

Subsidies mediate interactions between communities across space

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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.

Spatial flows between ecosystems are ubiquitous in nature. Research on spatial ecology and meta-community dynamics demonstrated the fundamental role of dispersal for species coexistence and biodiversity at local and regional scales (Mouquet and Loreau 2002, Leibold et al. 2004, Holyoak et al. 2005, Seymour et al. 2015). In parallel, ecosystem ecology and ecosystem-level studies have shown that spatial flows of resources are also fundamental drivers of community dynamics (Polis et al. 1997, 2004, Harvey et al. 2016). In natural ecosystems, many communities have a net heterotrophic functioning and productivity relies on subsidies coming from neighbouring ecosystems. For instance benthic marine- or freshwater-systems rely on detritus inputs sinking from pelagic waters (Fitzgerald and Gardner 1993, Schindler and Scheuerell 2002), and at aquatic-terrestrial boundaries, ecosystems experience strong bi-directional resource-exchanges, with riverine vegetation subsidizing river or lake communities with dead-organic matter (Hall et al. 2000, Cole and Caraco 2001, Richardson et al. 2010), while riparian systems benefit from nitrogen-rich inputs of emergent aquatic insects (Baxter et al. 2005, Gratton and Vander Zanden 2009, Dreyer et al. 2015), or fish carcasses (Hocking and Reimchen 2009). The quantification of these

resource spatial flows (thereafter called subsidies), and the recognition of their importance for local community dynamics by meta-community ecology, eventually led to a formal integration of community and ecosystem perspectives on spatial flows within the meta-ecosystem framework, accounting for both organism dispersal and resource exchanges between ecosystems (Loreau et al. 2003, Massol et al. 2011, 2017).

Previous studies on allochthonous subsidies generally investigated subsidy effects on recipient communities from a donor-controlled perspective, thus without consideration of the reciprocal effects on both connected ecosystems (Cole et al. 2006). Reframed into a spatial perspective however, subsidies could be considered as a vector of indirect interactions between community dynamics, with donor community dynamics modulating the quantity and quality of exported resources. Both composition (species traits) and structure (trophic interactions) of communities control the quantity and quality of detritus locally produced, and potentially exported to other ecosystems as subsidies. On the one hand, the population dynamics and life cycles of the species composing a community determine the amount of detritus produced locally (e.g. subsidy pulses triggered by 17-year

emergence cycles of cicadas reported by Menninger et al. 2008). On the other hand, species functional traits determine detritus quality via their stoichiometry (Sitters et al. 2015). Indeed, key species functional traits such as autotrophy translate into carbon-nutrient ratios biased toward high values due to their carbon-fixing photosynthesis activities, compared to the content of heterotrophic species (see Sterner and Elser 2002, Sterner 2009 for cross-taxon comparisons). Through a direct effect on the stoichiometric balance and the degradability of building block molecules, community composition modulates not only detritus composition, but also the rate at which detritus is made available as a new resource for subsidized communities (Enriquez et al. 1993, Scott and Binkley 1997, Allison 2012), such as plant litter composition driving decomposition rates in forest and stream ecosystems worldwide (Cornwell et al. 2008, García-Palacios et al. 2016).

Community structure and the strength of species interactions within a community should also affect the quantity and quality of detritus by modulating the biomass distribution across trophic levels (Shurin et al. 2006). Empirical studies, for instance, showed that in a wide range of ecosystems, changes in one trophic level induce trophic cascades over an entire food web, which leads to drastic changes in biomass distributions (Schmitz et al. 2000, Carpenter et al. 2001, Jackson et al. 2001, Frank et al. 2005). Beyond the traditional focus on species loss and local productivity change, the spatial consequences for subsidy-connected ecosystems of these structural changes and the subsequent modified detritus production have still to be investigated.

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

Here we propose a test of such indirect 'neighbour effects' with experimental microcosm meta-ecosystems. We used aquatic microbial communities consisting of bacteria feeding on organic resources, various autotroph and bacterivorous protists, and a top predator. The microcosms were mimicking a wide range of natural ecosystems, from heterotrophic, such as in stream or benthic waters, to autotrophic, such as forests or pelagic phytoplankton-based ecosystems, and from resource to predator dominated. We built two-patch meta-ecosystems connecting ecosystems only by spatial subsidies (spatial flows of detritus and inorganic resources, and no organisms dispersing). In one ecosystem we manipulated species traits (autotroph versus heterotroph species

and consumer body size), while in the other ecosystem we manipulated community structure by adding a competitor or a predator (Fig. 1). We followed temporal changes in community dynamics (i.e. species density and biomass) in each ecosystem, and then compared the dynamics between connected and isolated ecosystems to test if communities with different structures and compositions could affect each other only through subsidy exchanges. Specifically we asked whether autotroph versus heterotroph community dynamics could have differential impacts on neighbours, and whether the addition of a species inducing novel trophic interactions (e.g. competition or predation) could affect neighbour dynamics in the absence of organism dispersal.

