

Extinction and Ecosystem Function Debt Across Dispersal Rate and Behaviour in a Heterogeneous Metacommunity Model

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1 **Title: Extinction and ecosystem function debt across dispersal rate and behavior**
2 **in a heterogeneous metacommunity model**

3

4 **A short running title:** Extinction and ecosystem function debt

5 The codes can be accessed via the link:

6 https://datadryad.org/stash/share/z0Mrqixl9wJEzgLN7GRi9oThNqiz7EoA0t3rm89_t

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8

9 **Abstract**

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

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

22 **Results:** We reveal three species extinction regimes as dispersal increases: 1. species
23 most adapted to the removed habitat are most at risk; 2. similarly adapted species are
24 also at risk; 3. patch removal shifts competitive balance among the few species
25 coexisting at high dispersal, where competition is strong. We find surprisingly that
26 destruction of habitat can hasten the extinction of those species best adapted to harsh

27 environments, and that the proportion of diversity at risk from extinction actually
28 increases with dispersal because competition is intense there. Finally, there can be a
29 small ecosystem credit, but extinction debt, when dispersers reroute to potentially
30 more favorable remaining habitats (directed dispersal), especially when harsh
31 environments are removed. However, ecosystem debt occurs and can be large under
32 undirected dispersal.

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

37

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

40

41 **Introduction**

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

54 As well as causing extinction debt, habitat disturbance also causes ecosystem
55 function debt, which refers to the delayed loss of ecosystem functions such as
56 productivity or biomass (Haddad *et al.* 2015; Isbell *et al.* 2015). Ecosystem function
57 debt results from species loss and is therefore correlated with extinction debt (Haddad
58 *et al.* 2015; Isbell *et al.* 2015). However, it is possible for ecosystem function to

59 recover after habitat disturbance, even in the absence of species reintroductions. This
60 is because disturbance alters the competitive abilities of species, allowing productive
61 species to dominate entire habitats. We refer to the increase in ecosystem function
62 after habitat disturbance as ecosystem function credit. Extinction debt attracts the
63 most attention because it provides time windows for conservation actions to rescue
64 rare species from extinction (Hanski & Ovaskainen 2002; Malanson 2008; Wearn *et*
65 *al.* 2012; Halley *et al.* 2014; Highland & Jones 2014; Chen & Peng 2017; Otto *et al.*
66 2017; Figueiredo *et al.* 2019; Makishima *et al.* 2021; Ridding *et al.* 2021). However,
67 studies of ecosystem function debt/credit are limited (also mentioned by Gonzalez *et*
68 *al.* 2009), and as far as we know, none of these studies consider a heterogeneous
69 landscape.

70 The severity of extinction debt is usually measured as the number or
71 proportion of “delayed extinctions as a consequence of ecosystem perturbation” as
72 definition by Figueiredo *et al.* (2019), which means the number / proportion of
73 species extinct in the long run as a result of the perturbation, minus the number /
74 proportion of species extinct immediately after it. Similar definitions are used in the
75 other studies (Kuussaari *et al.* 2009; Jackson & Sax 2010; Halley *et al.* 2016;
76 Figueiredo *et al.* 2019). Meanwhile, a given species’ extinction risk could be

77 measured by the time delay index, that is the persistence time of extinct species since
78 habitat loss (Hanski & Ovaskainen 2002). If the time delay index of a species is
79 higher, its extinction risk is lower (Grimm & Wissel 2004). Previous theoretical
80 studies have extrapolated ecosystem function debt from the number of species lost
81 based on correlations between community biomass and species richness (Isbell *et al.*
82 2015). Ecosystem function debt/credit could be measured more directly as the amount
83 of biomass lost in the long run minus the amount lost immediately after habitat
84 disturbance: if this figure is positive then ecosystem function credit has occurred; if it
85 is negative, then ecosystem function debt has occurred.

86 Environmental heterogeneity in space is key to maintaining and shaping
87 species richness and ecosystem function (Ben-Hur & Kadmon 2020; Davies *et al.*
88 2021; Thompson *et al.* 2021). In recent decades there have been a number of
89 theoretical advances towards understanding environmentally heterogeneous
90 landscapes, through the study of metacommunity models with discrete communities
91 of different environmental conditions, all linked by dispersal (Thompson *et al.* 2014;
92 Fournier *et al.* 2017; Thompson & Gonzalez 2017; Thompson *et al.* 2017; Leibold &
93 Chase 2018; Thompson *et al.* 2020). These models have also begun to be employed in
94 the development of theories of extinction debt, though they have only explicitly

95 considered the effects of environmental heterogeneity on extinction debt to a limited
96 degree (see related studies in Mouquet *et al.* 2011; Thompson *et al.* 2017).

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

111 We use this metacommunity modeling approach to consider additional
112 questions fundamental to understanding the nature of extinction and ecosystem

113 function debt in a heterogeneous landscape (see Fig 1B). This includes basic
114 questions such as how extinction debt is distributed across the species adapted to
115 different environmental conditions, and how this may depend on how the lost habitat
116 fits into the distribution of habitats represented, and the rate of dispersal between
117 patches. We also ask whether the overarching effects of dispersal on extinction and
118 ecosystem function debts, and whether the basic tendency towards ecosystem function
119 debt one expects in homogeneous environments, is the same in heterogeneous
120 environments. When landscapes are homogeneous, one would anticipate, and recent
121 theory using a neutral model framework shows (Thompson *et al.* 2019), that higher
122 dispersal among patches would generally limit these debts. One would also anticipate
123 that patch removal can have only negative or at best no consequences for the
124 ecosystem functioning in the remaining patches. However, habitat heterogeneity
125 creates circumstances under which these ideas may not apply. Species competing
126 along an environmental gradient may do so more intensely when their dispersal rate is
127 higher, in which case their competitive balance may be more sensitive to patch
128 removal. Also, when a patch is removed, species better adapted to other patches could
129 fare better under directed dispersal, and hence ecosystem function in the remaining
130 patches may in fact improve. We answer these questions using an existing

131 metacommunity modeling approach based on consumer-resource dynamics, allowing
132 us to explicitly consider community biomass rather than drawing on correlations with
133 species richness. To answer our questions regarding the influence of dispersal, we add
134 to this metacommunity modeling approach the different potential dispersal behaviors
135 possible when habitat is destroyed. In addition, we link the observed metacommunity
136 extinction and ecosystem function debt behaviors with the effects of patch destruction
137 on heterogeneous metapopulations, by studying the behavior of a similar model of a
138 single species population in heterogeneous patches linked by dispersal.

139 **Model and Methods**

140 *Model framework*

141 Our model is comparable to the model used by Mouquet and Loreau (2003) which is
142 well-known for its predictions regarding the effects of dispersal on diversity and
143 ecosystem function in a heterogeneous metacommunity (Mittelbach & McGill 2019).
144 It captures the dynamics of a set of competing species in local patches that vary in
145 their environmental conditions (and hence dominant competitors) and are connected
146 by dispersal to form a metacommunity. We use a formulation of this model similar to
147 that used by Loreau *et al.* (2003), which models competition through resource
148 consumption rather than the local patch dynamics considered in the original model,

149 thus allowing clearer consideration of not just diversity, but also ecosystem function.

150 This metacommunity model has been studied extensively and is the core approach

151 used in recent developments in metacommunity theory (Leibold & Chase 2018; Ai &

152 Ellwood 2022).

153 Our model is not linked with a particular biological system, for example it could

154 describe grass competing for soil nitrogen (Loreau *et al.* 2003). We set varied

155 environments for habitat patches, such as surface soil temperatures of various plant

156 systems, and we allow species to differ in their traits, such as the temperature at which

157 each species has its maximum competitive ability for soil nitrogen (Tilman 1999).

