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

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Diversity and Distributions

18. Nov. 2024

1   **Title: Extinction and ecosystem function debt across dispersal rate and behavior**

2   **in a heterogeneous metacommunity model**

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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/z0Mrqixl9wJEzgLJN7GRi9oThNqiz7EoA0t3rm89_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

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

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

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

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

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 benigh 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 $t=2\times10^7$, which corresponds to

274    $2\times10^7\times0.2=4\times10^6$ 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

23

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.

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

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 statemen**t:

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

552 https://datadryad.org/stash/share/z0Mrqixl9wJEzgLJN7GRi9oThNqiz7EoA0t3rm89_t

553 M.

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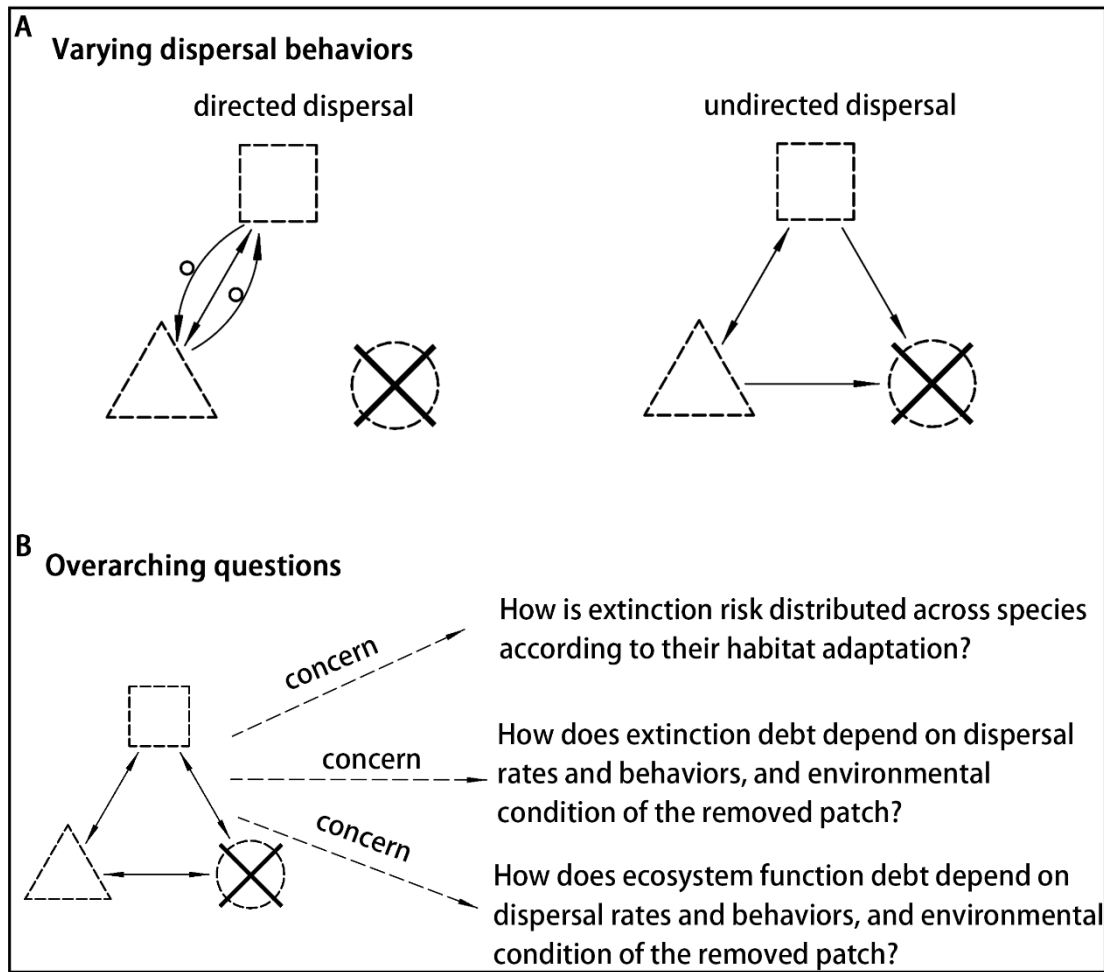698   and the extinction debt. *Nature*, 371, 65-66.

