Patch size mediates the effects of resource flows on biodiversity and productivity at different scales.

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**Abstract**

Patch size is a key factor driving biodiversity and productivity. Larger habitat patches contain more species and can be hubs of dispersal and resource flows in a network of multiple patches. However, from an ecosystem perspective mostly the identity and type of ecosystem and resource flows have been studied with respect to biodiversity and ecosystem dynamics. However, we do not know how patch size affects the biodiversity of multi-patch systems through exchanges of non-living resources. Here, we investigated the effects of patch size asymmetry on the biodiversity of two-patch meta-ecosystems connected through flows of non-living resources. We conducted highly replicated microcosm experiments, mimicking resource flows between differently sized patches of otherwise identical ecosystems. 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 and isolated ecosystems, respectively. Therefore, effects of patch size distribution on biodiversity can be modulated by resource flows, highlighting the role of cross-ecosystem dynamics affecting local community composition.

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

**Introduction**

Patch size is a key factor driving biodiversity and ecosystem function. Ecologists have known for a long time that larger patches or ecosystems harbour more biodiversity than smaller patches (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), and has been empirically and experimentally corroborated many times ever since (e. g., Baguette et al., 2000; Hill et al., 1996; Kareiva, 1985). The reason why larger patches or 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) shaping this pattern are being still debated (). 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, more niche diversity, and less ecological drift (e.g., …). This phenomenon by which larger patches have lower extinction rates and thus higher richness is the subject of extensive theoretical, comparative, and experimental extensions (e.g.,). In recent years, it has been also shown that patch size can also change ecosystem function. For example, larger patches can be more productive because they have species richness which allows them to use resources more efficiently (complementarity effects) (Delong & Gibert, 2019). Larger patches can also have higher decomposition rates because …. (LeCraw et al., 2017; Yang et al., 2021).

The impact of patch size on the biodiversity of multiple patches has mostly focused on the role of dispersal connecting systems. Concurrently, most ecosystems are also connected through spatial flows of non-living resources (e.g., leaf litter, carcasses, and inorganic nutrients ; herein, "resource flows") (Gounand et al., 2018) which is known to affect productivity and richness of ecosystems (refs). 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 flows. 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 metre of reach (Gratton & Vander Zanden, 2009). Similarly, the size of a river watershed determines the effects of resource inflow. The larger a watershed, the more diluted its fertilisation from 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. Hitherto, work on meta-ecosystem dynamics has largely focussed on systems of equal-sized ecosystems (but see Harvey et al.), thereby ignoring how differences in patch size may modulate local and regional richness and productivity through variation in patch size.

Here, we tested if and how patch size mediates the influence of resource flows on biodiversity using a protist microcosm experiment. We constructed two-patch meta-ecosystems (Loreau et al., 2003) in which resources were exchanged between patches following disturbance. We compared biodiversity and productivity in two-patch meta-ecosystems where we manipulated the relative size of local patches while keeping constant total meta-ecosystem size. We found that patch size asymmetry significantly influences biodiversity and productivity. Meta-ecosystems with asymmetric patch sizes exhibited higher β- diversity but lower productivity and 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 community composition and biomass at a local level (i.e., single patches).

**Materials and methods**

*Experimental design*

We studied how asymmetry in patch size mediates the effect of resource flows on biodiversity in meta-ecosystems using a protist microcosm experiment (Altermatt et al., 2015). Specifically, our experiment involved two-patch meta-ecosystems starting with the identical initial communities and connected by non-living resources (see Fig. 1) and respective isolated controls. We here refer to single patches with their size as a capital letter and the size of their connected patch as underscore (e.g., small connected to large = SL). Isolated single patches don’t have an underscore (e.g., small isolated = S). We refer to two-patch systems by combining their two patches notation (e.g., meta-ecosystem with a small and a large connected patches = SLLs). We studied meta-ecosystems of identical total size (45 ml), but with different patch size symmetry. In one treatment, named SLLS, patches were of different size (a small patch of 7.5 ml and a large patch of 37.5 ml). In the second treatment, named MMMM, patches were of identical size (22.5 ml). Further, we had the respective isolated controls with resource fluxes locally recycled (herein, “resource retention”). We manipulated reciprocal resource flows in the absence of dispersal.

