Patch size mediates the effects of resource flow on biodiversity at different scales.

\*, , , †

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: [EmanueleGiacomuzzo@gmail.com](mailto:EmanueleGiacomuzzo@gmail.com) +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): 127
* Number of words in the main text (excluding abstract, acknowledgements, references, table, and figure legends): 4289
* Number of words in each text box: no text box
* Number of figures: 4
* Number of references: 49
* Number of figures, tables, and text boxes: 4

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**

Patch size is a key factor driving biodiversity. Because it influences dispersal, ecologists have long acknowledged patch size as a crucial factor for the biodiversity of multi-patch systems. However, we don't know if patch size can affect the biodiversity of multi-patch systems also through exchanges of non-living resources (e.g., leaf litter, nutrients, and carcasses). Here, we investigate the effects of patch size asymmetry on the biodiversity of two patches exchanging non-living resources (i.e., meta-ecosystems). We did this by using a protist microcosm experiment. We found that meta-ecosystems with asymmetric patch sizes had higher β diversity but lower α and γ diversity than meta-ecosystems with symmetric patch sizes. Our findings demonstrate that patch size can affect biodiversity not only through dispersal but also through resource flow.

Keywords (max 10): homogenisation, differentiation, detritus, nutrients, scaling, subsidies, allochthonous input, disturbance, conservation, landscape

**Introduction**

Patch size is a key factor driving biodiversity. Ecologists have known for a long time that larger ecosystems harbour more biodiversity (species-area relationship) (Matthews et al., 2021). 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). Since then, we detected how larger ecosystems harbour a higher biodiversity of plants (Crawley & Harral, 2001), animals (Rahbek, 1997), and even bacteria (Horner-Devine et al., 2004). The reason why larger ecosystems harbour more biodiversity is still an ongoing field of research (Warren et al., 2022). The main explanation for the phenomenon has been that larger ecosystems have more colonisation, as they have more immigration (Baguette et al., 2000; Hill et al., 1996; Kareiva, 1985), and less extinction, as they have less emigration (Baguette et al., 2000; Hill et al., 1996; Kareiva, 1985; Kindvall, 1999; McPeek & Holt, 1992; Poethke & Hovestadt, 2002; Turchin, 1986). This explanation comes from the study of biodiversity on islands, which we call Island Biogeography Theory (MacArthur & Wilson, 1963, 1967). Among explanations other than migration, larger ecosystems should have more species because they have more habitat types where each species can find its niche (ref) and less ecological drift (Orrock & Watling, 2010), making it less likely for rare populations to go extinct.

Additionally, it's not just the size of an individual patch that drives its biodiversity. Also, the size of multiple patches plays a crucial role in driving their biodiversity. First of all, the larger the total size of those ecosystems the more biodiversity persists (Tilman et al., 1994). This is why we see that habitat loss decreases biodiversity (Pimm & Raven, 2000). Second of all, the relative size of those ecosystems can also influence biodiversity. This influence of the relative size of ecosystems on biodiversity stems from research that happened in the context of natural reserve design (Diamond, 1975). Ecologists and conservation scientists are interested in knowing whether a single large or several small ecosystems harbour more biodiversity (Fahrig et al., 2022). The size of ecosystems determines their biodiversity, with their fragmentation having positive or negative effects on biodiversity possibly according to how much species disperse, how heterogeneous patches are, and how important is for population persistence to spread their extinction risk across multiple patches (Fahrig et al., 2022).

However, researchers studying the impact of patch size on the biodiversity of multiple patches have only focused on how ecosystems are connected through dispersal. They ignored an additional connection among ecosystems which drives biodiversity: the spatial flows of non-living resources (herein, "resource flows"). Examples of non-living resources are leaf litter, carcasses, and inorganic nutrients. Ecosystems worldwide are connected through resource flows (Gounand et al., 2018). We know that resource flows can have either positive or negative effects on biodiversity. For example, the biodiversity of plants on sand dunes in Sardinia can be increased when they receive algal wrack from the sea (Del Vecchio et al., 2017). In contrast, the plant biodiversity of rainforests in British Columbia can be decreased when they receive algal wrack (Obrist et al., 2022) or salmon carcasses (Hocking & Reynolds, 2011) from the ocean. We also know that patch size can influence resource flow. For example, the size of a body of water regulates the amount of resources that leave it. The larger a lake or a river, the more insects emerge from it per perimeter metre (Gratton & Vander Zanden, 2009). Similarly, the size of a river watershed determines the effects of resource inflow. The larger a watershed, the less it gets fertilised by salmon carcasses (Hocking & Reimchen, 2009). As resource flows can influence biodiversity and patch size can influence resource flows, the hypothesis that patch size influences biodiversity through resource flows comes naturally.

Here, we test if patch size can mediate the influence of resource flows on biodiversity using a protist microcosm experiment (Altermatt et al., 2015). We constructed two-patch systems in which resources were exchanged between patches following disturbance, creating what we refer to as meta-ecosystems (Loreau et al., 2003). No dispersal between patches occurred. We compared meta-ecosystems with the same total volume but with patches of equal size (i.e., two medium-sized patches) or different sizes (i.e., one small and one large patch). Our findings revealed that patch size asymmetry had a significant influence on biodiversity. Meta-ecosystems with asymmetric patch sizes exhibited higher β diversity but lower mean α and γ diversity compared to meta-ecosystems where patches were of the same size. Additionally, we found that patch size asymmetry played a crucial role in shaping biodiversity and biomass at a local level (i.e., single patches). We were able to isolate the effect of resource flow on the patterns we observed by comparing Small-Large meta-ecosystems to systems made of one small and one large isolated patch (Small-Large isolated). This revealed that resource flow counteracts the effects of patch size per (which is the effects of patch size if the patches were to be isolated). It was attested by Small-Large meta-ecosystems having higher mean α diversity but lower β diversity than Small-Large isolated. Ultimately, our study suggests that we might be asking the wrong question. Asking how the size of ecosystems of the same type (e.g., forest) influences biodiversity through dispersal might not be enough. Instead, a better question might be asking how the size of ecosystems of different types (e.g., forests and lakes) influences biodiversity through its effects on both resource flow and dispersal.

