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Dendritic network structure and dispersal affect temporal dynamics of diversity and species persistence

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Landscape connectivity structure, specifically the dendritic network structure of rivers, is expected to influence community diversity dynamics by altering dispersal patterns, and subsequently the unfolding of species interactions. However, previous comparative and experimental work on dendritic metacommunities has studied diversity mostly from an equilibrium perspective. Here we investigated the effect of dendritic versus linear network structure on local (α-diversity), among (β-diversity) and total (γ-diversity) temporal species community diversity dynamics. Using a combination of microcosm experiments, which allowed for active dispersal of 14 protists and a rotifer species, and numerical analyses, we demonstrate the general importance of spatial network configuration and basic life history tradeoffs as driving factors of different diversity patterns in linear and dendritic systems. We experimentally found that community diversity patterns were shaped by the interaction of dispersal within the networks and local species interactions. Specifically, α-diversity remained higher in dendritic networks over time, especially at highly connected sites. β-diversity was initially greater in linear networks, due to increased dispersal limitation, but became more similar to β-diversity in dendritic networks over time. Comparing the experimental results with a neutral metacommunity model we found that dispersal and network connectivity alone may, to a large extent, explain α- and β-diversity dynamics. However, additional mechanisms, such as variation in carrying capacity and competition–colonization tradeoffs, were needed in the model to capture the detailed temporal diversity dynamics of the experiments, such as a general decline in γ-diversity and long-term dynamics in α-diversity.

Understanding the factors that influence the distribution, persistence and underlying temporal dynamics of species diversity patterns is a major focus of ecology. It is now commonly accepted that spatial dynamics, that is the specific connectivity pattern of the landscape and the dispersal therein, can significantly alter community composition, diversity and counteract local extinctions (Leibold et al. 2004, Holyoak et al. 2005, Baguette et al. 2013). These spatial dynamics have often been studied from a temporally stationary perspective. Therefore, a better understanding of the temporal dynamics of diversity patterns is needed, especially in habitats that are dynamic and highly prone to both species invasions and changes in network structures.

A prime example of such spatial networks are dendritic riverine ecosystems, which occur frequently in nature and have a complex but predictable structure (Rodriguez-Iturbe and Rinaldo 1997, Fagan 2002, Brown and Swan 2010, Altermatt 2013, Peterson et al. 2013). These ecosystems maintain high species diversity compared to other ecosystems, given their small global coverage (Vörösmarty et al. 2010, Dijkstra et al. 2013). Furthermore, they are important dispersal pathways (Barták et al. 2013) and are frequently invaded by non-native species, resulting in large temporal changes in community diversity (Leuven et al. 2009, Mari et al. 2011), which is often facilitated by anthropogenic changes in landscape network structure (Leuven et al. 2009, Lynch et al. 2011).

Much research has focused on understanding current and equilibrium-state community diversity patterns within dendritic networks (Grant et al. 2007, Peterson et al. 2013, Mari et al. 2014) and empirically observed community diversity patterns in river ecosystems have been linked to the specific dendritic river network structure (Muneepeerakul et al. 2008, Carrara et al. 2012, Altermatt 2013, Altermatt et al. 2013, Liu et al. 2013). For example, headwater sites have relatively low species diversity (Muneepeerakul et al. 2008, Carrara et al. 2012, Liu et al. 2013), but provide refuge for rare species and contribute to high among-community diversity (Muneepeerakul et al. 2008, Finn et al. 2011, Altermatt 2013, Liu et al. 2013, Göthe et al. 2013, but see Besemer et al. 2013). By contrast, increased landscape connectivity, for example due to man-made canals and river transport, can result in a homogenization of species diversity across riverine communities (Leuven et al. 2009, Lynch et al. 2011).

Parallel to empirical observations, many theoretical studies have assessed why dendritic networks harbour greater

mean species richness at confluence sites, but lower richness at headwater sites, compared to less connected networks (e.g. linear networks). Again, most of these studies took into account dispersal and subsequent diversity patterns in an equilibrium state (Fagan 2002, Muneepeerakul et al. 2008, Economo and Keitt 2010, Mari et al. 2014). However, such an approach does not allow addressing how, or if, different processes affect the temporal diversity-dynamics in dendritic networks. A recent stochastic model (Carrara et al. 2012) exemplified how characteristic diversity patterns in dendritic networks might persist over many. However, parallel experimental work comparing dendritic versus two-dimensional networks investigated community diversity patterns at a single time point (Carrara et al. 2012, 2014), preventing the empirical evaluation of spatio-temporal dynamics. Importantly, these experiments were performed using manipulated passive dispersal, which was achieved by pipetting small amounts of the culture medium and organisms between the patches, as the patches were physically not connected. While such studies are important for establishing the empirical and theoretical basis of community dynamics in complex networks, additional investigations are needed to fully test the applicability of these principles. Specifically, simplified approaches without active dispersal remove the consequences of interspecific differences in dispersal abilities and, by definition, eliminate competition–colonization tradeoffs (Cadotte 2007, Limberger and Wickham 2011). The occurrence of regional (across sites) and local (within sites) species tradeoffs, however, has been shown to be specifically important in affecting spatial species diversity patterns (Kneitel and Chase 2004, Boulangeat et al. 2012, Baguette et al. 2013). Therefore, active dispersal needs to be taken into account, such that organisms can themselves disperse between physically connected sites or patches. Only recently have experiments included active dispersal and temporal observations to assess population and community diversity dynamics in linear and dendritic networks (Seymour and Altermatt 2014, Giometto et al. 2014). However, they looked at only one species/network type (Giometto et al. 2014) or utilized a small-scale spatial setup (Seymour and Altermatt 2014). Additionally, these studies were not able to track species' dispersal and interactions, nor to link the observed dynamics to a mechanistic model.

