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

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**Abstract**

Patch size is a key factor driving biodiversity. Larger habitat patches contain more species and can be hubs of dispersal and resource flows in a network of multiple patches. Yet, from an ecosystem perspective mostly the identity and type of ecosystem and resource flows have been studied with respect to biodiversity and ecosystem dynamics. ~~Because it influences dispersal, ecologists have long acknowledged patch size as a crucial factor for the biodiversity of multi-patch systems~~ It is less known if and 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. Thus, effects of patch size distribution on biodiversity can be modulated by resource flows, highlighting the role of cross-ecosystem dynamics affecting local community composition. ~~Our findings demonstrate that patch size can affect biodiversity not only through dispersal but also through resource flow.~~

Keywords: 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 patches or ecosystems harbour more biodiversity (species-area relationship) than smaller patches (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), and has been empirically and experimentally corroborated many times ever since (e.g. ). The reason why larger patches or ecosystems harbour more biodiversity is still an ongoing field of research (Warren et al., 2022), with MacArthur and Wilson’s (1963, 1967) work out outlying how extinction rates on larger islands are lower. In particular, larger ecosystems have more species because they have more habitat types and more niche diversity and less ecological drift, respectively. This results in lower extinction rates and thus higher richness, a phenomenon that has resulted in extensive theoretical, comparative and experimental extensions (e.g., ), yet the individual roles (e.g., including speciation) being still debated (). 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) .

Additionally, it is 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).

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 (herein, "resource flows") which is known to affect productivity and richness of ecosystems (refs).

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 (Altermatt et al., 2015). We constructed two-patch meta-ecosystems in which resources were exchanged between patches following disturbance (Loreau et al., 2003). We compared meta-ecosystems of the same total size but with the individual patches being either of equal size (i.e., two medium-sized patches) or different sizes (i.e., one small and one large patch). We found 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 variability 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 connected by exchanging non-living resources (see Fig. 1) and respective isolated controls. We studied meta-ecosystems of identical total size (45 ml), but with different patch size distributions. In one treatment, named Small-Large, 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 Medium-Medium, patches were of identical size (22.5 ml). Further, we had the respective isolated controls with internal (local) resource fluxes/recycling only.

Each meta-ecosystem consisted of initially identical communities of microbial organisms. We manipulated reciprocal resource flows in the absence of dispersal. 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 meta-ecosystems by bootstrapping (without replacement) all possible pairs of patches to reflect Small-Small, Small-Large, and Medium-Medium meta-ecosystems. ~~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 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*

Our focal communities consisted of nine 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.), 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. We pipetted 7.5 ml, 22.5 ml, and 37.5 ml of the master-mix into 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.

*Disturbance and resource flow*

We applied local disturbances that were then associated with between-ecosystem resource flows (vs. internal flows only). 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 had 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 ofa a ha in the low disturbance treatment, and a a a , respectively.We boiled the respective volume in a microwave, 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. 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.

*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. 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. ~~Along with filming our treatments during the experiment, the day before day zero we filmed~~ We also took videos of all protist monocultures to construct a training dataset 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). 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. We measured the total area of protists (as area per volume medium), and subsequently use this “bioarea” as a proxy of biomass, which is a fair assumption given the roundish shape of all protists. 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 local biodiversity (a-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*

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 flow. 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.

Meta-ecosystem level: effects of patch size

To examine the effects of patch size on meta-ecosystems, we compared Small-Large and Medium-Medium meta-ecosystems. 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 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.

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.

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.

**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 biomass (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. 2ap = 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 biomass (purple lines in Fig. S6, p = 0.003). Resource flow influenced mean α diversity, β diversity, and total biomass without interacting with time. There was no evidence of resource flows affecting meta-ecosystems of identical patch size (i.e., Medium-Medium). This was attested by Medium-Medium isolated having the same mean α, β, γ diversity (green lines in Fig. 2, p > 0.1), and total biomass (green lines in Fig. S6, p > 0.1) as Medium-Medium isolated.

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

Also at a local level, resource flow affected both biodiversity and relative biomass (biomass per volume). In Small-Large meta-ecosystems, resource flow changed the biodiversity of small patches (Fig. 3a) and the relative biomass 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, p = 0.002) and more productive (grey vs orange lines in Fig. 3b, 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, 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 biomass of their patches. There was weak evidence of resources flowing between medium patches made them slightly more biodiverse (Fig. S8, p = 0.081) and productive (Fig. S8, p = 0.062) than 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. S7bp = 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 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 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 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, resource flow homogenised biodiversity (lower β diversity) in these meta-ecosystems and maintained higher biodiversity across patches (higher mean α diversity) compared to isolated systems without resource flows between small and large patches . The effects of resource flow were mediated by patch size, and consequently there was no difference between meta-ecosystems of identical sized patches, irrespective of reciprocal resource flow 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 flow.

