Climate change in metacommunities: dispersal gives double-sided effects on persistence

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Climate change is increasingly affecting the structure and dynamics of ecological communities both at local and at regional scales, and this can be expected to have important consequences for their robustness and long-term persistence. The aim of the present work is to analyse how the spatial structure of the landscape and dispersal patterns of species (dispersal rate and average dispersal distance) affects metacommunity response to two disturbances: (i) increased mortality during dispersal and (ii) local species extinction. We analyse the disturbances both in isolation and in combination. Using a spatially and dynamically explicit metacommunity model, we find that the effect of dispersal on metacommunity persistence is two-sided: on the one hand, high dispersal significantly reduces the risk of bottom-up extinction cascades following the local removal of a species; on the other hand, when dispersal imposes a risk to the dispersing individuals, high dispersal increases extinction risks, especially when dispersal is global. Large-bodied species with long generation times at the highest trophic level are particularly vulnerable to extinction when dispersal involves a risk. This suggests that decreasing the mortality risk of dispersing individuals by improving the quality of the habitat matrix may greatly increase the robustness of metacommunities.

Keywords: dispersal mortality; extinctions; food webs; migration; rescue effect; spatial model

1. INTRODUCTION

Ongoing climate change causes a variety of threats to ecosystems, several of which have strong connections to spatial setting and species dynamics [1–4]. Species’ geographical ranges, timing of ecological processes and dispersal patterns are likely to change drastically [4–7] with profound effects on populations and communities. Additionally, climate change is one of the factors expected to further exacerbate the already high rates of biodiversity loss [8,9], for example, by augmenting destruction and fragmentation of natural habitats—one of the major causes of the current biodiversity crisis [10–12]. These problems in isolation can have severe consequences for ecosystem persistence; and in concert they can potentially push species and ecological systems over their tolerance limit [1].

The response of ecological communities to disturbances is affected by both local (interactions among species coexisting within habitat patches) and regional processes (movement of species between habitat patches) [13,14]. At the local scale, food web structure has been shown to affect the ability to cope with disturbances such as species loss [15–19]. At the regional scale, number and distribution of habitat patches as well as species dispersal abilities have implications for the long-term persistence of interacting species [20–24]. Therefore, when studying the effects of climate change, it is important to take both local and regional dynamics into consideration.

In the framework of metacommunities, local communities are open and connected to each other through dispersal of potentially interacting species [13]. Species’ dispersal in the landscape can be described by their ‘dispersal kernel’—the function that describes the probability of dispersal to different distances [25] and can widely influence community patterns [26]. Dispersal of species between local communities may alleviate the risk of extinction cascades following species losses through recolonizations and rescue effects [13]. However, dispersal might also pose a risk to the dispersing individuals [27] that is likely to increase with distance travelled [7,28]. Climate change may cause the habitats and the areas between habitats to become more inhospitable, for example, via habitat degradation and fragmentation [2,3]. Also, changes in timing can cause ecological mismatch—the process in which crucial ecological events occur in a non-favourable time of the year—for example, reproduction occurring after the peak in primary production in the receiving habitat [2,29]. If these processes occur before species can adapt it can cause increased, presumably extensive, mortality for the migrants. The costs for the individuals...
dispersing can be severe, especially for longer distances where differences in timing is larger [7]. If mortality during dispersal is high, recolonizations and rescue mechanisms will no longer be effective and extinction cascades caused by local species loss might therefore be impossible. Also, this increased mortality alone could have drastic consequences for the communities.

A species’ body size is directly or indirectly coupled to other characteristics of the species, such as the metabolism affecting biological rates [30] and mobility [31,32]. This has direct consequences for how a species moves between habitats, both short-distance movements and long-distance migrations. Incorporation of some kind of size structure is therefore desirable when analysing spatial ecological phenomena.

