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

Emanuele Giacomuzzo1,2\*, Tianna Peller1,2, Isabelle Gounand3, Florian Altermatt1,2†

1 Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, Switzerland

2 Department of Aquatic Ecology, Eawag: Swiss Federal Institute of Aquatic Science and Technology, Dübendorf, Switzerland

3 Institut d'écologie et des sciences de l'environnement (iEES Paris), Sorbonne Université, CNRS, UPEC, CNRS, IRD, INRA, Paris, France

\* Corresponding author: Emanuele.Giacomuzzo@eawag.ch +41767908556

† Corresponding author: [Florian.Altermatt@eawag.ch](mailto:Florian.Altermatt@eawag.ch)

* Journal: Ecology Letters
* Article type: Letter
* Short running title (abbreviated form of title of less than 45 characters including spaces): Size affects diversity through resource flows.
* Number of words in the abstract (maximum 150):
* Number of words in the main text (excluding abstract, acknowledgements, references, table, and figure legends):
* Number of words in each text box: no text box
* Number of figures:
* Number of references:
* Number of figures, tables, and text boxes:

Statement of authorship: All authors designed the study. EG performed the experiment and analysed the data. EG wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

Data accessibility statement: if the manuscript is accepted, we agree to archive the data of our experiment in a public repository (Dryad, Figshare or Hal) and to include the DOI of such dataset at the end of the article.

**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. Spatial flows of non-living resources are also a driver of biodiversity and ecosystem function. However, whether ecosystem size and resource flows can interact to affect biodiversity and ecosystem function has been overlooked. Hence, we do not know whether ecosystem size can affect the biodiversity of multiple ecosystems through flows of non-living resources. Here, we investigated the effects of ecosystem size asymmetry on the biodiversity of two-ecosystem meta-ecosystems connected through flows of non-living resources. We conducted highly replicated microcosm experiments, mimicking resource flows between differently sized ecosystems of otherwise identical ecosystems. We found that meta-ecosystems with asymmetric ecosystem sizes had higher β- diversity but lower α-diversity and ecosystem function (total biomass) than their disconnected counterparts. In contrast, meta-ecosystems with symmetric ecosystem sizes had the same α- and β- diversity, as well ecosystem function, of their disconnected counterpart, attesting that resource flows had an effect only when happening between ecosystems of different size. Therefore, how ecosystem size distribution affects biodiversity can be modulated by resource flows, highlighting how cross-ecosystem dynamics can affect local community composition.

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 reason why larger ecosystems harbour more biodiversity is still an ongoing field of research (Warren et al., 2022) and the individual roles of different processes (e.g., speciation, dispersion) shaping this pattern are still being 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). This phenomenon by which larger ecosystems have lower extinction rates and thus higher richness is the subject of 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 species richness which allows them to use resources more efficiently (complementarity effects) (Delong & Gibert, 2019).

Spatial flows 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 another factor known to affect 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). Resource flows can also change ecosystem function (e.g., Marcarelli et al., 2011; Menninger et al., 2008; Samways & Cunjak, 2015), such as, for example, by providing carbon to unproductive ecosystems (Polis & Hurd, 1996). 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 resource flows amounts and effects. 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 and ecosystem size can influence resource flows, the hypothesis that ecosystem size can influence biodiversity and ecosystem function through resource flows comes naturally. Meta-ecosystem ecology provides a useful framework to test this hypothesis, as it explicitly considers ecosystems connected by spatial flows of resources (Gounand et al., 2018; Loreau et al., 2003).

Here, we tested if and how ecosystem size mediates the influence of resource flows on biodiversity and ecosystem function using a protist microcosm experiment. We constructed two-ecosystem meta-ecosystems connected by resources flows between ecosystems following disturbance. We compared biodiversity in two-ecosystem 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). As evidence that the effects of resource flows were mediated by differences in ecosystem size, resource flows had no effect on either α- diversity, β- diversity, or ecosystem function 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 using an aquatic protist community (Altermatt et al., 2015). Specifically, we compared two-ecosystem meta-ecosystems with either symmetric or asymmetric sizes and connected by non-living resources (see Fig. 1), starting with identical initial communities. We evaluated the resource flows effect by comparing connected systems with pairs of disconnected ecosystems of the same size and symmetry properties (controls; referred to as disconnected meta-ecosystems). Our compared meta-ecosystems were of identical total size (volume: 45 ml), but symmetric meta-ecosystems consist of two ecosystems of identical size (22.5 ml), while asymmetric meta-ecosystems consist in a small ecosystem of 7.5 ml and a large ecosystem of 37.5 ml. Symmetric and asymmetric meta-ecosystems are called MMMM and SLLs, respectively, with S, M, L referring to Small, Medium, and Large ecosystems respectively and subscripts to the size of the connected ecosystem. Thus, respective disconnected controls of the resource effect were called, 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.

