

# Spatially cascading effect of perturbations in experimental meta-ecosystems

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#### 25 Abstract

26 Ecosystems are linked to neighbouring ecosystems not only by dispersal, but also by 27 the movement of subsidy. Such subsidy couplings between ecosystems have important 28 landscape-scale implications because perturbations in one ecosystem may affect 29 community structure and functioning in neighboring ecosystems via increased/decreased 30 subsidies. Here, we combine a general theoretical approach based on harvesting theory 31 and a two-patch protist meta-ecosystem experiment to test the effect of regional 32 perturbations on local community dynamics. We first characterized the relationship 33 between perturbation regime and local population demography on detritus production 34 using a mathematical model. We then experimentally simulated a perturbation gradient 35 affecting connected ecosystems simultaneously, thus altering cross-ecosystem subsidy 36 exchanges. We demonstrate that the perturbation regime can interact with local 37 population dynamics to trigger unexpected temporal variations in subsidy pulses from 38 one ecosystem to another. High perturbation intensity initially led to highest level of 39 subsidy flows, however the level of perturbation interacted with population dynamics to 40 generate a crash in subsidy exchange over-time. Both theoretical and experimental results 41 show that perturbation regime interacting with local community dynamics can induce a 42 collapse in population levels for recipient ecosystems. These results call for an integrative 43 management of human-altered landscapes that takes into account regional dynamics of 44 both species and resource flows.

45

#### 46 Introduction

47 The importance of allochthonous subsidies for biological community persistence and 48 functioning in recipient ecosystems has been long recognized [1-3]. Ecosystems are 49 linked to neighbouring ecosystems through their shared boundaries by the spatial 50 movement of resources, despite wide variations in magnitude and type of inputs (e.g., 51 movement of prey, detritus, nutrient). Allochthonous inputs to the recipient ecosystem 52 subsidize primary producer biomass, consumer biomass [4–6], and strongly modulate the 53 dynamics and structure of food webs [7,8]. These spatial flows may even trigger complex 54 dynamical feedbacks between ecosystems (meta-ecosystem dynamics), acting at different 55 trophic levels. Over the last decade, extensive conceptual and theoretical work has 56 suggested that meta-ecosystem dynamics, by integrating spatial flows of energy, material 57 and organisms, may have important implications for the stability of biological 58 communities [9,10] and the unfolding of ecosystem processes [9,11–14]. As a direct 59 consequence of such a coupling of energy/resource release and spatial transport between 60 ecosystems, perturbations in one ecosystem will likely affect community structure and 61 functioning in neighbouring ecosystems via increased or decreased subsidies. 62 Such a scenario is expected to be common in natural systems under recurrent 63 perturbation dynamics [15]. For instance, spatial flows of nutrients and detritus from a 64 forest to a lake or a river are greatly affected following a fire due to increased erosion and 65 nutrient runoff [16-18]. Because perturbation pressure is usually intensified in humanmanaged regions, the dependence of spatial flows on perturbations is expected to be even 66 67 stronger. This is well exemplified by the effect of biomass harvesting and fertilization in 68 agricultural systems leading to higher resource runoffs in streams, which in turn leads to

69 higher primary production in downstream lakes and potentially to eutrophication issues 70 [19]. Such changes in ecosystem budgets (carbon and nutrient) following fire, 71 overgrazing or intensive agricultural practices have been widely studied by ecosystem 72 and forest ecologists for their direct impacts on neighbouring ecosystems [18–21]. 73 However, rather than directly impacting subsidies (e.g. by leaching of agricultural 74 fertilizers), perturbations can also trigger indirect effects between communities by 75 modifying local community dynamics such that outflowing subsidies are increased or 76 decreased. This can occur if some specific traits of the local community or population 77 interact with perturbation frequency or intensity to increase or decrease local detritus 78 production, generating variations in spatial subsidies to connected ecosystems. The 79 historical divide between community and ecosystem ecology impeded a unification of 80 these perspectives despite its potential significance for understanding connected-81 ecosystem dynamics and the cascading effect of perturbations across the landscape [22]. 82 In the context of global changes, many perturbations are likely to affect resource exchanges between ecosystems, either directly (e.g., agricultural nutrient loads) or 83 84 indirectly with impacts on communities triggering modifications of outflowing subsidies 85 (e.g., habitat fragmentation, resource exploitation). This suggests that spatial variations in 86 ecosystem processes and services in human-altered landscapes will be at least partly 87 determined by meta-ecosystem dynamics [23], and their alteration following community 88 response to perturbations. 89 In this study we propose a demonstration of meta-ecosystem dynamics under 90 perturbations by studying the effects of perturbation-induced cross-ecosystem subsidy