Here, we experimentally and theoretically investigated the effect of dendritic versus linear network structure on local species richness (α-diversity), species similarity among sites (β-diversity) and persistence of total species richness (γ-diversity) over time. We conducted microcosm experiments to observe the spatio-temporal dynamics of species diversity of actively dispersing individuals over many generations, utilizing 14 protist and a rotifer species. Such microcosms experiments allow the testing of general principles and provide qualitative insights into metacommunity ecology (Holyoak and Lawler 2005). Additionally, we studied these processes and patterns in numerical models of increasing complexity. We started with a neutral metacommunity model, which reflects differences due to network structure only, and then extended our analysis to more complex models including a competition–colonization tradeoff and variation in species' carrying capacity. Our main goal was a qualitative comparison of the models and the data, in order to understand the minimal processes needed to drive characteristic diversity patterns in dendritic networks, and how they unfold over time at macroecologically relevant scales.

Methods

Experimental setup and sampling

For our experiment we used a set of 14 protist and one rotifer species, henceforth collectively referred to as protists. The 15 species were cultured in protist medium, along with a set of common freshwater bacteria as a food source (*Serratia fonticola*, *Brevibacillus brevis* and *Bacillus subtilis*). Protist medium was made by adding 0.2 g l^{-1} protozoan pellet to tap water, autoclaving and then cooling to room temperature before use (for all methodological details see Altermatt et al. 2015). All protist species are primarily bacterivores; however, some species may predate on smaller species, or are capable of photosynthesis (Supplementary material Appendix 1 Table A1) (Altermatt et al. 2011a, Carrara et al. 2012).

We used two different types of microcosms (networks) in our experiment (in analogy to Fagan 2002), namely a linear network and a bifurcating dendritic network (Supplementary material Appendix 1 Fig. A1). Both types allowed species to freely move within the network (for details see also Seymour and Altermatt 2014). Networks were made of fifteen sections of silicon tubing (35 cm) connected by L- and Y-connecters. The total length (525 cm) and volume (250 ml) were the same for both network types. Per network, fifteen T-connectors, with vertical openings for sampling, were inserted, such that each of the fifteen sites per edge of the network could be sampled individually. To avoid laminar flow during the sampling procedure, we used silicon stoppers, which we placed on all site openings except the one being sampled. The ends of the networks were secured using metal clamps to prevent leakage. Medium in the networks was stagnant and there was no flow throughout the experiment, as the focus was as on the network structure. Per network type, we used five independent replicates.

Two weeks prior to the start of the experiment, we established fresh protist cultures for each of the 15 species. We added 25 ml of stock protist culture to 125 ml of fresh protist medium in previously autoclaved Erlenmeyer flasks containing two wheat seeds, and allowed the protists to grow to carrying capacity. Twelve hours prior to protist inoculation, networks were filled with 250 ml of protist medium and inoculated with the above-described set of freshwater bacteria. At the start of the experiment, each network site was inoculated with 1.5 ml of one of the fifteen protist species at their respective carrying capacity. We initialized each site with a single species to allow for colonization dynamics. We first calculated the centrality of all sites in the linear and dendritic networks, using closeness centrality l_i calculated as $l_i = \frac{1}{n}\sum d_{ij}$ (Newman 2010), which gives the mean geodesic distance from site i to j, averaged over all nodes j in the network. We then assigned each protist species randomly to a unique initial network site where it was inoculated. We thereby assured that the centrality ranking of the starting site

of a given species assigned in the linear network reflected the centrality ranking of the starting site for the same species in the dendritic network. This procedure was independently replicated across the five network replicates, to create five network pairs (one linear and one dendritic network per pair) with different random species assignments. This guaranteed that the observed patterns were uniquely due to differences in network structure and not initial starting position, as the starting position for each species was randomized across replicates.

All sites were routinely sampled over time by removing 0.5 ml of the medium from each network site, which was replaced with 0.5 ml of fresh medium inoculated with bacteria. Sampling occurred every four days for 24 days, with two additional samplings at day 32 and day 40 (i.e. 8-day intervals). Thereby, we collected data on species presence and abundance in all 10 network replicates (i.e. in total 150 local sites) at nine time-points. To reduce the workload to a manageable level, we staggered the counting so that two network pairs were counted on one day, two network pairs the next day and the last network pair on the third day. We used a stereomicroscope to estimate abundances of all protists in 0.5 ml of the sampled medium. If the species density was too high to be accurately counted, we diluted the sample until an appropriate measure could be taken (Altermatt et al. 2011b). Species densities and species presence were measured directly after sampling and with the individuals being alive (see also Altermatt et al. 2011b).

Statistical analyses

All statistical analyses were done using the program R, ver. 2.15.1 (<www.r-project.org/>). We used abundance-based species diversity estimates (α-diversity, β-diversity, γ-diversity), calculated as true diversity in the terminology of Jost (2006), using the R package simba (Jurasinski 2012). True β-diversity is calculated independently of α- and γ-diversity, and reflects the actual number of species differing between sites (Jost 2006). We tested for the differences in α-, β- and γ-diversity between linear and dendritic networks using generalized additive models (gam), using the R-package mgcv (Wood 2011). In these models, the response variable was the diversity measure and the explanatory variable was the network type. We included time as a smoothing term due to the nonlinear relationship of the response variable over time (Zuur et al. 2009). We calculated the mean occupancy for each species by counting the number of occupied sites for each species (while present in at least one site) and averaging across the replicates for each network type.

Metacommunity models

Overview

In analogy to the microcosm experiments, we modelled the meta-community dynamics of 15 species across 15 local sites. These sites were arranged in either dendritic or linear networks of local communities connected by dispersal and the connectivity patterns followed exactly the experimental setup. Our model takes into account demographic stochasticity as well as both intra- and inter-specific competitive interactions. We explored four scenarios. First, a neutral model, in which all demographic parameter values do not differ per se between species (Hubbell 2001, Etienne and Rosindell 2011). Second, a non-neutral model that takes into account species-specific variation in carrying capacity as observed in the experiments (Supplementary material Appendix 1 Table A1). Third, a model including a competition–colonization tradeoff, that is, species with higher dispersal rates are assumed to be less competitive. Fourth, a model that includes competition colonization tradeoffs and species-specific differences in carrying capacity. Such, competition colonization tradeoffs have been commonly observed in a large number of protist (Cadotte 2007, Limberger and Wickham 2011) and other species (Whitham 1978, Nunney 1990, Turnbull et al. 2004).