*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’s logistically difficult to separate living species from non-living resources, spatial flows were associated with disturbances, whose mortality effect was controlled in the disconnected 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 disconnected 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 made 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 5s 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 disconnected 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 disconnected 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 disconnected 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 asymmetric meta-ecosystems (SLLS; Fig. 2 purple solid versus dashed lines) but not in symmetric meta-ecosystems (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 disconnected 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 more 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 disconnected (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, on the presence or absence of the connection, as small ecosystems when connected to other small ecosystems were more biodiverse (dotted vs dashed brown lines in Fig. 3a, p = 0.012) than when disconnected (SS vs S). We observed a similar but weak 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 disconnected (SL vs SS). However, the results were not significant.

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 disconnected (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 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 disconnected (MM vs M), yet the effect was not significant.

**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 ecosystems with more similar communities (lower β diversity) but maintained higher biodiversity across ecosystems (higher mean α diversity) than asymmetric disconnected meta-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 were 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 impacted their α- and β- diversity by increasing the biodiversity of the small ecosystem. We could think of two ways small 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). Nutrient-wise, we always made flow the same amount of nutrients between the connected ecosystems, although in different forms (i.e., detritus, dissolved form), as we transferred the same volume. However, if there was a higher density of photosynthetic species in larger ecosystems, for instance due to slower competitive exclusion dynamics, then 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, 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.

Furthermore, our study shows how the effect of resource flows on an ecosystem’s diversity can be influenced by the size of the 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 LL). 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 the fact 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 first 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.

**Acknowledgements**

We thank Silvana Käser and Samuel Hürlemann for their valuable assistance in the lab. We also acknowledge Heng Zhang for his support in statistical analysis and Frank Pennekamp and Felix Moerman for their helpful guidance with the BEMOVI package. This project received funding from the Swiss National Science Foundation (grant no. 10030\\_197410) and the University of Zurich Research Priority Programme on Global Change and Biodiversity (URPP GCB), acquired by F.A. I.G. was supported by …

**References**

Altermatt, F., Fronhofer, E. A., Garnier, A., Giometto, A., Hammes, F., Klecka, J., Legrand, D., Mächler, E., Massie, T. M., Pennekamp, F., Plebani, M., Pontarp, M., Schtickzelle, N., Thuillier, V., & Petchey, O. L. (2015). Big answers from small worlds: A user’s guide for protist microcosms as a model system in ecology and evolution. *Methods in Ecology and Evolution*, *6*(2), 218–231. https://doi.org/10.1111/2041-210X.12312

Anderson, W. B., & Wait, D. A. (2001). Subsidized island biogeography hypothesis: Another new twist on an old theory. *Ecology Letters*, *4*(4), 289–291. https://doi.org/10.1046/j.1461-0248.2001.00226.x

Babler, A. L., Pilati, A., & Vanni, M. J. (2011). Terrestrial support of detritivorous fish populations decreases with watershed size. *Ecosphere*, *2*(7). https://doi.org/10.1890/ES11-00043.1

Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1). https://doi.org/10.18637/jss.v067.i01

Bray, R. J., & Curtis, J. T. (1957). An Ordination of the Upland Forest Communities of Southern Wisconsin. *Ecological Monographs*, *27*(4), 325–349.

Cortes, C., Vapnik, V., & Saitta, L. (1995). Support-Vector Networks. *Machine Learning*, *20*, 273–297.

Del Vecchio, S., Jucker, T., Carboni, M., & Acosta, A. T. R. (2017). Linking plant communities on land and at sea: The effects of Posidonia oceanica wrack on the structure of dune vegetation. *Estuarine, Coastal and Shelf Science*, *184*, 30–36. https://doi.org/10.1016/j.ecss.2016.10.041

Delong, J. P., & Gibert, J. P. (2019). Larger area facilitates richness-function effects in experimental microcosms. *American Naturalist*. https://doi.org/10.5061/dryad.48cn500

Dimitriadou, E., Hornik, K., Leisch, F., Meyer, D., & Maintainer, A. W. (2006). *Misc Functions of the Department of Statistics (e1071), TU Wien*.

Fahrig, L. (2003). Effects of Habitat Fragmentation on Biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, *34*, 487–515. https://doi.org/10.1146/annurev.ecolsys.34.011802.132419

Forster, J. R. (1778). *Observations made during a voyage round the world*. University of Hawaii Press. https://doi.org/10.5962/bhl.title.50538

Fukami, T. (2004). Assembly history interacts with ecosystem size to influence species diversity. *Ecology*, *85*(12), 3234–3242. https://doi.org/10.1890/04-0340

Gilbert, B., & Levine, J. M. (2017). Ecological drift and the distribution of species diversity. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1855). https://doi.org/10.1098/rspb.2017.0507

Gounand, I., Harvey, E., Ganesanandamoorthy, P., & Altermatt, F. (2017). Subsidies mediate interactions between communities across space. *Oikos*, *126*(7), 972–979. https://doi.org/10.1111/oik.03922

