Extinction and ecosystem function debt across dispersal rate and behavior in a heterogeneous metacommunity model

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Abstract

Aim: Habitat destruction causes “extinction debt” and is also thought to produce ecosystem function debt, but theory of their magnitude and nature is limited. Heterogeneous landscapes are fundamental to the maintenance of species richness and ecosystem function, whilst directed or undirected dispersal behavior, such as dispersal of seeds by animals or by the wind, is also important, especially after habitat destruction. We therefore consider extinction and ecosystem function debt under different dispersal rates and behaviors in heterogeneous landscapes.

Methods: We use a classic heterogeneous metacommunity model to capture the dynamics of competing species in local patches linked by dispersal and varying in environmental conditions. We remove one patch at a time, and measure extinction debt and ecosystem function debt by the number / proportion of delayed extinctions and the amount of biomass change, respectively.

Results: We reveal three species extinction regimes as dispersal increases: 1. species most adapted to the removed habitat are most at risk; 2. similarly adapted species are also at risk; 3. patch removal shifts competitive balance among the few species coexisting at high dispersal, where competition is strong. We find surprisingly that destruction of habitat can hasten the extinction of those species best adapted to harsh environments, and that the proportion of diversity at risk from extinction actually increases with dispersal because competition is intense there. Finally, there can be a small ecosystem credit, but extinction debt, when dispersers reroute to potentially more favorable remaining habitats (directed dispersal), especially when harsh environments are removed. However, ecosystem debt occurs and can be large under undirected dispersal.

Main conclusions: The magnitude and nature of extinction and ecosystem function debts depend on species dispersal rates and behaviors, as well as the environmental conditions of the disturbed habitats. Conservation actions will be more successful if they consider these factors.

Keywords: habitat loss, directed/undirected dispersal, extinction regimes, harsh/benign environment, resource consumption, species conservation

Introduction

Habitat destruction causes species extinctions (Fahrig 2003; Jackson & Fahrig 2013; Horváth *et al.* 2019; Chase *et al.* 2020) and interferes with ecosystem functions and ecosystem services (Isbell *et al.* 2015). Some species in disturbed habitats disappear immediately (Krauss *et al.* 2010), for example in the case of habitat conversion or chemical spillages. Some species are able to remain in the habitat during and after disturbance, depending on the time scales and severity of the disturbance (Ceballos *et al.* 2015). Other species, having survived the initial disturbance, crowd into the remaining habitat patches (Ewers & Didham 2006). For those species not destroyed immediately, the habitat disturbance may cause future extinctions across multiple trophic levels (Krauss *et al.* 2010). "Extinction debt" describes the delayed species extinctions occurring after environmental disturbance (Tilman *et al.* 1994; Kuussaari *et al.* 2009).

As well as causing extinction debt, habitat disturbance also causes ecosystem function debt, which refers to the delayed loss of ecosystem functions such as productivity or biomass (Haddad *et al.* 2015; Isbell *et al.* 2015). Ecosystem function debt results from species loss and is therefore correlated with extinction debt (Haddad *et al.* 2015; Isbell *et al.* 2015). However, it is possible for ecosystem function to recover after habitat disturbance, even in the absence of species reintroductions. This is because disturbance alters the competitive abilities of species, allowing productive species to dominate entire habitats. We refer to the increase in ecosystem function after habitat disturbance as ecosystem function credit. Extinction debt attracts the most attention because it provides time windows for conservation actions to rescue rare species from extinction (Hanski & Ovaskainen 2002; Malanson 2008; Wearn *et al.* 2012; Halley *et al.* 2014; Highland & Jones 2014; Chen & Peng 2017; Otto *et al.* 2017; Figueiredo *et al.* 2019; Makishima *et al.* 2021; Ridding *et al.* 2021). However, studies of ecosystem function debt/credit are limited (also mentioned by Gonzalez *et al.* 2009), and as far as we know, none of these studies consider a heterogeneous landscape.

The severity of extinction debt is usually measured as the number or proportion of “delayed extinctions as a consequence of ecosystem perturbation” as definition by Figueiredo *et al.* (2019), which means the number / proportion of species extinct in the long run as a result of the perturbation, minus the number / proportion of species extinct immediately after it. Similar definitions are used in the other studies (Kuussaari *et al.* 2009; Jackson & Sax 2010; Halley *et al.* 2016; Figueiredo *et al.* 2019). Meanwhile, a given species’ extinction risk could be measured by the time delay index, that is the persistence time of extinct species since habitat loss (Hanski & Ovaskainen 2002). If the time delay index of a species is higher, its extinction risk is lower (Grimm & Wissel 2004). Previous theoretical studies have extrapolated ecosystem function debt from the number of species lost based on correlations between community biomass and species richness (Isbell *et al.* 2015). Ecosystem function debt/credit could be measured more directly as the amount of biomass lost in the long run minus the amount lost immediately after habitat disturbance: if this figure is positive then ecosystem function credit has occurred; if it is negative, then ecosystem function debt has occurred.

Environmental heterogeneity in space is key to maintaining and shaping species richness and ecosystem function (Ben-Hur & Kadmon 2020; Davies *et al.* 2021; Thompson *et al.* 2021). In recent decades there have been a number of theoretical advances towards understanding environmentally heterogeneous landscapes, through the study of metacommunity models with discrete communities of different environmental conditions, all linked by dispersal (Thompson *et al.* 2014; Fournier *et al.* 2017; Thompson & Gonzalez 2017; Thompson *et al.* 2017; Leibold & Chase 2018; Thompson *et al.* 2020). These models have also begun to be employed in the development of theories of extinction debt, though they have only explicitly considered the effects of environmental heterogeneity on extinction debt to a limited degree (see related studies in Mouquet *et al.* 2011; Thompson *et al.* 2017).

Species dispersal behavior, a crucial component of metacommunities before and after habitat disturbance, can be modelled in different ways. Most animals are active dispersers, easily orientating themselves and moving purposefully in the direction of habitats with sufficient resource (Bowler & Benton 2005; Croteau 2010). Most plants disperse passively, in the direction of whichever organism or abiotic dispersal agent is transporting the seed. Seeds dispersed by animals benefit from active dispersal, thus avoiding unsuitable habitats (Bowler & Benton 2005; Nield *et al.* 2020; Mason *et al.* 2022) whereas seeds dispersed by the wind cannot avoid unsuitable habitats (Zona 2017). In this study, we distinguish between these two dispersal behaviors (Fig. 1A). One in which the individuals previously dispersing to the disturbed habitat instead disperse to remaining habitats, in other words the individuals change direction to available habitats (hereafter referred to as “directed dispersal”), and another where those individuals continue to disperse to the disturbed habitat and are lost (hereafter referred to as “undirected dispersal”).