Our model allowed us to track mean α-, mean β- and γ-diversity and compare the model outputs to the empirical data collected in the microcosms. This relatively simple model implementation is not thought to generate specific quantitative predictions, nor did we parameterize the model with previously recorded life-history data. Rather, we aimed at understanding the effects of relevant mechanisms in generating the observed diversity patterns. If the main driver of experimentally observed diversity patterns is network structure (linear versus dendritic), the neutral model should be able to qualitatively capture these diversity dynamics.

Local population dynamics

We assumed that all species are limited in their population growth by a finite amount of resources. Therefore, local population dynamics follow the logistic growth equation provided by Beverton and Holt (1957). An individual of species i in patch p produces a mean number of daughter cells $\lambda_{i,p,t}$ per time step (t):

$$\lambda_{i,p,t} = \lambda_{i,0} \frac{1}{1+(\lambda_{i,0}-1)/K_{i,p,t}N_{i,p,t}} \quad (1)$$

with $N_{i,p,t}$ as the population size of species i in patch p at time t. λ_{i0} is the growth rate of species i and $K_{i,p,t}$ is its carrying capacity. As one time step in the model corresponds to one generation, such a time-step is roughly analogous to one day in the experiment (the species used have generation times of approximately 0.5–2 days, Carrara et al. 2012). We included demographic stochasticity by modelling reproduction as a Poisson process, meaning that every individual produces an integer number of daughter cells drawn from a Poisson distribution with mean $\lambda_{i,p,t}$.

For simplicity, we assumed that inter-specific interactions are mediated by competition for resources. This effect is captured by the competition coefficient $\alpha_{i,j}$ which can be easily interpreted in biological terms: an individual of species j has $\alpha_{i,j}$ times the effect on species i as i has on itself. If for example $\alpha_{i,j} = 2$ the impact of species j on i is twice as strong as the intra-specific interaction of species i. We model this impact as affecting a species' carrying capacity in analogy to the Lotka–Volterra model of inter-specific interactions:

$$K_{i,p,t} = K_{i,0} \times \frac{C_{i,p,t}}{C_{i,p,t} + \sum_{i \neq j} \alpha_{i,j} C_{i,p,t}} \quad (2)$$

with $K_{i,0}$ as the carrying capacity of species i in isolation and $C_{j,p,t}$ as the population density of species j in patch p at time t ($C_{i,p,t} = N_{i,p,t} / K_{i,p,t}$).

Dispersal

Dispersal was defined by dendritic or linear connectivity matrices, which followed the experimental setup exactly. Dispersal is additionally influenced by an emigration rate (d_i) which captures the relative number of individuals that emigrate from a given site to a connecting site. As a standard, we assumed that $B(d_i, N_{i,p,t})$ individuals leave patch p per connecting vertex. The function B returns an integer number of emigrants drawn from a binomial distribution with d_i as the success probability and $N_{i,p,t}$ as the number of trials. The alternative is to assume that $B(d_i, N_{i,p,t})$ individuals leave patch p and that this number is divided equally among the connecting vertices. In additional analyses we found that this assumption does not change our results qualitatively (results not shown). In the experiment there were no a priori (and no known) mortality costs associated with dispersal. Therefore, we also did not assume any dispersal mortality in the model, such that all emigrants will immigrate into their target patch defined by the respective connectivity matrix.

Competition–colonization tradeoff

In a non-neutral model we implemented a competition–colonization tradeoff. This tradeoff allows us to determine the competition coefficient $\alpha_{i,j}$ for a pair of species i and j if their respective dispersal rates d_i and d_j are known. Generally, the competition coefficient $\alpha_{i,j}$ of a species j as a function of the difference in dispersal abilities relative to another species i should be monotonically decreasing with the restriction that $\alpha_{i,j} > 0$ (otherwise Eq. 2 does not hold) and that $\alpha_{i,j} = 1$ if the dispersal rates are identical. Consequently, we chose an exponential tradeoff function of the form

$$a_{i,j} = e^{-\tau(d_j - d_i)} \quad (3)$$

where τ defines the steepness to the tradeoff function, that is, the strength of the tradeoff. Note that we also tested a linear relationship and that the results were not altered qualitatively.

Numerical analyses

We iterated our simple meta-community model for $t_{max} = 50$ iterations, which roughly corresponded to the duration of the experiments (covering on average about 50 generations for the species used). We assumed that dispersal occurs before reproduction. We additionally ran simulations for $t_{max} = 500$ iterations to analyse the system's behaviour at (quasi-) equilibrium (Supplementary material Appendix 1 Fig. A10). Our standard scenario is a neutral model (standard parameter values see Table 1). We complemented this scenario with the above described competition–colonization tradeoff model which only differs in the parameters d_i and $\alpha_{i,j}$, as defined by Eq. 3. In addition we analysed the effect of adding variation in carrying capacities, as this was the case in the experiment (Supplementary material Appendix 1 Table A1). In the latter scenario the carrying capacities were randomly assigned with $K_{i,0} \in [10,100,1000,10000]$.

All numerical analyses were initialized, in analogy to the microcosm experiments, with one randomly chosen species at carrying capacity per patch. The model output was used to calculate diversity indices following the method described above for the empirical results. See Table 1 for an overview of all tested parameter combinations and Supplementary material Appendix 1 Fig. A5–A10 for a sensitivity analysis. We ran 100 replicates per simulation run and 25 replicates for the sensitivity analysis. All simulations were performed in R, ver. 2.15.1 (<www.r-project.org/>).

Table 1. Parameters explored in the models, their meanings and tested values. Standard values are highlighted in bold font. In the non-neutral models including the colonization–competition tradeoff species were attributed a randomly drawn emigration rate (d_i, drawn from a uniform distribution between 0.05 and 0.3) and the strength of inter-specific interactions ($\alpha_{i,j}$) was calculated using Eq. 5. Note that the effect of τ and t_{max} was only analyzed for the standard values of the other parameters.