158 Biomass of a species would increase if that species inhabits a patch where the soil

159 temperature is optimal. In this example, the model is attempting to capture the

160 dynamics of the biomass of different plant species on a heterogeneous landscape

161 through competition for soil nitrogen. The competitive ability of the species depends

162 on the match between the soil temperature of the patch and the optimal temperature of

163 the species.

164 The metacommunity consists of M patches, each with a different value of an

165 environmental condition, connected by dispersal rate a . Each patch is numbered from

166 1 to M . The environmental value (such as the surface soil temperature after

167 normalization) of the first patch is $E_1=1$, then the adjoining patch is defined as $E_j=E_{j-1}$ -
168 $1/(M-1)$ where j is from 2 to M . There are S species in each patch initially, numbered
169 from 1 to S . The optimal niche value of the first species is $H_1=1$, and remaining
170 species are defined as $H_i=H_{i-1}/(S-1)$ where i is from 2 to S . The species competitive
171 ability in each patch is determined by the match between species' optimal niche value
172 and the environmental value of a patch. Under these definitions, in the case of
173 maximal potential diversity (our focus), where there are as many species as patches
174 (i.e. $M=S$), the first species is the best competitor in the first patch, the second species
175 is the best competitor in the second patch, and so on. We refer to the patches towards
176 the center of the range of environmental conditions as the habitats with benign
177 environments, and the patches with extreme environmental values, such as 0 or 1, as
178 the habitat with harsh environments. Patches with benign environments are suitable
179 for all species, whereas patches with harsh environments are suitable only for those
180 species adapted to that patch. Note that those patches are not necessarily spatially
181 central in our model, in which all patches are assumed equally connected to focus on
182 environmental heterogeneity between patches rather than dispersal limitation. Hence,
183 species with extreme optimal environmental values close to 0 or 1 are best adapted to
184 patches with harsh environments, whereas species with mid-range environmental

185 values are best adapted to benign environments.

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

$$190 \quad \frac{dR_j(t)}{dt} = I_j - l_j R_j(t) - R_j(t) \sum_{i=1}^S C_{ij} P_{ij}(t) \quad (1)$$

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

$$195 \quad C_{ij} = \frac{1.5 - |H_i - E_j|}{b} \quad (2)$$

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

$$198 \quad \frac{dP_{ij}(t)}{dt} = e C_{ij} R_j(t) P_{ij}(t) - m P_{ij}(t) + a \left(\frac{1}{M-1} \sum_{k=1, k \neq j}^M P_{ik}(t) - P_{ij}(t) \right) \quad (3)$$

199 where e is the rate of conversion of resource into new biomass, and m is the rate of
200 loss of biomass of each species in each patch. The first term describes the
201 consumption and conversion of biomass by species; the second term describes the
202 decrease in species biomass as species die; the third term describes species

203 immigration from other patches; the fourth term describes species emigration to other
204 patches. The parameter a is the per-capita rate at which individuals are moving out
205 of a patch, and the proportion of dispersers coming into any given patch is then $\frac{1}{M-1}$,
206 where M is the number of patches (Plitzko & Drossel 2015).

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

215 *Simulated patch removal and dispersal behaviors*

216 We ran each simulation to reach the first approximate equilibrium (when the total
217 biomass of all species is a fixed point and the biomass of each species becomes
218 saturated, see Fig. S1), and then removed *a patch* from the metacommunity and ran
219 the model until the second approximate equilibrium. We carried out this patch
220 removal and subsequent simulation individually for each patch. We included two

221 different dispersal behaviors that would have major consequences for the structure of
222 the metacommunity once the habitat is lost. Under directed dispersal, when we
223 remove a patch, we remove all of its connections to other patches, lowering the
224 number of patches M by 1 in the third term of Eq. 3 (since the same dispersers are
225 now spread over fewer patches), and maintain dispersal between the remaining
226 patches. Under undirected dispersal, we do not remove a patch and its connections
227 from the system. Instead, we assume that the patch was destroyed permanently for
228 any species, but dispersal to it is still occurring through the existing connections
229 (Fig.1A). Species dispersing to the destroyed patch would die immediately.

230 *Model parameters*

231 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
232 and j . Some of these parameters were set as they were in other studies (Loreau *et al.*
233 2003; Gonzalez *et al.* 2009; Shanafelt *et al.* 2015; Thompson *et al.* 2017). If the total
234 biomass of a species across the whole metacommunity fell below five, we considered
235 the species extinct in the metacommunity. This metacommunity scale extinction
236 cutoff is comparable to, but leads to simpler and faster code than, the patch-scale
237 cutoff of 0.1 used in previous studies (Loreau *et al.* 2003; Shanafelt *et al.* 2015), as it
238 is equal to 0.1 times the number of patches M . Furthermore, the small population size

239 effects that influence extinction risk (breakdown of mating and defense systems, and
240 demographic or environmental stochasticity effects) may be more accurately
241 considered as acting at the metacommunity scale when there is significant dispersal.
242 We studied patch removal under various consumption rates and magnitudes by
243 varying b (which consumption rates are inversely proportional to) from 10, 20, 21, 22,
244 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,
245 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
246 behavior of the model was consistent with b close to values causing collapse of the
247 metacommunity (b above 24).

248 *Metapopulation simulations*

249 To improve our overall understanding of community-level observations, we also
250 designed a metapopulation model to look at the effects of patch removal at the
251 species-level. The metapopulation is a version of the model with three patches (i.e. the
252 $M=3, S=1$ case of our model). This kind of metapopulation model is able to eliminate
253 the interaction between species, instead focusing on the match between the
254 environmental condition of the removed patch and the optimal niche of the species. A
255 metapopulation with three patches is the simplest topology, as it is still a
256 metapopulation after one patch is removed. Moreover, the consequences of removing

257 a patch would be more obvious in this kind of metapopulation than in
258 metapopulations with many patches. We considered two scenarios, one in which the
259 species was best adapted to the patch with harsh environmental condition, and one in
260 which the species was best adapted to the patch with benign environmental condition.
261 These scenarios correspond to the patches with harsh and benign environment in the
262 metacommunity model, where each patch has the best adapted species. The
263 environmental condition E for the three patches was 1, 0.98 and 0.96 (these were the
264 first three patches in the metacommunity model) in both scenarios, while the species
265 optimal niche value was $H=1$ in the first scenarios and $H=0.98$ in the second scenarios
266 (these were the first and second species in the metacommunity model). We removed
267 patches with different environmental conditions and assessed the extinction risk and
268 ecosystem function debt in the metapopulation model, allowing a deeper insight into
269 the metacommunity results. For the metapopulation simulations we used $I=67.6$,
270 $a=0.01$ and $b=10$.

271 *Experimental Design*

272 Each simulation ran for 4×10^6 generations (specifically, we set per-capita death rate
273 as $m=0.2$, and simulated the model from $t = 0$ to $t = 2 \times 10^7$, which corresponds to
274 $2 \times 10^7 \times 0.2 = 4 \times 10^6$ generations) to reach approximate equilibrium (Fig. S1), at

275 which point *a patch* was removed, before continuing to run for 4×10^6 generations to
276 reach a second approximate equilibrium post habitat destruction. We explained patch
277 removal under directed and undirected dispersal behavior in the section *Simulated*
278 *patch removal and dispersal behaviors*.

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

293 removal allowed us to specify extinction regimes across dispersal and resource
294 consumption rates.