Gounand, I., Little, C. J., Harvey, E., & Altermatt, F. (2018). Cross-ecosystem carbon flows connecting ecosystems worldwide. *Nature Communications*, *9*(1), 4825. https://doi.org/10.1038/s41467-018-07238-2

Gratton, C., & Vander Zanden, M. J. (2009). Flux of aquatic insect productivity to land: Comparison of lentic and lotic ecosystems. *Ecology*, *90*(10), 2689–2699. https://doi.org/10.1890/08-1546.1

Gravel, D., Guichard, F., Loreau, M., & Mouquet, N. (2010). Source and sink dynamics in meta-ecosystems. *Ecology*, *91*(7), 2172–2184. https://doi.org/10.1890/09-0843.1

Gravel, D., Mouquet, N., Loreau, M., & Guichard, F. (2010). Patch dynamics, persistence, and species coexistence in metaecosystems. *American Naturalist*, *176*(3), 289–302. https://doi.org/10.1086/655426

Hanski, I., & Ovaskainen, O. (2000). The metapopulation capacity of a fragmented landscape. *Nature*, *404*(6779), 755–758. https://doi.org/10.1038/35008063

Harvey, E., Gounand, I., Fronhofer, E. A., & Altermatt, F. (2018). Disturbance reverses classic biodiversity predictions in river-like landscapes. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1893). https://doi.org/10.1098/rspb.2018.2441

Harvey, E., Gounand, I., Fronhofer, E. A., & Altermatt, F. (2020). Metaecosystem dynamics drive community composition in experimental, multi-layered spatial networks. *Oikos*, *129*(3), 402–412. https://doi.org/10.1111/oik.07037

Hocking, M. D., & Reimchen, T. E. (2009). Salmon species, density and watershed size predict magnitude of marine enrichment in riparian food webs. *Oikos*, *118*(9), 1307–1318. https://doi.org/10.1111/j.1600-0706.2009.17302.x

Hocking, M. D., & Reynolds, J. D. (2011). Impacts of Salmon on Riparian Plant Diversity. *Science*, *331*(6024), 1609–1612. https://doi.org/10.1126/science.1201079

Kallimanis, A. S., Mazaris, A. D., Tzanopoulos, J., Halley, J. M., Pantis, J. D., & Sgardelis, S. P. (2008). How does habitat diversity affect the species-area relationship? *Global Ecology and Biogeography*, *17*(4), 532–538. https://doi.org/10.1111/j.1466-8238.2008.00393.x

Knoll, L. B., Vanni, M. J., & Renwick, W. H. (2003). Phytoplankton primary production and photosynthetic parameters in reservoirs along a gradient of watershed land use. *Limnology and Oceanography*, *48*(2), 608–617. https://doi.org/10.4319/lo.2003.48.2.0608

LeCraw, R. M., Romero, G. Q., & Srivastava, D. S. (2017). Geographic shifts in the effects of habitat size on trophic structure and decomposition. *Ecography*, *40*(12), 1445–1454. https://doi.org/10.1111/ecog.02796

Loreau, M., Daufresne, T., Gonzalez, A., Gravel, D., Guichard, F., Leroux, S. J., Loeuille, N., Massol, F., & Mouquet, N. (2013). Unifying sources and sinks in ecology and Earth sciences. *Biological Reviews*, *88*(2), 365–379. https://doi.org/10.1111/brv.12003

Loreau, M., Mouquet, N., & Holt, R. D. (2003). Meta-ecosystems: A theoretical framework for a spatial ecosystem ecology. *Ecology Letters*, *6*(8), 673–679. https://doi.org/10.1046/j.1461-0248.2003.00483.x

Luo, M., Wang, S., Saavedra, S., Ebert, D., & Altermatt, F. (2022). Multispecies coexistence in fragmented landscapes. *Proceedings of the National Academy of Sciences*, *119*(37). https://doi.org/10.1073/pnas.2201503119

MacArthur, R. H., & Wilson, E. O. (1963). An Equilibrium Theory of Insular Zoogeography. *Evolution*, *17*(4), 373–387. https://doi.org/10.2307/2407089

MacArthur, R. H., & Wilson, E. O. (1967). *The Theory of Island Biogeography*. Princeton University Press. https://doi.org/10.1515/9781400881376

Marcarelli, A. M., Baxter, C. V., Mineau, M. M., & Hall, R. O. (2011). Quantity and quality: Unifying food web and ecosystem perspectives on the role of resource subsidies in freshwaters. *Ecology*, *92*(6), 1215–1225. https://doi.org/10.1890/10-2240.1

Marleau, J. N., & Guichard, F. (2019). Meta-ecosystem processes alter ecosystem function and can promote herbivore-mediated coexistence. *Ecology*, *100*(6), 1–11. https://doi.org/10.1002/ecy.2699

Marleau, J. N., Guichard, F., & Loreau, M. (2014). Meta-ecosystem dynamics and functioning on finite spatial networks. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1777). https://doi.org/10.1098/rspb.2013.2094

