1 **Landscape heterogeneity buffers biodiversity of meta-food-webs under global**

2 **change through rescue and drainage effects**

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15 **Summary**

16 **The impacts of habitat fragmentation and eutrophication on biodiversity have been**

17 **studied in different scientific realms. Metacommunity research[1–5] has shown that**

18 **reduction in landscape connectivity may cause biodiversity loss in fragmented**

19 **landscapes. Food-web research addressed how eutrophication increases biomass**

20 **accumulations at high trophic levels causing the breakdown of local biodiversity [6–**

21 **9]. However, there is very limited understanding of their cumulative impacts as they**

22 **could amplify or cancel each other. Here, we show with simulations of meta-food-**

23 **webs that landscape heterogeneity provides a buffering capacity against increasing**

24 **nutrient eutrophication. An interaction between eutrophication and landscape**

25 **homogenization precipitates the decline of biodiversity. We attribute our results to**

26 **two complementary mechanisms related to source and sink dynamics. First, the**

27 **"rescue effect" maintains local biodiversity by rapid recolonization after a local**

28 **crash in population densities. Second, the "drainage effect" allows a more uniform**

29 **spreading of biomass across the landscape, reducing overall interaction strengths**

30 **and therefore stabilizing dynamics. In complex food webs on large spatial networks**

31 **of habitat patches, these effects yield systematically higher biodiversity in**

32 **heterogeneous than in homogeneous landscapes. Our meta-food-web approach**

33 **reveals a strong interaction between habitat fragmentation and eutrophication and**

34 **provides a mechanistic explanation of how landscape heterogeneity promotes**

35 **biodiversity.**

36

37 Increasing human demands for production of goods in natural landscapes have caused

38 habitat fragmentation and homogenisation, eutrophication and increasing land-use

39 intensity. This resulted in an erosion of biodiversity and associated ecosystem services at

40 global scales. Habitat fragmentation describes how production areas dissect continuous

41 natural landscapes into habitat patches embedded in a landscape matrix whose hostility

42 for the species increases with land-use intensity. Increasing nutrient inputs from

43 agricultural practices yield biomass accumulations at higher trophic levels, eroding

44 biodiversity by increased species' interaction strengths[6,9]. Despite growing evidence on

45 the importance of these global change factors, we still do not understand how their

46 interaction drives biodiversity changes. While fragmentation and eutrophication are

47 often studied in isolation, complex feedback loops in multi-trophic food webs can

48 generate non-linearities in the response of biodiversity, which is rendering our

49 knowledge of the interactive effects of these stressors in natural landscapes fraught with

50 uncertainty. The high-dimensional interplay between spatial and trophic processes

51   prevents experimental studies on such complex interactions. Simulations of spatial food

52   web dynamics are therefore needed to reveal the mechanisms underlying how these

53   global change stressors interact.

54   One key challenge is the integration of spatial processes connecting local populations

55   across habitat patches into metapopulations and interaction processes connecting local

56   species into complex food webs (Fig. 1). Traditionally, independent and mostly separated

57   research areas have addressed these two types of ecological networks. First,

58   metacommunity theory describes how dispersing individuals connect local populations

59   across complex spatial networks of habitat patches[10]. Depending on their size and quality,

60   patches can comprise large source populations that yield a net dispersal flux of individuals

61   to small sink populations[1,4] (Fig. 1a). These source-sink dynamics[11] can facilitate

62   persistence of small populations by rescue effects[12], which is undermined by increasing

63   fragmentation or land-use intensity that prevent successful dispersal. Second, food-web

64   theory addresses how biomass fluxes (i.e. energy and matter) between species drive

65   population dynamics (Fig. 1b). Weak biomass fluxes can cause consumer extinction due

66   to energy limitations while strong biomass fluxes can result in top-heavy consumer-

67   resource biomass pyramids with unstable dynamics[6,9]. Eutrophication in particular

68   increases all biomass fluxes and thus undermines biodiversity of local food webs[7].

69   Although both research areas documented strongly negative effects of either

70   fragmentation or eutrophication on biodiversity, the interplay of these stressors in

71   complex natural communities has remained virtually untapped.

72   So far, studies synthesizing spatial and trophic processes have been limited to small

73   species motifs such as food chains[13,14]. They showed that dispersal can synchronize

74   population dynamics, which reduces biodiversity by correlated local extinctions[15,16].