**Materials and methods**

*Experimental design*

We studied how patch size mediates the effect of resource flows on biodiversity using a protist microcosm experiment (Altermatt et al., 2015). Specifically, our experiment involved creating meta-ecosystems consisting of two patches exchanging non-living resources. For a graphical representation of our experimental design, see Fig. 1. We studied two main meta-ecosystems, both with a total volume of 45.0 ml, but with different patch sizes. The first meta-ecosystem, named Small-Large, had a small patch (7.5 ml) and a large patch (37.5 ml). The second meta-ecosystem, named Medium-Medium, had two medium-sized patches of identical size (22.5 ml). Each meta-ecosystem consisted of two protist cultures. No organism dispersed, as during resource flow everything inside the material transferred between patches was killed (see Disturbance & resource flow section). As we observed that part of the cultures evaporated, we added water and medium regularly to keep the volume of cultures consistent (see Appendix S1 in Supporting Information).

To determine the effects of resource flow, we created isolated patches (Fig. 1). Isolated patches, including small (7.5 mL), medium (22.5 mL), and large (37.5 mL) sizes, generated resources which were then poured back into the patch that they generated from. From these isolated patches, we derived systems consisting of two isolated patches, which we refer to as two-patch isolated systems. Each "Small-Large isolated" was constructed with one small and one large isolated patch. Each "Medium-Medium isolated" was constructed with two medium isolated patches (medium patches could not be identical). We could tell whether resource flow had an effect by comparing Small-Large meta-ecosystems and Small-Large isolated, or by comparing Medium-Medium meta-ecosystems and Medium-Medium isolated.

To understand the effects of the size of the connected patch, we established two control meta-ecosystems. The first consisted of two small patches (Small-Small meta-ecosystems). The second consisted of two large patches (Large-Large meta-ecosystems). To tell what the effect of the size of the connected patch was, we compared patches that were connected to either small or large patches. We did this first by comparing small patches connected to other small patches against small patches connected to large patches. Then, by comparing large patches connected to small patches against large patches connected to other large patches.

*Experimental setup*

Preparing for the experiment, we cultured 11 microbial species, which we refer to collectively as protists. These included nine water ciliates (*Euplotes aediculatus*, *Colpidium* sp., *Loxocephalus* sp., *Paramecium aurelia*, *Paramecium caudatum*, *Spirostomum* sp., *Spirostomum teres*, *Tetrahymena cf. pyriformis*, and *Blepharisma* sp.), one alga (*Euglena gracilis*), and one rotifer (*Cephalodella* sp.). We cultured protists in autoclaved bottles with standard protist medium (0.46 g of Protozoa Pellet by Carolina per L of water), two wheat seeds, and a bacterial mix (*Serratia fonticola*, *Bacillus subtilis*, and *Brevibacillus brevis*) constituting 5 % of the total culture volume. See Altermatt et al. (2015) for the protocols we used to cultivate protists.

At the start of the experiment (day zero), we created the protist community by filling a large, autoclaved bottle with equal volumes of the eleven protist species. We supplemented the bottle with a standard protist medium (15 % of the volume). We pipetted the protist community from this large bottle into 110 sterile 50 ml centrifuge tubes (SPL life sciences skirted conical centrifuge tubes, Naechon-myeon, Korea). Each tube represented a patch. We pipetted 7.5 ml, 22.5 ml, and 37.5 ml into the small, medium, and large patches, respectively. The cultures were then randomized on foam boards and kept in an incubator (memmert IPP750plus, Schwabach, Germany) at 20 °C with constant lighting for the remainder of the experiment.

*Disturbance & resource flow*

Our experiment consisted of comparing meta-ecosystems with symmetric (Medium-Medium) and asymmetric (Small-Large) patch sizes. Each meta-ecosystem consisted of two patches connected by resource flow. To connect the two patches within each meta-ecosystem through resource flow, every four days (starting on day five) we boiled a portion of the community in each patch, representing a local disturbance. We boiled this part of the community by transferring it to an external tube and then placing it in a microwave (Sharp R-202, Ostaszewo, Poland). The portion of the community was then poured into the connected patch, creating a bidirectional resource flow. To make the isolated patches comparable to meta-ecosystem patches, we also boiled part of their community, the same volume as with connected patches. In this case, however, we poured it back to the originating patch.

Each treatment was crossed with two levels of disturbance: low and high. In low-disturbance treatments, we boiled 5.25 ml of each patch; in high-disturbance patches, we boiled 6.75 ml. As a fixed volume was boiled in each patch, the smaller the patch the more it was disturbed. At low disturbance, 70 % of small patches, 23.3 % of medium patches, and 14 % of large patches were disturbed. At high disturbance, 90 % of small patches, 30 % of medium patches, and 18 % of large patches were disturbed. The effects of patch size on biodiversity were stronger when disturbance and resource flow were high, so we focused the remaining part of this paper on the high disturbance treatment. For additional details regarding the effects of patch size on meta-ecosystems in the low-disturbance treatment, please refer to Appendix S2.

