Biological invasions are globally affecting ecosystems, causing local species loss and altering ecosystem functioning. Understanding how such biological invasions occur and succeed is thus of high priority. Both local properties and the spatial network structure have been shown to be determinants of invasion success, and the identification of spatial invasion hubs directly promoting invasion dynamics is gaining attention. Spatial dynamics, however, could also indirectly alter invasion success by shaping pre-invasion local community structure: in many ecosystems, such as riverine networks, regional properties such as patch size distribution are known drivers of local community structures, which themselves may affect the establishment success of invading species. Using microcosm experiments in dendritic networks, we disentangled how inherent patch size distribution and dispersal along specific network topologies shaped local resident communities, and, subsequently, affected the establishment success of invading species. After controlling for regional scale effects of connectivity on pre-invasion diversity, we find that patch size distributions independently shaped pre-invasion community diversity and invasion success, with no direct effect of pre-invasion diversity on invasion success. Our results suggest that 1) landscape configuration plays an underestimated role in invasion success and that 2) invasion success should follow predictable landscape-scale patterns in riverine networks given non-random patch-size distribution.

Keywords: biodiversity change, dendritic networks, invasive species, microcosm experiment, protists

Introduction

Biodiversity is rapidly changing worldwide and declines are predicted to continue for the coming decades (Chapin et al. 2000, Sala et al. 2000, Pereira et al. 2010). One major factor contributing to this decline are biological invasions, often occurring as a by-product of increased human mobility, global trade and changes in habitat or ecosystem properties (Sala et al. 2000, Mooney and Cleland 2001). Species invading new...
ecosystems can partially or completely out-compete, predate or displace native species, with subsequent impacts on ecosystem functioning (Clavero and García-Berthou 2005, Pereira et al. 2010), calling for a mechanistic understanding of species invasion success and the ecological drivers of it.

Invasion success has been linked to local properties of the communities and ecosystems (Stachowicz et al. 1999, Levine et al. 2004, Mächler and Altermatt 2012, Kempel et al. 2013), but also to regional properties and spatial landscape structures (Deckers et al. 2005, Mari et al. 2014, Altermatt and Fronhofer 2018). The former is relatively straightforward: local conditions related to resource availability and the functional niche of each resident species will directly influence the establishment success of an invading species. As such, biodiversity and other properties of the community have been proposed as important local modulators of species invasion success (Levine and D’Antonio 1999, Stachowicz et al. 1999, Levine et al. 2004). Overall, most studies indicate a positive effect of species diversity in reducing species invasions (Elton 1933, Tilman 1997, Wardle 2001, Kennedy et al. 2002, but see Hooper et al. 2005 on the possible scale-dependency of this effect), mostly because a diverse community is assumed to already have filled the available niches with resident species efficiently using the available resources. Consequently, it is more difficult for an invader to establish and persist.

The effects of regional connectivity and spatial landscape structure are more complex. Firstly, spatial dynamics directly modulate how invading species get to a specific location, and thereby affect invasion dynamics. In this context, the spatial unfolding of invasion fronts (Giometto et al. 2014, Williams et al. 2016), as well as the significance of specific hubs in spatial networks on invasion success have been receiving increasing attention (Morel-Journel et al. 2019). Secondly, however, the physical configuration of the landscape and the spatial dynamics it generates will also modulate invasion success indirectly by influencing local community structure and dynamics such as diversity or identity of species found locally (MacArthur and Wilson 1963, Holoyak et al. 2005, Holland and Hastings 2008, Pillai et al. 2011, McIntosh et al. 2018).

As virtually all species live in a spatial landscape of connected habitats, this spatial perspective is highly relevant. These intricate effects of spatial dynamics on invasion success are expected in all spatially structured landscapes, but may be especially pronounced in spatial networks with a complex but also non-random spatial structure (Rodriguez-Iturbe and Rinaldo 1997).

A classic example of such landscapes are dendritic riverine networks, which are also among the ecosystems most strongly affected by invasive species (Leuven et al. 2009, Reid et al. 2019). Riverine networks follow well described topological structure and have general properties that are highly conserved across all rivers globally (Rodriguez-Iturbe and Rinaldo 1997, Altermatt 2013), including their hierarchic structure with physical flows and inherent scaling of hydrologic parameters with catchment area. These dendritic networks are scale-free (i.e. fractal) and shaped by universal physical processes. Importantly, their unique features, such as scaling of patch size distribution with drainage area, found in these networks irrespective of their individual unique realization and natural riverine networks can be very closely approximated with so-called optimal channel networks (Rodriguez-Iturbe and Rinaldo 1997, Carraro et al. 2020). The latter allow them to be studied in a formalized way. A key aspect and inherent feature of these networks is that position in the network, patch size/catchment area and further topological aspects are intrinsically correlated.

