Ecosystem size mediates the effects of resource flows on biodiversity and ecosystem function at different scales.

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**Abstract**

Ecosystem size and resource flows are key factors driving biodiversity and ecosystem function. However, the question of whether and how these drivers interact has been largely overlooked. Here, we investigated how ecosystem size asymmetry affects biodiversity and function of two-patch meta-ecosystems connected through flows of non-living resources. We conducted a microcosm experiment, mimicking spatial resource flows between ecosystems of different sizes, yet otherwise identical properties, or between ecosystems of the same size. Meta-ecosystems with asymmetric ecosystem sizes displayed higher α- diversity but lower β-diversity and ecosystem function (total biomass) than their unconnected counterparts. At the same time, such an effect was not found for meta-ecosystems of identical patch sizes. Our work demonstrates how the size of ecosystems, interconnected via resource flows, can modulate cross-ecosystem dynamics, having implications for biodiversity and function across scales.

Keywords: homogenisation, differentiation, detritus, nutrients, scaling, subsidies, allochthonous input, disturbance, species-area relationship, landscape

**Introduction**

Ecosystem size is a key factor driving biodiversity. Ecologists have long known that larger ecosystems harbour more biodiversity than smaller ecosystems (species-area relationship; MacArthur & Wilson, 1963). The concept dates back to the late 1700s during the second Pacific voyage of James Cook. There, naturalists Johann Reinhold Forster and Georg Forster noted that 'Islands only produce a greater or less number of species, as their circumference is more or less extensive' (Forster, 1778), which has been empirically and experimentally corroborated many times since (e.g., Fukami, 2004; Losos & Ricklefs, 2009; Wilson, 1961). The various reasons why larger ecosystems harbour more biodiversity remains an ongoing area of research (Losos & Ricklefs, 2009), and the individual roles of different processes (e.g., speciation, dispersion) contributing to this pattern are still debated (e.g., Valente et al., 2020). The main explanation for this phenomenon has been that species go extinct at lower rates in larger ecosystems (MacArthur & Wilson, 1963, 1967), as they have more habitat types (Kallimanis et al., 2008; Williams, 1943), more niche diversity (e.g., Ren et al., 2022), and less ecological drift (e.g., Gilbert & Levine, 2017), with extensive theoretical, comparative, and experimental extensions (e.g., Hanski & Ovaskainen, 2000; Luo et al., 2022; Wang & Altermatt, 2019). Furthermore, ecosystem size can also influence ecosystem function (LeCraw et al., 2017; Yang et al., 2021). For example, larger ecosystems can be more productive because their community composition allows them to use resources more efficiently (complementarity effects) (Delong & Gibert, 2019).

Furthermore, ecosystems are rarely isolated in space. Spatial flows and subsidies of non-living resources among ecosystems (e.g., leaf litter, carcasses, inorganic nutrients; herein, "resource flows"; see Gounand et al., 2018 for a review) are—next to ecosystem size—a key abiotic factor affecting biodiversity and ecosystem function. For example, salmon carcasses–likely transported from rivers to land by wolves and bears–can decrease riparian plant biodiversity by promoting the dominance of nutrient-rich species (Hocking & Reynolds, 2011). Subsidies from marine algal wrack can either increase plant biodiversity on sand dunes (Del Vecchio et al., 2017) or decrease plant biodiversity in rainforests on tiny islands (Obrist et al., 2022). As another example, aquatic insects can increase the function (production) of riparian birds which feed on them (Nakano & Murakami, 2001). Supporting such empirical evidence, meta-ecosystem theory predicts that resource flows can affect biodiversity by modifying species interactions and persistence (Gravel, Mouquet, et al., 2010; Marleau et al., 2014; Peller et al., 2022). For example, resource flows can delay competitive exclusion by increasing locally available resources (Gounand et al., 2017) or instead prevent the local establishment of dispersing species by increasing the abundance of the resident competitors (Gravel, Mouquet, et al., 2010). Furthermore, resource flows should increase meta-ecosystem production if they transport resources from ecosystems good at producing biomass to ecosystems good at transforming non-living resources into consumers (Harvey et al., 2023). However, despite widespread recognition that ecosystem size and resource flows can, individually, affect biodiversity and ecosystem function, their interactive effect has largely been overlooked.

These two drivers likely interact since ecosystem size influences the amount and the effect of resource flows. For example, the size of a body of water regulates the amount of resources it exports: the larger a lake or river, the more insects emerge from it per metre of reach (Gratton & Vander Zanden, 2009). Whereas, the size of the receiving watershed would determine the effects of aquatic resource import: for instance, the larger a watershed, the more diluted its fertilisation from salmon carcasses (Hocking & Reimchen, 2009). As resource flows can influence biodiversity and ecosystem function, and ecosystem size can influence resource flows, the hypothesis that ecosystem size can influence biodiversity and ecosystem function through resource flows emerges naturally as a general concept.

