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ECOGRAPHY

Research article

Disturbance-driven alteration of patch connectivity determines local biodiversity recovery within metacommunities

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Understanding the capacity of ecological systems to withstand and recover from disturbances is a major challenge for ecological research in the context of environmental changes. Past research has mostly focused on the local effects of disturbances on biodiversity recovery, while alterations of inter-patch connectivity induced by disturbances have received comparatively less attention. Here, we investigated the effect of disturbances on local biodiversity recovery within metacommunities. Our specific focus was on drying river networks, which are characterised by a high variability of patch connectivity. We found marked variations of local biodiversity recovery among sites and among groups of organisms with contrasting dispersal modes, which were explained by the amount of patch connectivity loss due to drying events. Local communities of flying organisms recovered more efficiently from drying events than organisms with strictly aquatic dispersal due to the capacity of the former group to overcome hydrological connectivity loss. As a general rule, loss of patch connectivity decreases community recovery, regardless of patch location in the river network, dispersal mode or drying spatial extent. The relationship between patch connectivity loss and community recovery we found in river networks is general and applicable to any spatial network with a high variability of patch connectivity.

Keywords: dispersal, drying events, intermittent rivers, metacommunity, river network, species richness

Introduction

Most ecological systems are exposed to a wide range of environmental fluctuations and disturbances, both natural and induced by humans. These disturbances vary in intensity, frequency, duration and spatial extent (Sousa 1984, Miller et al. 2011, Donohue et al. 2016, Thom and Seidl 2016). Pulse disturbances are a specific type of disturbances, which cause a sudden increase in population mortality and alter community composition for a limited period of time (Bender et al. 1984, Jentsch

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and White 2019). Such disturbances can have multiple origins, such as wildfires (Turco et al. 2018), forest cutting (Nordén et al. 2019), flooding (Woodward et al. 2016, Rolls et al. 2018) or drying events (Messager et al. 2021, Sarremejane et al. 2021). They are likely to increase in frequency and intensity due to climate change in most regions of the world (Coumou and Rahmstorf 2012, Harris et al. 2018), questioning the capacity of ecological systems and organisms to withstand and recover from recurrent pulse disturbances (Jacquet et al. 2020).

Although some organisms have developed resistance traits to cope with disturbance events (e.g. seed banks, eggs or resting stages that survive in extreme conditions), much of the resilience of ecological communities, defined as their capacity to recover a pre-disturbance state after a disturbance, depends on species recolonization from undisturbed neighbouring habitats (Tonkin et al. 2018, Van Looy et al. 2019). Metapopulation theory has outlined the key role of species dispersal capabilities and landscape structure to determine metapopulation persistence and species extinction probability (Hanski and Ovaskainen 2000). Furthermore, works on graph theory showed that patch connectivity is positively related to local species richness, both in random networks (Bunn et al. 2000, Urban and Keitt 2001, Limdi et al. 2018), lattice landscapes (Laroche et al. 2020), as well as dendritic networks (Muneepeerakul et al. 2008, Carrara et al. 2014, Tonkin et al. 2018).

Traditional approaches in metacommunity ecology have focused on average properties at the metacommunity scale rather than on the inter-patch variability of these properties (Leibold and Chase 2018, Leibold et al. 2022). However, patch connectivity can be highly variable within spatially structured landscapes, such as river networks, where most sites are isolated and few ones are highly connected (Brown and Swan 2010, Brown et al. 2011, Tonkin et al. 2018, Borthagaray et al. 2020). The inherent variability of patch connectivity in metacommunities is likely to have important implications for biodiversity recovery, questioning the use of average metrics at the metacommunity scale (Leibold et al. 2022). The link between patch connectivity and local biodiversity recovery in metacommunities facing disturbances has not been explicitly investigated yet, and it remains unclear whether and when disturbances can trigger a loss of community recovery via an alteration of patch connectivity. In particular, disturbances can vary in duration, frequency, spatial extent and spatial location (Zelnik et al. 2018, Kéfi et al. 2019), with potentially different effects on patch connectivity (Horváth et al. 2019, Borthagaray et al. 2020).

Drying river networks are suitable systems for studying the resilience of metacommunities to recurrent disturbances. They are ubiquitous worldwide, as large proportion as 51–60% of global stream length is dry for at least one month each year (Messager et al. 2021), and their extent is likely to increase with ongoing global change in most regions of the world (Harris et al. 2018, Spinoni et al. 2018). Drying events have a two-fold effect on riverine metacommunities: first, they cause sudden mortality in patches that dry up (Soria et al. 2017) and, second, they temporarily increase patch isolation, thus altering patch connectivity and metacommunity dynamics (Gauthier et al. 2021). Drying events in upstream or downstream reaches are likely to have different effects on metacommunity dynamics in river networks. Patches in the most upstream reaches are also the most isolated ones, while patches located further downstream are better connected. Hence, drying events in downstream reaches are likely to generate more pronounced river network fragmentation compared with drying events in upstream reaches, with potential indirect effects on the local biodiversity of upstream communities.

Organisms inhabiting river networks are characterised by various dispersal modes (e.g. swimming, drifting or flying) and the importance of landscape connectivity in determining their metacommunities strongly differ among these modes (Kärnä et al. 2015). The dispersal of aquatic organisms is constrained by watercourse distances between local patches and, therefore, by river structure, while the dispersal of organisms with a flying adult stage (e.g. most insects) is limited by the overland distances and terrestrial landforms between local patches (Cañedo-Argüelles et al. 2015, Heino et al. 2017, Gauthier et al. 2021, Larsen et al. 2021). Several empirical studies on riverine metacommunities outlined that each dispersal mode can be associated with specific biodiversity patterns and resilience to drying events (Sarremejane et al. 2017, 2020a, Gauthier et al. 2021).