We use this metacommunity modeling approach to consider additional questions fundamental to understanding the nature of extinction and ecosystem function debt in a heterogeneous landscape (see Fig 1B). This includes basic questions such as how extinction debt is distributed across the species adapted to different environmental conditions, and how this may depend on how the lost habitat fits into the distribution of habitats represented, and the rate of dispersal between patches. We also ask whether the overarching effects of dispersal on extinction and ecosystem function debts, and whether the basic tendency towards ecosystem function debt one expects in homogeneous environments, is the same in heterogeneous environments. When landscapes are homogeneous, one would anticipate, and recent theory using a neutral model framework shows (Thompson *et al.* 2019), that higher dispersal among patches would generally limit these debts. One would also anticipate that patch removal can have only negative or at best no consequences for the ecosystem functioning in the remaining patches. However, habitat heterogeneity creates circumstances under which these ideas may not apply. Species competing along an environmental gradient may do so more intensely when their dispersal rate is higher, in which case their competitive balance may be more sensitive to patch removal. Also, when a patch is removed, species better adapted to other patches could fare better under directed dispersal, and hence ecosystem function in the remaining patches may in fact improve. We answer these questions using an existing metacommunity modeling approach based on consumer-resource dynamics, allowing us to explicitly consider community biomass rather than drawing on correlations with species richness. To answer our questions regarding the influence of dispersal, we add to this metacommunity modeling approach the different potential dispersal behaviors possible when habitat is destroyed. In addition, we link the observed metacommunity extinction and ecosystem function debt behaviors with the effects of patch destruction on heterogeneous metapopulations, by studying the behavior of a similar model of a single species population in heterogeneous patches linked by dispersal.

Model and Methods

Model framework

Our model is comparable to the model used by Mouquet and Loreau (2003) which is well-known for its predictions regarding the effects of dispersal on diversity and ecosystem function in a heterogeneous metacommunity (Mittelbach & McGill 2019). It captures the dynamics of a set of competing species in local patches that vary in their environmental conditions (and hence dominant competitors) and are connected by dispersal to form a metacommunity. We use a formulation of this model similar to that used by Loreau *et al.* (2003), which models competition through resource consumption rather than the local patch dynamics considered in the original model, thus allowing clearer consideration of not just diversity, but also ecosystem function. This metacommunity model has been studied extensively and is the core approach used in recent developments in metacommunity theory (Leibold & Chase 2018; Ai & Ellwood 2022).

Our model is not linked with a particular biological system, for example it could describe grass competing for soil nitrogen (Loreau *et al.* 2003). We set varied environments for habitat patches, such as surface soil temperatures of various plant systems, and we allow species to differ in their traits, such as the temperature at which each species has its maximum competitive ability for soil nitrogen (Tilman 1999). Biomass of a species would increase if that species inhabits a patch where the soil temperature is optimal. In this example, the model is attempting to capture the dynamics of the biomass of different plant species on a heterogeneous landscape through competition for soil nitrogen. The competitive ability of the species depends on the match between the soil temperature of the patch and the optimal temperature of the species.

The metacommunity consists of M patches, each with a different value of an environmental condition, connected by dispersal rate a. Each patch is numbered from 1 to M. The environmental value (such as the surface soil temperature after normalization) of the first patch is E_1=1, then the adjoining patch is defined as E_j=E_{j-1}-1/(M-1) where j is from 2 to M. There are S species in each patch initially, numbered from 1 to S. The optimal niche value of the first species is H_1=1, and remaining species are defined as H_i=H_{i-1}-1/(S-1) where i is from 2 to S. The species competitive ability in each patch is determined by the match between species' optimal niche value and the environmental value of a patch. Under these definitions, in the case of maximal potential diversity (our focus), where there are as many species as patches (i.e. M=S), the first species is the best competitor in the first patch, the second species is the best competitor in the second patch, and so on. We refer to the patches towards the center of the range of environmental conditions as the habitats with benign environments, and the patches with extreme environmental values, such as 0 or 1, as the habitat with harsh environments. Patches with benign environments are suitable for all species, whereas patches with harsh environments are suitable only for those species adapted to that patch. Note that those patches are not necessarily spatially central in our model, in which all patches are assumed equally connected to focus on environmental heterogeneity between patches rather than dispersal limitation. Hence, species with extreme optimal environmental values close to 0 or 1 are best adapted to patches with harsh environments, whereas species with mid-range environmental values are best adapted to benign environments.

Within patches, species compete for a resource, with species' resource consumption and therefore competitive ability in the patch determined by the match between their niche value and the environmental value of the patch. The dynamics of the biomass of the resource in patch *j*, R_j, follow (Loreau *et al.* 2003):

$$\frac{dR_j(t)}{dt} = I_j - l_j R_j(t) - R_j(t) \sum_{i=1}^{S} C_{ij} P_{ij}(t) \qquad (1)$$

where I_j is the rate of input, and l_j is the rate of loss of resource in patch *j*. Species *i* consumes the resource in patch *j* at a rate defined by C_{ij} that depends on the difference between the optimal niche value of species *i* H_i, and the environmental condition of patch *j*, E_j (modified from Gonzalez *et al.* 2009):

$$C_{ij} = \frac{1.5 - |H_i - E_j|}{b} \quad . \qquad (2)$$

where *b* determines the overall magnitude of resource consumption of all species. The dynamics of P_{ij}(t), the biomass of species *i* in patch *j* at time *t*, follow:

$$\frac{dP_{ij}(t)}{dt} = eC_{ij}R_j(t)P_{ij}(t) - mP_{ij}(t) + a\left(\frac{1}{M-1}\sum_{k=1,k\neq j}^{M} P_{ik}(t) - P_{ij}(t)\right) \qquad (3)$$

where *e* is the rate of conversion of resource into new biomass, and *m* is the rate of loss of biomass of each species in each patch. The first term describes the consumption and conversion of biomass by species; the second term describes the decrease in species biomass as species die; the third term describes species immigration from other patches; the fourth term describes species emigration to other patches. The parameter a is the per-capita rate at which individuals are moving out of a patch, and the proportion of dispersers coming into any given patch is then $\frac{1}{M-1}$, where M is the number of patches (Plitzko & Drossel 2015).

Our model assumes that the environment is constant within each patch, but environmental variation occurs between patches (Ai & Ellwood 2022). In Loreau *et al.* (2003), the environmental value of each patch was the function of time and the initial environmental value of each patch, making the C_{ij} of each patch also a function of time. The Loreau *et al.* (2003) study considered spatial insurance effects, and how the diversity and functioning of the metacommunity emerges from the spatial dynamics of new species coming into and proliferating in local communities as the local environment changes.

Simulated patch removal and dispersal behaviors

We ran each simulation to reach the first approximate equilibrium (when the total biomass of all species is a fixed point and the biomass of each species becomes saturated, see Fig. S1), and then removed *a patch* from the metacommunity and ran the model until the second approximate equilibrium. We carried out this patch removal and subsequent simulation individually for each patch. We included two different dispersal behaviors that would have major consequences for the structure of the metacommunity once the habitat is lost. Under directed dispersal, when we remove a patch, we remove all of its connections to other patches, lowering the number of patches M by 1 in the third term of Eq. 3 (since the same dispersers are now spread over fewer patches), and maintain dispersal between the remaining patches. Under undirected dispersal, we do not remove a patch and its connections from the system. Instead, we assume that the patch was destroyed permanently for any species, but dispersal to it is still occurring through the existing connections (Fig.1A). Species dispersing to the destroyed patch would die immediately.