*Sampling*

To determine the abundance, species identity, biomass, and characteristics of protists in each patch, every four days we took one 0.2 ml sample of each patch, which we filmed for five seconds under a dissecting microscope (Pennekamp et al., 2015; Pennekamp & Schtickzelle, 2013). Sampling started on day zero. Two exceptions were made to our sampling method. First, at the start of the experiment (day zero), we characterised communities by filming 12 samples of the cultures inside the large bottle from which they were inoculated. Second, during the last two time points (days 24 and 28), we sampled patches twice to minimise the error from detecting individuals in sparse cultures. Along with filming our treatments during the experiment, the day before day zero we filmed the protist monocultures used to assemble the experiment. This was done to construct a training dataset for species identification. We took enough videos of each monoculture to capture at least 100 individuals of each species.

*Quantifying biomass and biodiversity*

To characterise protist communities in the videos we took during sampling, we employed the R-package BEMOVI (Altermatt et al., 2015). First, we extracted moving particles' abundance and traits (e.g., speed, shape, size) in the videos. The traits were then used to filter out particles that were not protists. For example, we filtered out particles that moved too fast to be a protist. Biomass was inferred from the sum of the area of the protists, named bioarea. Biodiversity was computed in two steps. First, we identified protist species using a support vector machine model (Cortes et al., 1995) that employed all extracted traits as predictor variables and protist monocultures as a training dataset. For this, we used the r-package "e1071" (Dimitriadou et al., 2006). Second, we calculated biodiversity indices as follows. For each patch, we calculated biodiversity as Shannon Index (Shannon, 1948). For each meta-ecosystem and isolated two-patch system, we calculated mean α diversity as the mean Shannon Index among patches, β diversity as the Bray-Curtis index (Bray & Curtis, 1957) among patches, and γ diversity as the total number of species persisting at the meta-ecosystem level.

*Statistical analysis*

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, as their inclusion would hinder our understanding of the impact of disturbances and resource flow. To evaluate the influence of a predictor variable on a response variable, we followed these steps. We examined the effects of the predictor variable and its interaction with time by comparing a full model to a null model using ANOVA. The full model included as fixed effects: the predictor variable, time, and the interaction between the predictor variable and time. As random effects, it considered the impact of replicates on both the intercept and the slope of the relationship between the response variable and time, with a correlation between the intercept and slope. The null model mirrored the full model but without the predictor variable (also without its interaction with time). Similarly, we assessed the influence of the predicting variable alone (without its interaction with time) by comparing with ANOVA a reduced model with the null model. The reduced model was the same as the full model but without the interaction between the predicting variable and time.

Meta-ecosystem level: effects of patch size asymmetry

To examine the effects of patch size asymmetry on meta-ecosystems, we compared Small-Large and Medium-Medium meta-ecosystems. Our predicting variable was patch size asymmetry (symmetric vs asymmetric) and our response variables were mean α diversity, β diversity, γ diversity, and total bioarea density (the sum of the bioarea density of both patches).

Meta-ecosystem level: effects of resource flow

To examine the impact of resource flow on meta-ecosystems, we compared meta-ecosystems with isolated two-patch systems. First, Small-Large meta-ecosystems and Small-Large isolated two-patch systems. Second Medium-Medium meta-ecosystems and Medium-Medium isolated two-patch systems. For each of these two comparisons, we performed multiple comparisons iteratively, resulting in a distribution of p-values and ΔAIC. Each iteration involved two-patch isolated systems with differently combined patches (without resampling). The presented p-value and ΔAIC are the means of their respective distributions. Our predicting variable was resource flow (present vs absent) and our response variables were mean α diversity, β diversity, γ diversity, and total bioarea density.

Patch level: effects of resource flow

To investigate the effects of resource flow at a local level, we had to ask two questions. First, does resource flow among patches of the same size have an effect? We did this by comparing (i) small patches connected to small with small isolated patches and (i) large patches connected to large with large isolated patches. As a predicting variable, we used the connection of the patch (connected vs isolated). Our response variables were biodiversity (Shannon Index) and bioarea density.

Second, we asked: does the size of the connected patch have an effect? This was answered by comparing patches connected to patches of the same size to patches connected to patches of different sizes. We did this by comparing small connected to large patches to small connected to small patches and large connected to small patches to large connected to large patches. As a predicting variable, we used the size of the connected patch (same size vs different size). Also, here our response variables were biodiversity (Shannon Index) and bioarea density.

Patch level: effects of patch size per se

To investigate the impact of patch size per se, independently from resource flow, we compared small, medium, and large isolated patches. Our predicting variable was patch size (small vs medium vs large), and our response variables were biodiversity (Shannon Index) and bioarea density.

**Results**

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

At a meta-ecosystem level, patch size asymmetry influenced mean α, β, and γ diversity (Fig. 2). This was supported by comparing Small-Large meta-ecosystems and Medium-Medium meta-ecosystems. Small-Large meta-ecosystems compared to Medium-Medium exhibited higher β diversity (solid lines in Fig. 2b, strong evidence, p = 0.002), lower α diversity (solid lines in Fig. 2a, strong evidence, p = 0.003), and a lower γ diversity (solid lines in Fig. 2c, strong evidence, p = 0.004). Patch size asymmetry influenced α and β diversity by interacting with time. Despite its impact on biodiversity, patch size asymmetry did not influence meta-ecosystem total bioarea (solid lines in Fig. S6, no evidence, p > 0.1).

At a meta-ecosystem level, resources flow impacted mean α and β diversity only when happening between patches of different sizes (Fig. 2). This was supported by comparing first Small-Large meta-ecosystems to Small-Large isolated and then Medium-Medium meta-ecosystems to Medium-Medium isolated. Small-Large meta-ecosystems compared to Small-Large isolated had lower β diversity (purple lines in Fig. 2b, moderate evidence, p = 0.012) and higher mean α diversity (purple lines in Fig. 2a, moderate evidence, p = 0.019). However, there was no evidence that resource flow influenced γ diversity (purple lines in Fig. 2c, no evidence, p > 0.1). Furthermore, resource flow decreased total bioarea (purple lines in Fig. S6, strong evidence, p = 0.003). Resource flow influenced mean α diversity, β diversity, and total bioarea without interacting with time. There was no effect of resource flow between the two medium patches. This was attested by Medium-Medium isolated having the same mean α, β, γ diversity (green lines in Fig. 2, no evidence, p > 0.1), and total bioarea (green lines in Fig. S6, no evidence, p > 0.1) as Medium-Medium isolated.