91 exchanges on each ecosystem's biological community and function over time. First, we

92 used a mathematical model inspired from general harvesting theory that couples 93 population demographics to recurrent perturbations, from which we extracted the 94 analytical prediction that detritus levels closely depend on the interaction between local 95 species dynamics and perturbation regime, and that they follow a hump-shaped 96 relationship with perturbation intensity. We then experimentally tested this prediction and 97 analysed its spatial consequences on neighbouring community dynamics using two-patch meta-ecosystems containing contrasting protist communities: one heterotrophic, and one 98 99 autotrophic community. Such a configuration is commonly seen in many natural 100 ecosystems such as the coupling found between lake benthic (or stream) and forest (or 101 cropland) ecosystems. We simulated a perturbation gradient affecting both ecosystems 102 simultaneously and altering cross-ecosystem subsidy exchanges. The perturbation 103 consisted in the sampling of a certain volume corresponding to the perturbation 104 intensity/subsidy diffusion level (0%, 5%, 30% and 80% of total volume) from each 105 ecosystem. Living protists were subsequently turned into dead biomass and the sample 106 transferred to the recipient ecosystem. Perturbations and subsidy diffusion events 107 occurred repeatedly at controlled intervals, over a three-week period. In parallel, we 108 monitored changes in protist and bacteria density, and percentage oxygen availability as a 109 proxy for ecosystem functioning in each ecosystem.

110

111 Methods

112 Model description

113 Resource subsidies are often linked to perturbations. Mortality triggered by

114 perturbations fuels the detritus pool that can serve as new resources for organisms, which

115 can be transferred to other ecosystems as subsidies. For instance, during a storm there 116 may be increased leaf litter input from the riparian vegetation into rivers, or in marine 117 fisheries discarded by-catch may feed benthic marine ecosystems [24]. We analysed a 118 simple population model, derived from classic harvesting theory, to understand how 119 subsidies depend on population growth rate (r) and carrying capacity (K), as well as on 120 the frequency (f) and intensity (I) of perturbations. We describe the dynamics of a 121 population density N with a simple logistic model:

122 
$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) \quad [1]$$

123 The population, initially at carrying capacity, is subjected to recurrent perturbations. 124 At a frequency f, a perturbation provokes the death of a fraction I of the population, 125 which characterizes the intensity of the perturbation. This fraction is removed from N, 126 and is considered as a subsidy. This leads to the following equation to characterize 127 subsidy dynamics:

128 
$$S(nT) = N_{P-}(nT) * I$$
 [2]

129 with T = 1/f the time between two perturbations (period), n the number of the 130 perturbation, and  $N_{P-}$  the biomass of the population at the time nT just before the 131 perturbation. We analytically derived the solution of S(nT), the level of subsidy at 132 equilibrium, and the conditions under which the system is not crashing.