Model parameters

Model parameters were: M=50, S=50, e=0.2, m=0.2, I_j=165, l_j=10, $P_{ij}(0)$=10 for all i and j. Some of these parameters were set as they were in other studies (Loreau *et al.* 2003; Gonzalez *et al.* 2009; Shanafelt *et al.* 2015; Thompson *et al.* 2017). If the total biomass of a species across the whole metacommunity fell below five, we considered the species extinct in the metacommunity. This metacommunity scale extinction cutoff is comparable to, but leads to simpler and faster code than, the patch-scale cutoff of 0.1 used in previous studies (Loreau *et al.* 2003; Shanafelt *et al.* 2015), as it is equal to 0.1 times the number of patches M. Furthermore, the small population size effects that influence extinction risk (breakdown of mating and defense systems, and demographic or environmental stochasticity effects) may be more accurately considered as acting at the metacommunity scale when there is significant dispersal. We studied patch removal under various consumption rates and magnitudes by varying *b* (which consumption rates are inversely proportional to) from 10, 20, 21, 22, 23, 24, and dispersal rates from 0.01, 0.02, 0.03, 0.04, 0.05, 0.06, 0.07, 0.08, 0.09, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, 1. These *b* values were chosen to confirm that the behavior of the model was consistent with *b* close to values causing collapse of the metacommunity (*b* above 24).

Metapopulation simulations

To improve our overall understanding of community-level observations, we also designed a metapopulation model to look at the effects of patch removal at the species-level. The metapopulation is a version of the model with three patches (i.e. the M=3, S=1 case of our model). This kind of metapopulation model is able to eliminate the interaction between species, instead focusing on the match between the environmental condition of the removed patch and the optimal niche of the species. A metapopulation with three patches is the simplest topology, as it is still a metapopulation after one patch is removed. Moreover, the consequences of removing a patch would be more obvious in this kind of metapopulation than in metapopulations with many patches. We considered two scenarios, one in which the species was best adapted to the patch with harsh environmental condition, and one in which the species was best adapted to the patch with benign environmental condition. These scenarios correspond to the patches with harsh and benigh environment in the metacommunity model, where each patch has the best adapted species. The environmental condition *E* for the three patches was 1, 0.98 and 0.96 (these were the first three patches in the metacommunity model) in both scenarios, while the species optimal niche value was *H*=1 in the first scenarios and *H*=0.98 in the second scenarios (these were the first and second species in the metacommunity model). We removed patches with different environmental conditions and assessed the extinction risk and ecosystem function debt in the metapopulation model, allowing a deeper insight into the metacommunity results. For the metapopulation simulations we used *I*=67.6, *a*=0.01 and *b*=10.

Experimental Design

Each simulation ran for 4×10^6 generations (specifically, we set per-capita death rate as *m*=0.2, and simulated the model from $t = 0$ to $t =$ 2×10^7, which corresponds to 2×10^7×0.2=4×10^6 generations) to reach approximate equilibrium (Fig. S1), at which point *a patch* was removed, before continuing to run for 4×10^6 generations to reach a second approximate equilibrium post habitat destruction. We explained patch removal under directed and undirected dispersal behavior in the section *Simulated patch removal and dispersal behaviors*.

We also ran each simulation without patch removal for 8×10^6 generations, to compare with the patch removal case, and to identify whether species go extinct due to metacommunity dynamics or habitat loss. For a given species, 1) if it goes extinct before the first approximate equilibrium, this extinction is caused by metacommunity dynamics; 2) if it goes extinct during the first to second approximate equilibrium, but the persistence time is shorter when we remove a patch than when we don't, habitat loss has hastened the extinction of the species already destined for extinction due to metacommunity dynamics; 3) if it goes extinct during the first to second approximate equilibrium under patch removal but not without it , then the extinction is driven by habitat loss; 4) if it does not go extinct during the first to second approximate equilibrium, then it's extinction risk is not substantially affected by metacommunity dynamics or habitat loss. We only focused on the species which go extinct due to habitat loss, or whose extinction is hastened by habitat loss, i.e. species falling into categories 2 and 3 above. Revealing the nature of these extinctions due to patch removal allowed us to specify extinction regimes across dispersal and resource consumption rates.

We recorded the biomass of all species in each patch at the first approximate equilibrium of each simulation to see the distributions of community composition and ecosystem function along heterogeneous environments. We also recorded the persistence times of each species across the whole metacommunity after patch removal to measure the risk intensity of *each extinct species due to patch removal* as the inverse of persistence time (unit as generations^-1, as recommended by Grimm and Christian in 2004). To measure the magnitude of extinction debt, we calculated the number of extinct species as the total number of extinct species at the second approximate equilibrium minus the number of species going extinct immediately after patch removal. The proportion of species going extinct was calculated as the number of extinct species divided by the number of species before removal but after the initial approximate equilibrium. To study total ecosystem function debt, we calculated the total biomass change as the mean biomass across the M-1 remaining patches at the second approximate equilibrium minus the mean biomass of each patch before removal, and we also calculated the immediate biomass change as the mean biomass in the M-1 remaining patches after patch removal minus the mean biomass before removal. Under both directed and undirected dispersal, biomass change was given by the total biomass change minus the immediate biomass change upon patch removal. The proportion of biomass change was the biomass change over the mean biomass of each patch before removal. With these data, we analyzed how the magnitude of extinction and ecosystem function debt changed with dispersal rate and the environmental condition of each removed patch under directed and undirected dispersal behaviors.

We used the forward Euler method to simulate the differential equations with dt=0.01. The simulation code was written in Java, and data were analyzed in R version 4.1.3 (R 2022).

Results

Extinction regimes under different dispersal and consumption rates

Dispersal and consumption rates determine which species go extinct after habitat loss. We distinguish three extinction regimes (Fig. 2A) outside of a low consumption rate zone where no species can coexist before patch removal (white area in Fig.2A).

Under low dispersal and medium to high consumption rates (green area in Fig. 2A), removing a patch causes the species best adapted to it to go extinct under both directed and undirected dispersal (Fig. 2B and 2C). Hence in this regime, only the species best adapted to the patch being removed are at risk. However, that risk (measured as the inverse of persistence time) varies and is highest under the removal of the harsh environment patches (Fig. 2B and 2C). The extinction risk pattern in this regimes makes intuitive sense given the pattern of biomass found before patch removal, in which the biomass of each species is quite low other than in the patch it is best adapted to (Fig. S2A).

Under medium dispersal rates and medium to high consumption rates (blue area in Fig. 2A), removing a patch can cause both the species adapted to it and the next most closely adapted species to go extinct under both directed and undirected dispersal (Fig. 2D-G). This makes sense given the pattern of biomass found before patch removal (Fig. S2B and S2C) in this extreme, where species have substantial biomass in patches similar to the ones they are best adapted to, and hence removal of such patches could have a large impact on their metacommunity biomass. In addition, species adapted to harsh environments already destined for extinction may go extinct faster due to patch removal under directed dispersal (Fig. 2D), even when patches with very benign environments are removed (see Fig. S3, where the persistence time of species with optimal niche value as 0.16 in the case without removal is 5.8×10^5 generations, but it is 1.34×10^5 when patch with environmental condition as 0.51 is removed). In this regime, the species best adapted to the removed patch is at the greatest risk, and the risk intensity decreases with the difference between the species preferred condition and the environment of the removed patch (Fig. 2D-G).