Matias, M. G., Underwood, A. J., Hochuli, D. F., & Coleman, R. A. (2010). Independent effects of patch size and structural complexity on diversity of benthic macroinvertebrates. *Ecology*, *91*(7), 1908–1915. https://doi.org/10.1890/09-1083.1

Menninger, H. L., Palmer, M. A., Craig, L. S., & Richardson, D. C. (2008). Periodical cicada detritus impacts stream ecosystem metabolism. *Ecosystems*, *11*(8), 1306–1317. https://doi.org/10.1007/s10021-008-9194-4

Obrist, D. S., Fitzpatrick, O. T., Brown, N. E. M., Hanly, P. J., Nijland, W., Reshitnyk, L. Y., Wickham, S. B., Darimont, C. T., Reynolds, J. D., & Starzomski, B. M. (2022). Scale-dependent effects of marine subsidies on the island biogeographic patterns of plants. *Ecology and Evolution*, *12*(9), e9270. https://doi.org/10.1002/ece3.9270

Obrist, D. S., Hanly, P. J., Kennedy, J. C., Fitzpatrick, O. T., Wickham, S. B., Ernst, C. M., Nijland, W., Reshitnyk, L. Y., Darimont, C. T., Starzomski, B. M., & Reynolds, J. D. (2020). Marine subsidies mediate patterns in avian island biogeography. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1922). https://doi.org/10.1098/rspb.2020.0108

Peller, T., Marleau, J. N., & Guichard, F. (2022). Traits affecting nutrient recycling by mobile consumers can explain coexistence and spatially heterogeneous trophic regulation across a meta‐ecosystem. *Ecology Letters*, *25*(2), 440–452. https://doi.org/10.1111/ele.13941

Pennekamp, F., & Schtickzelle, N. (2013). Implementing image analysis in laboratory-based experimental systems for ecology and evolution: A hands-on guide. *Methods in Ecology and Evolution*, *4*(5), 483–492. https://doi.org/10.1111/2041-210X.12036

Pennekamp, F., Schtickzelle, N., & Petchey, O. L. (2015). BEMOVI, software for extracting behavior and morphology from videos, illustrated with analyses of microbes. *Ecology and Evolution*, *5*(13), 2584–2595. https://doi.org/10.1002/ece3.1529

Polis, G. A., & Hurd, S. D. (1996). Linking marine and terrestrial food webs: Allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. *American Naturalist*, *147*(3), 396–423. https://doi.org/10.1086/285858

Ren, H., Svenning, J. C., Mi, X., Lutz, J. A., Zhou, J., & Ma, K. (2022). Scale-dependent species–area relationship: Niche-based versus stochastic processes in a typical subtropical forest. *Journal of Ecology*, *110*(8), 1883–1895. https://doi.org/10.1111/1365-2745.13924

Sabo, J. L., Finlay, J. C., Kennedy, T., & Post, D. M. (2010). The Role of Discharge Variation in Scaling of Drainage Area and Food Chain Length in Rivers. *Science*, *330*(6006), 965–967. https://doi.org/10.1126/science.1196005

Samways, K. M., & Cunjak, R. A. (2015). Increases in benthic community production and metabolism in response to marine-derived nutrients from spawning Atlantic salmon (Salmo salar). *Freshwater Biology*, *60*(8), 1647–1658. https://doi.org/10.1111/fwb.12597

Shannon, C. E. (1948). A Mathematical Theory of Communication. *The Bell System Technical Journal*, *27*(3), 379–423.

Valente, L., Phillimore, A. B., Melo, M., Warren, B. H., Clegg, S. M., Havenstein, K., Tiedemann, R., Illera, J. C., Thébaud, C., Aschenbach, T., & Etienne, R. S. (2020). A simple dynamic model explains the diversity of island birds worldwide. *Nature*, *579*(7797), 92–96. https://doi.org/10.1038/s41586-020-2022-5

Wang, S., & Altermatt, F. (2019). Metapopulations revisited: the area-dependence of dispersal matters. *Ecology*, *100*(9). https://doi.org/10.1002/ecy.2792

Warren, R. J., Costa, J. T., & Bradford, M. A. (2022). Seeing shapes in clouds: the fallacy of deriving ecological hypotheses from statistical distributions. *Oikos*, *2022*(11). https://doi.org/10.1111/oik.09315

Williams, C. B. (1943). Area and the number of species. *Nature*, *152*(3853), 264–267. https://doi.org/10.1038/152264a0

Wilson, E. O. (1961). The Nature of the Taxon Cycle in the Melanesian Ant Fauna. *The American Naturalist*, *95*(882), 169–193. https://doi.org/10.1086/282174

Wright, D. H. (1983). Species-Energy Theory: An Extension of Species-Area Theory. *Oikos*, *41*(3), 496. https://doi.org/10.2307/3544109

Yang, X., Wang, Y., Xu, Q., Liu, W., Liu, L., Wu, Y., Jiang, L., & Lu, J. (2021). Soil fertility underlies the positive relationship between island area and litter decomposition in a fragmented subtropical forest landscape. *CATENA*, *204*, 105414. https://doi.org/10.1016/j.catena.2021.105414

**Figure legends**

Figure 1: A protist microcosm experiment was used to study whether differences in ecosystem size can affect biodiversity through resource flows. We compared two-ecosystem meta-ecosystems with reciprocal resource flows compared to systems without resource flows. Meta-ecosystem 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 disconnected ecosystems treatments were crossed with two levels of disturbance, low and high, and each treatment 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 disconnected meta-ecosystems (SL).