From an ecological perspective, it is well known that dispersal and metacommunity dynamics are essential to properly describe the spatial linkage between communities in riverine networks (Altermatt 2013, Seymour et al. 2015, Tonkin et al. 2018). Also, connectivity and network structure are known to have a central role in shaping local population dynamics and species composition (Corre et al. 2015, Layeghifard et al. 2015, Altermatt and Fronhofer 2018). Specifically, riverine landscapes possess typical and invariant characteristics leading to higher species diversity at confluences of branches and in lower reaches of the stream (Fernandes et al. 2004, Muneepeerakul et al. 2007, Rodriguez-Iturbe et al. 2009). Experiments in dendritic landscapes have shown that those diversity patterns are primarily shaped by the connectivity of habitats and the directionality of dispersal between habitats (Carrara et al. 2014, Seymour et al. 2015), but can also be modulated by disturbances (Harvey et al. 2018).

Consequently, it has been speculated that predicting invasion dynamics requires a better understanding of regional influences related to landscape network structure (Mari et al. 2014). Previous work has thus independently studied the relationships between habitat size and diversity, connectivity and diversity, and the effect of species diversity on invasion success (Kennedy et al. 2002, Drakare et al. 2006, Carrara et al. 2012, Meier and Hofer 2016). However, little is known about the interactive effects of habitat connectivity, habitat size and species diversity on invasion success.

In this study, we experimentally tested how well-conserved habitat size distribution and connectivity in dendritic networks are shaping local community composition, and, subsequently, affecting the resistance of these communities to species invasions. We conducted microcosm experiments with protist and rotifer species, in which we first let the local ‘resident’ communities assemble across replicated dendritic networks with constant patch size spatial distribution and in isolated controls. We employed nearest-neighbor passive dispersal, and community assembly included both direct competition and ecological drift. Subsequently, a common invader species was added into each patch of the local communities and dispersal was halted (i.e. no dispersal occurred after invader had been added). This allowed us to address the invasibility of each community, and to disentangle effects of local community properties per se versus the regional dynamics influencing resident community assembly prior to invasion. In other words, we tested if and how the network structure and patch size distribution in generic dendritic networks ‘primes’ the local communities with respect to their invasibility or not. We assessed short- and long-term
invasion success. The invasion success was assessed for each local community individually, thereby disentangling effects of local properties with the effects of spatial network position. We investigated the effect of patch connectivity and patch size on invaders’ establishment using presence and absence data of invaders. We hypothesized that the invasion success is lower in large patches. Those larger more connected patches are expected to support higher species diversity when invasion starts, with assumed higher resource complementarity, higher proportion of used resources and therefore lower availability of resources for invaders (Wardle 2001). On the contrary, the invasion success was expected to be higher in small and more isolated patches with low resource complementarity and low species diversity, a low proportion of used resources, and higher resource availability for invaders. We also assumed that the imprint this spatial connectivity leaves on local communities subsequently reduces invasion success, because past dispersal dynamics (compared to the isolated controls) should have made communities more resistant to invading species by maintaining higher pre-invasion diversity.

**Methods**

We studied community assembly and subsequent invasion dynamics in experimental dendritic networks (Fig. 1). We used five independent landscape structures representing riverine dendritic networks (A–E), with 36 patches in each landscape (Supporting information). These landscapes were generated by an optimal channel networks (OCN) algorithm (Carraro et al. 2019, 2020). OCNs are spanning trees that reproduce all important and scale-free characteristics inherent to all natural stream networks (Carraro et al. 2020). Thus, their structure captures geomorphological and hydrological characteristics of rivers. Specifically, they reproduce connectivity, catchment area and patch size scaling distributions observed in real river systems. Importantly, in natural streams as well as in OCNs, these values are highly colinear, and thus their effects on ecological dynamics may go hand in hand (e.g. patch size and connectivity being positively correlated). OCNs are generated using a stochastic process, and thus many different realizations of networks can be generated, but all with overall the same properties. In this case, to ensure

![Figure 1. Experimental setup. Five dendritic landscapes, each with 36 connected patches following a realistic patch size scaling structure, as well as 40 single patch controls were each inoculated with the same community of five protist species and one rotifer. Subsequent community structure and biodiversity was shaped by dispersal and species interactions over a period of 21 days (single patch controls without dispersal). Thereafter, dispersal was halted, and the species _Spirostomum_ sp. was added to each patch, and its invasion (establishment) success was assessed at two subsequent time points. The colour of the patches represents species biodiversity patterns (light green: low diversity, dark green: high diversity).](image_url)
comparability to previous studies, the five specific realized OCNs used were the same as in previous experiments (see Appendix in Carrara et al. 2014). For logistic reasons, patch sizes were binned in four categories (3, 5.2, 9, 18 ml), and as a control we had 10 isolated replicates (isolated ‘control’) for each of these patch sizes (in total 40 control patches; Fig. 1). Importantly, some of the variables examined, such as position in the network and patch size, are inherently linked in these dendritic riverine networks. The chosen statistical approach allowed us to specifically describe these dependencies.

We introduced five protist and one rotifer species (subsequently all referred to as ‘protists’) into each patch and then monitored the subsequent community assembly shaped by dispersal, species interactions and ecological drift (phase 1; Fig. 1). We then halted dispersal, and assessed the invasibility potential of each of these communities, by introducing an invading species to each of these communities after three weeks of community assembly (phase 2). We investigated invasion success by measuring presence or absence of the invader on day four (8 generations, termed short-term invasion success) and day seven post-invasion (14 generations, termed long-term invasion success). Importantly, this design allowed us to separate the effect of spatial dynamics on community assembly (phase 1) from the subsequent test of invasion potential (phase 2), which was done for each of the patches independently.