295 We recorded the biomass of all species in each patch at the first approximate
296 equilibrium of each simulation to see the distributions of community composition and
297 ecosystem function along heterogeneous environments. We also recorded the
298 persistence times of each species across the whole metacommunity after patch
299 removal to measure the risk intensity of *each extinct species due to patch removal* as
300 the inverse of persistence time (unit as generations⁻¹, as recommended by Grimm
301 and Christian in 2004). To measure the magnitude of extinction debt, we calculated
302 the number of extinct species as the total number of extinct species at the second
303 approximate equilibrium minus the number of species going extinct immediately after
304 patch removal. The proportion of species going extinct was calculated as the number
305 of extinct species divided by the number of species before removal but after the initial
306 approximate equilibrium. To study total ecosystem function debt, we calculated the
307 total biomass change as the mean biomass across the M-1 remaining patches at the
308 second approximate equilibrium minus the mean biomass of each patch before
309 removal, and we also calculated the immediate biomass change as the mean biomass
310 in the M-1 remaining patches after patch removal minus the mean biomass before

311 removal. Under both directed and undirected dispersal, biomass change was given by
312 the total biomass change minus the immediate biomass change upon patch removal.
313 The proportion of biomass change was the biomass change over the mean biomass of
314 each patch before removal. With these data, we analyzed how the magnitude of
315 extinction and ecosystem function debt changed with dispersal rate and the
316 environmental condition of each removed patch under directed and undirected
317 dispersal behaviors.

318 We used the forward Euler method to simulate the differential equations with
319 $dt=0.01$. The simulation code was written in Java, and data were analyzed in R
320 version 4.1.3 (R 2022).

321 **Results**

322 *Extinction regimes under different dispersal and consumption rates*

323 Dispersal and consumption rates determine which species go extinct after habitat loss.

324 We distinguish three extinction regimes (Fig. 2A) outside of a low consumption rate
325 zone where no species can coexist before patch removal (white area in Fig.2A).

326 Under low dispersal and medium to high consumption rates (green area in Fig.
327 2A), removing a patch causes the species best adapted to it to go extinct under both
328 directed and undirected dispersal (Fig. 2B and 2C). Hence in this regime, only the

329 species best adapted to the patch being removed are at risk. However, that risk
330 (measured as the inverse of persistence time) varies and is highest under the removal
331 of the harsh environment patches (Fig. 2B and 2C). The extinction risk pattern in this
332 regimes makes intuitive sense given the pattern of biomass found before patch
333 removal, in which the biomass of each species is quite low other than in the patch it is
334 best adapted to (Fig. S2A).

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

347 removed). In this regime, the species best adapted to the removed patch is at the
348 greatest risk, and the risk intensity decreases with the difference between the species
349 preferred condition and the environment of the removed patch (Fig. 2D-G).

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

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

362 We consider the dependence of extinction debt on dispersal rate, measuring extinction
363 debt as the number (Fig. 3A, B) and the proportion (Fig. 3C, D) of species going
364 extinct in the whole metacommunity. Generally, the mean number of extinct species

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

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

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

383 extinct than removing a patch with harsh environmental conditions (Fig. 4A, B).

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

395 *Verifying extinction debt and ecosystem function credit mechanisms in*

396 *metapopulations*

397 Under directed dispersal, habitat loss benefitted the mean biomass in the remaining
398 patches in the metapopulation analysis. The poorer the match between the species and
399 the environment in the removed patch, the higher the mean biomass for each of the
400 remaining patches (Fig.5A). We also hypothesized that extinction risk is often highest

401 when harsh habitat patches are removed in our metacommunity model because the
402 species in those patches were on average more poorly adapted to remaining patches.
403 In support of this, we found that the metapopulation experienced the greatest risk of
404 extinction upon removal of the best patch for the species when that best patch was a
405 harsh environment rather than a benign environment (Fig. 5B). Under undirected
406 dispersal, the population went extinct regardless of which patch was removed.

407 **Discussion**

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

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

421 In our model, the number of species is equal to the number of patches, and each
422 species has a patch to which it is best adapted. For example, the species with $H_i = 0.5$
423 is best adapted to the patch with $E_j = 0.5$. The diagonal in each panel of Fig. 2
424 indicates the species best adapted to each patch. As in previous studies, species
425 sorting under low dispersal rates allowed each species to dominate its preferred patch
426 (Mouquet & Loreau 2003; Suzuki & Economo 2021; Ai & Ellwood 2022). Hence,
427 removing a patch tends to cause the species better adapted to this patch to go extinct,
428 resulting in the diagonal risk zones in Fig. 2B-G. Species with central niches have
429 numerous relatively suitable habitats and are therefore less at risk than species with
430 extreme niches and few suitable habitats. We show that this can be understood in
431 terms of the principles applying to metapopulations, in that removing the best patch
432 for that species creates less of a risk if that patch is benign than if that patch is a harsh
433 environmental condition relative to the gradient experienced by that metapopulation
434 (Fig. 5B). At medium dispersal rates, species transit quickly between patches, and
435 hence patches with similar environmental conditions play important roles in
436 maintaining species even though they are sub-optimal patches. Regardless of which

437 patch is removed, the species adapted to harsh environments are at greater risk of
438 extinction; their low competitive ability prevents them from increasing their
439 productivity in any of the patches, and habitat loss reduces their biomass and further
440 exacerbates their extinction.

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

450 *Ecosystem debts under undirected dispersal but credits under directed dispersal*

451 Under directed dispersal in metapopulations, the harsher the removed patch, the
452 higher the mean biomass became for remaining patches (Fig. 5A). Dispersers which
453 previously dispersed to the less productive patches dispersed to more productive
454 patches after patch removal, which increased the biomass. Similar patterns could be

455 seen in the metacommunities, especially when harsh patches were removed (Fig. 4C,
456 E and G). However, while the mean biomass increased greatly in the metapopulation,
457 it increased only slightly in the metacommunity (see y-axis of Fig. 3E, G and 5A), and
458 in addition, removing a patch caused the whole biomass of the metacommunity to
459 decrease, whereas it increased in the metapopulation (Fig. 5A). This is because in the
460 metacommunity, the removed patch may have been the worst habitat for some
461 species, but the best habitat for other species, hence removing a patch would cause the
462 mean biomass of some species to increase and others to decrease. Moreover,
463 removing any patch from a metacommunity caused species to lose habitat, thus
464 increasing extinction, whereas in a metapopulation only the removal of the best patch
465 would cause it to go extinct.

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

472 *Comparison with existing theory of extinction and ecosystem function debt*

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

482 The specific assumptions of perfect trade-offs in Tilman's model have been
483 criticized as being unrealistic (Loehle & Li 1996; Banks 1997; Malanson 2008).
484 Moreover, relaxing the assumptions leads to very different results, such as species
485 losses occurring more quickly than predicted by the model with perfect trade-off.
486 Moreover, this included not just competitive species, but all types of species could go
487 extinct due to habitat destruction (Loehle & Li 1996; Banks 1997). In addition, recent
488 studies (Li *et al.* 2020; Liao *et al.* 2022; Zhang *et al.* 2023) relaxed the strict
489 competition-colonization trade-offs through weakening relative competition strength
490 or violating the strict hierarchical competition by considering intransitive competition,

491 and found that the species loss oscillated with disturbance extent rather than following
492 a simple monotonic relationship as predicted. Even in these studies, the best
493 competitor suffered the most impact as the disturbance extent increases (see Fig.2 in
494 Liao *et al.* 2022).

