Modelling biological and resource fluxes in fluvial meta-ecosystems

Matthew Talluto (matthew.talluto@uibk.ac.at)[1,*], Rubén del Campo (ruben.del-campo@uibk.ac.at)[1], Edurne Estévez (Edurne.Estevez-Cano@uibk.ac.at)[1,2], Thomas Fuß (thomas.fuss@uibk.ac.at)[1], Lukas Thuile Bistarelli (Lukas.Thuile-Bistarelli@uibk.ac.at)[1], Jan Martini (jan.martini@uibk.ac.at)[1], and Gabriel A. Singer (gabriel.singer@uibk.ac.at)[1]

[1]Department of Ecology, University of Innsbruck, Innsbruck, Austria
[2]Faculty of Science and Technology, University of the Basque Country (UPV/EHU), Spain
[*]Author for correspondence. Address:
University of Innsbruck
Department of Ecology
Technikerstrasse 25
A-6020 Innsbruck, Austria
tel: +43 (0)512 507-51738

Paper type:
Short title: Modelling fluvial meta-ecosystems
Keywords: fluvial meta-ecosystems, biodiversity, ecosystem functioning, river networks

Abstract

Meta-ecosystem theory predicts that cross-ecosystem flows of energy, nutrients, and organisms have important implications for local community assembly and ecosystem functioning. Developments in the theory also have the potential to enhance our understanding of biodiversity-ecosystem functioning relationships. Meta-ecosystem theory is particularly well-suited to the study of rivers, because water flow forces strong spatial interrelationships among connected ecosystems. However, models that address flows of both resources and organisms and explicitly link both are lacking. We present a model and associated R-package for cross-ecosystem flows of both resources and organisms that can be used to predict their distribution in river networks, as well as meta-ecosystem functioning. The model incorporates feedbacks between these two crucial components. To illustrate the capabilities of the model, we present an in silico experiment and analysis, as well as providing sample code.

1 Introduction

In river networks, the flow of water enforces strong spatial connections among local ecosystems. This flow enables relatively large fluxes of energy, nutrients, and organisms and has profound implications for community assembly and ecosystem functioning (EF). Recent developments in the theory of meta-ecosystems have provided a solid conceptual framework for describing how both organisms and material interact in such a spatial context, and how this interaction can influence the spatial distribution of EF (Loreau et al. 2003; Gravel et al. 2010; Harvey et al. 2023). Moreover, the actual spatial structure of the river network, and the degree to which this structure differentially influences the movement of organisms and materials, may significantly impact EF at the scale of the entire network (Talluto et al. {in press}).

Understanding the effects of biodiversity on EF has long been a central goal of ecological research (Bannar-Martin et al. 2018). Researchers have long hypothesised that ecosystems with more species would exhibit higher levels of ecosystem functioning (Margalef 1963). Biodiversity is generally an important driver of EF (Cardinale et al. 2012; Hooper et al. 2012) and can be as important as abiotic drivers (e.g., climate Duffy et al. 2017). However, recent experiments and models have revealed complex effects of diversity on ecosystem functioning (i.e., positive, negative and no effects; see Pennekamp et al. 2018), pointing to non-linear and probably highly context dependent biodiversity-ecosystem functioning relationships (Thébault and Loreau 2006; Little and Altermatt 2018). This further suggests that the classic view that ecosystem functioning depends only on the diversity of organisms might be overly simplistic. For example, species identity, in addition to species richness, can be a key determinant of ecosystem function due to the effects of morphology, behaviour, and physiology on the acquisition, use and allocation of resources (Hooper et al. 2005; Díaz et al. 2013; Gagic et al. 2015). Moreover, different resources can contain different essential nutrients and carbon compounds that determine lability and palatability; thus resource properties can also strongly determine consumption and processing rates (Cornwell et al. 2008).

Fluvial systems are ideal for the study of meta-ecosystems generally, and for the interrelationship between biodiversity and EF, because rivers are embedded in a terrestrial matrix and organized in networks, which have a hierarchical dendritic structure that strongly interconnects local ecosystems via the downstream flow of water. In other words, the physical and geographical structure of river networks promotes the exchange of resources and organisms between aquatic and the surrounding terrestrial ecosystems, but also among different locations in the river (Cid et al. 2022; Battin et al. 2008). This structure ultimately has a strong influence on how organisms and resources are distributed in space.

In order to better integrate the theory of meta-ecosystems with actual field studies, we need both (i) highly resolved spatio-temporal data on resources and consumers within fluvial meta-ecosystems (FMEs), and (ii) a new generation of models operating at the meta-ecosystem level (Talluto et al. {in press}). These models should link community composition with resource properties and dynamics. The availability

of datasets is rapidly increasing thanks to technological developments such as DNA sequencing, size-exclusion chromatography, mass spectrometry and infrared spectroscopy (Sleighter and Hatcher 2008; Huber et al. 2011; Tremblay et al. 2011; Baird and Hajibabaei 2012). These datasets are unprecedented in both breadth—covering a great spatial extent, such as entire river networks—and depth—capturing much more biological and chemical diversity at a single location than has ever been possible (Altermatt et al. 2020). However, we still lack models that can provide the context for these datasets at the appropriate spatio-temporal scales (Gounand et al. 2018; but see Harvey et al. 2023).

Developing fluvial meta-ecosystem models presents important challenges due to the unique properties and structure of river networks. For one, biodiversity-EF relationships are likely strongly scale dependent (Gonzalez et al. 2020). This is because the spatial configuration of river networks imposes unique and strong controls on both organisms and resource fluxes. However, the distribution of these ecosystem components is driven by different mechanisms. Resources highly depend on structure of the surrounding terrestrial ecosystem (i.e., land cover shapes the nature of the resources that are transferred to the river corridor) and are passively transported by flow (Roebuck et al. 2020). In contrast, the distribution of consumers is driven by the interplay between (i) stochastic processes (e.g., extinctions); (ii) dispersal (including both flow-mediated downstream dispersal but also active dispersal and transport by other organisms); (iii) local environmental factors, including resource properties, that filter species from the regional species pool; and (iv) biotic interactions (Leibold et al. 2004; Urban 2004; Heino et al. 2015).

Here, we develop a meta-ecosystem model that explicitly couples the distribution and fluxes of both resources and their consumers in FMEs. We construct this model by joining two commonly-used model types in fluvial ecosystem and community ecology: reaction-transport models (for resources), and metacommunity models (for organisms). By linking these two models, we allow for feedbacks between the consumers and the resources they are sustained on. These feedbacks are essential to enable a more mechanistic understanding of the connections between the processes underlying community assembly, resulting biodiversity patterns, and ecosystem functioning. Our model structure facilitates developing and testing *in-silico* hypotheses regarding FME properties, including interactions among local- and regional-scale patterns in biodiversity and ecosystem functioning (i.e., resource consumption), spatial structure of the river network, and the effects of changes in connectivity, flow, and the terrestrial matrix. We provide an implementation of the model via an R-package as well as some worked examples with sample code and data.

