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

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**Abstract**

Ecosystem size is a key factor driving biodiversity and ecosystem function. Larger ecosystems contain more species and can be hubs of dispersal and resource flows in a network of multiple ecosystems. However, whether and how ecosystem size and resource flows interact to affect biodiversity and ecosystem function has been largely overlooked. Here, we investigated how ecosystem size asymmetry affects biodiversity of two-ecosystem meta-ecosystems connected through flows of non-living resources. We conducted highly replicated microcosm experiments, mimicking resource flows between ecosystems of different size, yet otherwise being identical. We found that meta-ecosystems with asymmetric ecosystem sizes had higher β-diversity but lower α-diversity and ecosystem function (total biomass) than their unconnected counterparts, while such an effect was not found for meta-ecosystems of identical patch sizes. Our work gives a demonstration of how cross-ecosystem dynamics modulated by differences in patch sizes, with cascading effects on biodiversity and direct implication on conservation and management of spatially connected ecosystems.

Keywords: homogenisation, differentiation, detritus, nutrients, scaling, subsidies, allochthonous input, disturbance, conservation, landscape

**Introduction**

Ecosystem size is a key factor driving biodiversity. Ecologists have known for a long time 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 '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; Matias et al., 2010; Wilson, 1961). The various reasons why larger ecosystems harbour more biodiversity is still an ongoing field of research REF 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 the 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 change ecosystem function (LeCraw et al., 2017; Yang et al., 2021). For example, larger ecosystems can be more productive because they have community compositions which allows them to use resources more efficiently (complementarity effects) (Delong & Gibert, 2019).

Yet, ecosystems are rarely isolated in space, and 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. For example, salmon carcasses transported from rivers to land by wolves and bears can decrease riparian plant biodiversity by making communities dominated by nutrient-rich species (Hocking & Reynolds, 2011). Other examples show that subsidies from marine algal wrack can either increase or decrease plant biodiversity, on sand dunes (Del Vecchio et al., 2017) or rainforests on tiny islands (Obrist et al., 2022), respectively. Likewise, 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 local 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). However, despite recognition that both ecosystem size and resource flows can affect biodiversity and ecosystem function, their interactive effect on biodiversity has largely been overlooked.

Ecosystem size can influence the amount and 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 a river, the more insects emerge from it per metre of reach (Gratton & Vander Zanden, 2009), while 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, while also ecosystem size can influence resource flows, the hypothesis that ecosystem size can influence biodiversity and ecosystem function through resource flows emerges as a generic and natural phenomenon.

Here, we tested if and how ecosystem size mediates the influence of resource flows on biodiversity and ecosystem function using a protist microcosm experiment (REF). We constructed two-ecosystem meta-ecosystems connected by resources flows between ecosystems following disturbance. We compared biodiversity in two-patch meta-ecosystems where we manipulated the relative size of local ecosystems (symmetric vs asymmetric sizes) while keeping constant total meta-ecosystem size. We found that ecosystem size asymmetry significantly influences biodiversity through resource flows. Resource flows in meta-ecosystems with asymmetric ecosystem sizes increased their α-diversity and decreased their β- diversity and ecosystem function (total biomass). Contrastingly, resource flows had no effect on either α-diversity, β-diversity, or ecosystem function, respectively, in meta-ecosystems with symmetric ecosystem sizes.

**Materials and methods**

*Experimental design*

We studied how asymmetry in ecosystem size mediates the effect of resource flows on biodiversity in meta-ecosystems via a microcosm experiment containing an aquatic protist community (Altermatt et al., 2015). Specifically, we compared two-patch meta-ecosystems with either symmetric or asymmetric sizes (yet identical total size) either connected by non-living resources or unconnected (see Fig. 1). All replicates started with identical initial communities. We evaluated the resource flows effect by comparing connected systems 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 being composed of two identical sized patches (each 22.5 ml), while asymmetric meta-ecosystems being composed of a 7.5 ml and a 37.5 ml patch, respectively. Symmetric and asymmetric meta-ecosystems are called MMMM and SLLs, respectively, with S, M, 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. Respective unconnected controls of the resource effect are referred to as 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 above combinations were replicated x-fold.

