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Isabelle Gounand, Eric Harvey, Pravin Ganesanandamoorthy, Florian
Altermatt

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1 **Title:** Subsidies mediate interactions between communities across space.

2 **Authors:** Isabelle Gounand*^{1,2}, Eric Harvey^{1,2}, Pravin Ganesanandamoorthy², Florian
3 Altermatt^{1,2}

4

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7 ***Corresponding author:**

8 Isabelle Gounand: isabelle.gounand@eawag.ch; ORCID: 0000-0002-0675-3973

9

10 **E-mails:**

11 EH Eric.Harvey@eawag.ch; ORCID: 0000-0002-8601-7326

12 PG Pravin.Ganesanandamoorthy@eawag.ch;

13 FA florian.altermatt@eawag.ch; ORCID: 0000-0002-4831-6958

14

15 **Affiliations**

16 ¹Department of Evolutionary Biology and Environmental Studies, University of Zurich,
17 Winterthurerstrasse 190, CH-8057 Zürich, Switzerland.

18 ²Eawag, Swiss Federal Institute of Aquatic Science and Technology, Department of
19 Aquatic Ecology, Überlandstrasse 133, CH-8600 Dübendorf, Switzerland.

20

21 Abstract

22 Most spatial ecology focuses on how species dispersal affects community
23 dynamics and coexistence. Ecosystems, however, are also commonly connected by
24 flows of resources. We experimentally tested how neighbouring communities indirectly
25 influence each other in absence of dispersal, via resource exchanges. Using two-patch
26 microcosm meta-ecosystems, we manipulated community composition and dynamics,
27 by varying separately species key functional traits (autotroph *versus* heterotroph species
28 and size of consumer species) and trophic structure of aquatic communities (species
29 growing alone, or in presence of competitors or predators). We then analysed the effects
30 of species functional traits and trophic structure on communities connected through
31 spatial subsidies in the absence of actual dispersal. Both functional traits and trophic
32 structure strongly affected dynamics across neighbouring communities. Heterotroph
33 communities connected to autotroph neighbours developed better than with heterotroph
34 neighbours, such that coexistence of competitors was determined by the functional traits
35 of the neighbouring community. Densities in autotroph communities were also strikingly
36 higher when receiving subsidies from heterotroph communities compared to their own
37 subsidies when grown in isolated ecosystems. In contrast, communities connected to
38 predator-dominated ecosystems collapsed, without any direct contact with the predators.
39 Our results demonstrate that because community composition and structure modify the
40 distribution of biomass within a community, they may also affect communities connected
41 through subsidies through quantitative and qualitative changes of detritus flows. This
42 stresses that ecosystem management should account for such interdependencies
43 mediated by spatial subsidies, given that local community alterations cascade across

44 space onto other ecosystems even if species dispersal is completely absent.

45

46 Introduction

47 Spatial flows between ecosystems are ubiquitous in nature. Research on spatial
48 ecology and meta-community dynamics demonstrated the fundamental role of dispersal
49 for species coexistence and biodiversity at local and regional scales (Mouquet and
50 Loreau 2002, Leibold et al. 2004, Holyoak et al. 2005, Seymour et al. 2015). In parallel,
51 ecosystem ecology and ecosystem-level studies have shown that spatial flows of
52 resources are also fundamental drivers of community dynamics (Polis et al. 1997, 2004,
53 Harvey et al. 2016). In natural ecosystems, many communities have a net heterotrophic
54 functioning and productivity relies on subsidies coming from neighbouring ecosystems.
55 For instance benthic marine- or freshwater-systems rely on detritus inputs sinking from
56 pelagic waters (Fitzgerald and Gardner 1993, Schindler and Scheuerell 2002), and at
57 aquatic-terrestrial boundaries, ecosystems experience strong bi-directional resource-
58 exchanges, with riverine vegetation subsidizing river or lake communities with dead-
59 organic matter (Hall et al. 2000, Cole and Caraco 2001, Richardson et al. 2010), while
60 riparian systems benefit from nitrogen-rich inputs of emergent aquatic insects (Baxter et
61 al. 2005, Gratton and Vander Zanden 2009, Dreyer et al. 2015), or fish carcasses
62 (Hocking and Reimchen 2009). The quantification of these resource spatial flows
63 (thereafter called subsidies), and the recognition of their importance for local community
64 dynamics by meta-community ecology, eventually led to a formal integration of
65 community and ecosystem perspectives on spatial flows within the meta-ecosystem
66 framework, accounting for both organism dispersal and resource exchanges between
67 ecosystems (Loreau et al. 2003, Massol et al. 2011, Massol et al. in review).

