Identifying the combined effects of patch quality and connectivity on metacommunity dynamics

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Abstract

Food webs are dynamic due to spatial and temporal heterogeneity differently affecting species and the strength of their trophic interactions. This research determines how variation in patch quality and connectivity is linked to changes in heterogeneity, and how it impacts metacommunity food web dynamics. A mathematical model was parametrised using existing community data to represent a community response to habitat quality changes, and a dispersal component was aggregated and parametrised using previous research to represent metacommunity responses to connectivity. Using this model, different combinations of patch quality and connectivity levels were tested to identify metacommunity responses. Patch quality had the strongest effect on diversity and food web metrics, while connectivity modified these effects strongly in food web metrics and metacommunity composition.

Introduction

Ecology seeks to understand the many natural processes that affect species and their interactions (Levin 2009). In a world with ever-increasing anthropogenic impacts, important areas of study in the field typically revolve around biodiversity, species interactions, and their persistence in changing environments (Loreau 2009). With rapid losses of biodiversity being observed in many environments in the world (Cardinale *et al.* 2012, Hooper *et al.* 2012), it has been shown that species interactions are very important for the maintenance of community dynamics and biodiversity (Loreau *et al.* 2003, Ives & Cardinale 2004, Thompson *et al.* 2017, Thompson & Gonzalez 2017). Food web theory (*e.g.* McCann 2012, Thompson *et al.* 2012) provides a framework to integrate the study of biodiversity to that of species interactions.

Though community dynamics are important to determine populations fluctuations and aggregate species stability (Cottingham *et al.* 2001), there is much more to an ecological system than individual communities. Communities connected through dispersal have been shown to affect each other's dynamics and biodiversity (Thompson & Gonzalez 2017, Leibold *et al.* 2004). This part of Ecology, known as metacommunity theory, is a powerful tool for better understanding the workings of ecological systems, but is relatively new and under continuous growth. Metacommunity theory combines community and spatial ecology, and its subject of study is a set of communities that are potentially interacting through species dispersal (Leibold *et al.* 2004).

Metacommunity theory has brought forth many interesting findings about the functioning of ecological systems, and here I focus on the effects of dispersal and patch quality on metacommunities. Dispersal within a metacommunity has been shown to have profound effects on communities within it, in respect to its species interactions (Thompson & Gonzalez 2017), genetic makeup (Watts *et al.* 2015), species function (Thompson *et al.* 2017), and species

identity (Downes *et al.* 2017), to list a few. Research centered around patch quality is less prevalent (*e.g.* Mortelliti *et al.* 2010, Chisholm *et al.* 2011, Becker & Hall 2015), so expanding the knowledge of the effects of patch quality on metacommunities is one of the primary goals of this study. Additionally, understanding the effects of changing dispersal is imperative in conservation, as shown in previous research with the importance of stepping-stones (Saura *et al.* 2014) as strategies to enhance connectivity (Bélisle *et al.* 2001).

In this study I address the question of how habitat quality and connectivity interact to affect metacommunities, and test the hypothesis that patch quality and connectivity affect diversity and food web metrics. I predict that increasing patch quality will increase diversity and food web metrics, and that intermediate connectivity will maximise these metrics.

Methods

Microcosm community data

A dataset from a microcosm experiment was analyzed to understand its community dynamics and properties. The microcosm experiment in question was performed from November 16 to December 15, 2016 by Carina Firkowski and Janvi Patel. This microcosm experiment consists of eight species of protists (*Blepharisma* sp., *Euplotes* sp., *Colpidium* sp., *Paramecium aurelia*, *Paramecium bursaria*, *Spirostomum sp.*, *Tetrahymena pyriformis*, and *Vorticella* sp.) and one rotifer species (*Lepadella* sp.). These species have previously been studied by Cadotte (2007) and Firkowski (unpublished) as well as many others (*e.g.* Haddad *et al.* 2008, Carrara *et al.* 2012, Altermatt *et al.* 2015), which will allow for better understanding of the properties not being measured in this microcosm study, such as carrying capacity and food web structure. The microcosm data being used describes the abundance of each species in a community over a 30-day period under high, intermediate, and low initial resource availability treatments, in a total of 8 replicates per treatment level.

Microcosm statistical analysis

Using the microcosm community data, I assessed the equilibrium effect of patch quality on diversity as the Shannon index, richness as the number of species present, Pielou's evenness index, and productivity as total community mass per unit of time (sum of average mass of species multiplied by abundance). I used ANOVAs and Tukey tests to determine if the differences in each metric were significant between treatment levels.

I visualised patch quality's effect on equilibrium communities' composition using a CCA plot. To quantify the patch quality effect, I used a permutational ANOVA to determine significance in the differences in community composition, and Marti Anderson's PERMDISP2 procedure to analyse variance homogeneity in Bray-Curtis dissimilarities between groups. I applied an ANOVA and Tukey tests to determine significance in group dispersion differences.

For the time series effect of patch quality on community compositions, I visualised the effect of patch quality over time using the PCA vectors at each timestep. The effect over time was quantified using a permutational ANOVA, followed by the Marti Anderson's PERMDISP2 procedure. An ANOVA and Tukey tests were used to determine significance in group dispersion differences.

The effect of patch quality on the temporal correlation of species abundances, calculated as Gross' synchrony (Gross *et al.* 2014), was assessed using ANOVA and Tukey tests.

I applied a square root data transformation to ensure normality and constant variance. All analyses were performed in R version 3.4.2, along with Rstudio 1.1.383. Code can be found at https://github.com/TristanGarry/TG_microcosm_analysis1.

Simulation of metacommunity dynamics

The results from the microcosm experiment were used to parametrize a mathematical model with the objective of analysing the effect of patch quality and connectivity on metacommunity dynamics. The mathematical model is a spatially explicit species interaction metacommunity (SESIM) model (Firkowski *et al.* unpublished), and consists of a Lotka-Volterra model (Thompson *et al.* 2014, Thompson & Gonzalez 2017) with a metacommunity food web structure (Ives & Cardinale 2004).