Here, we design a model of river metacommunity to generate controlled biodiversity patterns in perennial conditions, as well as biodiversity trajectories following various scenarios of drying spatial extent, duration and location. We use this controlled simulation setting to investigate local recovery of freshwater biodiversity from drying events 1) between simulated disturbance scenarios, 2) between local patches of a given simulation and 3) between organisms with specific dispersal modes. Our central prediction is that the variability of local biodiversity recovery will mirror the variability of patch connectivity, with isolated communities being likely less resilient than highly connected ones because they receive a smaller number of individuals via dispersal (Fig. 1). To test this prediction, we propose a novel index of connectivity that integrates species dispersal capabilities as well as the alteration of patch connectivity induced by recurrent disturbances. We make three specific predictions: first, we expect that community recovery following a disturbance will be higher in a well-connected patch than in a more isolated one (Fig. 1a–c). Second, the alteration of connectivity due to disturbances is expected to indirectly affect the local biodiversity of unaffected patches via increased patch isolation (Fig. 1d–f). Third, we expect community recovery to differ between dispersal modes, which have contrasted dispersal pathways within the river network and, therefore, contrasted capabilities to overcome losses of patch connectivity (Fig. 1g–i).

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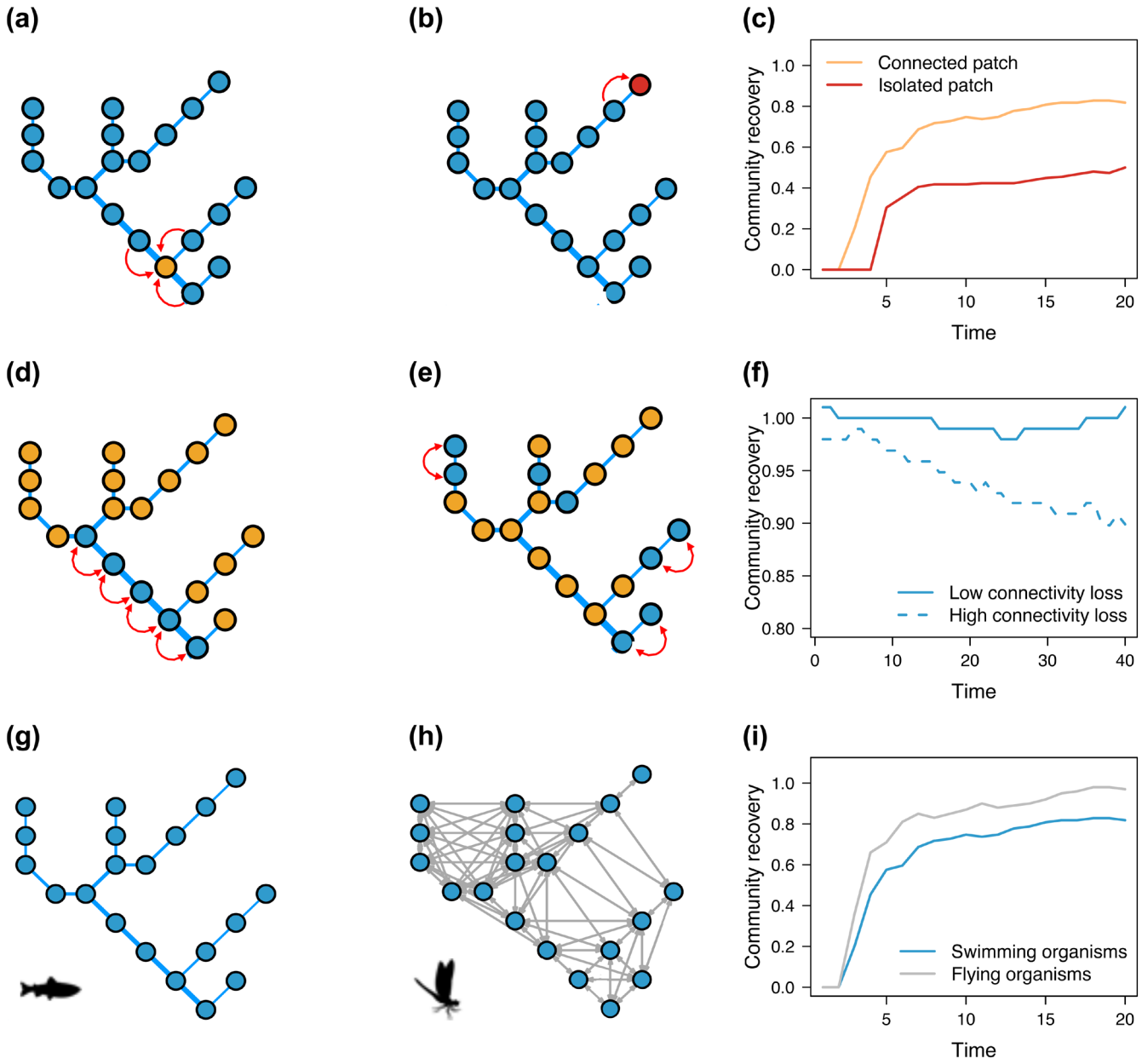

Figure 1. Theoretical expectations. (a–c) Community recovery following a disturbance that causes the death all individuals present in a patch is expected to be higher in a well-connected patch, which receives more individuals from unaffected neighbouring communities via dispersal (e.g. a, in orange), than in a more isolated patch (e.g. b, in red). Blue lines represent the waterways between patches of a river network. Unaffected patches are in blue and red arrows represent dispersal from unaffected neighbouring patches. (d–f) Local biodiversity of unaffected patches (in blue) can be impacted indirectly if a disturbance significantly increases patch isolation. This is the case in panel (e), where unaffected patches are highly isolated, but not in panel (d). Patches affected or unaffected by disturbances are in orange and blue, respectively, and red arrows represent dispersal between unaffected patches. (g–i) Community recovery is expected to be lower for swimming organisms (in blue) than flying organisms (in grey) due to differences in patch connectivity. Blue lines represent waterways between patches in panel g) and lines connect patches located at a maximum overland distance of 2 km in panel e).

