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

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The integration of ecosystem processes over large spatial extents is critical to predicting whether and how local and 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. Through simulating a forest-lake-stream meta-ecosystem, our model illustrates 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.

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. 2017, 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), and 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 currently no theoretical model investigating the spatial flow of both abiotic (i.e. resources, nutrients) and biotic (i.e. organisms) ecosystem 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 understand and therefore predict 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. 2021). 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 (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 (Fig. 1). 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 (Fig. 1). The combined effects of
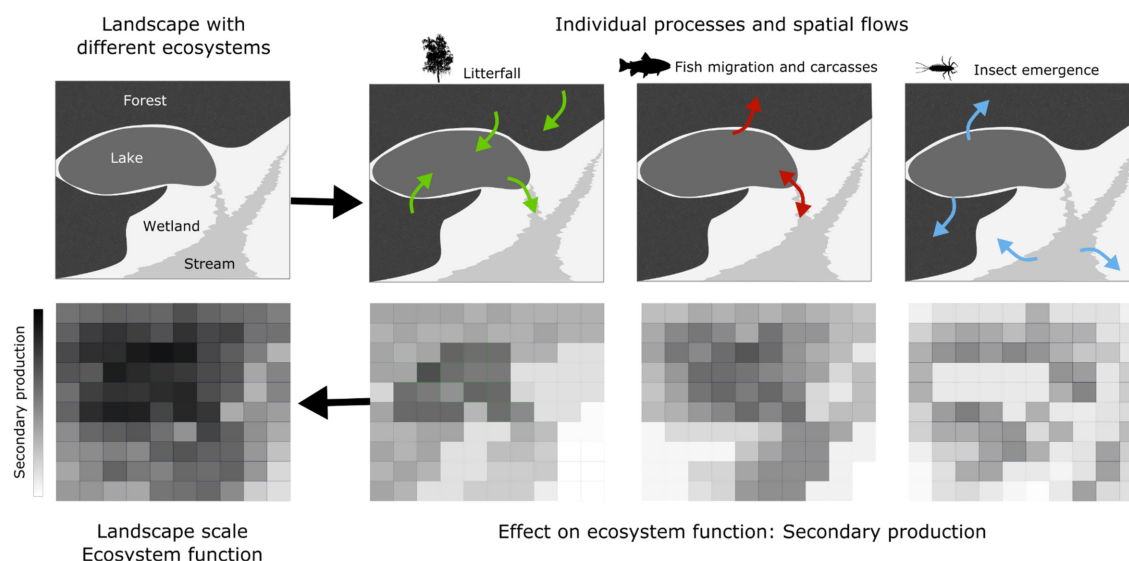

Figure 1. Conceptual diagram showing how different components of a meta-ecosystem contribute to function(s). Top right panels focus on one specific process each (arrows). Bottom right panels show an example of how the associated spatial flows would influence secondary production in a rasterized representation 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.

those flows of abiotic and biotic ecosystem compartments, however, should predict functioning at the whole landscape scale (Fig. 1).

The large body of empirical research on flows of materials and organisms 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 by Marcarelli et al. 2020). Taken as a whole, however, past studies clearly demonstrated that multiple abiotic and biotic flows interact and flow reciprocally across different ecosystems in watersheds (see section below for a short review of studies and flows). 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 (Fig. 1). The theory we derive in the next sections can be reduced to models integrating various combinations of the three individual type of flows listed above, but the full strength of our novel approach is in the integration of these three types.

Meta-ecosystem dynamics across different ecosystems involve spatial couplings where a specific species (or ecosystem compartment) 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 subsidize 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', 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 patches will, in turn, subsidize downstream fish patches (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 patch) 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 patches to landscape extents. We thus need a modelling framework capable of incorporating these factors while also faithfully representing local interactions.

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 (Harvey et al. 2020). 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) (Knight et al. 2005, McCoy et al. 2009). 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.

A meta-ecosystem model for landscape ecosystem functions

In this section, we present a model that allows representation of many types of flows and thus represents a more realistic application of the theory to empirical meta-ecosystems (Fig. 2). We first describe how we model the structure of individual ecosystems and the flows between local ecosystem compartments (Fig. 2a–b). We then illustrate how our modelling choices allow us to integrate numerous spatial flows across landscapes (Fig. 2c). Throughout this conceptual description, we articulate our general mathematical

