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44 designing the research during the working group, EH wrote the first draft of the manuscript,
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49

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52

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58 **Abstract**

59 The integration of meta-ecosystem processes over large spatial extent is critical to predicting
60 whether and how global changes might impact biodiversity and ecosystem functions. Yet, there
61 remains an important gap in meta-ecosystem models to predict multiple ecosystem functions
62 (e.g., carbon sequestration, elemental cycling, trophic efficiency) across different ecosystem
63 types (e.g., terrestrial-aquatic, benthic-pelagic). We derive a generic meta-ecosystem model to
64 predict ecosystem function at landscape extents by integrating the spatial dimension of natural
65 systems as spatial networks of different habitat types connected by cross-ecosystem flows of
66 materials and organisms. This model partitions the physical connectedness of ecosystems from
67 the spatial flow rates of materials and organisms, allowing the representation of all types of
68 connectivity across ecosystem boundaries as well as the interaction(s) between them. The model
69 predicts that cross-ecosystem flows maximize the realization of multiple functions at landscape
70 extent. Spatial flows, even the ones that significantly reduce the overall amount of nutrients in
71 the meta-ecosystem, can reallocate nutrients to more efficient ecosystems, leading to greater
72 levels of productivity at both local and regional scales. This '*cross-ecosystem efficiency*
73 *hypothesis*' is a general and testable hypothesis emphasizing the complementarity and
74 interconnectedness among ecosystems and the importance of addressing ecosystem diversity for
75 meta-ecosystem function.

76 **Context: Ecosystem function(s) at the landscape scale**

77 The flows of resources, materials, and species can connect different types of ecosystems
78 within a landscape (Polis *et al.* 1997; Loreau *et al.* 2003; Massol *et al.* 2011). Meta-ecosystem
79 theory has been proposed to study these spatial flows across coupled ecosystems, while stressing
80 how spatial and temporal changes in biodiversity within each ecosystem can affect ecosystem
81 functions at the meta-ecosystem scale (Loreau *et al.* 2003; Gravel *et al.* 2010; Gounand *et al.*
82 2014; Marleau *et al.* 2014). Meta-ecosystem theory, however, has recently been criticised for
83 lack of connection to empirical research (Massol *et al.* 2011; Harvey *et al.* 2016; Gounand *et al.*
84 2018a) and there is a current push to develop empirically motivated meta-ecosystem models.

85 Classic meta-ecosystem theory tends to focus on measuring how flows influence the
86 stability of meta-ecosystems (Marleau *et al.* 2010; Gounand *et al.* 2014; McCann *et al.* 2021).
87 Yet, there remains an important gap in meta-ecosystem models to predict how ecosystem
88 connections influence functions other than stability (e.g., production, carbon sequestration,
89 elemental cycling, and trophic efficiency) at both local and landscape scales. To address this gap,
90 meta-ecosystem theory expanded the two-patch ecosystem approach (Gravel *et al.* 2010;
91 Marleau *et al.* 2010) to multi-patch systems (Marleau *et al.* 2014; McCann *et al.* 2021) where all
92 patches are of the same ecosystem type (i.e., terrestrial-terrestrial, aquatic-aquatic, but see
93 Leroux & Loreau 2012). However, there is no current theoretical model investigating the spatial
94 flow of both abiotic (i.e., resources, nutrients) and biotic (i.e., organisms) compartments across
95 different ecosystem types (e.g., terrestrial-aquatic), in multi-patch systems (Massol *et al.* 2017;
96 Gounand *et al.* 2018a). The theoretical and empirical integration of meta-ecosystem processes at
97 a broad spatial extent is critical to predicting and therefore understanding whether and how
98 global changes may impact biodiversity and ecosystem functions at the landscape scale.