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

506 *Implications of our results for biodiversity conservation*

507 Extinction debt provides a window for species restoration and landscape
508 management (Kuussaari *et al.* 2009; Wearn *et al.* 2012), but which recovery plans

509 should be applied depends on many factors. Huxel and Hastings (1999) concluded
510 that, “either restoring patches adjacent to occupied patches or reintroducing the
511 species into restored patches increases the efficacy of the recovery effort”. Our results
512 indicate that the type of extinction regime must be identified before deciding which
513 species to protect during restoration efforts, since different species are at risk in
514 different regimes. For example, when the most adapted species is most at risk, efforts
515 should focus on reintroducing the lost habitat and its best competitors, whereas in the
516 regime in which species adapted to the neighboring patches are also at risk, restoring
517 the adjacent patches should also be a priority. In some management cases, such as
518 quantifying the size of reservation areas with limited resources, protecting habitats
519 with benign environments should be prioritized, because losing this type of habitat
520 will cause the most extinction and ecosystem function debt since a wide range of
521 species are adapted to those habitats. Our model suggests that, regardless of which
522 habitats are lost, the total biomass of the whole metacommunity is lower, so the
523 habitats with harsh environments should also be protected. Undirected dispersal may
524 cause species to continue dispersing to the destroyed habitat, meaning that restoring
525 the lost habitat immediately would be a good way of restoring species richness and
526 ecosystem function. In summary, our results suggest that restoration actions should be

527 guided by extinction regime, dispersal behaviors, and landscape heterogeneity.

528 *Future Directions*

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

540 *Conclusion*

541 We developed a new theory of extinction and ecosystem function debt in a
542 heterogeneous landscape. Habitat loss hastens the extinction of species adapted to
543 extreme environments, and always causes extinction debt under both directed and
544 undirected dispersal. Interestingly, habitat loss causes ecosystem function debts under

545 undirected dispersal, but credits under directed dispersal. Both extinction debt and
546 ecosystem function credit/debt increase with dispersal rate. Our study indicates that
547 extinction regime, dispersal behavior, and the environmental conditions of habitats
548 should be considered before taking conservation actions to mitigate the effects of
549 habitat loss.

550 **Data availability statement:**

551 This theoretical study has no data; codes are available at link:

552 https://datadryad.org/stash/share/z0Mrqix19wJEzgLJN7GRi9oThNqiz7EoA0t3rm89_t

553 M.

554 **References**

555 Ai, D. & Ellwood, M.D.F. (2022). A spatially implicit model fails to predict the
556 structure of spatially explicit metacommunities under high dispersal.

557 *Ecological Modelling*, 474, 110151.

558 Banks, J.E. (1997). DO IMPERFECT TRADE-OFFS AFFECT THE EXTINCTION
559 DEBT PHENOMENON? *Ecology*, 78, 1597-1601.

560 Ben-Hur, E. & Kadmon, R. (2020). Heterogeneity–diversity relationships in sessile
561 organisms: a unified framework. *Ecology Letters*, 23, 193-207.

562 Bowler, D.E. & Benton, T.G. (2005). Causes and consequences of animal dispersal

563 strategies: relating individual behaviour to spatial dynamics. *Biological*
564 *Reviews*, 80, 205-225.

565 Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M. & Palmer, T.M.
566 (2015). Accelerated modern human-induced species losses: Entering the sixth
567 mass extinction. *Science advances*, 1, e1400253.

568 Chase, J.M., Blowes, S.A., Knight, T.M., Gerstner, K. & May, F. (2020). Ecosystem
569 decay exacerbates biodiversity loss with habitat loss. *Nature*, 584, 238-243.

570 Chen, Y. & Peng, S. (2017). Evidence and mapping of extinction debts for global
571 forest-dwelling reptiles, amphibians and mammals. *Scientific Reports*, 7,
572 44305.

573 Croteau, E.K. (2010). Causes and Consequences of Dispersal in Plants and Animals.
574 *Nature Education Knowledge*, 3(10):12.

575 Davies, A.B., Tambling, C.J., Ranc, N., Marneweck, D.G., le Roux, E., Druce, D.J. *et*
576 *al.* (2021). Spatial heterogeneity facilitates carnivore coexistence. 102,
577 e03319.

578 Ewers, R.M. & Didham, R.K. (2006). Confounding factors in the detection of species
579 responses to habitat fragmentation. *Biological Reviews*, 81, 117-142.

580 Fahrig, L. (2003). Effects of Habitat Fragmentation on Biodiversity. *Annual Review of*

581 *Ecology, Evolution, and Systematics*, 34, 487-515.

582 Figueiredo, L., Krauss, J., Steffan-Dewenter, I. & Sarmiento Cabral, J. (2019).

583 Understanding extinction debts: spatio-temporal scales, mechanisms and a

584 roadmap for future research. *Ecography*, 42, 1973-1990.

585 Fournier, B., Mouquet, N., Leibold, M.A. & Gravel, D. (2017). An integrative

586 framework of coexistence mechanisms in competitive metacommunities.

587 *Ecography*, 40, 630-641.

588 Gonzalez, A., Mouquet, N. & Loreau, M. (2009). Biodiversity as spatial insurance the

589 effects of habitat fragmentation and dispersal on ecosystem functioning. In:

590 *Biodiversity, Ecosystem Functioning , and Human Wellbeing* (eds. Naeem, S,

591 Bunker, D, Hector, A, Loreau, M & Perrings, C). Oxford University Press, pp.

592 134-146.

593 Grimm, V. & Wissel, C. (2004). The intrinsic mean time to extinction: a unifying

594 approach to analysing persistence and viability of populations. *Oikos*, 105,

595 501-511.

596 Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D. *et al.*

597 (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems.

598 *Science advances*, 1, e1500052.

- 599 Halley, J.M., Monokrousos, N., Mazaris, A.D., Newmark, W.D. & Vokou, D. (2016).
600 Dynamics of extinction debt across five taxonomic groups. *Nature*
601 *Communications*, 7, 12283.
- 602 Halley, J.M., Sgardeli, V. & Triantis, K.A. (2014). Extinction debt and the species–
603 area relationship: a neutral perspective. *Global Ecology and Biogeography*,
604 23, 113-123.
- 605 Hanski, I. & Ovaskainen, O. (2002). Extinction Debt at Extinction Threshold.
606 *Conservation Biology*, 16, 666-673.
- 607 Highland, S.A. & Jones, J.A. (2014). Extinction debt in naturally contracting
608 mountain meadows in the Pacific Northwest, USA: varying responses of
609 plants and feeding guilds of nocturnal moths. *Biodiversity and Conservation*,
610 23, 2529-2544.
- 611 Horváth, Z., Ptacnik, R., Vad, C.F. & Chase, J.M. (2019). Habitat loss over six
612 decades accelerates regional and local biodiversity loss via changing
613 landscape connectance. *Ecology Letters*, 22, 1019-1027.
- 614 Isbell, F., Tilman, D., Polasky, S. & Loreau, M. (2015). The biodiversity-dependent
615 ecosystem service debt. *Ecology Letters*, 18, 119-134.
- 616 Jackson, H.B. & Fahrig, L. (2013). Habitat Loss and Fragmentation. In: *Encyclopedia*

617 *of Biodiversity* (ed. Levin, SA). Elsevier.

618 Jackson, S.T. & Sax, D.F. (2010). Balancing biodiversity in a changing environment:
619 extinction debt, immigration credit and species turnover. *Trends in Ecology &*
620 *Evolution*, 25, 153-160.

621 Krauss, J., Bommarco, R., Guardiola, M., Heikkinen, R.K., Helm, A., Kuussaari, M.
622 *et al.* (2010). Habitat fragmentation causes immediate and time-delayed
623 biodiversity loss at different trophic levels. *Ecology letters*, 13, 597-605.

624 Kuussaari, M., Bommarco, R., Heikkinen, R.K., Helm, A., Krauss, J., Lindborg, R. *et*
625 *al.* (2009). Extinction debt: a challenge for biodiversity conservation. *Trends*
626 *in Ecology & Evolution*, 24, 564-571.