To understand the effects of the size of the connected patch, we established two control meta-ecosystems. The first consisted of two small patches (SSSS). The second consisted of two large patches (LLLL) (see Fig. 1). 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 by comparing (i) SL and SS and then (ii) LS and LL.

*Experimental setup*

Our initial communities consisted of nine heterotrophic ciliates (*Euplotes aediculatus*, *Colpidium* sp., *Loxocephalus* sp., *Paramecium aurelia*, *Paramecium caudatum*, *Spirostomum* sp., *Spirostomum teres*, *Tetrahymena cf. pyriformis*, and *Blepharisma* sp.), one photosynthetic flagellate (*Euglena gracilis*), 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*) 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 (SPL life sciences skirted conical centrifuge tubes, Naechon-myeon, Korea), with each tube representing a patch. At the start, we pipetted 7.5 ml, 22.5 ml, and 37.5 ml of the master-mix to constitute the small, medium, and large patches, respectively. The replicates were randomized in position and kept in an incubator (Memmert IPP750plus, Schwabach, Germany) at 20 °C with constant lighting for the remainder of the experiment.

*Disturbances and* *resource flows*

We applied local disturbances associated with between-ecosystem resource flows or local recycling flows only (isolated controls). Every four days (starting on day five) we boiled a portion of the community in each patch for 30 seconds, representing a local disturbance. We investigated whether … by having two levels of disturbances, either boiling 5.25 ml of each patch (low disturbance) or boiling 6.75 ml (high disturbance). This resulted in a disturbance rate of 70 % of a small patch, 23.3 % of a medium patch , and 14 % of a large patch in the low disturbance treatment, and 90 % of a small patch , 30 % of a medium patch , and 18 % of a large patch, respectively. We boiled the respective volume in a microwave (boiling killed organisms preventing dispersal), and subsequently let it cool down to room-temperature. We then poured it back to the respective recipient patch, creating a bidirectional resource flow. In the isolated controls, the same volume was disturbed, but poured back to the originating patch to control for the mortality associated with cross-ecosystem resource flows. We here focus on the results of the high disturbance level, yet give the low disturbance level in Appendix S2. Throughout the experiment, the total volume of the patches was held constant by compensating evaporation loss with deionised water (see Appendix S1).

*Sampling*

To determine the abundance, species identity, biomass, and characteristics of protists in each patch, we took one 0.2 ml sample of each patch 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 disturbance. We took a 5s video of each sample at xx magnification, using xx camera (Pennekamp et al., 2015; Pennekamp & Schtickzelle, 2013). At the last two time points (days 24 and 28), we took two samples per patch 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). First, we extracted moving particles' traits (e.g., speed, shape, size) in the videos, using these traits to filter out particles that were not protists and obtain an average abundance of protist individuals per volume. We also measured 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. Biodiversity was computed in two steps. First, we 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. Second, we calculated local biodiversity (α-diversity, also averaged at the meta-ecosystem level) using the Shannon Index (Shannon, 1948), among-community diversity (β- diversity) as the Bray-Curtis index (Bray & Curtis, 1957), and total biodiversity (γ- diversity) as the total number of species persisting at the meta-ecosystem level.

*Statistical analysis*

To understand the effects of resource flow on biodiversity and productivity 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, as their inclusion would interfere with our understanding of the impact of disturbances and resource flows. To evaluate the influence of a predictor variable on a response variable, 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.

We used the isolated controls to create virtual meta-ecosystems (that is, pairing two patches to calculate the diversity levels, yet without having these patches connected by flows of resources). We constructed these virtual control meta-ecosystems by bootstrapping (without replacement) all possible pairs of isolated patches to compare to SLLS and MMMM

Meta-ecosystem level: effects of patch size

To examine the effects of patch size on meta-ecosystems, we compared SLLS and MMMM. Our predicting variable was patch size distribution (asymmetric vs. symmetric patch sizes) and our response variables were mean α- diversity, β- diversity, γ- diversity, and total biomass density (the sum of the biomass density of both patches).

Meta-ecosystem level: effects of resource flows

To examine the impact of resource flows on meta-ecosystems, we compared meta-ecosystems with isolated two-patch systems. First, SLLS and SL. Second MMMM and MM. 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 flows (present vs absent) and our response variables were mean α diversity, β diversity, γ diversity, and total biomass density.