Parameter	Meaning	Tested values
$K_{i,0}$	carrying capacity	10, 100, **1000**, 10000
$\lambda_{i,0}$	growth rate	1.5, **2**, 3, 4
d_i	emigration rate	0, 0.05, **0.1**, 0.2, 0.3
$\alpha_{i,j}$	strength of inter-specific interactions	0, 1, 1.25, **1.5**, 1.75, 2
τ	strength of the competition–colonization tradeoff	0, 1, 2, 3, **4**, …, 10
t_{max}	simulation time	**50**, 500

Results

Microcosm experiments

We observed significantly different species diversity patterns between the linear and dendritic networks. These differences not only persisted over long time-spans, but also showed pronounced spatio-temporal dynamics (Fig. 1, 2). Overall, species diversity at the network level (γ-diversity) was 15 at the start of the experiment (15 unique species) and steadily declined to an average of 6.8 species for linear networks and 7.8 species for dendritic networks (Fig. 2A). This effect of network type on γ-diversity over time was significant ($p = 0.029$; in the following, all detailed statistical results are given in Supplementary material Appendix 1 Table A2).

Species richness per site (mean α-diversity) was by default 1 at the start of the experiment (1 unique species per location) and increased to a maximum average of 6.5 species for the dendritic networks (day 16) and 4.9 species for the linear networks (day 8, Fig. 1, 2B). Subsequently, mean α-diversity decreased again, resulting in an average of 5.1 species (dendritic networks) and 4.0 species (linear networks) at the end of the experiment (Fig. 2B). We found a highly significant effect of network type on α-diversity ($p < 0.001$), based on our gam model (Fig. 2A, Supplementary material Appendix 1 Table A2), as well as a highly significant smoothing term. We found that α-diversity consistently differed between network types over time, and that there were on average three more species (38% increase) at interior sites of both network types, compared to the external sites (Fig. 1, Supplementary material Appendix 1 Fig. A2–A3).

The mean number of species differing between sites (mean β-diversity) was 15 at the start of the experiment since all sites had a unique species and there were 15

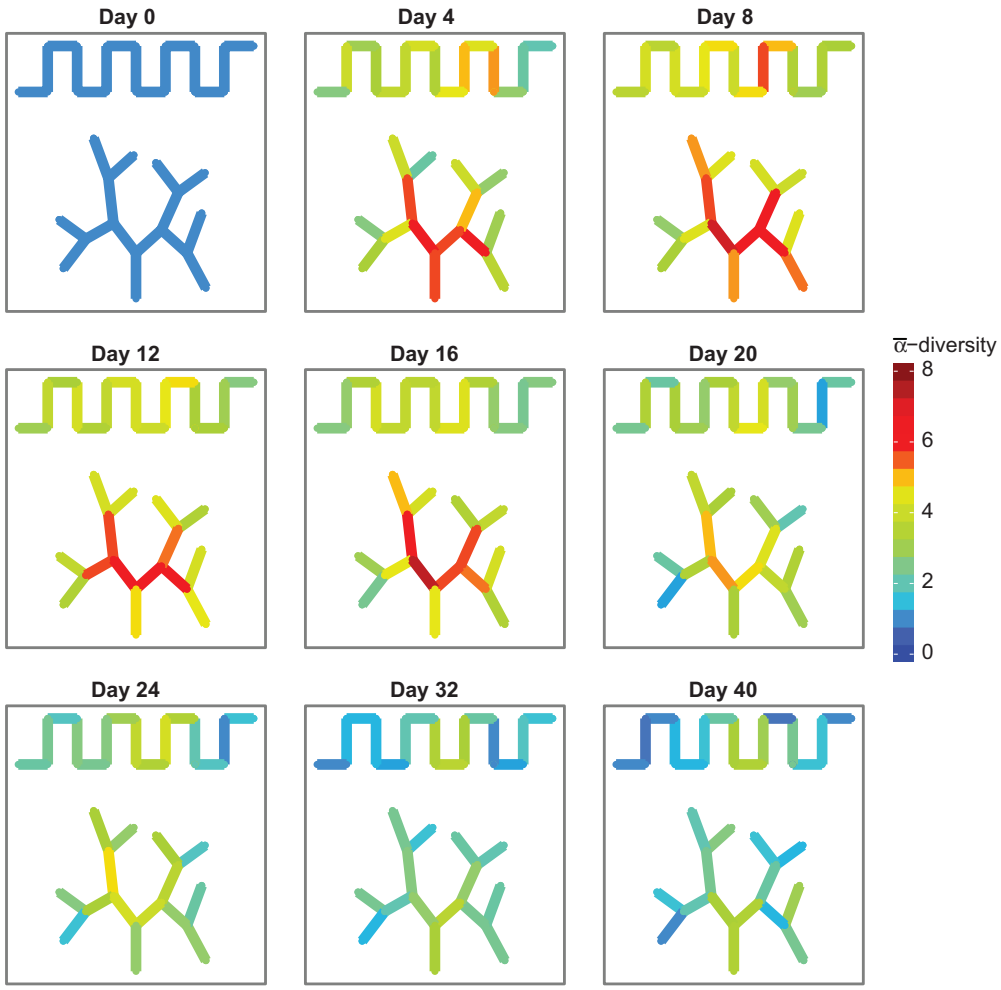

Figure 1. Spatio-temporal dynamics of mean α-diversity across linear and dendritic networks. Mean α-diversity across the five replicates per network type is given for each site as a color gradient from red to blue (i.e. from low to high diversity). At day 0, every site was initialized with one species.

unique species in total. We observed a sharp decline in mean β-diversity from day 0 to day 4, where mean β-diversity was 2.6 for the linear networks and 3.3 for the dendritic networks. At the end of the experiment, mean β-diversity was 1.5 in linear networks and 1.7 in dendritic networks (Fig. 2C). Throughout the experiment, we measured consistently and significantly higher β-diversity in the linear networks compared to the dendritic networks ($p < 0.001$; Fig. 2C, Supplementary material Appendix 1 Table A2). The high β-diversity at the beginning of the experiment is mostly reflected in the pairwise-distance among sites, whereby sites further from each other showed the highest β-diversity at the start of the experiment (Supplementary material Appendix 1 Fig. A4).