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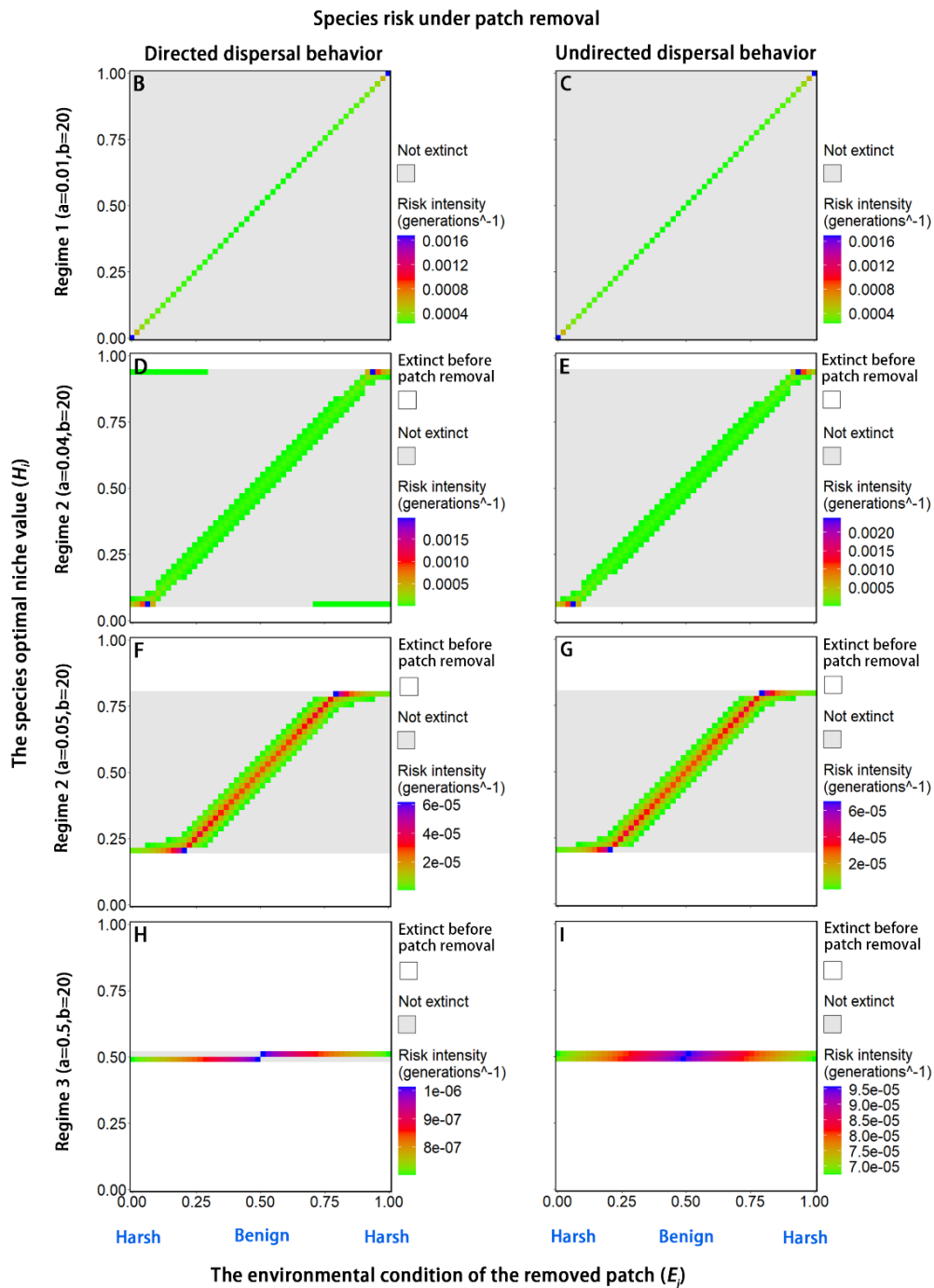**A Varying dispersal behaviors**

directed dispersal   undirected dispersal

B Overarching questions

concern — — — How is extinction risk distributed across species according to their habitat adaptation?

concern — — — How does extinction debt depend on dispersal rates and behaviors, and environmental condition of the removed patch?