75   However, consumer dispersal can also induce compensatory dynamics[17] and dampen

76   oscillations[18], which prevents extinctions. Moreover, dispersal may increase resilience of

77   complex food webs by reducing strong interspecific interactions[19] depending on the

78   trophic level that is dispersing[18]. The relative strength of these potentially counteracting

79   positive and negative effects of dispersal on population persistence depends on the

80   trophic interaction structure[14]. While these studies have demonstrated interactions

81   between spatial and trophic processes in small modules, the study of impacts on

82   biodiversity in large spatial networks with many species has remained in its infancy.

83   Traits of organisms play an important role in both spatial and trophic processes. In

84   metacommunities, body mass and movement mode determine which patches compose

85   species-specific spatial networks[20]. Similarly, the propagation of energy fluxes through

86   food webs is driven by species' interaction strengths that depend strongly on body

87   masses[8]. Although metapopulation and food-web theories have been developed mostly

88   independently, they have identified the same important drivers (i.e. body mass), and the

89   same currencies (i.e. biomass fluxes). To date, a trophic metacommunity framework

90   incorporating spatial use properties is still lacking[21]. Also, as spatial and trophic processes

91   in real landscapes are coupled (Fig. 1c), a mechanistic understanding of global change

92   effects on ecosystems will benefit from an integrated approach. We address this challenge

93   by synthesizing metapopulation and food-web models that use allometric scaling

94   relationships of spatial and trophic processes as a unifying principle into a meta-food-web

95   model. We identify key mechanisms complementary to the rescue effect in landscapes

96   under eutrophication and isolation (Fig. 1).

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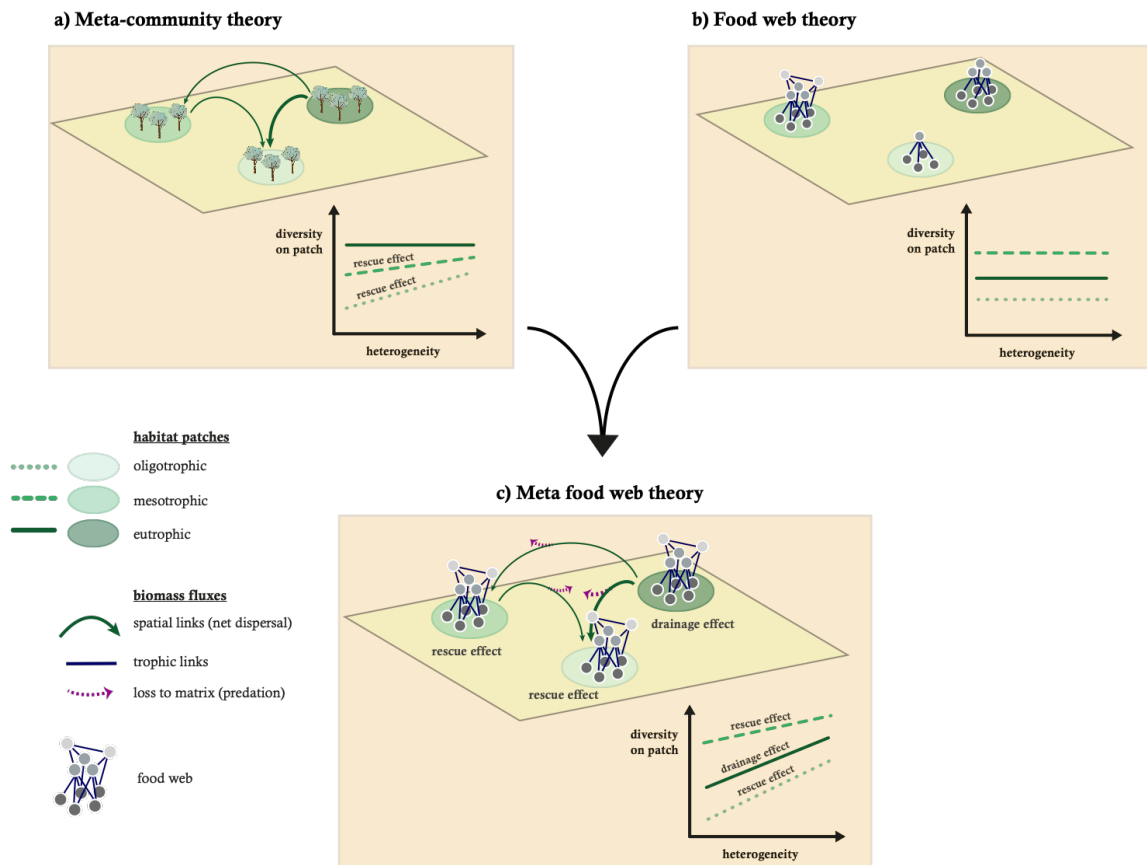
Fig. 1. Conceptual figure illustrating the synthesis of metacommunity theory and food-web theory into meta-food-web theory. Panel a) illustrates metacommunity dynamics with net dispersal from larger (nutrient richer patches) to smaller populations (nutrient poorer patches) and the associated rescue effect on local diversity. Panel b) illustrates local food-web dynamics on patches with different nutrient richness and the effect of the paradox of enrichment on local diversity. Panel c) illustrates the synthesis of metacommunity and food web dynamics and the interaction of respective key effects and their consequence for biodiversity.