Mean occupancy per species was on average 0.7 sites higher in dendritic networks compared to linear networks, with 14 of 15 species occupying more sites in the dendritic networks. Mean species occupancy ranged from 1 to 9.4 across all networks with a significant effect of network type on mean occupancy based on a paired t-test ($t_{14} = 4.4$, $p < 0.001$, pairing done with respect to species identity, i.e. mean occupancy per species in linear versus dendritic networks).

Metacommunity model

Depending on the models' assumptions (i.e. increasing model complexity) and the level of diversity considered (α-, β- and γ-diversity), our metacommunity models (Fig. 3) were able to consistently reflect the experimental findings (Fig. 2). Already the simplest model (neutral model) was able to reflect some of the temporal diversity patterns: The structural differences of linear and dendritic networks and dispersal within resulted in an initial increase in α-diversity and an overall decrease in β-diversity (Fig. 3A), as observed in the experiment (Fig. 2). However, the neutral model was not able to explain the decrease in α-diversity after an intermediate peak, as observed in the experiments (Fig. 1, 2). A possible explanation for the decline in α-diversity is that differential inter-specific competitive interactions exist as a consequence of a competition–colonization tradeoff (Fig. 3B) as suggested by the high qualitative consistency between the model incorporating a competition–colonization tradeoff and the empirical data. However, this model still does not fully reflect the empirically observed dynamics in γ-diversity decay. Additional processes leading to global species extinctions, for example due to variation in carrying

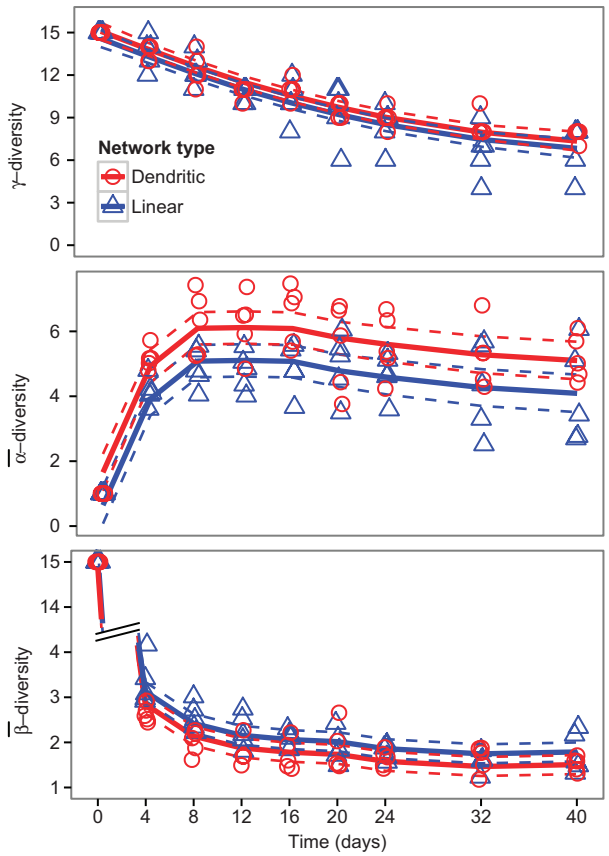

Figure 2. Mean diversity patterns over time for dendritic (red) and linear (blue) networks. Mean values were calculated across the five replicates per network type. The panels show true γ-diversity (A), true α-diversity (B) and true β-diversity (C) across linear and dendritic networks over time, with gam-fitted curves. Dashed lines represent the 95% percent confidence intervals of the respective gam model. Note for panel C (β-diversity), the *y*-axis is split, due to a steep drop in β-diversity from day 0 to day 4. The *y*-axis for all panels can be interpreted as number of species, but the true diversity measures were calculated using species' abundances.

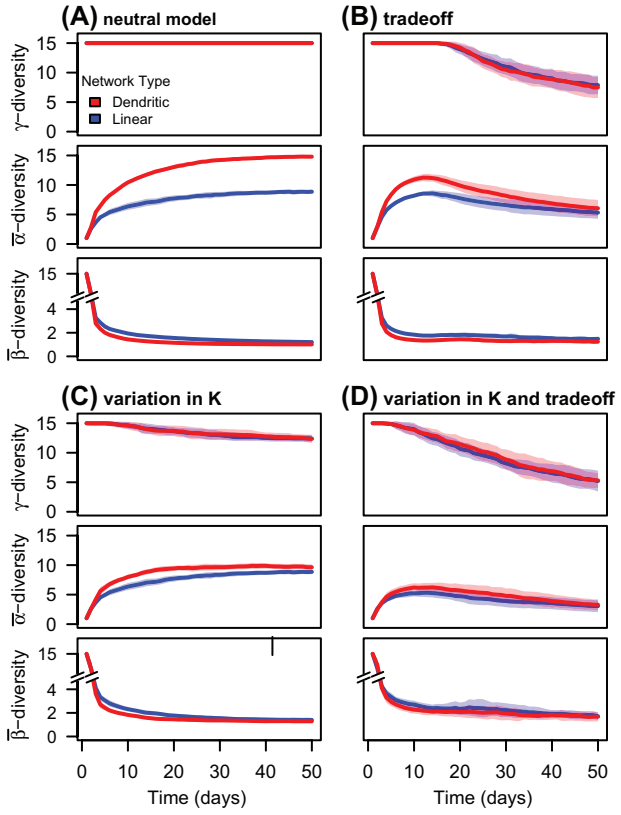

Figure 3. Diversity dynamics in the metacommunity model. The upper left panels (A) show results for the neutral model (here: $K_{i,0} = 1000$, $\lambda_0 = 2$, $d_i = 0.1$, $\alpha_{ij} = 1$). Note that γ-diversity does not decrease on the time scales depicted here due to high carrying capacities that reduced drift (see Supplementary material Appendix 1 Fig. A10 for long-term dynamics). The upper right panels (B) show results from an analogous model that includes a competition–colonization tradeoff (Eq. 3; $\tau = 4$). The lower left panels (C) show results for a model with variation in carrying capacities (abbreviated as *K*) keeping all other parameters constant (here: $\lambda_0 = 2$, $d_i = 0.1$, $\alpha_{ij} = 1$). The lower right panel (D) combines the effects of variation in carrying capacity and a competition–colonization tradeoff (Eq. 3; $\tau = 4$). The figure shows results (mean and standard deviation) of 100 replicate simulation runs. Note for panels on β-diversity, the *y*-axis is split. See Supplementary material Appendix 1 Fig. A5–A10 for a sensitivity analysis and long-term dynamics.

capacity (as observed in the empirical system; Supplementary material Appendix 1 Table A1) are required to fully match the temporal dynamics of γ-diversity observed in the experiment (Fig. 3D; note that variation in *K* alone is not enough to reproduce the empirical pattern consistently; Fig. 3C). Thus, while the neutral model which captures only the effect of network structure on diversity was able to explain short-term diversity dynamics, only the model incorporating both a competition–colonization tradeoff and variation in K was able to match all empirically observed long-term diversity patterns (α-, β- and γ-diversity).