Patch level: effects of resource flows

To investigate the effects of resource flows at a local level, we had to ask two questions. First, do resource flows among patches of the same size have an effect? We did this by comparing (i) SS to S and (i) LL to L.

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 (i) SL to Ss and (i) LS to LL .

Patch level: effects of patch size per se

To investigate the impact of patch size per se, independently from resource flows, we compared small, medium, and large isolated patches.

**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). Specifically, SLLS exhibited lower α diversity compared to MMMM (p = 0.002), higher β diversity (p = 0.003), and lower γ diversity (p = 0.004) across time (solid lines in Fig2, panels a, b, c,, respectively). 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 biomass (solid lines in Fig. S6, no evidence, p > 0.1).

At a meta-ecosystem level, resource flows impacted mean α and β diversity, without interacting with time, but only when happening between patches of different sizes (Fig. 2 compare solid and dotted lines). SLLS had a lower β diversity (p = 0.012) and a higher mean α diversity (p = 0.019)compared to SL pairs (purple lines in Fig. 2a and 2b, respectively). However, resource flows did not influence γ diversity (purple lines in Fig. 2c, p > 0.1). Furthermore, resource flows decreased total biomass (purple lines in Fig. S6, p = 0.003). By contrast, resource flows did not affect α, β, γ diversity and total biomass in meta-ecosystems of identical patch size (MMMM vs MM, green lines in Fig. 2, S6 p > 0.1).

*Effects of resource flows at the level of single patches*

Also at a local level, resource flows affected both biodiversity and relative biomass (biomass per volume). Being connected to large patches increased diversity in small patches (grey vs orange lines in Fig. 3a, p = 0.002) as well as biomass (grey vs orange lines in Fig. 3b, p = 0.019) than if they were isolated. In contrast, being connected to a small patch decreased biomass in large patches compared to when isolated (black vs blue lines in Fig. 3a, p = 0.001), without affecting their biodiversity (black vs blue lines in Fig. 3a, p > 0.1). We observe a weak trend of resources flow slightly increasing biodiversity (Fig. S8, p = 0.081) and biomass (Fig. S8, p = 0.062) in medium patches compared to if they were isolated, yet the effect was not significant.

The impact on a patch was also dependent on the size of the patch it was connected to. In small patches, the connection with large patches increased biodiversity and relative biomass 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, p = 0.012) and productive (grey solid vs dotted orange lines in Fig. S7b 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 , p = 0.013) and productive (solid orange vs dotted orange lines in Fig. S7b, p = 0.06). Time interacted with resource flows (S vs Ss) to influence biodiversity. Time also interacted with both resource flows (Ss vs S) and patch size (small connected to large vs Ss) to influence relative biomass.

In large patches, the connection with small patches decreased their relative biomass (solid blue vs solid black lines in Fig. S7b, p = 0.036). This effect was mediated difference in size of the patch connected to. When large patches were connected to other large patches, the effect disappeared (dotted blue vs solid blue lines in Fig. S7b, 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 relative biomass was influenced by time.~~

**Discussion**

Our microcosm experiment shows that patch size asymmetry can mediate the effects of resource flows on biodiversity. Meta-ecosystems with asymmetric patch sizes (SLLS) 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 (MMMM). By isolating the effects of resource flows in shaping this pattern, we show that resource flows counteract the effects of patch size per se. Differences in patch size per se (SL vs MM) acted as a differentiating force, increasing the β diversity of patches and decreasing their mean α diversity. Resource flows between patches of different sizes (SLLS vs SL) 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.

R esources flows between small and large patches , homogenised biodiversity (lower β diversity) in these meta-ecosystems and maintained higher biodiversity across patches (higher mean α diversity) compared to isolated systems . The effects of resource flows were mediated by patch size, and consequently there was no difference between meta-ecosystems of identical sized patches, irrespective of reciprocal resource flows or not .

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 also influence biodiversity indirectly through its effects on resource flows.

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 flows, 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 flows should impact biodiversity. For example, resource flows 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.

Finally, we unravel effects of patch size at a local level, both of the target patch, as well as the size of the patch connected to. 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 flows 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 flows coming from a patch of the same size changing the biodiversity of small patches (S vs Ss) 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 flows 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 first evidence that differences in patch size can indirectly affect biodiversity in meta-ecosystems through resource flows. As resource exchanges are a common phenomenon, we expect that this phenomenon could be of common relevance. While we demonstrated an effect of resource flows modulation of biodiversity in patches of different size yet otherwise same quality, resources are often also exchanged among ecosystems of different types, which could even agrevate the effect demonstrated. 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.