Here, we tested if and how the size of interconnected ecosystems mediates the influence of resource flows on biodiversity and ecosystem function using a protist microcosm experiment (Altermatt et al., 2015; Benton et al., 2007; Cadotte & Fukami, 2005). We constructed two-patch meta-ecosystems connected by resource flows between ecosystems (we use “patch” as a synonym for “ecosystem”). We manipulated (i) the relative size of the two patches within the meta-ecosystem (symmetric vs asymmetric sizes) while keeping the total size of the meta-ecosystem constant and (ii) the connection between the two ecosystems (connected vs unconnected). Our results showed that ecosystem size asymmetry significantly influences biodiversity and ecosystem function through resource flows. Specifically, we observed resource flows increasing α-diversity and a decreasing β-diversity and ecosystem function (total biomass) in asymmetric meta-ecosystems, when comparing their connected to their unconnected treatment. Contrastingly, resource flows did not affect α-diversity, β-diversity, or ecosystem function in symmetric meta-ecosystems, as shown by comparing symmetric connected and unconnected meta-ecosystems.

**Materials and methods**

*Experimental design*

We studied how asymmetry in ecosystem size mediates the effect of resource flows on biodiversity and ecosystem function in meta-ecosystems via a microcosm experiment involving an aquatic protist community (Altermatt et al., 2015). Specifically, we compared two-patch meta-ecosystems with either symmetric or asymmetric sizes (yet identical total meta-ecosystem size), and either connected by non-living resource flows or unconnected (see Fig. 1). All replicates started with identical initial communities and we evaluated the resource flow effect by comparing connected meta-ecosystems with pairs of unconnected ecosystems of the same size and symmetry properties (controls, referred to as unconnected meta-ecosystems). Meta-ecosystems were of identical total size (volume: 45 ml), with symmetric meta-ecosystems composed of two identical sized patches (each 22.5 ml), and asymmetric meta-ecosystems composed of a 7.5 ml and a 37.5 ml patch, respectively. We call symmetric meta-ecosystems MMMM and asymmetric meta-ecosystems SLLs, with S, M, and L referring to Small (7.5 ml), Medium (22.5 ml), and Large (37.5 ml) ecosystems, respectively, and subscripts referring to the size of the connected ecosystem. We call the respective unconnected controls of the resource effect (unconnected meta-ecosystems) MM and SL (without subscripts).

To understand the effects of the size of the connected ecosystem, we also established two control meta-ecosystems connecting two small ecosystems (SSSS) and two large ecosystems (LLLL), respectively (see Fig. 1). To understand what the effect of the size of the connected ecosystem was, we compared local ecosystems that were connected to either small or large ecosystems. We did this by comparing SL with SS and LS with LL. All the above combinations were replicated five-fold.

*Experimental setup*

Our initial communities consisted of eight heterotrophic ciliates (*Blepharisma* sp., *Colpidium* sp., *Loxocephalus* sp., *Paramecium aurelia*, *Paramecium caudatum*, *Spirostomum* sp., *Spirostomum teres*, and *Tetrahymena cf. pyriformis*), two mixotrophic ciliates able to photosynthesise (*Euglena gracilis* and *Euplotes aediculatus*), and one rotifer (*Cephalodella* sp.), subsequently all referred to as “protists”. We cultured protists in pre-autoclaved bottles with standard protist medium (0.46 g of Protozoa Pellet by Carolina per L of water) and a bacterial mix (*Serratia fonticola*, *Bacillus subtilis*, and *Brevibacillus brevis*) serving as food for protists and constituting 5 % of the total culture volume. See Altermatt et al. (2015) for further details and protocols.

At the start of the experiment (day zero), we established a master mix of the protist community consisting of all 11 species mixed at 1/11 of their carrying capacity and supplemented with a standard protist medium (standard protist medium constituted 15 % of the master mix volume). The experiment was conducted in 50 ml centrifuge tubes, with each tube representing an ecosystem. We pipetted 7.5 ml, 22.5 ml, and 37.5 ml of the master mix to constitute the small, medium, and large ecosystems, respectively. The replicates were randomised in position and kept in an incubator at 20 °C with constant lighting for the remainder of the experiment.

*Disturbances and* *non-living* *resource flows*

Because it is logistically difficult to separate living species from non-living resources, spatial flows were associated with disturbances, whose mortality effect was controlled in the unconnected ecosystems. More specifically, every four days (starting on day five), we boiled a fixed volume of the community of each ecosystem for 30 seconds to kill every organism, thereby turning all organisms into non-living resources (i.e., local disturbance). After boiling the sampled volumes in a microwave, we let them cool down to room temperature and then poured them into the connected recipient ecosystems, creating bidirectional resource flows. In the unconnected controls, the same volume was disturbed but poured back to the originating ecosystem to control for the mortality associated with cross-ecosystem resource flows (‘resource retention’ in Fig. 1). We here focus on the results of the high disturbance level yet give the results for the low one in Appendix S4. This is because resource flow effects on biodiversity were mediated by patch size at both low and high disturbance, but ecosystem function only at high disturbance. Throughout the experiment, the total volume of the ecosystems was held constant by compensating evaporation loss with deionised water (see Appendix S1).

*Sampling*

To determine the abundance, species identity, biomass, and traits of protists in each ecosystem, we took videos of 0.2 ml samples from each ecosystem every four days, starting at day zero. While the first two time points (days 0 and 4) took place before the first disturbance, all other time points were always taken three days after the disturbance to leave communities to recover as much as possible from disturbances. We took a 5 s-video of each sample at 1.6x magnification, using a Hamamatsu Orca Flash 4.0 (Herrsching am Ammersee, Germany) camera. During the last two time points (days 24 and 28), we took two samples per ecosystem to reduce the sampling error and increase the chances of detecting individuals at low densities (each metric was averaged across the two samples). We also took videos of all protist monocultures to construct a training dataset of each species’ traits for species identification. We took sufficient videos of each monoculture to capture at least 100 individuals of each species.