*Patch level: effects of resource flow*

At a local level, resource flow affected both biodiversity and bioarea density. In Small-Large meta-ecosystems, resource flow changed the biodiversity of small patches (Fig. 3a) and the bioarea density of both small and large patches (Fig. 3b). Being connected to large patches (instead of being isolated) made small patches more biodiverse (grey vs orange lines in Fig. 3a, strong evidence, p = 0.002) and more productive (grey vs orange lines in Fig. 3b, moderate evidence, p = 0.019) than if they were isolated. In contrast, being connected to a small patch (instead of being isolated) made large patches less productive (black vs blue lines in Fig. 3a, strong evidence, p = 0.001) without affecting their biodiversity (black vs blue lines in Fig. 3a, no evidence, p > 0.1). Resource flow in Medium-Medium meta-ecosystems also impacted both the biodiversity and bioarea density of their patches. Resources flowing between medium patches made them more biodiverse (Fig. S8, weak evidence, p = 0.081) and productive (Fig. S8, weak evidence, p = 0.062) than if they were isolated.

At a local level, how a connection impacted a patch was dependent on the size of the patch it was connected to. In small patches, the connection with large patches increased biodiversity and bioarea density more than the connection with other small patches. Small patches when connected to other small patches were more biodiverse (grey solid vs dotted orange lines in Fig. S7a, moderate evidence, p = 0.012) and productive (grey solid vs dotted orange lines in Fig. S7b, weak evidence, p = 0.071) than when isolated. When connected to large patches they were even more biodiverse (solid orange vs dotted orange lines in Fig. S7a, moderate evidence, p = 0.013) and productive (solid orange vs dotted orange lines in Fig. S7b, weak evidence, p = 0.06). Time interacted with resource flow (small isolated vs small connected to small) to influence biodiversity. Time also interacted with both resource flow (small connected to small vs small isolated) and patch size (small connected to large vs small connected to small) to influence bioarea density.

In large patches, the connection with small patches decreased their bioarea density (solid blue vs solid black lines in Fig. S7b, moderate evidence, p = 0.036). This effect was only through the size of the connected patch. When large patches were connected to other large patches there was no effect on bioarea density (dotted blue vs solid blue lines in Fig. S7b, no evidence, p > 0.01).

*Patch level: effects of patch size per se*

Patch size impacted the biomass and biodiversity of isolated patches (Fig. 4). Larger patches were more biodiverse (Fig. 4a, strong evidence, p < 0.001) and productive (Fig. 4b, strong evidence, p < 0.001). The effect of patch size on biodiversity and bioarea density was influenced by time.

**Discussion**

Our microcosm experiment shows that patch size asymmetry can mediate the effects of resource flow on biodiversity. Meta-ecosystems with asymmetric patch sizes (Small-Large meta-ecosystems) maintained two patches whose biodiversity was more differentiated (higher β diversity) but maintained lower biodiversity across patches (lower mean α diversity) and sustained fewer total species (lower γ diversity) compared to meta-ecosystems with symmetric patch sizes (Medium-Medium meta-ecosystems). By isolating the effects of resource flow in shaping this pattern, we show that resource flow counteracts the effects of patch size per se. Differences in patch size per se (Small-Large vs Medium-Medium isolated) acted as a differentiating force, increasing the β diversity of patches and decreasing their mean α diversity. Resource flows between patches of different sizes (Small-Large meta-ecosystems vs Small-Large isolated) acted as a homogenising force, decreasing β diversity and decreasing mean α diversity. The observed effects in meta-ecosystems were due to patch size, as it had a stronger effect than resource flows.

When resources flowed between small and large patches in Small-Large meta-ecosystems, resource flow homogenised their biodiversity (lower β diversity) and allowed them to maintain higher biodiversity across patches (higher mean α diversity) compared to when small and large patches were isolated (Small-Large isolated). The effects of resource flow were mediated by patch size, as the biodiversity of Medium-Medium meta-ecosystems and Medium-Medium isolated was the same.

The impact of patch size on the biodiversity of multiple ecosystems has predominantly been researched in the context of its influence on dispersal. Both implicitly through the study of ecosystems of the same type (Fahrig, 2003) and explicitly by studying metapopulations (Hanski, 2015). However, ecosystems are connected also through resource flows, which can also influence biodiversity (Del Vecchio et al., 2017; Hocking & Reynolds, 2011; Obrist et al., 2020, 2022). Here, we show that patch size can influence biodiversity also through its effects on resource flow. Our results suggest that when studying how patch size influences biodiversity we might have missed a key way via which patches are connected.

Furthermore, resource flows link ecosystems of different types (Gounand et al., 2018). So far, ecologists have studied how patch size impacts ecosystems of the same type connected by dispersal. For example, we might have studied how the size of forests influences their biodiversity (Chase et al., 2020). However, ecosystems of different types can also be connected through resource flows (Gounand et al., 2018). For example, riparian forests and rivers can be connected through resource flow, as riparian forests provide leaves to streams (Marks, 2019), and streams provide forests with fish carcasses (Gende et al., 2007). Therefore, considering the size of a single ecosystem type might not be enough. Instead, we might have to consider the size of multiple ecosystem types, which are connected.