99 Empirical examples of spatial flows of energy, materials, or organisms coupling different
100 ecosystems abound and have recently been reviewed (see reviews in Gounand *et al.* 2018b;
101 Montagano *et al.* 2019; Peller *et al.* 2020). Several of these studies focus on how cross-
102 ecosystem exchanges or allochthonous flows affect dynamics at the ecotone (Richardson & Sato
103 2015). What is missing are studies investigating the functional implications of meta-ecosystem
104 dynamics at broader multi-patch spatial extents than the ecotone itself (but see Iwata *et al.* 2003;
105 Largaespada *et al.* 2012). Yet, the effects of material and organismal flows are likely to
106 propagate or even accumulate across landscapes driving regional variation in ecosystem
107 function. In watersheds, for instance, different cross-ecosystem flows (e.g., litterfall, fish
108 migration) will operate at different spatial scales and thus contribute to ecosystem functions (e.g.,
109 primary and secondary production) at multiple spatial extents (Figure 1). The combined effects
110 of those flows of abiotic and biotic compartments, however, should predict functioning at the
111 whole landscape scale (Figure 1).

112 Here, we derive a meta-ecosystem model to predict ecosystem function(s) at landscape
113 extents by integrating the spatial dimension of ecosystems as spatial networks of different habitat
114 types connected by cross-ecosystem flows of materials and organisms. This meta-ecosystem
115 model partitions the physical connectedness of ecosystems from the spatial flow rates of
116 materials and organisms allowing the representation of all types of connectivity across ecosystem
117 boundaries as well as the interaction(s) between these two properties. We use this model to make
118 testable predictions on ecosystem function at landscape extents, using watersheds as an example,
119 and to investigate the impacts of perturbations on cross-ecosystem flows and corresponding
120 functions.

121

122 **Empirical meta-ecosystem – from the interface between ecosystems to the landscape**

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

130 Previous studies have shown that inputs of terrestrial detritus to aquatic ecosystems are
131 very common (Gounand *et al.* 2018b, 2020), and they can limit benthic invertebrate production
132 and contribute to fish diet (Richardson 1991; Kawaguchi *et al.* 2003; Wallace *et al.* 2015) (see
133 Figure 2a arrow A). Conversely, emerging aquatic insects contribute to the diets of terrestrial
134 consumers (Nakano & Murakami 2001; Sabo & Power 2002; Iwata *et al.* 2003; Baxter *et al.*
135 2005; Marczak & Richardson 2007; Bultman *et al.* 2014) (see Figure 2a arrow B). Movements of
136 organisms, organic matter, and nutrients also occur within ecosystems either passively following
137 directional flows along the dendritic network (upstream to downstream e.g., particulate organic
138 matter, see Figure 2a arrow C) or actively via organismal movement (downstream to upstream
139 e.g., fish migrations, Figure 2a,b arrows D and H). Biomass and resources can also be exchanged
140 vertically between benthic and pelagic lake zones via the sinking and resuspension of plankton
141 and organic matter (Jyväsjärvi *et al.* 2013; Matisoff *et al.* 2017) (see Figure 2a arrows E and F).

142 The large body of empirical research on flows of materials and organisms in watersheds
143 highlight how different types of spatial flows have been studied mostly in isolation, and ignoring
144 their bi-directional property (Schindler & Smits 2017, but see review in Marcarelli *et al.* 2020).

145 Taken as a whole, however, the data clearly demonstrate that multiple abiotic and biotic flows
146 interact and flow reciprocally across different ecosystems in watersheds. The different flows can
147 be separated into three broad categories: (1) **trophic flows within each ecosystem patch** (e.g.,
148 biomass transfer along the food chain at one location), (2) **spatial flows among patches of the**
149 **same ecosystem type** (e.g., ungulates foraging across different forest patches), and (3) **spatial**
150 **flows across patches of different ecosystem types** (flows at the ecotone of two different
151 ecosystem types, e.g., forest-lake). We surmise that by integrating these three types of flows into
152 meta-ecosystem theory, we can predict the drivers of variations in ecosystem function across
153 landscapes (Figure 1). The theory we derive in the next section can be reduced to models
154 integrating various combinations of the three individual components listed above, but the full
155 strength of our novel approach is in the integration of these three flow types.