133

134 Experimental design

Our general model showed that the amount of perturbation-induced subsidy produced
locally is strongly dependent on the interaction between demography parameters (e.g.,
growth rate) and perturbation regime (e.g., intensity, see 'results' section below). We

138 propose to test these predictions and their consequences at the landscape level. To do so, 139 we built a factorial protist microcosm experiment composed of two-patch meta-140 ecosystems linked by different intensity of perturbation-induced subsidy pulse (0, 5%, 141 30%, 80%, thereafter referred to as diffusion treatment) and by species dispersal 142 (with/without dispersal; see Fig. 1). We had four replicates of each treatment combination 143 at the meta-ecosystem level, resulting in a total of 24 meta-ecosystems, each composed of 144 two connected patches, and 4 unconnected controls (56 microcosms, see Fig. 1). The 145 experiment lasted 21 days and took place in a controlled culture room at 20 °C and 146 constant light. The position of replicate groups was randomized across the shelves in the 147 culture room to control for possible micro-condition differences. 148 In order to study effects of subsidy exchanges between contrasting ecosystem types in 149 a representative way, we built two-patch meta-ecosystems consisting of one heterotrophic 150 protist community (ecosystem 1) and one autotrophic protist community (ecosystem 2). 151 The heterotrophic community was composed of four bacteriophagous ciliate protist 152 species: Colpidium sp., Paramecium aurelia, Spirostomum sp., and Tetrahymena 153 pyriformis. The autotrophic community was composed of the photosynthetic flagellate 154 Euglena gracilis. This autotrophic species has a slow growth rate relative to most species 155 in the heterotrophic community (except for Spirostomum sp.). These contrasting growth 156 rates between the two ecosystems are essential to test the spatial consequences of our 157 model predictions on the interaction between demography and perturbation intensity (see 158 above). For details on culture conditions and experimental procedures, see [25] and [26]. 159 Each microcosm consisted of a 250 mL Schott bottle filled to 100 mL. Microcosms 160 were assembled by first filling each Schott bottle with 75 mL of pre-autoclaved standard

161 protist medium (Carolina Biological Supply, Burlington NC, USA), and 5 mL of a

162 bacteria solution composed of three species (Serratia fonticola, Bacillus subtilis and

163 Brevibacillus brevis). After 24 hours, to allow time for bacteria growth, we added 20 mL

164 of protist solution with each protist species at carrying capacity (5 mL per species for

165 heterotrophic communities, and 20 mL of *Euglena gracilis* for autotrophic communities).

166 Thus, protist communities were added at 20% of their carrying capacity and were allowed

167 to grow 24 hours before the first diffusion event.

168

169 Diffusion and dispersal procedures

170 For each diffusion level (0, 5%, 30%, and 80%), a corresponding volume (0, 5, 30, 171 and 80 mL) was sampled from each microcosm and microwaved to turn living cells into 172 detritus. After a 3 hours cooling period at ambient temperature (20 °C), the microwaved 173 samples were poured into the respective neighbouring recipient ecosystems. Dispersal 174 was unidirectional, from the autotrophic to the heterotrophic community, to test whether 175 the introduction of an autotroph species could interact synergistically with subsidy 176 diffusion and enhance microbial activity and ecosystem functioning. Dispersal was 177 performed simultaneously with the diffusion procedure. It was done by sampling 5 mL 178 (corresponds to an average of 1450 Euglena cells) from the autotrophic microcosm that 179 was then poured directly into the heterotrophic microcosm of the corresponding meta-180 ecosystem. Because detritus and nutrient were also dispersed at the same time via the 181 medium, the 5 mL was subtracted from the volume taken for subsidy diffusion from the 182 autotrophic community. The logistical difficulty to disperse species without also 183 diffusing medium (i.e., nutrient and detritus) did not permit having a 'no-diffusion with