Methods

Experimental design

To test the indirect influence of community composition on one another via cross-ecosystem subsidies, we performed a two-patch meta-ecosystem experiment with protists growing in microcosm ecosystems solely connected by subsidies (spatial flows of detritus). We varied species traits in ecosystem 1 and trophic structure in ecosystem 2 according to a factorial design (Fig. 1). In ecosystem 1 we grew one of these three species with contrasting traits alone (monocultures): the autotroph flagellate *Euglena gracilis*

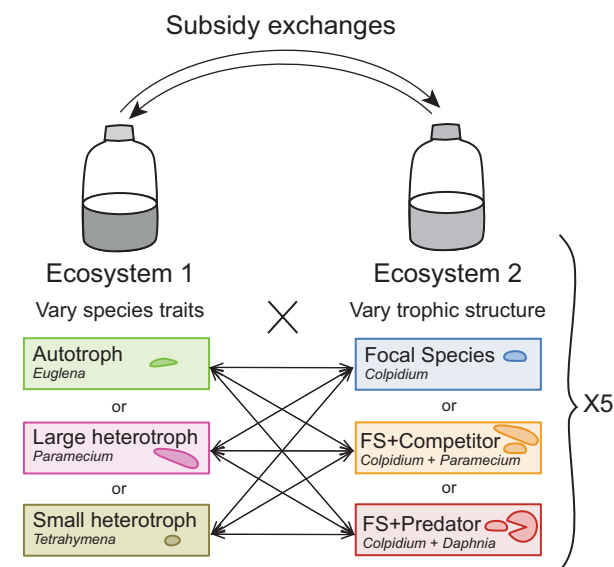


Figure 1. The experimental design consists of two-patch meta-ecosystems linked by reciprocal exchanges of detritus and resources (subsidies). In ecosystem 1, we varied the dominant functional trait of the species present (either *Euglena gracilis*, *Paramecium aurelia* or *Tetrahymena pyriformis*). In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

(~35 μm), a large bacterivorous ciliate (*Paramecium aurelia*, ~96 μm), or a small bacterivorous ciliate (*Tetrahymena pyriformis*, ~30 μm). In ecosystem 2, our focal species, *Colpidium striatum*, a small bacterivorous ciliate (~45 μm) was grown alone, or either with *Paramecium aurelia* as a competitor, or was submitted to predation by the generalist filter feeding waterflea *Daphnia magna* (~0.5 to 2 mm). Treatments are hereafter called Autotroph, Large heterotroph and Small heterotroph in ecosystem 1 and Focal Species (FS), FS+ Competitor, FS+ Predator in ecosystem 2. We connected ecosystem 1 and ecosystem 2 only by subsidy exchanges (detritus, including inorganic resources present in the growing medium), and prohibited any type of species dispersal. We had a five-fold replication of the nine meta-ecosystem types (all possible combinations of ecosystems 1 and 2), as well as the control ecosystems without diffusion, resulting in an experiment consisting of 45 independent 2-patch meta-ecosystems and 30 isolated 1-patch ecosystems (120 microcosms).

Experiment setup

Ecosystems were assembled in microcosms of 250 ml Schott bottles filled with 100 ml culture medium. All organisms (bacteria, protists and waterfleas) used in the experiment were grown in pre-autoclaved protist suspension filtered through Whatman filters (0.31 g protist pellets 1 l^{-1} tap water). Microcosms were assembled with 75 ml protist medium, 5 ml of bacterial culture (*Serratia fonticola*, *Bacillus subtilis* and *Brevibacillus brevis*; added one day prior to protist addition), and completed with 20 ml of protist culture at carrying capacity (10 ml per species in the competition treatment). For the predation treatment, we added four equal-sized juvenile *Daphnia magna* to each microcosm. More details on protist culture and experimental procedures are found in Altermatt et al. (2015). Microcosms were randomized within the five replicate blocks, and the experiment took place at 20°C and constant lighting. We replaced all *Daphnia* that died within the first six days due to initial conditions (i.e. insufficient oxygen-levels in the freshly autoclaved medium).