*Experimental setup*

Our initial communities consisted of eight heterotrophic ciliates (*Colpidium* sp., *Loxocephalus* sp., *Paramecium aurelia*, *Paramecium caudatum*, *Spirostomum* sp., *Spirostomum teres*, *Tetrahymena cf. pyriformis*, and *Blepharisma* sp.), 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 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 standard protist medium (15 % of the 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 turn every organism into non-living resources (i.e., local disturbance). We investigated whether resource flows level affect our results by considering two levels of disturbances, either boiling 5.25 ml of each ecosystem (low disturbance) or boiling 6.75 ml (high disturbance), which represented 70 % and 90 % of a small ecosystem, 23.3 % and 30 % of a medium ecosystem, and 14 % and 18 % of a large ecosystem, respectively in the low and high disturbance treatments. After boiling the sampled volumes in a microwave, we subsequently let them cool down to room-temperature, and then poured them to 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. As resource flows influenced diversity only at high resource flows / disturbance level, we here focus on the results of the high disturbance level yet give the results for the low disturbance level in Appendix S2. 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 (day 0 and 4) took place before the first disturbance, all other time points were always taken three days after the disturbance to leave communities recover as much as possible from disturbances. We took a 5 s video of each sample at 1.6x magnification, using Hamamatsu Orca Flash 4.0 (Herrsching am Ammersee, Germany) camera. At the last two time points (days 24 and 28), we took two samples per ecosystem to reduce the sampling error and increase 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, and used these traits to filter out particles that were not protists and obtain an average abundance of protist individuals per volume. We also measured as a proxy for ecosystem function protist biomass. 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) that employed 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 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.

To examine resource flows effects at the meta-ecosystem level, 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. For each of comparisons, we performed multiple comparisons iteratively, 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 Tables S1 for the p values associated with meta-ecosystem models.

To examine resource flow effects at the ecosystem level, we investigated whether the size of the connected ecosystem influenced resource flows 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 and LL to L. To test the influence of the resource flow connection or size on a response variable (Shannon Index, biomass), we made the same model comparisons as at the meta-ecosystem level (but without iterations). See Tables 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 (green lines in Fig. 2a and 2b, respectively, p > 0.1), as well as total biomass (green lines in Fig. 2d, p > 0.1), compared to MM pairs. Resource flows did not influence γ-diversity in either asymmetric or symmetric meta-ecosystems, as SLLS had the same γ-diversity as SL pairs (purple lines in Fig. 2c, p > 0.1) and MMMM had the same γ-diversity as MM pairs (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 dashed brown lines in Fig. 3a, p = 0.002) and biomass (solid vs dashed 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) Second, the presence or absence of the connection, as small ecosystems when connected to other small ecosystems were more diverse (dotted vs dashed 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, as being connected to large led to greater biomass (solid vs dotted brown lines in Fig. 3b, p = 0.06) than when connected to small ecosystems (SL vs SS), as well as being connected to other small ecosystems (dotted vs dashed brown lines in Fig. 3b p = 0.071) instead of being unconnected (SL vs SS).

Also at the local level, large ecosystems that were connected to small ecosystems were similar in their biodiversity (solid vs dashed blue lines in Fig. 3a, p > 0.1) but had lower biomass (solid vs dashed blue lines in Fig. 3b, p = 0.001) than when unconnected (LS vs L). For large ecosystems, the connection with small ecosystems decreased their biomass (solid vs dotted 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 (dotted vs dashed blue lines in Fig. 3b, p > 0.01) (LL vs L).

We observe a weak, yet marginally non-significant, trend of resource flows slightly increasing biodiversity (Fig. S8, p = 0.081) and biomass (Fig. S8, p = 0.062) in medium ecosystems compared to if they were unconnected (MM vs M).