*Quantifying biomass and biodiversity*

We used the R-package BEMOVI to identify and characterise protist species in the communities (Altermatt et al., 2015; Pennekamp et al., 2015; Pennekamp & Schtickzelle, 2013). We first extracted moving particles' traits (e.g., speed, shape, size) in the videos. We then used these traits to filter out particles that were not protists and obtain an average abundance of protist individuals per volume. We also measured protist biomass as our focal ecosystem function. We calculated the total area of protists (as area per volume medium) and subsequently used this “bioarea” as a proxy of biomass (hereafter referred to as “biomass”), which is a fair assumption given the roundish shape of protists. We then identified protist species using a support vector machine model (Cortes et al., 1995; r-package “e1071”: Dimitriadou et al., 2006), employing traits extracted from species monocultures as predictor variables. Last, we calculated local biodiversity (α-diversity) using the Shannon Index (Shannon, 1948). At the meta-ecosystem scale, we calculated biodiversity through (i) mean local diversity (mean α-diversity) as the Shannon Index averaged across ecosystems, (ii) among-community diversity (β-diversity) as the Bray-Curtis index (Bray & Curtis, 1957), and (iii) total biodiversity (γ-diversity) as the total number of species persisting at the meta-ecosystem level.

*Statistical analysis*

To understand the effects of resource flows on biodiversity over time in symmetric and asymmetric meta-ecosystems, we performed statistical analysis using mixed-effect models with the 'lme4' package in R (Bates et al., 2015). The analysis excluded the initial two time points preceding the disturbances (grey zones in all figures), as their inclusion would interfere with our understanding of the impact of disturbances and resource flows.

At the meta-ecosystem level, to examine resource flow effects, we compared SLLS to SL and MMMM to MM. SL and MM were virtual meta-ecosystems created from unconnected ecosystems, that is, pairing two ecosystems to calculate the diversity and total biomass (yet without having these ecosystems connected by flows of resources). We constructed these virtual control meta-ecosystems by creating all possible pairs (without replacement) of unconnected ecosystems (25 SL pairs and 10 MM pairs). To test the influence of the resource flow connection on a response variable (α-, β-, γ- diversity, total biomass), we examined the effects of the resource flow connection and its interaction with time by comparing a full model (including the predictor variable interacting with time as a fixed effect) to a null model (including only time as a fixed effect) using ANOVA. Significant results indicated that the predictor variable interacted with time to affect the response variable. Similarly, we assessed the influence of the predictor variable alone (without its interaction with time) by comparing with ANOVA a reduced model (including the predictor variable and time as fixed effects) with the null model. Significant results indicated that the predictor variable affected the response variable without interacting with time. In the full, reduced, and null models, random effects considered the impact of replicates on the correlated intercept and the slope of the relationship between the response variable and time. We performed multiple comparisons iteratively when comparing (i) asymmetric connected to asymmetric unconnected meta-ecosystems and (ii) symmetric connected to symmetric unconnected meta-ecosystems, resulting in a distribution of p-values. Each iteration involved unconnected meta-ecosystems with differently paired ecosystems (without resampling). The presented p-values are the means of their respective distributions. See Table S1 for the p values associated with meta-ecosystem models.

At the local level, we investigated whether the size of the connected ecosystem influenced resource flow effects–comparing SL to SS and LS to LL–and whether resource flows had an effect when happening between ecosystems of the same size–comparing SS to S, MM to M, and LL to L. To test the influence of the resource flow connection or connected ecosystem size on a response variable (Shannon Index, biomass), we made the same model comparisons as at the meta-ecosystem level (but without iterations). See Table S2 for the p-values associated with ecosystem models.

**Results**

At the meta-ecosystem level, resource flows increased mean α-diversity, decreased β-diversity, and decreased total biomass in meta-ecosystems with asymmetric patch sizes (SLLS; Fig. 2 purple solid versus dashed lines) but not in meta-ecosystems with identical (symmetric) patch sizes (MMMM; Fig. 2 green solid versus dashed lines): SLLS had a higher mean α-diversity (p = 0.019), lower β-diversity (p = 0.012), and lower total biomass (p = 0.003) compared to SL unconnected meta-ecosystems (purple lines in Fig. 2a, 2b, 2d respectively). MMMM had the same mean α- and β-diversity and total biomass (green lines in Fig. 2a, 2b, and 2d, respectively, p > 0.1) as MM. Resource flows did not influence γ-diversity in either asymmetric or symmetric meta-ecosystems. That is, SLLS had the same γ-diversity as SL (purple lines in Fig. 2c, p > 0.1), and MMMM had the same γ-diversity as MM (green lines in Fig. 2c, p > 0.1).