We use a bioenergetic model to analyse population dynamics across a gradient of complexity from simple (tri-trophic food chain on a single patch) to complex systems (40-species food web on 50 habitat patches). This model employs body masses as the unifying trait that determines not only trophic links and interaction strengths of the food webs but also the dispersal ranges. Dispersal rates depend on local net growth rates, summarizing

112   resource availability, competition and predator pressure arising from local trophic

113   dynamics[22].

114

115   Firstly, on a single patch, low nutrient supply for a tri-trophic food chain causes predator

116   starvation (Fig. 2a, extinction, left side). Increasing nutrient supply first promotes

117   predator equilibrium biomass densities (Fig. 2a, survival, equilibrium) and therefore top-

118   heavy biomass pyramids causing biomass oscillations (Fig. 2a, survival, oscillation), which

119   paradoxically eventually yield predator extinction (Fig. 2a, extinction, right side). Such

120   extinctions due to unstable oscillations under eutrophication have first been described as

121   the "paradox of enrichment"[6]. Subsequently, they were generalized to systems with an

122   increased energy flux to the predator relative to its loss rate[9,23]. Turning around this

123   "principle of energy flux", however, also suggests that an additional drainage effect arises

124   from energy transfer from large populations (sources) to small populations (sinks),

125   preventing unstable dynamics in top-heavy systems. Consistent with this hypothesis, we

126   find that increasing emigration rates that drain biomass out of a eutrophic location can

127   prevent predator extinction by reducing oscillations (Fig. 2b). Spatial fluxes tend to

128   increase with dispersal rates and the underlying variability in the landscape. This

129   demonstrates the drainage effect as a mechanism by which spatial processes can stabilize

130   trophic population dynamics in heterogeneous landscapes.

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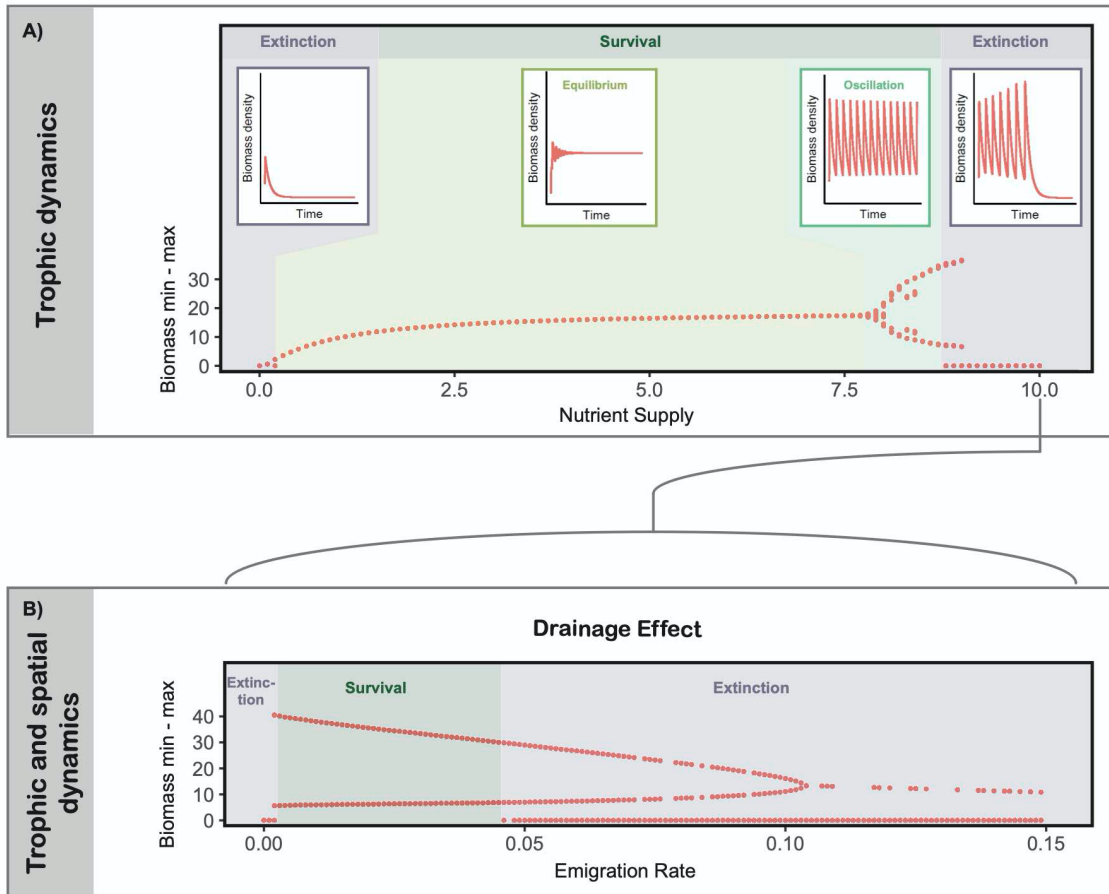
Fig. 2: Top predator dynamics of a tri-tropic food chain on a single patch. A) Exemplary time series of biomass densities of the predator at different nutrient supply concentrations (boxes; from left to right: 0.1 (oligotrophic); 3 (mesotrophic); 8.5 and 10 (eutrophic)) corresponding to points in the bifurcation diagram showing maximum and minimum biomass density (y-axis) across a gradient of nutrient supply concentrations (x-axis). B) Bifurcation diagram showing maximum and minimum biomass density (y-axis) when enabling emigration across a gradient of emigration rates (x-axis) with a nutrient supply concentration of 10, which corresponds to the last point in panel A).

