A general meta-ecosystem model to predict ecosystem functions at landscape extents

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Abstract

The integration of ecosystem processes over large spatial extents is critical to predicting whether and how global changes may impact biodiversity and ecosystem functions. Yet, there remains an important gap in meta-ecosystem models to predict multiple functions (e.g., carbon sequestration, elemental cycling, trophic efficiency) across ecosystem types (e.g., terrestrial-aquatic, benthic-pelagic). We derive a flexible meta-ecosystem model to predict ecosystem functions at landscape extents by integrating the spatial dimension of natural systems as spatial networks of different habitat types connected by cross-ecosystem flows of materials and organisms. We partition the physical connectedness of ecosystems from the spatial flow rates of materials and organisms, allowing the representation of all types of connectivity across ecosystem boundaries as well as the interaction(s) between them. Through simulating a forest-lake-stream meta-ecosystem, our model illustrated that even if spatial flows induced significant local losses of nutrients, differences in local ecosystem efficiencies could lead to increased secondary production at regional scale. This emergent result, which we dub the 'cross-ecosystem efficiency hypothesis', emphasizes the importance of integrating ecosystem diversity and complementarity in meta-ecosystem models to generate empirically testable hypotheses for ecosystem functions.

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Abstract

The integration of ecosystem processes over large spatial extents is critical to predicting whether and how global changes may impact biodiversity and ecosystem functions. Yet, there remains an important gap in meta-ecosystem models to predict multiple functions (e.g., carbon sequestration, elemental cycling, trophic efficiency) across ecosystem types (e.g., terrestrial-aquatic, benthic-pelagic). We derive a flexible meta-ecosystem model to predict ecosystem functions at landscape extents by integrating the spatial dimension of natural systems as spatial networks of different habitat types connected by cross-ecosystem flows of materials and organisms. We partition the physical connectedness of ecosystems from the spatial flow rates of materials and organisms, allowing the representation of all types of connectivity across ecosystem boundaries as well as the interaction(s) between them. Through simulating a forest-lake-stream meta-ecosystem, our model illustrated that even if spatial flows induced significant local losses of nutrients, differences in local ecosystem efficiencies could lead to increased secondary production at regional scale. This emergent result, which we dub the 'cross-ecosystem efficiency hypothesis', emphasizes the importance of integrating ecosystem diversity and complementarity in meta-ecosystem models to generate empirically testable hypotheses for ecosystem functions.

Keywords: metacommunity, cross-ecosystem subsidy, spatial networks, aquatic-terrestrial linkages, ecosystem function, landscape scale

Context: Ecosystem function(s) at the landscape scale

Flows of resources, materials, and organisms can connect different types of ecosystems within a landscape (Polis et al. 1997, Loreau et al. 2003, Massol et al. 2011). Meta-ecosystem theory has been proposed to describe these spatial flows across coupled ecosystems and explain how spatial and temporal changes in biodiversity within each ecosystem can affect functions at larger spatial scales (Loreau et al. 2003, Gravel et al. 2010, Gounand et al. 2014). The theory, however, has been challenged for lack of connection to empirical research (Massol et al. 2011, Harvey et al. 2016, Gounand et al. 2018a) and there is a current push to develop empirically motivated meta-ecosystem models.

Early meta-ecosystem theory used spatially implicit or two-patch ecosystem models to investigate how allochthonous flows impacted ecosystem stability and functioning (Loreau and Holt 2004, Gravel et al. 2010, Marleau et al. 2010, Gounand et al. 2014). The theory expanded through models that include multi-patch systems (Marleau et al. 2014, McCann et al. 2021), ecological stoichiometry (Marleau et al. 2015, Marleau and Guichard 2019), non-diffusive movement of organisms (Leroux and Loreau 2012, McLeod and Leroux 2021, Peller et al. 2022) and has been used to explain phenomena varying from nutrient colimitation (Marleau et al. 2015) to trophic functional structures (Jacquet et al. 2022). However, there is no current theoretical model investigating the spatial flow of both abiotic (i.e., resources, nutrients) and biotic (i.e., organisms) compartments across different ecosystem types (e.g., terrestrial-aquatic), in multi-patch systems (Massol et al. 2017, Gounand et al. 2018a). The theoretical and empirical integration of meta-ecosystem processes at a broad spatial extent is critical to understanding and therefore predicting whether and how global changes may impact biodiversity and ecosystem functions at the landscape scale.

Empirical examples of spatial flows of energy, materials, or organisms coupling different ecosystems abound and have recently been reviewed (Gounand et al. 2018b, Montagano et al. 2019, Peller et al. 2020). Several of these studies focus on how cross-ecosystem exchanges or allochthonous flows affect dynamics at the ecotone (Richardson and Sato 2015). What is missing are studies investigating the functional implications of meta-ecosystem dynamics at broader spatial extents than the ecotone (but see Iwata et al. 2003, Largaespada et al. 2012, Jacquet et al. 2022). The effects of material and organismal flows are likely to propagate or even accumulate across landscapes driving regional variation in ecosystem function. In watersheds, for instance, different cross-ecosystem flows (e.g., litterfall, fish migration) will operate at different spatial scales and thus contribute to ecosystem functions (e.g., primary and secondary production) at multiple spatial extents (Figure 1). The combined effects of those flows of abiotic and biotic compartments, however, should predict functioning at the whole landscape scale (Figure 1).

Here, we derive a meta-ecosystem model to predict ecosystem function(s) at landscape extents by integrating the spatial dimension of ecosystems as spatial networks of different habitat types connected by cross-ecosystem flows of materials and organisms. This meta-ecosystem model partitions the physical connectedness of ecosystems from the spatial flow rates of materials and organisms allowing the representation of all types of connectivity across ecosystem boundaries as well as the interaction(s) between these two properties. For example, organisms can have different life stages that perceive their physical environment differently (aquatic versus terrestrial stages) and/or can have different movement rates (winged versus non-winged). Thus, the impacts and the measurements of physical connectedness and rates of spatial flows are likely to be quite different, despite being key components of connectivity.

We use this model to generate testable predictions on ecosystem functions at landscape extents, using watersheds as an example, and to investigate the impacts of perturbations on cross-ecosystem flows and corresponding functions.

Empirical meta-ecosystem – from ecosystem boundaries to the landscape

Watersheds are a classic and relevant example to illustrate the potential of our proposed integrated meta-ecosystem approach because they are mosaics of terrestrial and aquatic ecosystems interconnected by spatial flows of materials, energy, and organisms (Hynes 1975). Moreover, because of their relevance as a unit for conservation and resource management, watersheds have been extensively studied and spatial flows of materials, as well as organisms, have been quantified in many watersheds (Figure 2 and Table S1 for an extensive review).

Previous studies have shown that inputs of terrestrial detritus to aquatic ecosystems are very common (Gounand et al. 2018b, 2020) , and they can limit benthic invertebrate production and contribute to fish diet (Richardson 1991, Kawaguchi et al. 2003, Marczak and Richardson 2007, Bultman et al. 2014, Wallace et al. 2015) (see Figure 2a arrow A). Conversely, emerging aquatic insects contribute to the diets of terrestrial consumers (Nakano and Murakami 2001, Sabo and Power 2002, Iwata et al. 2003, Baxter et al. 2005, Bultman et al. 2014) (see Figure 2a arrow B). Movements of organisms, organic matter, and nutrients also occur within ecosystems either passively following directional flows along the dendritic network (upstream to downstream e.g., particulate organic matter, see Figure 2a arrow C) or actively via organismal movement (downstream to upstream e.g., fish migrations, Figure 2a,b arrows D and H) (Peller et al. 2023). Biomass and resources can also be exchanged vertically between benthic and pelagic lake zones via the sinking and resuspension of plankton and organic matter (Jyväsjärvi et al. 2013, Matisoff et al. 2017) (see Figure 2a arrows E and F).

The large body of empirical research on flows of materials and organisms in watersheds highlights how different types of spatial flows have been studied mostly in isolation, ignoring their bi-directional property (Schindler and Smits 2017, but see review in Marcarelli et al. 2020). Taken as a whole, however, the data clearly demonstrate that multiple abiotic and biotic flows interact and flow reciprocally across different ecosystems in watersheds. The different flows can be separated into three broad categories: (1) **trophic flows within each ecosystem patch** (e.g., biomass transfer along the food chain at one location), (2) **spatial flows among patches of the same ecosystem type** (e.g., ungulates foraging across different forest patches), and (3) **spatial flows across patches of different ecosystem types** (flows at the ecotone of two different ecosystem types, e.g., forest-lake). We surmise that by integrating these three types of flows into meta-ecosystem theory, we can better represent variations in ecosystem functioning across landscapes (Figure 1). The theory we derive in the next section can be reduced to models integrating various combinations of the three individual components listed above, but the full strength of our novel approach is in the integration of these three flow types.

Using watersheds as a case study allows us to highlight (**1**) the biotic linkages that can emerge between ecosystems of different types (here terrestrial-aquatic) and (**2**) how cross-ecosystem biotic linkages at the ecotone interface are indirectly linked to the whole watershed via the connectivity structure of the landscape. Although we use watersheds to illustrate the usefulness of our model, the landscape perspective that we propose is relevant for any system for which spatial flows within ecosystem types (e.g., seagrass leaves decaying and flowing to an adjacent seagrass bed) and spatial flows across different ecosystem types (e.g., nutrients leaching from islands to the seagrass beds) are expected to interact and affect dynamics and functions at broader scales: marine-island, marine-freshwater, pelagic-benthic, and even, less intuitively, forest-grassland connections where behavioral movements within and across the two similar ecosystems can play an important role in driving divergence in trophic dynamics and productivity (Abbas et al. 2012, Leroux et al. 2017, Gounand et al. 2018b, García-Callejas et al. 2019).