At the local level, small ecosystems that were connected to large ecosystems had higher diversity (Shannon Index) (solid vs dotted brown lines in Fig. 3a, p = 0.002) and biomass (solid vs dotted brown lines in Fig. 3b, p = 0.019, connection interacted with time) than when unconnected (SL vs S). This effect on biodiversity can be broken down into two components. First, the size of the connected ecosystem, as being connected to large ecosystems led to greater biodiversity (solid vs dotted brown lines in Fig. 3a, p = 0.013) (SL vs SS). Second, the presence or absence of the connection, as small ecosystems when connected to other small ecosystems were more diverse (dashed vs dotted brown lines in Fig. 3a, p = 0.012) than when unconnected (SS vs S). We observed a similar but weak (marginally not significant) trend for biomass. That is, when a small ecosystem was connected to a large ecosystem, it led to greater biomass (solid vs dashed brown lines in Fig. 3b, p = 0.060) than when connected to small ecosystems (SL vs SS). Also, a small patch connected to another small patch sustained greater biomass (dashed vs dotted brown lines in Fig. 3b p = 0.071) than when unconnected (SS vs S).

Also at the local level, large ecosystems that were connected to small ecosystems were similar in their biodiversity (solid vs dotted blue lines in Fig. 3a, p > 0.1) but had lower biomass (solid vs dotted blue lines in Fig. 3b, p = 0.001) relative to when they were unconnected (LS vs L). For large ecosystems, however, the connection to small ecosystems decreased their biomass (solid vs dashed blue lines in Fig. 3b, p = 0.036) (LS vs LL). This effect was mediated by the size of the connected ecosystem, as when large ecosystems were connected to other large ecosystems, the effect was not observed (dashed vs dotted blue lines in Fig. 3b, p > 0.1) (LL vs L).

Finally, in medium ecosystems we observed a weak, yet marginally non-significant, trend of resource flows increasing biodiversity (Fig. S8, p = 0.081) and biomass (Fig. S8, p = 0.062) in connected ecosystems relative to those that were unconnected (MM vs M).

**Discussion**

Our microcosm experiment shows, as a proof-of-concept, that ecosystem size asymmetry can mediate the effects of bidirectional resource flows on biodiversity. Meta-ecosystems with asymmetric ecosystem sizes (SLLS) had more similar communities (lower β-diversity) but maintained higher biodiversity across the two patches (higher mean α-diversity) than asymmetric yet unconnected ecosystems (SL). The fact that these effects were not observed in meta-ecosystems with symmetric ecosystem sizes indicates a mediating role of ecosystem size. These results could be explained by the connection of the small ecosystem to a larger ecosystem, which increased the biodiversity of the small ecosystem (SL had greater biodiversity than SS and S) while the biodiversity of the large ecosystem remained unchanged (biodiversity was similar between Ls, LL, and L). As small and large ecosystems were identical aside from their size (resources, community composition, etc.), the effects of the connection can be attributed to ecosystem size. Ultimately, our findings suggest that considering the size of interconnected ecosystems can help us understand how bidirectional resource flows shape biodiversity.

Notably, we found resources flowing between ecosystems of different sizes impacted both α- and β-diversity by increasing the biodiversity of the smaller patch within the meta-ecosystem. Furthermore, it decreased total meta-ecosystem biomass by increasing the biomass of small patches but increasing the biomass of large patches. We suggest three ways small patches may have gained biodiversity and biomass, while large patches lost biomass. First, resource quantity: small ecosystems might have had a net import of resources. Although the volume exchanged between ecosystems was equivalent, larger ecosystems had a greater dominance of photosynthetic species than small ecosystems (Fig. S9), which might have increased carbon availability more in large versus small ecosystems. Consequently, small ecosystems may have imported a greater quantity of newly fixed carbon from large ecosystems relative to what they exported, creating . This net import of resources could have allowed small ecosystems to sustain more biodiversity as more resources allow more individuals to persist, promoting a greater abundance of rare species and preventing their extinction (species energy theory, see Wright, 1983). This mechanism could also apply to natural ecosystems, as according to the trophic island biogeography theory we would expect differences in the ratio between autotrophic and heterotrophic organisms between ecosystems of different sizes. Gravel 2011 parameterised a metacommunity model using 50 pelagic food webs (Scale and Structure in Natural Food Webs reference) and found that the larger an ecosystem the more consumers it should have. Second, resource quality: small ecosystems may have had a net import of good quality detritus (protist detritus). As large ecosystems were more productive in terms of protist biomass per volume, more protist detritus was moved from large to small ecosystems despite the same volume being exchanged. If the detritus of protists was of higher quality as a resource for the local community compared to other resource forms (e.g., bacterial detritus, inorganic nutrients), it would have sustained a higher growth of individuals and, therefore, higher biodiversity in the small ecosystem. This could be the case as protist growth is mainly driven by PUFAs (reference) and protists are rich in PUFAs (reference) while most bacteria lack it (reference). Third, resource heterogeneity: small ecosystems might have imported more heterogeneous resources than the ones they had. As there was greater protist diversity in large ecosystems, the corresponding exported detritus might have been more diverse with respect to carbon compounds and biomolecules, potentially creating more niches for protists to coexist in small ecosystems. This could have been the case as more biodiverse communities create more differentiated resources (find references in Moore 2004 that says that: ***diverse communities create diverse resources***) which then could increase the biodiversity of the communities they enter, as more diverse resources can increase biodiversity (Butler2003, Kang2004, Lake et al. 2000; Palmer et al. 2000, Moore & Hunt 1988; Yodzis 1988).