(a) All ecosystem stocks

(b) Local dynamics

(c) Landscape representation and spatial dynamics

(d) Mathematical matrix-based meta-ecosystem framework

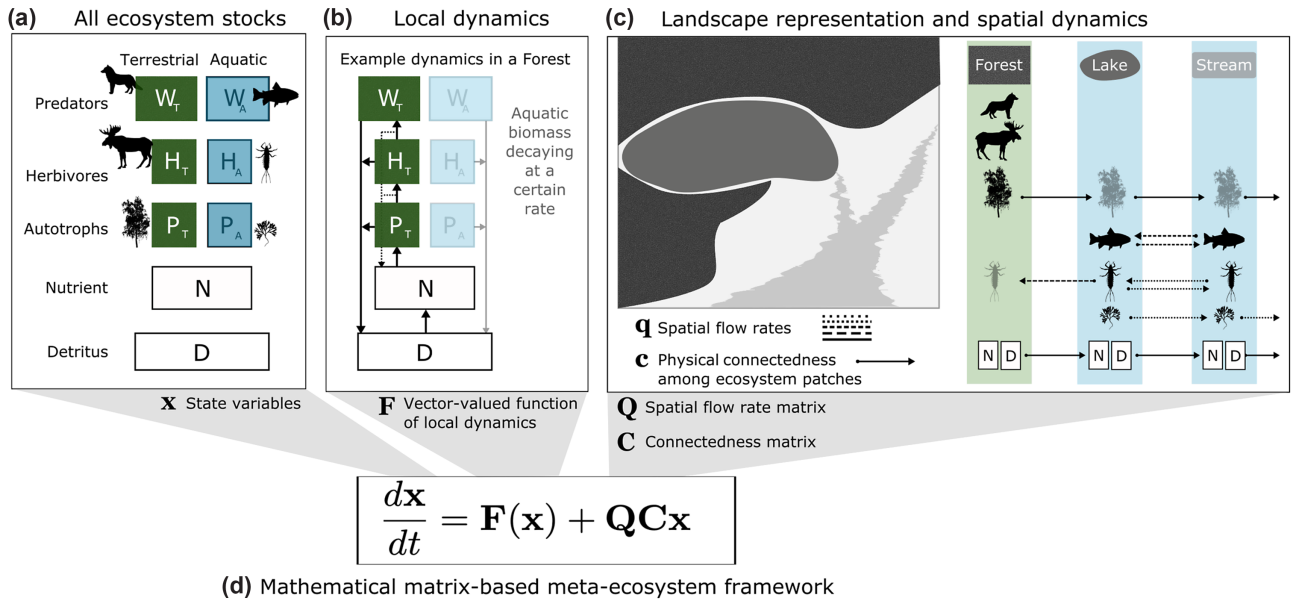$$\frac{d\mathbf{x}}{dt} = \mathbf{F(x)} + \mathbf{QCx}$$

Figure 2. 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 (Fig. 4). (a) All eight local 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 ecosystem compartments highlighted in green and blue, 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 ecosystem 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.

machinery (Fig. 2d) and provide concrete examples of how the model works (Box 1).

The first element of the model is that each ecosystem patch, independent of the type of ecosystem it is, contains all the possible ecosystem compartments found at the meta-ecosystem level (Fig. 2a). Concretely, this stipulation means that a river ecosystem would include a compartment for terrestrial herbivores, while a forest ecosystem would have a compartment for aquatic predators in a watershed meta-ecosystem (Fig. 2a). Therefore, we have compartments we would normally expect in an ecosystem model plus additional compartments that are, in many cases, devoid of any stocks (i.e. biomass, nutrient; Fig. 2a, Box 1). We label each compartment as x_{ik}, where i denotes local ecosystem patch i (e.g. a forest patch) and k denotes the type of compartment k (e.g. primary producer). We collect all the compartments into a vector $\mathbf{x}$, such that we first list the stock for a given compartment type in each local ecosystem in order (e.g. nutrients in the forest, the lake, the stream, etc.) and then list the next compartment type in each local ecosystem (e.g. terrestrial primary producer in the forest, the lake, the stream, etc.) and so on until they are all enumerated.

Mathematically, this makes $\mathbf{x} = [x_{11}, x_{21}, \ldots, x_{i1}, \ldots, x_{n1}, x_{12}, \ldots, x_{n2}, \ldots, x_{ik}, \ldots, x_{nm}]^T$ with n being the total number of ecosystem patches in the meta-ecosystem, m being the total

number of compartment types in the meta-ecosystem, and ^{T} being the transpose as $\mathbf{x}$ is a column vector. How these compartments change over time is due to flows of materials and energy that enter and leave them, such as trophic flows, immigration, excretion of wastes, dry deposition of nutrients, and other processes. Generically, we can write a system of ordinary differential equations to describe these changes, $d\mathbf{x}/dt = \mathbf{G(x)}$, where $\mathbf{G}$ is a vector-valued function describing rates of change of each ecosystem compartment across the meta-ecosystem due to the above ecological processes. To make $\mathbf{G}$ more tractable, we can decompose it into parts. For our purposes, following the formalism first proposed by Othmer and Scriven (1971) and then adapted by Jansen and Lloyd (2000), we first split $\mathbf{G}$ into two parts, i.e. $d\mathbf{x}/dt = \mathbf{G(x)} = \mathbf{F(x)} + \mathbf{QCx}$: *flows in local ecosystems*, which is captured by the term $\mathbf{F(x)}$, and *between ecosystem flows*, which is captured by the term $\mathbf{QCx}$ (Box 1, Fig. 2d).