68 Previous studies on allochthonous subsidies generally investigated subsidy

69 effects on recipient communities from a donor-controlled perspective, thus without
70 consideration of the reciprocal effects on both connected ecosystems (e.g. Cole et al.
71 2006). Reframed into a spatial perspective, however, subsidies could be considered as
72 a vector of indirect interactions between community dynamics, with donor community
73 dynamics modulating the quantity and quality of exported resources. Both composition
74 (species traits) and structure (trophic interactions) of communities control the quantity
75 and quality of detritus locally produced, and potentially exported to other ecosystems as
76 subsidies. On the one hand, the population dynamics and life cycles of the species
77 composing a community determine the amount of detritus produced locally (e.g. subsidy
78 pulses triggered by 17-year emergence cycles of cicadas reported by Menninger et al.
79 2008). On the other hand, species functional traits determine detritus quality via their
80 stoichiometry (Sitters et al. 2015). Indeed, key species functional traits such as
81 autotrophy translate into carbon-nutrient ratios biased toward high values due to their
82 carbon-fixing photosynthesis activities, compared to the content of heterotrophic species
83 (see Sterner and Elser 2002, Sterner 2009 for cross-taxon comparisons). Through a
84 direct effect on the stoichiometric balance and the degradability of building block
85 molecules, community composition modulates not only detritus composition, but also the
86 rate at which detritus is made available as a new resource for subsidized communities
87 (Enriquez et al. 1993, Scott and Binkley 1997, Allison 2012), such as plant litter
88 composition driving decomposition rates in forest and stream ecosystems worldwide
89 (Cornwell et al. 2008, García-Palacios et al. 2015).

90 Community structure and the strength of species interactions within a community
91 should also affect the quantity and quality of detritus by modulating the biomass

92 distribution across trophic levels (Shurin et al. 2006). Empirical studies, for instance,
93 showed that in a wide range of ecosystems, changes in one trophic level induce trophic
94 cascades over an entire food web, which leads to drastic changes in biomass
95 distributions (Schmitz et al. 2000, Carpenter et al. 2001, Jackson et al. 2001, Frank et al.
96 2005). Beyond the traditional focus on species loss and local productivity change, the
97 spatial consequences for subsidy-connected ecosystems of these structural changes
98 and the subsequent modified detritus production have still to be investigated.

99 Overall the tight link between community composition and dynamics, and local
100 detritus production triggers an indirect connection between communities connected by
101 subsidy exchanges: the recipient community fed by subsidies becomes indirectly linked
102 to the donor community dynamics through the qualitative and quantitative characteristics
103 of the exported resources. Such subsidy linkages between ecosystems imply that local
104 community composition and structure may matter for the functioning of neighbouring
105 communities even in the absence of species' dispersal. This hypothesis has
106 fundamental implications for the functioning of connected ecosystems and for their
107 response to anthropogenic pressure, since it postulates the spatial spread of local
108 perturbations. Any event that would modify local community composition and dynamics,
109 such as biological invasions, is susceptible to pass on neighbouring community
110 dynamics through subsidy disruption even if species dispersal cannot occur (e.g. Baxter
111 et al. 2004).

112 Here we propose a test of such indirect "neighbour effects" with experimental
113 microcosm meta-ecosystems. We used aquatic microbial communities consisting of
114 bacteria feeding on organic resources, various autotroph and bacterivorous protists, and

115 a top predator. The microcosms were mimicking a wide range of natural ecosystems,
116 from heterotrophic, such as in stream or benthic waters, to autotrophic, such as forests
117 or pelagic phytoplankton-based ecosystems, and from resource to predator dominated.
118 We built two-patch meta-ecosystems connecting ecosystems only by spatial subsidies
119 (spatial flows of detritus and inorganic resources, and no organisms dispersing). In one
120 ecosystem we manipulated species traits (autotroph *versus* heterotroph species and
121 consumer body size), while in the other ecosystem we manipulated community structure
122 by adding a competitor or a predator (see Fig. 1). We followed temporal changes in
123 community dynamics (i.e., species density and biomass) in each ecosystem, and then
124 compared the dynamics between connected and isolated ecosystems to test if
125 communities with different structure and composition could affect each other only
126 through subsidy exchanges. Specifically we asked whether autotroph *versus*
127 heterotroph community dynamics could have differential impacts on neighbours, and
128 whether the addition of a species inducing novel trophic interactions (e.g. competition or
129 predation) could affect neighbour dynamics in the absence of organism dispersal.