627 Leibold, M.A. & Chase, J.M. (2018). *Metacommunity Ecology, Volume 59*. Princeton
628 University Press.

629 Li, Y., Bearup, D. & Liao, J. (2020). Habitat loss alters effects of intransitive higher-
630 order competition on biodiversity: a new metapopulation framework.
631 *Proceedings of the Royal Society B: Biological Sciences*, 287, 20201571.

632 Liao, J., Barabás, G. & Bearup, D. (2022). Competition–colonization dynamics and
633 multimodality in diversity–disturbance relationships. *Ecology*, 103, e3672.

634 Loehle, C. & Li, B.-L. (1996). Habitat Destruction and the Extinction Debt Revisited.

635 *Ecological Applications*, 6, 784-789.

636 Loreau, M., Mouquet, N. & Gonzalez, A. (2003). Biodiversity as spatial insurance in
637 heterogeneous landscapes. *Proceedings of the National Academy of Sciences*,
638 100, 12765-12770.

639 Makishima, D., Sutou, R., Goto, A., Kawai, Y., Ishii, N., Taniguchi, H. *et al.* (2021).
640 Potential extinction debt due to habitat loss and fragmentation in subalpine
641 moorland ecosystems. *Plant Ecology*, 222, 445-457.

642 Malanson, G.P. (2008). Extinction debt: origins, developments, and applications of a
643 biogeographical trope. *Progress in Physical Geography: Earth and*
644 *Environment*, 32, 277-291.

645 Mason, D.S., Baruzzi, C. & Lashley, M.A. (2022). Passive directed dispersal of plants
646 by animals. *Biological Reviews*, 97, 1908-1929.

647 Mittelbach, G.G. & McGill, B.J. (2019). *Community Ecology (Second Edition)*.
648 Oxford University Press.

649 Mouquet, N. & Loreau, M. (2003). Community Patterns in Source - Sink
650 Metacommunities. *The American Naturalist*, 162, 544-557.

651 Mouquet, N., Matthiessen, B., Miller, T. & Gonzalez, A. (2011). Extinction debt in
652 source-sink metacommunities. *PloS one*, 6, e17567-e17567.

653 Nield, A.P., Nathan, R., Enright, N.J., Ladd, P.G. & Perry, G.L.W. (2020). The spatial
654 complexity of seed movement: Animal-generated seed dispersal patterns in
655 fragmented landscapes revealed by animal movement models. *Journal of*
656 *Ecology*, 108, 687-701.

657 Otto, R., Garzón-Machado, V., del Arco, M., Fernández-Lugo, S., de Nascimento, L.,
658 Oromí, P. *et al.* (2017). Unpaid extinction debts for endemic plants and
659 invertebrates as a legacy of habitat loss on oceanic islands. *Diversity and*
660 *Distributions*, 23, 1031-1041.

661 Plitzko, S.J. & Drossel, B. (2015). The effect of dispersal between patches on the
662 stability of large trophic food webs. *Theoretical Ecology*, 8, 233-244.

663 R, C.T. (2022). R: A language and environment for statistical computing. R
664 Foundation for Statistical Computing, Vienna, Austria.

665 Ridding, L.E., Newton, A.C., Keith, S.A., Walls, R.M., Diaz, A., Pywell, R.F. *et al.*
666 (2021). Inconsistent detection of extinction debts using different methods.
667 *Ecography*, 44, 33-43.

668 Shanafelt, D.W., Dieckmann, U., Jonas, M., Franklin, O., Loreau, M. & Perrings, C.
669 (2015). Biodiversity, productivity, and the spatial insurance hypothesis
670 revisited. *J Theor Biol*, 380, 426-435.

671 Suzuki, Y. & Economo, E.P. (2021). From species sorting to mass effects: spatial
672 network structure mediates the shift between metacommunity archetypes.
673 *Ecography*, 44, 715-726.

674 Thompson, P.L. & Gonzalez, A. (2017). Dispersal governs the reorganization of
675 ecological networks under environmental change. *Nature Ecology &*
676 *Evolution*, 1, 0162.

677 Thompson, P.L., Guzman, L.M., De Meester, L., Horváth, Z., Ptacnik, R.,
678 Vanschoenwinkel, B. *et al.* (2020). A process-based metacommunity
679 framework linking local and regional scale community ecology. *Ecology*
680 *Letters*, 23, 1314-1329.

681 Thompson, P.L., Kéfi, S., Zelnik, Y.R., Dee, L.E., Wang, S., de Mazancourt, C. *et al.*
682 (2021). Scaling up biodiversity–ecosystem functioning relationships: the role
683 of environmental heterogeneity in space and time. *Proceedings of the Royal*
684 *Society B: Biological Sciences*, 288, 20202779.

685 Thompson, P.L., Rayfield, B. & Gonzalez, A. (2014). Robustness of the spatial
686 insurance effects of biodiversity to habitat loss. *Evolutionary Ecology*
687 *Research*, 16, 445-460.

688 Thompson, P.L., Rayfield, B. & Gonzalez, A. (2017). Loss of habitat and connectivity

689 erodes species diversity, ecosystem functioning, and stability in
690 metacommunity networks. *Ecography*, 40, 98-108.

691 Thompson, S.E.D., Chisholm, R.A. & Rosindell, J. (2019). Characterising extinction
692 debt following habitat fragmentation using neutral theory. *Ecology Letters*, 22,
693 2087-2096.

694 Tilman, D. (1999). THE ECOLOGICAL CONSEQUENCES OF CHANGES IN
695 BIODIVERSITY: A SEARCH FOR GENERAL PRINCIPLES. *Ecology*, 80,
696 1455-1474.

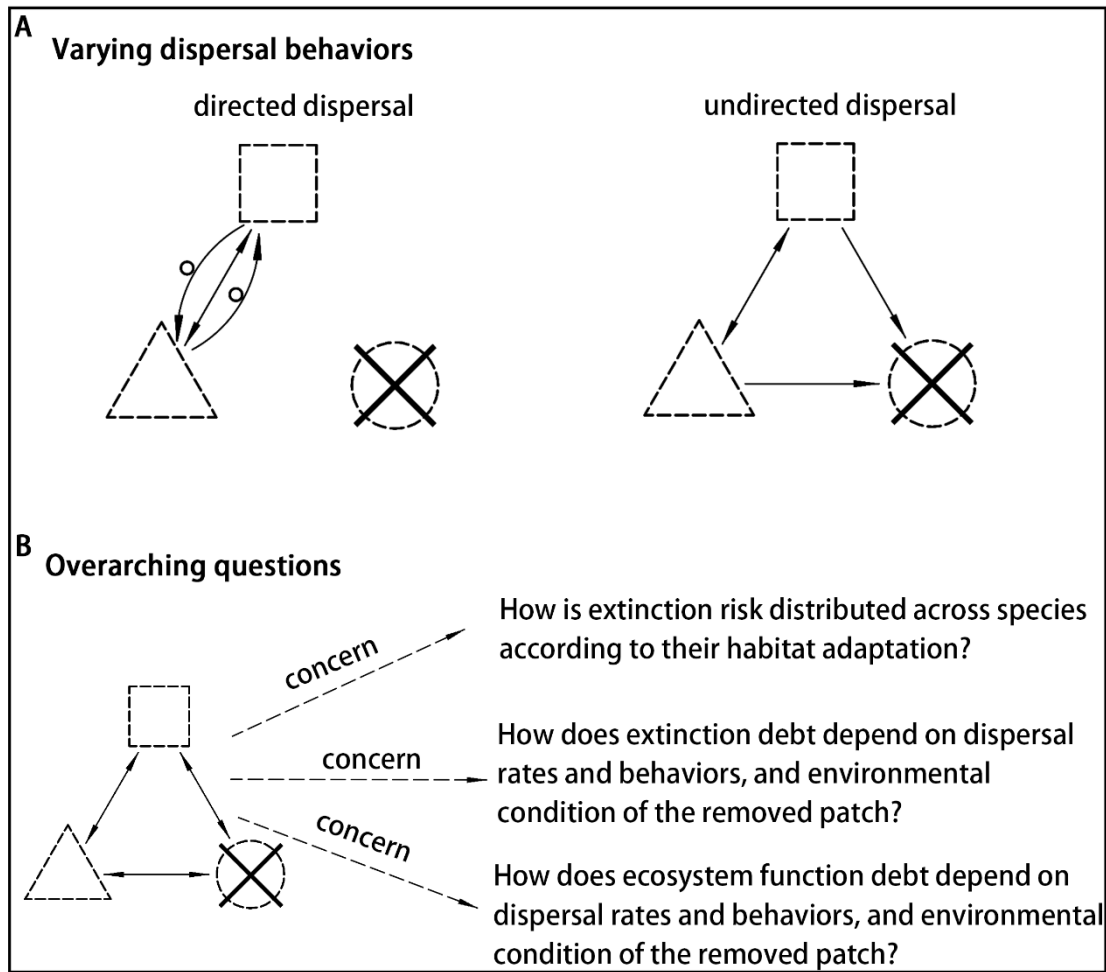
697 Tilman, D., May, R.M., Lehman, C.L. & Nowak, M.A. (1994). Habitat destruction
698 and the extinction debt. *Nature*, 371, 65-66.