Flows in local ecosystems are flows between ecosystem compartments within the same ecosystem type, e.g. a grasshopper eating a plant in a forest (Fig. 2b). As mentioned earlier, we have ecosystem compartments in these local ecosystems that we would not normally consider, such as having a terrestrial predator in an aquatic ecosystem or aquatic herbivore in a terrestrial ecosystem. Yet, if they are physically in the ecosystem, such as a bear in a river or a mayfly in a field, there

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' ($\mathcal{A_L}$) and the other being a 'stream' ($\mathcal{A_S}$). 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 ecosystem compartment (N), a detritus ecosystem compartment (D), primary producer ecosystem compartments (P), herbivore ecosystem compartments (H), and predator ecosystem compartments (W). Since it is highly likely that aquatic and terrestrial biotic ecosystem compartments would differ greatly, we explicitly model them separately in each ecosystem.

Each local ecosystem type Z ($Z = \{\mathcal{A_L}, \mathcal{A_S}, \mathcal{T}\}$) 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 ($Y = \{\mathcal{A_L}, \mathcal{A_S}, \mathcal{T}\}$, $Y \neq Z$), 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, respectively. 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:

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

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

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

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

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

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

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

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

This set of equations represents a subset of $\mathbf{F}(\mathbf{x})$ specifically those associated with a single ecosystem (i.e. $[f_{i,1}(\mathbf{x}_i)\ f_{i,2}(\mathbf{x}_i)$ … $f_{i,m}(\mathbf{x}_i)]^T$). 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, these are in the Supporting information.

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. $F_{P_Z}\left(N_Z, P_Z\right) = \gamma_{P_Z} P_Z N_Z$. We also tested saturating functions like Monod/Type II, e.g. $F_{P_Z}\left(N_Z, P_Z\right) = \dfrac{\alpha_{P_Z} P_Z N_Z}{\beta_{P_Z} + N_Z}$, 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.

will be local flows impacting organisms and other ecosystem compartments (Fig. 2b). As a corollary, the flows associated with an ecosystem compartment need not match in different ecosystems, i.e. a mayfly in a river feeds while they do not in the field. This formalism provides a great deal of flexibility in describing dissimilar ecosystems that can share organisms and materials, which is generally not possible in other meta-ecosystem models.

Formally, for a given ecosystem compartment x_{ik}, we can describe its local flows as a function of all ecosystem compartments in ecosystem patch i, $f_{i,k}(\mathbf{x}_i)$, where $\mathbf{x}_i = (x_{i1}, x_{i2}, …, x_{im})$. Furthermore, if $\mathbf{x}_i = \mathbf{x}_j$, i.e. the stocks in ecosystem patch i and j are equal, we generally do not require the flows to be equal, i.e. $f_{i,k}(\mathbf{x}_i) \neq f_{j,k}(\mathbf{x}_j)$ (Box 1 for examples). The totality of local flows in the meta-ecosystem is therefore composed by each of these functions arranged into a column vector, i.e. $\mathbf{F}(\mathbf{x}) = [f_{1,1}(\mathbf{x}_1), f_{2,1}(\mathbf{x}_2), …, f_{i,1}(\mathbf{x}_i), …, f_{n,1}(\mathbf{x}_n), f_{1,2}(\mathbf{x}_1), …, f_{n,2}(\mathbf{x}_n), …, f_{i,k}(\mathbf{x}_i), …, f_{n,m}(\mathbf{x}_n)]^T$. With $\mathbf{F}(\mathbf{x})$ defined, we can now turn to our next set of flows.

Between ecosystem flows are the spatial flows that cross the boundaries of one ecosystem patch to enter a different ecosystem patch (Fig. 2c). 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. We note here that while foraging can be modelled as a spatial trophic interaction (McCann et al. 2005, Garcia-Callejas et al. 2019, Peller et al. 2022), foraging is split into a spatial flow component (which is part of the $\mathbf{QCx}$ term) and a local trophic flow term (which is part of the $\mathbf{F}(\mathbf{x})$ term) in our model. Our approach, since we have an existing ecosystem compartment for the foraging organism's stock to be tracked, allows us to loosen the coupling between movement

and consumption and allows other local processes that may involve the foraging organism (nutrient recycling, other trophic and non-trophic interactions) to be easily specified.