**Community set-up and community assembly**

We used five freshwater protist and rotifer species for the community assembly: *Loxocephalus* sp., *Tetrahymena* sp., *Colpidium striatum*, *Dexiostoma campyllum*, *Paramecium caudatum* and *Cephalodella* sp. (a rotifer), in the following all referred to as ‘resident protist species’. These resident species were kept in a nutrient medium (Protist Pellet Medium, 0.46 g l−1) inoculated with the bacteria *Serratina fonticola*, *Brevibacillus brevis* and *Bacillus subtilis* as a food source. All protists and the rotifer are bacterivorous, and are thus directly competing for the same set of resources. Competitive hierarchy, body size distribution and community dynamics of this set of species is very well established (Warren 1996, McGrady-Steed et al. 1997, Holyoak and Lawler 2005, Altermatt et al. 2011, Giometto et al. 2013, Carrara et al. 2015, Pennekamp et al. 2018), with generation times of about 0.25–2 days, depending on the species (Carrara et al. 2012 for details). All these species have been used in many previous experiments, showing that they can form communities of varying diversity, and that outcome of direct competition between them is also shaped by environmental settings, such as patch size or disturbances. Previous to the experiment, all species had been kept as monocultures and kept under sterile conditions following Altermatt et al. (2015), where also further details on all experimental methods can be found.

At the onset of the experiment, we mixed the six resident species monocultures with a focal density of 33.3 individuals ml−1 per species (community-mix). From this community-mix we distributed 3 ml to all patches, such that it contained on average 100 individuals of each of the six resident species. Starting at these densities, well-below carrying capacity, allowed us to look at species assembly dynamics. We topped up the volume in the respective patches with protist medium to reach the final focal volumes (3, 5.2, 9, 18 ml).

We then applied a dispersal treatment twice a week (in total 5 times during 21 days). We applied undirected nearest neighbor dispersal along the network structure, using a method with mirror landscapes developed by Carrara et al. (2012) to avoid long-tailed dispersal. This particular type of density-independent dispersal assumes an equal per capita dispersal rate for all different species and therefore excludes competitive colonisation tradeoffs (Carrara et al. 2012). By using a nearest-neighbour dispersal, our results are directly comparable to previous experimental and theoretical work, and are specifically matching the dispersal mode generally used in most theoretical models (see a summary in Harvey et al. 2018). Dispersal is assumed to shape community assembly by counteracting local extinctions due to species interactions or ecological drift. At each dispersal step, patches were well-mixed and then a volume of 200 µl was transferred into each neighboring patch using the mirror landscape (Supporting information). In the isolated single patch controls no dispersal was conducted, but a volume of 200 µl was pipetted out and back into the same patch to control for the handling effect.

**Invasion assay**

*Spirostomum* sp. was chosen as the invader to these communities. It is a species that directly competes with the resident species for a common resource (bacteria), has a population growth rate of 0.57 day−1, its competitive ability is intermediate to the other species (for details and all species population growth rates and competitive abilities, see also Carrara et al. 2012, 2015), and it is known to be able to persist in the chosen patches and experimental settings. Importantly, this species was also chosen as invader because it is relatively large in comparison to the resident species (body length ~850 µm, for traits of all species see also Carrara et al. 2012), and thus can be tracked easily in the communities. Thereby, false-absences in the assessment of invasion success could be largely avoided.

Twenty-one days after the onset of the experiment, we stopped all dispersal, and added on average 10 *Spirostomum* sp. individuals in a volume of 200 µl to each patch. We intentionally added this invading species at an initially low number to match natural scenarios of species invasions. Four days and seven days after this invasion, presence or absence of the invader was assessed (referred to as short-term and long-term invasion success). To do so, we screened the invader’s presence in a subsample of 175 µl under a stereo microscope. When *Spirostomum* sp. was not present in the subsample screened for the long-term invasion success, we additionally screened a total volume of 1.5 ml.

In parallel, we used a video-based monitoring method to assess community structure and diversity of resident communities. We recorded and analyzed the community in each
patch of the connected dendritic landscapes and isolated single patch controls at three different time points: immediately preceding the invasion, four days after the invasion, and seven days after the invasion. The videos for community analysis were taken from 175 µl subsamples, of which a total volume of 34.4 µl was recorded for 5 s (25 frames per second, 16x fold magnification, full light) by a digital Orca Flash 4.0 camera. We closely followed the method and the R package BEMOVI developed and used by Pennekamp et al. (2015, 2017). The settings for BEMOVI script were the following: pixel size of 4.05 µm, difference lag of 10 frames, thresholds of 10–255 difference of pixel intensity, min particle size 5 pixels, max particle size 1000 pixels, link range 3 frames, displacement 16 pixels, detection frequency of 0.1 s, median step length of 3 pixels.