Discussion

Dendritic networks commonly occur in natural ecosystems, including riverine systems (Vannote et al. 1980, Grant et al. 2007, Finn et al. 2011, Altermatt 2013), and are theoretically expected to influence local and regional biodiversity patterns as well as species persistence (Muneepeerakul et al. 2008, Rodriguez-Iturbe et al. 2009). Experimental verifications, however, have focused on momentary diversity patterns (i.e. single snapshots in time; Carrara et al. 2012, 2014), thereby ignoring the spatio-temporal dynamics of dispersal and community composition. However, species diversity is often the result of spatio-temporal dynamics, including post-glacial recolonization, species sorting and species invasions. Therefore, studies of community composition in complex networks should not only include spatial, but also temporal perspectives (Yeakel et al. 2014).

Utilizing microcosm experiments with active dispersal in dendritic and linear networks, we found that community diversity patterns were driven by the interaction of dispersal and network structure as well as local species interactions (Fig. 1–3). We experimentally demonstrated that community diversity patterns characteristically observed in dendritic systems (Muneepeerakul et al. 2008, Rodriguez-Iturbe et al. 2009, Altermatt 2013) may not only be caused, but also

maintained over many generations due to the connectivity structure of dendritic networks. The experimentally observed dynamics were driven by dispersal of all species from individual network sites, and the different path lengths in linear versus dendritic networks. Consistent findings from the neutral metacommunity model, assuming only differences in network structure, suggest different network structures are the fundamental drivers of empirically observed β-diversity and initial α-diversity patterns. However, a purely neutralist perspective was not sufficient to reflect all experimentally observed α- and γ-diversity dynamics, especially in the long-term. These spatio-temporal diversity dynamics could only be captured by a metacommunity model, which included dispersal along the network structure, competition–colonization tradeoffs and species-specific variation in carrying capacity (Fig. 3). It is noteworthy that the individual processes contributing to the observed diversity patterns unfold differently in dendritic versus linear metacommunities over time, causing pronounced temporal dynamics of community diversity. All individual elements, network structure, competition–colonization tradeoffs and variation in carrying capacity have been individually shown to be important for driving community assembly (Cuddington and Yodzis 2002, Cadotte 2007, Muneepeerakul et al. 2008). Our numerical models of increasing complexity suggest all three processes in combination determine the experimentally observed spatio-temporal dynamics of diversity in dendritic networks (Fig. 3).

We acknowledge that the scope of microcosm experiments, as employed in our study, is to experimentally disentangle causalities and conceptually identify individual processes that can drive empirically observed patterns (reviewed by Holyoak and Lawler 2005). As such, our experiments inevitably leave out many aspects of the real world, as we did not mimic natural river systems or their detailed hydrological attributes such as flow or directional environmental gradients. Our work rather exemplifies the general importance of alternative connectivity patterns found in dendritic networks, active dispersal and species-specific tradeoffs in understanding spatio-temporal diversity patterns. Consequently, our findings are to be compared in a qualitative but not quantitative way to natural systems, and may especially be relevant for organisms exhibiting symmetric dispersal along dendritic networks, but need to be refined to include unidirectional drift.

Experimental findings

As expected, we found that the greater connectivity of dendritic networks increased local species richness (α-diversity) and species similarity among sites (β-diversity) over time compared to less connected linear networks (Fig. 1, 2). This is consistent with recent empirical and theoretical work showing that the dendritic structure of river networks, compared to linear networks, may increase species dispersal rates, which can lead to increased species diversity and metacommunity stability (Fagan 2002, Carrara et al. 2012, Altermatt et al. 2013, Liu et al. 2013, Peterson et al. 2013). However, previous studies used either passive dispersal (Carrara et al. 2012, 2014) or invasion scenarios into unoccupied landscapes (Seymour and Altermatt 2014) and did not consider temporal dynamics. By contrast, our experiment could address the temporal unfolding of dispersal and species interactions, as all sites were initially occupied by one species and allowed subsequent active colonization. The faster initial colonization (days 0–8 of the experiment) of the dendritic networks compared to the linear networks was mostly driven by decreased dispersal limitation as a result of the greater network connectivity within the dendritic network which could be explained with a simple neutral metacommunity model (Fig. 2, 3A). The relatively slow process of dispersal and colonization resulted in the spatial co-occurrence of species after an initial time delay of about 8–12 days, whereby local species richness was saturated. From that point onwards, additional model mechanisms to reflect the experimental findings, suggesting that species interactions and the potential effects of a colonization tradeoff (Cadotte 2007, Limberger and Wickham 2011) influenced the change in local (α-diversity) and global (γ-diversity) decay of species diversity (Fig. 2, 3B–D).

Interestingly, the above mentioned diversity patterns characteristic of dendritic networks persisted throughout long phases (> 20 days) of both of these processes, such that α-diversity remained higher in dendritic networks (Fig. 2), especially at central nodes of the network, and β-diversity among external versus internal nodes remained higher (Fig. 1, Supplementary material Appendix 1 Fig. A3). This time-span reflects 20–40 generations of our study organisms, and, while transitive, can still be highly relevant for many systems, especially those reset frequently due to disturbance.