Moreover, resources flowing between ecosystems of different sizes decreased meta-ecosystem function by increasing biomass in small patches and decreasing it in large patches, possibly through these three mechanisms. First: resource quantity. The net import of biomass to small patches and net export to large patches would have increased the biomass of small patches which now had more resources to produce new individuals while large patches now had less resources. Maybe the large patches had better recycling than small patches and that’s why moving resources to the small ecosystems reduced the total biomass of the meta-ecosystem. Second: resource quality. The import of good quality resources to the small ecosystems would increase biomass and bad quality resources to the large ecosystems would decrease, as a meta-ecosystem model showed that better quality subsidies cycle more easily through an ecosystem compartment increasing its function (cite here Osakpolor2023). At a meta-ecosystem level, having the good quality resource in the small ecosystems could have decreased production because these good quality resources were not taken up as much by the small ecosystem if it had a lower recycling because of its lower biodiversity, as it has been found in nature for decomposers (put here the reference of van der Plas 2019). Third: resource heterogeneity. Maybe moving resource heterogeneity more to the small patch changed productivity through nutrient co-limitation? Or through biodiversity?

Our study highlights that the size of the donor ecosystem, where resource flows originate, can shape the effect of resource flows on a recipient ecosystem’s diversity. In particular, in our experiment, biodiversity increased in a small ecosystem when connected to a larger one. The subsidised island biogeography theory (Anderson & Wait, 2001) states that resources flowing into an ecosystem can influence its biodiversity, making its biodiversity deviate from what we would expect from species-area relationships, especially in small ecosystems. This has been supported by field studies, for instance, with resource flows increasing the diversity of bird species more in smaller than in large islands (Obrist et al., 2020). Our results align with this finding, showing that resource flows between small ecosystems changed their biodiversity but not between large ecosystems. However, the characteristics of the connected ecosystem have been overlooked by this theory. Through integration with the meta-ecosystem framework, we add to the subsidised island biogeography that the effects of the resource flows may also be mediated by the characteristics of the exporter ecosystem, notably its size.

Decades of research on spatial subsidies have documented that donor ecosystems commonly vary in size (refs, e.g. Polis [4] Add references on how the donor ecosystem size matters). For example, islands which export nitrogen to coral reefs, kelp forests which exchange non-living resources with adjacent intertidal zones, etc… Moreover, evidence from natural systems supports our finding that the size of donor ecosystems can influence the biodiversity of recipient ecosystems. [3] Improve this previous phrase. For instance, an iconic empirical example of how the size of the connected ecosystem can influence the connected ecosystem is found in lakes and rivers embedded in terrestrial watersheds of different sizes. Notably, studies found that larger watersheds can (i) increase lake primary production, as they export more phosphorus (Knoll et al., 2003), (ii) sustain fewer lake consumers that rely on sediments, as they export lower quantities of sediments (lower water flow, gentler slopes, and increased sedimentation in terrestrial ecosystems) (Babler et al., 2011), and (iii) sustain longer river food chains, as they have more water flow, hence less hydrological variation and therefore a more stable environment (Sabo et al., 2010). [5] Add here about other types of system where the size of the donor ecosystem has an influence and maybe move all examples to the top. This, in conjunction with our findings, suggests that subsidised island biogeography (Anderson & Wait, 2001) would gain in integrating how the size of the connected ecosystems mediates the effects of resources on the shape of species-area relationships and possibly changes this relationship. According to our results, we expect, for example, that the diversity of macroinvertebrates in a lake might be higher than expected by their area only (according to subsidies island biogeography) when the lake is connected to a larger rather than a small forest. These effects could extend to biomass, too.

Beyond the net quantity of resources exchanged (which we controlled for), our experiment emphasises that the asymmetry in ecosystem size necessarily generates differences in the quality of exported resources through changes in community composition. We would expect that in nature differences in ecosystem size would cause differences in resource quality and cause effects through the following mechanisms. First, larger ecosystems may have resources that are more heterogeneous. Larger ecosystems generally have higher diversity within trophic levels (horizontal diversity, MacArthur1963, MacArthur1967) and higher number of trophic levels (vertical diversity or maximum food chain length, Post2000, Ward2017, Guo2023). Such higher species diversity should translate into higher resource heterogeneity when these species die, and their compounds remain in the environment (**reference: more diverse community create more diverse resources**). When a more heterogeneous detritus moves from a larger to a smaller ecosystem it should create more niches for species to coexist on (**reference: more resource diversity creates more niches**) in the small ecosystem, increasing its biodiversity. Second, larger ecosystems may have resources that are easier to take up and use. Larger ecosystems, by having more trophic levels, have more species that are rich in nitrogen (when compared to carbon, Elser2000, Scharler2015, Fagan2002) and therefore produce resources that are also richer in nitrogen. Such detritus from higher trophic levels can be more liable than the one of lower trophic levels (Yee2006). Therefore, when liable resources move from a large to a small ecosystem, they could cause resources to be taken up and use more quickly by species increasing their biodiversity and function.