To identify species, we used a random forest algorithm. This algorithm is based on decision trees using binary thresholds to divide the observations into the most probable class at the end node (Pennekamp et al. 2017). The information about morphological and movement features for classification were given from BEMOVI (Pennekamp et al. 2017).

**Statistical analyses**

We calculated Shannon diversity of the community in every patch using the R-package vegan (ver. 2.4-3, Oksanen et al. 2019). The degree connectivity of each patch (i.e. number of connecting nodes) and distance to outlet were calculated directly from the respective network adjacency matrices. Additionally to connectivity, distance to the outlet provides information about the position in the network. We analyzed the effects of landscape type (dendritic networks versus isolated controls), patch size and their interaction on diversity before the invasion using an analysis of variance (Anova). To correct for the non-independence of patches within the landscapes, we used a conservative approach and calculated the mean Shannon diversity values per patch size and dendritic network (five landscapes and four patch sizes, in total 20 mean values). In the controls, each value was independent, thus 10 replicates per patch sizes, in total 40 values.

Our main interest was to test for the indirect effect of landscape configuration on invasion success via an effect on pre-invasion community structure (diversity). Thus, as mentioned above, we stopped dispersal among patches prior to invasion by *Spirostomum sp.* (Fig. 1), allowing us to test the modulating effect of landscape configuration on pre-invasion diversity. To disentangle those direct and indirect paths statistically, we used a piecewise structural equation model (SEM) to analyze the invasion success of *Spirostomum sp.* in the dendritic networks using the R-package piecewiseSEM (ver. 2.1.0, Lefcheck 2016). SEMs are probabilistic models that unite predictor and response variables to evaluate multivariate causal relationships and hypothesis in complex network structures (Grace 2006, Fan et al. 2016). We tested the direct and indirect effects between the four explanatory variables distance to outlet, connectivity, patch size and pre-invasion Shannon diversity on the invasion success of *Spirostomum sp.* Network metrics are often highly correlated (see the Supporting information for the correlation between the three network metrics used individually for each of the dendritic landscapes) making it challenging to statistically disentangle their independent effects. Using SEMs allowed us to control for residual co-variance among our network metrics (distance to outlet, connectivity and patch size). We tested whether the five independent landscape structures (A–E) had an influence on the SEM results. For this purpose, we ran independent general linear mixed models on invasion success and diversity before invasion with and without random effects outside the SEM.

Statistical analyses were done in R (ver. 3.3.3 and ver. 4.0.2 (piecewise SEM), <www.r-project.org>.

**Results**

Dispersal in the dendritic landscapes affected community assembly and resulted in a characteristic diversity distribution: Shannon diversity index ($S_H$) immediately preceding the invasion varied between 0.32 and 1.42, with smallest values found in small and/or more isolated patches (Fig. 2, 3, Supporting information), while highest values were found in the largest patches. Overall, in dendritic landscapes, mean $S_H$ immediately preceding invasion increased steadily from small (3 ml) to large (18 ml) patches (mean $S_H$ with increasing patch size: 0.70, 0.74, 0.96, 1.09, Fig. 3). Although pre-invasion diversity seemed more variable (higher variance) in smaller patches, especially in the experimental connected landscapes, a Levene’s test of homogeneity demonstrated that this is not the case (in connected landscapes: df=3, F-value=0.92, p = 0.433; in controls: df=3, F-value=0.21, p = 0.89). Diversity in single patch controls also increased significantly with patch size (Fig. 3), but was on average not significantly lower in the isolated controls compared to the diversity in the dendritic network (all statistical details in the Supporting information).

We then analyzed invasion success of *Spirostomum sp.* in the landscapes (see Fig. 4 for short-term invasion success and the Supporting information for long-term invasion success) and the controls. The short-term invasion success of *Spirostomum sp.* in the dendritic landscapes was highest in the small patches (3 ml) and lowest in the large patches (18 ml). The mean proportion of successful invasions was 9.5 times higher in the small 3 ml patches (0.57) compared to the 18 ml patches (0.06).

The results of the piecewise SEM showed that patch size was the only significant explanatory variable for both the invasion success of *Spirostomum sp.* and for shaping Shannon diversity preceding invasion in the dendritic network structure (Fig. 5, Table 1: SEM: Fisher’s C = 1.36, p = 0.85, df = 4). Patch size had a direct positive effect on diversity prior to invasion and a direct negative effect on invasion success. However, because there were no direct effect of diversity before invasion on invasion success, there were also no indirect effect of patch size on invasion success (modulated by diversity before invasion).
Figure 2. Shannon diversity ($S_H$) of the resident communities immediately preceding the invasion of *Spirostomum* sp. across the dendritic landscapes (A–E) and the isolated single patch controls. Overall, small patches had lower diversity than large patches (light green: low diversity, dark green: high diversity).