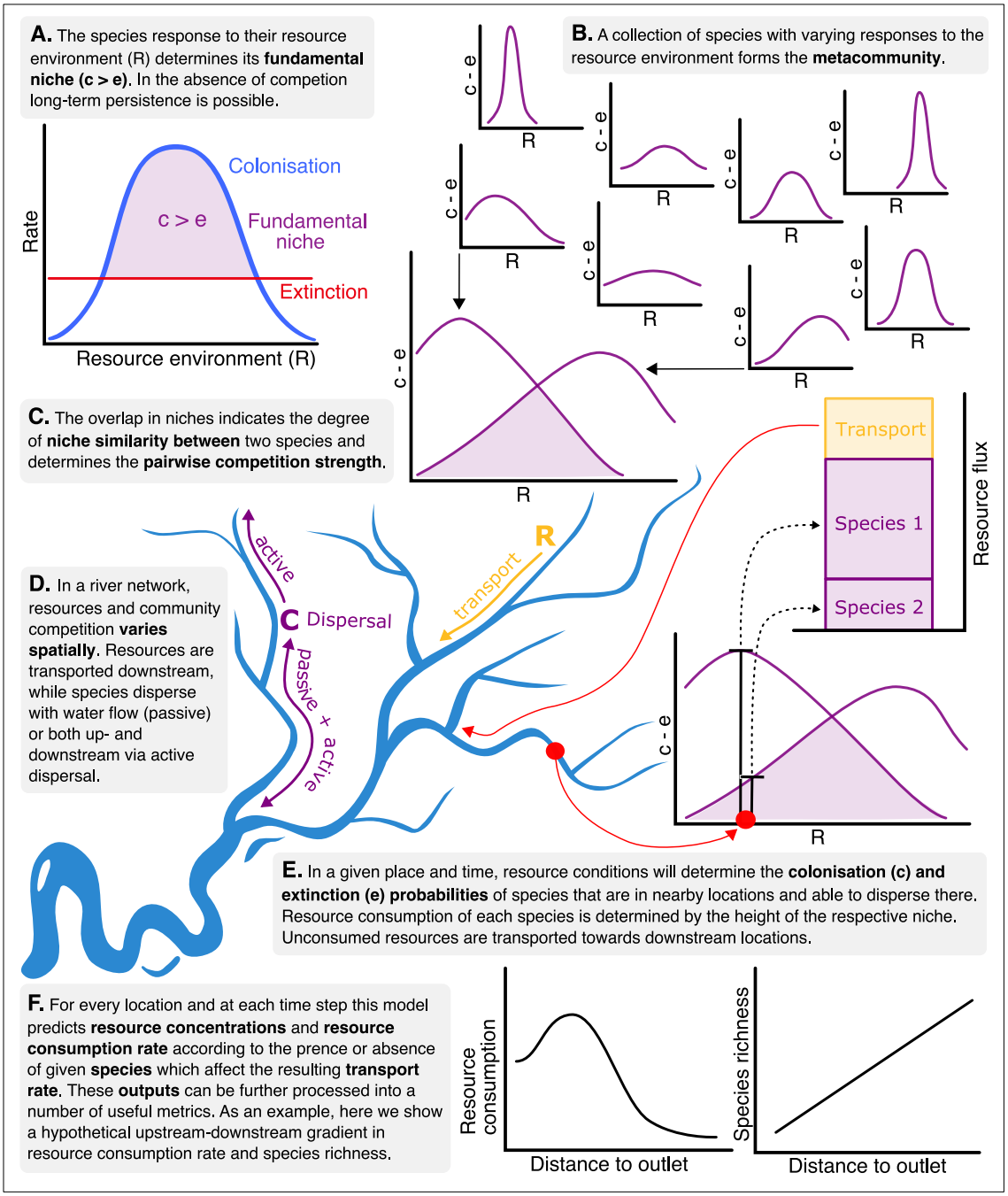

Figure 1: Conceptual diagram illustrating key model flows and outputs.

2 Materials & Methods

2.1 Model Description

Our conceptual starting point for modelling the biological community is metapopulation theory (Levins 1969). The classic metapopulation model tracks the number of occupied patches p in a landscape composed of h available patches as a function of the rates of colonisation and extinction of local populations within those patches:

$$\frac{dp}{dt} = cp\,(h - p) - pm \tag{1}$$

Occupied patches (p) experience extinction according to the extinction rate m, while unoccupied patches ($h - p$) are colonised according to the colonisation rate c. The additional p in the colonisation term takes dispersal into account; as more patches are occupied in the metapopulation as a whole, unoccupied patches are colonised more quickly due to increased dispersal from the occupied patches.

Hunt and Bonsall (2009) extended this model to multi-species communities by adding competition to the extinction term:

$$\frac{\partial p_i}{\partial t} = c_i p_i\,(h - p_i) - p_i \left(m_i + \sum_{j \in S \setminus \{i\}} o_{ij} p_j \right) \tag{2}$$

where the subscript i indicates a focal species, the subscript j a competitor, and $S \setminus \{i\}$ is the set of species in the local community excluding the focal species i. Here, the extinction rate is now broken into two terms. The first a species-specific intrinsic extinction rate m_i, representing, e.g., stochastic extinctions that are unrelated to other species in the local community. The o_{ij} term is the effect of competition between i and j on the extinction rate of i (multiplied by p_j because competition only occurs when species j is also present). For future clarity of notation, we assume all parameters are specific to a target species i and thus omit the subscript.

An important aspect of metacommunity dynamics is dispersal, which in the classic model is incorporated into the colonisation term using the prevalence p_i. In rivers, hydrological connections among habitat patches facilitates passive dispersal in the water. However, many organisms are capable of active dispersal (i.e., any dispersal not facilitated by the flow of water in the river channel), either overland or upstream along the streambed, and even organisms that cannot move themselves can be carried upstream by various processes (e.g., transport by organisms, wind, or humans; Kristiansen 1996). Because these two dispersal mechanisms are likely to occur at quite different rates, and because the rates will likely vary among different types of organisms, we break the dispersal portion of the colonisation term here into active (α) and passive (β) components, with the passive component additionally weighted by the discharge Q:

$$\frac{\partial p}{\partial t} = cp(\alpha + \beta Q)\,(h - p) - p \left(m + \sum_{j \in S \setminus \{i\}} o_j p_j \right) \tag{3}$$