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.

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 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 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 flow 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. Our study allowed us to demonstrate that patch size asymmetry can influence biodiversity through resource flows.

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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 flow. 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). ~~killed and made flow to the connected patch~~. 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. 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 “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 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) 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 small isolated 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 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**

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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 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).

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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.

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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.

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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.

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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) 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.

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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 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.

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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.

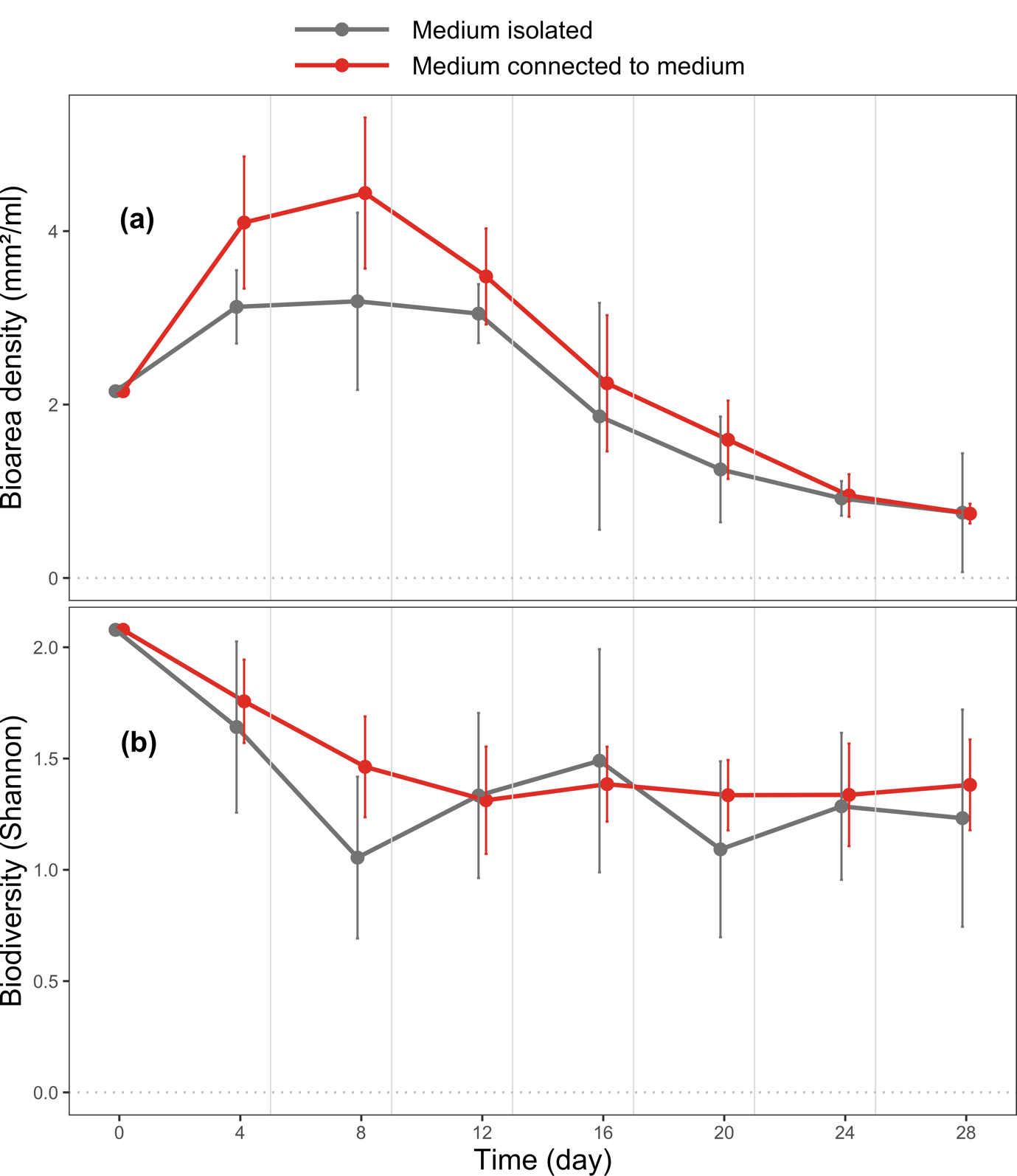


Figure S8. The connection with another medium patch made medium patches sustain (a) higher biodiversity and (b) higher bioarea density. Dots represent means across replicates; error bars represent 95 % confidence intervals; vertical grey lines represent disturbance events followed by resource flow. All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