**Discussion**

Our microcosm experiment shows 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). Notably, these effects were not observed in meta-ecosystems with symmetric ecosystem sizes, indicating a mediating role of ecosystem size. These results could be explained by the connection of the small ecosystem to a larger ecosystemincreasing its biodiversity (SL had greater biodiversity than SS and S). 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. In contrast, resource flows did not affect biodiversity in large ecosystems (biodiversity was similar between Ls, LL, and L). Ultimately, our study showed that the effects of bidirectional resource flows on biodiversity were mediated by ecosystem size.

Notably, we found resources flowing between ecosystems of different sizes impacting both α- and β-diversity by increasing the biodiversity of the ecosystem in the smaller patch. We could think of two ways small-patch ecosystems may have had more biodiversity. First, via a net import of resources into small ecosystems, as large ecosystems had a greater density of photosynthetic species than small ecosystems (Fig. S9). The total volume, and in principle also the total nutrient levels, of flows was reciprocal and a closed system at the meta-ecosystem scale, yet resource flow may have been in different form and bio-availability (e.g., detritus, dissolved form). However, through differences in community composition, in particular of the autotrophic species, total carbon availability could increase, for example through photosynthesis and slower competitive exclusion dynamics in large system. Consequently, small ecosystems could have imported more newly fixed carbon from large ecosystems than they exported. As large ecosystems had more photosynthetic individuals, they would enrich the system in carbon, creating more photosynthetic biomass, which created more detritus when they were disturbed, and therefore a large resource flow. The import of resources could then have allowed unproductive small ecosystems to sustain more biodiversity as more resources allow more individuals to persist, and therefore promoting greater population abundance of rare species and preventing their extinction (species energy theory, see Wright, 1983). This mechanism would create a source-sink dynamics of resources (Gravel, Guichard, et al., 2010): there is a net movement of newly fixed carbon from large to small ecosystems. Thus, our work supports a growing body of studies which suggest defining sources and sinks based on directions of spatial flows (Loreau et al., 2013). Second, as there is a higher 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. Third, as more detritus was moved from large to small ecosystems, if the detritus of protists was of higher quality than in 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.

Our study shows that meta-ecosystems of the same total size, yet differing in local ecosystem size, can differ in their biodiversity. Meta-ecosystem ecology shows that resource flows between ecosystems can impact biodiversity (e.g., Gounand et al., 2017; Gravel, Mouquet, et al., 2010; Marleau & Guichard, 2019; Peller et al., 2022). For example, meta-ecosystem theory predicts resource flows can influence persistence of species and the coexistence of competitors (Gounand et al., 2017; Gravel, Mouquet, et al., 2010). Detritus flowing from productive ecosystems could for instance allow the persistence of species in unproductive ecosystems that would otherwise go extinct (Gravel, Mouquet, et al., 2010). However, meta-ecosystem theory and previous experiments have typically assumed the size of connected ecosystems to be the same (but see Harvey et al., 2018, 2020), thereby ignoring how differences in ecosystem size observed in natural systems (e.g., Fahrig, 2003) may modulate local and meta-ecosystem richness through flows of resources. Our results suggest that integrating ecosystem size into meta-ecosystem ecology would help us further our comprehension of how resource flows shape biodiversity. In particular, we suggest that resource flowing into large ecosystems should have a limited influence, whereas meta-ecosystem theory generally predicts effects on all ecosystems.