Using the parametrized SESIM model, a five-patch network was simulated to equilibrium at 500 time-steps using 10 replicates. Three different connectivity patterns were compared, namely linear, circular, and global, allowing for dispersal within metacommunities with differing proportions of high and low quality patches (Fig. 1).
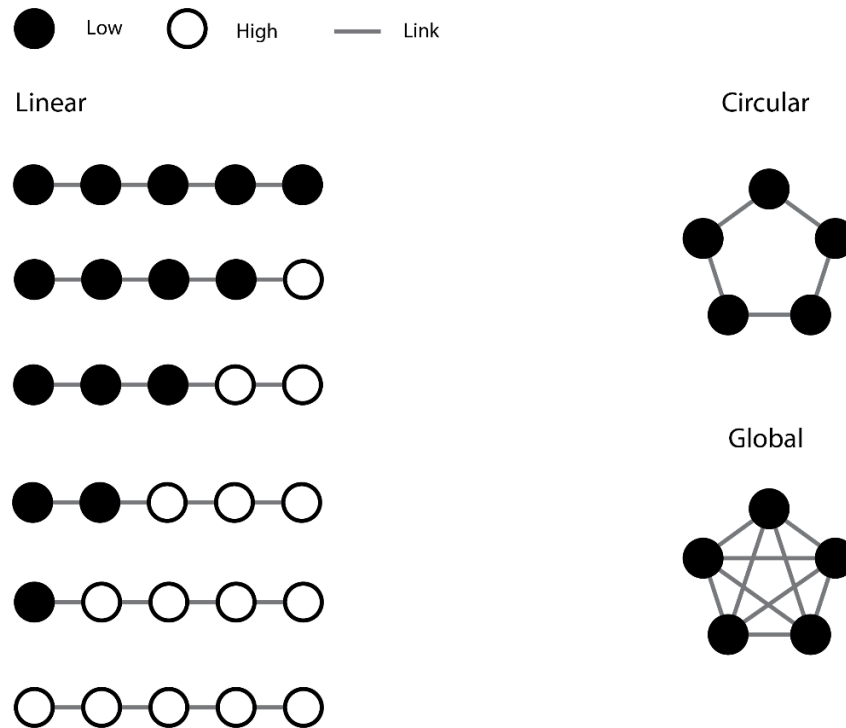

Figure 1. Simulation experimental design of connectivity patterns and patch quality levels. Each set of five patches represents one metacommunity. Links represent paths through which dispersal can occur, and are all equal in length. Low patches refer to low resource availability treatment level from the microcosm experiment, and high patches refer to the high resource availability treatment level from the microcosm experiment. The proportions of high and low quality patches shown in the linear connectivity were also applied to the circular and global connectivities.

Analyses of simulated data

Using the simulation results, I assessed the effect of patch quality and connectivity at local and regional scales on diversity as the Shannon index, richness as the number of species present, Pielou's evenness index, and productivity as total community mass per unit of time.

I determined patch quality and connectivity's effects on community composition heterogeneity using PCA and Cohen's d effect size. The multivariate community composition was summarized using PC axes 1 and 2, and these were used to determine the difference between treatments' composition. 'Between' effect size was obtained by calculating the differences in distance between each patch quality and connectivity treatment's multivariate points and the control's centroid (lowest patch quality and no connectivity). This provides a measure of the treatment's contribution to community composition heterogeneity in comparison to the control. 'Within' effect size was obtained by calculating the distances between each patch quality and connectivity treatments' multivariate points and their own group centroid. This determines the amount of community composition heterogeneity caused by patch quality and connectivity treatments. For both 'between' and 'within' effect sizes, the distances from the control multivariate points to the control's centroid functioned as the null hypothesis. These methods were used over the time series data to assess effect size over all time-steps, and also at the final time-step to assess effect size at equilibrium. The abundance data was standardized using the Hellinger method prior to analysis.

I used the coefficient of variation of species abundance to determine how the beneficial effect of high quality patches propagated across the metacommunity network. The coefficient of variation was calculated as the standard deviation of each community's abundances divided by its mean abundance. This coefficient allows for the identification of patterns of variation seen in high and low quality patches, allowing one to track their effects on both adjacent and more distant patches in the network. The abundance data was standardized using the Hellinger method prior to analysis.

To assess the local effect of patch quality and connectivity on food web structure I analysed changes in the following metrics: (a) number of links, as the number of realized trophic links in each patch; (b) link density, as number of links divided by the number of species present in each patch; (c) connectance, as number of links divided by the square of the number of species present in each patch; and (d) number of trophic levels, as the number of unique of trophic levels found in each patch.

All analyses were performed in R version 3.4.4, along with Rstudio 1.1.383. Code can be found at https://github.com/TristanGarry/connectivity-patchquality.

Results

Microcosm experiment

Results displayed a positive relationship between the examined metrics and patch quality (Fig. 2), and a significant effect of patch quality on the multivariate community data (Fig. 3). Overall, low quality patches exhibited greater dissimilarity to other patch qualities, than did high and intermediate patch qualities.
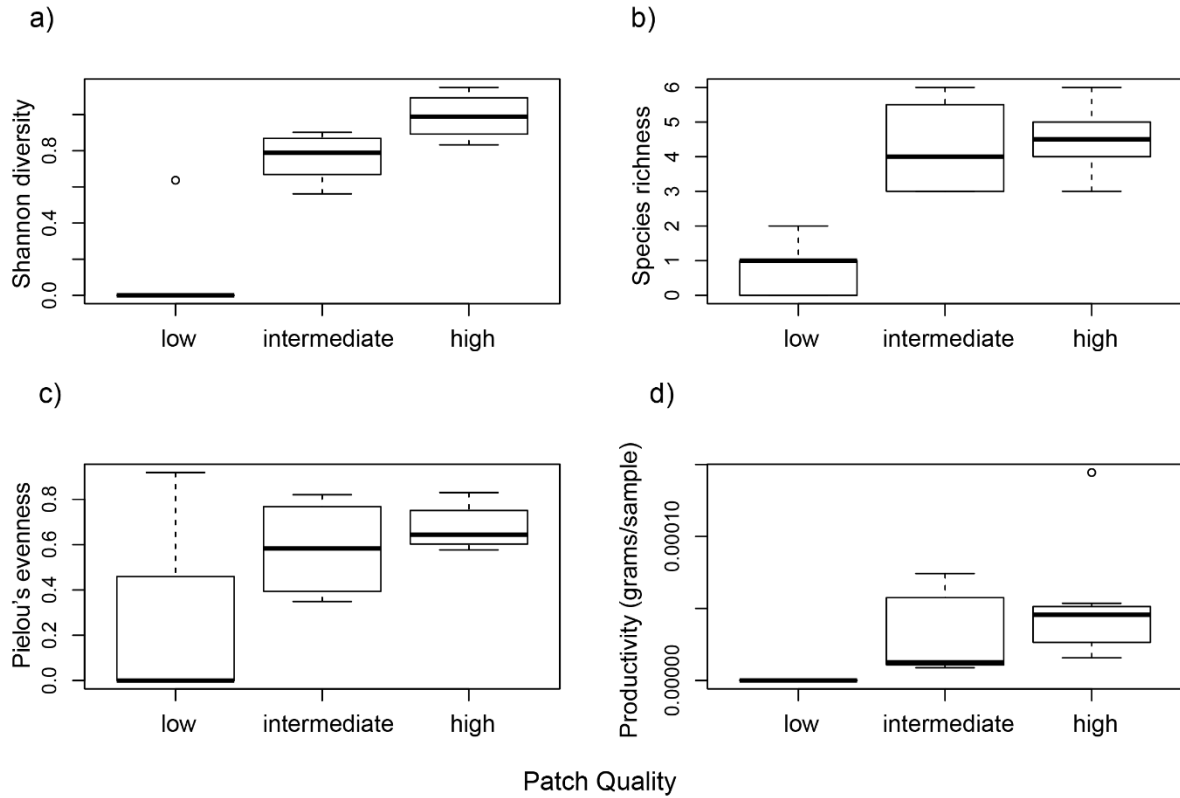
Figure 2. Effect of patch quality on the examined metrics at the final time-step (t=30). (a) Diversity calculated as Shannon's diversity, (b) species richness, (c) Pielou's evenness, and (d) community productivity in grams per sample. Significance is presented in Table 1.