Meta-ecosystem dynamics across different ecosystems involve spatial couplings where a specific trophic level contributes to different trophic levels in the connected ecosystems (Leroux and Loreau 2012, Montagano et al. 2019, Jacquet et al. 2022). Often, this occurs through the conversion of living to dead organic matter and eventually inorganic matter. For example, terrestrial herbivore insects falling in water can subsidize aquatic top-predators and decomposers at the same time, and also affect aquatic herbivores through indirect interactions by relaxing predation pressure via an alternative food source (Baxter et al. 2005, Allen and Wesner 2016, Montagano et al. 2019). Alternatively, predation pressure on aquatic herbivores may increase if terrestrial herbivores subside aquatic predators directly, generating a numerical response (Baxter et al. 2004, Sato et al. 2016, Takimoto and Sato 2020). Those indirect cross-ecosystem biotic interactions illustrate the permeability between ecosystems and the complexity of predicting how human actions in one ecosystem might affect coupled ecosystems (Leroux and Loreau 2012, Massol et al. 2017, Montagano et al. 2019).

Cross-ecosystem interactions also constitute a dominant mechanism by which changes in the processes in one locality can impact processes at a different location, even in the absence of dispersal (i.e., 'spatial cascade', see Gounand et al. 2017, García-Callejas et al. 2019). For instance, it has been shown that upstream forest cover contributes ~70% of all dissolved organic carbon loadings to watersheds of the North American Adirondack mountains (Canham et al. 2004), and the spatial configuration of forest patches in watersheds is a direct driver of leaf litter availability in headwater streams (Little and Altermatt 2018). Cascading effects in space can also occur through the active movement of organisms subsidized by terrestrial resources along the connectivity structure of the river network. For example, the movement of aquatic invertebrates subsidized by red alder detritus (favoured by human forest harvesting over other species) from upstream reaches that will, in turn, subsidize downstream fish habitats (Wipfli and Musslewhite 2004).

The magnitude of any spatial cascade across the landscape could be controlled by three main factors: (**1**) the level of biotic movement (dispersal or regular foraging movements within a habitat) of organisms acting as consumers at multiple locations (McCann et al. 2005), (**2**) the passive abiotic movement of altered nutrient or decaying detritus (Vannote et al. 1980), and (**3**) the constraints imposed by landscape configuration on these processes (Harvey and Altermatt 2019, McLeod and Leroux 2021). These factors need to be explicitly integrated to achieve the scaling up of ecosystem function from local to landscape extents. We thus need a modelling framework capable of incorporating these factors while also faithfully representing local interactions.

A meta-ecosystem model for landscape ecosystem functions

To start, we want to keep track of all organisms and materials that are interacting across the ecosystems that make up our meta-ecosystem. We keep track of their current state in a vector we label **x**. At a given time, we can examine the state of a given organism (say the grasshopper in the forest) or a given material (detritus in a lake) by looking corresponding element in the **x** vector, $x_{ki,}$ where the *k* denotes the type of ecosystem compartment (e.g. primary producer) and *i* denotes which ecosystem it is in (e.g. a patch of forest). The elements of the vector change over time as the organisms and materials interact within and between ecosystems, which we can represent with a system of differential equations $d\mathbf{x}/dt = \mathbf{G(x)}$, where **G** is a vector-valued function describing rates of change of each ecosystem compartment. Thus, **G(x)** is to capture vast complexity of ecological processes seen within the meta-ecosystem such as nutrient recycling, detritus decomposition, spatial flows of organisms and materials, trophic flows, etc.

To make **G(x)** more tractable, we can decompose it into parts. For our purposes, we first split **G** into two parts: *flows in local ecosystems* and *between ecosystem flows*. *Flows in local ecosystems* are flows between ecosystem compartments within the same ecosystem, e.g. a grasshopper eating a plant in a forest. We note that organisms from one ecosystem type may forage in another ecosystem, e.g. a bear in a river, and we will categorize that flow as local. This contrasts with other studies that modelled direct flows from one ecosystem to another across trophic levels, i.e., a consumer in one ecosystem consumes a resource in another (McCann et al. 2005, García-Callejas et al. 2019, Peller et al. 2022). However, such a spatial flow implicitly assumes that there is instantaneous movement between ecosystems for either the consumer and/or resource, and therefore tight coupling between consumption and movement. An alternative is to explicitly model the dynamics of a non-local compartment in its non-local ecosystem type (see Figure 3b) (Leroux and Loreau 2012). While this approach creates more variables to keep track of, it also helps us generalize our methods to more diverse situations and allows for cleaner mathematical treatment (Box 1).

We collect all these flows in the vector-valued function $\mathbf{F(x)}$, which is itself composed of *nm* functions, where *n* is the number of ecosystem compartments in the whole meta-ecosystem and *m* is the number of ecosystem patches (i.e. physically distinguishable ecosystems that may or may not be of the same type). Formally, $\mathbf{F(x)} = [f_{1,1}(\mathbf{x}_1),\ f_{2,1}(\mathbf{x}_2),\ \ldots,\ f_{i,1}(\mathbf{x}_i),\ \ldots,\ f_{n,1}(\mathbf{x}_n), f_{1,2}(\mathbf{x}_1),\ \ldots,\ f_{n,2}(\mathbf{x}_n),\ \ldots, f_{i,k}(\mathbf{x}_i),\ \ldots, f_{n,m}(\mathbf{x}_n)]^T$ where $\mathbf{x}_i = (x_{i,1}, \ldots, x_{i,k}, \ldots, x_{i,m})$ describe the local flows to and from ecosystem compartment *k* in ecosystem patch *i*.

Between ecosystem flows are the spatial flows that cross the boundaries of one ecosystem patch to enter a different ecosystem patch. The kinds of flows that we consider include migration (partial or complete; Peller et al. 2023), dispersal, bulk flows of materials, foraging, and any other transfer of biomass and/or materials from one ecosystem to another. Furthermore, we will allow that the flows may be unidirectional, bidirectional or be crossing ecosystem boundaries in different ways for different ecosystem compartments. For example, if a bird and a rat on a forested island travel to a neighboring forested island in the same lake, the bird will not need to enter the lake ecosystem, while the rat must.

Therefore, for a given ecosystem compartment *k*, we have its physical connectedness (or spatial structure) regarding the boundaries of the ecosystems within the meta-ecosystem, which we will call $\mathbf{C}_k$. This $\mathbf{C}_k$ is an *n* x *n* matrix whose elements, c_{ijk}, indicate if compartment *k* in ecosystem *i* is physically capable of sending a spatial flow to ecosystem *j* (Jansen and Lloyd 2000):

$$\mathbf{C}_k = \begin{pmatrix} c_{11k} & \cdots & c_{1nk} \\ \vdots & \ddots & \vdots \\ c_{n1k} & \cdots & c_{nnk} \end{pmatrix}$$

The diagonal entries of the $\mathbf{C}_k$ matrices are negative to indicate the export of organisms and materials from the focal ecosystem, while the off-diagonal entries are positive and represent the arrival of organisms and materials from other ecosystems. Unlike previous work (Marleau et al. 2010, 2014, 2015), we do not require $\mathbf{C}_k$ matrices to be symmetric and c_{iik} does not need to equal to the negative row sum of its other elements (i.e., $c_{iik} \neq \sum_{i=1}^{n} c_{ij}$). This means that the flows between ecosystems can be unidirectional or bidirectional (reciprocal) and they can leave the meta-ecosystem partially or entirely. We then combine these separate matrices together into the meta-ecosystem connectedness matrix, **C**:

$$\mathbf{C} = \bigoplus_{k=1}^{m} (\mathbf{C}_k)^T = \begin{pmatrix} (\mathbf{C}_1)^T & \mathbf{0} & \cdots & \mathbf{0} \\ \mathbf{0} & (\mathbf{C}_2)^T & \cdots & \mathbf{0} \\ \vdots & \vdots & \ddots & \vdots \\ \mathbf{0} & \mathbf{0} & \cdots & (\mathbf{C}_m)^T \end{pmatrix}$$

Where ^{T} indicates we take the transpose of the $\mathbf{C}_k$ matrix and ‘’ is the direct sum (note; we use the transpose as the **C** matrix will be on the left-hand side of **x**, rather than on the right-hand side as in other models such as Marleau et al. 2015). For the rates of flow of each ecosystem compartment, we use a separate matrix **Q** that describes how frequently these ecosystem boundaries are crossed. For this study, we deliberately simplify our **Q** matrix such that an ecosystem compartment does not vary how fast it crosses ecosystem boundaries independent of the ecosystem that it is in. With this assumption, each ecosystem compartment has only one rate of flow, q_k, and we organize all these rates into the diagonal matrix **Q’**, which is m x m as we have m ecosystem compartments. Since these rates are invariant across the meta-ecosystem, we create the **Q** matrix by multiplying **Q'** with an n x n identity matrix, ($\mathbf{I}_{(n,n)}$), as we have n ecosystem patches, through the use of the Kronecker tensor product, which generates an nm x nm matrix:

$$\mathbf{Q}' = \begin{pmatrix} q_1 & 0 & \dots & 0 \\ 0 & q_2 & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & q_m \end{pmatrix} \qquad \mathbf{I}_{(n,n)} = \begin{pmatrix} 1 & 0 & \dots & 0 \\ 0 & 1 & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & 1 \end{pmatrix}$$

$$\mathbf{Q} = \mathbf{Q}' \otimes \mathbf{I}_{(n,n)} = \begin{pmatrix} q_1\mathbf{I}_{(n,n)} & \mathbf{0} & \dots & \mathbf{0} \\ \mathbf{0} & q_2\mathbf{I}_{(n,n)} & \dots & \mathbf{0} \\ \vdots & \vdots & \ddots & \vdots \\ \mathbf{0} & \mathbf{0} & \dots & q_m\mathbf{I}_{(n,n)} \end{pmatrix},$$

where q_k is the between ecosystem spatial flow rate for ecosystem compartment k and **0** is an n x n zero matrix. Note that if the spatial flow of one compartment is affected by the stock of another compartment, then **Q'** (and therefore **Q**) is no longer diagonal (for example, if a parasite is completely dependent on its host for its movement across the landscape). Furthermore, if there are ecosystem-specific differences in spatial flow rates (for example, certain genotypes/phenotypes in an ecosystem disperse more readily than those found in another ecosystem), then we can replace the identity matrix with a weighted diagonal matrix instead.