In order to produce a model where the meta-community also interacts with the environment, it is necessary to further extend this model to incorporate local (and potentially dynamic) non-biological conditions in specific patches. More recent theoretical (Holt and Keitt 2000; Holt et al. 2005) and empirical (Talluto et al. 2017) work has extended the single-species Levins model (eqn. 1) by fitting the colonisation and extinction rates as functions of local climatic conditions. The result is a dynamic range model with long-term occupancy driven by the balance of local colonisation and extinction (Talluto et al. 2017). We combine this approach with the multi-species Hunt model (eqn. 2) by redefining the c and m terms to be functions of the quality q_x of a focal patch x:

$$\begin{aligned} c_x &= f(q_x) \\ m_x &= g(q_x) \end{aligned} \tag{4}$$

The shape of these two functions is flexible; for example, Talluto et al. (2017) defined them as quadratic functions of local climate conditions. Our more general approach here can incorporate local climatic and/or habitat conditions, and dynamic resource concentrations into the q term. We explore these possibilities further in the case studies. For now, we consider the case where $q_x = [R]_x$, the concentration of an essential resource. We can use a simple reaction-transport model (Soetaert and Herman 2009) to describe the fluctuations of this resource concentration in time (since all terms relate to a focal patch, the subscript x has been omitted for clarity).

$$\frac{\partial R}{\partial t} = \sum_{i \in S} R\rho_i(R) - \frac{QR - \sum Q_u R_u}{Al} \tag{5}$$

The right-hand term here gives loss due to advective transport, where Q is the discharge of the focal patch (in volumetric units per unit time; we use $\mathrm{m}^3\ \mathrm{s}^{-1}$ throughout), Q_u and R_u are discharge and resource concentrations of upstream patches (including lateral input, if relevant), A is the cross-sectional area (m^2), and l is the stream length of the patch (m). The left-hand term is the reaction component. We consider here only reaction due to biological activity, and postulate that the net reactive change in a patch is the sum of a set of resource use functions, $\rho_i(R)$, of all species S in the local community. Each ρ_i function describes the impact of a species on the resource in units of s^{-1}. The forms of these functions will depend on which resources are being modelled.

2.2 Implementation

We provide an implementation of the model in an R-package **flume** (FLUvial Meta-Ecosystem model) (Talluto 2023), and demonstrate some capabilities via case studies and sample code. In this section we describe some of the implementation details that are flexible in the formulation of the model above, but for which we have made specific choices in software. A full list of model parameters and default values from the package is available in Table 1.

Table 1: Model parameters with default values and values used for case studies.

Symbol	Description	Default Value	Case Study 1
c_μ	Niche location	$0 - 1^*$	$0.1 - 0.9$
c_σ	Niche breadth	$c_{\mu,2} - c_{\mu,1}{}^\dagger$	0.1
c_γ	Colonisation scale	5×10^{-6}	6×10^{-6}
m_γ	Extinction scale	2×10^{-7}	1.25×10^{-7}
α	Active dispersal rate	0.1	$0.05 - 2.8$
β	Passive dispersal rate	0.1	0.1
o_γ	Competition scale	0.001	$0.001, 0.1$
r	Resource use scale	5×10^{-4}	5×10^{-4}

*Uniformly distributed across the range, depending on the number of species.

† i.e., the distance between niche locations of adjacent species.

2.2.1 Patch quality

Patch quality is defined by two functions describing the impact of quality on colonisation and extinction (eqn. 4). We modelled the colonisation niche (i.e., the shape of the c function) as a Gaussian curve (Austin 1999). Thus, for a single resource, the niche shape can be defined by three parameters: location (c_μ), breadth (c_σ), and scale (c_τ):

$$c(R) = c_\tau e^{\frac{-(R-c_\mu)^2}{2c_\sigma^2}} \tag{6}$$

With multiple niche dimensions, the niche shape is similarly described by a multivariate Gaussian. Extinctions in the model are constant with respect to the environment, controlled only by a scale parameter (m_γ) determining the overall background rate of stochastic extinctions.

2.2.2 Competition

Our metacommunity model includes a competition term ($\sum o_i j p_j$), allowing for totally independent pairwise (and potentially asymmetrical) competition coefficients among species. In practise, pairwise competition strength is extremely difficult to estimate. Thus, we make a simplifying assumption that the strength of competition will be proportional to the degree of overlap in two species' fundamental niches (defined as the difference between colonisation and extinction, excluding the competition term). We further add a scale parameter o_γ (which is constant by default but can vary by species pair). In flume, we compute this as the integral of a piecewise function defined by the lesser of the two species' niches when both niches are positive (i.e., within the fundamental niche of the species), and zero otherwise:

$$o_{ij} = o_{\gamma,ij} \int \begin{cases} c_i(R) - m_i(R) & 0 < c_i(R) - m_i(R) \leq c_j(R) - m_j(R) \\ c_j(R) - m_j(R) & 0 < c_j(R) - m_j(R) < c_i(R) - m_i(R) \\ 0 & 0 \geq c_j(R) - m_j(R) \\ 0 & 0 \geq c_i(R) - m_i(R) \end{cases}$$

2.2.3 Resource use functions

In principle, we expect that a species' total resource consumption in a site will be correlated with abundance (or biomass) (Díaz et al. 2003; Winfree et al. 2015). Although we do not track abundance in our model, we can make the simplifying assumption that abundances will be higher when species are closer to their niche optima (Holt et al. 1997; but see McGill 2012). Thus, the consumption $\rho_i(R_x)$ for species i at site x (eqn 5) will be proportional to the overall niche height at that site $c_{i,x} - m_{i,x}$ (eqn. 4). We can further allow that species vary in their overall ability to use resources, scaling the resource use function by a species-specific consumption constant r_i:

$$\rho_i(R_x) = \begin{cases} r_i \frac{c_{i,x} - m_{i,x}}{\max(c_i - m_i)} & c > m \\ 0 & c \leq m \end{cases} \tag{7}$$

Here we scale the niche height by the maximum niche height to allow us to interpret this term as the fraction of a species' maximum consumption rate, and to interpret r_i as that maximum rate. Finally, we assume that when a species is outside it's equilibrium habitat (i.e., when $m > c$; Talluto et al. 2017), that resource consumption is negligible and can be ignored.

2.2.4 Stochastic simulations

For analysis, we discretised the model in space and time. We thus consider a series of habitat patches representing stream reaches. Each reach is characterised by two fundamental state variables: the resource vector $\mathbf{R}$, giving the concentration of each resource, and the community vector $\mathbf{C}$, which gives the absence (denoted by zeroes) or presence (denoted by ones) of all possible species in the community. For any time interval Δt we can then compute the probability of observing colonisations and extinctions for a species i (eqn. 3):

$$\begin{aligned} \mathrm{pr}\left(\mathbf{C}_{i,t+\Delta t} = 1 \mid \mathbf{C}_{i,t} = 0\right) &= 1 - \mathrm{e}^{-c_i p_i (\alpha_i + \beta_i Q)\Delta t} \\ \mathrm{pr}\left(\mathbf{C}_{i,t+\Delta t} = 0 \mid \mathbf{C}_{i,t} = 1\right) &= 1 - \mathrm{e}^{-(\sum m_{ij}\mathbf{C}_{j,t} + m_i)\Delta t} \end{aligned} \tag{8}$$

Here, the prevalence term p_i indicates local prevalence, i.e., the number of occupied reaches within dispersal range. We consider only the case of nearest neighbour dispersal, so p_i is the sum of the occupancy states of reaches immediately up- and downstream of the focal reach; longer distance dispersal can be incorporated via the regional species pool (see §2.3).