Our study also shows how the effect of resource flows on a recipient ecosystem’s diversity can be influenced by the size of the donor ecosystem where the resource flows originate. 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 are in line with this finding, showing that resource flows between small ecosystems changed their biodiversity (Ss was more diverse than S), but not between large ecosystems (LL was as diverse as L). However, whether the size of the connected ecosystem influences the effects of resource flows has been overlooked by subsidised island biogeography. Here, we showed that the biodiversity of an ecosystem is greater when connected to a larger ecosystem relative to when connected to an ecosystem of the same size (SL was more diverse than SS). Field studies already support that the size of the connected ecosystem can influence the connected ecosystem. For example, some studies found that larger watersheds can (i) increase lake primary production, as they transport more phosphorus (Knoll et al., 2003), (ii) sustain fewer lake consumers that rely on sediments, as sediments are transported less (lower water flow, gentler slopes, and increased sedimentation) (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). Therefore, we suggest that subsidised island biogeography (Anderson & Wait, 2001) should not only study how the size of the focus ecosystems mediates the effects of resources on the shape of species-area relationships but also how the size of the connected ecosystems changes this relationship. For example, we might find that the diversity of macroinvertebrates in a lake might be higher than expected by their size (according to subsidies island biogeography) when the lake is connected to a larger rather than a small forest. These effects could extend to biodiversity too.

In conclusion, our experiment provides experimental evidence that asymmetry in ecosystem size can indirectly affect biodiversity 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 of ecosystems of the same type, resources are 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: We conducted a protist microcosm experiment to study whether differences in ecosystem size can affect biodiversity through resource flows. We compared two-patch meta-ecosystems with reciprocal resource flows compared to unconnected systems without resource flows. Meta-ecosystems were composed either of identical or different individual ecosystem-sizes, yet with total overall 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 and release the resources, and either put back to 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 its 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: Resource flow influence diversity and ecosystem function in asymmetric meta-ecosystems, but not in symmetric meta-ecosystems. Asymmetric connected meta-ecosystems (SLLS) sustained (a) higher mean α-diversity, (b) lower β-diversity, and (d) lower total biomass than asymmetric unconnected meta-ecosystems (SL). (c) lower γ diversity during the experiment. For meta-ecosystems, dots represent means across replicates. For “unconnected”, dots represent the mean of all possible combinations of these 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 are slightly jittered to improve figure clarity.

Figure 3: In SLLS, the connection between small and large ecosystems influenced single ecosystems' (a) biodiversity and (b) relative biomass. In terms of diversity, the connection had only an effect on small ecosystems (SL had greater diversity than SS and S; LS had similar diversity than LL and L). In terms of biomass, the connection increased the biomass of small ecosystems (SL had greater biomass than SS and S) and decreased the biomass of large ecosystems (LS had less biomass than LL and L). Biomass: bioarea density (mm2/ml). Dots represent means across replicates; error bars represent 95 % confidence intervals; vertical grey lines show the timing of the disturbance events. Points are slightly jittered to improve figure clarity.

**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

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Figure 3.

**Appendix S1 Experimental design: volume balance**

During the experiment, the volume of ecosystems was kept constant and inevitable losses through sampling (for the videos and evaporation were balanced and replenished. Three days before each sampling day, we added protists medium of the same volume to be sampled (0.2 ml), to avoid a decrease in total volume. Secondly, we counteracted evaporation losses by replenishing with autoclaved deionised water the volumes that evaporated. 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 sligthly 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 Results: low disturbance**

*Meta-ecosystem level: effects of ecosystem size asymmetry*

Ecosystem size asymmetry affected the β diversity of meta-ecosystems as at high resource flows. But unlike at high resource flows, it did not influence the α or γ diversity of meta-ecosystems (Fig. S1). This was supported by comparing SLLS to MMMM. SLLS exhibited higher β diversity than MMMM (solid lines in Fig. S1b, weak evidence, p = 0.08). They did not differ in their α (solid lines in Fig. S1a, no evidence, p > 0.1) or γ diversity (solid lines in Fig. S1c, no evidence, p > 0.1). As also at high resource flows, ecosystem size did not affect productivity (solid lines in Fig. S2, no evidence, p > 0.1).