Patch quality had a significant positive effect on all metrics (Fig. 2). Diversity (Fig. 2a) was greatly affected by patch quality ($F_{2,21} = 67.419$, $p < 0.001$). Richness (Fig. 2b; $F_{2,21} = 32.109$, $p < 0.001$), evenness (Fig 2c; $F_{2,17} = 4.8299$, $p = 0.021$), and productivity (Fig. 2d; $F_{2,21} = 6.5137$, $p = 0.006$) were also significantly affected by patch quality, but less drastically as seen by the F-statistic values. Table 1 summarises results for the mentioned tests.

Table 1. F-statistics and p-values for specific metrics' ANOVA tests.

	Diversity	Richness	Evenness	Productivity
F	67.419	32.109	4.8299	6.5137
p-value	< 0.001	< 0.001	0.021	0.006

As predicted, communities under low and high patch quality were deemed to be significantly different in all metrics: diversity ($p < 0.001$), richness ($p < 0.001$), evenness ($p = 0.018$), and productivity ($p = 0.005$). Communities under intermediate and high patch quality differed significantly in diversity ($p = 0.029$), while not being significantly different in richness ($p = 0.882$), evenness ($p = 0.717$), and productivity ($p = 0.344$). Communities under intermediate

and low patch quality were significantly different in richness ($p < 0.001$) and diversity ($p < 0.001$), but were not significantly different in evenness ($p = 0.065$) and productivity ($p = 0.103$). All p-values presented above are summarised in Table 2.

Table 2. p-values for pairwise Tukey tests for the effect of patch quality on Shannon diversity, species richness, Pielou's evenness and community productivity. Significance: *** ≤ 0.001, ** ≤ 0.01, * ≤ 0.05, . ≤ 0.1.

	Diversity	Richness	Evenness	Productivity
Low - High	<0.001 ***	<0.001 ***	0.018 *	0.005 **
Intermediate - High	0.029 *	0.882	0.717	0.344
Low - Intermediate	<0.001 ***	<0.001 ***	0.065 .	0.103

A CCA ordination (Fig. 3) constrained by patch quality explained a large amount of variation in communities' composition (adjusted $R^2 = 0.6085$), with the first CCA axis accounting for 12.26% of the explained variation, and the second CCA axis for an additional 1.31% of the explained variation. The high and intermediate patch qualities overlapped in the first CCA axis and were reasonably close in the second CCA axis. This strengthens the results from Figure 2, indicating that the intermediate and high patch qualities are less dissimilar from each other than they are from the low patch qualities.
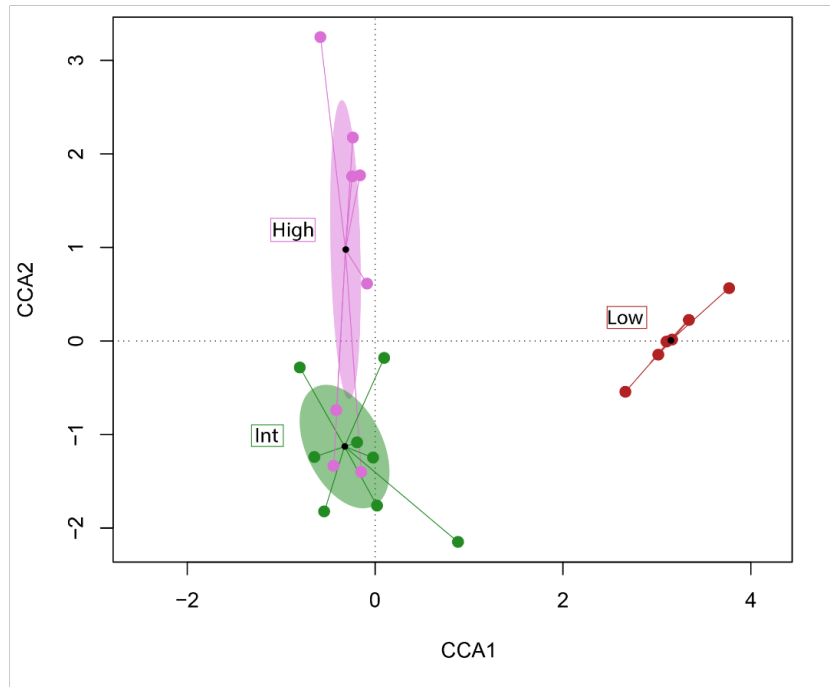

Figure 3. CCA plot of the community composition at the final time-step (t = 30). Each coloured point represents one replicate. Shaded ovals indicate a 95% confidence interval of the multivariate community composition for each patch quality level, while solid lines connect replicates to the group's centroid, represented by black points.

A permutational ANOVA also supported the results of community composition dissimilarities between patch qualities at the final time-step, based on 200 permutations ($F_{2,21}$ = 43.856, p = 0.005) and 999 permutations ($F_{2,21}$ = 43.856, p = 0.001). At least part of the differences in community composition between patch qualities can be explained by dispersion heterogeneity at the final time-step ($F_{2,21}$ = 18.768, p < 0.001). This is visually represented by the end community composition in Figure 3, where intermediate patch qualities show the greatest community composition dispersion. Pairwise differences in community composition dispersion homogeneity at the final time-step were also significant between low and high (p = 0.005), low and intermediate (p < 0.001), and intermediate and high (p = 0.049) patch qualities.
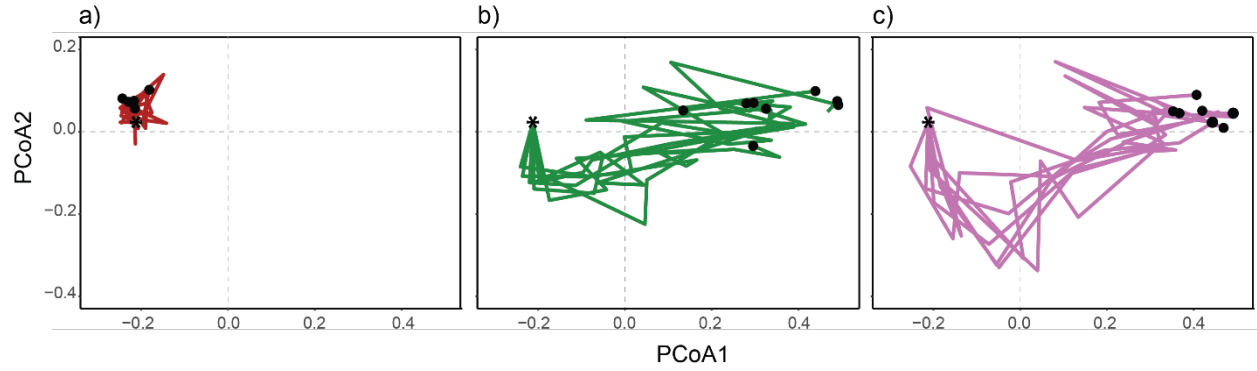

Figure 4. Assembly trajectory per patch quality. Principal Coordinates plots show community composition over time. (a) Low, (b) intermediate, and (c) high patch quality. Black asterisks show the initial community composition, lines represent the assembly trajectory of one community replicate, and black dots represent the end community composition.