130

131 Methods

132 Experimental design

133 To test the indirect influence of community composition on one another via cross-
134 ecosystem subsidies, we performed a two-patch meta-ecosystem experiment with
135 protists growing in microcosm ecosystems solely connected by subsidies (spatial flows
136 of detritus). We varied species traits in Ecosystem 1 and trophic structure in Ecosystem
137 2 according to a factorial design (Fig. 1). In Ecosystem 1 we grew one of these three
138 species with contrasting traits alone (monocultures): the autotroph flagellate *Euglena*
139 *gracilis* (~35 μm), a large bacterivorous ciliate (*Paramecium aurelia*, ~96 μm), or a small
140 bacterivorous ciliate (*Tetrahymena pyriformis*, ~30 μm). In Ecosystem 2, our focal
141 species, *Colpidium striatum*, a small bacterivorous ciliate (~45 μm) was grown alone, or
142 either with *Paramecium aurelia* as a competitor, or was submitted to predation by the
143 generalist filter feeding waterflea *Daphnia magna* (~0.5 to 2 mm). Treatments are
144 hereafter called “Autotroph”, “Large heterotroph” and “Small heterotroph” in Ecosystem
145 1 and “Focal Species” (FS), “FS+Competitor”, “FS+Predator” in Ecosystem 2. We
146 connected Ecosystem 1 and Ecosystem 2 only by subsidy exchanges (detritus,
147 including inorganic resources present in the growing medium), and prohibited any type
148 of species dispersal. We had a five-fold replication of the nine meta-ecosystem types (all
149 possible combinations of Ecosystems 1 and 2), as well as the control ecosystems
150 without diffusion, resulting in an experiment consisting of 45 independent 2-patch meta-
151 ecosystems and 30 isolated 1-patch ecosystems (120 microcosms).

152

153 Experiment setup

154 Ecosystems were assembled in microcosms of 250 mL Schott bottles filled with 100 mL
155 culture medium. All organisms (bacteria, protists, and waterfleas) used in the experiment
156 were grown in pre-autoclaved protist pellet suspension filtered through Whatman filters
157 (0.31 g protist pellets 1 L⁻¹ tap water; Protist pellets from Carolina Biological Supply,
158 Burlington NC, USA). Microcosms were assembled with 75 ml protist medium, 5 mL of
159 bacterial culture (*Serratia fonticola*, *Bacillus subtilis* and *Brevibacillus brevis*; added one
160 day prior to protist addition), and completed with 20 mL of protist culture at carrying
161 capacity (10 mL per species in the competition treatment). For the predation treatment,
162 we added four equal-sized juvenile *Daphnia magna* to each microcosm. More details on
163 protist culture and experimental procedures are found in Altermatt et al. (2015).
164 Microcosms were randomized within the 5 replicate blocks, and the experiment took
165 place at 20 °C and constant lighting. We replaced all *Daphnia* that died within the first
166 six days due to initial conditions (i.e., insufficient oxygen-levels in the freshly autoclaved
167 medium).

168

169 Diffusion

170 Ecosystem 1 and 2 were connected by bi-weekly reciprocal subsidy exchanges.
171 These spatial flow events consisted in sampling 30 mL from each ecosystem,
172 microwaving these samples for 100 seconds, until they reached a full boil, to turn all
173 living biomass into detritus, and then adding it into the respective connected ecosystem
174 after a cooling period of two hours at ambient temperature (20 °C). This diffusion

175 method mimics detritus flows associated with recurrent perturbation-induced mortality.
176 Isolated controls were also submitted to the same perturbations, but the microwaved
177 samples were added back in the microcosm of origin to isolate the diffusion effects from
178 perturbation-induced mortality.

179

180 Samplings and measurements

181 In parallel, we tracked changes in community dynamics in each microcosm during
182 one month. We measured population densities every Tuesday and Friday (i.e., twice a
183 week), leaving as much time as possible for protist growth after each diffusion event
184 (occurring on Wednesdays and Saturdays). At each measurement point we took two 0.5
185 mL samples per microcosm, one to measure protist density by video analysis, the other
186 to measure bacterial dynamics by flow cytometry. The volumes sampled were
187 considered sufficiently small to not affect local dynamics (Altermatt et al. 2011) and thus
188 did not need to be replaced by fresh medium. We recorded one 5 s-video per sample
189 following a standardized video procedure (Pennekamp and Schtickzelle 2013, Altermatt
190 et al. 2015). From each video we extracted densities of moving individuals along with
191 morphometric and movement information, such as cell size and speed. This was
192 achieved using the R-package *bemovi* (Pennekamp et al. 2015) coupled to the image
193 analysis free-ware ImageJ (ImageJ, National Institute of Health, USA). The additional
194 traits measured served to discriminate species identity in mixtures (competition
195 treatment), provided as inputs to trait distance analysis with the *svm* algorithm (e1071 R-
196 package Meyer et al. 2014), and to calculate bio-areas as a proxy for biomass. Since
197 automated particle detection relies on movement, the method systematically

198 underestimated densities of *Euglena gracilis*, which is much less mobile than the other
199 species. Therefore, we complemented density estimates of this species with visual
200 counts from the videos. To exclude false positives, we also performed a visual check of
201 all videos where a protist species had less than 3 individuals per frame. We counted
202 *Daphnia* individuals visually. Finally, we measured the total abundance of the 3-species
203 bacterial community on a flow cytometer (BD Accuri™ C6 cell counter) on SYBR green
204 fixed samples (dilution x1000), following a standard protocol (Altermatt et al. 2015).