Material and methods

Metacommunity dynamics in dendritic river networks

Dendritic river network

We adapted the individual-based simulation algorithm of metacommunity dynamics in discrete time of Jabot et al. (2020) to riverine landscapes. We generated a virtual river network (so-called optimal channel network, OCN) with the R-package 'OCNnet' (Carraro et al. 2020, 2021). OCNs are structures that reproduce the topological connectivity and scaling features of real river networks. We built a virtual river network on a square lattice spanning an area of 156.25 km^2 (25 × 25 cells with 0.5 km cell side), with an outlet

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located close to the bottom left corner of the lattice. We used a threshold area of 1.25 km^2 (5 cells) to partition the river network into n = 124 patches, which are depicted in Fig. 2a (see Carraro et al. (2020, 2021) for detailed information on OCNs generation). We assumed that environmental conditions in perennial river networks are homogeneous across the network, and thus specifically focused on the combined effects of landscape structure and species dispersal on biodiversity dynamics. This assumption is particularly suited to model biodiversity dynamics in systems experiencing recurrent disturbance events, such as drying events or flooding (Datry et al. 2016, 2017, Sarremejane et al. 2021).

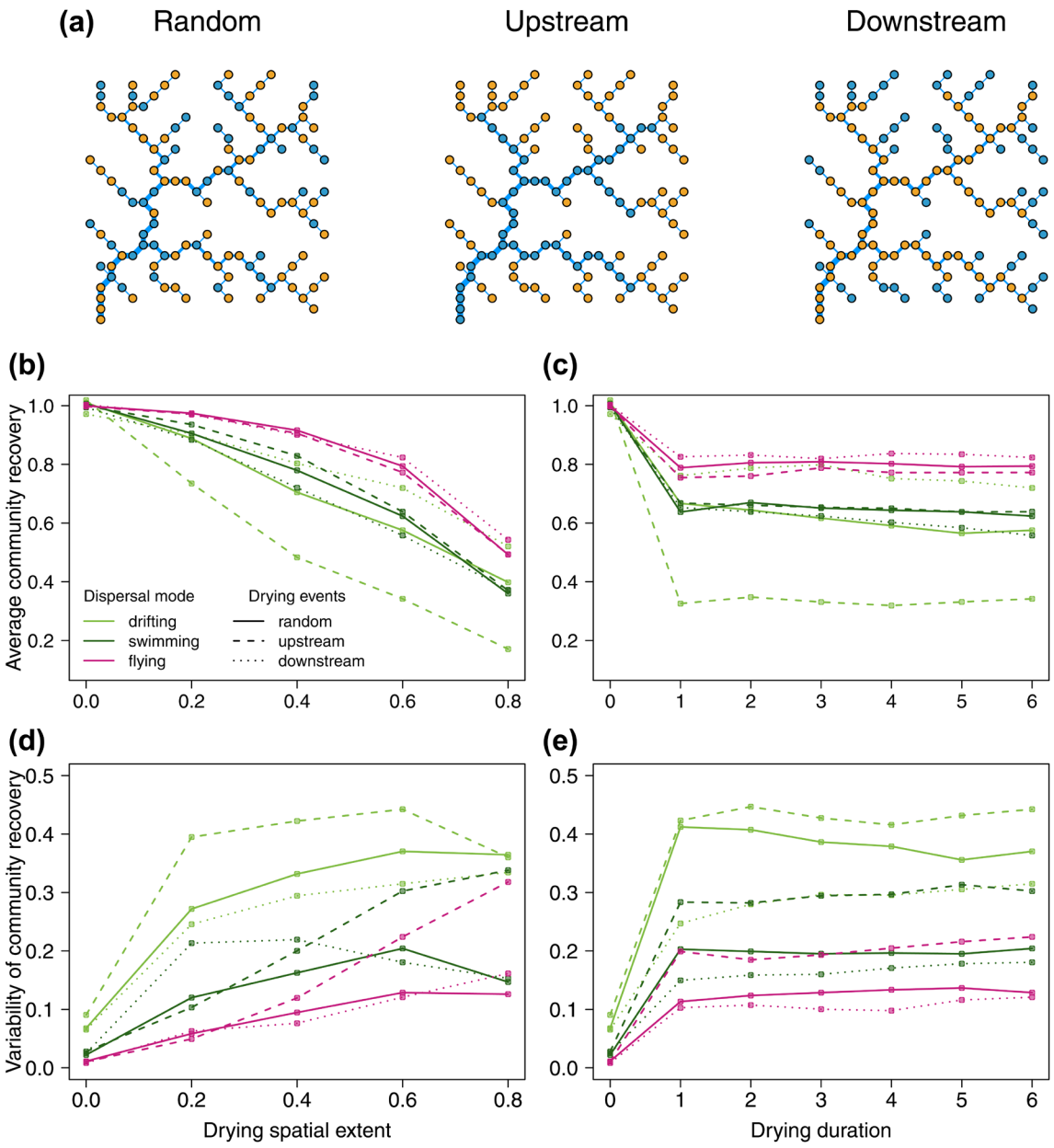

Figure 2. Effects of drying spatial extent, duration and location on average and inter-patch variability of community recovery for three dispersal modes. (a) Location of patches affected (in orange) and unaffected (in blue) by drying events in the river network for three scenarios of drying location: random, upstream and downstream, drying spatial extent $E = 0.6$ in this example. The river network is composed of 124 habitat patches, the river mouth is located at the bottom left corner of the lattices. Community recovery corresponds to local species richness relative to control (perennial) conditions ($SR_{Drying}/SR_{Control}$). Variability of community recovery is estimated by the standard deviation of community recovery over all habitat patches. (b, d) Effects of drying spatial extent, drying duration was fixed to 6 months. (c, e) Effects of drying duration, drying spatial extent was fixed to 0.6. Drifting, swimming and flying organisms are in light green, dark green and pink, respectively. Random, upstream and downstream drying locations are illustrated by solid, dashed and dotted lines, respectively. The relative effects of each variable on community recovery are provided in the Supporting information.

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Community dynamics

We considered a regional species pool of 100 species, each species having the same regional frequency (Supporting information). Each local community had a carrying capacity of $K = 5000$ individuals, therefore local populations of species were composed of 50 individuals on average (Supporting information). Both dispersal-driven regional processes and local demographic processes (births and deaths) drove biodiversity dynamics. In each local patch and at each time step, we simulated four processes taking place sequentially: 1) mortality, 2) reproduction, 3) dispersal and 4) establishment, which accounts for competition for resources (fixed carrying capacity K in local patches). At each time step, we simultaneously updated community composition in all patches.

Mortality

We modelled individual mortality in the metacommunity at each time step as a Bernoulli draw with fixed mortality probability d. In addition, the occurrence of drying events influenced patch viability and therefore individual mortality. We added a component to the model of Jabot et al. (2020) to account for pulse increase of individual mortality induced by drying events. At a given time t, a local patch could be dry or wet. A drying event occurring at time t in patch i caused the death of all organisms in patch i (i.e. all species densities are set to zero). Hence, we assumed that organisms did not have resistance strategies to cope with drying events (e.g. resting stages, adaptations to survive in sediments) and were not able to leave a patch when it became dry.