(c) lower γ diversity during the experiment. For meta-ecosystems, dots represent means across replicates. For “disconnected”, dots represent the mean of all possible combinations of these disconnected ecosystems assembled as virtual meta-ecosystems with the respective ecosystem size structure. Tot biomass: total 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 scientific experiment

Description automatically generated

Figure 1.

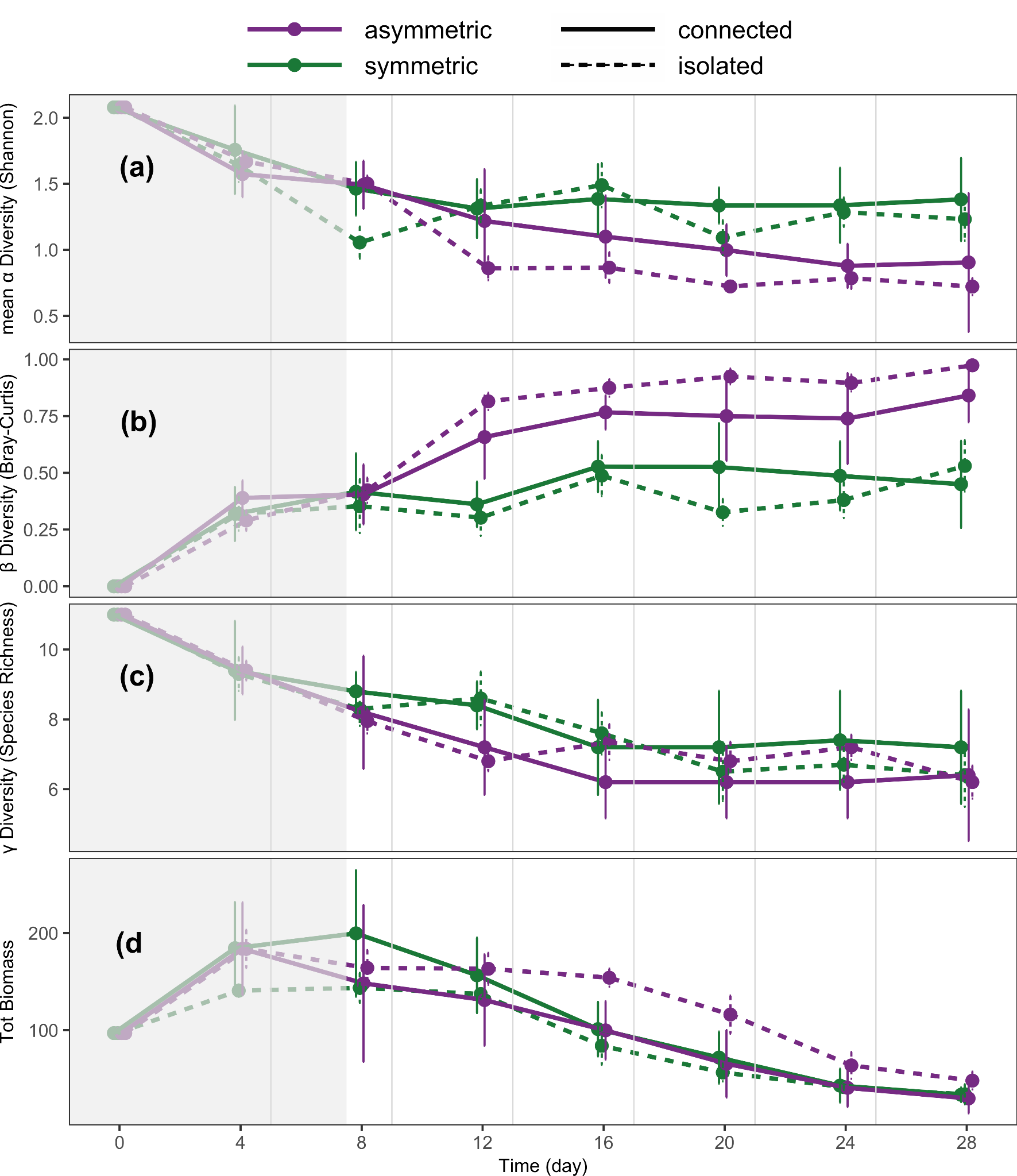


Figure 2.