205

206 Analyses

207 We characterized the indirect effects of neighbouring communities on each other
208 through subsidy flows using log response-ratios of protist densities at each time point,
209 for the different neighbour treatments (either species traits or trophic structure) in the
210 connected ecosystem, with 95% confidence intervals (CI). The responses were tested
211 relative to controls without diffusion, such that CIs not comprising zero reveal significant
212 effects of diffusion, while none overlapping CIs between neighbour treatments reveal a
213 significant neighbour effect. We tested the effects of trophic structure on neighbour
214 community dynamics by comparing the density of species in Ecosystem 1 (each
215 monoculture) when connected to different communities driven by specific interactions in
216 Ecosystem 2 (i.e. FS, FS+Competitor, FS+Predator). Conversely, we tested the effects
217 of functional traits on neighbour community dynamics by comparing the density of our
218 focal species, *Colpidium striatum*, in Ecosystem 2 when connected to different species
219 population with specific functional traits in Ecosystem 1 (i.e. Autotroph, Large
220 heterotroph, Small heterotroph). We studied the potential interaction with time by

221 running generalized linear models (GLM) on log response-ratios with species traits or
222 trophic interaction in the connected ecosystem and time as explanatory variables. We
223 used Gaussian distributions as link functions to avoid overestimation of positive effects
224 due to the ratio (Berlow et al. 1999). The effect of species traits in Ecosystem 1 on
225 competitive outcome in Ecosystem 2 was also tested with a GLM on the density of
226 *Colpidium* relative to *Paramecium* (using the relative proportion), with species traits in
227 the connected ecosystem and time as explanatory variables. For each GLM, the level of
228 significance and the effect size of each factor, and their interactions, were assessed
229 using a standard F test (Type II analysis of deviance). For each significant term of
230 interest we ran post-hoc pairwise comparisons (with Tukey adjusted p-values) to
231 evaluate specific contrast among variables. When time was not significantly affecting the
232 terms of interest we performed the post-hoc analysis on simplified GLM sub-models
233 (without the effect of time) in order to avoid unnecessary inflations of type II error
234 (Nakagawa 2004).

235 Lastly, because neighbour effects can originate from changes in both subsidy
236 quantity and quality, we examined approximated biomass (bio-areas) at the different
237 trophic levels (bacteria, protist, predator) according to community characteristics
238 (species traits or trophic structure) to bring an element of interpretation, assuming that
239 the different trophic levels produce different qualities of detritus. For bacteria we took a
240 constant mean individual area of $1 \mu\text{m}^2$, assuming no significant change of size over the
241 experiment (bio area = $1 \mu\text{m}^2 * \text{cell counts}$). For protists, we measured mean individual's
242 area directly from the video analysis, and extrapolated it to the total population
243 (Pennekamp et al. 2015). Bio-area of *Daphnia* was estimated visually based on four size

244 classes. To test protist and bacteria bio-area differences among communities along time
245 we ran four different GLM with either species traits (Ecosystem 1) or trophic structure
246 (Ecosystem 2) and time as explanatory variables. We studied residual distributions to
247 select the most appropriate link function (Gamma or Gaussian). All analyses were
248 conducted with R 3.1.2 (R Development Core team, 2014), using the 'car' package (Fox
249 and Weisberg 2011) for type II analysis of deviance, and the 'lsmeans' package for post
250 hoc pairwise comparisons (Lenth 2013).

251 Results

252 Subsidy-mediated effects on population density

253 Both local community functional traits (autotrophy *versus* heterotrophy) and
254 trophic structure induced strong significant effects on connected communities via
255 subsidy exchanges and in the absence of dispersal (see Supplementary material
256 Appendix 1 Table A1 and Appendix 2 Table A2). At the end of the experiment,
257 population densities of our focal species in Ecosystem 2 were significantly higher when
258 connected to autotroph compared to heterotroph communities ($F_{2,60} = 39.40$, $p < 0.0001$
259 in Focal Species and FS+Competitor treatments (see Supplementary material Appendix
260 1 Table A1, and Appendix 5 Table A5 for post-hoc multiple comparisons) or compared
261 to isolated communities (Fig. 2, panels a and b). The only exception was in the
262 FS+Predator treatment where predation resulted in the extinction of the focal species
263 irrespective of functional traits in the connected community (Fig. 2c). Predators drove
264 protist to extinction and concentrated all the biomass in their body, which cascaded on
265 detritus quality and negatively affected population density in subsidy-connected
266 communities in Ecosystem 1 compared to the focal species grown alone (FS) (Fig. 3,
267 $p < 0.0001$ for the factor “trophic structure” on each community; see Supplementary
268 material Appendix 1 Table A2 for the GLM and Appendix 5 Tables A5 for post-hoc
269 multiple comparisons). Moreover, the benefit (or not) of being a connected *versus* an
270 isolated community depended on species functional traits. Some species were relatively
271 insensitive to spatial subsidies when connected to FS or FS+Competitor communities
272 (e.g. Large heterotroph, Fig. 3b). In contrast, the autotroph did always far better when
273 connected to heterotroph communities, regardless of the trophic structure, compared to

274 isolated autotroph communities, which received only their own autotroph detritus (Fig.
275 3a: confidence intervals above the zero line). At last, consumer size (Large versus Small
276 heterotroph) did not impact significantly species density in the connected ecosystem.