Changing resource concentration can be computed for each reach using a variety of numerical integration techniques. The flume package uses the lsoda algorithm implemented in the DeSolve R-package (Soetaert et al. 2010).

2.3 Initial & Boundary Conditions

Boundary conditions in the model are used to represent external input into the river network (e.g., input of resources and organisms from the terrestrial environment, or overland flow of water and groundwater contributing to discharge). Rivers are not closed systems, and because of the downstream flow of water, all material would be rapidly flushed downstream without user-provided boundary conditions. For each reach in the model, we implemented a virtual upstream "reach" representing this input. The resource concentrations and community composition of these virtual reaches are constant and must be supplied by the user at model initialisation. Discharge from virtual reaches is not user supplied, rather it is computed as the growth in discharge from one reach to the next moving downstream, according to the growth in catchment area and defined by hydraulic scaling relationships (Burgers et al. 2014). By default, flume will use the boundary conditions as initial conditions as well, but this can be overriden. The actual resource concentration and community composition of the virtual reaches can vary depending on modelling needs; for example, community composition could be uniform and contain all possible species to represent a classical "regional species pool" from metacommunity modelling, or resource concentrations could vary among headwaters or from upstream to downstream to represent land use gradients.

2.4 Temporal resolution

The time scale of the model determines how frequently colonisation and extinction steps are performed; community state is constant within time steps. The temporal resolution set via a parameter passed at model initialisation, with units determined by the units of discharge. The default value is 86400, which, assuming discharge is in units of $m^3 s^{-1}$, corresponds to 24 hours. Thus, using default parameters, community composition can change once per day, while resources are integrated continuously throughout the day. Longer time steps can be set to simulate slower community dynamics and improve computation time, with the potential downside that this allows resource concentrations to change more while community composition is constant.

2.5 Model output

After a simulation run, the model returns an object containing all model parameters and complete state (i.e., the model is resumable). The object also contains a complete history of all state variables, consisting of reach by time by resource and reach by time by species arrays. Resource fluxes (transport and consumption) are also returned for every reach and time step and are the primary metrics of ecosystem function returned by the model. The package also includes a variety of convenience functions for plotting and for computing aggregate metrics for both community and resource state.

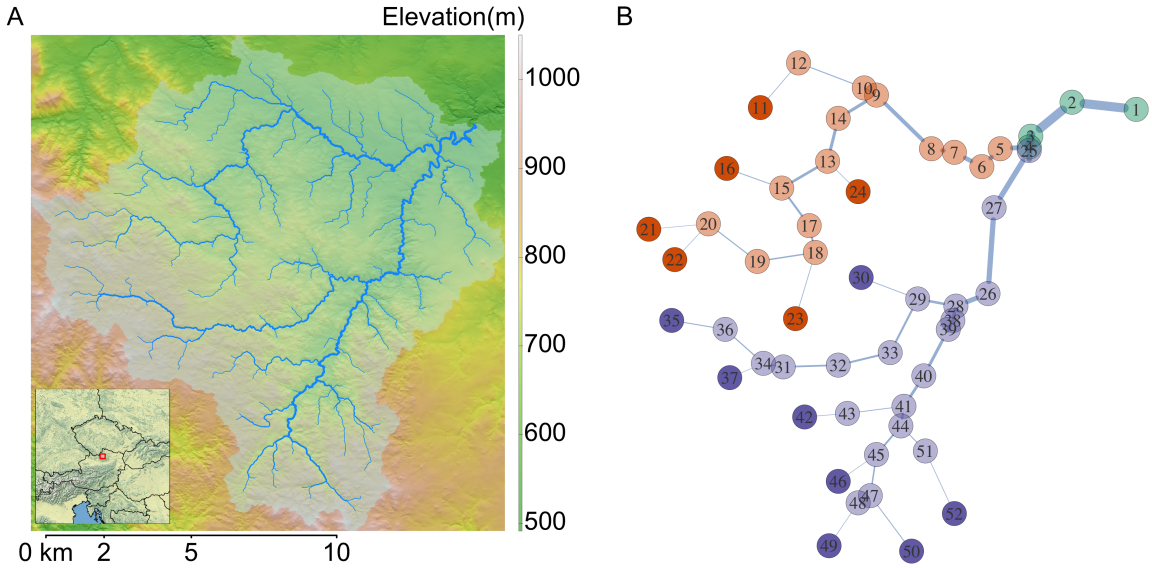

Figure 2: (A) Delineated Kamp river network, with the drainage area shown shaded. Line weights are proportional to Strahler stream order. Location of the river network within central Europe is shown in the inset. (B) Schematic of the network Kamp river network after conversion for use with flume. Line weights are proportional to discharge, which range from 0.05–0.88 $m^3 s^{-1}$. The network has been segmented into approximately 2-km reaches (which are assumed to be exactly equal length for modelling purposes); each node in the schematic is a reach midpoint. Node hues indicate membership in either the left tributary (orange), the right tributary (purple), or the mainstem (turquoise). Darker colours indicate headwater nodes.

2.6 Sample river network

In order to demonstrate some features of the package and explore the behaviour of the model, we created a representation of the Kamp river in Austria to use as the spatial setting for simulations. This river network is included with the package, along with other sample networks, and a vignette is included to help users generate a network from a digital elevation model.

3 Case studies

3.1 Case Study 1: effects of dispersal on biodiversity-EF relationships

A good match of local environmental conditions and niches of occurring species leads to high local ecosystem functioning. A strong match can only be achieved if species with fitting niches are available at a local site. A large regional species pool (i.e., high γ diversity) makes it more likely that species with fitting niches are available, translating to a positive biodiversity-EF relationship. However, γ diversity can only increase functioning if species are able to get to appropriate habitats. Thus, dispersal may be an essential mediator of biodiversity-EF relationships. If species are dispersal limited, then many niches may be vacant, resulting in low efficiency of local communities. On