Reproduction

Individuals produced juveniles at a constant rate r, so that the number of juveniles produced by each individual during one step was a Poisson draw with parameter r. In the following, we considered equal mortality and reproduction rates ($r = d$) for sake of simplicity.

Dispersal

We considered three specific modes of dispersal that are commonly observed in riverine communities: 1) drifting, with downstream flow-directed dispersal along the waterway (e.g. plant seeds and macroinvertebrate larvae), 2) swimming, with bidirectional dispersal along the waterway (e.g. fishes) and 3) flying, with overland dispersal (e.g. insects with flying adult stage). For all dispersal modes, a proportion $(1 - m)$ of the individuals remained in the local patches, while a proportion m dispersed to neighbouring patches. For drifting dispersal, individuals dispersed to the patch situated downstream only (i.e. maximum drifting distance equals 0.5 km). For swimming dispersal, individuals dispersed to patches that were connected by water flow, which could be located upstream or downstream (i.e. maximum swimming distance equals 0.5 km). For flying dispersal, individuals dispersed to the patches situated closer than a threshold overland distance of 2 km (Fig. 1h), corresponding to a maximum flying distance that has been reported in the literature for mayflies (Ephemeroptera) (Kovats et al. 1996). Note that species in other groups of aquatic insects, such as dragonflies (Odonata) and caddisflies (Trichoptera), can show larger dispersal distances than mayflies (Sarremejane et al. 2017).

As illustrated in Fig. 1g–h, the resulting dispersal pathways strongly differed among aquatic and aerial dispersal groups within the river network. Drying events also impacted individual dispersal by generating a sudden decrease in patch connectivity. If a drying event occurred at time step t in patch i, no individuals dispersed to neighbouring patches and the individuals coming from neighbouring patches did not survive (i.e. all individuals are set to zero in patch i). We also included long-distance dispersal (LDD) from the regional pool at a constant rate in each patch (Supporting information). This spatially implicit dispersal process allowed upstream patches to be recolonized by drifting organisms and maintained regional richness (Jabot et al. 2020).

Establishment

Each patch had a fixed carrying capacity of K individuals. The number of recruited individuals $N(t)$ in a patch at time t followed a Poisson distribution with mean equal to $K–N(t)$, where $N(t)$ was the number of surviving individuals in the patch after the mortality step. No individual was recruited whenever $N(t)$ was larger than K. The number $N_j(t)$ of recruited individuals of each species j followed a multinomial draw with probabilities proportional to the numbers of individuals of each species j reaching the focal patch, including local offspring.

Drying scenarios

At each time step, a regional drying event could occur and was defined by 1) its spatial extent E, that is the fraction of patches that dried-up, 2) its duration D, that is the number of consecutive time steps with drying conditions and 3) its location L (Supporting information). We tested three distinct scenarios regarding drying location: 1) random distribution of dry patches, 2) patches located upstream being preferentially subject to drying, 3) patches located downstream being preferentially subject to drying (e.g. due to combined effects of drought and water extraction).