When considering the complete time-series data, a two-way permutational ANOVA showed that community composition was significantly affected by the interaction between time and patch quality ($F_{2,219}$ = 42.261, p = 0.001). Overall, intermediate and high patch qualities had similar community composition dispersions over time, with an initial negative (time-step 3) and final positive (time-step 30) effect of patch quality on community composition dispersions. Low and high community dispersions were significantly different for the majority of time-steps, where low patch qualities showed lower mean dispersions than high patch qualities at all time-steps. Low and intermediate community dispersions showed the same trends as the low and high dispersions. All p-values and differences are presented in Table 3.

Table 3. Differences in community composition dispersion homogeneity at each time-step obtained through PERMDISP2. Significance: *** ≤ 0.001, ** ≤ 0.01, * ≤ 0.05, . ≤ 0.1.

Time-step	Int-High difference	Int-High p-value	Low-High difference	Low-High p-value	Low-Int difference	Low-Int p-value
3	-0.032	0.005 **	-0.039	0.001 ***	-0.008	0.672
6	0.006	0.955	-0.030	0.324	-0.036	0.206
9	-0.031	0.467	-0.076	0.023 *	-0.044	0.232
13	0.044	0.099 .	-0.042	0.112	-0.086	0.006 **
17	-0.020	0.526	-0.084	0.000 ***	-0.064	0.006 **
21	-0.030	0.677	-0.144	0.001 ***	-0.114	0.011 *
24	0.086	0.053 .	-0.079	0.083 .	-0.165	0.000 ***
27	0.057	0.340	-0.178	0.001 ***	-0.235	0.000 ***
30	0.071	0.049 *	-0.099	0.005 **	-0.170	0.000 ***

Patch quality had a non-linear effect on community synchrony, although only marginally significant ($F_{2,21}$ = 3.388, p = 0.053). As seen in Figure 4, while low patch quality showed a low level of synchrony (μ = 0.310, sd = 0.109), intermediate (μ= 0.020, sd = 0.151) and high patch qualities (μ= 0.084, sd = 0.110) showed values of synchrony undistinguishable from independent fluctuations in abundances. The intermediate-high (p = 0.751) and low-high (p = 0.194) pairwise differences were deemed non-significant, while low-intermediate (p = 0.049) pairwise differences were significant.
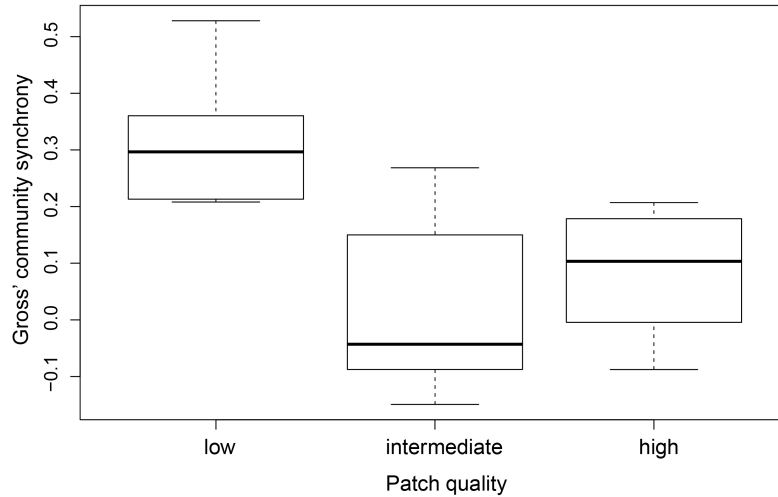

Figure 5. Gross' community synchrony for each patch quality.

Mathematical Model

As in the microcosm experiment, the model's diversity metrics increased greatly between low and high quality patches. Of the diversity metrics, Shannon's diversity, richness, and Pielou's evenness fit the microcosm metrics quantitatively well, while productivity fit the microcosm qualitatively well. The identity of species at equilibrium was also similar in the microcosm and the model. Connectivity schemes strongly altered the response of food web metrics and community composition to patch quality, and had a weaker effect on the response to patch quality in diversity metrics.
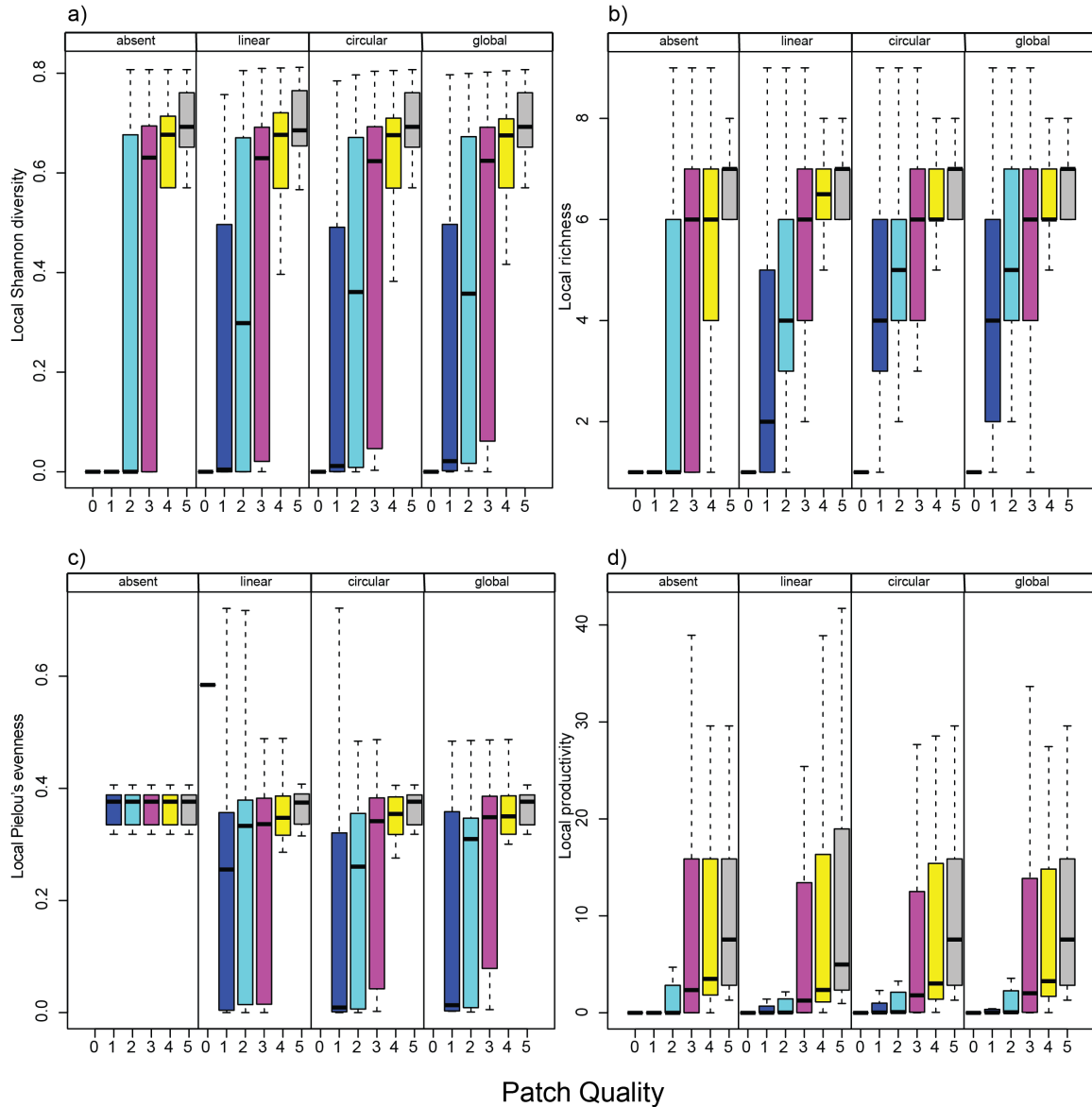