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

167 productivity (Abbas *et al.* 2012; Leroux *et al.* 2017; Gounand *et al.* 2018b; García-Callejas *et al.*
168 2019).

169 Meta-ecosystem dynamics of spatial flows across different ecosystems involve spatial
170 couplings where a specific trophic level contributes to different trophic levels in the connected
171 ecosystems (Leroux & Loreau 2012; Montagano *et al.* 2019). Often, this occurs through the
172 conversion of living to dead organic matter and eventually inorganic matter. For example,
173 terrestrial herbivore insects falling in water can subsidize aquatic top-predators and decomposers
174 at the same time, and also affect aquatic herbivores through indirect interactions by relaxing
175 predation pressure via an alternative food source (Baxter *et al.* 2005; Allen & Wesner 2016;
176 Montagano *et al.* 2019). Those indirect cross-ecosystem biotic interactions illustrate the
177 permeability between ecosystems and the complexity of predicting how human actions in one
178 ecosystem might affect coupled ecosystems (Leroux & Loreau 2012; Massol *et al.* 2017;
179 Montagano *et al.* 2019).

180 Cross-ecosystem interactions also constitute a dominant mechanism by which changes in
181 the processes in one locality can impact processes at a different location, even in the absence of
182 dispersal (i.e., ‘spatial cascade’, see Gounand *et al.* 2017; García-Callejas *et al.* 2019). For
183 instance, it has been shown that upstream forest cover contributes ~70% of all dissolved organic
184 carbon loadings to watersheds of the North American Adirondack mountains (Canham *et al.*
185 2004), and the spatial configuration of forest patches in watersheds is a direct driver of leaf litter
186 availability in headwater streams (Little & Altermatt 2018). Cascading effects in space can also
187 occur through the active movement of organisms subsidized by terrestrial resources along the
188 connectivity structure of the river network. This is exemplified by the movement of aquatic
189 invertebrates subsidized by red alder detritus (itself favored by human forest harvesting of other

190 species) from upstream reaches that will, in turn, subsidize downstream fish habitats (Wipfli &
191 Musslewhite 2004).

192 The magnitude of any spatial cascade across the landscape could be controlled by three
193 main factors: (1) the level of biotic movement (dispersal or regular foraging movements within a
194 habitat) of organisms acting as consumers at multiple locations (McCann *et al.* 2005), (2) the
195 passive abiotic movement of altered nutrient or decaying detritus (*sensus* Vannote *et al.* 1980),
196 and (3) the constraints imposed by landscape configuration on these processes (Harvey &
197 Altermatt 2019; McLeod & Leroux 2021). These factors need to be explicitly integrated to
198 achieve the scaling up of ecosystem function from local to landscape extent.

199 **A meta-ecosystem model for landscape ecosystem function**

200 Here, we derive a meta-ecosystem model which integrates trophic flows within ecosystem
201 patches (Figure 3), spatial flows among ecosystems of the same type (Figure 2 arrows C and D),
202 and spatial flows across different ecosystem types (Figure 2 arrows A and B) in what would be
203 by default a multi-patch system (e.g., a leaf falling from the terrestrial ecosystem into a lake that
204 then decomposes as it moves between connected aquatic ecosystems). Mathematical tractability
205 of such complexity is challenging and likely a reason why there is a gap in meta-ecosystem
206 models that have patches that do not share the same ecosystem compartments. To overcome the
207 complexity involved in integrating the three components above, we generalized a matrix
208 approach to spatial networks (Figure 3).