699 Wearn, O.R., Reuman, D.C. & Ewers, R.M. (2012). Extinction debt and windows of
700 conservation opportunity in the Brazilian Amazon. *Science*, 337, 228-232.

701 Zhang, H., Bearup, D., Barabás, G., Fagan, W.F., Nijs, I., Chen, D. *et al.* (2023).
702 Complex nonmonotonic responses of biodiversity to habitat destruction.
703 *Ecology*, 104, e4177.

704 Zona, S. (2017). Fruit and Seed Dispersal of *Salvia* L. (Lamiaceae): A Review of the
705 Evidence. *The Botanical Review*, 83, 195-212.

706



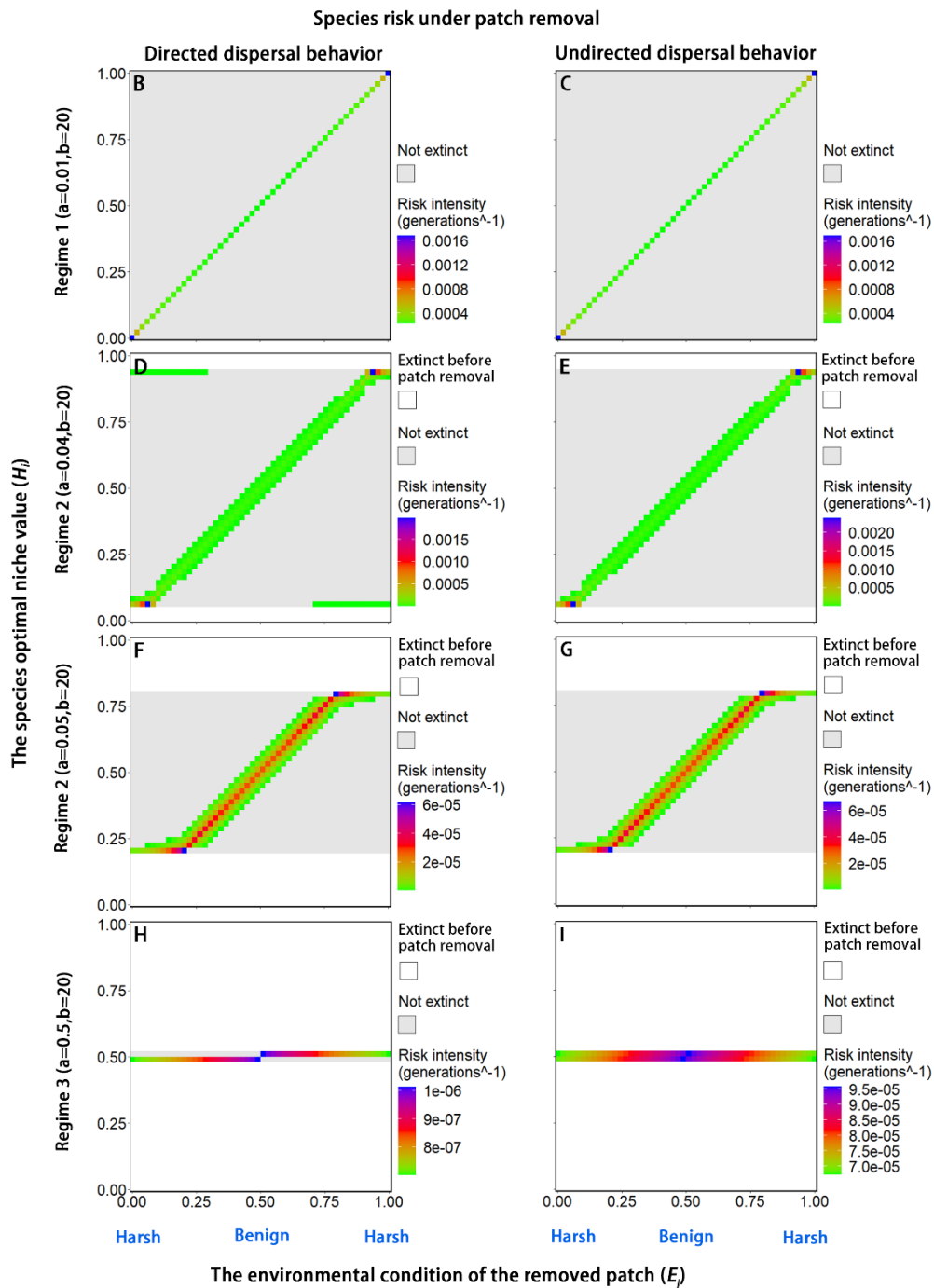
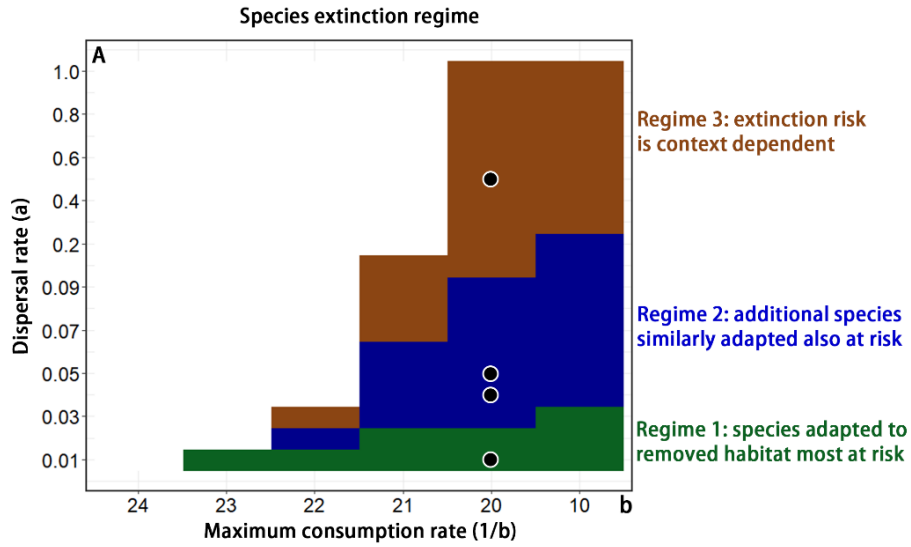
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710 **Figure 1 Dispersal behavior and questions asked.** Different shapes with dashed
 711 outlines represent patches with different environmental conditions. The solid line with
 712 arrows indicates the direction of dispersal between patches. Panel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