Diffusion

Ecosystem 1 and 2 were connected by bi-weekly reciprocal subsidy exchanges. These spatial flow events consisted in sampling 30 ml from each ecosystem, microwaving these samples for 100 s, until they reached a full boil, to turn all living biomass into detritus, and then adding it into the respective connected ecosystem after a cooling period of two hours at ambient temperature (20°C). This diffusion method mimics detritus flows associated with recurrent perturbation-induced mortality. Isolated controls were also submitted to the same perturbations, but the microwaved samples were added back in the microcosm of origin to isolate the diffusion effects from perturbation-induced mortality.

Samplings and measurements

In parallel, we tracked changes in community dynamics in each microcosm during one month. We measured

population densities every Tuesday and Friday (i.e. twice a week), leaving as much time as possible for protist growth after each diffusion event (occurring on Wednesdays and Saturdays). At each measurement point we took two 0.5 ml samples per microcosm, one to measure protist density by video analysis, the other to measure bacterial dynamics by flow cytometry. The volumes sampled were considered sufficiently small to not affect local dynamics (Altermatt et al. 2011) and thus did not need to be replaced by fresh medium. We recorded one 5 s-video per sample following a standardized video procedure (Pennekamp and Schtickzelle 2013, Altermatt et al. 2015). From each video we extracted densities of moving individuals along with morphometric and movement information, such as cell size and speed. This was achieved using the R-package *bemovi* (Pennekamp et al. 2015) coupled to the image analysis free-ware *ImageJ*. The additional traits measured served to discriminate species identity in mixtures (competition treatment), provided as inputs to trait distance analysis with the *svm* algorithm (e1071 R-package Meyer et al. 2014), and to calculate bio-areas as a proxy for biomass. Since automated particle detection relies on movement, the method systematically underestimated densities of *Euglena gracilis*, which is much less mobile than the other species. Therefore, we complemented density estimates of this species with visual counts from the videos. To exclude false positives, we also performed a visual check of all videos where a protist species had less than three individuals per frame. We counted *Daphnia* individuals visually. Finally, we measured the total abundance of the three-species bacterial community on a flow cytometer on SYBR green fixed samples (dilution $\times 1000$), following a standard protocol (Altermatt et al. 2015).

Analyses

We characterized the indirect effects of neighbouring communities on each other through subsidy flows using log response-ratios of protist densities at each time point, for the different neighbour treatments (either species traits or trophic structure) in the connected ecosystem, with 95% confidence intervals (CI). The responses were tested relative to controls without diffusion, such that CIs not comprising zero reveal significant effects of diffusion, while none overlapping CIs between neighbour treatments reveal a significant neighbour effect. We tested the effects of trophic structure on neighbour community dynamics by comparing the density of species in ecosystem 1 (each monoculture) when connected to different communities driven by specific interactions in ecosystem 2 (i.e. FS, FS+ Competitor, FS+ Predator). Conversely, we tested the effects of functional traits on neighbour community dynamics by comparing the density of our focal species, *Colpidium striatum*, in ecosystem 2 when connected to different species population with specific functional traits in ecosystem 1 (i.e. Autotroph, Large heterotroph, Small heterotroph). We studied the potential interaction with time by running generalized linear models (GLM) on log response-ratios with species traits or trophic interaction in the connected ecosystem and time as explanatory variables. We used Gaussian distributions as link functions to avoid overestimation of positive effects due to the ratio (Berlow et al. 1999). The effect of species traits

in ecosystem 1 on competitive outcome in ecosystem 2 was also tested with a GLM on the density of *Colpidium* relative to *Paramecium* (using the relative proportion), with species traits in the connected ecosystem and time as explanatory variables. For each GLM, the level of significance and the effect size of each factor, and their interactions, were assessed using a standard F-test (type II analysis of deviance). For each significant term of interest we ran post hoc pairwise comparisons (with Tukey adjusted p-values) to evaluate specific contrast among variables. When time was not significantly affecting the terms of interest we performed the post hoc analysis on simplified GLM sub-models (without the effect of time) in order to avoid unnecessary inflations of time II error (Nakagawa 2004).