*Meta-ecosystem level: effects of resource flows*

As at high resource flows levels, resources flowing between small and large ecosystems impacted their α and β diversity but not their γ diversity (Fig. S1). This was supported by comparing SLLS and SL. SLLS had lower β-diversity (purple lines in Fig. S1b, strong evidence, p = 0.007), higher mean α diversity (purple lines in Fig. S1a, strong evidence, p = 0.002), and the same γ diversity (purple lines in Fig. S1c, no evidence, p > 0.1). However, unlike at high resource flows, there was no evidence that the movement of resources changed productivity. SLLS had the same total biomass as SL (purple lines in S2, no evidence, p > 0.1). Resource flows interacted with time to influence α- and β-diversity in SLLS. As at high levels of resource flows, there was no evidence for an effect of resource flows between two medium ecosystems on mean α, β, and γ diversity (green lines in Fig. S1, no evidence, p > 0.1). Contrary to high resource flows, resource flows increased the productivity of MMMM. MMMM had higher biomass density than MM (green lines in Fig. S2, moderate evidence, p = 0.026).

A graph of different types of lines

Description automatically generated with medium confidence

Figure S1. Meta-ecosystem ecosystem size asymmetry influenced biodiversity. Meta-ecosystems with asymmetric ecosystem sizes (SLLS) sustained higher β diversity (b) but same α (a) and γ diversity (c). 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 are slightly jittered to improve figure clarity.

A graph of different sizes and colors

Description automatically generated

Figure S2. ecosystem size asymmetry had no effect on the meta-ecosystem total biomass. This was attested by comparing SLLS to MMMM. This was attested by SLLS having the same biomass as SL. Resource flowing between medium ecosystems affected total biomass density, as MMMM were more productive than MM. 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.

*ecosystem level: effects of resource flows*

As with high resource flows, resource flows in SLLS changed biodiversity and productivity at a local level (Fig. S3). The connection to large ecosystems made small ecosystems more biodiverse (solid orange vs solid grey lines in Fig. S3a, strong evidence, p = 0.001) and more productive (solid orange vs solid grey lines in Fig. S3b, strong evidence, p = 0.004). The connection to small ecosystems made large ecosystems less biodiverse (solid blue vs solid black lines in Fig. S3a, strong evidence, p = 0.001) and less productive (solid blue vs solid black lines in Fig. S3a, weak evidence, p = 0.064) than if they were unconnected. The effect of the connection on the biodiversity of large ecosystems was not detected at high resource flows. Time interacted with the connection to influence the biodiversity of small and large ecosystems and the biomass of large ecosystems. Resource flows in MMMM impacted only the productivity but not the biodiversity of their ecosystems. Resources flowing between medium ecosystems impacted their productivity but not their biodiversity. Medium ecosystems connected to other medium ecosystems compared to unconnected medium ecosystems were more productive (S4b, strong evidence, p = 0.003) but as biodiverse (S4a, no evidence, p > 0.1).

Unlike with high resource flows, how a connection impacted an ecosystem was dependent on the size of the ecosystem it was connected to only for small ecosystems (Fig. S3). The size of the connected ecosystem influenced the biodiversity and productivity of the small ecosystems. Being connected to a small instead of being unconnected did not influence its biodiversity (grey solid vs dotted orange lines in Fig. S3a, no evidence, p > 0.1) or productivity (grey solid vs dotted orange lines in Fig. S3b, no evidence, p > 0.1). However, being connected to a larger ecosystem it increased its biodiversity (solid orange vs solid grey lines in Fig. S3a, very strong evidence, p < 0.001) and biomass (solid orange vs solid grey lines in Fig. S3b, very strong evidence, p < 0.001).

For large ecosystems, only the connection had an effect, not the size of the connected ecosystem. Being connected to another large ecosystem decreased large ecosystems' biodiversity (solid blue vs solid black lines in Fig. S3a, weak evidence, p = 0.064) and productivity (solid blue vs solid black lines in Fig. S3b, no evidence, p > 0.1). Being connected to a small ecosystem decreased its biodiversity the same as being connected to a large ecosystem (dotted blue vs solid blue lines in Fig. S3a, no evidence, p > 0.1) and biomass (dotted blue vs solid blue lines in Fig. S3b, no evidence, p > 0.1). In small ecosystems, time interacted with ecosystem size and connection to influence biodiversity. In large ecosystems, time interacted with connection to influence biodiversity and biomass.