Under high dispersal and high consumption rates (dark brown area in Fig. 2A), the metacommunity is dominated by two species before patch removal (Fig. S2D), removing a patch may cause one of the remaining species to go extinct (Fig. 2H) under directed or undirected dispersal with high consumption rates (Fig. S4), or all of them to go extinct under undirected dispersal with relatively low consumption rates (Fig. 2I). In cases where the metacommunity has an odd number of patches and is dominated by only one species before patch removal (Fig. S5), that species persisted after patch removal, in both the directed and undirected dispersal cases. Hence in this regime, extinction risk is sensitive to the patch structure and dispersal context. See Fig. S6 as the rescaled version of Fig.2.

The magnitude of extinction debt and ecosystem function debt or credit under various dispersal rates

We consider the dependence of extinction debt on dispersal rate, measuring extinction debt as the number (Fig. 3A, B) and the proportion (Fig. 3C, D) of species going extinct in the whole metacommunity. Generally, the mean number of extinct species first increased and then decreased with dispersal rate in both the directed and undirected dispersal cases for all consumption rates (Fig. 3A, B). However, the proportion of species going extinct increased with dispersal rate for all three maximum consumption rates under both directed and undirected dispersal, because total species richness before patch removal declines with dispersal at high dispersal (Fig. 3C, D). Under directed dispersal behavior, habitat loss can result in some small benefits to the mean ecosystem function of the remaining patches for all consumption and dispersal rates (y-axis are positive in Fig. 3E, G). This benefit had a mostly positive relationship with dispersal rate under all consumption rates, especially when measured as a proportional increase in biomass (Fig. 3G). Under undirected dispersal, there was always an ecosystem function debt. Mean and proportional biomass decreases were largely more substantial under higher dispersal rates (Fig. 3F, H).

The magnitudes of extinction debt and ecosystem function debt or credit with environmental conditions of the removed patch

Variation in extinction debt with environmental conditions of the removed patch occurred in regime 2 (in the other two regimes a single species went extinct regardless of which patch was removed). Under both directed and undirected dispersal, removing a patch with benign environmental conditions caused more species to go extinct than removing a patch with harsh environmental conditions (Fig. 4A, B).

Under directed dispersal behavior and at low dispersal rates, a small ecosystem function credit occurred no matter which patch was removed (Fig. 4C). At medium to high dispersal, larger ecosystem function credit occurred only when harsh patches were removed (Fig. 4E, G). Under undirected dispersal, there was always an ecosystem function debt (Fig. 4D, F, H). In most scenarios, the relationship between change in average biomass of remaining patches and the position on the environmental gradient of the lost patch was U-shaped (Fig. 4C-H)—meaning that change was always the least positive or the most negative when patches with benign environments were removed. In other words, the removal of the benign patches had either the least benefit, or caused the largest debt, depending on whether there were ecosystem credits or debts.

Verifying extinction debt and ecosystem function credit mechanisms in metapopulations

Under directed dispersal, habitat loss benefitted the mean biomass in the remaining patches in the metapopulation analysis. The poorer the match between the species and the environment in the removed patch, the higher the mean biomass for each of the remaining patches (Fig.5A). We also hypothesized that extinction risk is often highest when harsh habitat patches are removed in our metacommunity model because the species in those patches were on average more poorly adapted to remaining patches. In support of this, we found that the metapopulation experienced the greatest risk of extinction upon removal of the best patch for the species when that best patch was a harsh environment rather than a benign environment (Fig. 5B). Under undirected dispersal, the population went extinct regardless of which patch was removed.

Discussion

Existing theory of extinction and ecosystem function debt is limited, especially for heterogeneous landscapes. Here we contribute to the foundations of this theory through the study of the effects of patch removal in a metacommunity model with patches differing in environmental conditions. We find a number of behaviors that make intuitive sense, such as the likelihood of highly adapted species going extinct, and patches with benign environment causing more extinctions when removed. We also find more surprising behaviors, such as the exacerbation of already existing extinction risk of species adapted to harsh environments, even when patches with very different environmental conditions were removed, an increase in the proportion of species going extinct with dispersal, with the possibility of ecosystem credit in the remaining patches under one of the two types of dispersal we explored.

Trends in extinction risk across species, with different patches removed, and with dispersal

In our model, the number of species is equal to the number of patches, and each species has a patch to which it is best adapted. For example, the species with H_i =0.5 is best adapted to the patch with E_j =0.5. The diagonal in each panel of Fig. 2 indicates the species best adapted to each patch. As in previous studies, species sorting under low dispersal rates allowed each species to dominate its preferred patch (Mouquet & Loreau 2003; Suzuki & Economo 2021; Ai & Ellwood 2022). Hence, removing a patch tends to cause the species better adapted to this patch to go extinct, resulting in the diagonal risk zones in Fig. 2B-G. Species with central niches have numerous relatively suitable habitats and are therefore less at risk than species with extreme niches and few suitable habitats. We show that this can be understood in terms of the principles applying to metapopulations, in that removing the best patch for that species creates less of a risk if that patch is benign than if that patch is a harsh environmental condition relative to the gradient experienced by that metapopulation (Fig. 5B). At medium dispersal rates, species transit quickly between patches, and hence patches with similar environmental conditions play important roles in maintaining species even though they are sub-optimal patches. Regardless of which patch is removed, the species adapted to harsh environments are at greater risk of extinction; their low competitive ability prevents them from increasing their productivity in any of the patches, and habitat loss reduces their biomass and further exacerbates their extinction.

At high dispersal rates and with an even number of patches, mass effects generate two dominant species (with H_i around 0.5, see Fig. S2) that are well-matched regional best competitors because they are equal in the number of patches they are better adapted to. Patch removal can then disrupt this balance and cause extinction of one of the species, or both if they both require large numbers of patches to persist, further leading to horizontal risk zones (Fig.2H and I). This constitutes a high proportion of species going extinct at high dispersal (Fig. 3C, D), since the regional species richness is so low at high dispersal, due to increased competition for patches (Mouquet & Loreau 2003; Ai & Ellwood 2022).

Ecosystem debts under undirected dispersal but credits under directed dispersal

Under directed dispersal in metapopulations, the harsher the removed patch, the higher the mean biomass became for remaining patches (Fig. 5A). Dispersers which previously dispersed to the less productive patches dispersed to more productive patches after patch removal, which increased the biomass. Similar patterns could be seen in the metacommunities, especially when harsh patches were removed (Fig. 4C, E and G). However, while the mean biomass increased greatly in the metapopulation, it increased only slightly in the metacommunity (see y-axis of Fig. 3E, G and 5A), and in addition, removing a patch caused the whole biomass of the metacommunity to decrease, whereas it increased in the metapopulation (Fig. 5A). This is because in the metacommunity, the removed patch may have been the worst habitat for some species, but the best habitat for other species, hence removing a patch would cause the mean biomass of some species to increase and others to decrease. Moreover, removing any patch from a metacommunity caused species to lose habitat, thus increasing extinction, whereas in a metapopulation only the removal of the best patch would cause it to go extinct.

Under undirected dispersal, biomass decreased in remaining patches after patch removal (Fig. 3F, H). This was driven partly by the fact that a higher proportion of species went extinct at high dispersal rates under undirected dispersal than under directed dispersal (Fig. 3C, D). Also, and perhaps more importantly, under undirected dispersal none of the individuals dispersing to destroyed habitats contribute to ecosystem function.