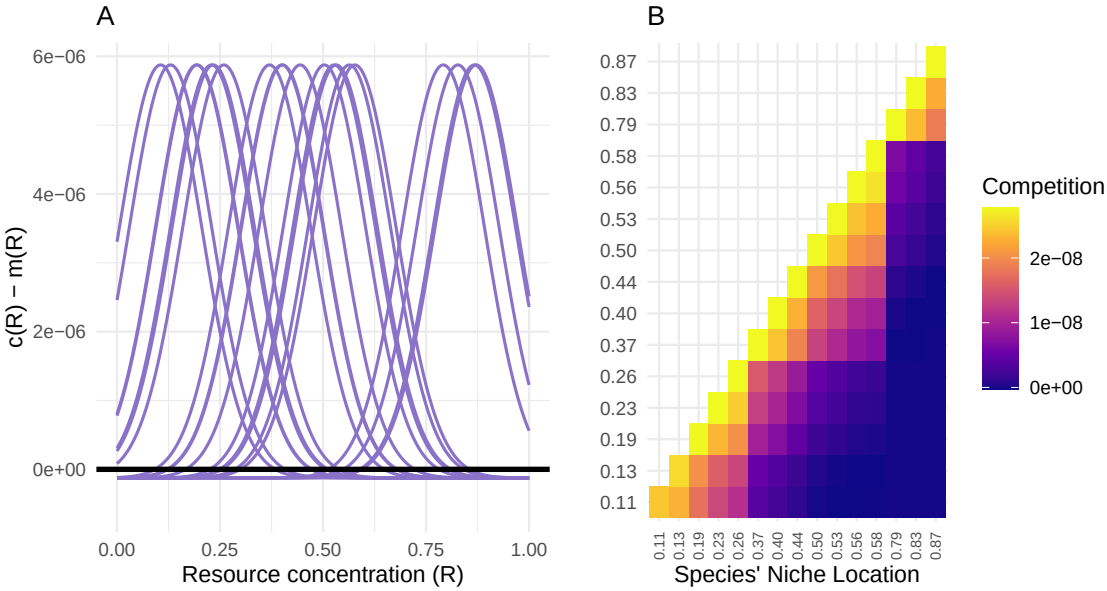

Figure 3: Visualisation of (A) niches and (B) strength of competition for a sample metacommunity of 20 species. In (A), the vertical axis is the difference between the colonisation term $c(R)$ and the extinction term $m(R)$. The height of this curve represents the net rate of change of occupied patches for given resource conditions for each species. Values greater than zero indicate conditions under which the species is able to persist in the long-term and represent the species' fundamental niches. In (B), species are ordered following their niche location (i.e., the location on the resource axis of the optimum in A). Colours indicate pairwise competition strength, which are proportional to the degree of niche overlap.

the other hand, high dispersal can lead to communities structured primarily by mass effects, resulting in communities with many redundant species or with species that are not well-adapted to local conditions (Mouquet and Loreau 2003; Declerck et al. 2013; Horváth et al. 2016). In other words, dispersal being either too low or too high can lead to a mismatch between environment and species and may reduce the strength of biodiversity-EF relationships.

We developed scenarios to see whether flume can reproduce the expectation that biodiversity-EF relationships are stronger at intermediate dispersal. We included γ diversity and the strength of competition as additional variables, to determine if they mediate any effect of dispersal on biodiversity-EF relationships. We started with a template metacommunity consisting of 50 species. All species had identical niche parameters (Table 1), with the exception of the niche location, which was randomly selected on the interval (0.1, 0.9). We scaled resource concentrations such that they were approximately between 0 and 1, for simplicity. From this template, we generated scenarios consisting of either a high- (40 species) or low- (20 species) diversity metacommunity. These scenarios were generated by drawing species randomly from the template metacommunity; for each diversity scenario, we generated a total of ten metacommunities this way, each with different randomly drawn species (Fig. 3).

For each of the ten species lists, we ran simulations while varying dispersal ability

and the strength of competition. Competition strength was varied by adjusting the competition scale parameter. In this way, local competition was always dependent on the number and niche parameters of species present, but globally competition was scaled up or down according to the scenario. We ran a high-competition scenario ($o_\gamma = 0.1$) and a low-competition scenario ($o_\gamma = 0.001$). We varied dispersal by changing the active dispersal component (α) from $\alpha = 0.4$ to $\alpha = 2.8$, in steps of 0.4. We additionally added a "nearly zero" dispersal scenario where $\alpha = 0.05$, for a total of eight total dispersal scenarios. We used a small value instead of zero for α to avoid species being permanently lost from upstream reaches due to no upstream dispersal (and no immigration from outside the river network). The passive dispersal parameter was held at a constant low level ($\beta = 0.1$). All combinations of competition, γ-diversity, species lists, and dispersal ability resulted in 320 total scenarios. Additionally, to capture variability in the stochastic model, we replicated each individual scenario 8 times. All scenarios were run at a temporal resolution of 1 day, and for a total of 90 time steps. Initial and boundary conditions for resources were set to vary between 0.1 and 0.9 and were spatially autocorrelated, simulating a resource gradient due to, e.g., land use differences across the river network. Initial species locations were determined randomly with a per-species target prevalence of 20% of reaches occupied. When reporting results, we report all figures as a temporal average from the final 30 time steps. Taking the last time steps allows the model time to "forget" initial conditions, while averaging over time reduces some noise simply due to random fluctuations in colonisation/extinction of species. We use the total resource consumption rate (i.e., in units of $mass \times volume^{-1} \times time^{-1}$) as the measure of ecosystem function, and species richness as the measure of biodiversity.

Overall biodiversity-EF relationships were positive for all scenarios. Unsurprisingly, increasing dispersal rates had a positive influence on local biodiversity (Fig. 4). Thus, the higher dispersal scenario represents a shift in metacommunity structuring towards mass effects, whereby local diversity reflects the immigration of species that are not necessarily strongly adapted for the local conditions.

The extent to which mass effects reduced the efficiency of resource processing and the strength of the biodiversity-EF relationship depended both on gamma diversity and competition strength. When competition was weak, we observed little relationship between the biodiversity-EF slope and the dispersal ability of species when diversity was low, but a weak negative relationship when diversity was high (Fig. 5). For both of these scenarios, there was no hump shape; i.e., the theoretical prediction that dispersal facilitates strong biodiversity-EF relationships up until mass effects result in poorly adapted communities was not supported when competition was weak. In contrast, with strong competition, we observed a pronounced hump in the relationship between the biodiversity-EF slope and dispersal ability. In high diversity-high competition scenarios, the decline in the biodiversity-EF slope was quite rapid following its maximum, suggesting that with many available species, mass effects quickly overwhelm local sorting (Fig. 5b). For low diversity-high competition scenarios, this decline was more gradual.