A graph of different colored lines

Description automatically generated

Figure S3. In small ecosystems the size of the connected ecosystem impacted the biodiversity (a) and (b) biomass density of a ecosystem. In large ecosystems the size of the connected ecosystem did not impact neither the biodiversity (a) nor the (b) biomass density of an ecosystem. Dots represent means across replicates; error bars represent 95 % confidence intervals; vertical grey lines represent disturbance events. All ecosystems were sampled on the same day. Points were jittered to make the figure clear.

A graph of a number of bloat and a number of bloat

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Figure S4. The connection with another medium ecosystem did not affect (i) the biodiversity of medium ecosystems, but it increased their (b) 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 jittered to make the figure clear.

*Ecosystem level: effects of ecosystem size per se*

As in the high disturbance treatment, ecosystem size impacted the biomass and biodiversity of unconnected ecosystems (Fig. S5). Larger ecosystems were more biodiverse (Fig. S5a, strong evidence, p < 0.001) and productive (Fig. S5b, strong evidence, p < 0.001). The effect of ecosystem size on biodiversity and biomass density was influenced by time.

A graph of different types of data

Description automatically generated with medium confidence

Figure S5. The larger the unconnected ecosystem, the higher biomass (a) and biodiversity (b) it sustained throughout the experiment. Dots represent means across replicates; error bars represent 95 % confidence intervals; vertical grey lines represent disturbance events. All ecosystems were sampled on the same day. Points were jittered to make the figure clear.

**Appendix S3 Results: High disturbance**

A graph of different sizes and colors

Description automatically generated

Figure S6. ecosystem size asymmetry had no effect on the meta-ecosystem total biomass. This was attested by comparing SLLS to MMMM. Resource flowing between small and large ecosystems decreased productivity. This was attested by SLLS with a lower total biomass than SL. Resource flowing between medium ecosystems had no effect on total biomass density, as MMMM were as productive as MM. 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 jittered minimally along the x-axis to make the figure clear.

A graph of different colored lines

Description automatically generated

Figure S7. The size of the connected ecosystem influenced the biodiversity (a) and (b) total biomass of small ecosystems. But only the (b) total biomass of large ecosystems. Dots represent means across replicates; error bars represent 95 % confidence intervals; vertical grey lines show the timing of the disturbance events. Points are minimally jittered along the x-axis to improve figure clarity.