Comparison with existing theory of extinction and ecosystem function debt

Tilman et al. (1994), one of the most influential theoretical studies of extinction debt, concluded that when habitats are lost, extinction risk is greatest for the system's best competitor. Implemented within the competition-colonization trade-off framework, Tilman's model revealed that habitat destruction weakens the colonization rate of all species, but it especially impacts the system's best competitor because of its lower colonization rate. Whereas Tilman's model relied on the strength of trade-offs between competition and colonization, our model focuses on heterogeneous metacommunities, and hence the "best competitor" varies across habitats according to their environmental condition.

The specific assumptions of perfect trade-offs in Tilman's model have been criticized as being unrealistic (Loehle & Li 1996; Banks 1997; Malanson 2008). Moreover, relaxing the assumptions leads to very different results, such as species losses occurring more quickly than predicted by the model with perfect trade-off. Moreover, this included not just competitive species, but all types of species could go extinct due to habitat destruction (Loehle & Li 1996; Banks 1997). In addition, recent studies (Li *et al.* 2020; Liao *et al.* 2022; Zhang *et al.* 2023) relaxed the strict competition-colonization trade-offs through weakening relative competition strength or violating the strict hierarchical competition by considering intransitive competition, and found that the species loss oscillated with disturbance extent rather than following a simple monotonic relationship as predicted. Even in these studies, the best competitor suffered the most impact as the disturbance extent increases (see Fig.2 in Liao *et al*. 2022).

Mouquet *et al.* (2011) investigated extinction debt in heterogeneous metacommunities, concluding that less competitive species at the regional scale are more strongly affected by habitat destruction, especially at high dispersal rates. Here we noted that these regionally less competitive species, adapted to harsh environments, had relatively low biomass before habitat loss (Fig. S2B, S2C). We found that in fact, because of the metacommunity dynamics, these species went extinct even without habitat loss, but it took a long time. Habitat loss can accelerate their extinction but it is not the root cause. In nature, it is difficult to identify the drivers of species extinctions because most systems are not at a steady state, and so species extinctions might result from community dynamics, or extrinsic factors such as habitat loss.

Implications of our results for biodiversity conservation

Extinction debt provides a window for species restoration and landscape management (Kuussaari *et al.* 2009; Wearn *et al.* 2012), but which recovery plans should be applied depends on many factors. Huxel and Hastings (1999) concluded that, “either restoring patches adjacent to occupied patches or reintroducing the species into restored patches increases the efficacy of the recovery effort”. Our results indicate that the type of extinction regime must be identified before deciding which species to protect during restoration efforts, since different species are at risk in different regimes. For example, when the most adapted species is most at risk, efforts should focus on reintroducing the lost habitat and its best competitors, whereas in the regime in which species adapted to the neighboring patches are also at risk, restoring the adjacent patches should also be a priority. In some management cases, such as quantifying the size of reservation areas with limited resources, protecting habitats with benign environments should be prioritized, because losing this type of habitat will cause the most extinction and ecosystem function debt since a wide range of species are adapted to those habitats. Our model suggests that, regardless of which habitats are lost, the total biomass of the whole metacommunity is lower, so the habitats with harsh environments should also be protected. Undirected dispersal may cause species to continue dispersing to the destroyed habitat, meaning that restoring the lost habitat immediately would be a good way of restoring species richness and ecosystem function. In summary, our results suggest that restoration actions should be guided by extinction regime, dispersal behaviors, and landscape heterogeneity.

Future Directions

Metacommunity theory is the theoretical framework for this model, and there are some limiting assumptions which could be relaxed in future studies. First, most natural landscapes are not spatially implicit, and community composition and ecosystem function depend on the spatial configuration of patches, such as distance between patches, topologies of metacommunities, patch size and shape etc. (Suzuki & Economo 2021; Ai & Ellwood 2022; Zhang *et al.* 2023). Meanwhile, some other parameters in our model could also be relaxed, for example, set variable dispersal ability in species, or set variable dispersal networks (Zhang et al. 2020), or consider the stage structure in the dispersal process, or even associate the dispersal among patches with metacommunity topologies. These kinds of assumptions would help to generalize the model and the results.

Conclusion

We developed a new theory of extinction and ecosystem function debt in a heterogeneous landscape. Habitat loss hastens the extinction of species adapted to extreme environments, and always causes extinction debt under both directed and undirected dispersal. Interestingly, habitat loss causes ecosystem function debts under undirected dispersal, but credits under directed dispersal. Both extinction debt and ecosystem function credit/debt increase with dispersal rate. Our study indicates that extinction regime, dispersal behavior, and the environmental conditions of habitats should be considered before taking conservation actions to mitigate the effects of habitat loss.

Data availability statement:

This theoretical study has no data; codes are available at link: https://datadryad.org/stash/share/z0Mrqixl9wJEzgLJN7GRi9oThNqiz7EoA0t3rm89_tM.