* Also, differences in ecosystem size may underlie differences in functional diversity (Smith2013, Kunz2024, Tew2022, but see Karadimou2016). In our case, it generated differences in net autotrophy (more photosynthesis in proportion in larger ecosystems). Differences in functional diversity may induce differences in resource limitations (C versus N, find a reference for this). In this configuration, resource flows stoichiometric asymmetry could be the vector of spatial complementarity in resource use (cf. Harvey et al. 2023 and Pichon et la 2023), which increases productivity at the basis of the food web and possibly, by this way, of diversity in a bottom-up mechanism.

Also, by influencing biodiversity, ecosystem size should influence the stoichiometry of its resources (Stribel2009).

[6]Add references, including Moore and invasives species paper by Tianna

In conclusion, our experiment provides experimental evidence that asymmetry in ecosystem size can indirectly affect biodiversity and function in meta-ecosystems through its effects on resource flows. As resource flows are a common phenomenon, we expect our findings to be of broad relevance. While we demonstrated that ecosystem size mediates the effects of resource flow on the biodiversity and function of ecosystems of the same type, resources often also flow among ecosystems of different types, which could even aggravate the effect demonstrated. This connection among ecosystems of different types is often overlooked in studies examining the effects of ecosystem size variations on biodiversity, as they focus on the effects of the fragmentation of a single ecosystem type (mainly forests) on biodiversity. Consequently, this could imply that when aiming to conserve the biodiversity of a habitat, it might be necessary to consider how ecosystem size changes resource flow between ecosystems of the same size, as well as resource flows connecting it with ecosystems of different types surrounding it.

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**Figure legends**

Figure 1**: experimental design.**

We conducted a protist microcosm experiment to study whether differences in ecosystem size can affect biodiversity and function through resource flows. We compared two-patch meta-ecosystems with reciprocal resource flows to unconnected meta-ecosystems without resource flows. Meta-ecosystems were composed either of symmetric or asymmetric individual ecosystem sizes, yet with a total identical volume. All ecosystems in the experiment started with the same protist community of 11 species. To create resource flows, a fixed volume (red portion of the ecosystem) of each ecosystem was removed, heated to kill all organisms to turn them into non-living resources, and either put back into the ecosystem (no resource flows) or reciprocally exchanged between ecosystems (resource flows). Importantly, while the volume disturbed in each ecosystem was equal, the smaller the ecosystem, the higher the percentage of disturbance compared to the ecosystem’s overall volume. Consequently, smaller ecosystems experienced greater disturbance compared to larger ecosystems. The meta-ecosystems and unconnected ecosystems treatments were crossed with two levels of disturbance, low and high, and each treatment combination was replicated five times.

Figure 2: **time series of diversity and biomass at a meta-ecosystem scale.**

(a) mean α-diversity, (b) β-diversity, (c) γ-diversity, and (d) total (Tot) biomass of the meta-ecosystem was calculated as bioarea (mm2) in asymmetric and symmetric (purple vs green) and connected and unconnected meta-ecosystems (solid versus dotted lines). For connected meta-ecosystems, dots represent means across replicates. For unconnected meta-ecosystems, dots represent the mean of all possible combinations of unconnected ecosystems assembled as virtual pairs of ecosystems with the respective ecosystem size structure. Error bars represent 95 % confidence intervals; vertical grey lines represent disturbance events followed by resource flows. Points were minimally jittered along the x-axis to make the figure clear. The area in grey indicates time points not considered for analysis, as meta-ecosystems were sampled before the first disturbance and resource flow.

Figure 3: **time series of diversity and biomass at a local scale.**

(a) biodiversity (Shannon index) and (b) biomass (bioarea per volume in mm2/ml). Dots represent means across replicates; error bars represent 95 % confidence intervals; vertical grey lines represent disturbance events followed by resource flows. All systems were sampled on the same day. Points were minimally jittered along the x-axis to make the figure clear. The area in grey indicates time points not considered for analysis, as ecosystems were sampled before the first disturbance and resource flow.

**Figures**

A diagram of a meta-ecosystems

Description automatically generated

Figure 1.

A graph of different colored lines

Description automatically generated

Figure 2.

A graph of different colored lines

Description automatically generated with medium confidence

Figure 3.

**Appendix S1 Experimental design: volume balance**

During the experiment, we kept the volume of ecosystems constant by replenishing the inevitable losses of volume that occurred through sampling and evaporation. Three days before each sampling day, we added the protist medium equal to the same volume to be sampled (0.2 ml) to avoid a decrease in total volume. Secondly, we counteracted evaporation losses by replenishing the volumes that evaporated with autoclaved deionised water. Right before the first two disturbances, we added 1.0 ml of deionised water to all tubes right before each disturbance. However, before the third exchange event, we observed slightly higher than anticipated evaporation rates, and the ecosystems were, on average, 1.17 ml (SD = 0.37) smaller than their initial volumes. Therefore, before the third exchange and after each subsequent exchange, we refilled the ecosystems with water until they reached their initial volume.