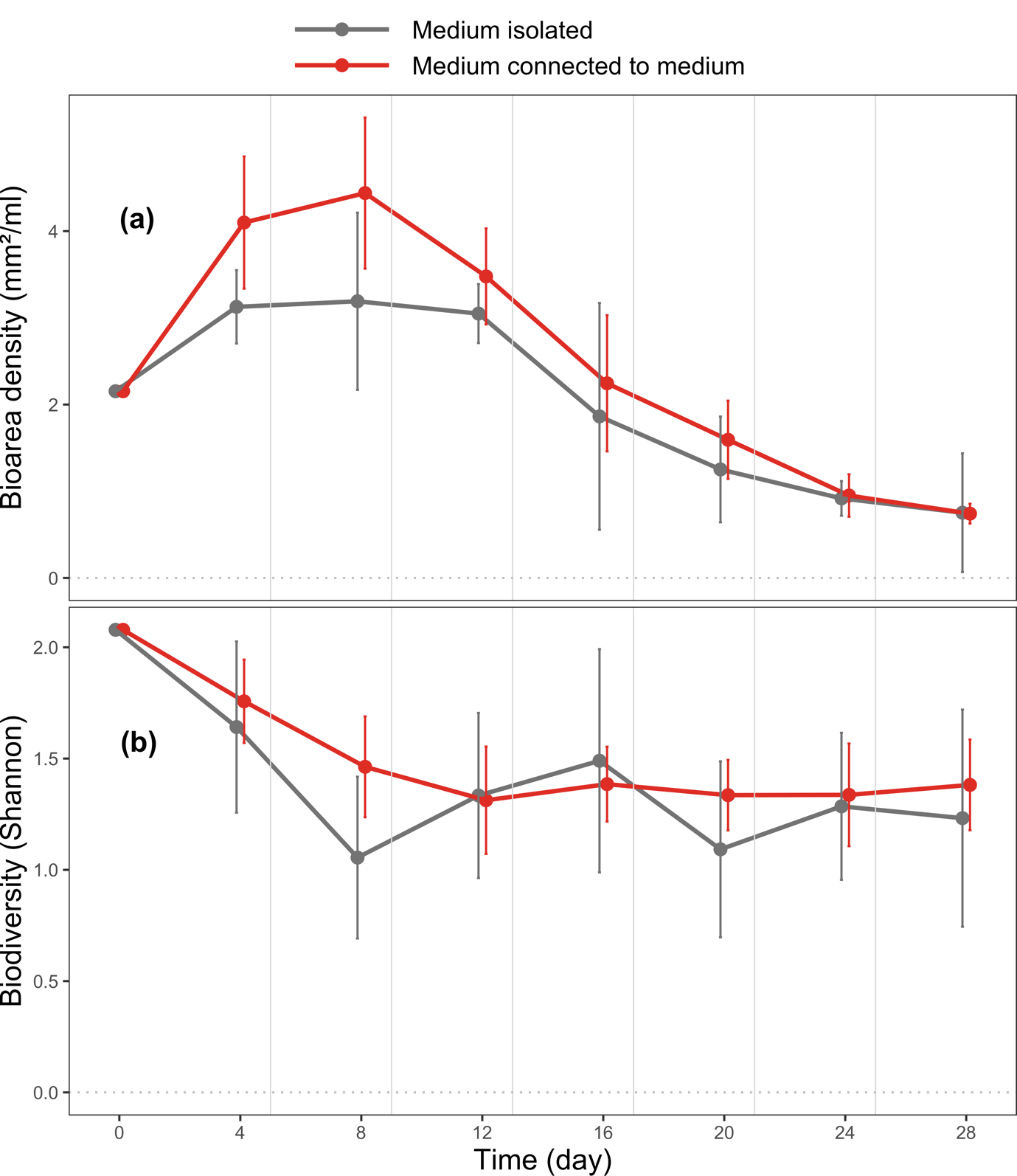


Figure S8. The connection with another medium ecosystem made medium ecosystems sustain (a) higher biodiversity and (b) higher biomass density. Dots represent means across replicates; error bars represent 95 % confidence intervals; vertical grey lines represent disturbance events followed by resource flows. All systems were sampled on the same day. Points were minimally jittered along the x-axis to make the figure clear.