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Figure captions

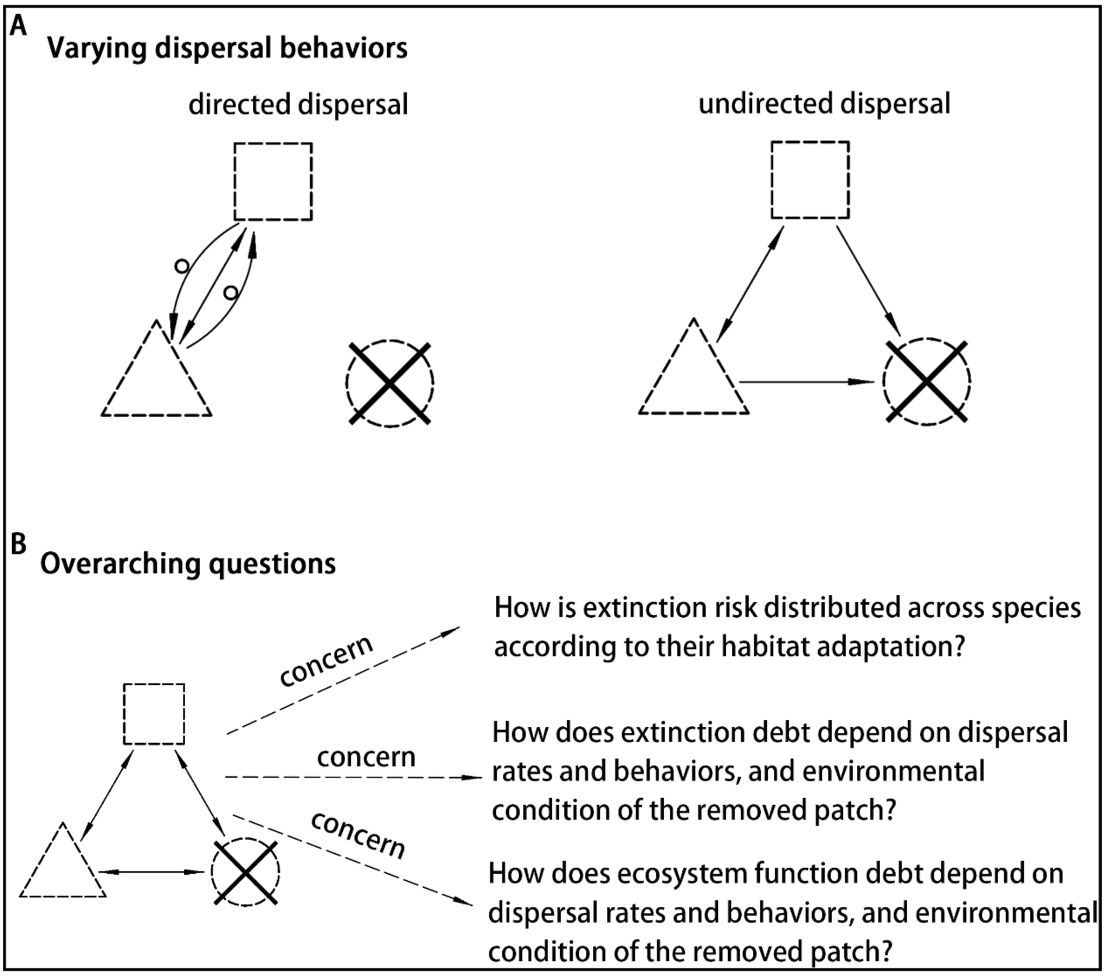
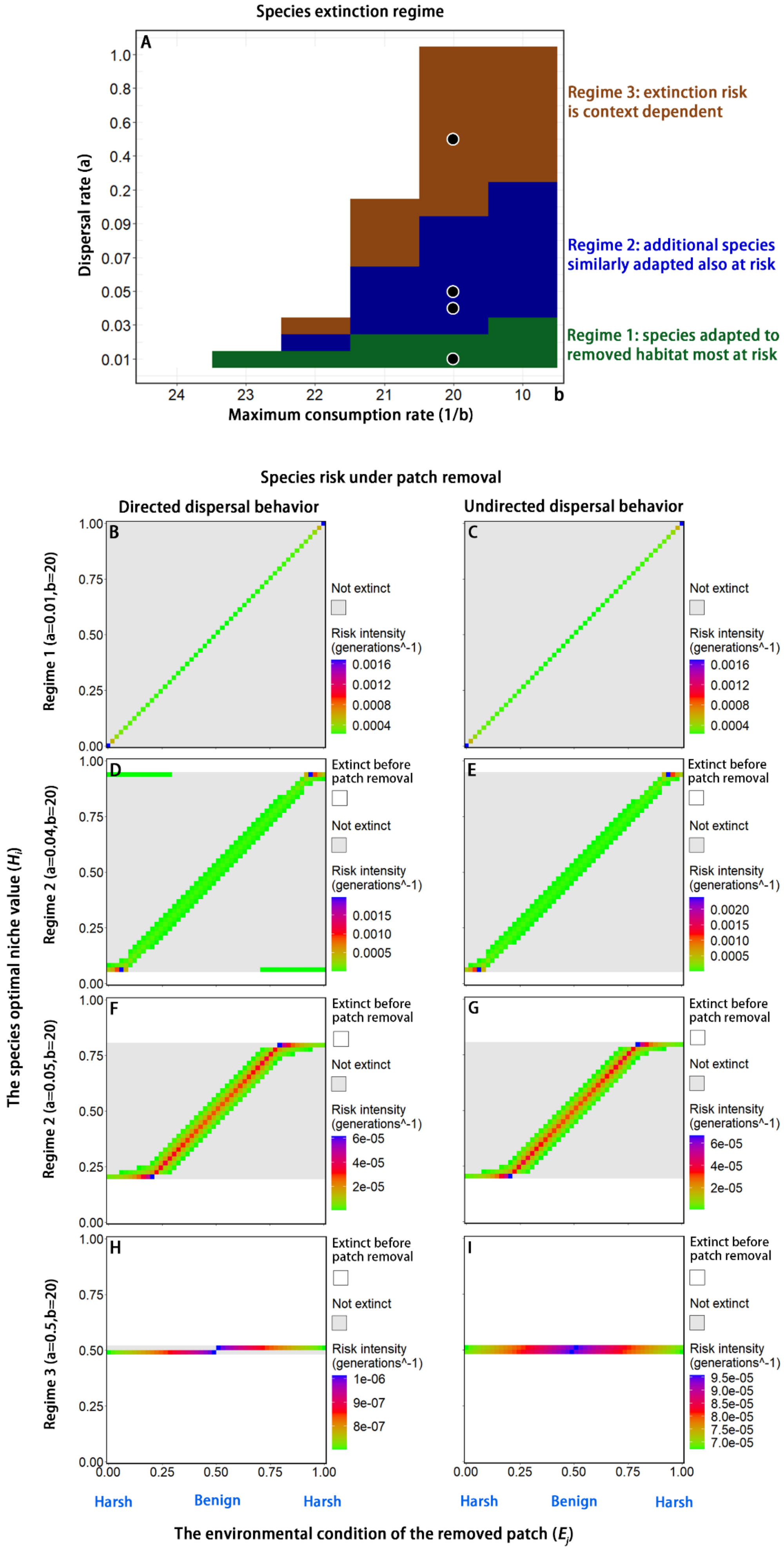


Figure 1 Dispersal behavior and questions asked. Different shapes with dashed outlines represent patches with different environmental conditions. The solid line with arrows indicates the direction of dispersal between patches. Panel A shows the two dispersal behaviors we consider: directed dispersal (left panel) and undirected dispersal (right panel). Under directed dispersal, the individuals which were dispersing to the destroyed habitat patch instead disperse to remaining habitats, represented by lines with round shapes if we remove a round patch. Under undirected

dispersal, individuals continue to disperse to the destroyed habitat (represented by lines with single arrows) and are lost. Panel B shows a diagram illustrating the patch removal in a heterogeneous metacommunity and lists the questions raised when a patch is removed, for example, the round patch has been removed here. Questions are explained in detail in the main text. For simplicity, we show a metacommunity with three patches, but our model includes 50 patches.



Species extinction regime
A
Dispersal rate (a)
Maximum consumption rate (1/b)
Regime 3: extinction risk is context dependent
Regime 2: additional species similarly adapted also at risk
Regime 1: species adapted to removed habitat most at risk
Species risk under patch removal
Directed dispersal behavior
Undirected dispersal behavior
Regime 1 (a=0.01,b=20)
Regime 2 (a=0.04,b=20)
Regime 2 (a=0.05,b=20)
Regime 3 (a=0.5,b=20)
The species optimal niche value (H_i)
Extinct before patch removal
Not extinct
Risk intensity (generations^-1)
Harsh
Benign
Harsh
The environmental condition of the removed patch (E_j)

Figure 2 The regimes of extinction behavior under patch removal in the space of possible consumption and dispersal rates (A), and the patterns of extinction risk after patch removal in each regime (B-I). In panel A, the colored areas represent distinct extinction regimes, whereas the four black dots indicate the values of consumption and dispersal rates where we have shown species risk in panels B-I. In the white area to the left of the colors in A, no species can persist in the metacommunity even in the absence of patch removal. In B-I, squares of color indicate the extinction risk (measured as the inverse of the number of generations the species persists after patch removal) of the species with the corresponding environmental niche value (H_i) on the vertical axis, under removal of the patch with the corresponding environmental condition (E_j) on the horizontal axis. Hence colors on the diagonal indicate a species' extinction risk when the patch it is best adapted to (the patch for which $E_j = H_i$) is removed, and colors just to the left and right of the diagonal indicate its risk when a patch close in environmental condition to its environmental niche value is removed. White areas mean that species went extinct before patch removal due to metacommunity dynamics, grey areas mean that species did not go extinct under removal of that patch, and colorful areas mean that species went extinct due to patch removal. As dispersal increases, the pattern of extinction risk changes from only the species best adapted to the removed habitat being at risk (first dot, B-C), to species adapted to similar habitats also being at risk (2nd and 3rd dots, D-G). In the latter, species with edge environmental niches may also be hastened towards extinction when very different habitat patches are removed (2nd dot, D). At high dispersal (4th dot, H-I), only 1-2 species persist before patch removal, and one or both are vulnerable to extinction upon patch removal. Extinction regimes (panel A) are the same both under directed and undirected dispersal. See text for a detailed description of these regimes.