We also show that the size of meta-ecosystems can alter their biodiversity. Meta-ecosystem theory predicts that resource flow should impact biodiversity. For example, resource flow can influence the biodiversity of competitors. Resources flowing too fast from empty to occupied patches should decrease biodiversity, as they should prevent a fugitive species from persisting (Gravel et al., 2010). Or if resources are transported between two ecosystems by consumers that feed in one patch and defecate in the other should allow the coexistence of the two consumers and increase biodiversity (Peller et al., 2021). However, meta-ecosystem theory has always considered the size of ecosystems to be the same. In light of our results, we believe that integrating patch size into meta-ecosystem theory would help us further our comprehension of how resource flows shape biodiversity.

Additionally, we unravel the effects of patch size at a local level. We show that the biodiversity of a patch can depend upon the size of the connected patch, in addition to the size of the patch. We already knew that the size of a patch could change how much of an effect resource flow had on the biodiversity of such a patch. We knew that resources could have more of an impact on the biodiversity of small patches compared to the biodiversity of large patches, as attested by smaller patches having higher biodiversity of birds in tiny islands in British Columbia (Obrist et al., 2020). This is what we also found here, attested by resource flow coming from a patch of the same size changing the biodiversity of small patches (small isolated vs small connected to small) but not of large patches (large isolated vs large connected to large). Therefore, we suggest that the study of how resources change the shape of species-area relationships – subsidised island biogeography (Anderson & Wait, 2001) – should take into consideration not only the size of the focus patch but also the size of its connected patches.

Our study shows how patch size can mediate the effects of resource flow on biodiversity. However, our data does not allow us to say why. The size of ecosystems influences certain of their ecological properties. For example, larger ecosystems can have longer food chains (Post et al., 2000; Ward & McCann, 2017), a higher ratio between consumers and preys (Gravel et al., 2011; McIntosh et al., 2018), and more stability (Greig et al., 2022). These properties could all affect resource flows and their effects, giving rise to the effects we observe. One explanation is that biodiversity was influenced by the quantity of resources that small and large patches exchanged. Large patches were more productive than small patches. Another explanation could be related to stoichiometry (Elser et al., 2000) or other measures of the quality of the resources that were exchanged – e.g., the content of highly unsaturated fatty acids (Twining et al., 2016).

In conclusion, our experiment provides the first evidence that differences in patch size can affect biodiversity through resource flows. Resource exchanges are a common phenomenon, linking different ecosystem types (Gounand et al., 2018). Therefore, we expect that this phenomenon should play out in ecosystems of all sorts, everywhere, and anytime. Furthermore, it is essential to note that resources are exchanged among ecosystems of different types, which could suggest that biodiversity might be contingent upon the size of ecosystems of different types interacting with each other. This aspect is often overlooked in studies examining the effects of patch 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 ecosystems of different types surrounding it. Our study allowed us to demonstrate that patch size asymmetry can influence biodiversity through resource flows. We are optimistic that promising discoveries lie ahead, which will elucidate the mechanisms behind why patch size changes biodiversity through resource flow. The impact of patch size on biodiversity via resource flows might now be a thrilling avenue for furthering our understanding of biodiversity.

**Acknowledgements**

We thank Silvana Käser and Samuel Hürlemann for their valuable assistance in the lab. We would also like to acknowledge Heng Zhang for his support in statistical analysis and Frank Pennekamp and Felix Moerman for their helpful guidance with the BEMOVI package. Additionally, we appreciate the contribution of ChatGPT in enhancing the clarity and conciseness of the manuscript. This study was part of the project “A meta-ecosystem perspective to understand diversity, productivity and stability of ecological systems (MetaPerspect)”. 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

Baguette, M., Petit, S., & Queva, F. (2000). Population spatial structure and migration of three butterfly species within the same habitat network: consequences for conservation. *Journal of Applied Ecology*, *37*(1), 100–108. <https://doi>.org/10.1046/j.1365-2664.2000.00478.x

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.

Chase, J. M., Blowes, S. A., Knight, T. M., Gerstner, K., & May, F. (2020). Ecosystem decay exacerbates biodiversity loss with habitat loss. *Nature*, *584*(7820), 238–243. <https://doi>.org/10.1038/s41586-020-2531-2

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

Crawley, M. J., & Harral, J. E. (2001). Scale Dependence in Plant Biodiversity. *Science*, *291*(5505), 864–868. <https://doi>.org/10.1126/science.291.5505.864

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

Diamond, J. M. (1975). The island dilemma: Lessons of modern biogeographic studies for the design of natural reserves. *Biological Conservation*, *7*(2), 129–146. <https://doi>.org/10.1016/0006-3207(75)90052-X

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

Elser, J. J., Fagan, W. F., Denno, R. F., Dobberfuhl, D. R., Folarin, A., Huberty, A., Interlandi, S., Kilham, S. S., McCauley, E., Schulz, K. L., Siemann, E. H., & Sterner, R. W. (2000). Nutritional constraints in terrestrial and freshwater food webs. *Nature*, *408*(6812), 578–580. <https://doi>.org/10.1038/35046058

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

Fahrig, L., Watling, J. I., Arnillas, C. A., Arroyo-Rodríguez, V., Jörger-Hickfang, T., Müller, J., Pereira, H. M., Riva, F., Rösch, V., Seibold, S., Tscharntke, T., & May, F. (2022). Resolving the SLOSS dilemma for biodiversity conservation: a research agenda. *Biological Reviews*, *97*(1), 99–114. <https://doi>.org/10.1111/brv.12792

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

Gende, S. M., Miller, A. E., & Hood, E. (2007). The effects of salmon carcasses on soil nitrogen pools in a riparian forest of southeastern Alaska. *Canadian Journal of Forest Research*, *37*(7), 1194–1202. <https://doi>.org/10.1139/X06-318