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**Figure legends**

Figure 1: A protist microcosm experiment was used to study whether differences in patch size can affect biodiversity through resource flows. We compared two-patch meta-ecosystems with reciprocal resource flows compared to systems without resource flows. Meta-ecosystem were composed either of identical or different individual patch-sizes, yet with total overall identical volume. ~~Additionally, we examined the effects of resource flow by creating isolated patches that did not interact with other patches.~~ All patches in the experiment started with the same protist community of 11 species. To create resource flows, a fixed volume (red portion of the patch) of each patch was removed, heated to kill all organisms and release the resources, and either put back to the patch (no resource flows) or reciprocally exchanged between patches (resource flows). Importantly, while the volume perturbed 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

Figure 2: Meta-ecosystem patch size asymmetry influenced biodiversity. Meta-ecosystems with asymmetric patch sizes (SLLS) 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 “isolated”, dots represent the mean of all possible combinations of these isolated patches assembled as virtual meta-communities with the respective patch size structure. 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 patches influenced single patches' (a) biodiversity and (b) relative biomass. In terms of biodiversity, the connection had only an effect on small patches. Small patches connected to large patches were more biodiverse than S patches. Large patches connected to small patches were as biodiverse as large isolated patches. In terms of biomass, the connection had an effect on both small and large patches. Small patches connected to large patches were more productive than S 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**

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Figure 1.

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Figure 2.

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Figure 3.

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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 SLLS and one large patch of a SLLS). 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 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, patch 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 patches 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 patches 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).

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Figure S1. Meta-ecosystem patch size asymmetry influenced biodiversity. Meta-ecosystems with asymmetric patch 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.

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Figure S2. Patch 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 patches 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.

*Patch 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 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 flows in MMMM 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.

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Figure S3. In small patches the size of the connected patch impacted the biodiversity (a) and (b) biomass density of a patch. In large patches the size of the connected patch did not impact neither the biodiversity (a) nor the (b) biomass 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.

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Figure S4. The connection with another medium patch did not affect (i) the biodiversity of medium patches, 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.

*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 biomass density was influenced by time.

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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**

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Figure S6. Patch 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 patches decreased productivity. This was attested by SLLS with a lower total biomass than SL. Resource flowing between medium patches 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

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Figure S7. The size of the connected patch influenced the biodiversity (a) and (b) total biomass of small patches. But only the (b) total biomass 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.