concern — — — How does ecosystem function debt depend on dispersal rates and behaviors, and environmental condition of the removed patch?
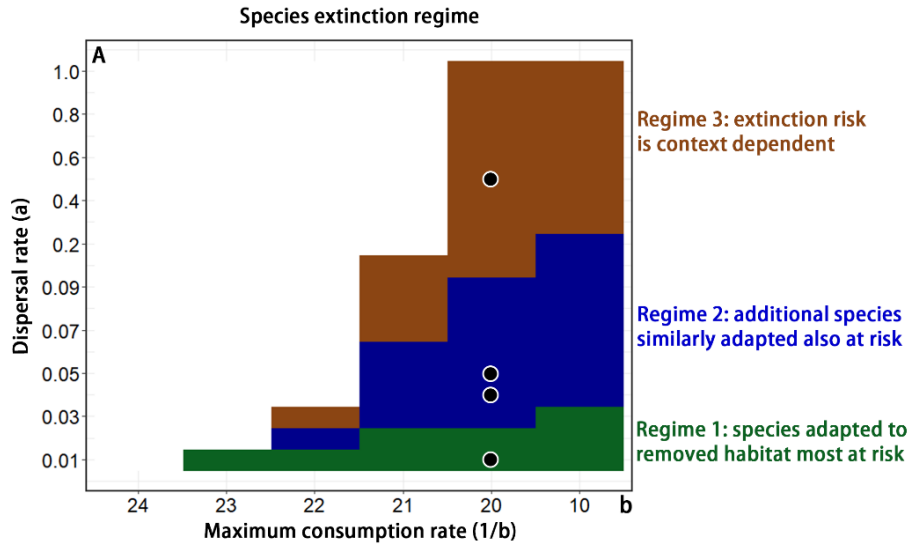
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710   **Figure 1 Dispersal behavior and questions asked.** Different shapes with dashed

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.

723

724

Species extinction regime

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

The species optimal niche value (H_i)

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

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.

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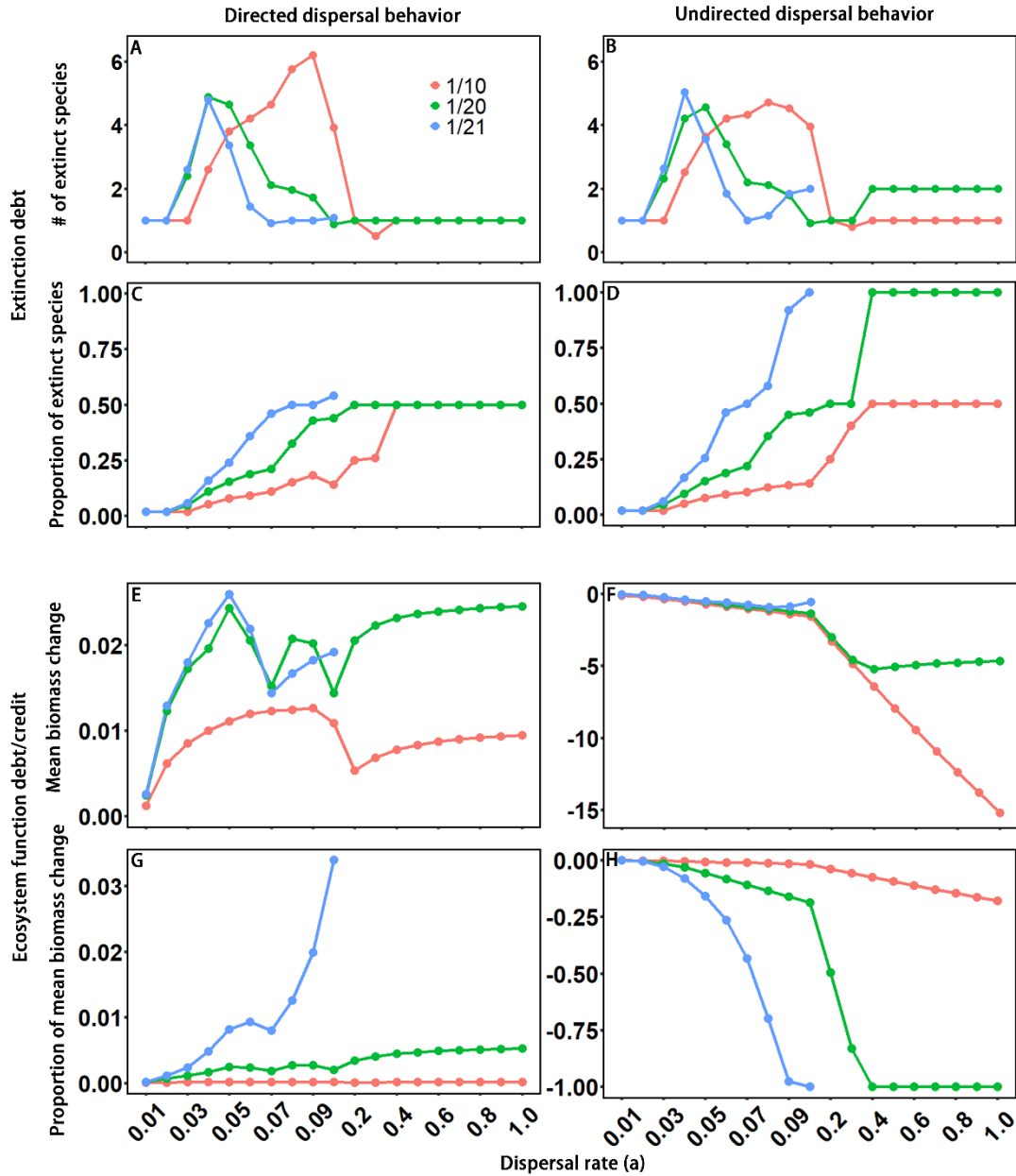
Figure 3 The magnitudes of extinction debt (A-D) and ecosystem function