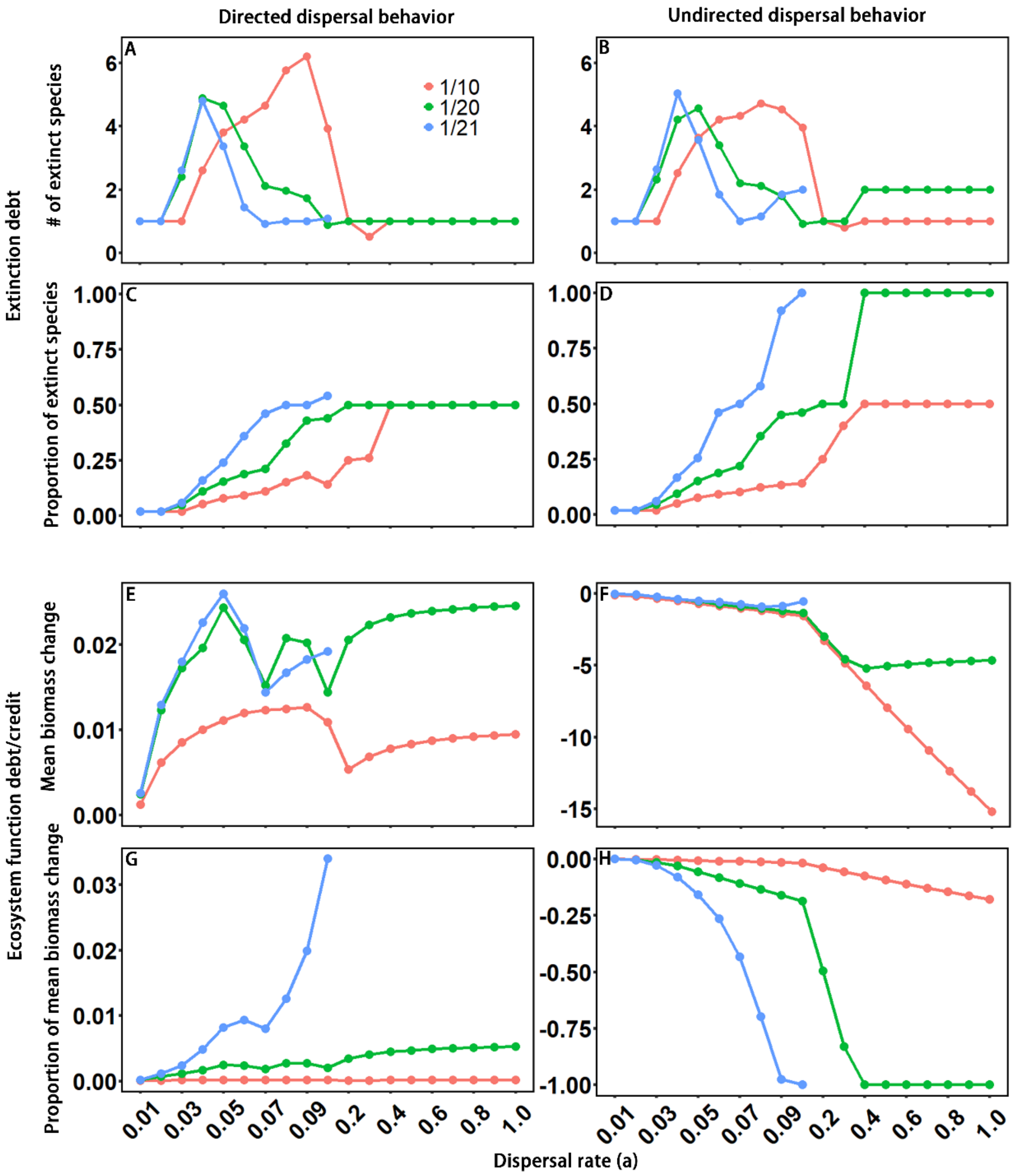


Figure 3 The magnitudes of extinction debt (A-D) and ecosystem function debt/credit (E-H) across dispersal rates. The left column of panels shows behaviors under directed dispersal, and the right undirected dispersal. Line colors differ by consumption rate as indicated in the legend in A. Extinction debt is shown as both the number of species going extinct (A, B) and the proportion of species going extinct (C, D). Ecosystem function debt/credit is shown as both the biomass change (E, F) and

proportion of biomass change (G, H). In panel E-H, positive y-axis means ecosystem function credit, whereas negative means ecosystem function debt. Key trends are that extinction debt generally increases with dispersal when measured as a proportion of species, and that directed dispersal can result in an ecosystem function credit (but extinction debt), while undirected dispersal always results in ecosystem debt. Note that results differ somewhat for an odd number of patches but on the whole extinction debt also increases with dispersal in that case.