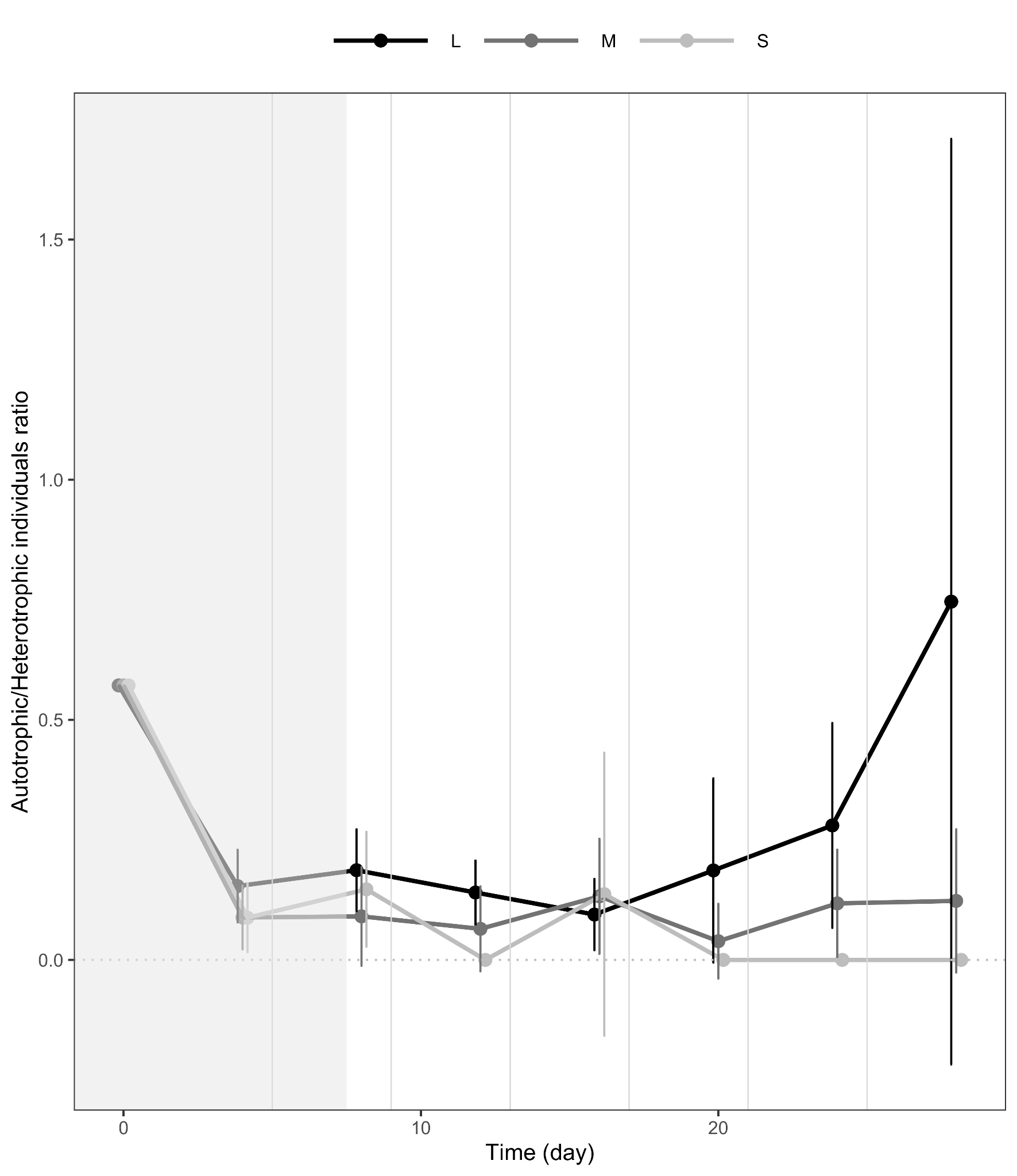


Figure S9. Larger ecosystems were denser with autotrophic individuals. P = 0.008, interaction with time.

**Appendix S4 comparisons p values**

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

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **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  (meta-ecosystem) | SLLS vs SL | .061 | **.019** | .002 | .483 |
| MMMM vs MM | .225 | .115 | .591 | .788 |
| β diversity  (meta-ecosystem) | SLLS vs SL | **.027** | **.012** | .007 | .075 |
| MMMM vs MM | .469 | .333 | .308 | .236 |
| γ diversity  (meta-ecosystem) | SLLS vs SL | .449 | .318 | .432 | .737 |
| MMMM vs MM | .576 | .62 | .282 | .242 |
| Total biomass  (meta-ecosystem) | 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. In bold the effects that passed a test with significance level below p = 0.05.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Response variable** | **Comparison** | **Full model**  **p (high disturbance)** | **Reduced model p (high disturbance)** | **Full model  p (low disturbance)** | **Reduced model p (low disturbance)** |
| Biomass  (ecosystem) | 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 |
| Shannon Index  (ecosystem) | 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 |