Here we investigate how metacommunity robustness is affected by two kinds of disturbances likely to result from climate change: (i) increased mortality for species during dispersal and (ii) local species extinctions. The two disturbance scenarios are addressed in isolation and in combination. We develop a general model that combines a dynamic model of species interactions in the local communities with a model of the coupling between local communities via species dispersal. Using this spatially and dynamically explicit model, we explore how species dispersal patterns (dispersal rate and dispersal distance) and the distribution of habitats affect the risk of local extinctions of species at different trophic levels. We show that if dispersal incurs a risk then this alone has a drastic effect on local species extinctions, especially for large-bodied species at high trophic level. We also show that the capacity for the dispersal of species among local communities to rescue consumers from becoming secondarily extinct following local loss of their resources is significantly reduced following the inclusion of a risk.

2. METHODS
(a) Local dynamics
We start with the construction of local ecological communities. Each local community consists of 12 coexisting species interacting across three trophic levels. The food web is triangular with six primary producers at the lowest trophic level. These species are consumed by four primary consumers, which are prey for the two secondary consumers. Omnivory is allowed. Connectance of local communities is set to $C = 0.09$, meaning that 13 links are randomly distributed with the constraints that (i) consumers have at least one feeding link to the trophic level directly beneath it, (ii) cannibalism is not allowed and (iii) feeding on species at higher trophic levels is not allowed. We choose to analyse these relatively small food webs given that we will couple up to eight populations of each species via dispersal between habitat patches (see below), which implies that we will model and follow the dynamics of up to 96 populations simultaneously.

The interactions within each local food web are described by a Rosenzweig–MacArthur model [33]:

$$\frac{dN_i}{dt} = N_i \left( r_i + \sum_{j=1}^{S} a_{ij} N_j \right),$$

where $dN_i/dt$ is the rate of change of density of species $i$ with respect to time in a community with $S$ species, $r_i$ is the intrinsic per capita growth/mortality rate of species $i$ and $a_{ij}$ is the per capita effect of species $j$ on the per capita growth rate of species $i$. We use a type II functional response (see following section). All species experience intraspecific competition, given by $a_{ii}$ and basal species also have interspecific competition, given by $a_{ij}$. For values of model parameters, see §2a(ii).

(i) Functional response type II
We use type II functional response for consumers in which

$$\begin{align*}
\tilde{a}_{ij} &= a_{ij} \quad j \in L(i), \\
\tilde{a}_{ij} &= \frac{h_{ij} a_{ij}}{1 + T \sum_{n \in R(i)} h_{ijn} a_{jn} N_n} \quad j \in C(i) \\
\tilde{a}_{ij} &= e \frac{h_{ij} a_{ij}}{1 + T \sum_{n \in R(i)} h_{ijn} a_{jn} N_n} \quad j \in R(i)
\end{align*}$$

(2.2)

Here $h_{ij}$ is the preference of predator $j$ for prey $i$, $a_{ij}$ is the intrinsic attack rate of predator $j$ on prey $i$, $T$ is the handling time needed for the predator to catch and consume the prey and $e$ is a measure of conversion efficiency, i.e. the rate at which resources are converted into new consumers. $L(i)$ is the set of species belonging to the same trophic level as species $i$, $C(i)$ contains the species that consume species $i$ and $R(i)$ contains the species being resources to species $i$.

Each predator has a maximum prey preference equal to 1, meaning that predators with only one prey has $h_{ij} = 1$. Predators with several prey species are assumed to have a high preference ($h_{ij} = 0.9$) for one of their prey species (assigned randomly) and equal lower preferences ($h_{ij} = 0.1/[$number of prey $- 1]$) for the others. For each consumer–prey interaction, the intrinsic attack rate, $a_{ij}$, is randomly drawn from the uniform distribution $[0,1]$. Handling time, $T_i$, is assumed to be the same for all consumers on all prey and is given the value of 1.