Subsequently, we studied this drainage effect in systems of two connected habitats across gradients of landscape hostility and habitat heterogeneity (represented by the difference in nutrient supply concentration of the two locations). Landscape hostility summarizes all factors that drive the loss of biomass during dispersal including higher metabolic costs

146   and increased mortality rates by predation pressure in the unsuitable landscape matrix.

147   Dispersal synchronizes unstable dynamics, causing predator extinction (Fig. 3, lower left

148   corner), in simulations without heterogeneity and without hostility. Increasing landscape

149   hostility yields drainage of biomass during dispersal, facilitates predator persistence and

150   then also reduces oscillations (Fig. 3, along the hostility axis). At very high levels of

151   landscape hostility, however, extreme death rates during dispersal cause predator

152   extinction. Similarly, increasing patch heterogeneity also enables predator persistence

153   and decreases oscillations (Fig. 3, along the heterogeneity axis). The drainage effect offers

154   general mechanistic explanations for these emergent patterns despite of some slightly

155   more complex patterns in population oscillations (e.g. some combinations of landscape

156   hostility and patch heterogeneity yield weak spatial links between patches and

157   desynchronization of biomass oscillation frequencies, see Supplement Fig. S2 for details).

158   For eutrophic patches, increased dispersal losses by landscape hostility or the coupling

159   with an oligotrophic patch (patch heterogeneity) both increase the biomass drainage

160   through increased net migration. For oligotrophic patches, however, there are differences

161   between effects of landscape hostility and patch heterogeneity. Drainage by landscape

162   hostility supresses small populations even more, whereas patch heterogeneity causes a

163   gain in biomass via dispersal that supports predator populations via rescue effects (see

164   Supplement Fig. S1). Patch heterogeneity thus creates dispersal fluxes in biomass that are

165   responsible for not only the well-known rescue effects[12] supporting small populations on

166   oligotrophic sink patches by net-immigration but also the drainage effects sustaining

167   large populations on eutrophic patches.