Simulations

We initialised the metacommunity with a multinomial draw of $K = 5000$ individuals from the regional pool in each patch. After a burn-in phase of 1000 steps, we modelled drying events occurring yearly over 10 years, corresponding to 520 weekly steps. We kept all biological parameters constant (m, d, r, K) and varied dispersal type (drifting, swimming and flying), drying spatial extent (0.2, 0.4, 0.6 and 0.8), drying duration (1–6 months) as well as drying location (upstream, random or downstream). This yielded a total of 219 independent simulations, including 3 simulations under control perennial conditions (i.e. one per dispersal mode, Supporting information). We recorded the composition of all patches at every simulation step (520 steps).

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We measured community recovery at each time step as the fraction of species present in drying river networks relative to control perennial conditions, that is $SR_{Drying}/SR_{Control}$, where SR_{Drying} and $SR_{Control}$ correspond to species richness in disturbed (drying) and undisturbed (perennial) river networks, respectively. The resulting temporal dynamics of community recovery in a river network experiencing yearly drying events is presented in the Supporting information. We used species richness to calculate community recovery rather than community composition, as several variables (e.g. number of species, species abundances) would jointly influence the calculation of community resilience otherwise, which would prevent a sound interpretation of the simulation results. We calculated community recovery at the end of the simulations, which were averaged over the last 20 steps in order to smooth the variability induced by stochasticity of metacommunity dynamics. We estimated the average and inter-patch variability of community recovery at the scale of the river network using respectively the mean and standard deviation of community recovery over all habitat patches at the end of the simulations.

Patch connectivity in spatial networks subject to disturbances

Ecologically scaled landscape indices incorporate the dispersal ability of an organism into the computation of landscape connectivity (Vos et al. 2001). They have been shown to have better abilities to predict metacommunity patterns (Laroche et al. 2020) and dynamics (Lalechère et al. 2017, Cunillera-Montcusi et al. 2021), and they are considered pivotal for designing efficient landscape conservation strategies (Meurant et al. 2018). A step forward is to incorporate the additional role played by disturbances in shaping landscape connectivity to gain a general understanding of biodiversity recovery in spatially structured landscapes. We defined patch connectivity as the probability that a local community receives individuals dispersing from all other communities of the metacommunity (Bunn et al. 2000, Urban and Keitt 2001, Laroche et al. 2020). Here, patch connectivity depends on 1) landscape structure, 2) species dispersal type and 3) spatial extent, duration and location of disturbances, which cause temporary alterations of patch connectivity. At a given time t, patch connectivity $C_j(t)$ quantifies the sum of link's weights between patch j and all patches of the network (Eq. 1):

$$C_j\left(t\right) = \sum_{i=1, i\neq j}^{n} l_{ij} w_i\left(t\right) \quad (1)$$

where n is the number of patches in the network, $w_i(t)$ is the viability of patch i at time t (ranging from 0 to 1, 0 if fully disturbed, 1 if undisturbed) and l_{ij} is the probability weight of the link between patches i and j, which decreases according to the formula $\exp(-d_{ij}/\lambda)$, where d_{ij} is the distance between patches i and j. We used flow directed, watercourse and overland distances to compute d_{ij} for drifting, swimming and flying organisms, respectively. The scaling parameter λ corresponds to average dispersal distance of the target species or dispersal group. We used an average dispersal distance $\lambda = 0.6$ km for aquatic organisms and $\lambda = 1.19$ km for aerial organisms, which accounts for dispersal to diagonal cells (the distance between two neighbouring cells is 0.5 km except for the ones in diagonal, where the distance is 0.71 km). Importantly, disturbed patches i at a given time t did not contribute to $C_j(t)$ as they were empty ($w_i(t) = 0$). Therefore, disturbance spatial extent, defined as the fraction of disturbed patches, necessarily decreased patch connectivity. Connectivity C_j of patch j under a given disturbance scenario was obtained by averaging all $C_j(t)$ over one year (Eq. 2):

$$C_j = \frac{1}{T}\sum_{t=1}^{T} C_j\left(t\right) \quad (2)$$

where T corresponds to the time period studied (e.g. one year). Hence, disturbance duration has a negative effect on patch connectivity C_j. We further defined patch connectivity loss as the connectivity in disturbed spatial networks relative to control (undisturbed) conditions, that is $(C_{Control} - C_{Disturbed})/(C_{Control} + 1)$, where $C_{Disturbed}$ and $C_{Control}$ correspond to connectivity metrics in disturbed and undisturbed spatial networks, respectively.

Output analysis

To evaluate the relative effects of drying spatial extent, drying location, duration, dispersal mode as well as patch ID on community recovery, we estimated which of these factors contributed to greater absolute variation in community recovery using a 5-factor analysis of variance (ANOVA), with community recovery at the end of the simulations as response variable (White et al. 2014). Similarly, we used linear and polynomial (i.e. with a quadratic term) regression models to compare the strength of the relationship between patch connectivity loss and community recovery among dispersal modes and scenarios of drying location.

Results

Effects of drying events on community recovery

Drying spatial extent, i.e. the fraction of patches that dry-up, had a negative effect on average community recovery for all dispersal modes (Fig. 2b). Smaller differences among drying locations were observed, except for drifting organisms (Fig. 2b). Furthermore, drying spatial extent increased the variability of community recovery within the metacommunity (Fig. 2d). Drying duration, i.e. the number of consecutive months with dry conditions, had a much smaller effect on the average and standard deviation of community recovery compared to drying spatial extent (Fig. 2c, e). A comparison of the relative magnitude of effects showed that drying spatial extent was the most influential driver of community

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recovery (30.7% of total variation), followed by the interaction between drying location and patch ID (20.5% of total variation, Supporting information). This interaction term encapsulates the connectivity of a focal patch and whether this patch is affected or not by drying events. The third most influential driver of community recovery was dispersal mode, followed by patch ID and the interaction between dispersal mode and drying location (5.4, 4.7 and 4.1% of the total variation, respectively (Supporting information)).