Figure 6. Effect of patch quality and connectivity on selected local metrics at equilibrium. (a) Local diversity calculated as Shannon's diversity, (b) Local species richness, (c) Local Pielou's evenness, and (d) local productivity in grams. Patch quality values indicate the number of high quality patches present in the network, with the remainder of patches being of low quality (see *Methods* Fig. 1).

Results showed a positive relationship between the examined diversity metrics and patch quality at a local scale (Fig. 6). Local diversity (Fig. 6a) was generally similar across all connectivity schemes, differing mostly for linear connectivity, showing the lowest mean diversity for patch qualities 1 and 2, and catching up to circular and global connectivities with higher patch qualities. Linear connectivity also showed the lowest richness values (Fig. 6b) in patch qualities 1 and 2, while circular and global connectivities were again very similar in richness. Evenness (Fig. 6c) gained considerable variation in the connected treatments compared to when connectivity was absent, with global connectivity having the least variation by a wide margin. Productivity (Fig. 6d) also showed a positive relationship with patch quality. Similar results were seen at the regional scale (Fig. S1).
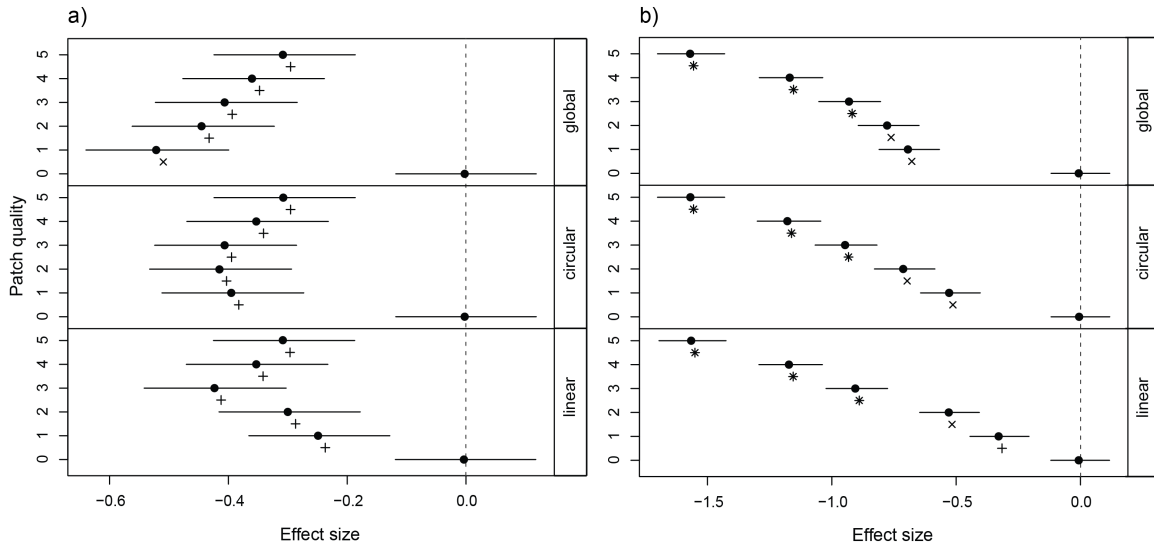

Figure 7. Cohen's effect size of patch quality and connectivity on community composition heterogeneity over the entire time series, calculated (a) between absent (control) and each connectivity and patch quality groups and (b) within absent (control) and each connectivity and patch quality groups. Patch quality values indicate the number of high quality patches present in the network, with the remainder of patches being of low quality (see *Methods* Fig. 1). Significance: + small effect, × medium effect, ∗ large effect.

An effect of patch quality and connectivity was also seen on the multivariate community data (Figs. 7 and 8). A PCA analysis of the community data summarized 49.37% of the variation in the data in the PC1 axis, and 20.21% in the PC2 axis. These PC axes were subsequently used to calculate the 'between' and 'within' effect sizes of patch quality and connectivity on community composition heterogeneity.

The 'between' overall effect size of community composition heterogeneity (Fig. 7a) showed a non-linear response to patch quality under the linear and circular connectivities. Linear connectivity showed the strongest effect size at patch quality 3, circular connectivity showed the strongest effect size at patch quality 2, and global connectivity showed the strongest effect at patch quality 1, demonstrating the increasing potential of connectivity to support source-sink dynamics. For 'within' overall effect size of community composition heterogeneity, all

connectivity schemes showed a positive relationship between effect size and patch quality, demonstrating the beneficial effect of increasing patch quality to spatial and temporal heterogeneity in community composition. Linear connectivity showed the most variation between patch quality treatment levels.
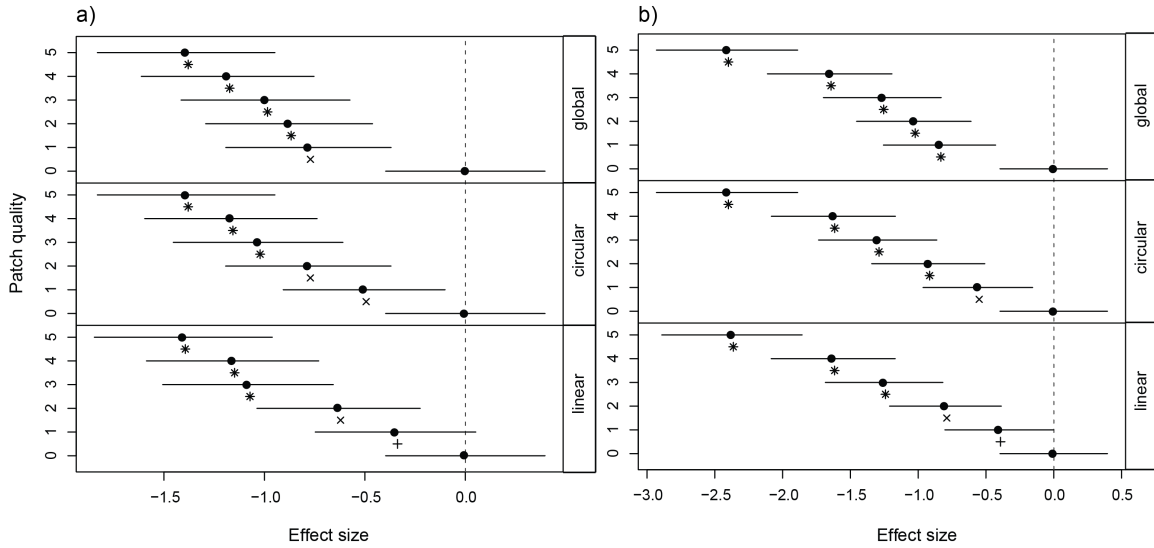

Figure 8. Cohen's effect size of patch quality and connectivity on community composition heterogeneity for the last time-step, calculated (a) between absent and each connectivity and patch quality groups and (b) within absent and each connectivity and patch quality groups. Patch quality values indicate the number of high quality patches present in the network, with the remainder of patches being of low quality (see *Methods* Fig. 1). Significance: + small effect, × medium effect, * large effect.