Figure 3. (A) Shannon diversity index ($S_H$) before invasion in the single patch controls and the landscape. Diversity is lowest in the small (3 ml) patch (mean = 0.70) and highest in the large (18 ml) patch (mean = 1.07). (B) Proportion of short-term invasion success in single patch controls and the landscapes. Four days after the invasion of *Spirostomum* sp., a volume of 175 µl was screened for the invader under a stereomicroscope. Numbers above the bars are according to the total numbers of patches. In both panels, standard errors of the mean are shown.
Figure 4. Short-term invasion success of *Spirostomum* sp. across the dendritic landscapes (A–E) and the isolated single patch controls.

Figure 5. Assumptions on causal relationships between the variables used in the structural equation model (SEM): distance to the outlet, connectivity, patch size and Shannon diversity ($S_H$) of the resident communities immediately preceding the invasion on the invasion success of *Spirostomum* sp. Significant coefficients ($p < 0.05$) of the SEM are shown as solid lines, non-significant as dashed lines. Negative relationships are shown in red. Unstandardized coefficients shown in brackets. The specific relationships to evaluate are the direct effect of patch size on invasion success, and the effect of diversity (modulated by patch size) on invasion success.
Table 1. Output of the piecewise structural equation model (SEM). Variables: distance to the outlet, connectivity, patch size and Shannon diversity ($S_0$) of the resident communities immediately preceding the invasion and invasion success of Spirostomum sp.

| Response | Predictor | Estimate | SE | df | Crit. value | p-value | St.est. | Signif. |
|----------|-----------|----------|----|----|-------------|---------|---------|---------|
| Invasion success | ~ distance to outlet + ... | S0 | -0.11 | 0.786 | 176 | -0.144 | 0.89 | -0.013 | *** |
| Invasion success | ~ connectivity + ... | Patch size | -0.24 | 0.737 | 176 | -3.21 | 0.0013 | -0.48 | *** |
| $S_0$ | Distance to outlet | -0.0038 | 0.012 | 176 | -3.03 | 0.7 | -0.027 | *** |
| $S_0$ | Connectivity | -0.0044 | 0.0154 | 176 | -0.29 | 0.78 | -0.024 | *** |
| $S_0$ | Patch size | 0.028 | 0.00056 | 176 | 4.95 | < 0.001 | 0.5 | *** |
| ~Patch size | ~ Connectivity | 0.63 | - | 178 | 10.7 | < 0.001 | 0.63 | *** |
| ~distance to outlet | ~ Patch size | -0.63 | - | 178 | -10.9 | < 0.001 | -0.63 | *** |

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05

Global goodness-of-fit: Fisher’s $C = 1.36$ with p-value = 0.85 and on 4 degrees of freedom

Coefficients:

| Response | Predictor | Estimate | SE | df | Crit. value | p-value | St.est. | Signif. |
|----------|-----------|----------|----|----|-------------|---------|---------|---------|
| Invasion success | ~ distance to outlet + ... | S0 | -0.11 | 0.786 | 176 | -0.144 | 0.89 | -0.013 | *** |
| Invasion success | ~ connectivity + ... | Patch size | -0.24 | 0.737 | 176 | -3.21 | 0.0013 | -0.48 | *** |
| $S_0$ | Distance to outlet | -0.0038 | 0.012 | 176 | -3.03 | 0.7 | -0.027 | *** |
| $S_0$ | Connectivity | -0.0044 | 0.0154 | 176 | -0.29 | 0.78 | -0.024 | *** |
| $S_0$ | Patch size | 0.028 | 0.00056 | 176 | 4.95 | < 0.001 | 0.5 | *** |
| ~Patch size | ~ Connectivity | 0.63 | - | 178 | 10.7 | < 0.001 | 0.63 | *** |
| ~distance to outlet | ~ Patch size | -0.63 | - | 178 | -10.9 | < 0.001 | -0.63 | *** |

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05

Individual $R^2$

| Response | Method | $R^2$ |
|----------|--------|-------|
| Invasion success | nagelkerke | 0.16 |
| 2003S0 | nagelkerke | 0.26 |

(Fig. 5). Neither connectivity nor distance to the outlet explained the community diversity patterns in the network structure prior to invasion. However, there was (as expected) a significant positive correlation between connectivity and patch size, and a significant negative correlation between distance to the outlet and patch size, which is an intrinsic characteristic of dendritic riverine networks, and is thus an indirect contributor to patch size as significant explanatory variable for the invasion success of Spirostomum sp. (Table 1). By prohibiting movement of Spirostomum sp. between patches, neither connectivity nor distance to the outlet could have a direct effect on invasion success. However, connectivity and distance to the outlet were the spatial components that shaped species diversity patterns in the network structure and consequently could indirectly affect the invasion success of Spirostomum sp. Distance to outlet, connectivity and patch size indirectly affect the invasion success of Spirostomum sp., via diversity patterns in the dendritic network.

Running general linear mixed effects models independent of the SEM showed no difference between the results when the independent landscape structures (A–E) were introduced as random factors or not (see Supporting information for statistical details). Model selection based on AIC supports the SEM models without random effects.

Discussion

Understanding invasion success of species has been a long-standing question in ecology (Elton 1933), and both local properties of the community as well as spatial dynamics/spatial network structures have been used to explain invasion success. We here experimentally addressed how these two views may go hand in hand: spatial dynamics, especially the spatial arrangement of patch size and dispersal among these patches, are shaping local communities, and can thereby indirectly modulate these communities’ resistance to invasions. This is likely a strongly understudied, but crucial mechanism: focusing on local or spatial drivers only will not give realistic understanding on how invasions in natural ecosystems emerge.