We investigated more in depth the variability of community recovery observed in the metacommunity for a drying spatial extent and duration fixed to $E=0.6$ and $D=6$ months (Fig. 3). We looked separately at drying and non-drying patches. First, we observed marked variations of community recovery between local communities in drying patches. This variation was observed 1) between dispersal modes, 2) between scenarios of drying location and 3) between local communities of the same metacommunity (i.e. within one box of Fig. 3a). Second, we observed indirect effects of drying events on the fraction of species present in non-drying patches (Fig. 3b). This indirect (mostly negative) effect of drying events was also strongly heterogeneous between non-drying patches (Fig. 3b).

More precisely, drifting organisms were the most affected by drying events occurring at upstream patches (Fig. 3a), which led to the extinction of all species initially present in drying patches, and to a lower fraction of species present in several non-drying patches. When drying events were located randomly or downstream, community recovery was highly variable between drying patches and few patches had even a greater richness relative to control (perennial) conditions, which led to a value of community recovery higher than one (Fig. 3a). This is due to model stochasticity and the comparison of very low values of species richness between simulation sets (i.e. control and drying conditions).

Swimming and flying organisms showed greater recovery from drying events located upstream than drifting organisms (Fig. 3a, yellow boxes). Swimming organisms had a lower community recovery than flying organisms when drying events were located randomly or downstream. Flying organisms were particularly affected by drying events located upstream (Fig. 3a), while swimming organisms were similarly affected by all drying locations (Fig. 3a). We further found indirect negative effects of drying events on the biodiversity of non-drying patches (Fig. 3b), which were particularly strong for swimming organisms when drying events occurred downstream or randomly (Fig. 3b, blue and dark blue boxes).

Relationship between community recovery and patch connectivity loss

We found a negative relationship between community recovery and loss of patch connectivity due to drying events, both in drying (Fig. 4a–c) and non-drying patches (Fig. 4d–f). In drying patches, community recovery of swimming organisms decreased linearly with connectivity loss (Fig. 4b), while community recovery of drifting and flying organisms

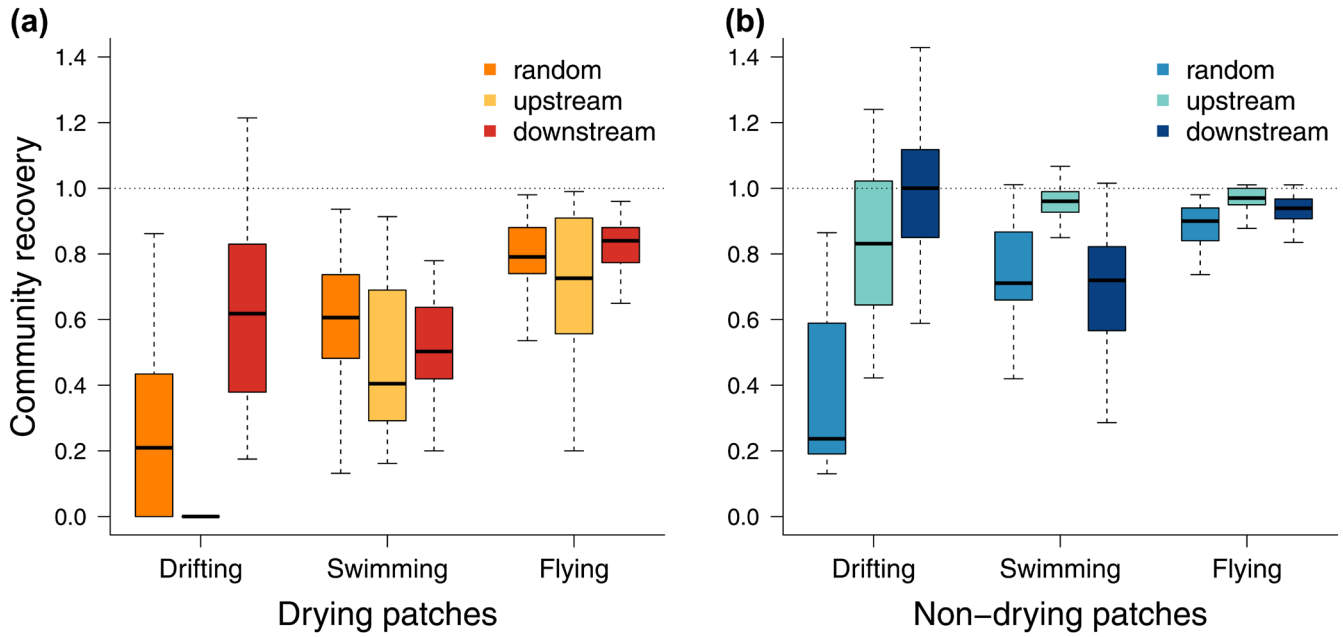

Figure 3. Community recovery in river networks experiencing yearly drying events for varying dispersal modes (drifting, swimming and flying) and scenarios of drying location (random, upstream and downstream). Community recovery corresponds to local species richness relative to control (perennial) conditions ($SR_{Drying}/SR_{Control}$) and is averaged over the last 20 steps of the simulations. Drying spatial extent: $E=0.6$, drying duration: $D=6$ months. (a) Community recovery in patches that dry-up. Orange, yellow and red boxes correspond to random, upstream and downstream scenarios of drying location, respectively. (b) Community recovery in patches that do not dry-up. Boxes in blue, turquoise and dark blue correspond to random, upstream and downstream scenarios of drying location, respectively.