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., Massol, F., Canard, E., Mouillot, D., & Mouquet, N. (2011). Trophic theory of island biogeography. *Ecology Letters*, *14*(10), 1010–1016. <https://doi>.org/10.1111/j.1461-0248.2011.01667.x

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

Greig, H. S., McHugh, P. A., Thompson, R. M., Warburton, H. J., & McIntosh, A. R. (2022). Habitat size influences community stability. *Ecology*, *103*(1), 1–14. <https://doi>.org/10.1002/ecy.3545

Hanski, I. (2015). Habitat fragmentation and species richness. *Journal of Biogeography*, *42*(5), 989–993. <https://doi>.org/10.1111/jbi.12478

Hill, J. K., Thomas, C. D., & Lewis, O. T. (1996). Effects of Habitat Patch Size and Isolation on Dispersal by Hesperia comma Butterflies: Implications for Metapopulation Structure. *The Journal of Animal Ecology*, *65*(6), 725. <https://doi>.org/10.2307/5671

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

Horner-Devine, M. C., Lage, M., Hughes, J. B., & Bohannan, B. J. M. (2004). A taxa-area relationship for bacteria. *Nature*, *432*(7018), 750–753. <https://doi>.org/10.1038/nature03073

Kareiva, P. (1985). Finding and Losing Host Plants by Phyllotreta: Patch Size and Surrounding Habitat. *Ecology*, *66*(6), 1809–1816. <https://doi>.org/10.2307/2937376

Kindvall, O. (1999). Dispersal in a metapopulation of the bush cricket, Metrioptera bicolor (Orthoptera: Tettigoniidae). *Journal of Animal Ecology*, *68*(1), 172–185. <https://doi>.org/10.1046/j.1365-2656.1999.00273.x

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

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

Marks, J. C. (2019). Revisiting the Fates of Dead Leaves That Fall into Streams. *Annual Review of Ecology, Evolution, and Systematics*. <https://doi>.org/10.1146/annurev-ecolsys-110218-024755

Matthews, T. J., Triantis, K. A., & Whittaker, R. J. (2021). *The Species–Area Relationship*. Cambridge University Press. <https://doi>.org/10.1017/9781108569422

McIntosh, A. R., McHugh, P. A., Plank, M. J., Jellyman, P. G., Warburton, H. J., & Greig, H. S. (2018). Capacity to support predators scales with habitat size. *Science Advances*, *4*(7). <https://doi>.org/10.1126/sciadv.aap7523

McPeek, M. A., & Holt, R. D. (1992). The Evolution of Dispersal in Spatially and Temporally Varying Environments. *The American Naturalist*, *140*(6), 1010–1027.

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

Orrock, J. L., & Watling, J. I. (2010). Local Community size mediates ecological drift and competition in metacommunities. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1691), 2185–2191. <https://doi>.org/10.1098/rspb.2009.2344

Peller, T., Andrews, S., Leroux, S. J., & Guichard, F. (2021). From Marine Metacommunities to Meta-ecosystems: Examining the Nature, Scale and Significance of Resource Flows in Benthic Marine Environments. *Ecosystems*, *24*(5), 1239–1252. <https://doi>.org/10.1007/s10021-020-00580-x

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

Pimm, S. L., & Raven, P. (2000). Extinction by numbers. *Nature*, *403*(6772), 843–845. <https://doi>.org/10.1038/35002708

Poethke, H. J., & Hovestadt, T. (2002). Evolution of density–and patch–size–dependent dispersal rates. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *269*(1491), 637–645. <https://doi>.org/10.1098/rspb.2001.1936

Post, D. M., Pace, M. L., & Hairston, N. G. Jr. (2000). Ecosystem size determines food-chain length in lakes. *Nature*, *405*, 1047–1049.

Rahbek, C. (1997). The Relationship Among Area, Elevation, And Regional Species Richness In Neotropical Birds. *The American Naturalist*, *149*(5), 875–902. <https://doi>.org/10.1086/286028

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

Tilman, D., May, R. M., Lehman, C. L., & Nowak, M. A. (1994). Habitat destruction and the extinction debt. *Nature*, *371*(6492), 65–66. <https://doi>.org/10.1038/371065a0

Turchin, P. B. (1986). Modelling The Effect of Host Patch Size on Mexican Bean Beetle Emigration. *Ecology*, *67*(1), 124–132. <https://doi>.org/10.2307/1938510

Twining, C. W., Brenna, J. T., Lawrence, P., Shipley, J. R., Tollefson, T. N., & Winkler, D. W. (2016). Omega-3 long-chain polyunsaturated fatty acids support aerial insectivore performance more than food quantity. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(39), 10920–10925. <https://doi>.org/10.1073/pnas.1603998113

Ward, C. L., & McCann, K. S. (2017). A mechanistic theory for aquatic food chain length. *Nature Communications*, *8*(1), 2028. <https://doi>.org/10.1038/s41467-017-02157-0

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

**Figure legends**

Figure 1: A protist microcosm experiment was used to study whether differences in patch size can affect biodiversity through resource flow. Bidirectional resource flows linked patches in what we call meta-ecosystems. No dispersal happened. Two meta-ecosystem types were at the centre of our analysis: one comprised of two medium-sized patches (Medium-Medium meta-ecosystem), and the other composed of one small and one large patch (referred to as Small-Large meta-ecosystem). These two meta-ecosystem types had the same total volume. Additionally, we examined the effects of resource flow by creating isolated patches that did not interact with other patches. These isolated patches served as a control for resource flow. All patches in the experiment started with the same protist community of 11 species. To create resource flow in meta-ecosystems, a fixed volume (red portion of the patch) of each patch was killed and made flow to the connected patch. We applied the same approach to isolated patches but returned the boiled material to the originating patch. It is important to note that although the volume killed in each patch was equal, the smaller the patch, the higher the percentage of disturbance compared to its overall volume. Consequently, smaller patches experienced greater disturbance compared to larger patches. The meta-ecosystems and isolated patches treatments were crossed with two levels of disturbance, low and high, and each treatment was replicated five times. Small-Small and Large-Large meta-ecosystems have been left out for clarity.