**Appendix S2 Autotrophic-heterotrophic ratio analysis**

At the local level, to examine the effects of ecosystem size, we investigated whether the size of unconnected ecosystems influenced the ratio between autotrophic and heterotrophic individuals (autotrophic-heterotrophic ratio) by comparing S, M, and L. To test the influence of ecosystem size on this ratio, we examined the effects of ecosystem size and its interaction with time by comparing a full model (including ecosystem size interacting with time as a fixed effect) to a null model (including only time as a fixed effect) using ANOVA. Significant results indicated that ecosystem size interacted with time to affect the autotrophic-heterotrophic ratio. Similarly, we assessed the influence of ecosystem size alone (without its interaction with time) by comparing with ANOVA a reduced model (including ecosystem size and time as fixed effects) with the null model. Significant results indicated that ecosystem size affected the response variable without interacting with time. In the full, reduced, and null models, random effects considered the impact of replicates on the correlated intercept and the slope of the relationship between the autotrophic-heterotrophic ratio and time.

**Appendix S3 Results: high disturbance**

Larger ecosystems were denser with autotrophic individuals, as attested by the autotrophic-heterotrophic ratio increasing with ecosystem size in unconnected ecosystems (Fig. S2, p = 0.026, ecosystem size interacted with time) (S vs M vs L).

A screenshot of a graph

Description automatically generated

Figure S1. The connection with another medium ecosystem shows a weak trend to increase (a) biodiversity and (b) biomass per volume. Dots represent means across replicates; error bars represent 95 % confidence intervals; vertical grey lines represent disturbance events followed by resource flows. All systems were sampled on the same day. Points were minimally jittered along the x-axis to make the figure clear. The area in grey indicates time points not considered for analysis, as meta-ecosystems were sampled before the first disturbance and resource flow.

A graph with lines and dots

Description automatically generated

Figure S2. Larger ecosystems were denser with autotrophic individuals. Dots represent means across replicates; error bars represent 95 % confidence intervals; vertical grey lines represent disturbance events followed by resource flows. All systems were sampled on the same day. Points were minimally jittered along the x-axis to make the figure clear. The area in grey indicates time points not considered for analysis, as meta-ecosystems were sampled before the first disturbance and resource flow.

**Appendix S4 Results: low disturbance**

At the meta-ecosystem level, resource flows increased mean α-diversity and decreased β-diversity in meta-ecosystems with asymmetric patch sizes (SLLS; Fig. S3 purple solid versus dashed lines) and increased total biomass in identical (symmetric) patch sizes (MMMM; Fig. S3 green solid versus dashed lines). SLLS had a higher mean α-diversity (p = 0.002, connection interacted with time), lower β-diversity (p = 0.007, connection interacted with time), same γ-diversity (p > 0.1), and same total biomass (p > 0.1) compared to SL (purple lines in Fig. S3a, S3b, S3c, S3d respectively). MMMM had the same mean α-, β-, and γ-diversity (green lines in Fig. S3a, S3b, and S3c, respectively, p > 0.1), but higher total biomass (green lines in Fig. S3d, p = 0.026), compared to MM.

At the local level, small ecosystems that were connected to large ecosystems had higher diversity (Shannon Index) (solid vs dotted brown lines in Fig. S4a, p = 0.001, connection interacted with time) than when unconnected (SL vs S). This effect on biodiversity was due to the size of the connected ecosystem, as being connected to large ecosystems led to greater biodiversity (solid vs dotted brown lines in Fig. S4a, p < 0.001, connection interacted with time) (SL vs SS). The presence or absence of the connection alone had no effect, as small ecosystems when connected to other small ecosystems were as diverse (dotted vs dashed brown lines in Fig. S4a, p > 0.1) than when unconnected (SS vs S).

Furthermore, small ecosystems connected to large ecosystems had higher biomass (solid vs dotted brown lines in Fig. S4b, p = 0.004) than unconnected (SL vs S). This effect on biomass was also due to the size of the connected ecosystem, as being connected to large ecosystems led to greater biomass (solid vs dashed brown lines in Fig. S4b, p < 0.001) (SL vs SS). The presence or absence of the connection alone had no effect, as small ecosystems, when connected to other small ecosystems, had as much biomass (dashed vs dotted brown lines in Fig. S4a, p > 0.1) as when unconnected (SS vs S).

Also at the local level, large ecosystems that were connected to small ecosystems had less biodiversity (solid vs dotted blue lines in Fig. S4a, p = 0.048, connection interacted with time) than when unconnected (LS vs L). This might have been due to the presence of the connection itself and not the size of the connected ecosystem, as large ecosystems had the same biodiversity when connected to different patch sizes (solid vs dashed blue lines in Fig. S4b, p > 0.1) (LS vs LL) but there was weak evidence of being connected to another large ecosystem decreased biodiversity (dashed vs dotted blue lines in Fig. S4b, p = 0.064) (LL vs L). We detected weak evidence for large ecosystems connected to small ecosystems to have less biomass (solid vs dotted blue lines in Fig. S4b, p = 0.064) than unconnected (LS vs L). However, this was not significant. We found no effect of the size of the connected ecosystem on biomass (solid vs dashed blue lines in Fig. S4, p > 0.1) (LS vs LL) and only weak evidence for the same size effect (dashed vs dotted blue lines in Fig. S4, p = 0.071, connection interacted with time) (LL vs L).

In medium ecosystems, we observed no effect of connection on biodiversity (dashed vs dotted lines in Fig. S5a, p > 0.1) in connected ecosystems compared to if they were unconnected (MM vs M). However, we observed increased biomass when ecosystems were connected (dashed vs dotted lines in Fig. S5b, p = 0.014, connection interacted with time) (MM vs M).