In our experimental dendritic networks, invasion success was modulated by patch size: both short- and long-term invasion success were higher in smaller patches (Fig. 4, 5, Supporting information). While there was also a strong effect of patch size on diversity, there was no significant direct effect of pre-invasion diversity on the invasion success: all explanatory power on invasion success remained on patch size, and there was not further variation explained by realized diversity in patches of identical size. While resident communities were shaped and emerged by the interplay of both local dynamics (ecological selection and drift) and spatial dynamics (dispersal, in this case along a well-defined and realistic habitat network structure), this thus did not translate into subsequent effects of spatial dynamics (dispersal and position in the network) on invasion success.

Most past studies have tested the impact of pre-invasion diversity while ignoring the spatial dynamic that led to that diversity. Especially in observational studies, this means that the ‘diversity’ effect contains the hidden influence of those processes that generated that diversity in the first place, for instance, if diversity before invasion is measured along a landscape of varying habitat sizes or connectivity level (as is the case for riverine networks). Here we were able to show that when controlling for regional properties (connectivity, patch size and distance to outlet), patch size becomes the
sole influencer of invasion success. Our main findings are about patch size and its effects on invasion success. In a riverine network, however, where patch size distribution is highly conserved and non-random, this outlines the possibility that 1) landscape configuration may play an underestimated role in invasion success (yet would need to be tested by conserving patch size distribution in the network or not) and that 2) invasion success should follow predictable landscape-scale patterns in riverine networks. Finally, in terms of mechanisms it suggests that 3) patch size influences invasion success via other (and not measured in this study) structuring properties of the resident community than just diversity (e.g. potentially by affecting the identity of the species present by favoring the presence of stronger competitors).

The direct effect of habitat network structure, and so-called ‘invasion hubs’ has been recently shown in studies of ecological invasions (Morel-Journel et al. 2019). Also, recent experimental and theoretical work indicated that the spatial percolation of local perturbations will be shaped (and potentially halted) by specific spatial network topologies (Gilarranz and Bascompte 2012, Gilarranz et al. 2015). In these studies, however, invasion was concurrently occurring with dispersal between patches. Here, we separated the effect of spatial dynamics (dispersal) and subsequent modulations of communities, altering their resistance to invasions. Our work now proposes that the regional scale properties of landscapes, such as patch size, are of highest overall relevance for independently shaping the local properties, namely community pre-invasion diversity and invasibility.

While invasion success has repeatedly been found to be negatively correlated with community diversity measures (Tilman 1997, Stachowicz et al. 1999, Naeem et al. 2000, Kennedy et al. 2002), there is still some controversy on how this plays out in natural systems, and it may be context-dependent. In contrast to many past studies we could not find evidence of biotic resistance generated by higher pre-invasion diversity (Harvey et al. 2016, Bullock et al. 2018). Likely, in our case, such diversity effects were not strong enough given the relatively low level and variation in species richness (max. six resident species) in our experimental set-up.

Biological invasions, and their consequences on natural communities, are likely to become even more important in the future (Ricciardi et al. 2017). By showing that well-known regional scale properties, such as patch size and connectivity, affect both pre-invasion diversity and invasion success, we unite two previously often disconnected lines of argumentation when understanding the (spatial) unfolding of invasions. Notably, however, the maintenance and management of spatial networks is a two-sided sword: regional scales properties such as patch size and connectivity as well as spatial dynamics can make local communities more resistant to invasions. However, they are also the way that biological invasions spread in space. While isolation and disconnecting spatial networks may seem a viable strategy to reduce the spread of biological invasions, we believe that this may be short-sighted: the lack of sufficient spatial dynamics will eventually lead to the loss of local diversity. We thus emphasize that it is essential to manage natural ecosystem networks as well as invasive species on a regional landscape level.

Speculations and alternative viewpoints

Importantly, and as a cautionary remark emerging from our exchange with and inputs by the reviewers, our study was done in networks in which patch size, patch size distribution and connectivity are inherently correlated (Supporting information), and their individual contributions to invasion success cannot be completely teased apart (but see Carrara et al. 2014). Thus, while our SEM approach identified patch size as the main explanatory factor modulating invasibility, patch size in these dendritic networks is inherently linked to position within the network, possibly making local and spatial properties shaping invasion success. This, however, would require further studies in which each landscape configuration would be replicated, and in which patch size distribution and network position would be disentangled (Carrara et al. 2014). Due to technical constraints this would be ideally addressed through simulation studies first. Finally, while we separated community assembly and dispersal from the invasion process, it is clear that in natural systems these processes often go hand in hand: invading species will also disperse between patches, possibly affect community structure and causing the opportunity for feedbacks on subsequent invasion success. We acknowledge that our experiment is simplistic in distinctly separating these processes in time, thereby omitting the possibility of non-trivial feedbacks among processes happening concurrently in nature.