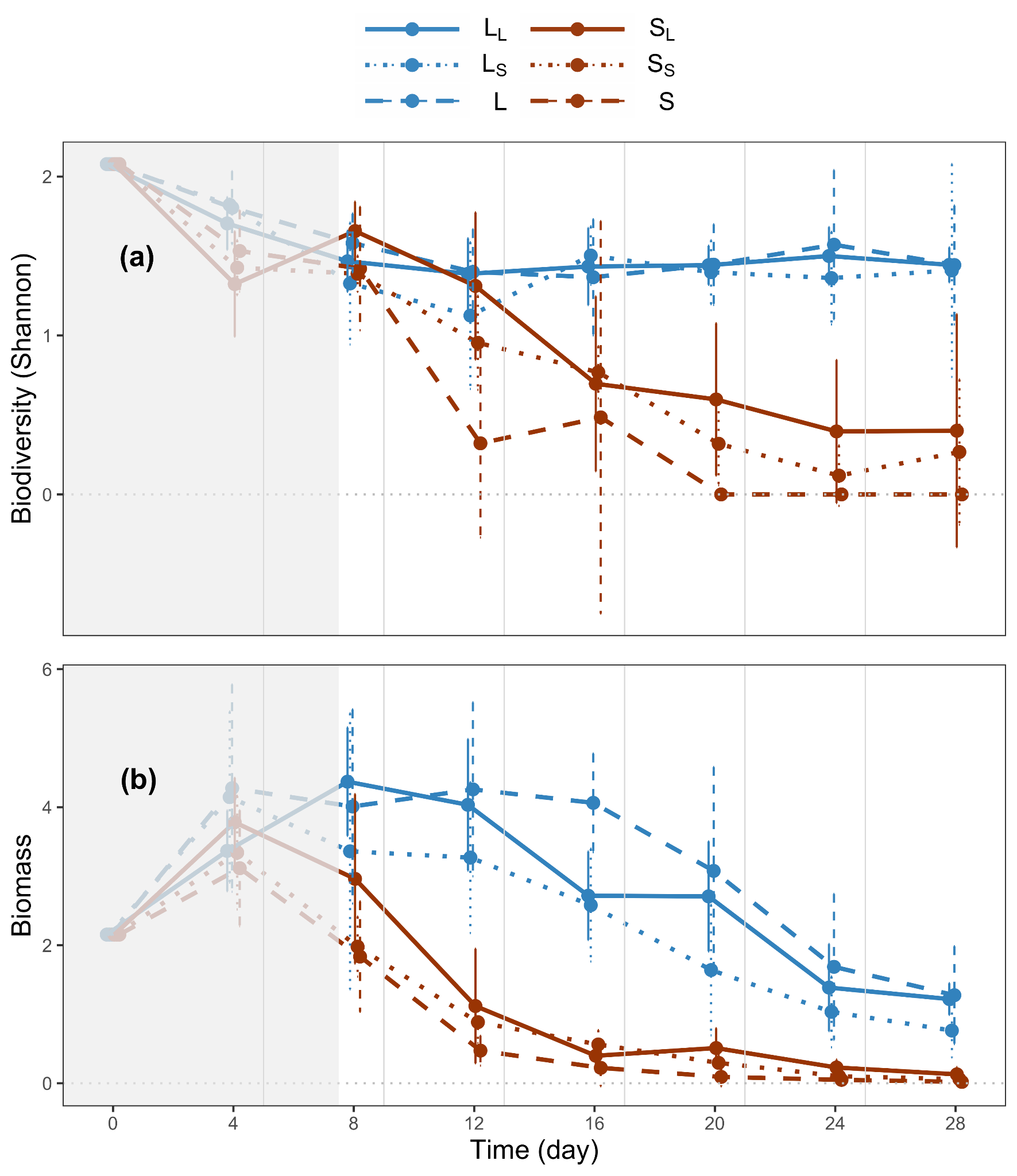


Figure 3.

**Appendix S1 Experimental design: volume balance**

During the experiment, we had to adapt to keep the volume of ecosystems constant. The first way we adapted was by changing the way we boiled ecosystems. For the first three disturbances, we boiled 15 tubes in a rack at 800 W for three minutes, which we noticed made evaporate ecosystems on a mean of 2.43 ml (SD = 0.87) per boiling event. To reduce evaporation loss, the last three disturbances were carried out by boiling four tubes for one minute, reducing evaporation to a mean of 1.25 (SD = 0.37) ml per tube per time point.

The second way we counteracted volume loss was by replenishing with medium the sampled volume. Three days before each sampling day, we added medium with the same volume we would have sampled (0.2 ml). We did not do it for the last sampling.

The third way we counteracted volume loss was 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 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.