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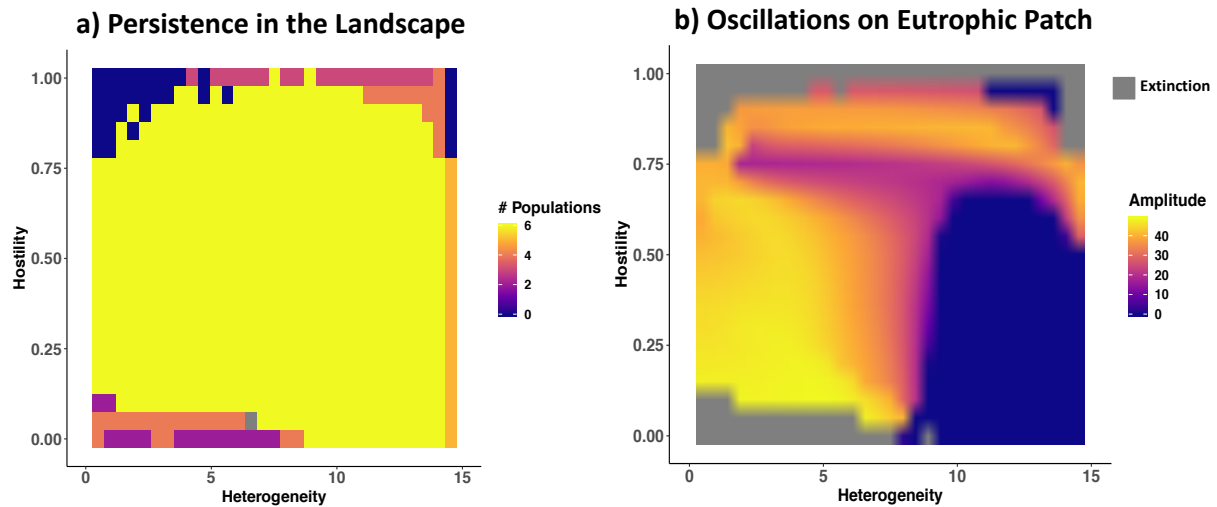
Fig. 3: Top predator dynamics of a tri-tropic food chain on two coupled patches. a) Heat map showing the number of persisting populations (colour coded; plant, herbivore and predator on 2 patches; maximum of 6) in the landscape across gradients of landscape heterogeneity (x-axis; difference in nutrient supply concentration across the two patches; on the left: two eutrophic patches, on the right: an eutrophic and an oligotrophic patch) and matrix hostility (y-axis). b) Heat map showing the amplitude of biomass density oscillations of the predator (z-axis; colour coded) in the (always) eutrophic patch across gradients of landscape heterogeneity (x-axis; difference in nutrient supply concentration between the two patches) and matrix hostility (y-axis). Amplitudes of 0 (blue) stand for an equilibrium state of the predator. Grey areas are where the predator went extinct.

178

To generalize the mechanistic understanding of drainage effects from food chains, we simulated the dynamics of a complex food web consisting of 10 plants and 30 animals on different complex landscapes containing 50 habitat patches (Fig. 4). We simulated homogeneous landscapes, where all patches have the same nutrient supply concentration.

183   These simulations were replicated across a gradient of nutrient supply concentrations

184   ranging from $10^{-0.8}$ (oligotrophic) to 10^2 (eutrophic). We also simulated three types of

185   heterogeneous landscapes with landscape averages being oligotrophic, mesotrophic or

186   eutrophic (Fig. 4). Nutrient supply concentration for each patch of heterogenous

187   landscapes is assigned randomly from the same gradient as in the homogeneous scenario,

188   but with a higher sampling density in the lower or higher nutrient supply values for

189   oligotrophic and eutrophic heterogeneous landscapes, respectively, and uniform

190   sampling for the mesotrophic heterogeneous landscapes. In line with our results from the

191   food chain simulations, we found that local species richness in homogeneous landscapes

192   is lowest on oligotrophic patches due to energy limitation. Higher nutrient supply first

193   increases species richness on mesotrophic patches before decreasing it again on

194   eutrophic patches (Fig. 4, purple). Species richness is highest in mesotrophic

195   heterogeneous landscapes because oligotrophic patches profit from the rescue effect and

196   eutrophic patches profit from the drainage effect (Fig. 4, orange). If there are only a few

197   oligotrophic patches in a eutrophic heterogeneous landscape, rescue and drainage effects

198   still increase local diversity, although the recue effect is weaker (Fig. 4, blue). Similarly, a

199   few eutrophic patches in an oligotrophic landscape foster local diversity through rescue

200   and drainage effects (Fig. 4, green). Thus, rescue effects and drainage effects also apply to

201   complex food webs in complex landscapes. This shows that the interaction of strong and

202   weak spatial and trophic biomass fluxes increases stability and species richness in

203   metacommunities.