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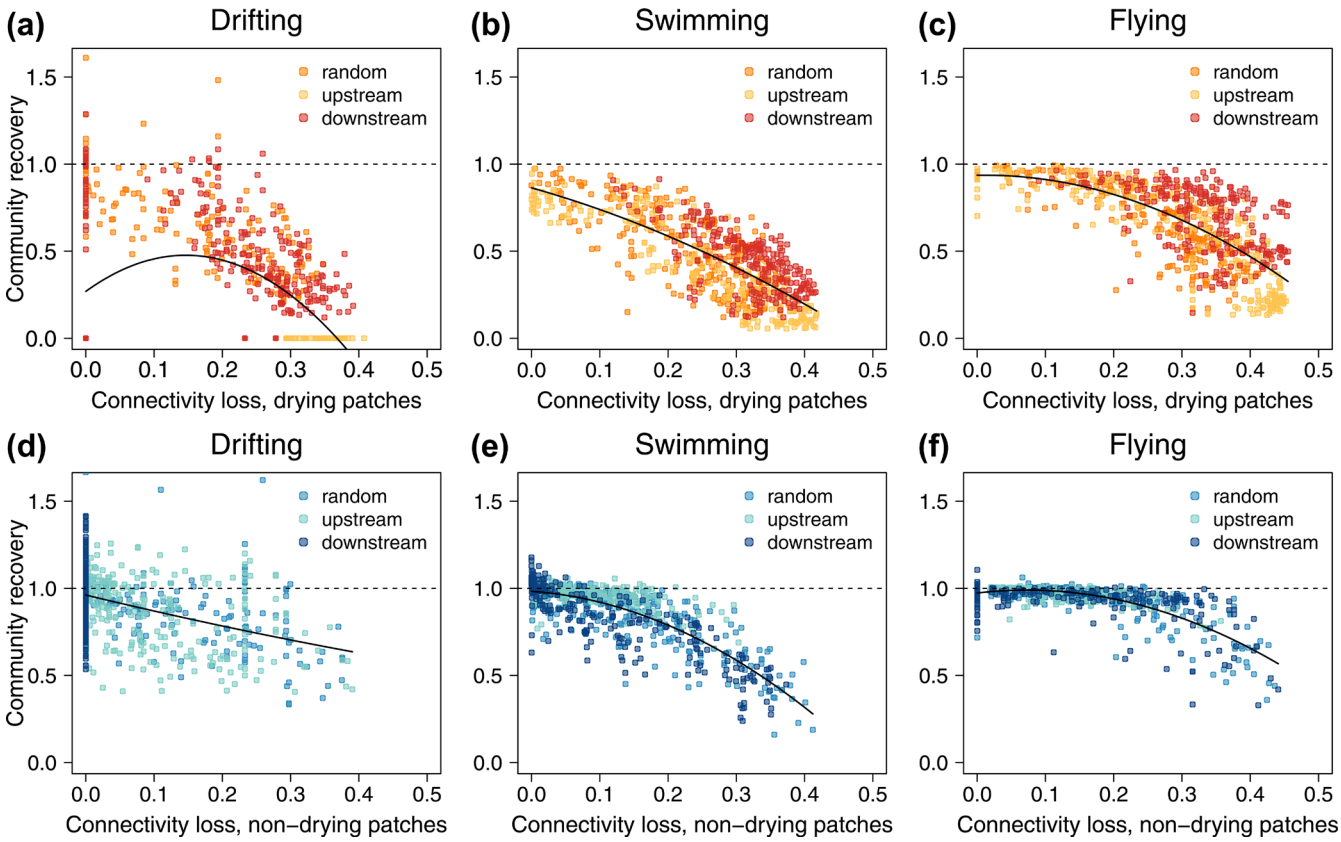

Figure 4. Relationship between connectivity loss and community recovery in drying and non-drying patches for varying dispersal modes. Drying duration: $D = 6$ months, all drying spatial extents are plotted. Black dotted lines indicate full recovery of species richness and solid lines are regression lines. (a–c) Drying patches, points in yellow, orange and red correspond to upstream, random and downstream location of drying events, respectively. Least-square ordinary regression for drifting ($R^2 = 0.11$), swimming ($R^2 = 0.61$) and flying organisms ($R^2 = 0.52$). (d–f) Non-drying patches, points in turquoise, blue and dark blue correspond to upstream, random and downstream location of drying events, respectively. Least-square ordinary regression for drifting ($R^2 = 0.19$), swimming ($R^2 = 0.69$) and flying organisms ($R^2 = 0.58$).

was nonlinear (Fig. 4a, c). Flying organisms had a higher proportion of local patches with high connectivity compared to other dispersal modes despite the occurrence of drying events, which explained the higher recovery ability of this group (Supporting information). In non-drying patches, we also found a negative relationship between community recovery and patch connectivity loss. This relationship was nonlinear for swimming and flying organisms, with a slow decrease followed by a sharper decline of community recovery as connectivity loss increased (Fig. 4e–f). Furthermore, drying events located upstream had a lower impact on the response of swimming and flying organisms to connectivity compared to other scenarios of drying location (Fig. 4e–f, Supporting information). Community recovery of drifting organisms in non-drying patches decreased linearly with connectivity loss when drying events were located upstream or downstream but was unrelated to connectivity loss when drying events were located downstream (Fig. 4d). The correlations between patch connectivity loss and community recovery are all robust to variations of input parameters (Supporting information).