Furthermore, a large evaporation which we did not anticipate happened to five high-level disturbance ecosystems during the first disturbance (two SLLS and one large ecosystem of a SLLS). Instead of being microwaved with other tubes containing also liquids, the tubes containing the material of these five ecosystems were microwaved with ten empty tubes. Adding 3.15 ml of water (right before the second resource exchange) compensated the higher evaporation to these tubes. We also microwaved these tubes with other filled tubes for the next disturbance events.

**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 jittered 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 disconnected. 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 disconnected 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 a 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 disconnected 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 a 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

Description automatically generated

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 disconnected 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 disconnected 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 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 slightly jittered to improve figure clarity.

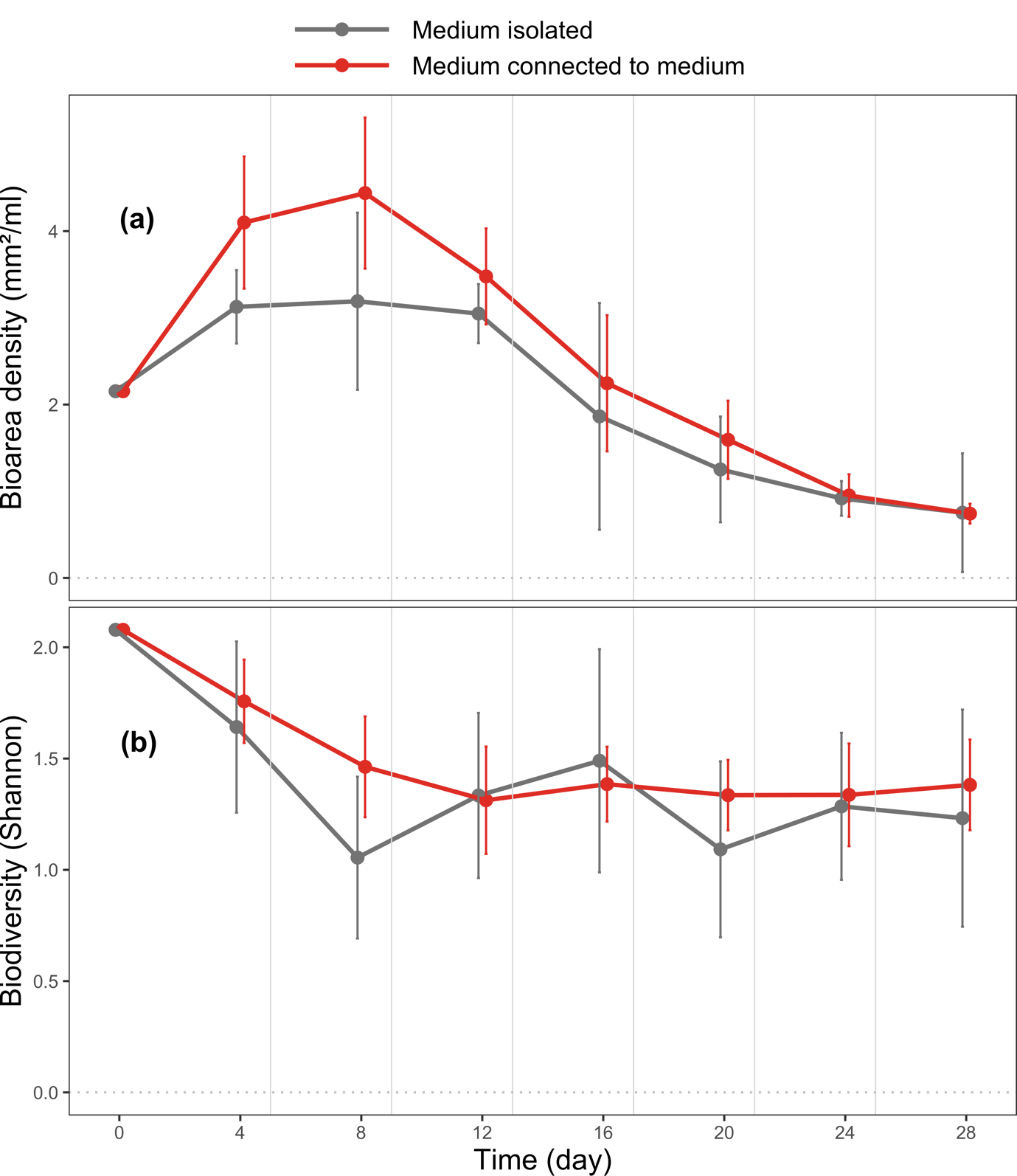


Figure S8. The connection with another medium ecosystem made medium ecosystems sustain (a) higher biodiversity and (b) higher biomass density. Dots represent means across replicates; error bars represent 95 % confidence intervals; vertical grey lines represent disturbance events followed by resource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