277

278 Subsidy-mediated effect on competition

279 While trophic structure in one ecosystem significantly impacted community
280 dynamics in the connected ecosystem, the reverse was also true: we found that the
281 competition outcome (in Ecosystem 2) strongly depended on species functional traits in
282 the connected ecosystem (Fig. 4, $F_{3,144} = 8.56$, $p < 0.0001$; see Supplementary material
283 Appendix 3 Tables A3 for full results of the GLM). At the end of the experiment,
284 coexistence between the two competitors (*Colpidium* and *Paramecium*) was only
285 observed in the meta-ecosystems with the autotroph as a neighbour (Fig. 4a). In the
286 presence of heterotrophic neighbours, we systematically observed competitive exclusion
287 of our focal species (*Colpidium*) by its competitor (Fig. 4b-d, with an exception in one
288 isolated replicate ecosystem), while it persisted over the course of the experiment when
289 connected to the autotroph community (Fig. 4a).

290

291 Changes in biomass distribution

292 We observed that the biomass distribution among trophic compartments (bacteria
293 / protists / predator) varies among community types, as inferred from bio-areas (Fig. 5;
294 Supplementary material Appendix 4 Tables A4). In the ecosystems where the predator
295 was present, both bacteria and protist biomass decreased dramatically within a few days

296 (Fig. 5, right side), and almost all biomass was concentrated at the predator level
297 (99.97% of the estimated bio-area at the end of the experiment). Protist and bacteria
298 biomasses did not differ between FS and FS+Competitor communities, but were
299 significantly lower in the FS+Predator community (adjusted p-value <0.0001 for every
300 pairwise comparison; see Supplementary material Appendix 5 Tables A5). Interestingly,
301 positive neighbour effects of the autotroph species on neighbour ecosystems occurred
302 despite the fact that autotroph protist biomass was generally lower or did not differ from
303 other neighbours (Fig. 5a, left side), but were associated with significantly higher
304 bacterial biomass (Fig. 5b, left side, see Supplementary material Appendix 5 Tables A5
305 for all multiple comparisons).

306 Discussion

307 Community ecology usually assumes that species dispersal and local interaction
308 dynamics are the main processes driving regional biodiversity and species coexistence
309 (Leibold et al. 2004, Holyoak et al. 2005). With our experiment, we show that exchange
310 of subsidies among ecosystems also shapes community dynamics by mediating indirect
311 interactions between communities. By integrating resource dynamics in meta-
312 communities, the meta-ecosystem concept offers an operational framework to envision
313 spatial feedbacks between resource and community dynamics at a large spatial scale
314 (Loreau et al. 2003). Here, we demonstrate in experimental meta-ecosystems that the
315 integration of feedbacks between community dynamics and spatial subsidies is needed
316 to understand ecosystem dynamics, and are essential to forecast the spatial spread of
317 local perturbations.

318 Our experiment reveals three striking subsidy-mediated effects among
319 communities solely connected by detritus spatial flows. First, autotroph communities
320 positively affected densities in the connected communities, such that the persistence of
321 our focal species in the presence of a competitor was tributary to these autotroph
322 subsidies. Second, population densities in the autotroph community heavily depended
323 on subsidies from heterotroph communities. Third, by contrast to these positive effects,
324 local predation negatively affected connected communities, even though the predator
325 was not allowed to disperse, but was only indirectly affecting them through the alteration
326 of subsidy flows. These three effects demonstrate that local community composition and
327 structure can strongly affect community dynamics in neighbouring ecosystems, even in
328 the absence of dispersal.

329 We explain the observed effects in terms of subsidy changes in quantity and
330 quality. The specific functioning of autotroph, heterotroph, and predation-pressured
331 communities impacted subsidies in contrasting ways. Photosynthetic activity by
332 autotrophs introduced new resources in the system otherwise closed, by fixing
333 atmospheric carbon, stored as carbohydrates (labile forms of carbon) or dissolved in the
334 medium by release activity (Baines and Pace 1991, Biersmith and Benner 1998, Guenet
335 et al. 2010). The greater bacteria densities in autotroph compared to heterotroph
336 communities likely profited from the exploitation of photosynthesis-derived dissolved
337 carbon (Børsheim et al. 2005). In addition, the small size of bacteria and their higher
338 surface/volume ratio may have enhanced recycling rates due to a greater proportion of
339 dead material exposed to decomposition (Berg 1984). Overall, even if not directly
340 measured, subsidies flowing from autotroph communities were undoubtedly more
341 abundant and more readily available than the ones flowing from heterotroph
342 communities. These rich subsidies subsequently triggered a bottom-up effect in the
343 neighbouring community resulting in higher densities of bacterivorous consumers.