Furthermore, we will allow that the flows may be unidirectional, bidirectional, or be crossing ecosystem boundaries in different ways for different ecosystem compartments (Fig. 2c, Mcleod and Leroux 2021). For example, if a bird and a rat on a forested island travel to a neighbouring forested island in the same lake, the bird will not need to enter the lake ecosystem, while the rat must. In addition, the rates of spatial flow across these boundaries for a given ecosystem compartment may vary between ecosystems. Using the rat again as an example, its rates of spatial flow from forest to lake is unlikely to be like that from lake to forest due to the physical medium, biomechanical differences between gait and swimming, etc.

This separation between the specification of the spatial arrangements and directionality of flows across the ecosystem boundaries (physical connectedness) and the rates of spatial flows across those boundaries is a key feature of our model. A benefit of this separation is that spatial flow rates (flow intensities) are commonly measured separately from physical connectedness for both organisms and materials, which can allow for easier model parameterization. In our model, both physical connectedness and the rates of spatial flows are represented by $nm \times nm$ matrices, $\mathbf{C}$ and $\mathbf{Q}$, respectively, that are multiplied together to give us the realized connectivity for the meta-ecosystem (Fig. 2d). The elements of these matrices could be functions of ecosystem compartments, say due to prey taxis, predator avoidance, or cross-emigration, or they could vary with time due to abiotic factors (like in spatio-temporal networks; (Fortin et al. 2021) or developmental cycles (Leroux and Loreau 2012). For this study, we used constant parameters for rates of spatial flows and physical

connectedness to simplify our analysis and make our results more intelligible.

To construct the $\mathbf{C}$ matrix, we consider the case where each ecosystem compartment has its own physical connectedness, $\mathbf{C}_k$, and there is no possibility of an organism or a material being transported by another. Then, $\mathbf{C}_k$ is an $n \times n$ matrix whose elements, c_{ijk}, indicate if ecosystem 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, $\mathbf{C}$:

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

where ^{T} indicates we take the transpose of the $\mathbf{C}_k$ matrix and $\oplus$ is the direct sum (note: we use the transpose as the $\mathbf{C}$ matrix will be on the left-hand side of $\mathbf{x}$, rather than on the right-hand side as in other models such as Marleau et al. 2015).

For our rates of spatial flows matrix $\mathbf{Q}$, its construction depends on our initial assumptions. In this study, we deliberately simplify our $\mathbf{Q}$ 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 organized all these rates into the diagonal matrix $\mathbf{Q}'$, which is $m \times m$ as we have m ecosystem compartments. Since these rates are invariant across the meta-ecosystem, we create the $\mathbf{Q}$ matrix by multiplying $\mathbf{Q}'$ with an $n \times n$ identity matrix, $(\mathbf{I}_{(n,n)})$, as we have n ecosystem patches, through the use of the Kronecker tensor product, which generates an $nm \times nm$ matrix:

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

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

where q_k is the between ecosystem spatial flow rate for ecosystem compartment k and $\mathbf{0}$ is an $n \times n$ zero matrix. Note that if the spatial flow of one ecosystem compartment is affected by the stock of another ecosystem compartment, then $\mathbf{Q}'$ (and therefore $\mathbf{Q}$) is no longer diagonal (e.g. 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 all ecosystem compartments, then we can replace the identity matrix with a weighted diagonal matrix instead. If these differences are ecosystem compartment-specific, we can instead multiply $Q' \otimes I_{(n,n)}$ by $\mathbf{W}$, where $\mathbf{W}$ is an $nm \times nm$ diagonal matrix with the weights as its elements.

With this model, we are now able to predict the significance of spatial flows in a simplified watershed meta-ecosystem (Box 1). Based on previous empirical work, we predict that spatial flows (as opposed to a 'no spatial flows' baseline scenario) would lead to 1) lower local stock and production in the most productive ecosystem, but 2) higher secondary production at the meta-ecosystem scale mainly because of 3) higher trophic efficiency at the meta-ecosystem scale. We expect this outcome as different ecosystem types are highly asymmetric in their primary production (terrestrial ecosystems are more autotrophic while on average aquatic ecosystems are more heterotrophic) (Gounand et al. 2020) and in their trophic efficiency (aquatic ecosystems move energy faster while terrestrial ecosystems tend to accumulate stock) (Shurin et al. 2002, Chapin et al. 2012). Thus, energy in a landscape tends to move among ecosystems that potentially share some levels of complementarity in functioning that should lead to emerging positive impact of spatial flows on productivity and trophic efficiency at the meta-ecosystem scale (Bartels et al. 2012, Gounand et al. 2017, Osakpolor et al. 2023, Pichon et al. in press).

