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## **Subsidies mediate interactions between communities across space**

Gounand, Isabelle ; Harvey, Eric ; Ganesanandamoorthy, Pravin ; Altermatt, Florian

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

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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  $\mu\text{m}$ ), a large bacterivorous ciliate (*Paramecium aurelia*, ~96  $\mu\text{m}$ ), or a small  
140 bacterivorous ciliate (*Tetrahymena pyriformis*, ~30  $\mu\text{m}$ ). In Ecosystem 2, our focal  
141 species, *Colpidium striatum*, a small bacterivorous ciliate (~45  $\mu\text{m}$ ) 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<sup>-1</sup> 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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544 Supplementary material (available online as Appendix oik-XXXXX at

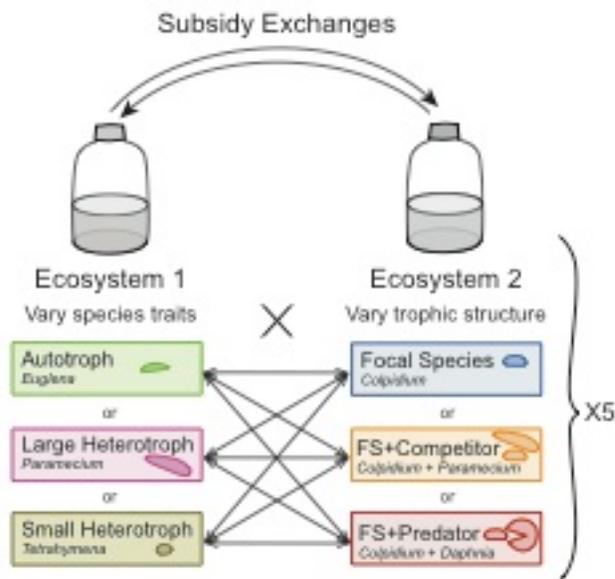
545 <[www.oikosjournal.org/readers/appendix](http://www.oikosjournal.org/readers/appendix)>). Appendix 1–5

546 Data available from the Dryad Digital Repository: XX

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548

## 549 Figure legends



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

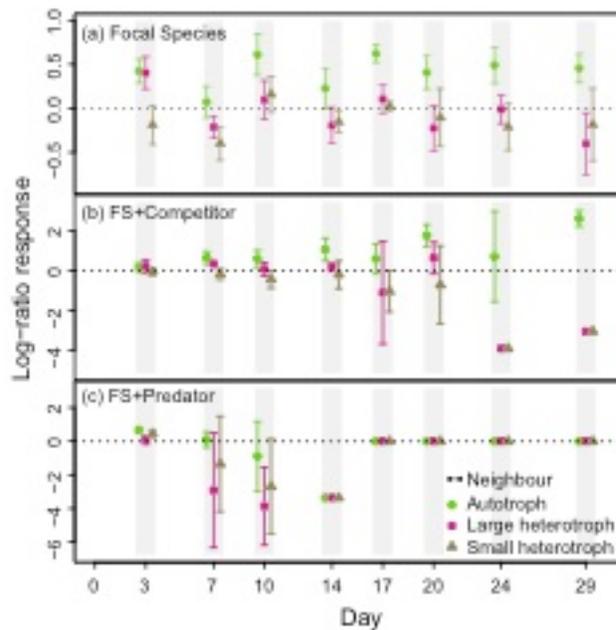
556 species with an additional competitor (FS + Competitor: *Colpidium striatum* with

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

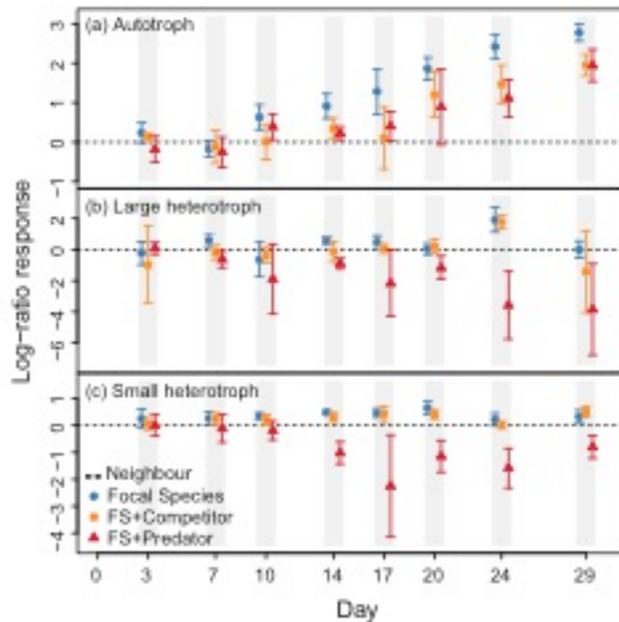
567 species. Bars give the 95% confidence interval (CI). Densities with CI not crossing the

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

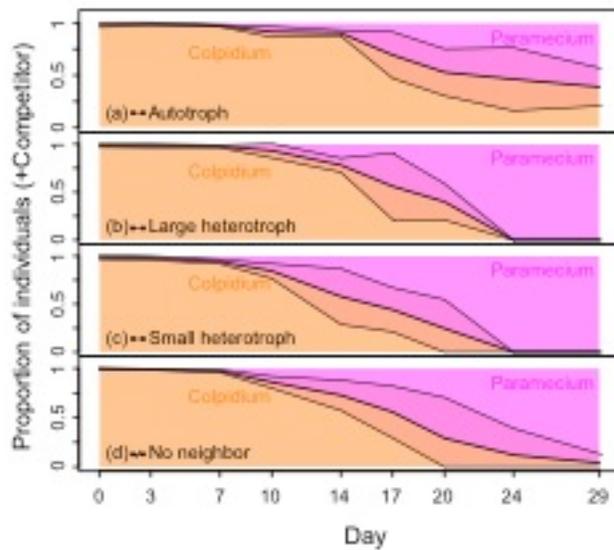
570 different trophic structure involving our focal species: (a) Focal Species, (b)

571 FS+Competitor, (c) FS+Predator.



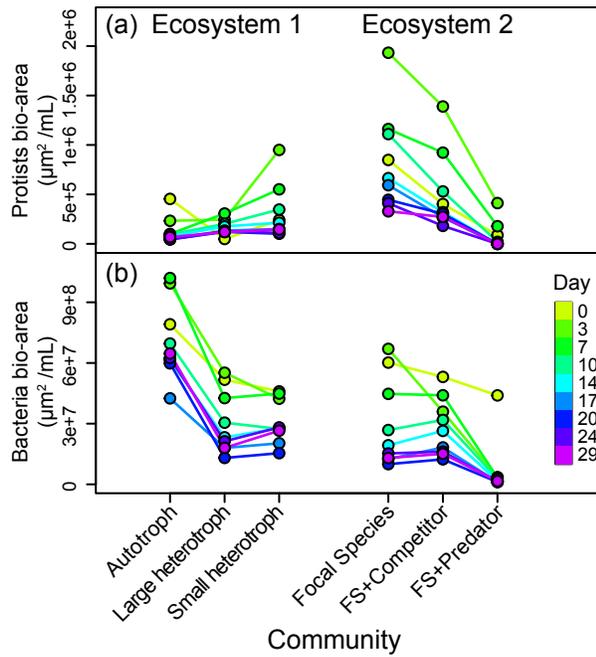
572

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