The effect sizes of at equilibrium community composition heterogeneity showed a positive relationship with connectivity and patch quality, demonstrating that both connectivity and patch quality contributed to increasing at equilibrium community composition heterogeneity. The beneficial effect of increasing connectivity to spatial heterogeneity in at equilibrium community composition is demonstrated by the 'between' (Fig. 8a) and 'within' effect sizes (Fig. 8b) under patch quality 1, increasing in effect size from linear, to circular, to global connectivity.
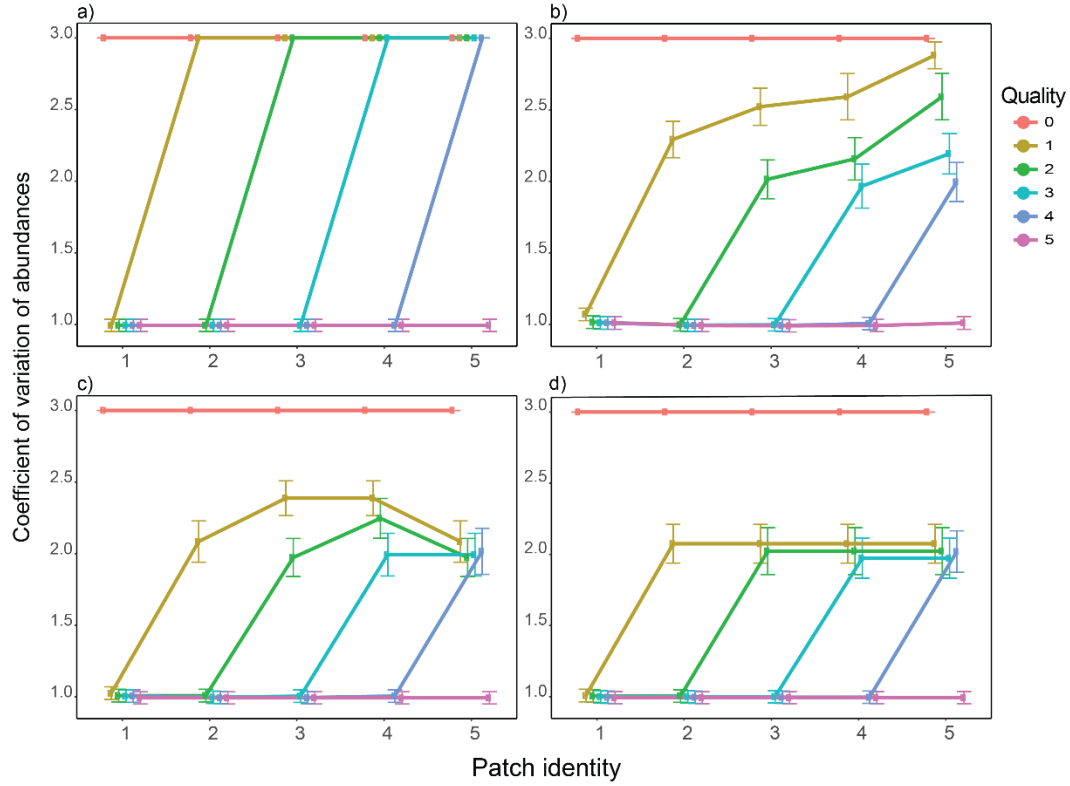
Figure 9. Effect of patch quality on the coefficient of variation of total community abundance. Connectivity: (a) absent, (b) linear, (c) circular, and (d) global. Quality values indicate the number of high quality patches present in the network, with the remainder of patches being of low quality (see *Methods* Fig. 1). Error bars represent standard error. Patch identity matches the patches as indicated in the methods section.

The coefficient of variation of the community abundances showed that effects of high quality patches propagated to adjacent patches. Effects of a single high quality patch could reach all five patches in the metacommunity (see patch quality 1 in Fig. 9b), reducing the variation in abundances of the remaining low quality patches in comparison to values under absent connectivity (Fig. 9a). Circular (Fig. 9c) and global connectivities (Fig. 9d) showed that with increasing connectivity high quality patches have a greater effect on all patches. However, even at the greatest connectivity level (Fig. 9d), low quality patches could still not be rescued to the equivalent levels of abundance variation as those of high quality patches.
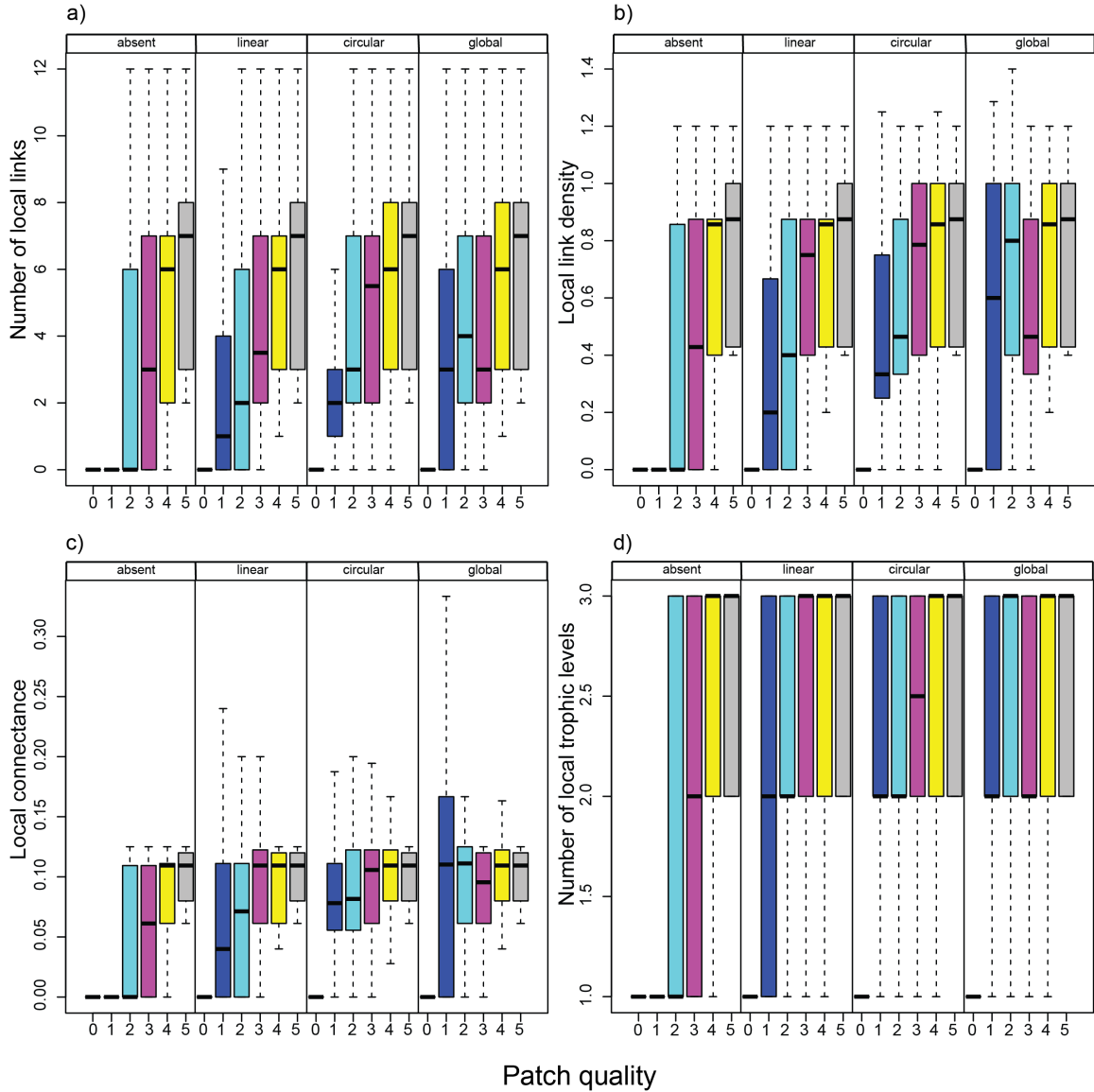
Figure 10. Effect of patch quality and connectivity on selected local food web metrics. (a) Total number of local links, (b) local link density, (c) local connectance, and (d) number of local trophic levels. Patch quality values indicate the number of high quality patches present in the network, with the remainder of patches being of low quality (see *Methods* Fig. 1).