344 Interestingly in the reverse direction also, subsidies from heterotroph communities
345 positively impacted autotroph community dynamics. This result stresses that neighbour
346 effects may not only happen via changes in subsidy abundance but also through
347 alterations to detritus stoichiometric balance. While not directly measured, the generally
348 greater ratio of nitrogen to carbon in heterotroph organisms (Elser et al. 2000, Sterner
349 2009) is a straightforward explanation for the higher densities of autotroph communities
350 when exchanging detritus with heterotroph communities compared to isolated controls,
351 along with likely ammonium release activity of the bacterivorous protists (Probyn 1987).

352 Overall, in our autotroph-heterotroph coupled ecosystems, heterotroph subsidies likely
353 relaxed autotroph nitrogen limitation, while autotroph subsidies fuelled heterotroph
354 growth with abundant labile carbon. Ecosystem couplings resulting in such resource
355 spatial complementarity are common between freshwater and riparian systems, with
356 riparian ecosystems exchanging abundant leaf litter against nitrogen-rich aquatic insects
357 (Baxter et al. 2005, Bartels et al. 2012), and thus highlight the general significance of our
358 findings.

359 By contrast, subsidies from communities with predators had negative effects on
360 neighbour community dynamics. We used a generalist predator species, capable of
361 consuming almost all protists and bacteria. Consequently, most of the biomass in these
362 ecosystems was concentrated at the highest trophic level, in the chitinous exoskeleton
363 of *Daphnia*. The molecular robustness of chitin as well as the low proportion of organic
364 material exposed to decomposition of larger organisms likely slowed down the recycling
365 process of predator detritus compared to other detritus (Berg 1984, Hamre et al. 2014).
366 The delay between slow recycling process and community dynamics triggered a spatial
367 cascade, leading to the accumulation of subsidies into recalcitrant form and to the
368 progressive starvation of neighbouring communities. It is noteworthy that in our closed
369 meta-ecosystems and in the absence of autotrophic species, the amount of subsidy
370 transferred is always the same (30% of total volume), therefore ruling out any local
371 collapse of subsidy to explain the negative effect of the predation. Therefore, the
372 observed indirect negative impact of predation on neighbour density likely comes from a
373 lower quality of subsidies. Beyond the specific effect of this particular predator, this
374 result stresses that changes in biomass distribution within a community may affect

375 neighbours by modifying subsidy characteristics.

376 Overall, our experiment shows general mechanisms by which natural
377 communities can indirectly but strongly influence each other's functioning, via the
378 abundance, stoichiometry and decomposability of detritus locally produced and
379 subsidizing other ecosystems. Measuring directly the stoichiometric changes in
380 subsidies produced by contrasted communities could be a natural extension of this
381 experiment to investigate these mechanisms further. We demonstrate that, next to
382 species dispersal (for example tested by Staddon et al. (2010)), spatial dynamics of
383 detritus are essential by themselves to understand the fundamental functioning of
384 connected ecosystems, as well as their response to perturbations. The importance of
385 subsidies is often studied only from the recipient ecosystem's local perspective (see
386 Marcarelli et al. 2011, Sitters et al. 2015 for reviews), and ecosystem managers usually
387 consider the threat of direct alterations to resource flows (e.g. nutrient pollution), but
388 rarely threats potentially induced by alterations of community structure or composition in
389 connected ecosystems (but see the crash of forest spider communities, induced by
390 prey-subsidy disruption following the invasion of a stream by an exotic fish in Baxter et
391 al. 2004). Our results suggest that any kind of perturbation (e.g. land-use change, over-
392 harvesting) can have wider repercussions in space than those observed on local
393 communities because of subsidy disruption (e.g. cascades across aquatic-terrestrial
394 boundaries: Greig et al. 2012, Fey et al. 2015, Schulz et al. 2015). The extent to which
395 local perturbations spatially cascade to other communities will depend on the strength of
396 the subsidy coupling between ecosystems, an essential piece of information on which
397 more research is needed. Our findings call for the adoption of a spatial perspective in

398 ecosystem management and restoration ecology that integrates fine-tuned knowledge of
399 resource spatial exchanges between ecosystems.

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404

405 Statement of authorship

406 IG, EH and FA designed the research; IG, EH and PG conducted the research and
407 processed the data; IG analysed the data and wrote the first draft of the manuscript. All
408 authors contributed to the final version of the manuscript.