Model interpretation

Our parallel numerical model aimed at pinpointing the mechanisms that are potentially responsible for the observed empirical patterns, and was not designed to fit the experimental system as exactly as possible, nor to predict its dynamics quantitatively. Thereby, it is in a broad class of models which aim at identifying the effects of general drivers of meta-population and -community dynamics, such as network structure (Fagan 2002, Mari et al. 2014), species interactions (Cuddington and Yodzis 2002) or patch dynamics (Reigada et al. 2015). Nevertheless, we not only found good agreement of the temporal diversity dynamics between the experiment (Fig. 2) and the models (Fig. 3), but also identified plausible mechanisms that likely drive the spatio-temporal community diversity patterns.

The model findings confirmed that α-diversity patterns are centrally influenced by the interaction of dispersal and the network structure (Fig. 3A). The higher connectivity of the dendritic networks led to a faster mixing of species compared to linear networks. In the absence of inter-specific interactions or very high dispersal rates we observed purely transient differences, whereby sites in dendritic networks saturated α-diversity earlier than sites in linear networks (Supplementary material Appendix 1 Fig. A6–A7). Inter-specific competition and other factors such as stochasticity (e.g. mediated by small carrying capacities; Supplementary material Appendix 1 Fig. A8 left panels) leading to local extinctions are then responsible for a saturation of α-diversity below the expected maximum of all species. As these extinctions are local, γ-diversity was not strongly depreciated, but the differences in α-diversity were temporarily stabilized

(Supplementary material Appendix 1 Fig. A10). A decrease in γ-diversity, as observed in the microcosm experiments, happened only after the introduction of a competition–colonization tradeoff as an additional mechanism (Fig. 3B). Such a tradeoff led to global species extinctions in the long run, as observed in our empirical (Fig. 2) and theoretical results (Fig. 3B–D). Finally, we took into account a cause of species extinctions that is not a function of dispersal: variation in carrying capacity (Fig. 3C–D). The empirical data suggested an important variation in this parameter and its incorporation allowed us to highly reproduce the empirical patterns (Fig. 3D).

Note that our model results are largely robust to changes in reproductive rate, the strength of inter-specific interactions, the dispersal rate, carrying capacity and the strength of the competition–colonization tradeoff. Higher reproductive rates and stronger inter-specific interactions (as long as intra- and inter-specific interactions are at least comparable in strength) generally sped up the systems' dynamics (Supplementary material Appendix 1 Fig. A5–A6; see Supplementary material Appendix 1 Fig. A10 for the long-term dynamics). Increasing dispersal rates and increased carrying capacity had a stabilizing effect (Supplementary material Appendix 1 Fig. A7–A8). This led to less local and global extinctions and to higher local species diversity. Increasing the strength of the competition–colonization tradeoff (Supplementary material Appendix 1 Fig. A9) does not alter our results qualitatively; again it only speeds up the systems' dynamics.

For the long-term dynamics of the system, the neutral model predicts that dendritic networks are able to sustain higher local and global species diversity (Supplementary material Appendix 1 Fig. A10). This is mainly due to altered dispersal patterns, which result in rescue effects and more generally in a homogenization of population sizes preventing local extinctions due to demographic stochasticity or inter-specific competition. Trivially, if we assume a competition–colonization tradeoff, the long-term stable state of both systems is identical, as the most competitive species will exclude all others. Note that a dendritic network structure slows down these dynamics.

Conclusions

Our experimental results suggest that contemporary diversity patterns in dendritic networks (Grant et al. 2007, Altermatt 2013, Peterson et al. 2013) are to an important extent driven by the characteristic connectivity of the network itself. Additional processes unfolding at different timescales, such as species interactions and local extinctions due to specific tradeoffs as well as the potential global loss of diversity due to stochastic or deterministic effects may modulate these patterns. The interplay of these processes likely drives the characteristic community diversity patterns observed in dendritic networks (Muneepeerakul et al. 2008, Rodriguez-Iturbe et al. 2009, Liu et al. 2013).

Importantly, many of these processes are currently influenced by anthropogenic activities, including modifications of network connectivity and introduction of non-native species (Leuven et al. 2009, Rodriguez-Iturbe et al. 2009, Lynch et al. 2011, Grant et al. 2012), thereby potentially affecting the community composition of all organisms. As the spatio-temporal unfolding of these processes and subsequent effects on community composition may be long lasting, transient dynamics and legacies of past modifications need to be considered when aiming at understanding diversity patterns in dendritic networks.

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References

Altermatt, F. 2013. Diversity in riverine metacommunities: a network perspective. – Aquat. Ecol. 47: 365–377.

Altermatt, F. et al. 2011a. Effects of connectivity and recurrent local disturbances on community structure and population density in experimental metacommunities. – PLoS ONE 6: e19525.

Altermatt, F. et al. 2011b. Interactive effects of disturbance and dispersal directionality on species richness and composition in metacommunities. – Ecology 92: 859–870.

Altermatt, F. et al. 2013. River network properties shape α-diversity and community similarity patterns of aquatic insect communities across major drainage basins. – J. Biogeogr. 40: 2249–2260.

Altermatt, F. et al. 2015. Big answers from small worlds: a user's guide for protist microcosms as a model system in ecology and evolution. – Meth. Ecol. Evol. in press. 6: 218–231.

Baguette, M. et al. 2013. Individual dispersal, landscape connectivity and ecological networks. – Biol. Rev. 88: 310–326.

Barták, V. et al. 2013. Spatial spread of Eurasian beavers in river networks: a comparison of range expansion rates. – J. Anim. Ecol. 82: 587–597.

Besemer, K. et al. 2013. Headwaters are critical reservoirs of microbial diversity for fluvial networks. – Proc. R. Soc. B 280: 20131760.

Beverton, R. J. H. and Holt S. J. 1957. On the dynamics of exploited fish populations. – Fish. Invest. Ministry Agric. Fish. Food (GB) Ser. II, No. 19.

Boulangeat, I. et al. 2012. Accounting for dispersal and biotic interactions to disentangle the drivers of species distributions and their abundances. – Ecol. Lett. 15: 584–593.