| 184 | dispersal' treatment (see below for statistical implications and Fig. 1). The herein used |
|-----|---|
| 185 | dispersal rate (i.e., 5%) corresponds to levels of dispersal rates that have been         |
| 186 | successfully applied in related experiments (e.g., [27,28]), and is arguably an           |
| 187 | intermediate to high value even for many natural systems (e.g., [29]). Experimentally,    |
| 188 | much lower dispersal rates (<0.01%) have been shown to significantly affect               |
| 189 | metacommunity dynamics (e.g., [30]).  |
| 190 |   |
| 191 | Measurements  |
| 192 | Measurements were synchronized with diffusion/dispersion procedures, with the             |
| 193 | measurements occurring every Tuesday (experimental days 0, 7, 14, 21) and Friday          |
| 194 | (experimental days 3, 10, 17), and diffusion/dispersion occurring every Wednesday and     |
| 195 | Saturday (see experimental calendar on Figure S1 in Online Supplementary Information).    |
| 196 | The last diffusion event was performed on day 15 to allow ecosystems to reach near        |
| 197 | equilibrium by day 21 (last measurement), and thus to evaluate the long-term impacts of   |
| 198 | our different diffusion treatments without its mortality effect.                          |
| 199 | On each measurement day we quantified oxygen concentration, protist and bacteria          |
| 200 | densities in each microcosm. Oxygen concentration was measured using sensors that         |
| 201 | were mounted in the microcosm bottles at a medium depth of 2 cm. The information from     |
| 202 | the sensors was collected through an optical fiber cable connected to an oxygen meter     |
| 203 | device (PreSens Fibox 4 Optical Oxygen Meters, Germany) controlling for water             |
| 204 | pressure and temperature. On each measurement day, two 0.5 mL samples were taken:         |
| 205 | one for protist and one for bacteria density analysis. Protist density was measured by    |
|     |   |

using a standardized video procedure [25,31]. In brief, a constant volume (17.6  $\mu$ L) of

207 each sample was placed under a dissecting microscope connected to a camera and a 208 computer for the recording of videos (5 seconds per video). Then, using an image 209 processing software (ImageJ, National Institute of Health, USA) we extracted the number 210 of moving organisms per video frame along with a suit of different traits for each 211 occurrence (e.g., speed, shape, size) that were used to filter out background movement 212 noise (e.g., particles from the medium, [31,32]). Finally, bacteria density was measured using standard flow cytometry on fresh SYBR green fixated cells using a BD Accuri<sup>TM</sup> 213 214 C6 cell counter (1/1000 dilution, following [25]). 215 Since detritus spatial flows were varying through time with species densities, we 216 estimated the effective amount of detritus transferred from the autotroph ecosystem by 217 simulating the logistic growth of *Euglena* from measured densities at each sampling day 218 (~48 hours before each diffusion treatment). Parameters for the growth curve were 219 extracted from control time series. We used the predicted numbers of Euglena individuals 220 multiplied by the diffusion intensity as a proxy for realized subsidy (see also model 221 description above, results section below, and the analysis of the general model). 222

#### 223 *Statistical analyses*

To test for the reciprocal effects of cross-ecosystem subsidy exchanges on protist and bacteria densities, and ecosystem oxygen level, we first ran one generalized linear model (GLM) for each variable, testing for the main and interacting effects among all treatments and time. We used standardized residuals *versus* fitted values plots, residuals distribution, variance over-dispersion, and log-likelihood information to select the most appropriate variance and link functions for each GLM model (i.e., Gamma for oxygen concentration,

230 and Gaussian on log-transformed data for bacteria and protist densities). The level of 231 significance and the effect size of each factor and their interactions were then assessed 232 using a standard F test (Type II analysis of deviance) on each GLM model. Finally, we 233 used *post-hoc* pairwise comparisons (with Tukey adjusted *p*-values) on sub-models to 234 extract the different contrasts of interest from significant terms in the main model. We 235 used sub-models to avoid inflations of type II error [33] given the high number of 236 potential pairwise comparisons in each main model. Because there was by definition no 237 direct control for the dispersal effect (no dispersal only treatment, see Fig. 1), this 238 treatment was removed from the main GLM models to avoid contrast imbalance. Instead, 239 we tested for dispersal effects using log-response ratios for each diffusion level with 95% 240 confidence intervals (see Fig. S2). 241 In a few microcosms we observed protist contaminations (e.g., Euglena individuals in 242 heterotrophic communities without dispersal), though mostly occurring at low densities. 243 To account for these contaminations, and to ensure that they did not bias our results, we 244 evaluated their impact on our analyses. We ran all of our GLM models with and without 245 the contaminated microcosms (see Tables S1, S2, and S3). We show that retaining the 246 replicates with contamination in the analysis did not affect the qualitative outputs of our 247 models, and that in all cases they made our interpretations overall more conservative by

248 increasing each model's residual variation. Therefore, we decided to retain all replicates

in the main analyses.