Acknowledgements – We thank Emanuel A. Fronhofer for support during data analysis and Chelsea J. Little for comments on a previous version of the manuscript.

Funding – Funding is from the Swiss National Science Foundation Grant no. PP00P3_150698 and the University of Zurich Research Priority Programme Global Change and Biodiversity (to FA).

Author contributions

Kathrin Holenstein: Conceptualization (equal); Data curation (equal); Formal analysis (lead); Investigation (equal); Methodology (equal); Visualization (lead); Writing – original draft (equal); Writing – review and editing (equal).

Eric Harvey: Conceptualization (equal); Formal analysis (equal); Investigation (supporting); Methodology (supporting); Supervision (equal); Validation (equal); Writing – original draft (supporting); Writing – review and editing (supporting).

Florian Altermatt: Conceptualization (equal); Formal analysis (supporting); Funding acquisition (lead); Investigation (supporting); Methodology (supporting);
Project administration (lead); Supervision (lead); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal).

Data availability statement
Data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.h9w0vr4jr> (Holenstein et al. 2021).

References

Altermatt, F. 2013. Diversity in riverine metacommunities: a network perspective. – Aquat. Ecol. 47: 365–377.
Altermatt, F. and Fronhofer, E. A. 2018. Dispersal in dendritic networks: ecological consequences on the spatial distribution of population densities. – Freshwater Biol. 63: 22–32.
Altermatt, F. et al. 2011. Interactive effects of disturbance and dispersal directionality on species richness and composition in metacommunities. – Ecology 92: 859–870.
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. – Methods Ecol. Evol. 6: 218–231.
Bullock, J. M. et al. 2018. Human-mediated dispersal and the rewiring of spatial networks. – Trends Ecol. Evol. 33: 958–970.
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.
Carrara, F. et al. 2015. Experimental evidence for strong stabilizing forces at high functional diversity of aquatic microbial communities. – Ecology 96: 1340–1350.
Carraro, L. et al. 2019. OCNet: optimal channel networks. – R-package ver. 0.1.1. CRAN. <https://cran.r-project.org/web/packages/OCNet/index.html>.
Carraro, L. et al. 2020. Generation and application of river network analogues for use in ecology and evolution. – Ecol. Evol. 10: 7537–7550.
Chapin, F. S. I. et al. 2000. Consequences of changing biodiversity. – Nature 405: 234–242.
Clavero, M. and García-Berthou, E. 2005. Invasive species are a leading cause of animal extinctions. – Trends Ecol. Evol. 20: 110.
Corre, N. L. et al. 2015. Patterns and scales of connectivity: temporal stability and variation within a marine metapopulation. – Ecology 96: 2245–2256.
Deckers, B. et al. 2005. Effects of landscape structure on the invasive spread of black cherry Prunus serotina in an agricultural landscape in Flanders, Belgium. – Ecography 28: 99–109.
Drakare, S. et al. 2006. The imprint of the geographical, evolutionary and ecological context on species–area relationships. – Ecol. Lett. 9: 215–227.
Elton, C. S. 1933. The ecology of invasions by animals and plants. – Univ. of Chicago Press.
Fan, Y. et al. 2016. Applications of structural equation modeling (SEM) in ecological studies: an updated review. – Ecol. Process. 5: 19.
Fernandes, C. C. et al. 2004. Amazonian ecology: tributaries enhance the diversity of electric fishes. – Science 305: 1960–1962.
Gillarranz, L. J. and Bascompte, J. 2012. Spatial network structure and metapopulation persistence. – J. Theor. Biol. 297: 11–16.
Gillarranz, L. J. et al. 2015. Inferring topology from dynamics in spatial networks. – Theor. Ecol. 8: 15–21.
Giometto, A. et al. 2013. Scaling body size fluctuations. – Proc. Natl Acad. Sci. USA 110: 4646–4650.
Giometto, A. et al. 2014. Emerging predictable features of replicated biological invasion fronts. – Proc. Natl Acad. Sci. USA 111: 297–301.
Grace, J. B. 2006. Structural equation modeling and natural systems. – Cambridge Univ. Press.
Harvey, E. et al. 2016. Bridging ecology and conservation: from ecological networks to ecosystem function. – J. Appl. Ecol. 54: 371–379.
Harvey, E. et al. 2018. Disturbance reverses classic biodiversity predictions in river-like landscapes. – Proc. R. Soc. B 285: 20182441.
Holenstein, K. et al. 2021. Data from: Patch size distribution affects species invasion dynamics in dendritic networks. – Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.h9w0vr4jr>.
Holland, M. D. and Hastings, A. 2008. Strong effect of dispersal network structure on ecological dynamics. – Nature 456: 792–794.
Holoyak, M. et al. 2005. Metacommunities. Spatial dynamics and ecological communities. – Univ. of Chicago Press.