Lastly, because neighbour effects can originate from changes in both subsidy quantity and quality, we examined approximated biomass (bio-areas) at the different trophic levels (bacteria, protist, predator) according to community characteristics (species traits or trophic structure) to bring an element of interpretation, assuming that the different trophic levels produce different qualities of detritus. For bacteria we took a constant mean individual area of $1 \mu\text{m}^2$, assuming no significant change of size over the experiment (bio-area = $1 \mu\text{m}^2 \times \text{cell counts}$). For protists, we measured mean individual's area directly from the video analysis, and extrapolated it to the total population (Pennekamp et al. 2015). Bio-area of *Daphnia* was estimated visually based on four size classes. To test protist and bacteria bio-area differences among communities along time we ran four different GLM with either species traits (ecosystem 1) or trophic structure (ecosystem 2) and time as explanatory variables. We studied residual distributions to select the most appropriate link function (Gamma or Gaussian). All analyses were conducted with R ver. 3.1.2 (<www.r-project.org>), using the 'car' package (Fox and Weisberg 2011) for type II analysis of deviance, and the 'lsmeans' package for post hoc pairwise comparisons (Lenth 2013).

Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.93hd6>> (Gounand et al. 2016).

Results

Subsidy-mediated effects on population density

Both local community functional traits (autotrophy versus heterotrophy) and trophic structure induced strong significant effects on connected communities via subsidy exchanges and in the absence of dispersal (Supplementary material Appendix 1 Table A1, A2). At the end of the experiment, population densities of our focal species in ecosystem 2 were significantly higher when connected to autotroph compared to heterotroph communities ($F_{2,60} = 39.40$, $p < 0.0001$ in Focal Species and FS+ Competitor treatments (see Supplementary material Appendix 1 Table A1 and Table A5 for post hoc multiple comparisons) or compared to isolated communities (Fig. 2a–b). The only exception was in the FS+ Predator treatment where predation resulted in the extinction of the

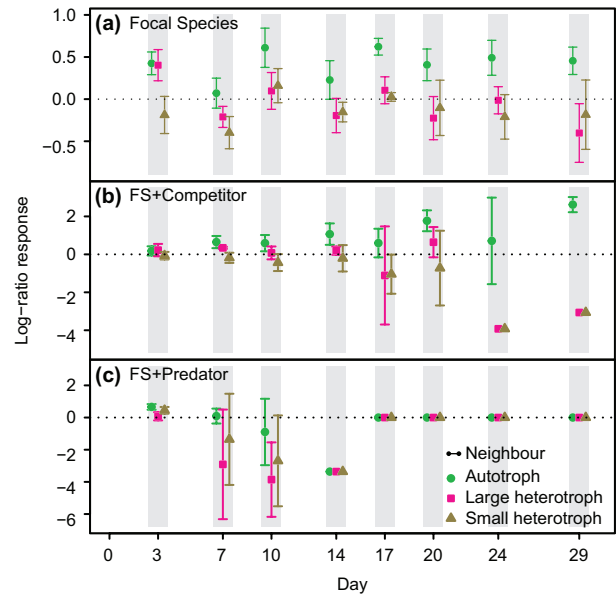


Figure 2. Effect of the species traits in ecosystem 1 on the density of focal species in ecosystem 2 (*Colpidium striatum*) over time, expressed as the log response-ratio (RR) of *Colpidium* density to detritus diffusion compared to the control without diffusion: $\text{Log RR} = \ln((N_{\text{Col}}^{\text{diff}+}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

focal species irrespective of functional traits in the connected community (Fig. 2c). Predators drove protist to extinction and concentrated all the biomass in their body, which cascaded on detritus quality and negatively affected population density in subsidy-connected communities in ecosystem 1 compared to the focal species grown alone (FS) (Fig. 3, $p < 0.0001$ for the factor 'trophic structure' on each community; see Supplementary material Appendix 1 Table A2 for the GLM and Table A5 for post hoc multiple comparisons). Moreover, the benefit (or not) of being a connected versus an isolated community depended on species functional traits. Some species were relatively insensitive to spatial subsidies when connected to FS or FS+ Competitor communities (e.g. Large heterotroph, Fig. 3b). In contrast, the autotroph did always far better when connected to heterotroph communities, regardless of the trophic structure, compared to isolated autotroph communities, which received only their own autotroph detritus (Fig. 3a: confidence intervals above the zero line). At last, consumer size (Large versus Small heterotroph) did not impact significantly species density in the connected ecosystem.