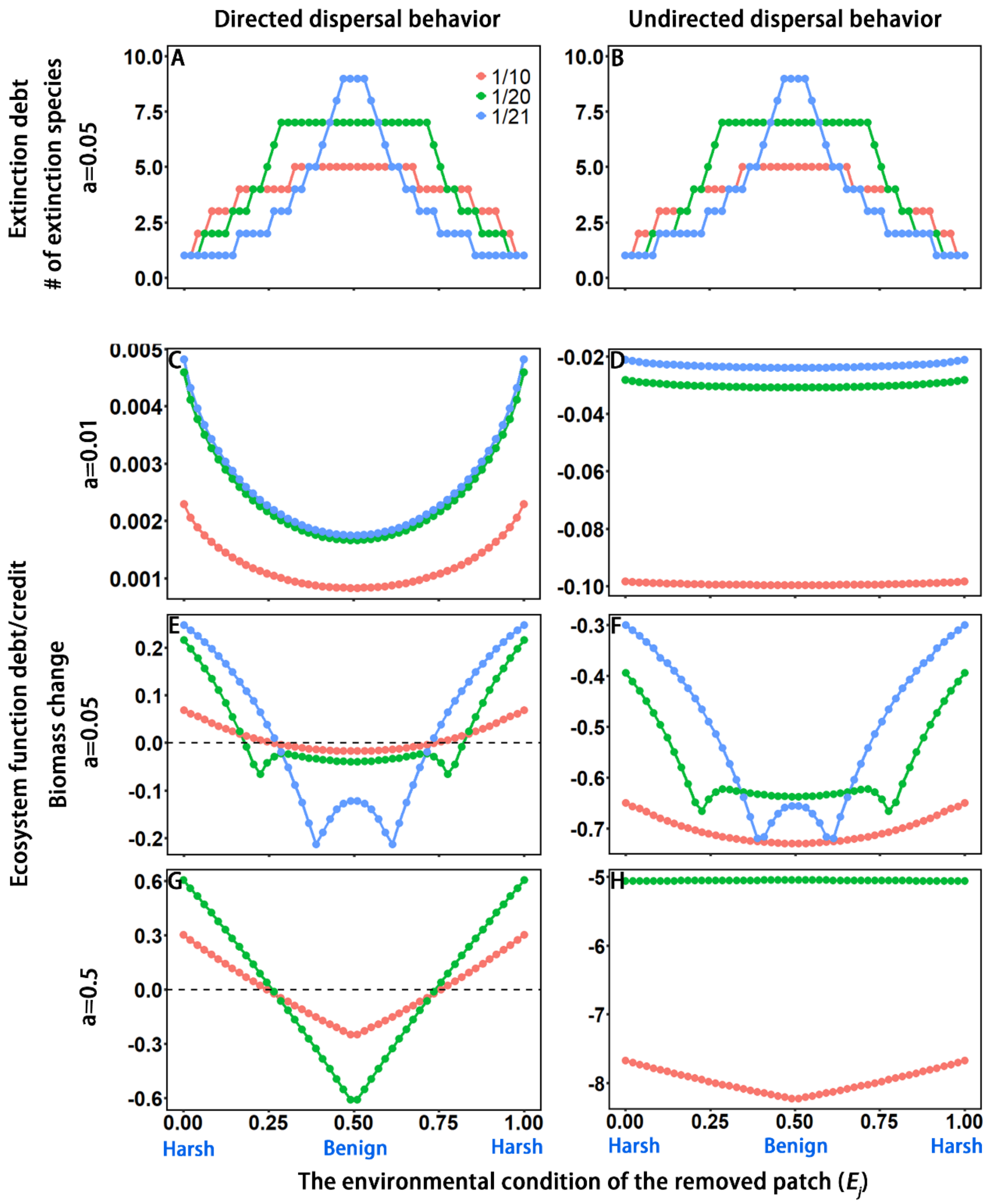


Figure 4 The dependence of the magnitude of extinction debt (A, B) and the magnitude of ecosystem function debt (C-H) on the environmental condition of the removed patch. The left column of panels shows behaviors under directed dispersal, and the right undirected dispersal. Line colors differ by consumption rate as indicated in the legend in A. Panels A and B represent the number of species going

extinct for dispersal rate a=0.05 in the extinction regimes "additional species similarly adapted also at risk". Panels C-H show ecosystem function debt/credit as the biomass change for three different dispersal rates (a=0.01, 0.05, and 0.5, from top to bottom row). The species cannot coexist when the dispersal rate is greater than 0.1 at low consumption rate (b=21), so there are no data for that consumption rate in the last row (G, H). The dotted line in panel E and G is for a change in biomass=0 since they include both positive and negative biomass change. In panel C-H, positive values on the y-axis mean ecosystem function credit, whereas negative values mean ecosystem function debt. A key trend is that the removal of benign habitats has the largest effects. There are 50 patches here. See details in the main text.

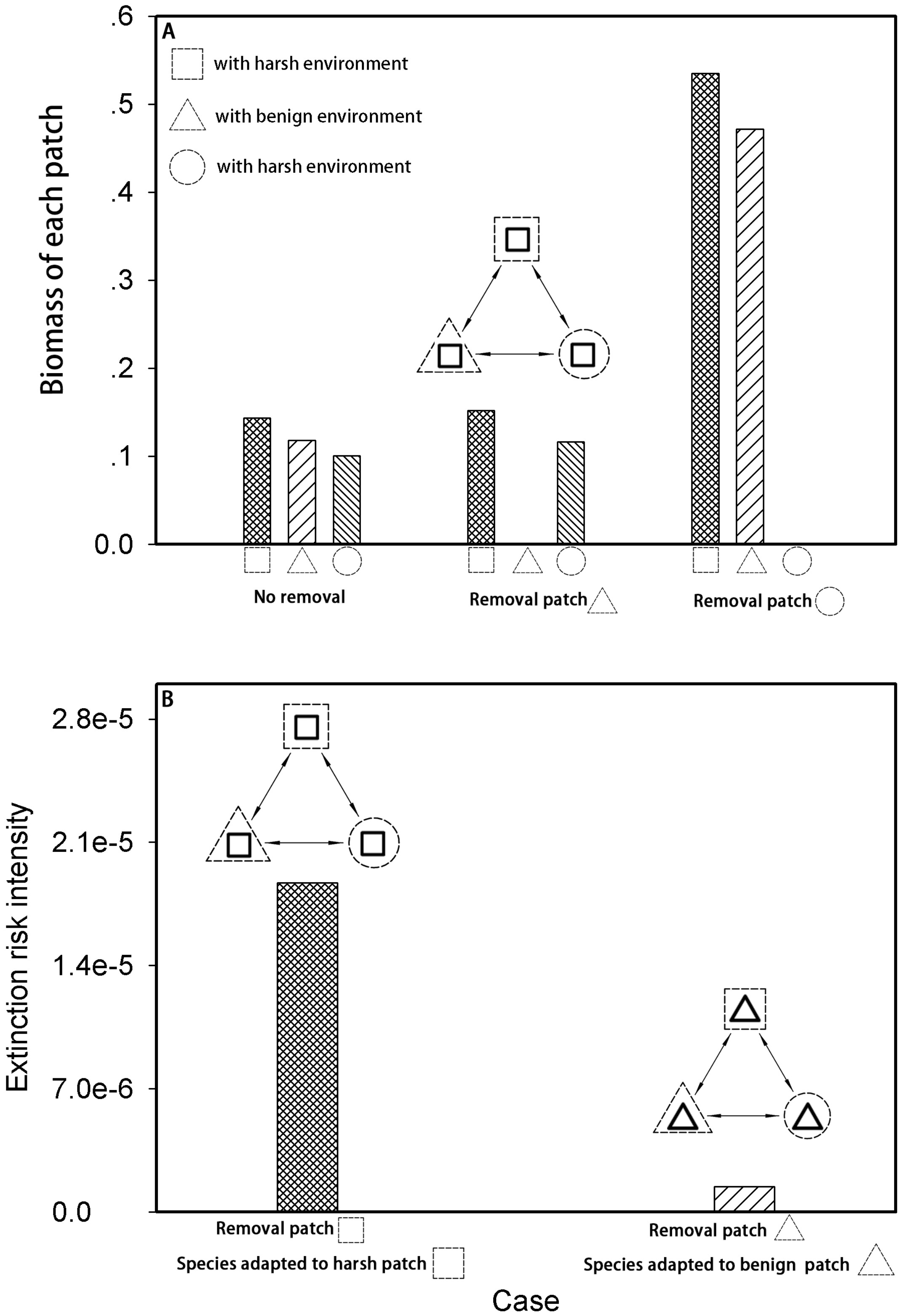


Figure 5 The biomass of each patch (A) and extinction risk intensity (B) with patch removal in a metapopulation. Each metapopulation has three patches (square,

triangle, and circle with dashed line) and one species (the shape with solid line). For the first scenario, i) the species (represented by a square solid line) is best adapted to the square patch (see the diagram in panel A and the left diagram in panel B) and that patch has a harsh environmental condition, while the triangle patch is the next-best patch, and the circle patch is the worst patch for the species (see *E* for patches and *H* for species in the main text); for the second scenario, ii) the triangle patch is the best patch for the species (represented by a triangle solid line) and has a benign environmental condition (see the right diagram in panel B, see detailed descriptions in the main text).