Finally, larger ecosystems were not denser with autotrophic individuals, as attested by ecosystem size not affecting the autotrophic-heterotrophic ratio in unconnected ecosystems (Fig. S6, p > 0.1) (S vs M vs L).

A graph of different colored lines

Description automatically generated

Figure S3. Resource flow influenced diversity in asymmetric meta-ecosystems, but not in symmetric meta-ecosystems, and ecosystem function in symmetric meta-ecosystems, but not in asymmetric meta-ecosystems. For connected meta-ecosystems, dots represent means across replicates. For unconnected meta-ecosystems, dots represent the mean of all possible combinations of unconnected ecosystems assembled as virtual meta-ecosystems with the respective ecosystem size structure. Total (Tot) biomass was calculated as bioarea (mm2). Error bars represent 95 % confidence intervals; vertical grey lines represent disturbance events followed by resource flows. All systems were sampled on the same day. Points were minimally jittered along the x-axis to make the figure clear. The area in grey indicates time points not considered for analysis, as meta-ecosystems were sampled before the first disturbance and resource flow.

A graph of different sizes and colors

Description automatically generated with medium confidence

Figure S4. In SLLS, the connection between small and large ecosystems influenced single ecosystems' (a) biodiversity and (b) relative biomass. Biomass: bioarea density (mm2/ml). Dots represent means across replicates; error bars represent 95 % confidence intervals; vertical grey lines represent disturbance events followed by resource flows. All systems were sampled on the same day. Points were minimally jittered along the x-axis to make the figure clear. The area in grey indicates time points not considered for analysis, as meta-ecosystems were sampled before the first disturbance and resource flow.

A graph of a number of red dots

Description automatically generated with medium confidence

Figure S5. The connection with another medium ecosystem made medium ecosystems sustain (a) the same biodiversity but (b) higher biomass density. Dots represent means across replicates; error bars represent 95 % confidence intervals; vertical grey lines represent disturbance events followed by resource flows. All systems were sampled on the same day. Points were minimally jittered along the x-axis to make the figure clear. The area in grey indicates time points not considered for analysis, as meta-ecosystems were sampled before the first disturbance and resource flow.

A graph with lines and points

Description automatically generated

Figure S6. Larger ecosystems were not denser with autotrophic. Dots represent means across replicates; error bars represent 95 % confidence intervals; vertical grey lines represent disturbance events followed by resource flows. All systems were sampled on the same day. Points were minimally jittered along the x-axis to make the figure clear. The area in grey indicates time points not considered for analysis, as meta-ecosystems were sampled before the first disturbance and resource flow.

**Appendix S5 p values of the comparisons**

Table S1. P values of the meta-ecosystems mixed effect models. The full and null models are compared to the null models. The effects that passed a test with a significance level below p = 0.05 are in bold.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Response variable** | **Comparison** | **Full model**  **p (high disturbance)** | **Reduced model p (high disturbance)** | **Full model  p (low disturbance)** | **Reduced model p (low disturbance)** |
| Mean  α-Diversity (Shannon) | SLLS vs SL | .061 | **.019** | **.002** | .483 |
| MMMM vs MM | .225 | .115 | .591 | .788 |
| β-Diversity (Bray-Curtis) | SLLS vs SL | **.027** | **.012** | **.007** | .075 |
| MMMM vs MM | .469 | .333 | .308 | .236 |
| γ-Diversity (Species Richness) | SLLS vs SL | .449 | .318 | .432 | .737 |
| MMMM vs MM | .576 | .620 | .282 | .242 |
| Total Biomass (mm2) | SLLS vs SL | **.011** | **.003** | .105 | .264 |
| MMMM vs MM | .167 | .356 | .078 | **0.026** |

Table S2. P values of the ecosystems mixed effect models. Both the full model and the reduced model are compared to the null model. The effects that passed a test with a significance level below p = 0.05 are in bold.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Response variable** | **Comparison** | **Full model**  **p (high disturbance)** | **Reduced model p (high disturbance)** | **Full model  p (low disturbance)** | **Reduced model p (low disturbance)** |
| Biodiversity (Shannon) | SL vs S | **.009** | **.002** | **.001** | **.031** |
| SL vs SS | **.045** | **.013** | **< .001** | **.004** |
| Ss vs S | **.040** | **.012** | .907 | .767 |
| MM vs M | .193 | .081 | .578 | .817 |
| LS vs L | .220 | .109 | **.048** | .330 |
| LS vs LL | .271 | .134 | .431 | .932 |
| LL vs L | .887 | .682 | .064 | .068 |
| Biomass (mm2/ml) | SL vs S | **.019** | **.032** | **.012** | **.004** |
| SL vs SS | .060 | .060 | **.001** | **< .001** |
| Ss vs S | .142 | .071 | .778 | .805 |
| MM vs M | .062 | .231 | **.014** | **.003** |
| LS vs L | **.003** | **.001** | .064 | .148 |
| LS vs LL | .085 | **.036** | .685 | .397 |
| LL vs L | .396 | .185 | .071 | .130 |
| Autotrophic/ Heterotrophic Individuals Ratio | S vs M vs L | **.026** | .109 | .161 | .291 |

To do before sending to Florian

* Check all the references
* Letter after the column upper/lower case
* Change detritus to resources
* Resource heterogeneity