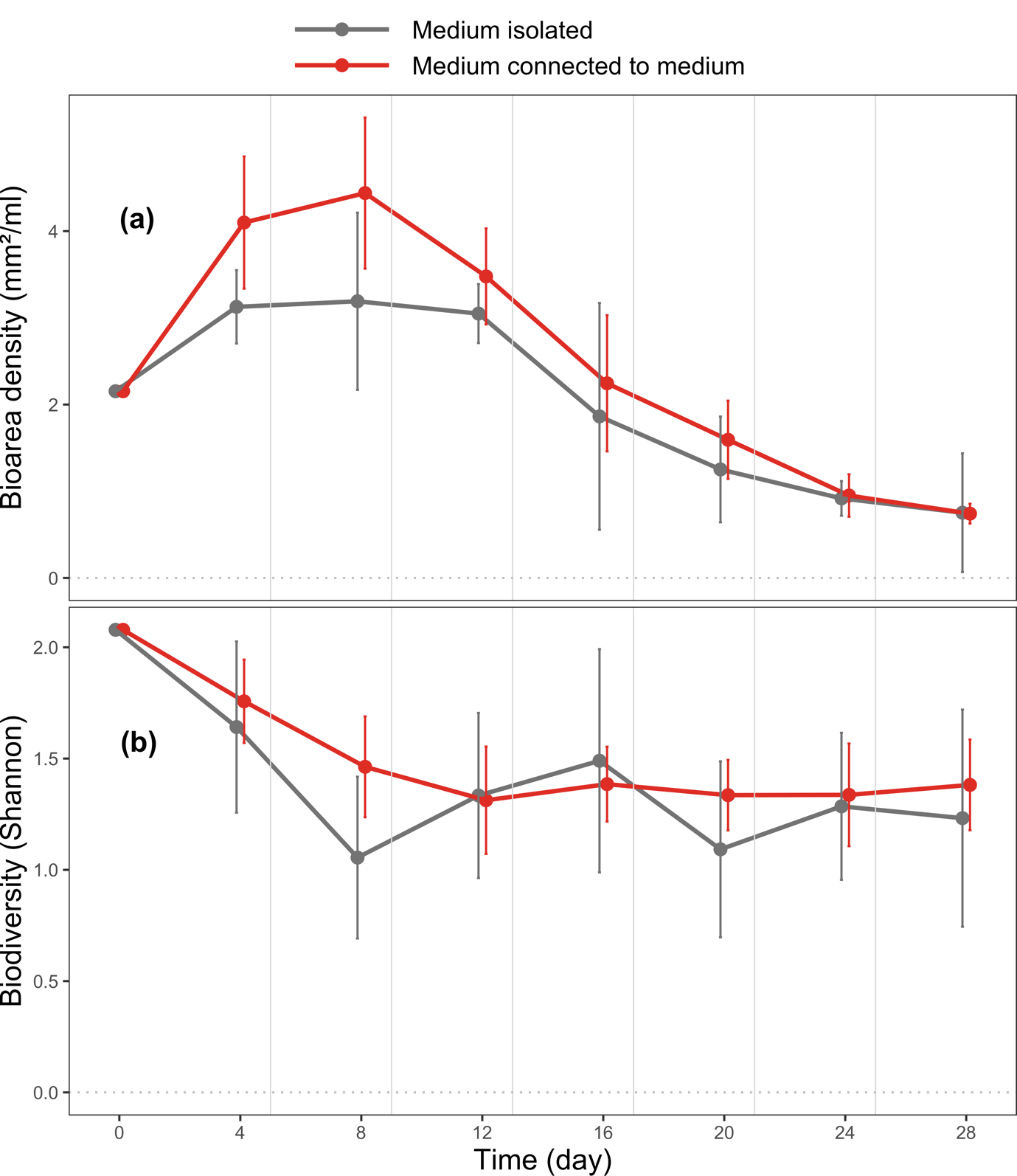


Figure S8. The connection with another medium patch made medium patches sustain (a) higher biodiversity and (b) higher biomass density. Dots represent means across replicates; error bars represent 95 % confidence intervals; vertical grey lines represent disturbance events followed by resource flows.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

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Response variable** | **Comparison** | **Full model**  **p (high disturbance)** | **Reduced model p (high disturbance)** | **Full model  p (low disturbance)** | **Full model p (low disturbance)** |
| Meta-ecosystem biomass | MMMM vs SLLS | .264 | .454 | .207 | .122 |
| SLLS vs SL | **.011 \*** | **.003 \*** | .105 | .264 |
| MMMM vs MM | .167 | .356 | .078 | **0.026** |
| Mean alpha diversity | MMMM vs SLLS | **.003 \*** | .056 | .464 | .293 |
| SLLS vs SL | .061 | **.019 \*** | **.002** | .483 |
| MMMM vs MM | .225 | .115 | .591 | .788 |
| Beta diversity | MMMM vs SLLS | **.002 \*** | **.016 \*** | .099 | .008 |
| SLLS vs SL | **.027 \*** | **.012 \*** | **.007** | .075 |
| MMMM vs MM | .469 | .333 | .308 | .236 |
| Gamma diversity | MMMM vs SLLS | **.014 \*** | **.004 \*** | .752 | .479 |
| SLLS vs SL | .449 | .318 | .432 | .737 |
| MMMM vs MM | .576 | .62 | .282 | .242 |
| Patch biomass | S vs M vs L |  |  |  |  |
| SL vs SS |  |  |  |  |
| Ss vs S |  |  |  |  |
| MM vs M |  |  |  |  |
| LS vs LL |  |  |  |  |
| LL vs L |  |  |  |  |
| Shannon Index | S vs M vs L |  |  |  |  |
| SL vs SS |  |  |  |  |
| Ss vs S |  |  |  |  |
| MM vs M |  |  |  |  |
| LS vs LL |  |  |  |  |
| LL vs L |  |  |  |  |

Meta-ecosystem models. Both the full model and the reduced model are compared to the null model.