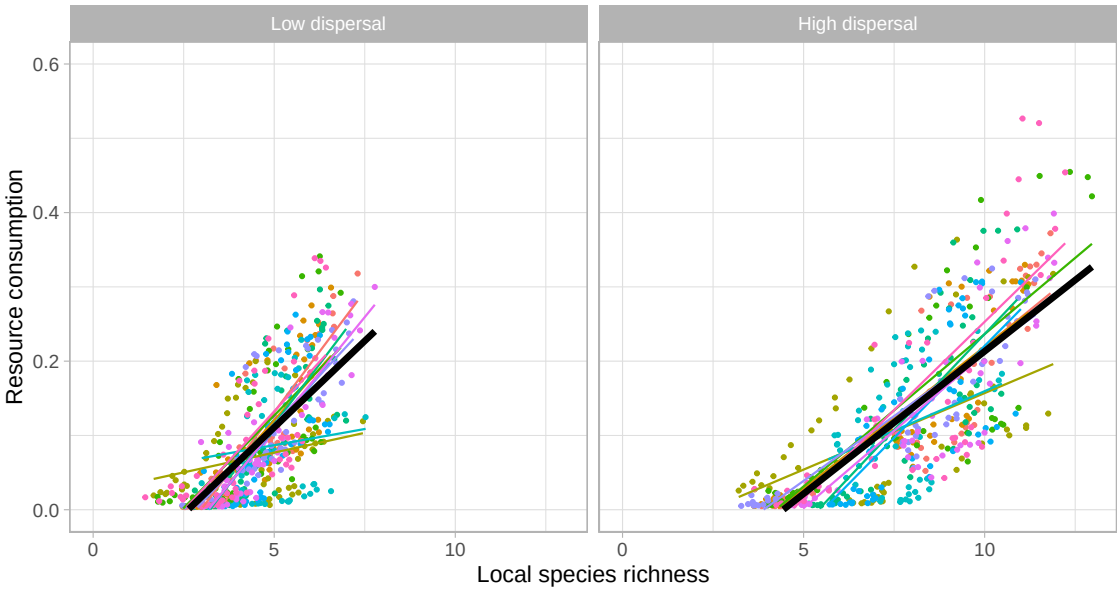

Figure 4: Biodiversity-ecosystem functioning relationships for two scenarios. Here, total resource consumption is a proxy for ecosystem function; units are arbitrary, but taken to be in $mass \times volume^{-1} \times time^{-1}$. Overall slopes for the two scenarios are similar, but the low-dispersal scenario (left panel) has reduced local diversity compared with the high-dispersal scenario (right panel). Both scenarios had low metacommunity gamma diversity (20 species) and moderately-high competition (competition scale = 0.1). Each point represents a single reach. Points and lines are coloured for separate replicate runs of each scenario (i.e,. the same parameters, but different random species lists). The black line shows the BEF relationship for all replicates together.

4 Discussion

We have presented here a new model for interacting community and resource dynamics in fluvial meta-ecosystems, along with an R-package *flume* implementing the model (Talluto 2023). Our model is based on coupling a patch dynamics model (similar to classical metapopulation models; Levins 1969) with a reaction transport model. We demonstrate with our case study that the model can be used to quickly explore hypotheses about the mechanisms structuring biodiversity-EF relationships. The model reproduced a hump-shaped relationship between dispersal and the biodiversity-EF slope under some conditions. In particular, the hump shape was only visible when competition was a strong influence in structuring the biological community, and was more pronounced with more diverse metacommunities (Fig. 5) Variation in the output across replicate simulations and due to different species in the metacommunities was low relative to the magnitude of the effects Here, we discuss further some potential applications of the model, and some challenges to its use.

4.1 Applications

One of the main applications of our model and the accompanying software is in rapidly exploring hypotheses relating to diversity and ecosystem function at the scale of

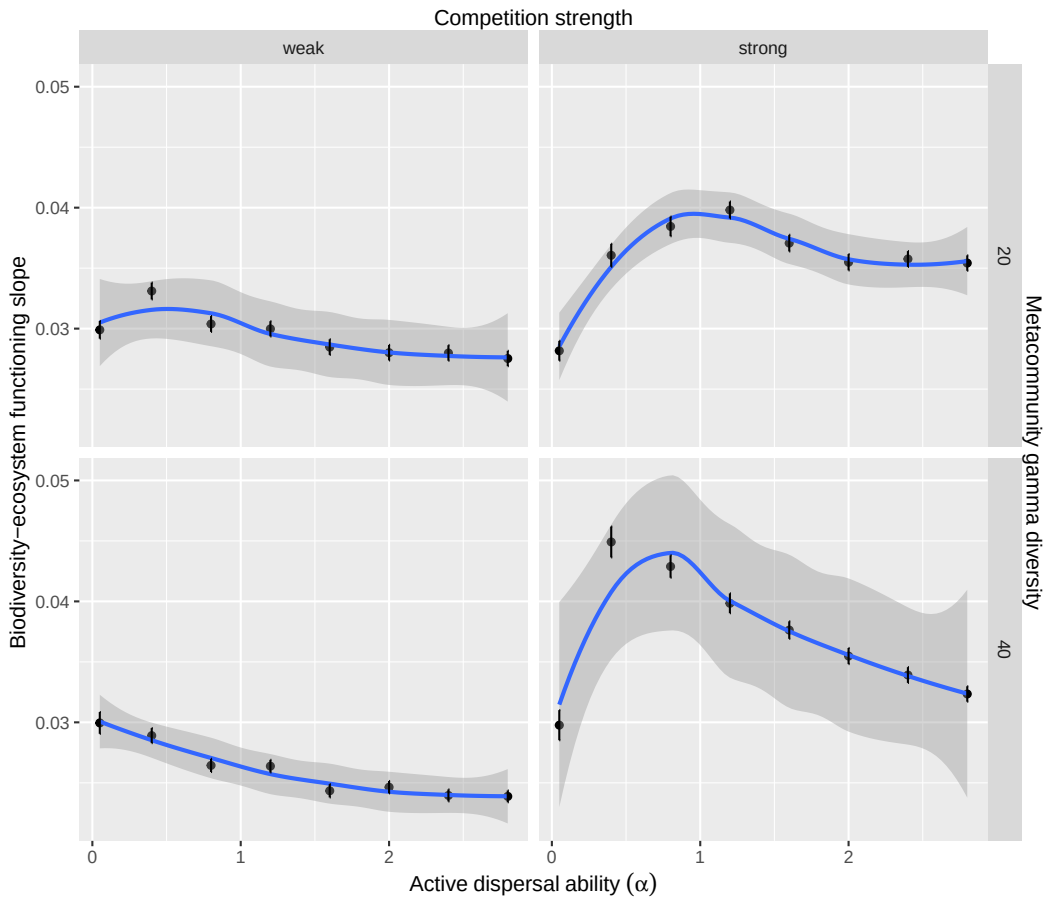

Figure 5: Strength of the biodiversity-EF relationship as a function of dispersal. Horizontal panels are for low (left) and high (right) competition scenarios, while vertical facets show low (top) and high (bottom) metacommunity diversity scenarios. A loess smoother has been added to show the relationships more clearly. When competition is weak, there is little relationship between dispersal and biodiversity-EF relationships. In contrast, strong competition facilitates a strong link between biodiversity and ecosystem function, with maximum slopes observed at low to intermediate dispersal rates.

entire river networks. Manipulations that are difficult or impossible to manage in the field or laboratory can easily be performed *in silico*. For example, changes in river network topology (e.g., due to human influence or changing precipitation patterns) can influence the balance between resource consumption and transport, and also change metacommunity dynamics (and associated feedbacks between the community and resource consumption). In the field, such changes can be studied either in time (e.g., by studying a single network before and after disruption), or in space (e.g., studying many networks with different spatial properties), but in both cases such studies are expensive and logistically difficult. Our model could be used to explore potentially fruitful avenues of research, to suggest experimental designs, and to evaluate potential important mechanisms before committing resources to a field study.