Connectivity had a very noticeable effect on food web metrics (Fig. 10). The total number of local links (Fig. 10a) varied greatly for patch quality 1 between connectivities, with circular connectivity showing the smallest variation, followed by linear, and then global connectivity. For patch quality 3, circular connectivity interestingly had the highest number of links. Similar results were seen for link density (Fig. 10b), here with circular connectivity having higher variation than the other two connectivities. Connectance showed the least amount of variation under circular connectivity (Fig. 10c), with global connectivity having a markedly high variation for patch quality 1. Interestingly, link density and connectance were more stable for

patch qualities 4-5 under linear and global connectivities. In linear and circular connectivities, there was a roughly linear relationship between the number of trophic levels (Fig. 10d) and patch quality. Global connectivity had a similar relationship, but experienced a drop in mean number of trophic levels at patch quality 3.

Discussion

Patch quality promoted increases in the microcosm's diversity metrics, finding supported by literature on the positive relationship between habitat quality and diversity metrics (Li & Stevens 2010). The observed relationships between quality and the metrics was non-linear. High quality and intermediate quality patches did not show significant differences in richness, evenness, and productivity (Table 2), suggesting that perhaps the gradient of habitat quality was not fully explored with the resource levels used in this experiment. This is also supported by the community composition dispersion results, as intermediate and high patch qualities showed considerable overlap (Fig. 3). However, since the relationship between habitat quality and species abundance is not always linear, tipping points in patch quality can determine community responses (Scheffer *et al.* 2009). An experiment with more resource increments could determine whether the full gradient was not explored and indeed responses to patch quality are linear, or whether a tipping point is situated between low and intermediate resource qualities.

The community composition data shows that, while intermediate and high patch qualities were similar in diversity metrics, their community composition dispersion was different (Table 3). Greater dispersion observed at intermediate resource quality could indicate a greater potential to resist disturbance and rapid changes (Wilcox *et al.* 2017). This relates to synchrony results, showing that intermediate resource quality had the lowest mean community synchrony, while differing significantly from synchrony levels under high resource quality. Low synchrony is often associated with greater ability to adapt to changes in the environment and persist in the face of disturbance (Gouhier *et al.* 2010). Hence, diversity, community composition and synchrony results suggest that intermediate patch quality might be the best patch quality overall for supporting communities in the long-term.

Simulation results supported the microcosm's results of increases in patch quality leading to increases in the diversity metrics. In patch qualities 1-5, the results were fairly linear (Fig. 6), while the difference between patch quality 0 and 1 was always the largest. The presence of even a single high quality patch in the network promoted source-sink dynamics, meaning that high quality patches were able to supplement low quality patches and greatly increase metrics, at both local (Fig. 6) and regional scales (Fig. S1). These dynamics were stronger in the circular and global connectivity schemes, indicating that the less connected linear scheme required more high quality patches to produce a similar rescue effect. The coefficient of variation (Fig. 9) further corroborates this result, by showing the propagation of high quality patches' effects across the networks. High quality patches had a greater effect in decreasing the coefficient of variation in circular and global connectivity schemes. However, it is interesting that even in the linear

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connectivity, a single high quality patch affected the variability in abundance in all patches in the network. This is encouraging, as it shows that even a single high quality patch can raise the viability of patches in a network, through having its effects propagate from patch to patch.

A potential tipping point in the diversity metrics was identified at patch quality 3 (Fig. 6). Diversity metrics for patch qualities 1 and 2 were characterised by low means and large variation, while patch qualities 4 and 5 were characterised by high means and small variation. Patch quality 3 however was usually characterised by a high mean and large variation, indicating that this may be the point at which communities can succeed, but are still at risk of stochastic effects or disturbance events. This is consistent with previous studies in source-sink dynamics which have found that there is an upper limit to the source-sink ratio under which these dynamics can occur (Mouquet *et al.* 2006).

Regional productivity was maximized in the linear connectivity scheme (Fig. S1). It has been shown that a single most competitive species can outperform competitively inferior species in the community, and hence be the main contributor to productivity (Aarsen 1997). This idea is supported by the greatest number of local extinction being observed in the linear connectivity scheme, suggesting that its high levels of productivity might be the result of the most productive organism dominating the community and available resources. This is also corroborated by the linear connectivity scheme showing the lowest values of community composition heterogeneity (with the exception of absent connectivity). This means that although the linear connectivity had the highest productivity, this may not be a proper signal of it having the healthiest community and may in fact be a signal of the opposite.