With these two matrices, **Q** and **C**, we can now fully describe between ecosystem flows by multiplying them together with the **x** vector, which when added to **F**(**x**) gives us the equation in Figure 3: $d\mathbf{x}/dt = \mathbf{F}(\mathbf{x}) + \mathbf{QCx}$. We emphasize here that our modelling framework allows for time-varying spatial parameters, as many ecosystems demonstrate strong temporal patterns in spatial flows. For example, we could allow for the connectedness and flow rate parameters to vary in time as landscapes change as in a spatio-temporal network (Fortin et al. 2021). In this way, we could incorporate changes in the probability of dispersal of organisms between ecosystems due to species-specific or ecosystem-wide changes over time. However, adding such variation in our model simulations would lead to additional complexities regarding the timing of flows and local processes (e.g., Leroux and Loreau 2012), and render our interpretations of the impacts of spatial processes much more difficult. We thus restrict our analysis to temporally invariant parameters and leave it to future work to explore the effects of timing.

This meta-ecosystem model allows representation of many types of flows and thus represents a more realistic application of the theory to empirical meta-ecosystems. First, there can be different local dynamics (trophic flows) within different ecosystems (or ecosystem patches) for each ecosystem compartment. For example, a terrestrial herbivore (e.g., grasshopper) will consume plants in the forest system, but if in ends up in the river, it will die without consuming any primary producers and its biomass will turn into detritus. This feature of the model makes it possible to appropriately model spatial flows across different ecosystem types because these types of flows often result in the material or organism moving across different compartments in the donor and recipient ecosystem (in our above-mentioned example, the flowing material is a living herbivore in the donor ecosystem while it is dead detritus in the recipient ecosystem). Second, each ecosystem compartment can have unique physical connectedness (see Figure 3d), which is likely to happen for species that differ in preferred habitat patches or foraging areas (McLeod and Leroux 2021). For example, an aquatic-terrestrial boundary may be more permeable for a terrestrial avian predator (e.g., osprey) foraging across habitat types than for a small terrestrial herbivore (e.g., snowshoe hare) foraging solely on land. Third, we can separate the effects of physical connectedness among ecosystems from the rate of spatial flows (flow intensity), which are normally measured separately from one another for both organisms and materials. The combination of the physical connectedness of ecosystems and the movement or flow potential leads to realized connectivity. With this model, we are now able to predict the impacts of spatial flows in a simplified watershed meta-ecosystem (Box 1).

Model application: a simulated forest-lake-stream meta-ecosystem

We apply the model to simulated watersheds (Box 1; Supplementary Materials). For our primary analysis, we utilize a watershed that is composed of two aquatic ecosystems (i.e., stream and lake) and one riparian forest ecosystem with a focus on production and trophic efficiency. We focused on these ecosystem functions because they can be affected by many human-induced perturbations (forest harvesting, fishing, etc.) and are linked with other biotic community and food web functions. Each ecosystem has its own local flows or internal dynamics of material transfer among its inorganic nutrients, autotrophic, and heterotrophic components (Figure 3a-b). To model flows in local ecosystems, we assumed a linear food chain for the biotic ecosystem compartments with Lotka-Volterra functional responses when they are in their local or donor ecosystem type (Figure 3). We also measured additional ecosystem functions (nutrient recycling), considered alternative watershed configurations, and examined changes in connectivity regimes in the supplementary materials to illustrate the flexibility of our approach (Supplementary Information).

The local ecosystem compartments can potentially flow across boundaries, such that an aquatic herbivore may enter a terrestrial environment, e.g., when aquatic insect larvae emerge to land for reproduction. Current meta-ecosystem theory typically models flows among ecosystems as diffusion, and therefore implicitly assumes that the material is of the same trophic level and composition in all patches and that it flows with the gradient in resources (i.e., from high to low density). Other studies modelled direct flows from one ecosystem to another across trophic levels, i.e., a consumer in one ecosystem consumes a resource in another (McCann et al. 2005, García-Callejas et al. 2019, Peller et al. 2022). However, such a flow implicitly assumes that there is instantaneous movement between ecosystems for either the consumer and/or resource, and therefore tight coupling between consumption and movement. An alternative is to explicitly model the dynamics of a non-local compartment in its non-local ecosystem type (see Figure 3b;Leroux and Loreau 2012). While this approach creates more variables to keep track of, it also helps us generalize our methods to more diverse situations and allows for cleaner mathematical treatment (Box 1).

For our primary analysis, we consider a forest that surrounds a lake and a stream that flows out of the lake (Figure 3) and common flows among these ecosystems (see Figure 2). Senescent plant biomass (e.g., leaves, branches), dead organic matter (e.g., topsoil), and inorganic nutrients can fall into and runoff in the lake, while aquatic insect herbivores (e.g., caddisfly) can emerge and enter the forest (Figure 3c). When biotic compartments flow from terrestrial to aquatic or from aquatic to terrestrial ecosystems, the biotic compartments considered here simply become dead organic material at a given rate as they can only survive a limited time in the recipient ecosystems (Figure 3b).

Nutrients, dead organic matter (detritus), senescent terrestrial plant biomass and phytoplankton flow passively downstream from the lake to the stream, while aquatic herbivores and carnivores can move actively upstream and between the stream and lake based on diffusive movements (Figure 3). Thus, while the ecosystems are all physically connected, the realized biotic connectivity (as defined by the **QC** matrix) is limited and much of the abiotic connectivity is unidirectional.

Simulation scenarios

We chose parameters to produce a realistic local flow hierarchy, such that the forest ecosystem has the greatest primary production, while the aquatic ecosystems are more efficient in the transfer of biomass between trophic levels and have faster mineralization (Gounand et al. 2020). We also use parameter ranges for spatial flow rates motivated by empirical work in order to explore relevant parameter space (see Table S1). Furthermore, our analysis focuses on functions and parameters that ensured a stable equilibrium in all ecosystems over the range of parameter values investigated. For this study, we run simulations where we vary the nutrient inputs to the local ecosystems to examine the impacts of nutrient supply on relative ecosystem functioning (see Supplementary Information for details on model parameterization).

To highlight the importance of spatial flows across different ecosystems, we first considered a non-spatial baseline scenario where all the forest, lake and stream were uncoupled from each other and compared it to three spatial scenarios where (i) the forest has nutrients, detritus, and producers flowing into the lake, the herbivores in the lake can go into the forest, and the stream and lake exchange organisms and materials (‘all flows’ scenario), (ii) the “all flows” scenario without forest producers entering the lake (‘no P_T flow’ scenario), and (iii) the “all flows” scenario without the lake herbivores entering the forest (‘no H_A flow’ scenario).

For our baseline scenario, only local processes are involved and thus generate expectations for compartment stocks (i.e. nutrients [N], detritus [D], producers [P], herbivores [H], predators [W]), ecosystem functions (primary producer, herbivore, and predator production), and trophic efficiencies (i.e., production of the top trophic level divided by the production of the lowest trophic level). Due to the Lotka-Volterra functional responses, changes in nutrient inputs in the baseline scenario only impacts the nutrient stocks of primary producers, detritus, and predators (Supplementary Information). This structure to the nutrient stocks has impacts on how tightly coupled changes to production are between trophic levels (e.g., primary production and herbivore production in a local ecosystem are linearly dependent on the local primary producer nutrient stocks, see Supplementary Information).

The meta-ecosystem in the baseline scenario generally has greater nutrient stocks than any of the spatial scenarios because the latter contain additional losses outside of the meta-ecosystem through directional flows out of the stream (Figure 4a). Primary production is also lower in the spatial scenarios due to this loss of nutrients (Figure 4b). However, as the overall meta-ecosystem is enriched through nutrient inputs to the forest, herbivore and predator production eventually exceed the baseline in the 'all flows' and 'no H_A flow' scenarios at the meta-ecosystem scale (Figures 4c,d). When we look at local ecosystem functioning, spatial flows reduce forest secondary production, while doubling secondary production in the stream (Figure 5). Our simulations showed limited effects of the aquatic subsidy (i.e., aquatic herbivores entering the forest) at the meta-ecosystem scale ('no H_A flow' scenario). These results were expected as aquatic herbivores have relatively low biomass and they do not integrate into the forest food chain (see Box 1). While these results could reinforce the perspective that the aquatic-terrestrial coupling is mostly unidirectional, we think caution is needed given empirical evidence that the qualitative aspect of aquatic subsidies (lower C:N ratio than terrestrial subsidy) can have significant implications for riparian communities (Bartels et al. 2012, Bultman et al. 2014, Sitters et al. 2015). Evaluating this evidence would have required a stoichiometric framework, which is outside the scope of our model.

The increase in production at the landscape level is due to better efficiencies in turning nutrients into consumer biomass when nutrients and organisms can flow between the forest, lake and stream (Figure 6). Under the baseline scenario, adding nutrients in the forest increases the nutrient stocks of the terrestrial primary producer, which lowers the meta-ecosystem trophic efficiency as the transfer of nutrients between terrestrial primary producers and consumers is much less efficient (Supplementary Information). However, spatial flows allow for a slower decline in meta-ecosystem trophic efficiency with increasing terrestrial nutrient inputs if terrestrial primary producers have a spatial flow (Figure 6a). Furthermore, if terrestrial primary producers have a spatial flow, the meta-ecosystems always maintain superior ecological trophic efficiency relative to the baseline scenario that only increases with increasing terrestrial nutrient enrichment (Figure 6a). Similar patterns in production and trophic efficiency held in the alternative watersheds (Supplementary Information). Once again, as nutrient enrichment in terrestrial ecosystems enters aquatic ecosystems through spatial flows, we observe gains in secondary production and in meta-ecosystem trophic efficiency (Supplementary Information).

These improvements in trophic efficiencies are a result of changes in the underlying efficiencies of the local ecosystems combined with the reallocation of nutrients within the meta-ecosystem (Figure 6b). Adding spatial flows modifies local trophic efficiencies, such that the lake's efficiency decreases, while the stream's efficiency increases (Figure 6b). The movement of aquatic predators leads to more of them entering the stream from the lake, which reduces measured trophic efficiency in the lake and increases it in the stream. This change at the top of the food chain outweighs the positive effects on trophic efficiency driven by the unidirectional flows of nutrients and primary producers in the lake, but reinforces the increase seen in the stream.

