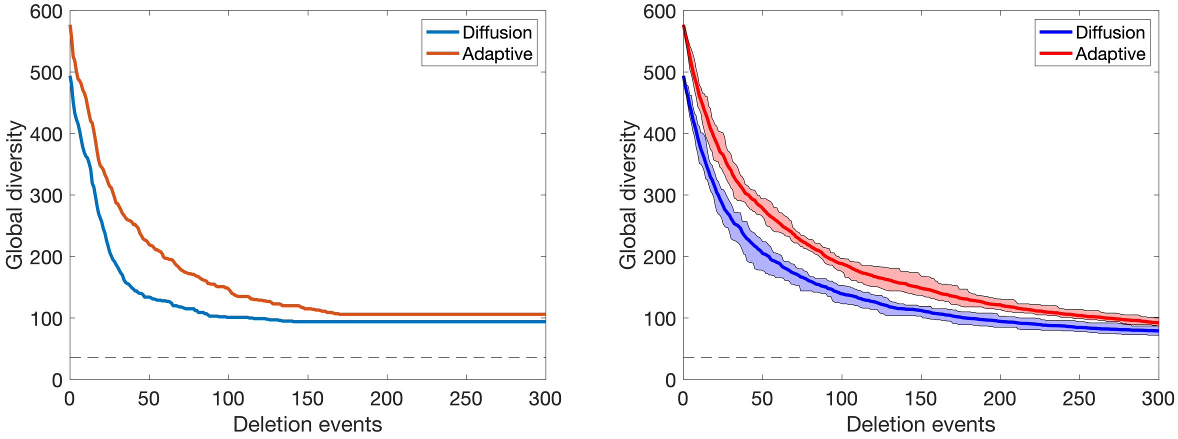
(d) Random-Displacement

Figure 5: Global diversity during sequential permanent patch removal in the two meta-communities.

Considering first the permanent deletion sequences, from the similarity of Figure 5(a) and 5(c), and also of Figure 5(b) to 5(d), sequential displacement of affected populations is as severe as eliminating them outright, so efforts to relocate evicted individuals amongst the closet habitats is of little benefit to conserving global biodiversity. The order of choosing habitats has very weak impact in this case, except that targeting the patch removal to start with the highest current diversity results in a more concave curve, particularly in the elimination case (Figure 5(a)), as the greatest losses are more keenly felt at the beginning of the sequence. This indifference is again due to the choice of migration rules that create a weak coupling between patches. As a result, all ten random deletion sequences for each variant demonstrated qualitatively similar behaviour.



(a) Targeted-Elimination (b) Random-Elimination



(c) Targeted-Displacement (d) Random-Displacement

Figure 6: Global diversity during sequential temporary patch removal in the two meta-communities.

Permitting re-colonisation, some distinctions between the migration models emerge. In the case of adaptive migration, eliminating local populations still leads to eventual collapse after 130-190 randomly-chosen patch destruction events (Figure 6(b)), by which time all 36 patches have likely been selected at least once. If the destruction events are targeted by diversity, this results in total annihilation after 36 events (Figure 6(a)). This is due to the adaptive migration rules giving rise to a isolated food webs in each of the remaining patches (as once local equilibrium has been reached, populations only leave when locally perturbed - usually by an invasive mutant). Therefore, local populations do not attempt to take advantage of the vacancies when neighbouring populations are eliminated, and simply await their own destruction. Sequences of displacement can be endured indefinitely, but global diversity is extremely limited (from 577 to fewer than 80 for random sequences (Figure 6(d))) as all species are forced to mix and as basal species that are well-adapted to feeding on the resource in the only patch they occupy are displaced. Due to the large number of patches and unique resources, many species in the meta-community feed primarily on the resource of their patch, so this effect will be significant. If the sequences are in order of decreasing diversity, eventually the system reaches an equilibrium where the algorithm alternates between a square of four neighbouring patches (with an irregular pattern that does not repeat after more than 800 events), leaving the other undisturbed and the global diversity static at 106 (Figure 6(c), blue). This yields the counter-intuitive result that random effects are *more* punishing to the meta-community than one that explicitly targets the highest-diversity patches.

The model with diffusive migration behaves in a broadly similar manner, with the main difference being that this meta-community is always able to persist for the full 1000 elimination events (Figure 6(a) and (b), blue). While these movement rules have been generally limiting compared to the adaptive movement, with lower initial global diversity and simpler food webs, it allows local populations mobility that is not dependent on local disruption to prompt emigration. Thus, a few species can spread and establish themselves in neighbouring patches after each habitat destruction event, and total annihilation is never quite achieved. However, only four non-resource species survive the targeted sequence, and between one and two in the case of random selection. Like the adaptive movement case, they can also survive repeated temporary displacement, and do so with substantially increased diversity (Figure 6(c) and (d), blue) by comparison.