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

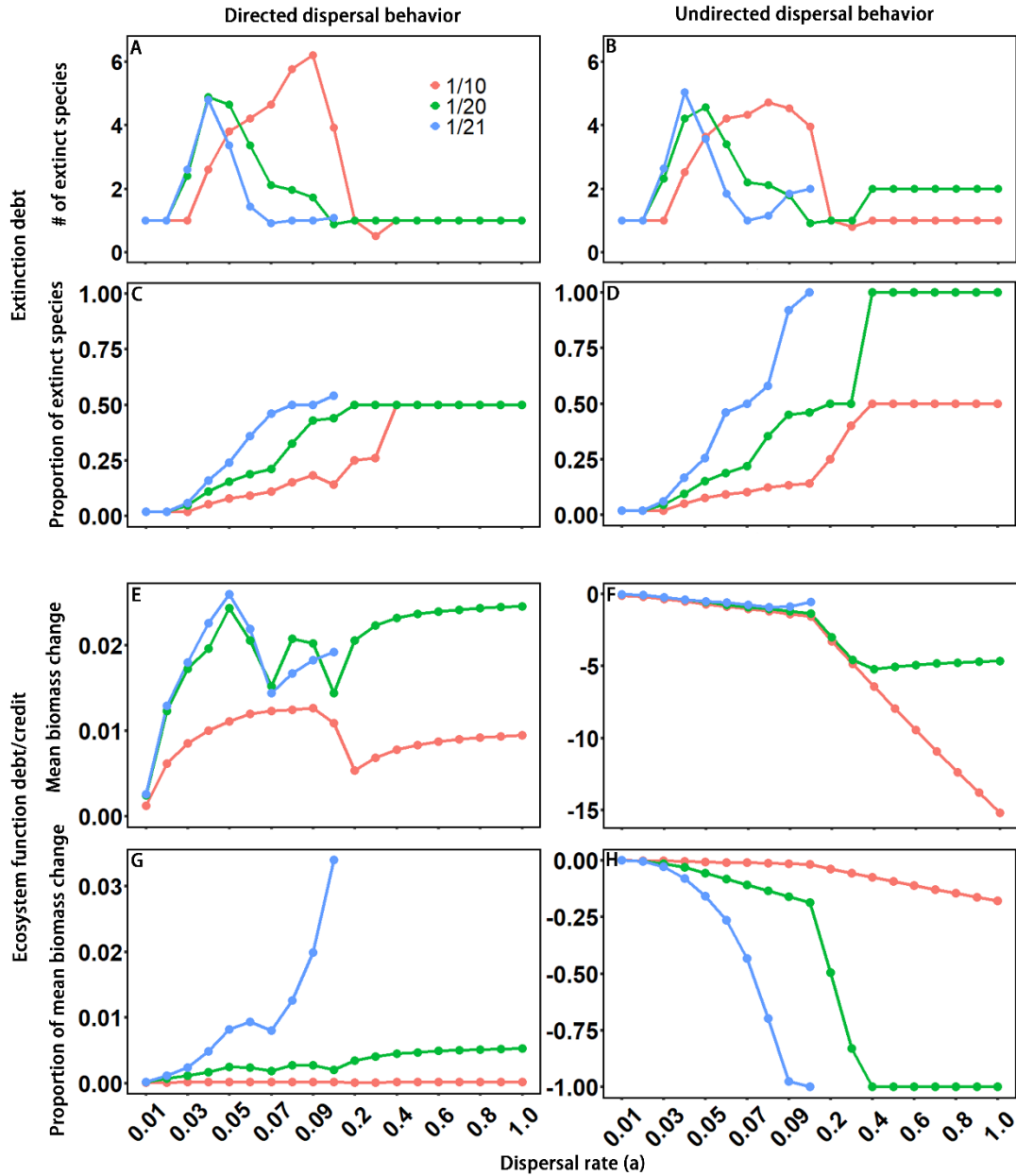
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726 **Figure 2 The regimes of extinction behavior under patch removal in the space of**
727 **possible consumption and dispersal rates (A), and the patterns of extinction risk**
728 **after patch removal in each regime (B-I).** In panel A, the colored areas represent
729 distinct extinction regimes, whereas the four black dots indicate the values of
730 consumption and dispersal rates where we have shown species risk in panels B-I. In
731 the white area to the left of the colors in A, no species can persist in the
732 metacommunity even in the absence of patch removal. In B-I, squares of color
733 indicate the extinction risk (measured as the inverse of the number of generations the
734 species persists after patch removal) of the species with the corresponding
735 environmental niche value (H_i) on the vertical axis, under removal of the patch with
736 the corresponding environmental condition (E_j) on the horizontal axis. Hence colors
737 on the diagonal indicate a species' extinction risk when the patch it is best adapted to
738 (the patch for which $E_j = H_i$) is removed, and colors just to the left and right of the
739 diagonal indicate its risk when a patch close in environmental condition to its
740 environmental niche value is removed. White areas mean that species went extinct
741 before patch removal due to metacommunity dynamics, grey areas mean that species
742 did not go extinct under removal of that patch, and colorful areas mean that species
743 went extinct due to patch removal. As dispersal increases, the pattern of extinction

744 risk changes from only the species best adapted to the removed habitat being at risk
745 (first dot, B-C), to species adapted to similar habitats also being at risk (2nd and 3rd
746 dots, D-G). In the latter, species with edge environmental niches may also be hastened
747 towards extinction when very different habitat patches are removed (2nd dot, D). At
748 high dispersal (4th dot, H-I), only 1-2 species persist before patch removal, and one or
749 both are vulnerable to extinction upon patch removal. Extinction regimes (panel A)
750 are the same both under directed and undirected dispersal. See text for a detailed
751 description of these regimes.
752



753

754 **Figure 3 The magnitudes of extinction debt (A-D) and ecosystem function**

755 **debt/credit (E-H) across dispersal rates.** The left column of panels shows behaviors

756 under directed dispersal, and the right undirected dispersal. Line colors differ by