All analyses were conducted with R 3.1.2 (R Development Core team, 2014), using the
'bemovi' package [32] for video analyses, the 'car' package [34] for type II analysis of

deviance, and the 'Ismeans' package for post hoc pairwise comparisons [35]. All data and the

R code to reproduce our main results and figures are available on Dryad [36].

254 Results

255 Model

273

256 We examined how changes in perturbation intensity, frequency and specific

257 demographic parameters (here intrinsic growth rate) can affect available subsidy levels.

258 We found that when a population has enough time to reach its carrying capacity between

259 perturbations, the level of subsidy remains almost constant (e.g. top dynamics in Fig. 2b).

260 However, when the perturbations are too frequent, too intense, or the population too slow

to recover, the population and subsidies decrease over time (Fig. 2b, dynamics "*r*-", "*I*+",

262 "*r*-/*I*+"). We can demonstrate (see Appendix S1 in Supplementary Information) that,

assuming initial density at carrying capacity (N(0) = K), if the growth rate and

264 perturbation regime satisfy the inequality:

265 rT + ln(1-I) > 0 [3],

the level of subsidies stabilizes to the following finite positive value:

267 
$$\frac{KI}{1+I\left(\frac{1}{1-a}-1\right)} \qquad [4],$$

with  $a = \frac{e^{-rT}}{1-I}$ . The amount of subsidy at equilibrium (equation [4]) decreases with decreasing *r* and increasing *f*, and follows a hump-shaped relationship with *I* (Fig. 2c). If inequality [3] is not satisfied, for instance with a combination of high perturbation intensity and low species growth rate, then both population and subsidies even tend to crash over time (Figs 2b "*r*-/*I*+" and 2c).

274 Experiment

| 275 | We found contrasting effects of the diffusion treatment in heterotroph versus autotroph                           |
|-----|---|
| 276 | ecosystems on protist density ( $F_{(3,333)} = 61.24$ , p<0.001, see Table S1 for full GLM table),                |
| 277 | and bacteria density ( $F_{(3,333)} = 3.65$ , p<0.01, see Table S2 for full GLM table). In the                    |
| 278 | autotroph ecosystems, Euglena gracilis, which is characterized by a slower growth rate                            |
| 279 | than the bacteriophagous species in the heterotroph ecosystems, was slow to recover from                          |
| 280 | each diffusion-induced mortality event, especially at high levels of diffusion (Fig. 3d).                         |
| 281 | The slow recovery at 80% diffusion level eventually resulted in a significant decline in                          |
| 282 | population densities from the beginning to the end of the experiment (adjusted p-value                            |
| 283 | <0.0001, Fig. 3d). As predicted by the model, this decline fed back along time on                                 |
| 284 | subsidies coming from autotroph ecosystems (Fig. 4c-f): At the beginning of the                                   |
| 285 | experiment (Fig. 4: Day 3), the 80% diffusion level generated a high amount of available                          |
| 286 | subsidy (estimated dead Euglena cells) to the heterotroph ecosystems (Fig. 4c). In the                            |
| 287 | heterotroph ecosystems, these subsidies sustained higher bacteriophagous protist                                  |
| 288 | densities ( $F_{(18,333)} = 3.00$ , p<0.001, Fig. 4a, and see Table S4 for all <i>post-hoc</i> multiple           |
| 289 | comparison results), paralleled by a decrease in bacteria density ( $F_{(18,333)} = 1.74$ , p<0.05,               |
| 290 | Fig. 4a, and Table S4). As a consequence of this increase in bacteria consumption, and                            |
| 291 | potentially bacteria turnover rates, oxygen concentration declined along the diffusion                            |
| 292 | gradient ( $F_{(18,333)} = 1.69 \text{ p} < 0.05$ , Fig. 4b, and Table S4). Over time, however, <i>Euglena</i> 's |
| 293 | difficulty to recover from the repeated 80% mortality (Fig. 3d) led to a drop in detritus                         |
| 294 | production that disrupted the amount of subsidies available to the heterotrophic                                  |
| 295 | ecosystems (Fig. 4f). As a consequence, by the end of the experiment (Fig. 4: Day 21),                            |
| 296 | the intermediate 30% diffusion level provided more subsidies to the heterotrophic                                 |