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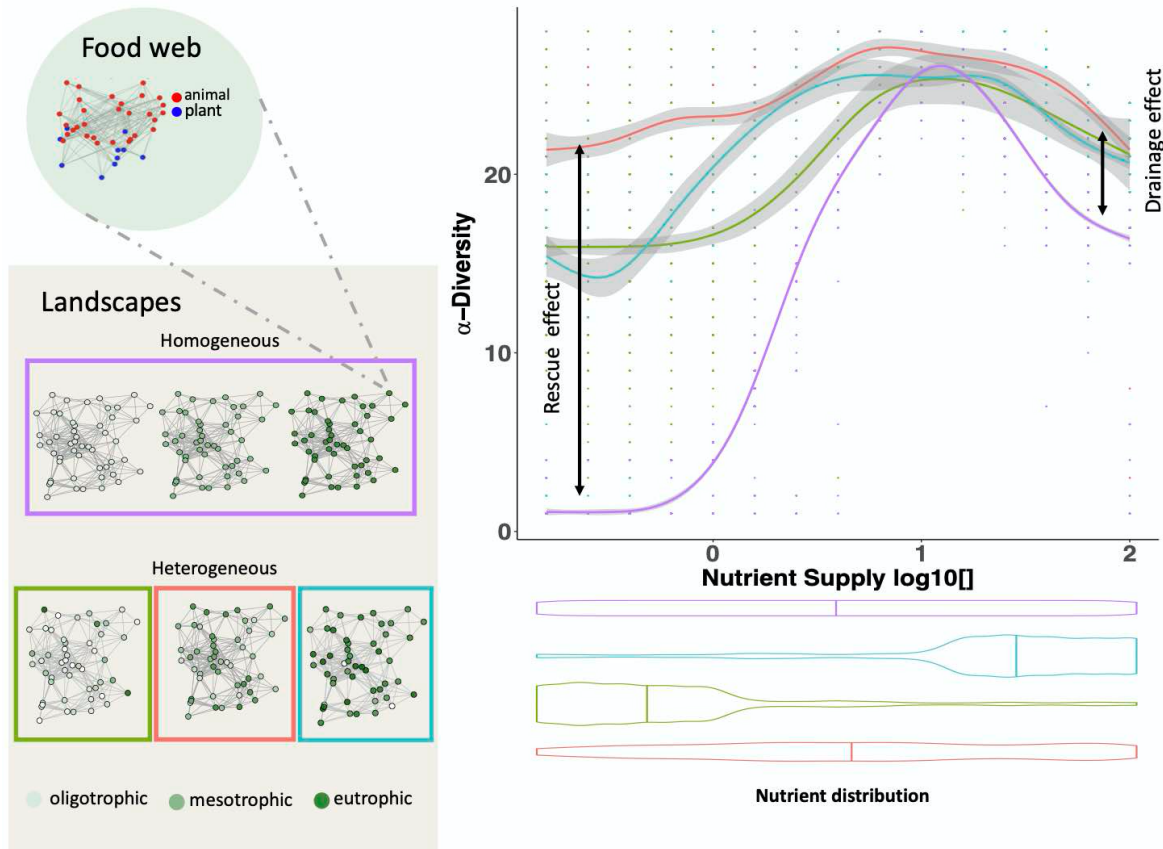
Fig. 4 Landscape heterogeneity drives biodiversity in complex meta-food-webs. Local diversity (y-axis) across a gradient of patch nutrient supply concentration in homogeneous (purple) and heterogeneous (green, orange, blue) landscapes. Violin plots below the x-axis show nutrient distributions within the landscape for each scenario. The meta-food-web consists of a complex food web of 10 plants and 30 animals and large homogeneous and heterogeneous landscapes with 50 habitat patches with different patch nutrient supply concentrations (nutrient supply concentrations on habitat patches are colour coded). Edges indicate dispersal links for an exemplary species with a dispersal range of 0.3. Lines are a smooth fit from a GAM model with 95% confidence intervals in ggplot2 and points represent the data.

Spatial processes in heterogenous landscapes stabilise local food-web dynamics and translate into higher diversity. This stresses the importance of addressing global change drivers in a meta-food-web framework. Various mechanisms are involved, all related to source-sink dynamics where energy moves from high biomass locations to low biomass locations. We have found that the well-known rescue effect allows persistence on

220   oligotrophic patches, while the novel drainage effect buffers eutrophic patches. Complex

221   interactions among these phenomena may further promote diversity. For instance,

222   nutrient spillover from a eutrophic to a neighbouring oligotrophic location may promote

223   local productivity and increase food-chain length[24]. Such spatial nutrient diffusion can

224   destabilize simple food chains and decrease spatial heterogeneity in a meta-ecosystem

225   model[18] and thus cross-ecosystem nutrient fluxes can change community composition[25].