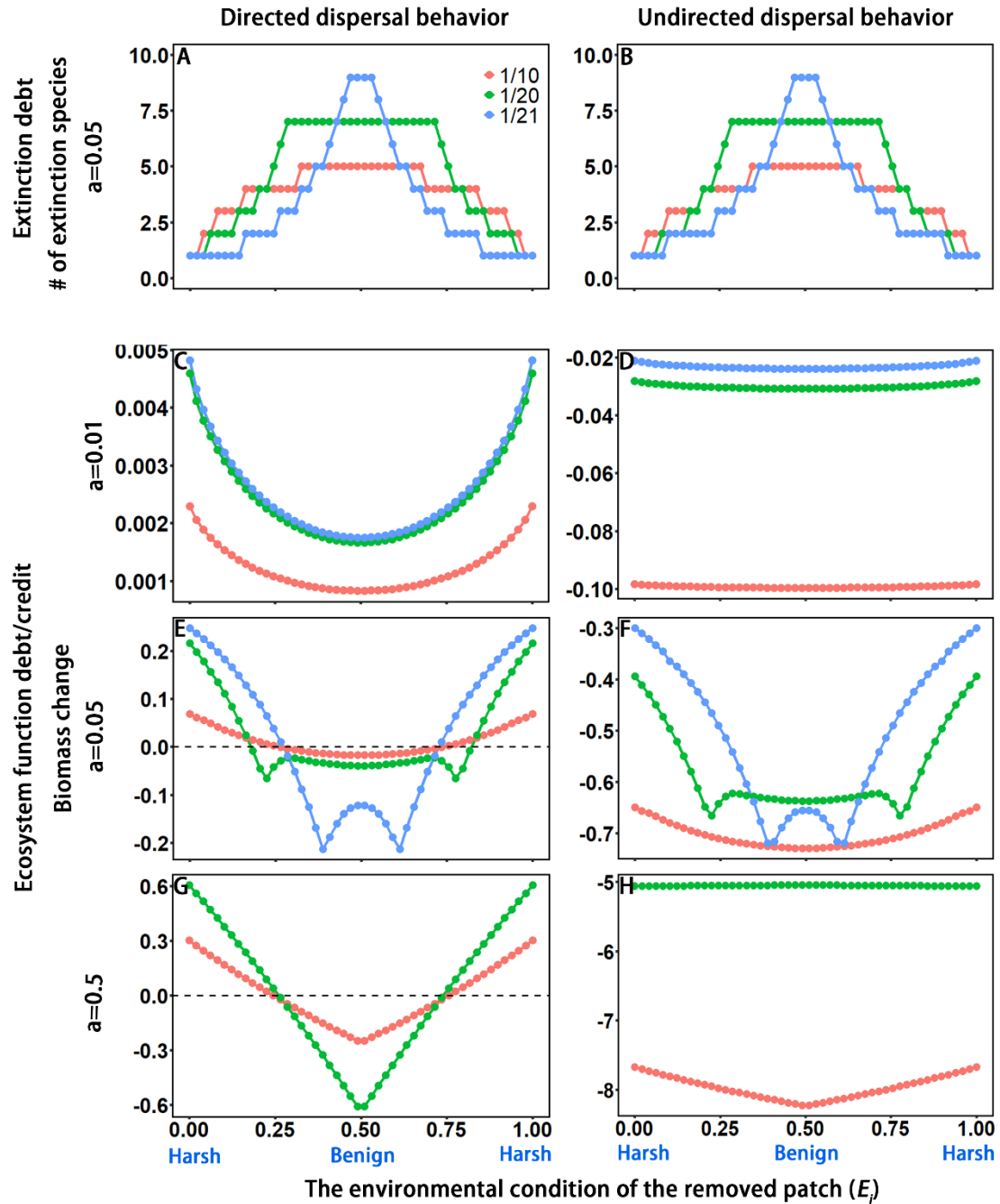
757 consumption rate as indicated in the legend in A. Extinction debt is shown as both the

758 number of species going extinct (A, B) and the proportion of species going extinct (C,

759 D). Ecosystem function debt/credit is shown as both the biomass change (E, F) and

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

767



768

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Figure 4 The dependence of the magnitude of extinction debt (A, B) and the

770

magnitude of ecosystem function debt (C-H) on the environmental condition of

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the removed patch. The left column of panels shows behaviors under directed

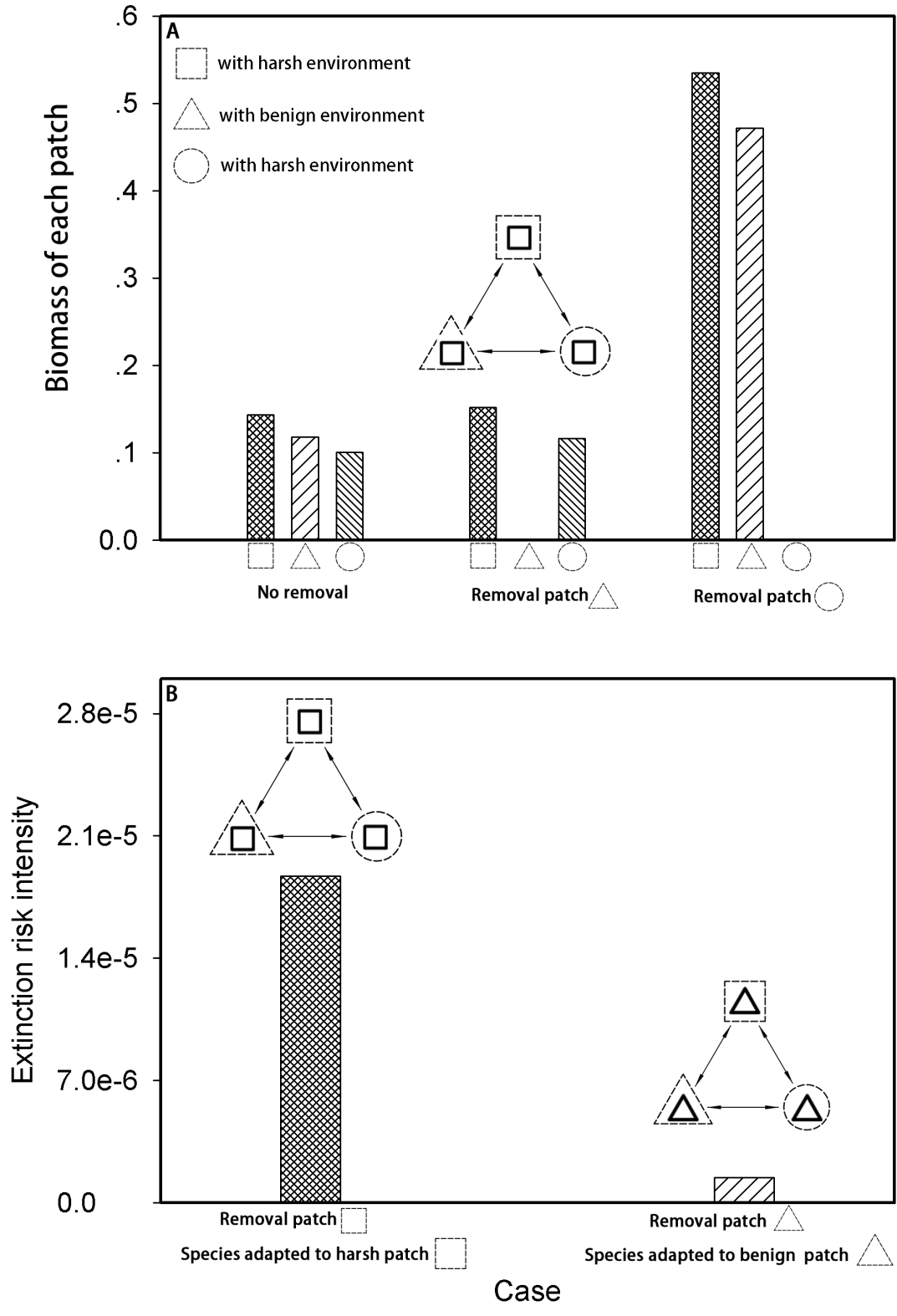
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dispersal, and the right undirected dispersal. Line colors differ by consumption rate as

773

indicated in the legend in A. Panels A and B represent the number of species going

774 extinct for dispersal rate $a=0.05$ in the extinction regimes “additional species similarly
775 adapted also at risk”. Panels C-H show ecosystem function debt/credit as the biomass
776 change for three different dispersal rates ($a=0.01$, 0.05 , and 0.5 , from top to bottom
777 row). The species cannot coexist when the dispersal rate is greater than 0.1 at low
778 consumption rate ($b=21$), so there are no data for that consumption rate in the last row
779 (G, H). The dotted line in panel E and G is for a change in biomass= 0 since they
780 include both positive and negative biomass change. In panel C-H, positive values on
781 the y-axis mean ecosystem function credit, whereas negative values mean ecosystem
782 function debt. A key trend is that the removal of benign habitats has the largest effects.
783 There are 50 patches here. See details in the main text.
784



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Figure 5 The biomass of each patch (A) and extinction risk intensity (B) with

788

patch removal in a metapopulation. Each metapopulation has three patches (square,

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