For the forest ecosystem, efficiencies only change from the baseline scenario if the terrestrial primary producers have a spatial flow, which leads to a decrease in local trophic efficiency (Figure 6b). The spatial flow of the terrestrial primary producers is key to the increased meta-ecosystem trophic efficiency: without it, nutrients remain “stuck” in the relatively inefficient terrestrial primary producer biomass and there is insufficient compensation to spatially induced losses in the trophic efficiency in the lake ecosystem (Figure 6). This mechanism also holds for alternative watersheds (Supplementary Information).

These simulation results show how spatial flows between different ecosystems can lead to complex responses at both local and meta-ecosystem scales. Spatial flows, even the ones that significantly reduce the overall amount of nutrients in the meta-ecosystem, can reallocate nutrients to more efficient ecosystems, leading to greater levels of secondary productivity at local and even regional scales. Thus, despite the relatively large loss of biomass in local ecosystems due to spatial exports of organisms and materials, the meta-ecosystem can maintain a high level of productivity. We termed this finding the ‘*cross-ecosystem efficiency hypothesis*’ because the meta-ecosystem trophic efficiencies can be greater in the spatial flow scenarios (Figure 6a). This general hypothesis emphasizes the complementarity and interconnectedness among ecosystems in the landscape and the importance of considering both local and coupled ecosystems when studying potential changes in ecosystem function following perturbations (e.g., resource extraction, connectivity loss). Therefore, while the application of our model is relatively simple, it provides a realistic scenario as it generated predictions that were not possible with previous meta-ecosystem theory. Thus, by utilizing tools to better integrate real world ecosystems into theory, we have expanded the possibilities of theory and can motivate empirical tests in the future.

Perspectives for predicting ecosystem functions across landscapes

Coupling functions in the landscape

The meta-ecosystem framework we developed highlights the interdependence among different ecosystems at the landscape scale. Local ecosystem properties and functions, when coupled with spatial flows, can be significantly altered and lead to landscape-level changes in function. In our simulations, we had an ecosystem with high primary production, slow mineralization, and poor trophic efficiency coupled to ecosystems with less primary production, faster mineralization, and higher trophic efficiencies. This 'spatial complementarity' can lead to co-dependencies between systems that share limiting resources through spatial flows (Gounand et al. 2017).

We showed that this complementarity also means that accounting for spatial flows across different ecosystem types can maximize nutrient use efficiency by transferring nutrients to more efficient ecosystems, thus maintaining functions across the landscape despite a net loss in nutrients for each ecosystem (Figure 4 and Supplementary Information). When spatial flows are accounted for, the energy and material lost by the terrestrial to the aquatic system is compensated at the meta-ecosystem level by the increase in herbivore and predator production in the aquatic system (Figure 5). Thus, the landscape can be perceived as an assembly line where each ecosystem type has its own 'niche' (e.g., biomass accumulation vs. production at different levels), and only by accounting for energy and material flows across those systems can we maximize the landscape of functions (hence the 'cross-ecosystem efficiency hypothesis', Figure 5).

Certain spatial flows, such as terrestrial primary producer biomass, were critical for maintaining 'cross-ecosystem' efficiency. Therefore, perturbations that could generate (or inhibit) a specific spatial flow of biomass from one ecosystem to another are important to consider in our framework. In watersheds, human activities such as damning, clearcutting forests, and establishing agricultural lands, can lead to widescale alteration in spatial flows, which then impact locally measured ecosystem properties and functioning (i.e. a spatial cascade). Furthermore, these local changes can then feedback on spatial flows, leading to the transmission and amplification of the original perturbations (see McCann et al. 2021). The approach we developed here emphasizes the importance of considering the mesoscale (watershed, landscape) as a scale of reference for understanding changes in ecosystem functions that are relevant for human societies.

Linking meta-ecosystem theory and empirical studies

We propose a meta-ecosystem model with three major components. First, the model integrates three flow types: flows in local ecosystems, spatial flows within the same ecosystem, and spatial flows across different ecosystems. Empirical studies showed that flows at all three levels are common (Figure 2, Table S1; see reviews in Allen and Wesner 2016, Gounand et al. 2018b, Montagano et al. 2019). Yet, existing theory usually focuses on only one of these components. Second, the framework we propose is flexible enough to incorporate abiotic and biotic flows at different scales. Empirical studies highlight that the spatial and temporal scales of abiotic and biotic flows may differ and that there are important interactions between abiotic and biotic flows (see review in McLeod and Leroux 2021), yet existing theory rarely captures these dynamics - especially in multi-patch models (Table S1, Figure 1). Third, our framework partitions the physical connectedness of ecosystems from the movement or flow potential (rate) of a compartment. For a flow to occur, there needs to be both physical connection and movement potential. This partitioning has three benefits; (i) it allows for a mathematically tractable way to model complex connectivity scenarios (i.e., K tensor product), (ii) it makes it possible to allow for variable flow scenarios across different local compartments, for instance in terms of directionality and differences of connectivity among trophic levels depending on species mobility, and this flexibility matches with empirical variability in ecosystem connections, and (iii) it provides a model framework to make predictions based on metrics that are often empirically measured or can be measured - for example, landscape permeability (e.g., terrain ruggedness, Chetkiewicz and Boyce 2009) and animal movement (e.g., movebank, Kranstauber et al. 2011). The model could also be used to determine the most important flows in and across ecosystems to focus future monitoring and research efforts. We illustrate how this model can be fit to a specific meta-ecosystem, and how it can be used to provide testable predictions in specific systems. In our forest-lake-stream meta-ecosystem case study, we predict that removing key flows (e.g., trees or terrestrial plants due to forestry practices) can cascade to impact stocks and productions at local and landscape scales (Figures 1, 4, 5, and 6), while emphasizing how complementarity in functions among ecosystem types can maximize ecosystem function in the landscape (‘*cross-ecosystem efficiency hypothesis*’).

Overall, we anticipate that our framework allows for the development of a suite of predictions for different ecosystems pertaining to how different flows mediate diverse ecosystem functions. The topology and the properties of our landscape were built on an empirical review of common flows (Table S1). While our specific results are tied to this landscape, our model framework is applicable to many other meta-ecosystems that vary in the productivity of their component ecosystems. For example, the model could explore how the demonstrated decline in Pacific salmon (e.g., Oke et al. 2020) can impact primary and secondary production of natal streams and riparian forests in the Pacific Northwest of North America. More broadly, ours and recent studies (Peller et al. 2020) suggest that more attention should be given to ecosystem diversity and their arrangement in the landscape if we are to properly understand and predict nutrient distribution at the landscape scale, especially in a context of global habitat fragmentation and land-use changes (IPBES 2019). Therefore, we need to better integrate connectivity loss across trophic levels to make testable predictions about the effects of reduced connectivity on ecosystem function at the mesoscale.

From a theory perspective, the model we propose is flexible enough to recover many existing meta-ecosystem model formulations. For example, by assuming that spatial flows only occur in the same compartment (i.e., herbivores flow to herbivores), our model can be simplified to study only spatial flows within the same ecosystem. The use of matrices in our framework makes for a good match between model predictions and empirical ecological data which are often readily presented as matrices (e.g., community, connectivity; Gravel et al. 2016). In addition, we advance our framework as a call for theoretical and empirical spatial ecologists to work together to study landscape-scale ecosystem functions. Much of the underlying theory focuses on stability as a key function, but other functions such as production and elemental cycling are also critical and more commonly measured in natural systems. Recent advances in spatial stoichiometry provide statistical methods to map empirical patterns in limiting nutrients across a landscape (Collins et al. 2017, Leroux et al. 2017, Soranno et al. 2019). These spatially explicit predictions of elemental surfaces can be used to partially parameterize meta-ecosystem models such as the one we propose here. Predictions can then be made on current and future functions.

Resource flows from one ecosystem to another are also known to vary at different time scales, from within a year to inter-annually (Spencer et al. 2005). Observational measurements of those flows could be established as a natural baseline against which flows following a perturbation could be simulated to analyze changes in the structural stability of the matrix or resilience (time of return to the natural baseline). This approach lends interesting insights on how to offset human impacts, urban development and land conversion, on cross-ecosystem flows, by providing information such as the amount/configuration of natural cover in riparian zones required to maintain underlying processes, especially in the context of a well-connected system like a river where effects can spread across the watershed. Thus, our approach can be useful to develop formal tests of landscape implications of local perturbations propagated via spatial cascades.

Finally, our framework can also be parametrized with empirical data, which could help to address questions about the functioning of natural systems in the face of perturbations. For instance, our approach could potentially shed new light on carbon sequestration at the landscape scale. Most carbon sequestration models assume homogeneous landscapes and ignore animals (Schmitz et al. 2018), but it is not clear how accounting for abiotic and biotic spatial flows in carbon might affect those predictions. Previous work has shown that carbon exchanges between ecosystems at large spatial scales can be highly significant (Gounand et al. 2018b). In that context, human-induced perturbations such as climate change, but also land use change and habitat fragmentation, could potentially alter carbon flows among ecosystems (Leroux et al. 2017), thus influencing carbon sequestration at regional and landscape extents. Yet, much research is needed to make the link between different types of perturbations and their impacts on spatial flows, and the cumulative effects of different types of perturbations on ecosystem functions in the landscape.

References

Abbas, F. et al. 2012. Roe deer may markedly alter forest nitrogen and phosphorus budgets across Europe. - Oikos 121: 1271–1278.

Allen, D. C. and Wesner, J. S. 2016. Synthesis: comparing effects of resource and consumer fluxes into recipient food webs using meta-analysis. - Ecology 97: 594–604.

Bartels, P. et al. 2012. Reciprocal subsidies between freshwater and terrestrial ecosystems structure consumer resource dynamics. - Ecology 93: 1173–1182.

Baxter, C. V. et al. 2004. Fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. - Ecology 85: 2656–2663.

Baxter, C. V. et al. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. - Freshwater Biology 50: 201–220.

Bultman, H. et al. 2014. Terrestrial deposition of aquatic insects increases plant quality for insect herbivores and herbivore density. - Ecol Entomol 39: 419–426.