Holoyak, M. and Lawler, S. P. 2005. The contribution of laboratory experiments on protists to understanding population and metapopulation dynamics. – In: Advances in ecological research. population dynamics and laboratory ecology. Academic Press, pp. 245–271.
Hooper, D. U. et al. 2005 Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. – Ecol. Monogr. 75: 3–35.
Kempel, A. et al. 2013. Determinants of plant establishment success in a multispecies introduction experiment with native and alien species. – Proc. Natl Acad. Sci. USA 110: 12727–12732.
Kennedy, T. A. et al. 2002. Biodiversity as a barrier to ecological invasion. – Nature 417: 636–638.
Layegheidfar, M. et al. 2015. Spatial and species compositional networks for inferring connectivity patterns in ecological communities. – Global Ecol. Biogeogr. 24: 718–727.
Lefcheck, J. S. 2016. piecewiseSEM: piecewise structural equation modelling in R for ecology, evolution and systematics. – Methods Ecol. Evol. 7: 573–579.
Leuven, R. S. E. W. et al. 2009. The river Rhine: a global highway for dispersal of aquatic invasive species. – Biol. Invas. 11: 1989.
Levine, J. M. and D’Antonio, C. M. 1999. Elton revisited: a review of evidence linking diversity and invasibility. – Oikos 87: 15–26.
Levine, J. M. et al. 2004. A meta-analysis of biotic resistance to exotic plant invasions. – Ecol. Lett. 7: 975–989.
MacArthur, R. H. and Wilson, E. O. 1963. An equilibrium theory of insular zoogeography. – Evolution 17: 373–387.
Mächler, E. and Altermatt, F. 2012. Interaction of species traits and environmental disturbance predicts invasion success of aquatic microorganisms. – PLoS One 7: e45400.
Mari, L. et al. 2014. Metapopulation persistence and species spread in river networks. – Ecol. Lett. 17: 426–434.
McGrady-Steed, J. et al. 1997. Biodiversity regulates ecosystem predictability. – Nature 390: 162–65.
McIntosh, A. R. et al. 2018. Capacity to support predators scales with habitat size. – Sci. Adv. 4: eaap7523.
Meier, E. S. and Hofer, G. 2016. Effects of plot size and their spatial arrangement on estimates of alpha, beta and gamma diversity of plants in alpine grassland. – Alp. Bot. 126: 167–176.
Mooney, H. A. and Cleland, E. E. 2001. The evolutionary impact of invasive species. – Proc. Natl Acad. Sci. USA 98: 5446–5451.
Morel-Journel, T. et al. 2019. Its all about connections: hubs and invasion in habitat networks. – Ecol. Lett. 22: 313–321.
Muneepeerakul, R. et al. 2007. A neutral metapopulation model of biodiversity in river networks. – J. Theor. Biol. 245: 351–363.
Naeem, S. et al. 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. – Oikos 91: 97–108.
Oksanen, J. et al. 2019. vegan: community ecology package. – R-package ver. 2.5-6. <https://cran.r-project.org/web/packages/vegan/index.html>.
Pennekamp, F. et al. 2015. BEMOVI, software for extracting behavior and morphology from videos, illustrated with analyses of microbes. – Ecol. Evol. 5: 2584–2595.
Pennekamp, F. et al. 2017. Dynamic species classification of microorganisms across time, abiotic and biotic environments – a sliding window approach. – PLoS One 12: e0176682.
Pennekamp, F. et al. 2018. Biodiversity increases and decreases ecosystem stability. – Nature 563: 109–112.
Pereira, H. M. et al. 2010. Scenarios for global biodiversity in the 21st century. – Science 330: 1496–1501.
Pillai, P. et al. 2011. Metacommunity theory explains the emergence of food web complexity. – Proc. Natl Acad. Sci. USA 108: 19293–19298.
Reid, A. J. et al. 2019. Emerging threats and persistent conservation challenges for freshwater biodiversity. – Biol. Rev. Camb. Phil. Soc. 94: 849–873.
Ricciardi, A. et al. 2017. Invasion science: a horizon scan of emerging challenges and opportunities. – Trends Ecol. Evol. 32: 464–474.
Rodriguez-Iturbe, I. and Rinaldo, A. 1997. Fractal river basins: 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.
Sala, O. E. et al. 2000. Global biodiversity scenarios for the year 2100. – Science 287: 1770–1774.
Seymour, M. et al. 2015. Dendritic network structure and dispersal affect temporal dynamics of diversity and species persistence. – Oikos 124: 908–916.
Stachowicz, J. J. et al. 1999. Species diversity and invasion resistance in a marine ecosystem. – Science 286: 1577–1579.
Tilman, D. 1997. Community invasibility, recruitment limitation and grassland biodiversity. – Ecology 78: 81–92.
Tonkin, J. D. et al. 2018. Metacommunities in river networks: the importance of network structure and connectivity on patterns and processes. – Freshwater Biol. 63: 1–5.
Wardle, D. A. 2001. Experimental demonstration that plant diversity reduces invasibility – evidence of a biological mechanism or a consequence of sampling effect? – Oikos 95: 161–170.
Warren, P. H. 1996. Dispersal and destruction in a multiple habitat system: an experimental approach using protist communities. – Oikos 77: 317–325.
Williams, J. L. et al. 2016. Rapid evolution accelerates plant population spread in fragmented experimental landscapes. – Science 353: 482–485.