Subsidy-mediated effect on competition

While trophic structure in one ecosystem significantly impacted community dynamics in the connected ecosystem, the reverse was also true: we found that the competition

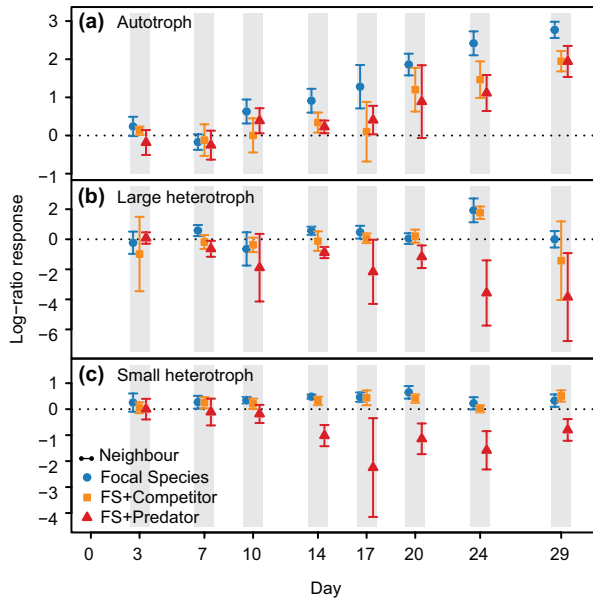


Figure 3. Effect of trophic structure in ecosystem 2 on the density of different species in ecosystem 1 via the diffusion of detritus over time, expressed as the log-ratio of density response to detritus diffusion compared to the control without diffusion: $\log \text{ response-ratio} = \ln((N^{\text{diff}+}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

outcome (in ecosystem 2) strongly depended on species functional traits in the connected ecosystem (Fig. 4, $F_{3,144} = 8.56$, $p < 0.0001$; see Supplementary material Appendix 1 Table A3 for full results of the GLM). At the end of the experiment, coexistence between the two competitors (*Colpidium* and *Paramecium*) was only observed in the meta-ecosystems with the autotroph as a neighbour (Fig. 4a). In the presence of heterotrophic neighbours, we systematically observed competitive exclusion of our focal species (*Colpidium*) by its competitor (Fig. 4b–d, with an exception in one isolated replicate ecosystem), while it persisted over the course of the experiment when connected to the autotroph community (Fig. 4a).

Changes in biomass distribution

We observed that the biomass distribution among trophic compartments (bacteria/protists/predator) varies among community types, as inferred from bio-areas (Fig. 5; Supplementary material Appendix 1 Table A4). In the ecosystems where the predator was present, both bacteria and protist biomass decreased dramatically within a few days (Fig. 5, right side), and almost all biomass was concentrated at the predator level (99.97% of the estimated bio-area at the end of the experiment). Protist and bacteria biomasses did not differ between FS and FS+ Competitor communities,

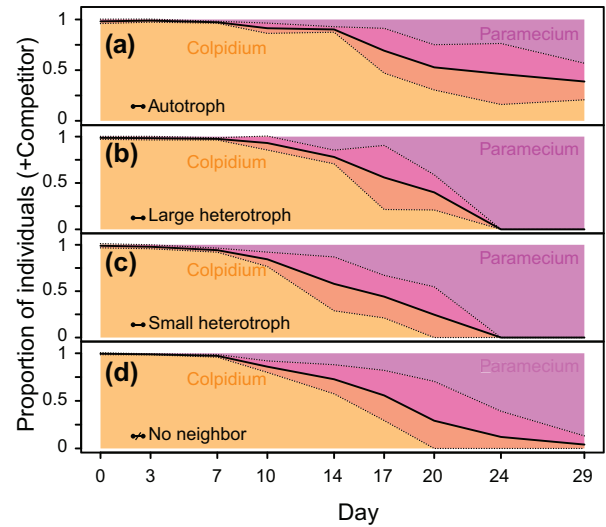


Figure 4. Effect of species trait in ecosystem 1 on the competition hierarchy between *Colpidium* (orange area) and *Paramecium* (pink area) in ecosystem 2 over time (FS+ Competitor treatment). The effect is expressed as the relative proportion of *Colpidium* versus *Paramecium* individuals (the two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

but were significantly lower in the FS+ Predator community (adjusted p -value < 0.0001 for every pairwise comparison; see Supplementary material Appendix 1 Table A5). Interestingly, positive neighbour effects of the autotroph species on neighbour ecosystems occurred despite the fact