Figure 2: Meta-ecosystem patch size asymmetry influenced biodiversity. Meta-ecosystems with asymmetric patch sizes (Small-Large meta-ecosystems) sustained (a) lower mean α diversity, (b) higher β diversity, and (c) lower γ diversity during the experiment. For meta-ecosystems, dots represent means across replicates. For Small-Large isolated, dots represent the mean of all possible combinations of small and large patches. For Medium-Medium isolated, dots represent the mean of all possible combinations of medium patches. Error bars represent 95 % confidence intervals; vertical grey lines represent disturbance events followed by resource flow. All systems were sampled on the same day. Points are slightly jittered to improve figure clarity.

Figure 3: In Small-Large meta-ecosystems, the connection between small and large patches influenced single patches' (a) biodiversity and (b) bioarea density. In terms of biodiversity, the connection had only an effect on small patches. Small patches connected to large patches were more biodiverse than small isolated patches. Large patches connected to small patches were as biodiverse as large isolated patches. In terms of bioarea density, the connection had an effect on both small and large patches. Small patches connected to large patches were more productive than small isolated patches. Large patches connected to small patches were less productive than large isolated patches. 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 4: The larger the isolated patch, the higher biodiversity (a) and biomass (b) it sustained throughout the experiment. 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.

A graph of different colored lines

Description automatically generated

Figure 2.

A graph of different colored lines

Description automatically generated

Figure 3.

A graph of two people

Description automatically generated with medium confidence

Figure 4.

**Appendix S1 Experimental design: volume balance**

During the experiment, we had to adapt to keep the volume of cultures constant. The first way we adapted was by changing the way we boiled cultures. For the first three disturbances, we boiled 15 tubes in a rack at 800 W for three minutes, which we noticed made evaporate cultures 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 cultures 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 cultures with water until they reached their initial volume.

Furthermore, a large evaporation which we did not anticipate happened to five high-level disturbance cultures during the first disturbance (two Small-Large meta-ecosystems and one large patch of a Small-Large meta-ecosystem). Instead of being microwaved with other tubes containing also liquids, the tubes containing the material of these five cultures 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 patch size asymmetry*

Patch size asymmetry affected the β diversity of meta-ecosystems as at high resource flow. But unlike at high resource flow, it did not influence the α or γ diversity of meta-ecosystems (Fig. S1). This was supported by comparing Small-Large to Medium-Medium meta-ecosystems. Small-Large meta-ecosystems exhibited higher β diversity than Medium-Medium meta-ecosystems (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 flow, patch size did not affect productivity (solid lines in Fig. S2, no evidence, p > 0.1).

*Meta-ecosystem level: effects of resource flow*

As at high resource flow levels, resources flowing between small and large patches impacted their α and β diversity but not their γ diversity (Fig. S1). This was supported by comparing Small-Large meta-ecosystems and Small-Large isolated. Small-Large meta-ecosystems 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 flow, there was no evidence that the movement of resources changed productivity. Small-Large meta-ecosystems had the same total bioarea as Small-Large isolated (purple lines in S2, no evidence, p > 0.1). Resource flow interacted with time to influence α and β diversity in Small-Large systems. As at high levels of resource flow, there was no evidence for an effect of resource flow between two medium patches on mean α, β, and γ diversity (green lines in Fig. S1, no evidence, p > 0.1). Contrary to high resource flow, resource flow increased the productivity of Medium-Medium meta-ecosystems. Medium-Medium meta-ecosystems had higher bioarea density than Medium-Medium isolated (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 patch size asymmetry influenced biodiversity. Meta-ecosystems with asymmetric patch sizes (Small-Large meta-ecosystems) 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 flow. 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. Patch size asymmetry had no effect on the meta-ecosystem total bioarea. This was attested by comparing Small-Large meta-ecosystems to Medium-Medium meta-ecosystems. This was attested by Small-Large meta-ecosystems having the same bioarea as Small-Large isolated. Resource flowing between medium patches affected total bioarea density, as Medium-Medium meta-ecosystems were more productive than Medium-Medium isolated. Dots represent means across replicates; error bars represent 95 % confidence intervals; vertical grey lines represent disturbance events followed by resource flow. All systems were sampled on the same day. Points were jittered to make the figure clear.

*Patch level: effects of resource flow*

As with high resource flows, resource flow in Small-Large meta-ecosystems changed biodiversity and productivity at a local level (Fig. S3). The connection to large patches made small patches 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 patches made large patches 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 isolated. The effect of the connection on the biodiversity of large patches was not detected at high resource flows. Time interacted with the connection to influence the biodiversity of small and large patches and the biomass of large patches. Resource flow in Medium-Medium meta-ecosystems impacted only the productivity but not the biodiversity of their patches. Resources flowing between medium patches impacted their productivity but not their biodiversity. Medium patches connected to other medium patches compared to isolated medium patches 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 patch was dependent on the size of the patch it was connected to only for small patches (Fig. S3). The size of the connected patch influenced the biodiversity and productivity of the small patches. Being connected to a small instead of being isolated 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 patch 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 patches, only the connection had an effect, not the size of the connected patch. Being connected to another large patch decreased large patches' 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 patch decreased its biodiversity the same as being connected to a large patch (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 patches, time interacted with patch size and connection to influence biodiversity. In large patches, time interacted with connection to influence biodiversity and biomass.