Model application: a watershed meta-ecosystem

Watersheds are a classic and relevant example to illustrate the potential of our proposed integrated meta-ecosystem
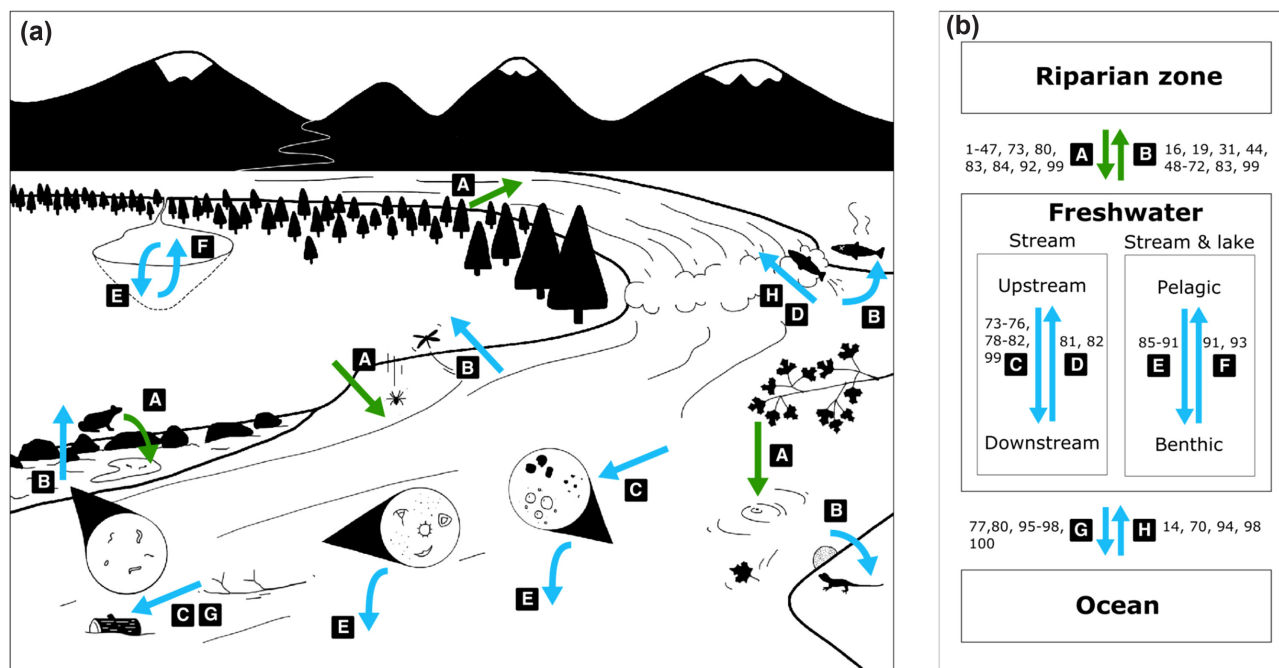
Figure 3. Spatial flows in watersheds. (a) Illustration and (b) schematic diagram of flows of material and organisms connecting the different habitats of a watershed. We provide 100 references quantifying these flows (identified by the numbers on the right panel), all available in Supporting information, 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, egg deposition of amphibians, leached nitrogen; (B) emergent insects and amphibians, fish carcasses caught by terrestrial consumers; (C) detritus, sediment dissolved organic carbon (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.

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 (Fig. 3, Supporting information 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) (Fig. 3a 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) (Fig. 3a 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 Fig. 3a arrow C) or actively via organismal movement (downstream to upstream e.g. fish migrations, Fig. 3a–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) (Fig. 3a arrows E and F).

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 behavioural 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).

A simulated forest-lake-stream meta-ecosystem

We apply the model to simulated watersheds (Box 1, Supporting information). 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 (Fig. 2a–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 (Fig. 2). We also measured additional ecosystem functions (nutrient recycling), considered alternative watershed configurations, and examined changes in connectivity regimes in the Supporting information to illustrate the flexibility of our approach (Supporting information).

For our primary analysis, we consider a forest that surrounds a lake and a stream that flows out of the lake (Fig. 2) and common flows among these ecosystems (Fig. 3). 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 (Fig. 2c). When biotic ecosystem compartments flow from terrestrial to aquatic or from aquatic to terrestrial ecosystems, the biotic ecosystem compartments considered here simply become dead organic material at a given rate as they can only survive a limited time in the recipient ecosystems (Fig. 2b).