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

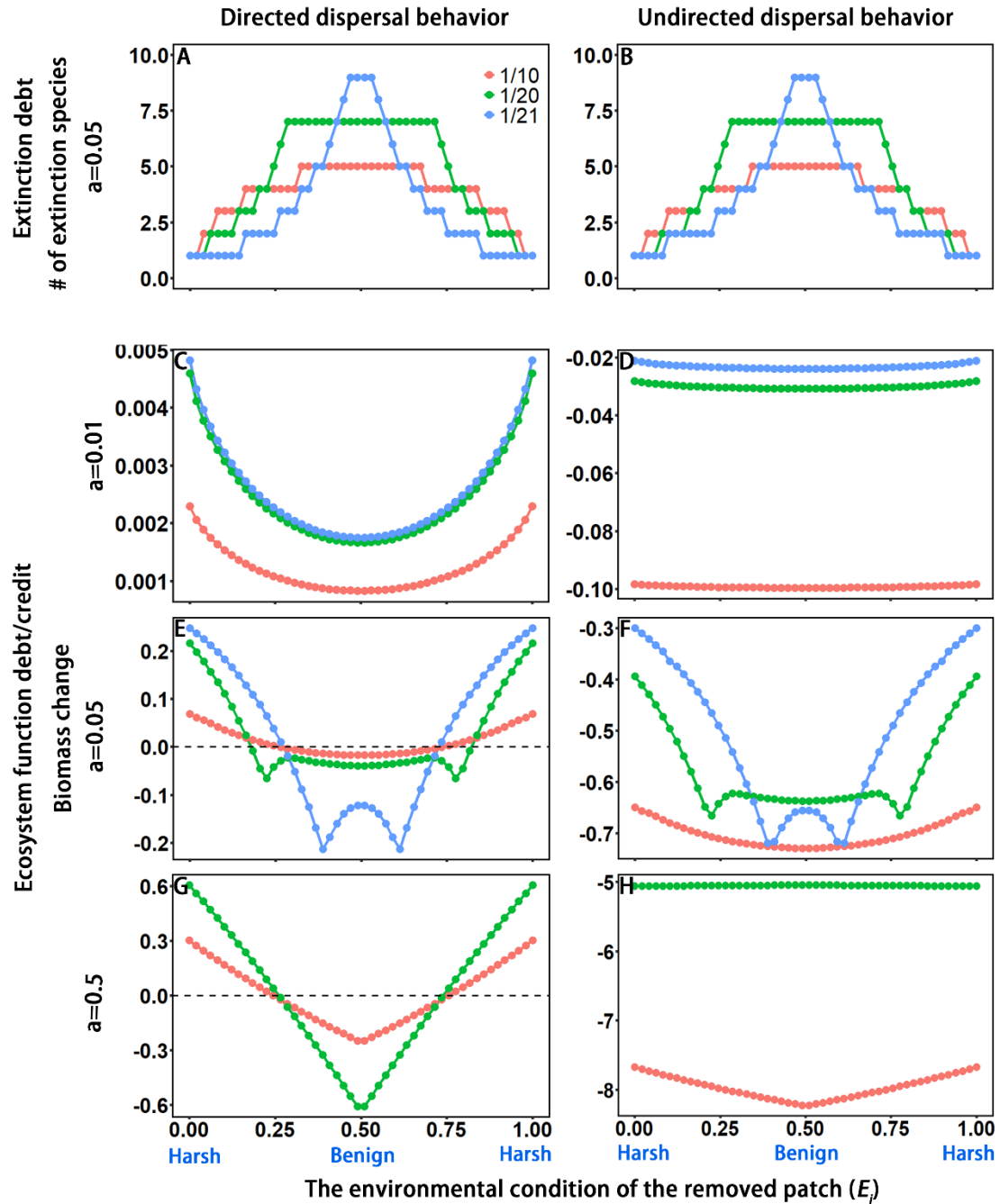under directed dispersal, and the right undirected dispersal. Line colors differ by