4.2 Calibration

Calibration of our model presents a number of challenges. Although the model parameters describe ecological processes, many of them will be very difficult to measure in practise. For example, measuring dispersal rates is possible, but our model expects dispersal in terms of the contribution to total colonisation flux (and incorporates both the movement of organisms as well as the successful establishment at the colonisation site). This is nearly impossible to measure in the field, although it could be measured or controlled for in laboratory conditions. However, measurement of dispersal in terms of relative rates of upstream and downstream dispersal is possible, as is measurement of how dispersal changes with distance; this could still be useful for calibration for establishing relationships among model parameters up to a constant.

At a higher level, many of the model's outputs are frequently measured under field conditions, such as bulk rates of ecosystem function or local and regional biodiversity patterns. Thus, reverse calibration becomes possible. Such a procedure would involve obtaining information from field or lab experiments that corresponds to particular model outputs (as well as inputs when possible). Then the calibration algorithm searches for parameter combinations that maximise the likelihood of the measured quantities given the model outputs. Because the model has many free parameters, some of which are likely exchangeable, simple optimisation algorithms are unlikely to produce sensible results. However, algorithms that perform better with multiple local optima, such as simulated annealing or Markov Chain Monte Carlo (MCMC) may be fruitful. Bayesian calibration using MCMC in particular has two benefits. First, a modeller can constrain model parameters using prior distributions, helping to narrow the search space and making it less likely that the model produces unrealistic parameter estimates. Second, full posterior inference allows for multiple parameter combinations to be included in the solution set and compared probabilistically. For example, a given data set may reveal that either active dispersal and competition are both very high, or dispersal and competition are very low, but only if there is also immigration from outside the river network. This kind of exercise could prove very useful in suggesting hypotheses and guiding future field studies. A major challenge of this approach is computational; MCMC may require many model runs to fully explore the parameter space, especially for high-dimensional models.

References

Altermatt, Florian, Chelsea J. Little, Elvira Mächler, Shaopeng Wang, Xiaowei Zhang et al. (2020). Uncovering the Complete Biodiversity Structure in Spatial Networks: The Example of Riverine Systems. *Oikos* 129.5, pp. 607–618.

Austin, Mike P. (1999). A Silent Clash of Paradigms: Some Inconsistencies in Community Ecology. *Oikos* 86.1, pp. 170–178.

Baird, Donald J. and Mehrdad Hajibabaei (2012). Biomonitoring 2.0: A New Paradigm in Ecosystem Assessment Made Possible by next-Generation DNA Sequencing. *Molecular Ecology* 21.8, pp. 2039–2044.

Bannar-Martin, Katherine H., Colin T. Kremer, S.K. Morgan Ernest, Mathew A. Leibold, Harald Auge et al. (2018). Integrating Community Assembly and Biodiversity to Better Understand Ecosystem Function: The Community Assembly and the Functioning of Ecosystems (CAFE) Approach. *Ecology Letters* 21.2, pp. 167–180.

Battin, Tom J., Louis A. Kaplan, Stuart Findlay, Charles S. Hopkinson, Eugenia Marti et al. (Feb. 2008). Biophysical Controls on Organic Carbon Fluxes in Fluvial Networks. *Nature Geoscience* 1.2, pp. 95–100.

Burgers, H. E. (Robin), Aafke M. Schipper and A. Jan Hendriks (2014). Size Relationships of Water Discharge in Rivers: Scaling of Discharge with Catchment Area, Main-Stem Length and Precipitation. *Hydrological Processes* 28.23, pp. 5769–5775.

Cardinale, Bradley J., J. Emmett Duffy, Andrew Gonzalez, David U. Hooper, Charles Perrings et al. (7th June 2012). Biodiversity Loss and Its Impact on Humanity. *Nature* 486.7401, pp. 59–67.

Cid, Núria, Tibor Erős, Jani Heino, Gabriel Singer, Sonja C Jähnig et al. (2022). From Meta-System Theory to the Sustainable Management of Rivers in the Anthropocene. *Frontiers in Ecology and the Environment* 20.1, pp. 49–57.

Cornwell, William K., Johannes H. C. Cornelissen, Kathryn Amatangelo, Ellen Dorrepaal, Valerie T. Eviner et al. (2008). Plant Species Traits Are the Predominant Control on Litter Decomposition Rates within Biomes Worldwide. *Ecology Letters* 11.10, pp. 1065–1071.

Declerck, Steven A. J., Christian Winter, Jonathan B. Shurin, Curtis A. Suttle and Blake Matthews (Mar. 2013). Effects of Patch Connectivity and Heterogeneity on Metacommunity Structure of Planktonic Bacteria and Viruses. *The ISME Journal* 7.3 (3), pp. 533–542.

Díaz, Sandra, Andy Purvis, Johannes H. C. Cornelissen, Georgina M. Mace, Michael J. Donoghue et al. (2013). Functional Traits, the Phylogeny of Function, and Ecosystem Service Vulnerability. *Ecology and Evolution* 3.9, pp. 2958–2975.

Díaz, Sandra, Amy J. Symstad, F. Stuart Chapin, David A. Wardle and Laura F. Huenneke (1st Mar. 2003). Functional Diversity Revealed by Removal Experiments. *Trends in Ecology & Evolution* 18.3, pp. 140–146.

Duffy, J. Emmett, Casey M. Godwin and Bradley J. Cardinale (Sept. 2017). Biodiversity Effects in the Wild Are Common and as Strong as Key Drivers of Productivity. *Nature* 549.7671, pp. 261–264.

Gagic, Vesna, Ignasi Bartomeus, Tomas Jonsson, Astrid Taylor, Camilla Winqvist et al. (22nd Feb. 2015). Functional Identity and Diversity of Animals Predict Ecosystem Functioning Better than Species-Based Indices. *Proceedings of the Royal Society B: Biological Sciences* 282.1801, p. 20142620.

Gonzalez, Andrew, Rachel M. Germain, Diane S. Srivastava, Elise Filotas, Laura E. Dee et al. (2020). Scaling-up Biodiversity-Ecosystem Functioning Research. *Ecology Letters* 23.4, pp. 757–776.

Gounand, Isabelle, Eric Harvey, Chelsea J. Little and Florian Altermatt (1st Jan. 2018). Meta-Ecosystems 2.0: Rooting the Theory into the Field. *Trends in Ecology & Evolution* 33.1, pp. 36–46.

Gravel, Dominique, Nicolas Mouquet, Michel Loreau and Frédéric Guichard (Sept. 2010). Patch Dynamics, Persistence, and Species Coexistence in Metaecosystems. *The American Naturalist* 176.3, pp. 289–302.

Harvey, Eric, Justin N. Marleau, Isabelle Gounand, Shawn J. Leroux, Carina R. Firkowski et al. (2023). A General Meta-Ecosystem Model to Predict Ecosystem Functions at Landscape Extents. *Ecography* 2023.11, e06790.