Discussion

Most studies on metacommunities have focused on average properties at the metacommunity level to capture the complexity of spatially structured systems, thereby overlooking the inherent heterogeneity within metacommunities (Leibold and Chase 2018, Leibold et al. 2022). Our results highlight the importance of analysing metacommunity heterogeneity to obtain a mechanistic understanding of biodiversity recovery in metacommunities characterised by high variability in patch connectivity, such as dendritic river networks. We found marked variation in local biodiversity recovery between simulated scenarios of drying events, between local patches in a given drying scenario, as well as between organisms with specific dispersal modes. The connectivity index we proposed incorporates the joint effects of dispersal mode and disturbance properties (i.e. spatial extent, spatial location and duration). This patch connectivity index provided a simple and unified explanation for the variation in community recovery between local patches and simulated scenarios: loss of connectivity decreases community recovery

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regardless of dispersal mode, drying spatial extent or patch location. Overall, our work highlights the mechanistic link between patch connectivity loss and community recovery in the context of metacommunities undergoing recurrent disturbances.

Predicting how ecological communities may respond to the increased intensities and frequencies of disturbances associated with climate change is particularly challenging, since the different characteristics of disturbance events (duration, intensity, frequency, spatial extent and spatial location) are known to have different impacts on community recovery and species richness (Jacquet and Altermatt 2020, Jacquet et al. 2020). For instance, Cunillera-Montcusí et al. (2021) demonstrated that wildfire size and spatial extent have qualitatively different impacts on the recovery of macroinvertebrate communities in freshwater ponds. Similarly, we found that increasing drying spatial extent decreased average community recovery, while drying duration had a smaller effect, echoing some recent empirical findings (Crabot et al. 2021). Furthermore, we showed that local species richness in non-drying patches also decreases with connectivity loss in a nonlinear way. This result is corroborated by the empirical findings of Horváth et al. (2019), who used a dataset on invertebrate species in ponds spanning six decades of habitat loss to demonstrate that habitat loss also translates into species loss within the remaining habitats. Using patch connectivity loss as a common currency is promising to gain general insights on the ecological impact of disturbances, which are expected to be more intense and more frequent in the future (Coumou and Rahmstorf 2012, Harris et al. 2018).

For the specific case of drying river networks, our study suggests some qualitative rules of thumb. First, spatial location of drying events has a comparatively second order effect on community recovery (except for drifting organisms, Fig. 3a), which is consistent with empirical observations on macroinvertebrate metacommunities (Datry et al. 2014, Leigh and Datry 2017), although rivers that naturally dry in their downstream sections show a higher resilience in some cases (Crabot et al. 2021). Second, drying spatial extent gradually alters biodiversity recovery and this effect accelerates once a threshold of connectivity loss is reached for flying organisms (Fig. 4c), which can be expected in river networks where most of the reaches (> 80%) are intermittent. To our knowledge, there is no empirical data that tested this pattern yet, which represents a key research gap for predicting the effects of increased river network fragmentation on biodiversity. Third, organisms with various dispersal modes are likely to be differently affected by increasing drying spatial extent: drifting organisms being impacted the most and flying organisms being impacted the least (Fig. 4). This corroborates recent empirical results (Sarremejane et al. 2017, Crabot et al. 2021, Gauthier et al. 2021) and calls for integrating dispersal abilities of organisms when assessing the effects of river network fragmentation by drying.

Our metacommunity model assumes that all environmental variables are similar between local patches. This is, however, an oversimplification as river networks are known to exhibit a wide range of variation of patch size and environmental conditions along the longitudinal gradient (Vannote et al. 1980, Carrara et al. 2014) as well as between different headwater sites (Heino et al. 2013, 2015), which are both exacerbated in drying river networks (Datry et al. 2016, Sarremejane et al. 2021). Our approach is based on the assumption that dispersal is the central process that determines community recovery in a metacommunity, which is closer to generality than realism. We nonetheless added some realism to the model with an explicit description of the landscape structure and the location of disturbance events, which was central to capture the internal variation of community recovery and connectivity loss in response to disturbances.

Many other ecological systems are subject to recurrent disturbances such as wildfires (Turco et al. 2018), forest cutting (Nordén et al. 2019) or flooding (Woodward et al. 2016). These types of events vary considerably in their spatial extent and location, and their effects on the connectivity of local communities could also be quantified and linked to biodiversity recovery. Human-managed habitats also face recurrent disturbances linked to agricultural activities such as tillage, fertilisation, crop harvest and rotation (Gaba et al. 2018), and silvicultural activities such as forest thinning or cutting (Senf and Seidl 2021). Understanding biodiversity dynamics and resilience in such recurrently disturbed systems requires developing quantitative frameworks in which transient dynamics following disturbance events is the rule rather than the exception (Pickett and White 1985, Fukami and Nakajima 2011). We demonstrated that variation of community recovery from drying events within a riverine metacommunity can be explained by an index of patch connectivity that encapsulates the influence of drying events on landscape connectivity. Our findings are based on a general model of metacommunity dynamics and can be transposed to other spatially structured systems characterised by a high heterogeneity of patch connectivity.

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Data availability statement

The article contains no original data. The code of the river metacommunity model is available from: <https://forgemia.inra.fr/lisc/r-package-cantal>.

Supporting information

The Supporting information associated with this article is available with the online version.

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