226   These meta-ecosystem approaches have synthesized nutrient fluxes with simple trophic

227   modules, and our meta-food-web approach provides a flexible tool to scale-up these

228   findings to the levels of landscape and food-web complexity that characterize natural

229   ecosystems.

230

231   In real landscapes, which suffer more and more from fragmentation, land-use

232   intensification and eutrophication due to human activities, managing connectivity and

233   heterogeneity is an important aspect of biodiversity conservation and restoration.

234   Traditionally, increasing landscape hostility due to higher dispersal mortality or

235   increased distances between habitat fragments have been perceived as threats to the

236   biodiversity of habitat patches as they reduce rescue effects[12]. Hence, wildlife bridges

237   across highways and other corridors to increase connectivity between habitat patches

238   have been propagated as important tools to remedy the consequences of land-use

239   intensification as the reduced hostility may benefit small sink populations by rescue

240   effects and thus lower extinction risks[26]. Our results, however, indicate that the

241   consequences of increasing habitat connectivity are highly context-dependent. We found

242   that higher connectivity between large populations can undermine biodiversity by

243   decreasing the drainage effect, whereas connecting large and small populations is

244   generally beneficial for both. Thus, in managing landscape connectivity, connections

245 between eutrophic and oligotrophic habitats or among oligotrophic habitats should be

246 enhanced to reduce the hostility effect. However, connections among eutrophic habitats

247 should only be established with caution, as a reduced hostility effect results in less

248 drainage effect and thus has the potential do destabilize both populations.

249 Broader implications for ecosystem services can arise as two habitat patches that suffer

250 from eutrophication may lose predatory pest control agents if they are well connected to

251 each other but may maintain pest control when coupled with less intensive or natural

252 habitats. Thus, the management of connectivity and heterogeneity in landscapes suffering

253 from fragmentation and eutrophication may benefit from fostering rescue and drainage

254 effects to maintain biodiversity and ecosystem services. Our meta-food-web approach has

255 revealed interactions between spatial and trophic dynamics beyond the rescue effect that

256 provide a mechanistic explanation of how landscape heterogeneity enhances biodiversity,

257 which facilitates new strategies for active landscape management to foster natural

258 biodiversity and ecosystem services.

259

260 **Author contributions**

261 R.R., U.B. and M.R.H. developed the idea, R.R. built the model, did the analyses and wrote

262 the first draft of the manuscript. M.R.H. designed the figures. All authors contributed to

263 the interpretation and the final version of this manuscript.

264

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270

Competing interests

271

272   None declared.

273

274   **Materials and Correspondence**

275   Requests should be addressed to U.B.

276

277   **Methods summary**

278   **Model**

279   We model a tritrophic food chain of one plant, one herbivore and one predator population

280   on one or two habitat patches and complex meta-food-webs consisting of 10 plants and

281   30 animals in different landscapes containing 50 patches. The feeding dynamics are

282   constant over all patches and are determined by the allometric food-web model by

283   Schneider et al. 2016[27]. We integrate dispersal as species-specific biomass flux between

284   habitat patches according to Ryser et al. 2019[28]. With the use of a dynamic bioenergetic

285   model we formulate feeding and dispersal dynamics in terms of ordinary differential

286   equations. The rate of change in biomass densities of a species are the sum of its biomass

287   loss by metabolism, being preyed upon and emigration and its biomass gain by feeding

288   and immigration. For detailed equations see Ryser et al. 2019[28] and for model parameters

289   see the supplement (TS1).

290   **Local food-web dynamics**

291   Following the allometric food-web model by Schneider et al. 2016[27] each species is fully

292   characterised by its average adult body mass. For the complex food web $\log_{10}$ body masses

293   were randomly drawn from a uniform distribution from 0 to 3 for plants and from 2 to 6

294   for animals. For the food chain the plant body mass was set to 10^2, the herbivore body

295   mass to 10^4 and the predator body mass to 10^6. We set mass ratios of the herbivore to the

296   plant and the predator to the herbivore to the optimum of 100, thus the respective

297   resource being a one-hundredth of its consumer's body mass. Trophic dynamical

298   parameters, such as metabolic rates and feeding rates, scale with body masses of model

299   species. Also, we assume a type II functional response. Capture rates were reduced to 5%

300   to achieve viable food chains and food webs with no interference competition.

301   **Nutrient model**

302   We have an underlying nutrient model with one nutrient that is driving the nutrient

303   uptake and therefore the growth rate of the plant population[8,27]. The nutrient model

304   consists of one nutrient, a nutrient turnover rate of 0.25 and a nutrient supply

305   concentration. The nutrient supply concentration was varied to get eutrophic and

306   oligotrophic patches (see Setup).