Heino, Jani, Adriano S. Melo, Tadeu Siqueira, Janne Soininen, Sebastian Valanko et al. (2015). Metacommunity Organisation, Spatial Extent and Dispersal in Aquatic Systems: Patterns, Processes and Prospects. *Freshwater Biology* 60.5, pp. 845–869.

Holt, R. D., J. H. Lawton, K. J. Gaston and T. M. Blackburn (1997). On the Relationship between Range Size and Local Abundance: Back to Basics. *Oikos* 78.1, pp. 183–190.

Holt, R.d. and T.h. Keitt (2000). Alternative Causes for Range Limits: A Metapopulation Perspective. *Ecology Letters* 3.1, pp. 41–47.

Holt, Robert D., Timothy H. Keitt, Mark A. Lewis, Brian A. Maurer and Mark L. Taper (2005). Theoretical Models of Species' Borders: Single Species Approaches. *Oikos* 108.1, pp. 18–27.

Hooper, D. U., F. S. Chapin III, J. J. Ewel, A. Hector, P. Inchausti et al. (2005). Effects of Biodiversity on Ecosystem Functioning: A Consensus of Current Knowledge. *Ecological Monographs* 75.1, pp. 3–35.

Hooper, David U., E. Carol Adair, Bradley J. Cardinale, Jarrett E. K. Byrnes, Bruce A. Hungate et al. (June 2012). A Global Synthesis Reveals Biodiversity Loss as a Major Driver of Ecosystem Change. *Nature* 486.7401 (7401), pp. 105–108.

Horváth, Zsófia, Csaba F. Vad and Robert Ptacnik (2016). Wind Dispersal Results in a Gradient of Dispersal Limitation and Environmental Match among Discrete Aquatic Habitats. *Ecography* 39.8, pp. 726–732.

Huber, Stefan A., Andreas Balz, Michael Abert and Wouter Pronk (1st Jan. 2011). Characterisation of Aquatic Humic and Non-Humic Matter with Size-Exclusion Chromatography – Organic Carbon Detection – Organic Nitrogen Detection (LC-OCD-OND). *Water Research* 45.2, pp. 879–885.

Hunt, Julia J.F.G. and Michael B. Bonsall (2009). The Effects of Colonization, Extinction and Competition on Co-Existence in Metacommunities. *Journal of Animal Ecology* 78.4, pp. 866–879.

Kristiansen, Jørgen (1st Oct. 1996). 16. Dispersal of Freshwater Algae — a Review. *Hydrobiologia* 336.1, pp. 151–157.

Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase et al. (2004). The Metacommunity Concept: A Framework for Multi-Scale Community Ecology. *Ecology Letters* 7.7, pp. 601–613.

Levins, Richard (1st Sept. 1969). Some Demographic and Genetic Consequences of Environmental Heterogeneity for Biological Control1. *Bulletin of the Entomological Society of America* 15.3, pp. 237–240.

Little, Chelsea J. and Florian Altermatt (2018). Species Turnover and Invasion of Dominant Freshwater Invertebrates Alter Biodiversity–Ecosystem-Function Relationship. *Ecological Monographs* 88.3, pp. 461–480.

Loreau, Michel, Nicolas Mouquet and Robert D. Holt (2003). Meta-Ecosystems: A Theoretical Framework for a Spatial Ecosystem Ecology. *Ecology Letters* 6.8, pp. 673–679.

Margalef, R. (Nov. 1963). On Certain Unifying Principles in Ecology. *The American Naturalist* 97.897, pp. 357–374.

McGill, Brian J. (1st Mar. 2012). Trees Are Rarely Most Abundant Where They Grow Best. *Journal of Plant Ecology* 5.1, pp. 46–51.

Mouquet, Nicolas and Michel Loreau (Nov. 2003). Community Patterns in Source-Sink Metacommunities. *The American Naturalist* 162.5, pp. 544–557.

Pennekamp, Frank, Mikael Pontarp, Andrea Tabi, Florian Altermatt, Roman Alther et al. (Nov. 2018). Biodiversity Increases and Decreases Ecosystem Stability. *Nature* 563.7729 (7729), pp. 109–112.

Roebuck, Jesse Alan Jr., Michael Seidel, Thorsten Dittmar and Rudolf Jaffé (7th Jan. 2020). Controls of Land Use and the River Continuum Concept on Dissolved Organic Matter Composition in an Anthropogenically Disturbed Subtropical Watershed. *Environmental Science & Technology* 54.1, pp. 195–206.

Sleighter, Rachel L. and Patrick G. Hatcher (June 2008). Molecular Characterization of Dissolved Organic Matter (DOM) along a River to Ocean Transect of the Lower Chesapeake Bay by Ultrahigh Resolution Electrospray Ionization Fourier Transform Ion Cyclotron Resonance Mass Spectrometry. *Marine Chemistry* 110.3-4, pp. 140–152.

Soetaert, Karline and Peter MJ Herman (2009). *A Practical Guide to Ecological Modelling*. Berlin: Springer.

Soetaert, Karline, Thomas Petzoldt and R. Woodrow Setzer (23rd Feb. 2010). Solving Differential Equations in R: Package deSolve. *Journal of Statistical Software* 33, pp. 1–25.

Talluto, Matthew (2023). *Flume: A Model For Fluvial Meta-Ecosystems. https://github.com/flee-group/flume*. Version 0.5.1.9002.

Talluto, Matthew, Rubén del Campo, Edurne Estévez, Florian Altermatt, Thibault Datry et al. ({in press}). Towards (Better) Fluvial Meta-Ecosystem Ecology: A Research Perspective. *npj Biodiversity*.

Talluto, Matthew V., Isabelle Boulangeat, Steve Vissault, Wilfried Thuiller and Dominique Gravel (12th June 2017). Extinction Debt and Colonization Credit Delay

Range Shifts of Eastern North American Trees. *Nature Ecology & Evolution* 1.7 (7), pp. 1–6.

Thébault, Elisa and Michel Loreau (1st Jan. 2006). The Relationship between Biodiversity and Ecosystem Functioning in Food Webs. *Ecological Research* 21.1, pp. 17–25.

Tremblay, Luc, Ghita Alaoui and Marc N. Léger (15th Nov. 2011). Characterization of Aquatic Particles by Direct FTIR Analysis of Filters and Quantification of Elemental and Molecular Compositions. *Environmental Science & Technology* 45.22, pp. 9671–9679.

Urban, Mark C. (2004). Disturbance Heterogeneity Determines Freshwater Metacommunity Structure. *Ecology* 85.11, pp. 2971–2978.

Winfree, Rachael, Jeremy W. Fox, Neal M. Williams, James R. Reilly and Daniel P. Cariveau (2015). Abundance of Common Species, Not Species Richness, Drives Delivery of a Real-World Ecosystem Service. *Ecology Letters* 18.7, pp. 626–635.