Canham, C. D. et al. 2004. A Spatially Explicit Watershed-Scale Analysis of Dissolved Organic Carbon in Adirondack Lakes. - Ecological Applications 14: 839–854.

Chetkiewicz, C.-L. B. and Boyce, M. S. 2009. Use of resource selection functions to identify conservation corridors. - Journal of Applied Ecology 46: 1036–1047.

Collins, S. M. et al. 2017. Lake nutrient stoichiometry is less predictable than nutrient concentrations at regional and sub-continental scales. - Ecological Applications 27: 1529–1540.

Fortin, M.-J. et al. 2021. Network ecology in dynamic landscapes. - Proceedings of the Royal Society B: Biological Sciences 288: 20201889.

García-Callejas, D. et al. 2019. Spatial trophic cascades in communities connected by dispersal and foraging. - Ecology 100: e02820.

Gounand, I. et al. 2014. The Paradox of Enrichment in Metaecosystems. - The American Naturalist 184: 752–763.

Gounand, I. et al. 2017. Subsidies mediate interactions between communities across space. - Oikos 126: 972–979.

Gounand, I. et al. 2018a. Meta-Ecosystems 2.0: Rooting the Theory into the Field. - Trends in Ecology & Evolution 33: 36–46.

Gounand, I. et al. 2018b. Cross-ecosystem carbon flows connecting ecosystems worldwide. - Nature Communications 9: 4825.

Gounand, I. et al. 2020. Global quantitative synthesis of ecosystem functioning across climatic zones and ecosystem types. - Global Ecology and Biogeography 29: 1139–1176.

Gravel, D. et al. 2010. Patch Dynamics, Persistence, and Species Coexistence in Metaecosystems. - The American Naturalist 176: 289–302.

Gravel, D. et al. 2016. Stability and complexity in model meta-ecosystems. - Nature Communications 7: 12457.

Harvey, E. and Altermatt, F. 2019. Regulation of the functional structure of aquatic communities across spatial scales in a major river network. - Ecology 100: e02633.

Harvey, E. et al. 2016. Bridging ecology and conservation: from ecological networks to ecosystem function. - J Appl Ecol 54: 371–379.

Hynes, H. B. N. 1975. The stream and its valley. - SIL Proceedings, 1922-2010 19: 1–15.

Iwata, T. et al. 2003. Stream meanders increase insectivorous bird abundance in riparian deciduous forests. - Ecography 26: 325–337.

Jacquet, C. et al. 2022. Meta-ecosystem dynamics drive the spatial distribution of functional groups in river networks. - Oikos in press.

Jansen, V. A. A. and Lloyd, A. L. 2000. Local stability analysis of spatially homogeneous solutions of multi-patch systems. - J Math Biol 41: 232–252.

Jyväsjärvi, J. et al. 2013. The importance of sedimenting organic matter, relative to oxygen and temperature, in structuring lake profundal macroinvertebrate assemblages. - Hydrobiologia 709: 55–72.

Kawaguchi, Y. et al. 2003. Terrestrial invertebrate inputs determine the local abundance of stream fishes in a forested stream. - Ecology 84: 701–708.

Kranstauber, B. et al. 2011. The Movebank data model for animal tracking. - Environmental Modelling & Software 26: 834–835.

Largaespada, C. et al. 2012. Meta-ecosystem engineering: Nutrient fluxes reveal intraspecific and interspecific feedbacks in fragmented mussel beds. - Ecology 93: 324–333.

Leroux, S. J. and Loreau, M. 2012. Dynamics of Reciprocal Pulsed Subsidies in Local and Meta. - Ecosystems 15: 48–59.

Leroux, S. J. et al. 2017. Stoichiometric distribution models: ecological stoichiometry at the landscape extent. - Ecol Lett 20: 1495–1506.

Little, C. J. and Altermatt, F. 2018. Landscape configuration alters spatial arrangement of terrestrial-aquatic subsidies in headwater streams. - Landscape Ecol: 1–13.

Loreau, M. and Holt, R. D. 2004. Notes and Comments Spatial Flows and the Regulation of Ecosystems. in press.

Loreau, M. et al. 2003. Meta-ecosystems: a theoretical framework for a spatial ecosystem ecology. - Ecology Letters 6: 673–679.

Marcarelli, A. M. et al. 2020. Magnitude and direction of stream–forest community interactions change with timescale. - Ecology 101: e03064.

Marczak, L. B. and Richardson, J. S. 2007. Spiders and subsidies: results from the riparian zone of a coastal temperate rainforest. - Journal of Animal Ecology 76: 687–694.

Marleau, J. N. and Guichard, F. 2019. Meta-ecosystem processes alter ecosystem function and can promote herbivore-mediated coexistence. - Ecology 100: e02699.

Marleau, J. N. et al. 2010. Nutrient flows between ecosystems can destabilize simple food chains. - Journal of Theoretical Biology 266: 162–174.

Marleau, J. N. et al. 2014. Meta-ecosystem dynamics and functioning on finite spatial networks. - Proceedings of the Royal Society of London B: Biological Sciences 281: 20132094.

Marleau, J. N. et al. 2015. Emergence of nutrient co-limitation through movement in stoichiometric meta-ecosystems. - Ecol Lett 18: 1163–1173.

Massol, F. et al. 2011. Linking community and ecosystem dynamics through spatial ecology. - Ecology Letters 14: 313–323.

Massol, F. et al. 2017. How life-history traits affect ecosystem properties: effects of dispersal in meta-ecosystems. - Oikos 126: 532–546.

Matisoff, G. et al. 2017. Sediment and nutrient distribution and resuspension in Lake Winnipeg. - Science of The Total Environment 575: 173–186.

McCann, K. S. et al. 2005. The dynamics of spatially coupled food webs. - Ecology Letters 8: 513–523.

McCann, K. S. et al. 2021. Landscape modification and nutrient-driven instability at a distance. - Ecology Letters 24: 398–414.

McLeod, A. M. and Leroux, S. J. 2021. Incorporating abiotic controls on animal movements in metacommunities. - Ecology 102: e03365.

Montagano, L. et al. 2019. The strength of ecological subsidies across ecosystems: a latitudinal gradient of direct and indirect impacts on food webs. - Ecology Letters 22: 265–274.

Nakano, S. and Murakami, M. 2001. Reciprocal subsidies: Dynamic interdependence between terrestrial and aquatic food webs. - PNAS 98: 166–170.

Oke, K. B. et al. 2020. Recent declines in salmon body size impact ecosystems and fisheries. - Nat Commun 11: 4155.

Peller, T. et al. 2020. From Marine Metacommunities to Meta-ecosystems: Examining the Nature, Scale and Significance of Resource Flows in Benthic Marine Environments. - Ecosystems in press.

Peller, T. et al. 2022. Traits affecting nutrient recycling by mobile consumers can explain coexistence and spatially heterogeneous trophic regulation across a meta-ecosystem. - Ecology Letters 25: 440–452.

Peller, T. et al. 2023. The significance of partial migration for food web and ecosystem dynamics. - Ecology Letters 26: 3–22.

Polis, G. A. et al. 1997. Toward an integration of landscape and food web ecology:The Dynamics of Spatially Subsidized Food Webs. - Annual Review of Ecology and Systematics 28: 289–316.

Richardson, J. S. 1991. Seasonal Food Limitation of Detritivores in a Montane Stream: An Experimental Test. - Ecology 72: 873–887.

Richardson, J. S. and Sato, T. 2015. Resource subsidy flows across freshwater–terrestrial boundaries and influence on processes linking adjacent ecosystems. - Ecohydrol. 8: 406–415.

Sabo, J. L. and Power, M. E. 2002. Numerical Response of Lizards to Aquatic Insects and Short-Term Consequences for Terrestrial Prey. - Ecology 83: 3023–3036.

Sato, T. et al. 2016. A test of the effects of timing of a pulsed resource subsidy on stream ecosystems. - J Anim Ecol 85: 1136–1146.

Schindler, D. E. and Smits, A. P. 2017. Subsidies of Aquatic Resources in Terrestrial Ecosystems. - Ecosystems 20: 78–93.

Schmitz, O. J. et al. 2018. Animals and the zoogeochemistry of the carbon cycle. - Science 362: eaar3213.

Sitters, J. et al. 2015. Spatial stoichiometry: cross-ecosystem material flows and their impact on recipient ecosystems and organisms. - Oikos 124: 920–930.

Soranno, P. A. et al. 2019. Spatial and temporal variation of ecosystem properties at macroscales. - Ecology Letters 22: 1587–1598.

Spencer, D. F. et al. 2005. Spatial and temporal variation in RGR and leaf quality of a clonal riparian plant: Arundo donax. - Aquatic Botany 81: 27–36.

Takimoto, G. and Sato, T. 2020. Timing and duration of phenological resources: Toward a mechanistic understanding of their impacts on community structure and ecosystem processes in stream food chains. - Ecological Research 35: 463–473.

Vannote, R. L. et al. 1980. The River Continuum Concept. - Can. J. Fish. Aquat. Sci. 37: 130–137.

Wallace, J. B. et al. 2015. Stream invertebrate productivity linked to forest subsidies: 37 stream-years of reference and experimental data. - Ecology 96: 1213–1228.

Wipfli, M. S. and Musslewhite, J. 2004. Density of red alder (Alnus rubra) in headwaters influences invertebrate and detritus subsidies to downstream fish habitats in Alaska. - Hydrobiologia 520: 153–163.

Figure Legends

Figure 1. Conceptual diagram showing how different components of a meta-ecosystem contribute to function(s). Top right panels focus on one specific process each (arrows). Bottom right panels show an example of how the associated spatial flows would influence secondary production in a rasterized representation of the landscape (darker colours have more influence). This can be understood as a log response ratio of an experiment where the flow is removed (response = secondary production with flow / secondary production without flow). The leftmost bottom panel presents the sum of flow effects. We propose a novel mathematical model to integrate the combined effect of those different types of flows at the landscape scale.