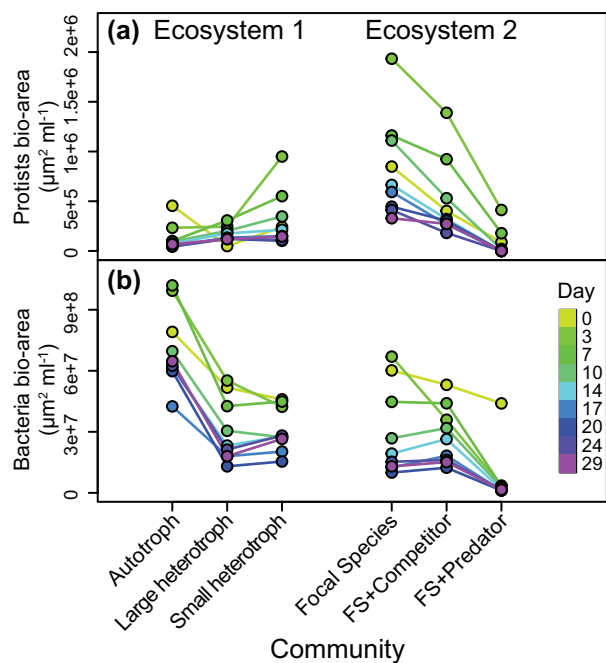


Figure 5. Bio-area of (a) protists and (b) bacteria over time (colours) for the different communities in each ecosystem. Points give the mean averaged over five replicates at a specific day (colours).

that autotroph protist biomass was generally lower or did not differ from other neighbours (Fig. 5a, left side), but were associated with significantly higher bacterial biomass (Fig. 5b, left side, see Supplementary material Appendix 1 Table A5 for all multiple comparisons).

Discussion

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

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

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

Interestingly in the reverse direction also, subsidies from heterotroph communities positively impacted autotroph community dynamics. This result stresses that neighbour effects may not only happen via changes in subsidy abundance but also through alterations to detritus stoichiometric balance. While not directly measured, the generally greater ratio of nitrogen to carbon in heterotroph organisms (Elser et al. 2000, Sterner 2009) is a straightforward explanation for the higher densities of autotroph communities when exchanging detritus with heterotroph communities compared to isolated controls, along with likely ammonium release activity of the bacterivorous protists (Probyn 1987). Overall, in our autotroph–heterotroph coupled ecosystems, heterotroph subsidies likely relaxed autotroph nitrogen limitation, while autotroph subsidies fuelled heterotroph growth with abundant labile carbon. Ecosystem couplings resulting in such resource spatial complementarity are common between freshwater and riparian systems, with riparian ecosystems exchanging abundant leaf litter against nitrogen-rich aquatic insects (Baxter et al. 2005, Bartels et al. 2012), and thus highlight the general significance of our findings.

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

Overall, our experiment shows general mechanisms by which natural communities can indirectly but strongly influence each other's functioning, via the abundance, stoichiometry and decomposability of detritus locally produced and subsidizing other ecosystems. Measuring directly the stoichiometric changes in subsidies produced by contrasted communities could be a natural extension of this experiment to investigate these mechanisms further. We demonstrate that, next to species dispersal (for example tested by Staddon et al. 2010), spatial dynamics of detritus are essential by themselves to understand the fundamental functioning of connected ecosystems, as well as their response to perturbations. The importance of subsidies is often studied only from the recipient ecosystem's local perspective (reviewed by Marcarelli et al. 2011, Sitters et al. 2015), and ecosystem

managers usually consider the threat of direct alterations to resource flows (e.g. nutrient pollution), but rarely threats potentially induced by alterations of community structure or composition in connected ecosystems (but see the crash of forest spider communities, induced by prey-subsidy disruption following the invasion of a stream by an exotic fish in Baxter et al. 2004). Our results suggest that any kind of perturbation (e.g. land-use change, over-harvesting) can have wider repercussions in space than those observed on local communities because of subsidy disruption (e.g. cascades across aquatic–terrestrial boundaries: Greig et al. 2012, Fey et al. 2015, Schulz et al. 2015). The extent to which local perturbations spatially cascade to other communities will depend on the strength of the subsidy coupling between ecosystems, an essential piece of information on which more research is needed. Our findings call for the adoption of a spatial perspective in ecosystem management and restoration ecology that integrates fine-tuned knowledge of resource spatial exchanges between ecosystems.

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References

Allison, S. D. 2012. A trait-based approach for modelling microbial litter decomposition. – *Ecol. Lett.* 15: 1058–1070.

Altermatt, F. et al. 2011. Interactive effects of disturbance and dispersal directionality on species richness and composition in metacommunities. – *Ecology* 92: 859–870.

Altermatt, F. et al. 2015. Big answers from small worlds: a user's guide for protist microcosms as a model system in ecology and evolution. – *Meth. Ecol. Evol.* 6: 218–231.