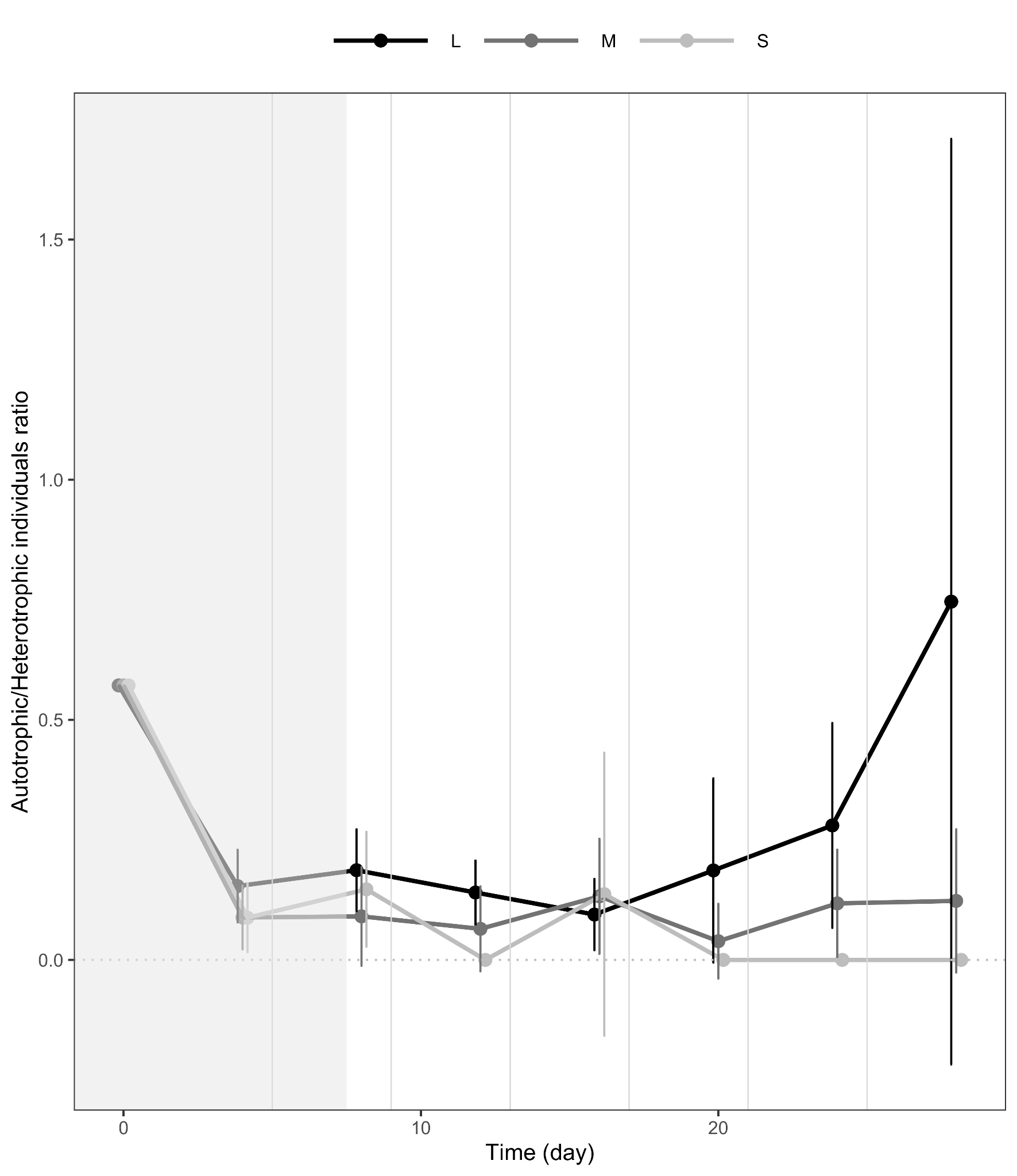


Figure S9. Larger ecosystems were denser with autotrophic individuals. P = 0.008, interaction with time.

**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 |

**Comments for co-authors**

* Figure 2. The labels are really small. Options are
  + I take off the words in parentheses (I would go for this one)
  + I put total biomass in another figure
  + We keep it like this
* Figure 3. I made this figure but not shown it to Tianna and Isabelle yey. I think the labels and lines are readable. Do you agree?
* *Figure 4.* I removed figure 4, as suggested by Isabelle, as the difference in biomass and productivity between small and large ecosystems can be shown when we show that resource flow had an effect.
* *Discussion 1st paragraph.* I changed the first paragraph of the discussion, as we now don’t compare SLLS vs MMMM but we compare (i) SLLS vs SL and (ii) MMMM vs MM.
* *Discussion possible other explanations paragraph.*Took off as I thought it was not that useful.
* *AIC.* I took off AIC as we didn’t mention it in the results (we selected the full or reduced model according to their p values).
* Ecosystem instead of ecosystem.
* Terms we agreed on with Isablle and Tianna:
  + Disconnected instead of isolated.
  + Symmetric
  + Biomass
  + Disconnected vs connected asymmetric meta-ecosystems. This allows us to refer to them as connected and disconnected meta-ecosytems.
* Discussion needs to be finished.
  + This needs to be expanded. *“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.“*