Figure 2. Spatial flows in watersheds. a) Illustration and b) schematic diagram of flows of material and organisms connecting the different habitats of a watershed. We provide one hundred references quantifying these flows (identified by the numbers on the right panel), all available in Table S1, providing flow quantifications for watersheds in temperate and cold climates (i.e., alpine, boreal, subarctic, arctic). The material of quantified flows are: A) Terrestrial detritus, leaves, and insects, eggs deposition of amphibians, leached nitrogen; B) Emergent insects and amphibians, fish carcasses caught by terrestrial consumers; C) Detritus, sediment DOC, invertebrates drifting, fish and insects migrating downstream; D) Fish and insects migrating upstream; E) Plankton sinking, organic matter; F) Resuspension of particles by wind, recycling of benthic phosphorus by fish; G) Sediment, particulate organic matter, nitrogen flowing downstream, phosphorus transported by salmon juveniles migrating downstream; H) Spawning salmon migrating upstream.

Figure 3. Overview of a meta-ecosystem model that integrates local trophic flows, spatial flows within the same ecosystem and/or across different ecosystem types, here illustrated for a

boreal watershed used as a case study in our simulations (see Fig. 4). **(a)** All eight ecosystem compartments included in the landscape, consisting of five trophic levels (detritus *(D),* inorganic nutrients *(N),* primary producers *(P),* herbivores *(H),* and predators *(W),* with terrestrial and aquatic specific biotic compartments highlighted in green and blue color, respectively). **(b)** Example of local forest dynamics describing within ecosystem trophic flows among ecosystem compartments including consumption dynamics, production of detritus by organisms, and recycling into nutrients. Dotted arrows represent the leaking of nutrients due to the relative lack of efficiency of trophic interactions. Transparency of aquatic compartments highlights that these stocks are decaying into detritus in the terrestrial ecosystem without any demographic dynamics. (**c**) Landscape representation with spatial dynamics decomposed between physical connectedness among ecosystem patches (**C)** for each ecosystem compartment between each ecosystem (heads and tails of the arrows), and spatial flow rates (**Q**) (the styles of the body of the arrow). **(d)** Mathematical representation of the meta-ecosystem. See text for full model description.

Figure 4. Effects of meta-ecosystem spatial flows and terrestrial nutrient inputs on (**a**) nutrient stock, **(b)** primary production, **(c)** herbivore production, and **(d)** predator production at the meta-ecosystem level relative to a local process only baseline scenario meta-ecosystem (no spatial flow scenario; dotted line). The spatial flow scenarios include 'all flows' (as specified in Figure 3; orange line), 'no P_T flow' (no exchange of terrestrial primary producer biomass between ecosystems; purple dashed line) and 'no H_A flow' (no exchange of aquatic herbivore biomass between ecosystems; green dashed dotted line). Full description of parameter values used to generate Figure 4 is in the Supplementary Material. Absolute values of stocks and production are available in Supplementary Figure S1.

Figure 5. Effects of meta-ecosystem spatial flows on secondary production at the ecosystem scale in (**a**) the forest, **(b)** the lake, **(c)** the stream, relative to a local process only baseline meta-ecosystem (no spatial flow scenario; dotted line) as terrestrial nutrient inputs vary. Secondary productions are the sum of herbivore and predator productions. Parameter values and scenarios are the same as in Figure 4. Absolute values of secondary production are available in supplementary Figure S2.

Figure 6. The ecosystem efficiencies at (**a**) meta-ecosystem and **(b)** ecosystem scales, that describe the transfer of nutrients from primary producers to predators, relative to the baseline scenario (dotted line), and as terrestrial and aquatic nutrient inputs vary. Efficiencies are computed by the ratio of predator to producer productions (equivalent to multiplying efficiencies at the two trophic transitions). Parameter values and scenarios are the same as in Figure 4. The trophic efficiencies at ecosystem scale (b) have distinct ranges among ecosystem types, which allow displaying them on the same panel. Labels indicate the ecosystem type just above the corresponding simulations for the three scenarios. Absolute values of trophic efficiencies are available in Supplementary Figure S3.