ecosystems than the 80% diffusion (Fig. 4f, adjusted p-values < 0.05) thus mirroring the</li>
model prediction of a hump-shaped relationship between perturbation intensity and
detritus production. This resulted into a significant peak of bacteria densities at 30%
(adjusted p-values<0.05, Fig. 4d, and Table S4) followed by a decline at 80% diffusion</li>
(adjusted p-value<0.05, Fig. 4d, and Table S4).</li>

302 In contrast to initial dynamics (Fig. 4a), protist and bacteria densities were positively rather than negatively associated by the end of the experiment (Fig. 4d). This temporal 303 304 change probably occurred because of an overall enrichment of the heterotroph 305 communities at 30% compared to 80% diffusion, owing to Euglena photosynthesis over 306 the course of the experiment. By the end of the experiment, and in the absence of recent 307 diffusion-induced perturbations (we stopped the diffusion treatment 6 days before the last 308 measurement - see "Methods" section), all heterotrophic and autotrophic ecosystems 309 converged to similar oxygen concentrations (Fig. 4e). This convergence in oxygen level, 310 in the absence of perturbations, likely developed because of similar overall biological rate 311 averaging between Euglena producing oxygen, but sustaining high density of oxygen-312 consuming bacteria in autotroph ecosystems, and low level of bacteria but likely with 313 high turnover due to higher level of protist density in heterotroph ecosystems. 314 The negative effect of diffusion-induced mortality on Euglena densities also meant 315 that in treatments where it dispersed to heterotrophic ecosystems its density was 316 systematically too low to have significant contributions on oxygen concentration or 317 protist density at 80% diffusion level (see Fig. S2), however it did significantly contribute 318 to increase protist density in heterotrophic ecosystems at low and intermediate diffusion 319 levels (day 21 only, Fig. S2b).

#### 320 Discussion

321 We experimentally showed how perturbation-induced cross-ecosystem subsidy 322 exchanges affect the local biological communities of two connected ecosystems with 323 contrasting demographic and natural history parameters. Our experimental results that 324 perturbations can lead to a decline of subsidy over-time also matched the outcome of our 325 theoretical model, which indicates that high levels of perturbations lead to collapsing 326 subsidies after initial positive effects. Thus, we found first experimental evidences of 327 meta-ecosystem effects on biological communities and ecosystem function (Figs. 3 and 328 4), and of spatially cascading effect of perturbations via a disruption of spatial flows 329 (Figs. 2, 4).

330 Exploring theoretical scenarios, we first derived the general conditions under which 331 local perturbations lead to the collapse of local detritus pool (Methods, eq. 4), disrupting 332 regional dynamics through the flow of detritus. Similar dynamics have been studied in 333 harvesting theory with a general focus on determining the optimal harvest effort (i.e., 334 perturbation intensity and frequency) for a maximal profit [37]. Here we stress the 335 indirect consequences of recurrent perturbations on connected ecosystems. In the 336 particular context of global changes, perturbations that kill a part of populations (e.g., 337 insect outbreaks, fires, storms) may occur in a more frequent or intense way [38]. Our 338 model shows that this may decrease subsidies to other systems (e.g., litter inputs into 339 rivers), the more severely as the intensity and frequency of the focal perturbations are 340 increasing if populations are slow to recover. This change in subsidy levels may affect 341 deeply the structure and functioning of the recipient community [39]. Previous empirical 342 work had shown the importance of directional resource spatial flows between ecosystems