A graph of different colored lines

Description automatically generated

Figure S3. In small patches the size of the connected patch impacted the biodiversity (a) and (b) bioarea density of a patch. In large patches the size of the connected patch did not impact neither the biodiversity (a) nor the (b) bioarea density of a patch. Dots represent means across replicates; error bars represent 95 % confidence intervals; vertical grey lines represent disturbance events. All patches 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 patch did not affect (i) the biodiversity of medium patches, but it increased their (b) bioarea density. Dots represent means across replicates; error bars represent 95 % confidence intervals; vertical grey lines represent disturbance events followed by resource flow. All systems were sampled on the same day. Points were jittered to make the figure clear.

*Patch level: effects of patch size per se*

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

A graph of different types of data

Description automatically generated with medium confidence

Figure S5. The larger the isolated patch, 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 patches 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. Patch size asymmetry had no effect on the meta-ecosystem total bioarea. This was attested by comparing Small-Large meta-ecosystems to Medium-Medium meta-ecosystems. Resource flowing between small and large patches decreased productivity. This was attested by Small-Large meta-ecosystems with a lower total bioarea than Small-Large isolated. Resource flowing between medium patches had no effect on total bioarea density, as Medium-Medium meta-ecosystems were as productive as Medium-Medium isolated. Dots represent means across replicates; error bars represent 95 % confidence intervals; vertical grey lines represent disturbance events followed by resource flow. 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 patch influenced the biodiversity (a) and (b) total bioarea of small patches. But only the (b) total bioarea of large patches. 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.

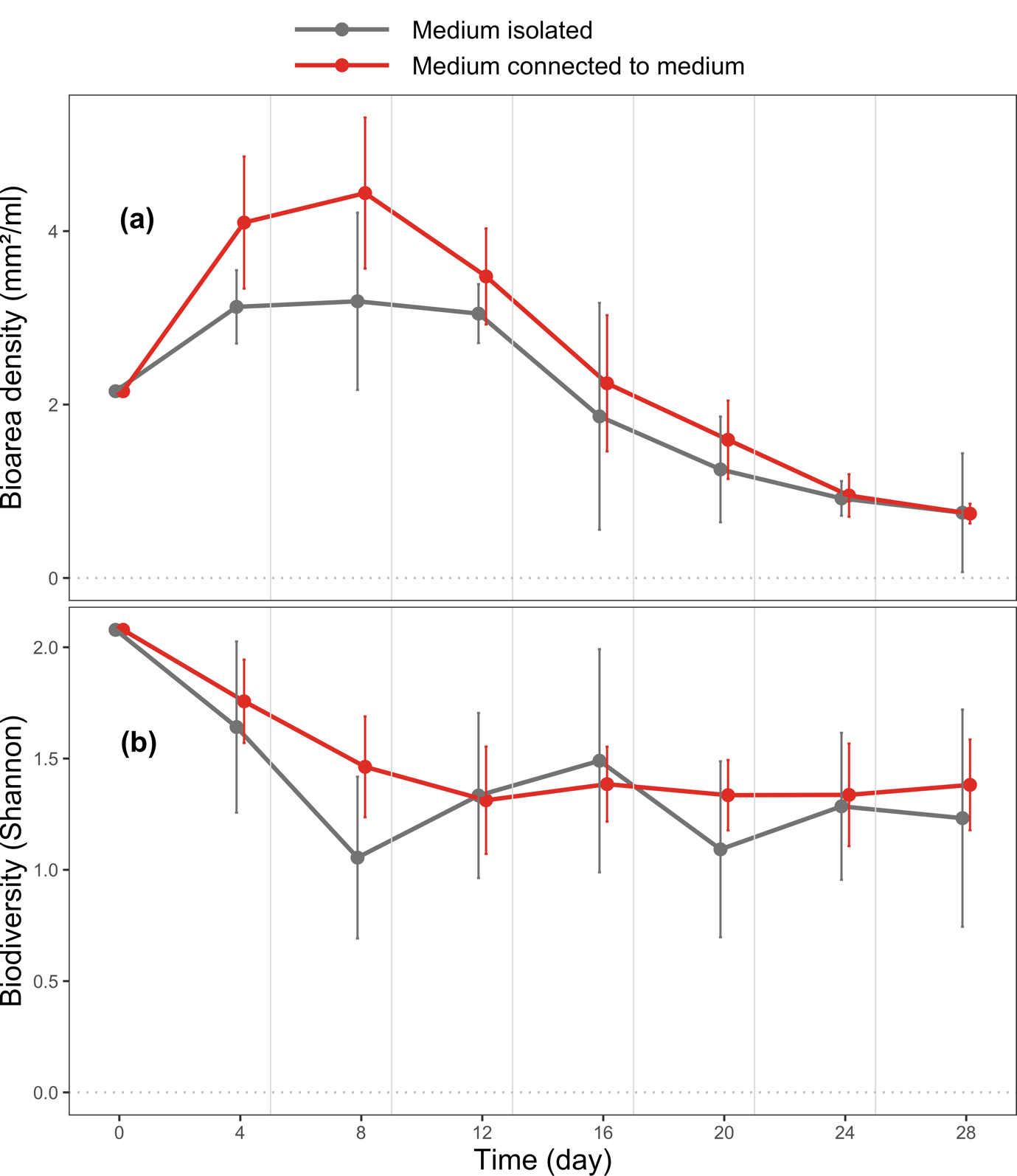


Figure S8. The connection with another medium patch made medium patches sustain (a) higher biodiversity and (b) higher bioarea density. Dots represent means across replicates; error bars represent 95 % confidence intervals; vertical grey lines represent disturbance events followed by resource flow. All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