(ii) Model parameters
For primary producers, intrinsic growth rates are randomly drawn from the uniform distribution $[0.5,2]$. For each patch, a new value is drawn. This is done in order to generate some spatial heterogeneity, mimicking that some patches in the landscape have higher primary production than others. Intrinsic mortality rates for consumers are generated in the following way: first values are randomly drawn from the uniform distribution $[-1,0]$, and the smallest of these values are assigned to the secondary consumers. For primary consumers the values are then multiplied by 0.1, and for carnivores the value is multiplied by 0.01. In this way, secondary consumers will always have lower mortality rates compared with their prey. This reflects the fact that body size often increases with trophic level [34], and larger body sizes often confer lower mortality rates [35]. The strength of
intraspecific competition among all species is randomly drawn from the interval [−1 0]. The strength of the interspecific competition among basal species is drawn at random from the uniform interval [−0.5 0]. Conversion efficiency, $c$, is set to 0.2 for links between adjacent trophic levels ($c < 1$ when the size of the consumer is larger than that of its prey). Omnivory links are assumed to be less efficient and conversion efficiency is therefore set to $e = 0.02$. The parametrization in the present study is similar to the ones used and motivated in earlier theoretical studies of food webs [15,17].

Note that in this model species’ body sizes are not directly entered. Instead, we enter the size structure by assuming species at higher trophic levels to be larger and therefore to have lower growth rates.

(b) Regional dynamics

Each patch is continually subject to migration events: per unit time, a fixed proportion, $m$, of each species’ population migrates from its current patch and disperses among the other patches. For a landscape of $s$ habitat patches, the number of individuals migrating from patch $q$ to patch $p$, per unit time, is given by

$$M_{i,p,q} = m(1 - td_{p,q})N_{i,q} e^{-d_{i,1} / c} \sum_{l \neq q} e^{-d_{i,l} / c}.$$

where $N_{i,q}$ is the density of species $i$ in patch $q$, the distance between the two patches is $d_{p,q}$ (for calculation, see §2c), and $c$ is a parameter [36]. Thus, the flow of migrants is greatest between patches separated by small distances; the strength of this bias is determined by $c$: lower values correspond to more localized dispersal (figure 1). We use two values of $c$ to model two types of dispersal kernels [25]: one when species have the capability and behaviour to disperse more locally in the landscape ($c = 0.1$, local dispersal), and one when species distribute themselves among the patches less dependent on the distance ($c = 1$, global dispersal).

Migration might pose some kind of risk to the individual, which should increase with distance travelled [28]. This is modelled by the term $(1 - td_{p,q})$ where $0 < \tau < 1$ quantifies the risk per unit distance. Here we use $\tau = 0$ and $\tau = 0.2$.

The change in densities in patch $p$, per unit time, as a result of migration is given by

$$\frac{dN_{i,p}}{dt} = \sum_{q=1,q \neq p} M_{i,p,q} - (mN_{i,p}).$$

where the first term represents flux in, and the second term flux out from patch $p$ of species of species $i$. The $q \neq p$ condition on the summation term indicates that no migrant may return to the patch it just vacated. The dynamics of species $i$ in patch $p$ are then given by

$$\frac{dN_{i,p}}{dt} = N_{i,p} \left( r_i + \sum_{j=1}^{S} \alpha_{j} N_{i,j} \right) + \hat{N}_{i,p}$$

The following parameters were varied: patch number ($s = 2$ to $s = 8$), dispersal rate (low $m = 0.001$ and high $m = 0.05$) and that for regulating dispersal distance—hereafter referred to as local ($c = 0.1$) versus global ($c = 1$) dispersal.

(c) Generating starting communities

The global habitat (the landscape) is a $25 \times 25$ cell grid, in which $s$ patches are allocated their positions at random—each patch being assigned a number between 1 and 625 at random. Each patch number corresponds to a specific $x$ and $y$ coordinate in the grid. The distance between patches, $d_{p,q}$ is calculated relative to the longest distance possible in the landscape, i.e. the distance between the outermost diagonal corners of the grid is set to 1, and distances between patches are determined relative to that point; $d$ is calculated based on the centre of the cell.