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 (Fig. 2). 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 (Supporting information). Furthermore, our analysis focuses on functions and
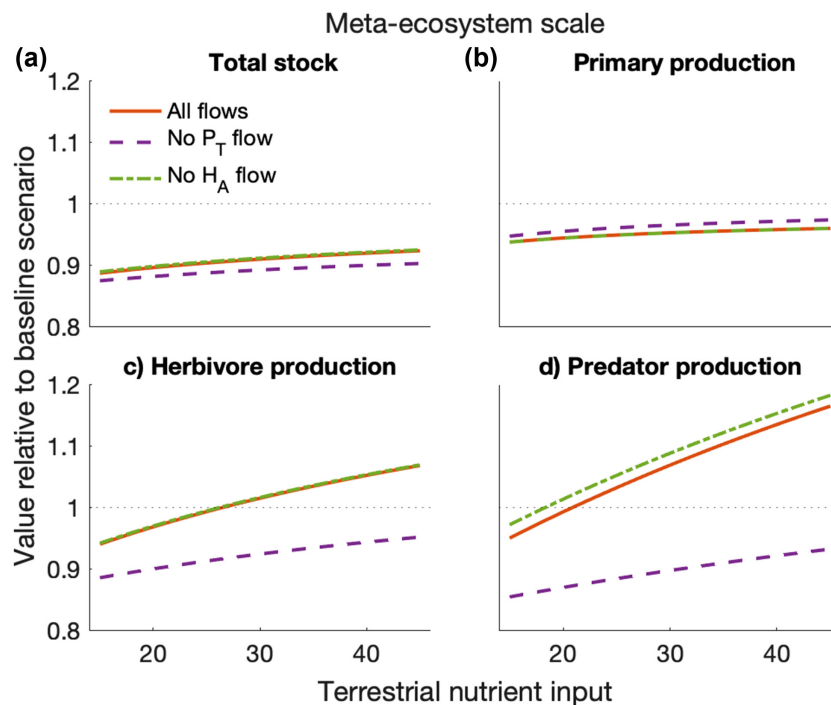

Figure 4. Effects of meta-ecosystem spatial flows and terrestrial nutrient inputs on (a) nutrient stock, (b) primary production, (c) herbivore production, and (d) predator production at the meta-ecosystem level relative to a local process-only baseline scenario meta-ecosystem (no spatial flow scenario; dotted line). The spatial flow scenarios include 'all flows' (as specified in Fig. 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 Fig. 4 is in the Supporting information. Absolute values of stocks and production are available in Supporting information.

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 (Supporting 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 the forest, lake, and stream were uncoupled from each other and compared it to three spatial scenarios where 1) 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), 2) the 'all flows' scenario without forest producers entering the lake ('no P_T flow' scenario), and 3) 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 ecosystem 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 impact the nutrient stocks of primary producers, detritus, and predators (Supporting 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 Supporting information).

Toward a cross-ecosystem efficiency hypothesis; results from the watershed case

As predicted, the meta-ecosystem in the baseline scenario (no spatial flows) generally has greater nutrient stocks than any of the scenarios with spatial flows because the latter contain additional losses outside of the meta-ecosystem through directional flows out of the stream (Fig. 4a). Primary production is also lower in the spatial scenarios due to this loss of nutrients (Fig. 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 (Fig. 4c–d). Given that the forest is the main producer of primary stock in the meta-ecosystem, it is not overly surprising that the 'no P_T flow' scenario leads to an overall decline, relative to baseline scenario, in secondary production at the meta-ecosystem scale (Fig. 4a–d). When we look at local ecosystem functioning, across ecosystem spatial flows reduce forest secondary production, while doubling secondary production in the stream (Fig. 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) because the 'all flows' and 'no H_A flows' scenarios perfectly overlap. These results were expected as aquatic herbivores have relatively low biomass and they do not integrate into the forest food chain (Box 1). While these results could reinforce the perspective that the aquatic-terrestrial coupling
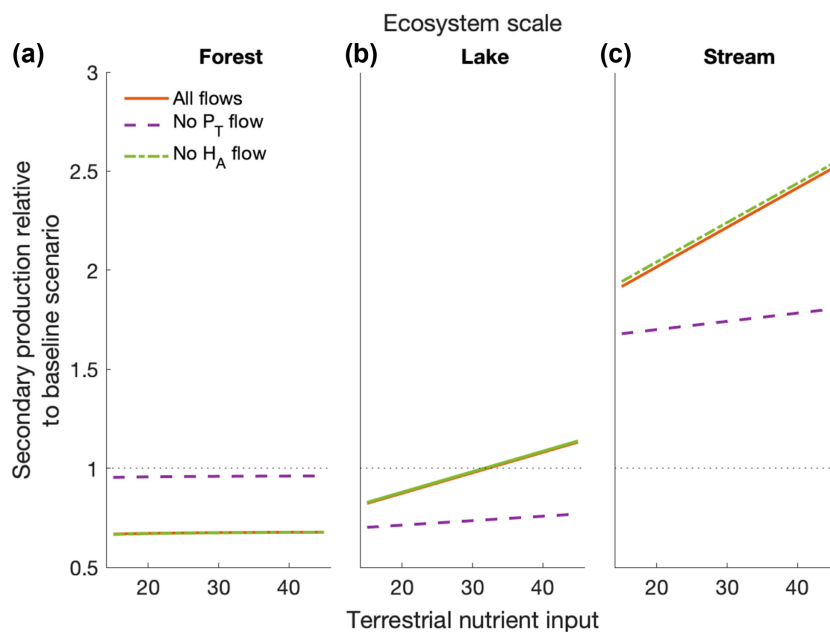