Baines, S. B. and Pace, M. L. 1991. The production of dissolved organic matter by phytoplankton and its importance to bacteria: patterns across marine and freshwater systems. – *Limnol. Oceanogr.* 36: 1078–1090.

Bartels, P. et al. 2012. Reciprocal subsidies between freshwater and terrestrial ecosystems structure consumer resource dynamics. – *Ecology* 93: 1173–1182.

Baxter, C. V. et al. 2004. Fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. – *Ecology* 85: 2656–2663.

Baxter, C. V. et al. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. – *Freshw. Biol.* 50: 201–220.

Berg, B. 1984. Decomposition of root litter and some factors regulating the process: long-term root litter decomposition in a Scots pine forest. – *Soil Biol. Biochem.* 16: 609–617.

Berlow, E. L. et al. 1999. Quantifying variation in the strengths of species interactions. – *Ecology* 80: 2206–2224.

Biersmith, A. and Benner, R. 1998. Carbohydrates in phytoplankton and freshly produced dissolved organic matter. – *Mar. Chem.* 63: 131–144.

Børsheim, K. Y. et al. 2005. Photosynthetic algal production, accumulation and release of phytoplankton storage carbohydrates and bacterial production in a gradient in daily nutrient supply. – *J. Plankton Res.* 27: 743–755.

Carpenter, S. R. et al. 2001. Trophic cascades, nutrients, and lake productivity: whole-lake experiments. – *Ecol. Monogr.* 71: 163–186.

Cole, J. J. and Caraco, N. F. 2001. Carbon in catchments: connecting terrestrial carbon losses with aquatic metabolism. – *Mar. Freshw. Res.* 52: 101–110.

Cole, J. J. et al. 2006. Differential support of lake food webs by three types of terrestrial organic carbon. – *Ecol. Lett.* 9: 558–568.

Cornwell, W. K. et al. 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. – *Ecol. Lett.* 11: 1065–1071.

Dreyer, J. et al. 2015. Quantifying aquatic insect deposition from lake to land. – *Ecology* 96: 499–509.

Elser, J. J. et al. 2000. Nutritional constraints in terrestrial and freshwater food webs. – *Nature* 408: 578–580.

Enriquez, S. et al. 1993. Patterns in decomposition rates among photosynthetic organisms: the importance of detritus C:N:P content. – *Oecologia* 94: 457–471.

Fey, S. B. et al. 2015. Recognizing cross-ecosystem responses to changing temperatures: soil warming impacts pelagic food webs. – *Oikos* 124: 1473–1481.

Fitzgerald, S. A. and Gardner, W. S. 1993. An algal carbon budget for pelagic-benthic coupling in Lake Michigan. – *Limnol. Oceanogr.* 38: 547–560.

Fox, J. and Weisberg, S. 2011. An {R} companion to applied regression. – Sage.

Frank, K. T. et al. 2005. Trophic cascades in a formerly cod-dominated ecosystem. – *Science* 308: 1621–1623.

García-Palacios, P. et al. 2016. The importance of litter traits and decomposers for litter decomposition: a comparison of aquatic and terrestrial ecosystems within and across biomes. – *Funct. Ecol.* 30: 819–829.

Gounand, I. et al. 2016. Data from: Subsidies mediate interactions between communities across space. – Dryad Digital Repository, <<http://dx.doi.org/10.5061/dryad.93hd6>>.

Gratton, C. and Vander Zanden, M. J. 2009. Flux of aquatic insect productivity to land: comparison of lentic and lotic ecosystems. – *Ecology* 90: 2689–2699.

Greig, H. S. et al. 2012. Warming, eutrophication, and predator loss amplify subsidies between aquatic and terrestrial ecosystems. – *Global Change Biol.* 18: 504–514.

Guenet, B. et al. 2010. Priming effect: bridging the gap between terrestrial and aquatic ecology. – *Ecology* 91: 2850–2861.

Hall, R. O. et al. 2000. Organic matter flow in stream food webs with reduced detrital resource base. – *Ecology* 81: 3445–3463.

Hamre, A. G. et al. 2014. Enzyme processivity changes with the extent of recalcitrant polysaccharide degradation. – *FEBS Lett.* 588: 4620–4624.

Harvey, E. et al. 2016. Spatially cascading effect of perturbations in experimental meta-ecosystems. – *Proc. R. Soc. B* 283: 20161496.

Hocking, M. D. and Reimchen, T. E. 2009. Salmon species, density and watershed size predict magnitude of marine enrichment in riparian food webs. – *Oikos* 118: 1307–1318.