343 for the maintenance of community structure and stability [2,7,40]. However, the temporal 344 feedbacks that can occur over time had only been investigated in theoretical terms, using 345 the meta-ecosystem framework [9,10,41]. Thus, in a second step we experimentally 346 demonstrated that meta-ecosystem dynamics have implications for natural ecosystems 347 under perturbation pressure because the way neighbouring ecosystems respond can 348 directly affect community dynamics and functioning in connected ecosystems. The link 349 between subsidy flow and perturbations, however, was not trivial because the direction of 350 the effect was completely reversed over time. Initially, the high level of diffusion-induced 351 mortality in the autotrophic ecosystem generated a peak in available subsidy for the 352 heterotrophic neighbour. By the end of the experiment, this high mortality level fed back 353 to generate an overall impoverishment in subsidy exchange, which significantly impacted 354 community composition and ecosystem dynamics in both ecosystems.

355 The analysis of the demographic mathematical model revealed the circumstances that 356 can lead (or not lead) to the observed temporal feedback in detritus exchanges (Fig. 2). 357 Slow species growth rates in a neighbouring ecosystem in combination with high 358 perturbation frequency and intensity generated the conditions for a collapse of the amount 359 of detritus exchanged over time (Fig. 2c bottom panel). For instance, slow-growing 360 woody plants of riparian forests exposed to recurrent fires are progressively replaced by 361 alien annuals of higher growth rates in Mediterranean areas [39,42]. Such high 362 perturbation regimes will both deforest and re-structure the autotrophic riparian 363 community towards a lower biomass system, and decline macro-invertebrate densities in 364 streams by reducing leaf litter inputs [43]. Here we show that, more generally, a habitat-

365 or ecosystem-specific response to any kind of perturbations can strongly impact
366 neighbouring ecosystems through the disruption of detritus flows.

367 Subsidy quality can also have important impacts on recipient ecosystems [44-46]. In 368 our experiment, the autotrophic protist species was not only a key species because of its 369 inability to recover from perturbation over time, but also because it could increase the 370 total level of resource in each ecosystem through photosynthetic activities. Thus, spatial 371 flows from autotroph ecosystems would have contained higher levels of resources than 372 flows from heterotrophic ecosystems. Over time such a local enrichment would have 373 increased the overall level of energy in the meta-ecosystems where autotrophs remained 374 abundant (e.g., 30% as opposed to 80% diffusion). Therefore, the feedback between 375 perturbation intensity and the slow recovery rate of autotrophs impoverished the meta-376 ecosystem under high perturbation pressure. This led to the observed change in the relationship between heterotrophic bacteria and protist density from initially negative to 377 378 positive at the end. This interpretation also lead to the important, but yet untested 379 hypothesis, that local species identity might play an essential role in mediating the 380 quantity and quality of among-ecosystems spatial flows.

Our results have important implications for the management of human-altered landscapes because conservation targets, such as in forest or grasslands, are usually localized in their actions, focussing on the most sensitive habitats or ecosystems. Our findings show that these management-induced disturbances (or preventions thereof) can directly affect dynamics in spatially coupled ecosystems, such as rivers or lakes, which are fed by resources from these "green" ecosystems [7,46–49]. We experimentally demonstrated, and showed also in a mathematical model, that the direction of the effects

388 depend on the temporal unfolding, the magnitude of disturbance and the type of 389 connected ecosystems (autotrophic vs. heterotrophic dominated). Increasing dispersal rate 390 by maintaining habitat connections can mitigate the deleterious effects of perturbation on 391 local communities [50], however our results suggest that high perturbation pressure can 392 hinder rescue effects when the dispersing populations are too slow to recover. Our study 393 calls for a more integrative management that takes into account regional dynamics related 394 to species and resource flows [51], and spatial variations in ecosystem functions [52,53]. 395 For instance, watershed conservation approaches could help to better integrate spatial 396 flows within river networks [23], and a better understanding of spatial flows between 397 forest and agricultural habitats would greatly improve agroforestry landscape 398 management, maximizing the delivery of ecosystem services. 399 We have demonstrated that cross-ecosystem subsidy exchanges can have far-reaching 400 implications for community dynamics and ecosystem processes beyond the generally 401 well recognized one-way allochthonous input of detritus [2,3]. The actual prevalence of 402 meta-ecosystems in natural landscapes is currently unknown but evidences suggest that 403 they might be ubiquitous to certain ecosystem boundaries [7,23]. The feedback between 404 demography, perturbations and changes in cross-ecosystem subsidy exchanges that we 405 demonstrated here suggests that meta-ecosystem dynamics might be even more 406 significant within fragmented and altered landscapes [54]. Yet our empirical 407 understanding of meta-ecosystems is strikingly insufficient, and more experiments are 408 needed to fully understand the potentially complex feedbacks triggered by spatial flows 409 that theory predicts [10–13], and to forecast how local perturbations can spread across 410 space in spatially structured landscapes [55,56].