The effect sizes show an interesting difference between early and late effects of patch quality and connectivity on community composition (Figs. 7 and 8), since the effect of patch quality on community composition was very variable between the overall effect and the equilibrium effect. This is particularly true for global connectivity, which showed opposite trends in the time series analysis versus the equilibrium analysis. This can be explained by considering that when connectivity is high, even a few high quality patches can have a strong influence on communities in low quality patches, and this is likely to have the strongest influence during early phases of community succession. As community succession progresses, the priority effect of low quality patches erodes, hence the overall large effect size values of patch quality 1 in global connectivity (Fig. 7a). This is also apparent under circular and linear connectivities, although at smaller degrees, with the largest effect size values seen in patch quality 2 and 3, respectively (Fig. 7a). Since these metacommunities are less connected, high quality patches have less influence in the assembly of low quality patches, so more patches are needed for a similar effect on community assembly. These results are supported by Chisholm *et al.* (2011), who found that diversity metrics are most strongly influenced by connectivity when patch quality is heterogenous. The equilibrium effect sizes (Fig. 8) however show that eventually the effects of connectivity are overcome by those of patch quality. This is interesting as it indicates a trade-off between connectivity and patch quality for early metacommunity assembly and at equilibrium

metacommunity dynamics. Seeing these effects explored in real-world systems would be interesting and could have important implications in conservation.

Food web metrics showed a different response than diversity metrics to the effects of connectivity and patch quality. Tipping points are seen later in diversity metrics than in food web metrics. In diversity metrics, a tipping point was identified at patch quality 3, while for food web metrics tipping points were more likely at lower patch qualities. Food web metrics usually presented the characteristic high mean and large variation values at patch qualities 1 or 2, depending on the connectivity schemes. Tipping points in food webs have been shown to be linked to the proportion of links removed. Allesina *et al.* (2015) showed that after 45% of the functional links are removed, disproportionately large damage is done by further removal of links. This might indicate that patch quality 2 metacommunities are sitting near the tipping point at which further removal of links will cause huge food web damage, and could explain the observed high mean and large variation values. Interestingly, global connectivity usually showed the largest variation in these metrics across all patches, but not the highest means. Overall, circular connectivity seemed like the best connectivity scheme in optimising food web metrics across all patch qualities: it usually had the lowest variation combined with the highest means.

The difference in tipping points between diversity and food web metrics seem to be driven by different factors. Diversity metrics are highly reliant on patch quality, while food web metrics are highly reliant on connectivity. The results obtained in this study could have implications for the identifications of tipping points, since I found evidence that food web metrics can provide early warning signals of tipping points. This also suggests for the potential use of food web metrics as early signs of recovery. Early warnings of tipping have been shown to come with increased variation, but tend to be shown across careful monitoring of time series data (Selkoe *et al.* 2015). Although this simulation does show the characteristic signs of increased variation before a collapse, a future work should investigate the effect of patch quality variation over time to see if these tipping points could be reproduced consistently in both food webs and diversity.

Conclusion

This research's objective was to better understand the effect of patch quality and connectivity on metacommunities. I found that as predicted, increasing patch quality increased diversity and food web metrics. Most diversity metrics were also maximized at the highest connectivity, except for productivity which was maximized in the least connected connectivity scheme. These results are in line with previous research and support that increasing habitat quality and connectivity will improve ecological systems. The community assembly of simulated data showed that connectivity affected the importance of patch quality at early succession stages. This has implications for conservation, as it indicates that connectivity is very important at early stages of recovery and succession of habitats with source-sink dynamics. The tipping points identified in food web metrics and diversity metrics were found at different patch qualities. Given more

research, this could provide insights into the identification of tipping points in natural communities, which has proven to be difficult.

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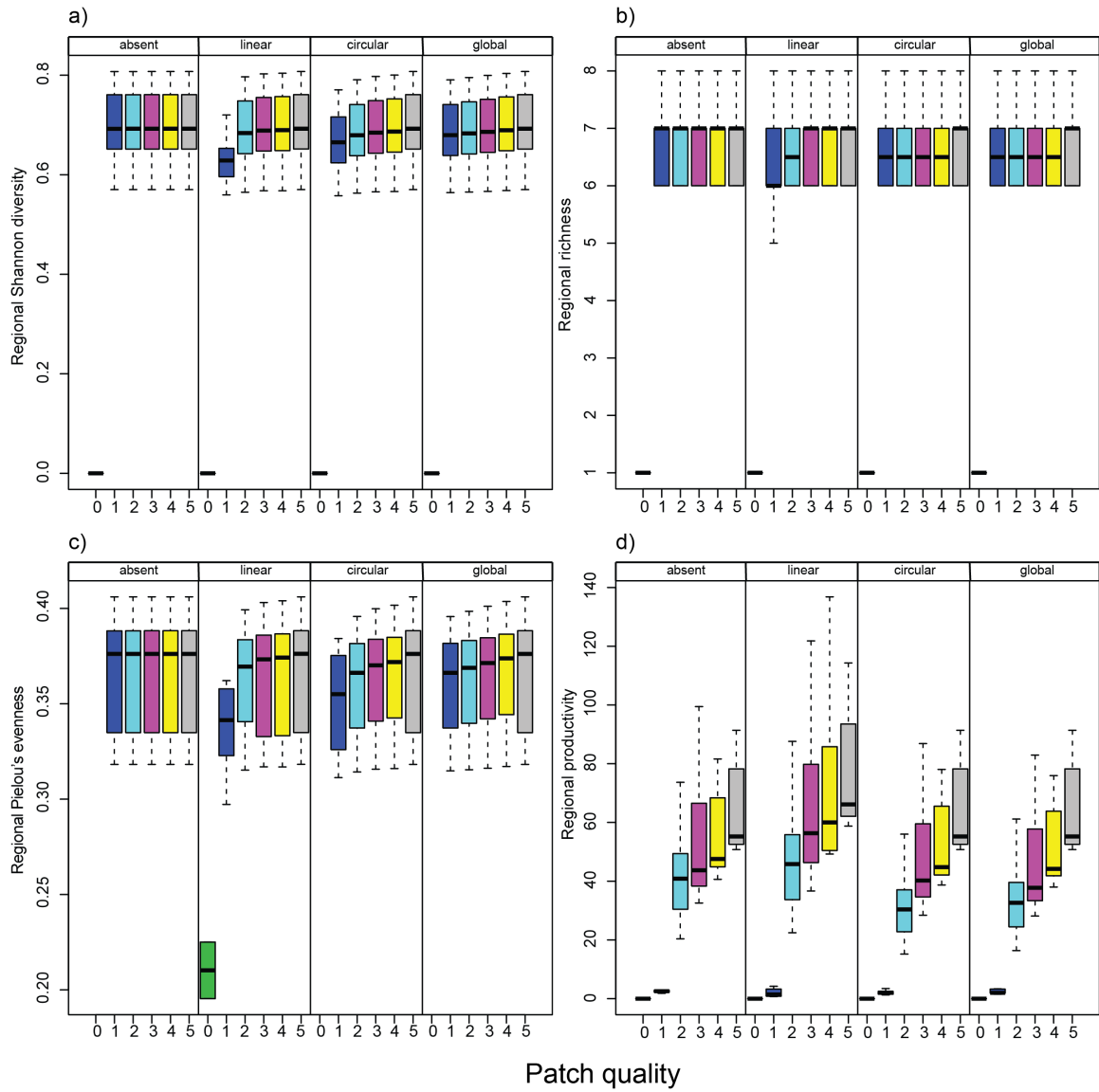
Supplementary Material

Figure S1. Effect of patch quality and connectivity on selected regional metrics at equilibrium. (a) Regional diversity calculated as Shannon's diversity, (b) regional species richness, (c) regional.