307   **Spatial dynamics**

308   We model dispersal between local communities as a dynamic process of emigration and

309   immigration, assuming dispersal to occur at the same timescale as the local population

310   dynamics[29]. Thus, biomass flows change dynamically between local populations and the

311   dispersal dynamics directly influence local population dynamics and vice versa[22].

312   Dispersal rates of animals are modelled with an adaptive emigration rate depending on

313   the net growth rate on the given patch. Dispersal ranges depend on the body masses of

314   our model species with larger species having a higher dispersal range. We model a hostile

315   matrix between habitat patches that does not allow feeding interactions to occur during

316   dispersal. Depending on the scenario, we define a landscape with one or two patches. In

317   cases with two patches, their locations are spatially explicit and were chosen in a way that

318   the distances between reflect the dispersal loss of the predator across the matrix hostility

319   gradient.

320   Emigration and immigration

321   Based on empirical observations[30] and previous theoretical frameworks[13,20,31], we

322   assume that the maximum dispersal distance of animal species increases with their body

323   mass. For simplicity, we do not let the plants disperse, as they don't move themselves and

324   the dispersal of plant propagules strongly depends on their dispersal strategy. We model

325   emigration rates as a function of each species' per capita net growth rate, which is

326   summarising local conditions such as resource availability, predation pressure, and inter-

327   and intraspecific competition[22]. Dispersal losses scale linearly with the distance between

328   two patches and are 100% in scenarios with only one patch or when the distance between

329   the two patches surpasses the dispersal range of an animal. Even though we model

330   dispersal losses according to dispersal distances, this loss term could also represent any

331   other sort of dispersal loss. For numerical reasons, we did not allow dispersal flows

332   smaller than 10^{-10}.

333   Numerical simulations

334   We initialised each local population with a biomass density randomly sampled from a

335   uniform probability density within the interval (0,10). Starting from these random initial

336   conditions, we numerically simulated food web and dispersal dynamics over 100,000

337   time steps by integrating the system of differential equations implemented in C++ using

338   procedures of the SUNDIALS CVODE solver version 2.7.0 (backward differentiation

339   formula with absolute and relative error tolerances of 10^{-10}) and the time series of

340   biomass densities were saved for last 10,000 time steps. For numerical reasons, a local

341   population was considered extinct and was set to 0 once its biomass density dropped

342   below 10^{-20}.

343   Equations and parameters

344   For detailed equations and parameters, see Ryser et al. 2019[28] and the Supplementary

345   Material.

Setup

347   To answer our questions, we model the following scenarios:

348   *Nutrient enrichment*: Simulations across a gradient of nutrient supply concentrations (0,

349   10) on one patch without emigration and therefore also no dispersal loss.

350   *Drainage effect*: Simulations across a gradient of maximal emigration rates (0, 0.15) on

351   one eutrophic patch with a nutrient supply concentration of 10.

352   *Hostility effect with two patches*: Simulations across a gradient of dispersal losses (0, 1) on

353   two eutrophic patches with a nutrient supply concentration of 15 on each and a maximal

354   dispersal rate of 0.05.

355   *Heterogeneity effect with two patches*: Simulations across a gradient of nutrient supply

356   concentrations (0, 15) on one of two patches with the other patch being a eutrophic patch

357   with a nutrient supply concentration of 15, a maximal emigration rate of 0.05 and no

358   dispersal loss.

359   *Interaction of hostility effect and heterogeneity effect*: For each level of heterogeneity

360   (difference in nutrient supply between the two patches) we simulated the whole gradient

361   of the hostility effect (dispersal loss of the predator from 0 to 1).

362   *Heterogeneity effect on complex food webs in complex landscapes*: For a complex meta-

363   food-web, we generated 5 random geometric graphs consisting of 50 patches. Each patch

364   was initialised with a complex food web consisting of 10 plant and 30 animal species. For

365   all random geometric graphs, we simulated 15 homogeneous landscapes, where all

366   patches have the same nutrient supply concentration with simulations across a gradient

367   of nutrient supply concentrations ranging from $10^{-0.8}$ (oligotrophic) to 10^2 (eutrophic) in

368   steps of 0.2 in the exponent, and 5 heterogeneous landscapes, where the nutrient supply

369   concentration for each patch is assigned randomly from the same gradient as in the

370   homogeneous scenario.

371

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