409

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413

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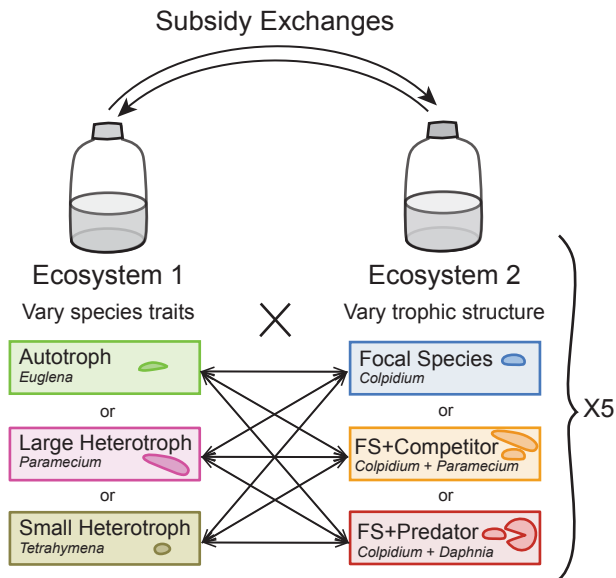
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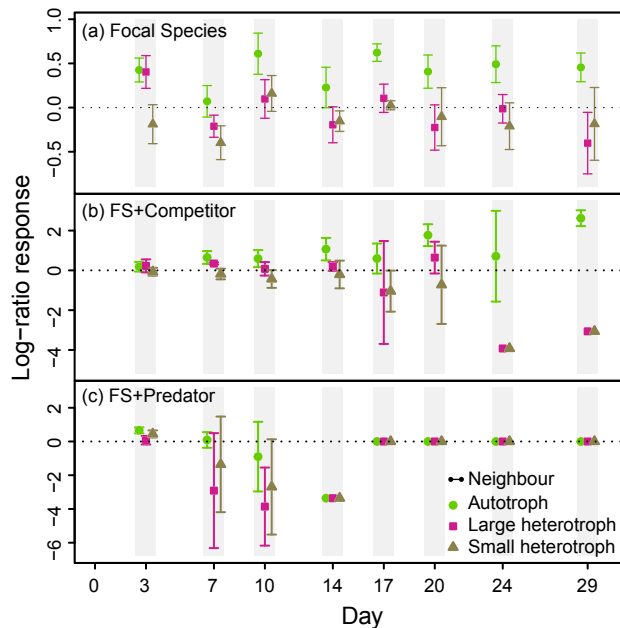
544 Supplementary material (available online as Appendix oik- 03922
545 at <www.oikosjournal.org/readers/appendix/oik-03922>). Appendix 1
546 Data available from the Dryad Digital Repository: <[http://](http://dx.doi.org/10.5061/dryad.93hd6)
547 dx.doi.org/10.5061/dryad.93hd6 >
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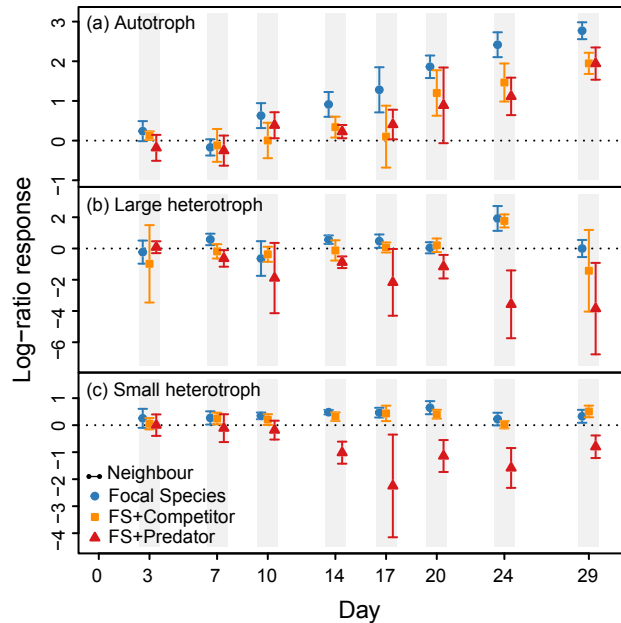
550

551 Figure 1. The experimental design consists of two-patch meta-ecosystems linked by
 552 reciprocal exchanges of detritus and resources (subsidies). In Ecosystem 1, we varied
 553 the dominant functional trait of the species present (either *Euglena gracilis*, *Paramecium*
 554 *aurelia*, or *Tetrahymena pyriformis*). In Ecosystem 2, we varied the trophic structure, by
 555 growing either a single species (*Colpidium striatum*; Focal Species (FS)), this same
 556 species with an additional competitor (FS + Competitor: *Colpidium striatum* with
 557 *Paramecium aurelia*), or in presence of a predator (FS + Predator: *Colpidium striatum*
 558 with *Daphnia magna*). The combination of these two variation levels gives nine different
 559 meta-ecosystems, each replicated five times. All ecosystems were inoculated with the
 560 respective above named species, a bacterial community and organic resources.