For each pair of patches, $p$ and $q$, the distance from $q$ to $p$ is calculated:

$$d_{p,q} = \sqrt{(X_p - X_q)^2 + (Y_p - Y_q)^2}.$$

where $X_p$ and $Y_p$ are the $x$ and $y$ coordinates for patch $p$, respectively, and $X_q$ and $Y_q$ are the $x$ and $y$ coordinates for patch $q$, respectively. The distance $d_{p,q}$ is then normalized relative to the longest possible distance in the grid

$$d_{p,q} = \frac{\delta_{p,q}}{\sqrt{((X_{\max} - 1)^2 + (Y_{\max} - 1)^2)}},$$

i.e. the distance between the outermost diagonal corners of the grid is set to 1, and distances between patches are determined relative to that point.

A system of $s$ persistent local starting communities is found. Each local community has the same structure but can vary in the growth rate of the primary producers.
(see §2a(ii)). Local communities are considered persistent if all species densities remain above predefined thresholds (see below) following numerical integration over 10 000 time units using a model with dispersal between local communities without a risk included. For initial species densities, we use the equilibrium densities of the corresponding system with type I functional response. In this way, we check that the system of local communities (the metacommunity) would be persistent in an environment without disturbances over a longer time period. To test the generality of findings, we generate a number of replicate metacommunities in which model parameters are sampled from the predefined distributions (see §2a(ii)). We keep generating replicates until 200 ‘persistent’ replicate metacommunities have been found. The two kinds of disturbances are then introduced.

(d) Disturbances

We investigate two disturbance scenarios, both in isolation and in combination: (i) increased mortality during the dispersal (hereafter dispersal mortality) and (ii) a forced extinction event: species is removed from the starting community in 50 per cent of the patches—that is, the species’ density is set to zero in a randomly selected 50 per cent of the patches. Removals are performed in absence \((\tau = 0)\) and presence \((\tau = 0.2)\) of the dispersal mortality. After introduction of the disturbance the system is integrated over 20 000 time units and the final densities are recorded. The procedure is repeated for removals of all species in the food web. The model allows species to have some degree of adaptation: if a consumer in one patch loses all its preys due to the forced removal then the consumer in that specific patch is allocated one new feeding link (weak) to a randomly selected species at the trophic level directly beneath it.

To reflect demographic stochasticity and Allee effects, we define absolute extinction thresholds below which species are considered extinct. These thresholds are set to different values for species at the three trophic levels. This is motivated by theory and empirical work [37] suggesting that demographic stochasticity should be stronger in species with high intrinsic birth and mortality rates than in species with low rates (in our model communities, these rates are higher for primary producers than for primary consumers, which in turn have higher rates than secondary consumers, see §2a(ii)). The threshold densities used are 0.02 for primary producers, 0.002 for primary consumers and 0.0002 for secondary consumers. These extinction thresholds are approximately two orders of magnitude smaller than the equilibrium densities of the respective species categories in the communities. The average densities between species at different trophic levels differ by one magnitude.

(e) Measuring local extinctions

The metacommunity’s response to the disturbances is measured as the proportion of possible local extinctions that is realized at the end of the simulation

\[
E_t = \frac{\sum_{p=1}^{s} \sum_{j=1}^{S_p} \epsilon_{pj}}{s(S_t)}
\]

(2.8)

and

\[
E_t = \frac{\sum_{p=1}^{s} \sum_{j=1}^{S_p} \epsilon_{pj}}{(s(S_t) - 1)}
\]

(2.9)

where \(\epsilon_{pj}\) is the number of local extinctions of species \(j\) in patch \(p\). This value can be either 1 or 0. \(S_t\) is the number of species in the trophic group of interest and \(s\) is the number of patches. When there is no forced species removal, all species are accounted for in the calculation and the denominator becomes \((sS_t)\). \(R\) stands for the removed species, meaning that population is not included in the calculation, therefore \(S_t - 1\) in the denominator. These separate calculations, depending on if there is a species removal or not, can affect the interpretation of the results when we do a direct comparison of the scenarios (see §4).