716 **Figure 1**

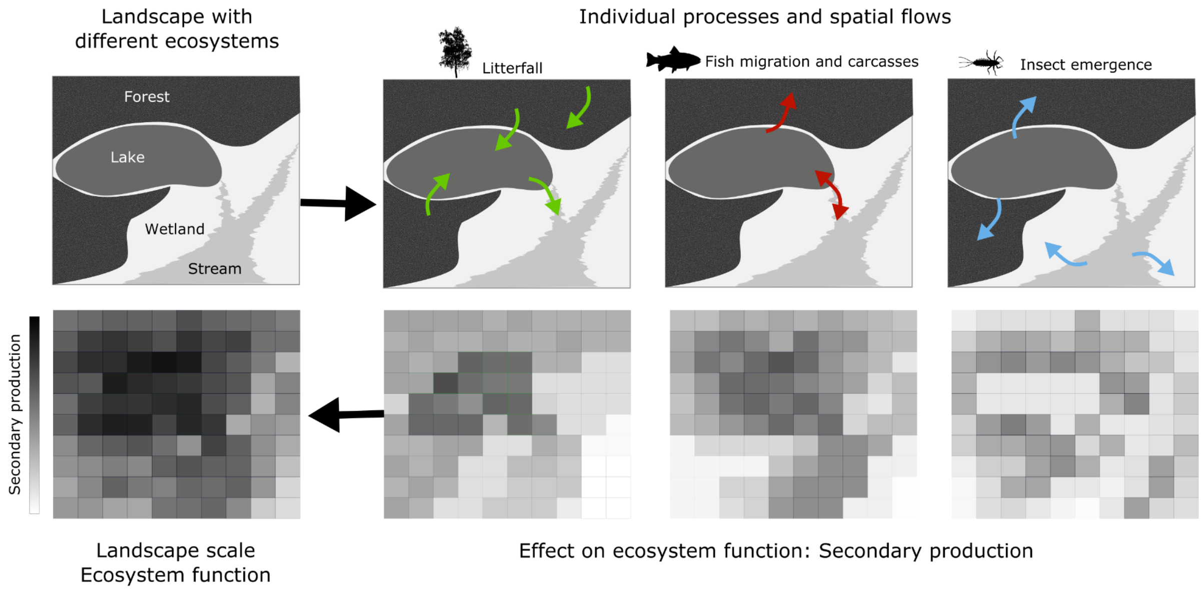

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Figure 2

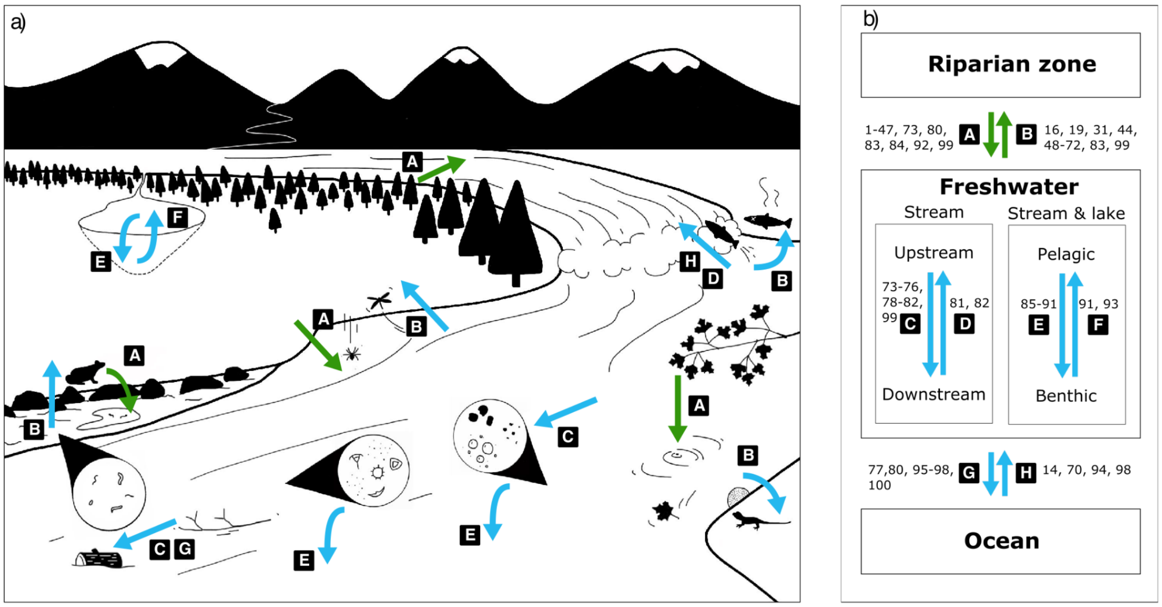
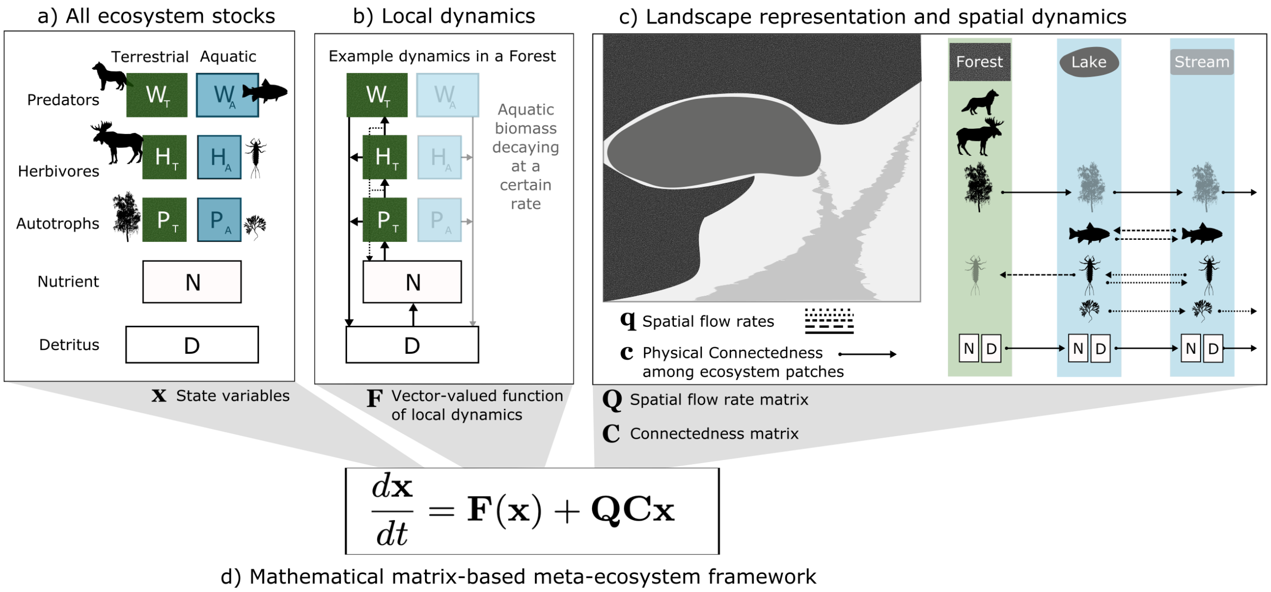
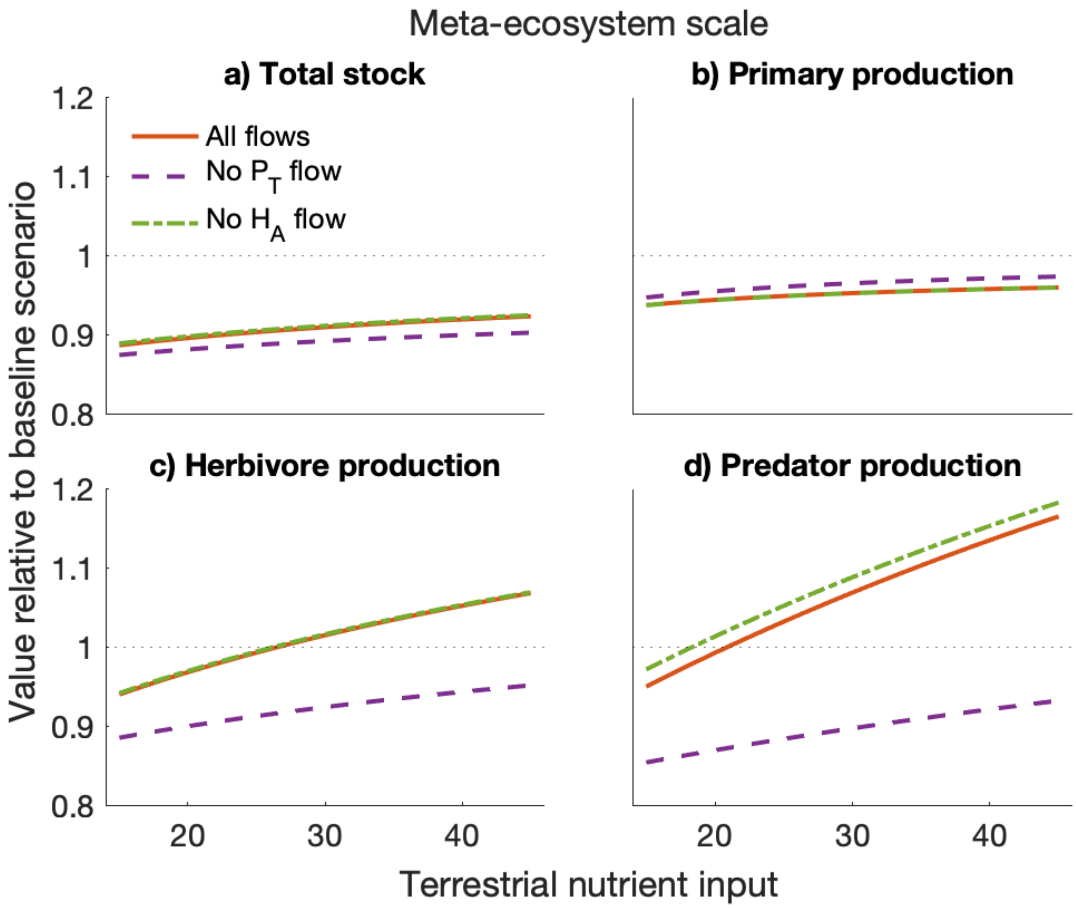

a)
b)
Riparian zone
1-47, 73, 80, 83, 84, 92, 99
A
B
16, 19, 31, 44, 48-72, 83, 99
Freshwater
Stream
Stream & lake
Upstream
73-76, 78-82, 99
C
81, 82
D
Downstream
Pelagic
85-91
E
91, 93
F
Benthic
77,80, 95-98, 100
G
H
14, 70, 94, 98
Ocean

Figure 3



a) All ecosystem stocks
Terrestrial
Aquatic
Predators
Herbivores
Autotrophs
Nutrient
Detritus
W_T
W_A
H_T
H_A
P_T
P_A
N
D
x State variables
b) Local dynamics
Example dynamics in a Forest
Aquatic biomass decaying at a certain rate
F Vector-valued function of local dynamics
c) Landscape representation and spatial dynamics
Forest
Lake
Stream
q Spatial flow rates
c Physical Connectedness among ecosystem patches
Q Spatial flow rate matrix
C Connectedness matrix
$$\frac{d\mathbf{x}}{dt} = \mathbf{F}(\mathbf{x}) + \mathbf{QCx}$$
d) Mathematical matrix-based meta-ecosystem framework

Figure 4



Meta-ecosystem scale
a) Total stock
b) Primary production
c) Herbivore production
d) Predator production
All flows
No P_T flow
No H_A flow
Value relative to baseline scenario
Terrestrial nutrient input
1.2
1.1
1
0.9
0.8
20
30
40

Figure 5

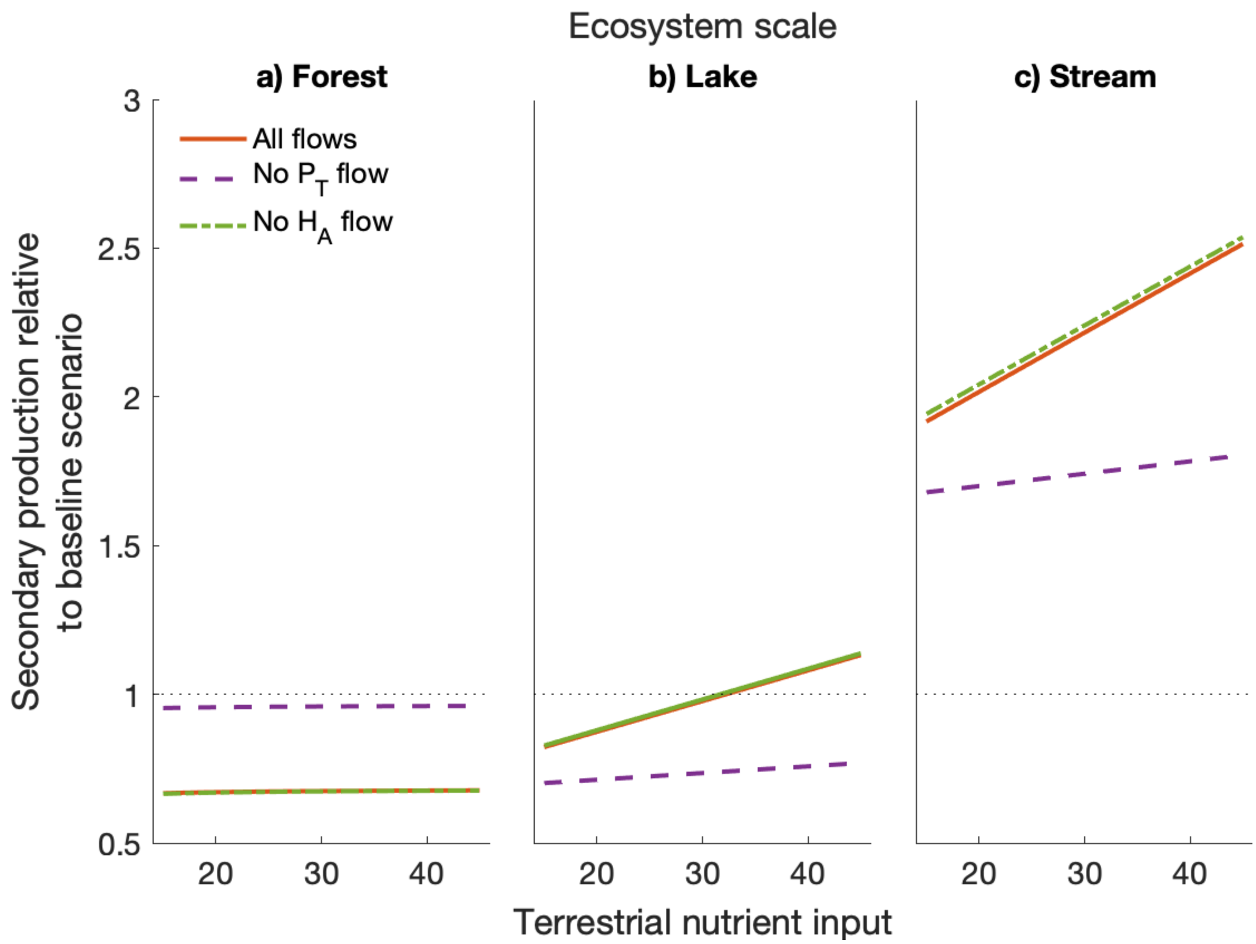
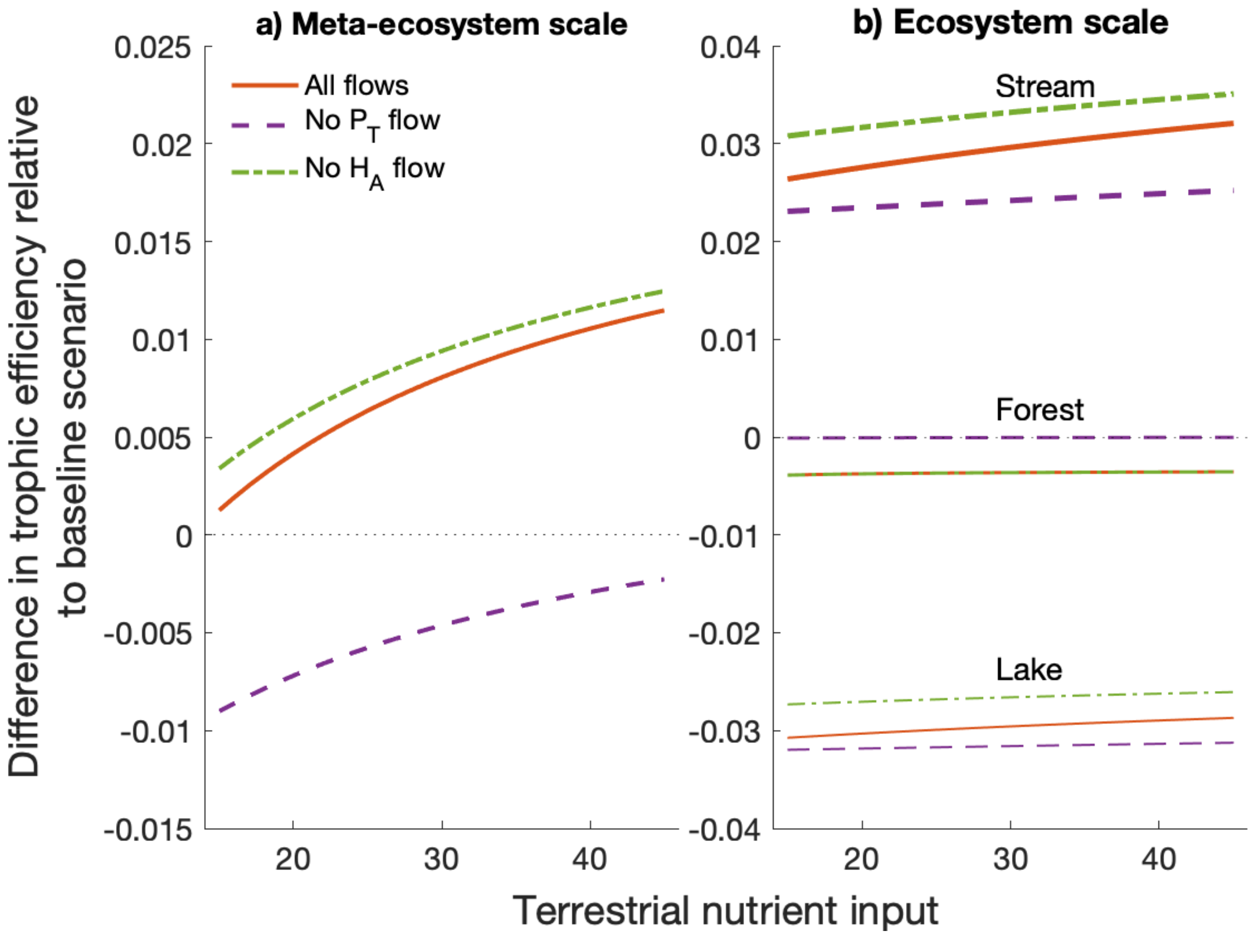