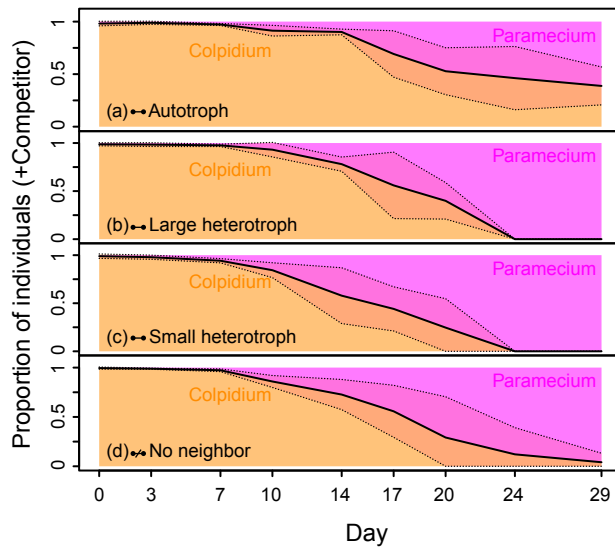
561

562 Figure 2. Effect of the species traits in Ecosystem 1 on the density of focal species in
 563 Ecosystem 2 (*Colpidium striatum*) over time, expressed as the log response-ratio (RR)
 564 of *Colpidium* density to detritus diffusion compared to the control without diffusion: Log
 565 $RR = \ln\left(\frac{N_{Col}^{diff+} + \min_D}{N_{Col}^{diff-} + \min_D}\right)$, with N the density and \min_D the minimal
 566 density detectable by our video analysis. Shapes and colours refer to the neighbour
 567 species. Bars give the 95% confidence interval (CI). Densities with CI not crossing the
 568 zero dotted lines differ significantly from the control. None overlapping CIs reveal protist
 569 densities significantly differing from each other. Each panel gives the results for a
 570 different trophic structure involving our focal species: (a) Focal Species, (b)
 571 FS+Competitor, (c) FS+Predator.



572

573 Figure 3. Effect of trophic structure in Ecosystem 2 on the density of different species in
 574 Ecosystem 1 via the diffusion of detritus over time, expressed as the log-ratio of density
 575 response to detritus diffusion compared to the control without diffusion: log response-
 576 ratio = $\ln\left(\frac{N^{\text{diff}+} + \min_D}{N^{\text{diff}-} + \min_D}\right)$, with N the density and \min_D the minimal
 577 density detectable by our video analysis. Shapes and colours refer to the neighbour
 578 trophic structure. Bars give the 95% confidence interval (CI). Densities with CI not
 579 crossing the zero dotted lines differ significantly from the control. None overlapping CIs
 580 reveal protist densities significantly differing from each other. Each panel gives the
 581 results for a different species with specific traits in Ecosystem 1: (a) Autotroph (*Euglena*
 582 *gracilis*), (b) Large heterotroph (*Paramecium aurelia*), (c) Small heterotroph
 583 (*Tetrahymena pyriformis*).

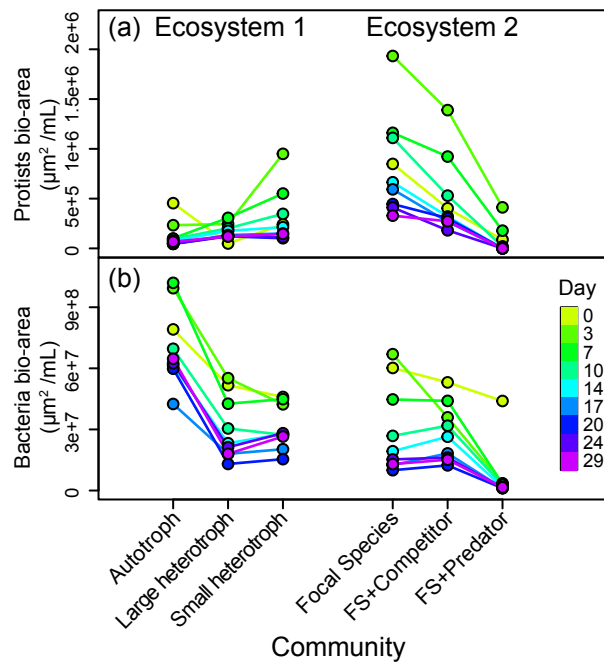


584

585 Figure 4. Effect of species trait in Ecosystem 1 on the competition hierarchy between
 586 *Colpidium* (orange area) and *Paramecium* (pink area) in Ecosystem 2 over time
 587 (FS+Competitor treatment). The effect is expressed as the relative proportion of
 588 *Colpidium* versus *Paramecium* individuals (the two competitors). Neighbour communities
 589 are either the Autotroph (*Euglena gracilis*), or the Large heterotroph (*Paramecium*
 590 *aurelia*) or the Small heterotroph (*Tetrahymena pyriformis*), in panel (a), (b), and (c)
 591 respectively. Barbells refer to subsidy connection. Panel (d) shows the control without
 592 diffusion. Dotted lines give the standard deviation.

593

594



595

596 Figure 5. Bio-area of (a) protists and (b) bacteria over time (colours) for the different
 597 communities in each ecosystem. Points give the mean averaged over five replicates at a
 598 specific day (colours).

599