For the partially removed species, we measure the ability for recolonization and the propensity for additional extinctions to occur. Recolonization is measured as the proportion of patches from which the species was initially removed that has a population size above the extinction threshold at the end of the simulation. The propensity for additional extinctions is measured as the proportion of the patches from which the species was not initially removed where it has gone locally extinct in the end of the simulation.

3. RESULTS

Primary and secondary consumers go extinct following both types of disturbances, whereas it is very rare that primary producers go extinct. Therefore, only extinction risks for consumer species are shown.

As expected, increased mortality during dispersal has the largest effect on the risk of local extinctions (the proportion of all possible local extinctions that are realized) when dispersal rate, \(m\), is high and dispersal is global (high \(c\)) (dashed lines in figures 2 and 3). Dispersal mortality has a relatively small effect on the risk of extinction when \(m\) is low. Secondary consumers—large-bodied species with long generation times at the highest trophic level—are more negatively affected by the dispersal mortality than primary consumers.

Risk of local extinctions following species removal depends on whether there is a risk involved in dispersal as well as on the dispersal pattern of species (dispersal rate, \(m\), and dispersal distance, \(c\)) and the number of habitat patches \((s)\) in the metacommunity. We find that high dispersal rate significantly reduces the risk of extinction cascades following the local removal of a species when dispersal poses no risk to the individuals (figures 2 and 3). We also see a few local extinction even without any of the disturbances present (black solid line in figure 3a,b). This is due to the fact that species with extremely slow generation times can, in rare cases, go extinct after the 10 000 initial time steps of the simulation.

On the other hand, high dispersal rate increases extinction risks when dispersal involves a risk, especially when dispersal is global (long dispersal distances) (figures 2 and 3). Secondary consumers are especially vulnerable to extinction when dispersal involves a risk and dispersal rate is high (figure 3c,d).
Moreover, we find that risk of local extinction decreases with increasing number of habitat patches in the landscape when dispersal involves a risk—dispersal rate is high and dispersal is local (low $c$) (figures 2c and 3c)—whereas it increase when dispersal is global (figures 2d and 3d).

In the results presented above, the removed species is not included in the measure of extinctions. As we remove a species from only 50 per cent of the patches, we can investigate how many of these patches are being recolonized by the species and how many patches where the species was not removed experience extinctions of the focal species. Overall, as expected, recolonization increases when dispersal rate ($m$) is high. The largest effect is on the primary producers, which never succeed in recolonizing when dispersal rate is low, but always succeed when dispersal rate is high, independent of whether a dispersal mortality is present or not. Primary consumers show a similar pattern but are slightly more affected by the presence of a dispersal mortality, which decreases the recolonization when dispersal rate is high. Secondary consumers, on the other hand, are significantly affected by the dispersal mortality when dispersal is high; without dispersal mortality, the recolonization rate is 100 per cent whereas with a risk present the rate is between 30 and 50 per cent (figure 4).

A similar analysis can be done for the risk of additional local extinctions of the locally removed species (i.e. extinctions in the patches where the species were not initially removed). Independent of the presence or the absence of a dispersal mortality, primary producers never experience additional extinctions. Secondary consumers, on the other hand, commonly endure additional extinctions when dispersal is high and a dispersal mortality is present. A similar but weaker trend holds for primary consumers (figure 5).

4. DISCUSSION
Global warming forces species to track their shifting habitat or adapt to new conditions within their present locations—processes that are critically influenced by species dispersal. Landscape degradation that may result from or correlate with climate change, such as habitat fragmentation, increased matrix hostility and decreased patch quality, will cause the demographic costs of migration and settlement to rise [38]. In addition, the dispersal phase is often stressful for individuals due to, for example, increased metabolic costs [30] and potential barriers in the landscape [39]. This can potentially exaggerate the negative effects of climate change. Climate change is likely to have profound and complex effects on local
as well as global ecological communities [40], which highlights the importance of analyses including both scales. Here we analyse how increased mortality during species dispersal affects the robustness of metacommunities, both in isolation and in concert with additional disturbances (local species extinctions).