Figure 5. Effects of meta-ecosystem spatial flows on secondary production at the ecosystem scale in (a) the forest, (b) the lake, (c) the stream, relative to a local process only baseline meta-ecosystem (no spatial flow scenario; dotted line) as terrestrial nutrient inputs vary. Secondary productions are the sum of herbivore and predator productions. Parameter values and scenarios are the same as in Fig. 4. Absolute values of secondary production are available in Supporting information.
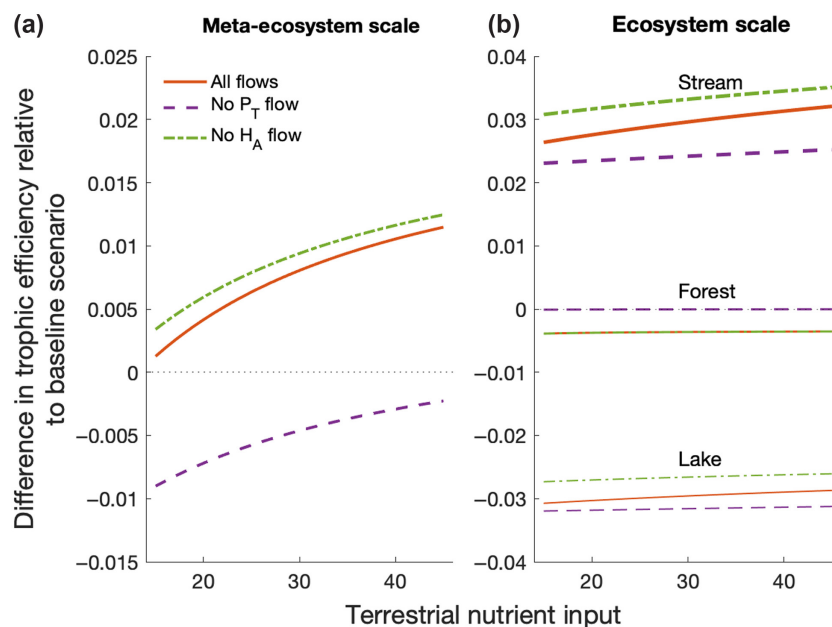
Figure 6. The ecosystem efficiencies at (a) meta-ecosystem and (b) ecosystem scales that describe the transfer of nutrients from primary producers to predators, relative to the baseline scenario (dotted line), and as terrestrial and aquatic nutrient inputs vary. Efficiencies are computed by the ratio of predator to producer productions (equivalent to multiplying efficiencies at the two trophic transitions). Parameter values and scenarios are the same as in Fig. 4. The trophic efficiencies at ecosystem scale (b) have distinct ranges among ecosystem types, which allow them to be displayed 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 Supporting information.

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 framework that can account for differences in resource quality, which is outside the scope of our model (Osakpolor et al. 2023).

The increase in production at the meta-ecosystem level is due to better efficiencies in turning nutrients into consumer biomass when nutrients and organisms can flow between the forest, lake, and stream (Fig. 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 (Supporting information). However, across ecosystem 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 (Fig. 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 (Fig. 6a). Similar patterns in production and trophic efficiency held in the alternative watersheds (Supporting 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 (Supporting 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 (Fig. 6b). Adding spatial flows modifies local trophic efficiencies, such that the lake's efficiency decreases, while the stream's efficiency increases, relative to the baseline scenario (Fig. 6b). The movement of aquatic predators leads to an increase of their biomass in the stream with a corresponding decrease in the lake. Therefore, this movement impacts predator production and leads to trophic efficiency being increased in the stream while being reduced in the lake. 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 from the forest, 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 (Fig. 6b). Given the inherent asymmetries in primary biomass production and in trophic efficiency among the different ecosystem types, 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 (Fig. 6). This