Holyoak, M. et al. 2005. Metacommunities: spatial dynamics and ecological communities. – Univ. of Chicago Press.

Jackson, J. B. et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. – *Science* 293: 629–637.

Leibold, M. A. et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. – *Ecol. Lett.* 7: 601–613.

- Lenth, R. V. 2013. lsmeans: least-squares means. – R package ver. 1.06-05.
- Loreau, M. et al. 2003. Meta-ecosystems: a theoretical framework for a spatial ecosystem ecology. – *Ecol. Lett.* 6: 673–679.
- Marcarelli, A. M. et al. 2011. Quantity and quality: unifying food web and ecosystem perspectives on the role of resource subsidies in freshwaters. – *Ecology* 92: 1215–1225.
- Massol, F. et al. 2011. Linking community and ecosystem dynamics through spatial ecology. – *Ecol. Lett.* 14: 313–323.
- Massol, F. et al. 2017. How life-history traits affect ecosystem properties: effects of dispersal in meta-ecosystems. – *Oikos* doi: 10.1111/oik.03893.
- Menninger, H. L. et al. 2008. Periodical cicada detritus impacts stream ecosystem metabolism. – *Ecosystems* 11: 1306–1317.
- Meyer, D. et al. 2014. e1071: Misc functions of the Department of Statistics (e1071), TU Wien. – R package ver. 1.6-3 <<http://CRAN.R-project.org/package=e1071>>.
- Mouquet, N. and Loreau, M. 2002. Coexistence in metacommunities: the regional similarity hypothesis. – *Am. Nat.* 159: 420–426.
- Nakagawa, S. 2004. A farewell to Bonferroni: the problems of low statistical power and publication bias. – *Behav. Ecol.* 15: 1044–1045.
- Pennekamp, F. and Schtickzelle, N. 2013. Implementing image analysis in laboratory-based experimental systems for ecology and evolution: a hands-on guide. – *Meth. Ecol. Evol.* 4: 483–492.
- Pennekamp, F. et al. 2015. BEMOVI, software for extracting behavior and morphology from videos, illustrated with analyses of microbes. – *Ecol. Evol.* 5: 2584–2595.
- Polis, G. A. et al. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. – *Annu. Rev. Ecol. Syst.* 28: 289–316.
- Polis, G. A. et al. 2004. Food webs at the landscape level. – Univ. of Chicago Press.
- Probyn, T. A. 1987. Ammonium regeneration by microplankton in an upwelling environment. – *Mar. Ecol. Prog. Ser.* 37: 53–64.
- Richardson, J. S. et al. 2010. Resource subsidies across the land-freshwater interface and responses in recipient communities. – *River Res. Appl.* 26: 55–66.
- Schindler, D. E. and Scheuerell, M. D. 2002. Habitat coupling in lake ecosystems. – *Oikos* 98: 177–189.
- Schmitz, O. J. et al. 2000. Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. – *Am. Nat.* 155: 141–153.
- Schulz, R. et al. 2015. Review on environmental alterations propagating from aquatic to terrestrial ecosystems. – *Sci. Total Environ.* 538: 246–261.
- Scott, N. A. and Binkley, D. 1997. Foliage litter quality and annual net N mineralization: comparison across North American forest sites. – *Oecologia* 111: 151–159.
- Seymour, M. et al. 2015. Dendritic network structure and dispersal affect temporal dynamics of diversity and species persistence. – *Oikos* 124: 908–916.
- Shurin, J. B. et al. 2006. All wet or dried up? Real differences between aquatic and terrestrial food webs. – *Proc. Biol. Sci.* 273: 1–9.
- Sitters, J. et al. 2015. Spatial stoichiometry: cross-ecosystem material flows and their impact on recipient ecosystems and organisms. – *Oikos* 124: 920–930.
- Staddon, P. et al. 2010. Connectivity, non-random extinction and ecosystem function in experimental metacommunities. – *Ecol. Lett.* 13: 543–552.
- Sterner, R. W. 2009. Nutrient stoichiometry in aquatic ecosystems. – In: *Encyclopedia of inland waters*. Elsevier, pp. 820–831.
- Sterner, R. W. and Elser, J. J. 2002. *Ecological stoichiometry. The biology of elements from molecules to the biosphere.* – Princeton Univ. Press.

Supplementary material (available online as Appendix oik-03922 at <www.oikosjournal.org/appendix/oik-03922>). Appendix 1.