Extinction of populations is a severe disturbance that could cause a cascade of secondary extinctions within communities [15–17,41] owing to both direct effects, when consumers lose their prey, and indirect effects, such as disruption of predator-mediated coexistence [42]. In our case, the extinction event implies that a large part of each local population of one species is lost simultaneously. Still, we observe relatively few extinctions of additional populations, compared with analyses of similar but closed communities [17].

In the spatial setting, global persistence is supported by rescue effects whereby exchange of individuals between patches contributes to the long-term survival of the metacommunity [13,43]. However, this positive effect of dispersal on persistence is complicated by indirect effects of dispersal and by interaction effects with other demographic traits or habitat characteristics [38]. For example, when demographic costs rise, either during the actual dispersal phase or the settlement process, we clearly observe an increase in the proportion of local populations going extinct. Depending on the dispersal pattern of the species, the increase can be substantial.

However, increasing mortality during dispersal has in isolation a comparable effect to the combined scenario, which highlights the severity of how a disturbance can affect populations over a continuum of time. In contrast to the instant extinction of local populations, the drainage of individuals caused by the dispersal mortality affects each population less compared with complete removal, but affects all populations simultaneously. Eventually, this process leads to additional losses of other local populations as well as extinctions owing to secondary effects.

The clear effect we observe from changing species dispersal patterns is coupled to factors directly affecting the proportion of individuals being subject to the dispersal mortality. First, increased dispersal rate means that a larger proportion of the populations are moving across the landscape and are thereby subject to increased mortality. Second, when dispersal is global, a larger proportion of the population are dispersing longer distances and are therefore affected by the distance-dependent dispersal mortality.

Our analysis suggests that the negative effects of climate change on metacommunity persistence could be mitigated by increased matrix quality, which can

![Figure 3](http://rstb.royalsocietypublishing.org/)

**Figure 3.** Local extinctions (the proportion of all possible local extinctions that occur, the removed species is not included) of secondary consumers. Solid lines indicate scenarios without risk included. Dashed lines show scenarios with risk included. The different lines show removal of primary producers (light grey), primary consumers (dark grey) and secondary consumers (black). White lines indicate scenarios without any species removal. Each point is an average over 200 replicates, and vertical bars show the s.e.
potentially be achieved by increasing the number of patches in the landscape. However, their positioning must impose a decrease of the maximum distance between patches for the effect to be positive. Here, given that we use relatively few patches in the metacommunities, it is not self-evident that more patches will give patches that are positioned closer to each other. In fact, when the distance is averaged over all patches in a metacommunity, the average distance is equal for all sizes of the metacommunities. However, the average minimum distance between two patches decreases significantly with increased number of patches (0.40 for a metacommunity with two patches versus 0.08 for eight patches). Local dispersal implies a smaller proportion of each population will disperse to patches far away, and therefore fewer individuals will experience the higher dispersal mortality. Global dispersal, on the other hand, implies that a larger proportion of each population is dispersing longer distances and is therefore affected by the dispersal mortality. In landscapes with a higher number of patches, the maximum distance between any two patches is on average larger (0.40 for a two patch community versus 0.70 for an eight patch community). Therefore, we observe a trend of increased proportion of local extinctions with increased number of patches when dispersal is global. In the light of climate change, a possible scenario is that suitable habitats are formed outside the original geographical range as its borders move. However, even if the number and area of suitable habitats were kept constant the shift would still have far-reaching consequences if the actual distance between patches were to change.