## 7. Discussion and conclusion

An allometric spatial eco-evolutionary model was utilised to construct two complex meta-foodwebs shaped by the feedback between ecological, evolutionary, and spatial dynamics. These each consist of 36 patches with explicit two-dimensional spatial structure and containing unique local compositions of species that have emerged dynamically during the simulation. The trade-off to this approach and the dispersal ruleset employed to rapidly obtain such a complex heterogeneous meta-community is the relatively low spatial range of most species and the weak coupling between neighbouring patches, in contrast to prior models of habitat destruction that typically involve fewer species each occupying many patches. This illustrates the essential conceit underpinning eco-evolutionary models: changes to the rules of species behaviour and their means of deciding when and how to move between environments has a crucial influence on the structure of the trophic meta-communities that emerge through evolution, and consequently on how that meta-community will be affected by a perturbation such as climate change or habitat destruction. We have tested the response of these systems to individual and repeated local disturbances, in the form of patch removal or displacement of the occupying populations - causing invasions of the neighbouring patches. While some previous studies have found omnivorous species to play an important role in meta-foodweb stability as a whole [11, 22, 23], we did not observe a relationship between the frequency of omnivory in a patch, and the impact of its disruption.

An important factor in this study is how we model the movement of populations in space. While both mechanisms allow the assembly of distinct local food webs (Figure 1-2), the adaptive migration model causes individual patches to exist in an isolated equilibrium unless they are actively perturbed within the patch. Thus, sequentially removing patches and eliminating their residing populace has little effect on local populations living in the remaining patches, and the entire meta-community perishes after all patches have been cleared even if they were open for re-colonisation (Figure 5(a)-(b), Figure 6(a)-(b), red). Similarly, the impact on global diversity of removing individual patches and eliminating their occupants will necessarily be governed by the number of unique species that resided there rather than any other factors such as the spatial location of the patch (Figure 3(a) compared to the other subfigures). Implementing a form of habitat destruction where affected local populations are displaced to neighbouring patches rather than simply removed from the system, also has highly damaging ecological consequences for the remaining patches in the meta-community (Figure 5(c)-(d), red), although total extinction is not reached if re-colonisation is permitted (Figure 6(c)-(d), red). However, constant mixing of species imposes severe limits on global diversity as highly-specialised basal species are displaced from the habitat where they are adapted to feed effectively, and as similar species from otherwise-isolated habitats are forced to share the same patch and compete for the same ecological niche.

Previous studies [45] indicated that a constant diffusion rule for migration from the beginning of the simulation would result in homogeneous low-diversity food webs in each patch, in agreement with other models that find intermediate spatial coupling to be most beneficial [11, 23]. Using such a rule, it is probable that temporary eliminations of patch populations would have low impact, as the vacated patch would be immediately re-colonised by the same species from surrounding patches. If species migrate between destruction events using the trait-limited diffusion mechanism implemented in this work, although the initial meta-community attains lower diversity and complexity compared to the adaptive migration mechanism, it will be able to persist throughout indeterminately many elimination events (Figure 6(a)-(b), blue), as vacated patches are re-colonised by neighbouring populations. This replicates the rescue effects of migration observed in other studies [52], and that in models of frequent patch loss (as is the case here) poor dispersers may suffer the most [28]. In our study, we can observe the results of these behavioural trade-offs on the meta-community, rather than species, level: if all species prefer to stay in their patch provided good conditions (adaptive migration), the end result is a more diverse meta-community of species who have existed for much longer times (Table 1), but which is unable to endure particularly calamitous events (Figure 6(b), red) due to their static behaviour. Meanwhile if all species adopt a strategy favouring constant dispersal independent of current fortunes, on a meta-community level significantly fewer species can co-exist at this stage in of evolutionary time, but the meta-network is more resilient to sustained habitat disruption. Moreover, this again demonstrates the impact of the model's ecological dynamics on both the structure of the meta-community assembled over an evolutionary timescale, and its influence on the response of that system on an ecological timescale to environmental challenges.

Under the diffusion mechanism of movement, individual patch deletion experiments yielded an interesting outcome for conservation applications: the destabilising influence of invasive species in a complex neighbouring ecosystem can be so great (Figure 3(a), and Figure 4) that if a local habitat with low diversity compared to others in the meta-network must be cleared of inhabitants, it is actually preferable to the global meta-community to ensure their elimination rather than carelessly dispersing them amongst adjacent environments. The role of invasive species in precipitating extinctions is widely-discussed in ecology [53], although in our simulations this is an extreme example. In contrast, it is preferable to displace the populations of relatively high-diversity patches which must be emptied, in order to maximise conserved global biodiversity. Furthermore, in real-life situations of conservation, it may be possible to identify habitats suitable for relocating the evicted species. This is particularly likely given the limitation of this model in that most species did not have sister populations in any other patch, which is unlikely to be the case for many real species, although it could apply to exactly the endangered species that such conservation efforts would be directed towards. Understanding how best to model allometric-scaling of dispersal in meta-communities is an ongoing challenge [54, 39], and future investigations with this model will pursue hybrids of the approaches employed in this paper combined with very low levels of diffusion to seek species with a more realistic distribution of close, intermediate and far-ranging evolved strategies. As more sophisticated spatially-explicit eco-evolutionary models are developed, we hope to obtain greater insights into how humanity should answer the pressing questions of natural habitat management and the environmental challenges ahead.

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