mechanism also holds for alternative watersheds (Supporting 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 (Fig. 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, change in connectivity). 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 (Fig. 4, Supporting 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 (Fig. 5). Classic meta-community theory has shown that trophic communities have evolved in response to resource availability and flows

that were constrained by the architecture of the landscape (Vannote et al. 1980, Harvey and MacDougall 2014). In that context, considering the cross-ecosystem flows simply points out the mismatch between the local production and the overall trophic community if ecosystems were considered in isolation. Thus, the landscape can be perceived as an assembly line where each ecosystem type has its own 'niche' (e.g. biomass accumulation versus 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', Fig. 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 damming, 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 (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 type, and spatial flows across different ecosystem types. Empirical studies showed that flows at all three levels are common (Fig. 3, Supporting information; see reviews by 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 by McLeod and Leroux 2021), yet existing theory rarely captures these dynamics – especially in multi-patch models (Fig. 1, Supporting information). Third, our framework partitions the physical connectedness of ecosystems from the movement or flow potential (rate) of an ecosystem compartment. For a flow to occur, there needs to be both physical connection and movement potential. This partitioning has three benefits: 1) it allows for a mathematically tractable way to model complex connectivity scenarios (i.e. K tensor product), 2) it makes it possible to allow for variable flow scenarios across different local ecosystem 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 3) 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 components or flows (e.g. trees or terrestrial plants due to forestry practices) can cascade to impact stocks and productions at local and landscape scales (Fig. 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 (Supporting information). 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 constituent ecosystems. For example, the model could explore how the demonstrated decline in Pacific salmon (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. 2021) 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 (Brondízio et al. 2019). This is also akin to the concept of 'land mosaic' where the multiple land uses found within agricultural landscapes are aggregated within a mosaic with a specific diversity, configuration and composition of land uses (Bennett et al. 2006). Therefore, the evidence is clear that we need to better integrate changes in connectivity 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 ecosystem 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). 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 the impacts of human activities, such as agricultural or urban development, on cross-ecosystem flows. For example, the model can provide information on the amount of natural riparian cover needed to maintain ecological processes within the context of well-connected systems such as a river and its surrounding 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. However, 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.

Author contributions

Eric Harvey: Conceptualization (lead); Funding acquisition (lead); Methodology (equal); Project administration (lead); Writing – original draft (lead); Writing – review and editing (lead). **Justin N. Marleau**: Conceptualization (lead); Formal analysis (lead); Methodology (lead); Writing – original draft (equal); Writing – review and editing (lead). **Isabelle Gounand**: Conceptualization (equal); Formal analysis (supporting); Visualization (lead); Writing – original draft (equal); Writing – review and editing (equal). **Shawn J. Leroux**: Conceptualization (equal); Formal analysis (supporting); Writing – original draft (equal); Writing – review and editing (equal); **Carina R. Firkowski**: Conceptualization (supporting); Visualization (supporting); Writing – original draft (equal); Writing – review and editing (equal). **Florian Altermatt**: Conceptualization (equal); Formal analysis (supporting); Writing – original draft (equal); Writing – review and editing (equal). **F. Guillaume Blanchet**: Conceptualization (equal); Formal analysis (supporting); Writing – original draft (equal); Writing – review and editing (equal). **Kevin Cazelles**: Conceptualization (equal); Writing – original draft (equal); Writing – review and editing (supporting). **Cindy Chu**: Conceptualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Cassidy C. D'Aloia**: Conceptualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Louis Donelle**: Conceptualization (equal); Writing – original draft (equal). **Dominique Gravel**: Conceptualization (equal); Formal analysis (supporting); Writing – original draft (equal); Writing – review and editing (equal). **Frédéric Guichard**: Conceptualization (equal); Formal analysis (supporting); Writing – original draft (equal); Writing – review and editing (equal). **Kevin McCann**: Conceptualization (equal); Writing – original draft (equal). **Jonathan L. W. Ruppert**: Conceptualization (equal); Writing – original draft (equal); Writing – review and editing (supporting). **Colette Ward**: Conceptualization (equal); Writing – original draft (equal); Writing – review and editing (supporting). **Marie-Josée Fortin**: Conceptualization (lead); Formal analysis (supporting); Methodology (supporting); Writing – original draft (equal); Writing – review and editing (equal).

Transparent peer review

The peer review history for this article is available at https://publons.com/publon/10.1111/ecog.06790.

Data availability statement

Data are available from the Open Science Framework Digital Repository: https://osf.io/sfbvk/ (Harvey et al. 2023).

Supporting information

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

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