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564 Figure 1. Each meta-ecosystem was composed of two ecosystems with contrasting protist communities: one heterotrophic (white background), and one autotrophic 565 566 community (green background). The two microcosms within each meta-ecosystem were 567 either linked by diffusion alone (movement of the brown compartment; brown line), or 568 diffusion and dispersal (movement of the blue compartment; blue line). The diffusion of 569 detritus was generated by a gradient of perturbation intensity (0, 5, 30, 80%) and 570 occurred by reciprocal transfer of medium without living organisms. With four replicates 571 per treatment combination, the experiment was composed of 24 meta-ecosystems and 4 572 unconnected pairs as controls for a total of 56 microcosms. P: protist community, B: 573 bacteria community, D: detritus, R: resource. 574



577 Figure 2. Interaction between species dynamics, perturbations and subsidies. Results 578 from a simple population model (defined in "Methods" section) showing (a) the changes 579 in density (green solid lines) through time of a species having a logistic growth rate r, 580 submitted to recurrent perturbations of intensity I at a frequency f. The intensity of the 581 perturbation is defined as the proportion of species dying suddenly and turned into subsidies. Panel (b) shows examples of species (green solid lines) and subsidy (grey 582 583 points) dynamics for different parameter sets. In the top dynamics ("ref.") the species can 584 reach its carrying capacity between two perturbations and subsidies are constant. Other 585 dynamics illustrate, from top to bottom, cases with a lower growth rate (r-), a greater 586 perturbation intensity (I+), or both (r-/I+), compared to the top dynamics. Panel (c) show

- the variation of subsidies at equilibrium according to perturbation intensity *I* and for
- 588 different growth rates r (blue colour refers to low growth rate while red to high ones).
- Points show the parameter couples used in panel (b). Values of parameters are: K = 9;
- 590 f = 1/30; in panel (b)  $r = \{0.13, 0.02, 0.13, 0.02\}$  and  $I = \{0.3, 0.3, 0.7, 0.7\}$  from top to
- 591 bottom; in panel (c)  $I \in [0,0.99]$  and  $r \in \{0.01,0.02,0.05,0.07,0.09,0.11,0.13\}$ .
- 592



Figure 3. Temporal dynamics for each diffusion level of protist densities in (a)
heterotroph and (d) autotroph ecosystems, bacteria densities in (b) heterotroph and (e)
autotroph ecosystems, oxygen concentration in (c) heterotroph and (f) autotroph
ecosystems. Panels a, b, d and e are presented on a log-scale. Bars represent ± standard
error for each experimental day. Dispersal and no dispersal treatments were lumped
together to produce the figure





Figure 4. Effect of diffusion at the beginning (a, b and c) and at the end (d, e and f) of the
experiment. The upper panels illustrate the effect of diffusion on protist and bacteria
densities at day 3 (a) and 21 (d). The middle panels illustrate the effect of diffusion on
oxygen concentration at day 3 (b) and 21 (e). The lower panels illustrate the estimated

- amount of detritus moved from the autotrophic to the heterotrophic ecosystem at the last
- 607 diffusion procedure before sampling day 3 (c) and 21 (f). Panels (a) and (d) are presented
- $608 \qquad \text{on a log-scale. Bars represent} \pm \text{standard error for each diffusion level.}$