Ecosystem scale
a) Forest
b) Lake
c) Stream
All flows
No P_T flow
No H_A flow
Secondary production relative to baseline scenario
3
2.5
2
1.5
1
0.5
20
30
40
Terrestrial nutrient input

Figure 6



a) Meta-ecosystem scale
b) Ecosystem scale
All flows
No P_T flow
No H_A flow
Stream
Forest
Lake
Difference in trophic efficiency relative to baseline scenario
Terrestrial nutrient input
0.025
0.02
0.015
0.01
0.005
0
-0.005
-0.01
-0.015
0.04
0.03
0.02
0.01
0
-0.01
-0.02
-0.03
-0.04
20
30
40

Box 1: Modelling the flows in terrestrial-aquatic landscapes

To highlight the potential of our framework, we developed scenarios that reflect the relative productivity and flows between ecosystems of different types through a set of mathematical models. In our modelled landscapes, we allow for one type of terrestrial ecosystem ($\mathcal{T}$) and two types of aquatic ($\mathcal{A}$) ecosystems that differ in terms of parameter values, with one type being a 'lake' ($\mathcal{A}_{\mathcal{L}}$) and the other being a 'stream' ($\mathcal{A}_{\mathcal{S}}$). For simplicity, we consider the case where a single limiting nutrient is limiting both the terrestrial and aquatic primary producers, and we follow the dynamics of nutrient stocks. In each ecosystem, there is an available inorganic nutrient compartment (*N*), a detritus compartment (*D*), primary producer compartments (*P*), herbivore compartments (*H*), and predator compartments (*W*). Since it is highly likely that aquatic and terrestrial biotic compartments would differ greatly, we explicitly model them separately in each ecosystem.

Each local ecosystem type Z ($Z = \{\mathcal{A}_{\mathcal{L}}, \mathcal{A}_{\mathcal{S}}, \mathcal{T}\}$) has its own specific available nutrient influx function, $I_{N_Z}(N_Z)$, and ecosystem compartment efflux functions, $E_{N_Z}(N_Z)$, $E_{D_Z}(D_Z)$, $E_{P_Z}(P_Z)$, $E_{H_Z}(H_Z)$, $E_{W_Z}(W_Z)$, $E_{P_{YZ}}(P_{YZ})$, $E_{H_{YZ}}(H_{YZ})$ and $E_{W_{YZ}}(W_{YZ})$, for the available nutrients, detritus, the native primary producers, the native herbivores, the native predators, the non-native primary producers, the non-native herbivores and the non-native predators from ecosystem type Y ($Y = \{\mathcal{A}_{\mathcal{L}}, \mathcal{A}_{\mathcal{S}}, \mathcal{T}\}$, $Y \neq Z$), respectively. Nutrients lost by organisms through the efflux functions are partially recycled at a constant proportion into the detritus, r_{P_Z}, r_{H_Z}, r_{W_Z}, $r_{P_{YZ}}$, $r_{H_{YZ}}$ and $r_{W_{YZ}}$ for the native primary producers, the native herbivores, the native predators, the non-native primary producers, the non-native herbivores and the non-native predators, respectively. The nutrients in the detritus become available again through mineralization, M_{D_Z}, and we ignore any of the more complex nutrient dynamics that are likely mediated by the microbial communities.

The transfer of nutrients to and between biotic ecosystem compartments are described by transfer functions, $F_{P_Z}(N_Z, P_Z)$, $F_{H_Z}(P_Z, H_Z)$, and $F_{W_Z}(H_Z, W_Z)$ for the native primary producers, the native herbivores and the native predators, respectively. Due to inefficiencies in assimilation and the maintenance of stoichiometric homeostasis, there are conversion efficiencies, κ_{H_Z} and κ_{W_Z}, for the native herbivore and native predator. The nutrients that are not consumed are instantly recycled to the available nutrient pool. Note that there are no transfer functions for the non-native organisms as they are assumed to simply enter the detrital pool at a given rate in this example. With these assumptions, we can describe the dynamics in a local ecosystem of type Z by the following set of ordinary differential equations:

$$\frac{dD_Z}{dt} = r_{P_Z}E_{P_Z}(P_Z) + r_{H_Z}E_{H_Z}(H_Z) + r_W E_{W_Z}(W_Z) + r_{P_{YZ}}E_{P_{YZ}}(P_{YZ}) + r_{H_{YZ}}E_{H_{YZ}}(H_{YZ}) + r_{W_{YZ}}E_{W_{YZ}}(W_{YZ}) - M_{D_Z}(D_Z) - E_{D_Z}(D_Z)$$

$$\frac{dN_Z}{dt} = I_{N_Z}(N_Z) - E_{N_Z}(N_Z) + M_{D_Z}(D_Z) - F_{P_Z}(N_Z, P_Z) + \left(1 - \kappa_{H_Z}\right)r_{H_Z}F_{H_Z}(P_Z, H_Z) + \left(1 - \kappa_{W_Z}\right)r_{W_Z}F_{W_Z}(H_Z, W_Z)$$

$$\frac{dP_Z}{dt} = F_{P_Z}(N_Z, P_Z) - E_{P_Z}(P_Z) - F_{H_Z}(P_Z, H_Z)$$

$$\frac{dH_Z}{dt} = \kappa_{H_Z}F_{H_Z}(P_Z, H_Z) - E_{H_Z}(H_Z) - F_{W_Z}(H_Z, W_Z)$$

$$\frac{dW_Z}{dt} = \kappa_{W_Z}F_{W_Z}(H_Z, W_Z) - E_{W_Z}(W_Z)$$

$$\frac{dP_{YZ}}{dt} = -E_{P_{YZ}}(P_{YZ})$$

$$\frac{dH_{YZ}}{dt} = -E_{H_{YZ}}(H_{YZ})$$

$$\frac{dW_{YZ}}{dt} = -E_{W_{YZ}}(W_{YZ})$$

This set of equations represents a subset of $\mathbf{F}(\mathbf{x})$ specifically those associated with a single ecosystem (i.e. $[f_{i,1}(\mathbf{x}_i)\, f_{i,2}(\mathbf{x}_i)\, \ldots\, f_{i,m}(\mathbf{x}_i)]^{\mathrm{T}}$). Thus, for the meta-ecosystem, we need to have one set of these equations per ecosystem and this gives us $\mathbf{F}(\mathbf{x})$. Due to the size of the spatial flow and physical connectedness matrices, we leave their presentation to the Supplementary Materials.

For our simulations, nutrient influx is a constant rate, $I_{N_Z} = i_{N_Z}$, efflux and mineralization functions are linear, e.g., $E_{D_Z} = e_{D_Z} D_Z$, and the transfer functions are Lotka-Volterra, e.g., $F_{P_Z}(N_Z, P_Z) = \gamma_{P_Z} P_Z N_Z$. We also tested saturating functions like Monod/Type II, e.g., $F_{P_Z}(N_Z, P_Z) = \frac{\alpha_{P_Z} P_Z N_Z}{\beta_{P_Z} + N_Z}$, donor-control (i.e., linear nutrient transfer from the trophic level below) and mixtures of transfer functions between trophic levels, but we settled on Lotka-Volterra equations as they allowed for a greater range of parameters that allowed for stable coexistence across the meta-ecosystem.