Brown, B. L. and Swan, C. M. 2010. Dendritic network structure constrains metacommunity properties in riverine ecosystems. – J. Anim. Ecol. 79: 571–580.

Cadotte, M. W. 2007. Competition–colonization tradeoffs and disturbance effects at multiple scales. – Ecology 88: 823–829.

Carrara, F. et al. 2012. Dendritic connectivity controls biodiversity patterns in experimental metacommunities. – Proc. Natl Acad. Sci. USA 109: 5761–5766.

Carrara, F. et al. 2014. Complex interaction of dendritic connectivity and hierarchical patch size on biodiversity in river-like landscapes. – Am. Nat. 183: 13–25.

Cuddington, K. and Yodzis, P. 2002. Predator–prey dynamics and movement in fractal environments. – Am. Nat. 160: 119–134.

Dijkstra, K. et al. 2013. Freshwater biodiversity and aquatic insect diversification. – Annu. Rev. Entomol. 59: 143–163.

Economo, E. P. and Keitt, T. H. 2010. Network isolation and local diversity in neutral metacommunities. – Oikos 119: 1355–1363.

Etienne, R. S. and Rosindell, J. 2011. The spatial limitations of current neutral models of biodiversity. – PLoS ONE 6: e14717.
Fagan, W. F. 2002. Connectivity, fragmentation, and extinction risk in dendritic metapopulations. – Ecology 83: 3243–3249.
Finn, D. S. et al. 2011. Small but mighty: headwaters are vital to stream network biodiversity at two levels of organization. – J. N. Am. Benthol. Soc. 30: 963–980.
Giometto, A. et al. 2014. Emerging predictable features of replicated biological invasion fronts. – Proc. Natl Acad. Sci. USA 111: 297–301.
Göthe, E. et al. 2013. Metacommunity structure in a small boreal stream network. – J. Anim. Ecol. 82: 449–458.
Grant, E. H. C. et al. 2007. Living in the branches: population dynamics and ecological processes in dendritic networks. – Ecol. Lett. 10: 165–175.
Grant, E. H. C. et al. 2012. Interbasin water transfer, riverine connectivity, and spatial controls on fish biodiversity. – PLoS ONE 7: e34170.
Holyoak, M. and Lawler, S. P. 2005. The contribution of laboratory experiments on protists to understanding population and metapopulation dynamics. – Adv. Ecol. Res. 37: 245–271.
Holyoak, M. et al. 2005. Metacommunities. Spatial dynamics and ecological communities. – Univ. of Chicago Press.
Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. – Princeton Univ. Press.
Jost, L. 2006. Entropy and diversity. – Oikos 113: 363–375.
Jurasinski, G. 2012. simba: a collection of functions for similarity analysis of vegetation. – GFZ Sci. Tech. Rep. STR10/10: 129–133.
Kneitel, J. M. and Chase, J. M. 2004. Tradeoffs in community ecology: linking spatial scales and species coexistence. – Ecol. Lett. 7: 69–80.
Leibold, M. A. et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. – Ecol. Lett. 7: 601–613.
Leuven, R. et al. 2009. The river Rhine: a global highway for dispersal of aquatic invasive species. – Biol. Invas. 11: 1989–2008.
Limberger, R. and Wickham, S. 2011. Competition–colonization tradeoffs in a ciliate model community. – Oecologia 167: 723–732.
Liu, J. et al. 2013. Effects of connectivity, dispersal directionality and functional traits on the metacommunity structure of river benthic diatoms. – J. Biogeogr. 40: 2238–2248.

Supplementary material (available online as Appendix oik.02354 at <www.oikosjournal.org/readers/appendix>). Appendix 1.

Lynch, H. J. et al. 2011. How restructuring river connectivity changes freshwater fish biodiversity and biogeography. – Water Resour. Res. 47: W05531.
Mari, L. et al. 2011. Hydrologic controls and anthropogenic drivers of the zebra mussel invasion of the Mississippi–Missouri river system. – Water Resour. Res. 47: W03523.
Mari, L. et al. 2014. Metapopulation persistence and species spread in river networks. – Ecol. Lett. 17: 426–434.
Muneepeerakul, R. et al. 2008. Neutral metacommunity models predict fish diversity patterns in Mississippi–Missouri basin. – Nature 453: 220–222.
Newman, M. E. J. 2010. Networks: an introduction. – Oxford Univ. Press.
Nunney, L. 1990. *Drosophila* on oranges: colonization, competition and coexistence. – Ecology 71: 1904–1915.
Peterson, E. E. et al. 2013. Modelling dendritic ecological networks in space: an integrated network perspective. – Ecol. Lett. 16: 707–719.
Reigada, C. et al. 2015. Metapopulation dynamics on ephemeral patches. – Am. Nat. 185: 183–195.
Rodriguez-Iturbe, I. and Rinaldo, A. 1997. Fractal river networks: chance and self-organization. – Cambridge Univ. Press.
Rodriguez-Iturbe, I. et al. 2009. River networks as ecological corridors: a complex systems perspective for integrating hydrologic, geomorphologic and ecologic dynamics. – Water Resour. Res. 45: W01413.
Seymour, M. and Altermatt, F. 2014. Active colonization dynamics and diversity patterns are influenced by dendritic network connectivity and species interactions. – Ecol. Evol. 4: 1243–1254.
Turnbull, L. A. et al. 2004. Seed mass and the competition/colonization tradeoff: competitive interactions and spatial patterns in a guild of annual plants. – J. Ecol. 92: 97–109.
Vannote, R. L. et al. 1980. The river continuum concept. – Can. J. Fish. Aquat. Sci. 37: 130–137.
Vörösmarty, C. J. et al. 2010. Global threats to human water security and river biodiversity. – Nature 467: 555–561.
Whitham, T. G. 1978. Habitat selection by pemphigus aphids in response to response limitation and competition. – Ecology 59: 1164–1176.
Wood, S. N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. – J. R. Stat. Soc. B 73: 3–36.
Yeakel, J. D. et al. 2014. Synchronisation and stability in river metapopulation networks. – Ecol. Lett. 17: 273–283.
Zuur, A. F. et al. 2009. Mixed effects models and extensions in ecology with R. – Springer.