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

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

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

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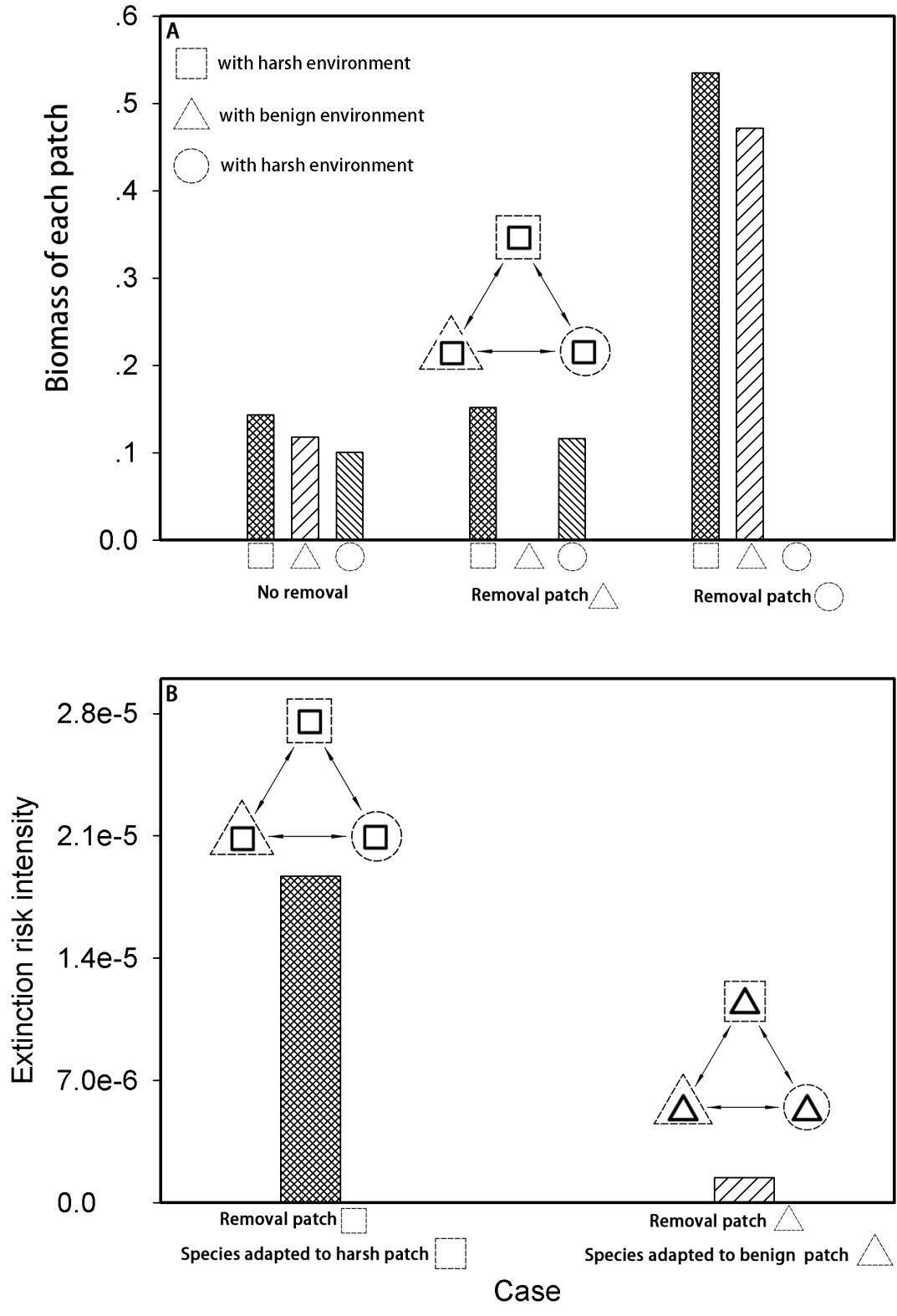
787 **Figure 5 The biomass of each patch (A) and extinction risk intensity (B) with**

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).

798