Species with different body size are affected differently by climate change. For example, larger-bodied species have higher metabolic costs and might be relatively more affected by an increased temperature [30] and face an increased risk of going extinct [44]. Additionally, species’ dispersal patterns have a clear link to body size, with larger species being more mobile [31,32]. The elevated extinction risk for secondary consumers stems from these multiple factors, which have the potential to catalyse each other. The underlying mechanisms depend on both species position in the network and characteristics coupled to body size. First, through bottom-up effects species at high trophic levels are negatively affected by the at-risk species at lower trophic levels. Second, species at higher trophic level are larger and therefore have longer generation times. Ecologists often assume that secondary consumers are more mobile on a per time unit basis (i.e. move over larger areas) [32]. Here we take a different approach by assuming that consumers are more mobile on a per generation basis. This increases the total amount of time an individual spends dispersing and naturally also the exposure to the dispersal mortality. Empirical studies have demonstrated the sensitivity of top predators to even small
disturbances [45–47], which probably stems from their susceptibility to indirect effects [48]. Disturbances to top predators can have far-reaching consequences owing to their wide-ranging distributions and long generation times, slowing recovery and thereby making their sensitivity even more alarming.

In figure 2c,d, we observe a decrease in proportion of local extinctions of secondary consumers when the other secondary consumer is removed. This can be explained by two factors. One is that due to the removal of a competitor, there is a release of resources for the secondary consumer that has not been removed. We see this reflected in an increase in density and decrease in local extinctions for the ‘unremoved’ secondary consumer. However, owing to the fact that we do not account for any of the extinctions, forced or not, of the removed secondary consumer, we also miss out those extinctions that would have happened despite the removal.

There have been numerous studies focusing on food web persistence and resistance against species loss, but most often performed in a closed setting. These studies have identified certain food web characteristics of importance for food web persistence and stability, for example, connectance and distribution of feeding interactions [16,17,49] and details of the allometric scaling [41,50]. Such characteristics of the local communities naturally interact with the spatial features and are therefore likely to have effects also in open ecological communities. Climate change (i.e. warming) can further affect the allometries [44,51], feeding rates [52] and the biomass–trophic level relationships [53] in the ecosystems, with important effects for stability. Additionally, if we were to take other types of interactions into account, such as mutualistic and competitive interactions, this would probably have effects on the persistence of the communities [54]. Whereas our study shows that it is important to take both the local and regional factors into account, it would be valuable to disentangle in detail their respective contributions when addressed in concert.

5. CAVEATS AND FUTURE DIRECTIONS

We have presented a model that has the ability to address numerous ecological phenomena, and include local population dynamics as well as spatial dynamics. However, several factors would be valuable to address in future analyses. The dispersal mortality considered here affects all populations. While this scenario is not unlikely, climate change might have more severe effects on certain species, for example, those that show less plasticity in their adaption to shifts in geographical range or those that experience a higher metabolic cost when temperature increases. In this case, our approach could potentially underestimate metacommunity robustness. On the other hand, the maximum dispersal rate used...
here is 20 per cent. For species where a majority of the population migrates every year (for example, migratory birds), this can be a large underestimate. In these cases, our approach would overestimate robustness.

6. CONCLUSIONS
As with all predictions of our ecosystems in the light of ongoing climate change, forecasting the identity and magnitude of the disturbances that follow are precarious, especially since multiple phenomena are likely to occur simultaneously. However, all species exist in a spatial setting and there is evidence that the spatial conditions for species will be strongly affected by climate change [1,2,8]. Binzer et al. [55] show that warming may have both positive and negative implications for the stability of ecological communities. Similarly, we show that by placing food webs in a spatial context the outcome of disturbance scenarios can change drastically and dispersal presents a double-sided effect on metacommunity robustness, depending on the degree of spatial coupling and the nature of species dispersal. Specifically, we here show that although species dispersal can, via rescue effects, halt avalanches of secondary extinctions, disruption of the dispersal attributable to demographic costs during the dispersal phase can be devastating for ecological communities, especially for species at high trophic level.

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REFERENCES