209 We derived a modified spatial network formulation that generalises earlier work to allow
210 us to handle less commonly modelled but empirically abundant spatial flows across different
211 ecosystems (Figure 3) (Othmer & Scriven 1971; Jansen & Lloyd 2000; Kouvaris *et al.* 2015). In

212 the equation presented in Figure 3a, \mathbf{x} is a vector containing elements x_{ki} representing the stock
 213 (i.e., mass of limiting nutrient) of ecosystem compartment k in ecosystem patch i , where k ranges
 214 from 1 to the total number of ecosystem compartments m , and where i ranges from 1 to the
 215 number of different ecosystem patches n (which could be of the same or of different ecosystem
 216 types). How \mathbf{x} varies over time t can be represented by a system of ordinary differential
 217 equations $d\mathbf{x}/dt = \mathbf{G}(\mathbf{x})$, where \mathbf{G} is a vector-valued function describing rates of change of each
 218 ecosystem compartment. We decompose \mathbf{G} in two parts: *flows in local ecosystems* and *between*
 219 *ecosystem spatial flows*. *Flows in local ecosystems* are collected in the vector-valued function
 220 $\mathbf{F}(\mathbf{x})$, while *between ecosystem spatial flows* (i.e., both spatial flows between discrete patches
 221 within the same ecosystem type and across different ecosystems types) are the result of the \mathbf{QCx}
 222 matrix multiplication where \mathbf{Q} is the matrix characterizing the *spatial flow rates* and \mathbf{C} is the
 223 matrix of *ecosystem physical connectedness*, both of which are $nm \times nm$ matrices because
 224 connectedness and flow rates are both species and ecosystem-specific. Similarly, the vector-
 225 valued function \mathbf{F} is composed of nm functions, $\mathbf{F}(\mathbf{x}) = [f_{1,1}(\mathbf{x}_1), f_{2,1}(\mathbf{x}_2), \dots, f_{i,1}(\mathbf{x}_i), \dots, f_{n,1}(\mathbf{x}_n),$
 226 $f_{1,2}(\mathbf{x}_1), \dots, f_{n,2}(\mathbf{x}_n), \dots, f_{i,k}(\mathbf{x}_i), \dots, f_{n,m}(\mathbf{x}_n)]^T$ where $\mathbf{x}_i = (x_{i,1}, \dots, x_{i,k}, \dots, x_{i,m})$ describe the local
 227 flows to and from ecosystem compartment k in ecosystem patch i . To be more concrete, the
 228 trophic flow of energy and nutrients in an ecosystem would be categorized in $\mathbf{F}(\mathbf{x})$, while the
 229 biomass of a herbivore that moves from one ecosystem to another divided by the time measured
 230 would be categorized in \mathbf{Q} and the direction of flows across the landscape would be categorized
 231 in \mathbf{C} .

232 Assuming that the spatial flow rate of an ecosystem compartment does not change between
 233 ecosystems, the matrix of spatial flow rates \mathbf{Q} is a diagonal matrix constructed by taking the

234 Kronecker tensor product of the traditional diagonal $m \times m$ flow (or diffusion or movement) rate
 235 matrix, which we denote as \mathbf{Q}' (Marleau *et al.* 2010, 2014, 2015; Marleau & Guichard 2019)
 236 with an $n \times n$ identity matrix ($\mathbf{I}_{(n,n)}$):

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

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

246 The matrix of ecosystem physical connectedness \mathbf{C} is a block diagonal matrix derived from
 247 the direct sum of the transpose of each ecosystem compartment k 's matrix of possible
 248 connections, \mathbf{C}_k , which is an $n \times n$ matrix whose elements, c_{ijk} , indicate if compartment k in
 249 ecosystem i is physically capable of sending a spatial flow to ecosystem j (Jansen & Lloyd
 250 2000):

251

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

252

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

253 The diagonal entries of the \mathbf{C}_k matrices are negative to indicate the export of organisms and
 254 materials from the focal ecosystem, while the off-diagonal entries are positive and represent the
 255 arrival of organisms and materials from other ecosystems. Note that we need to transpose the
 256 matrices due to the \mathbf{C} matrix being on the left-hand side of \mathbf{x} rather than on the right-hand side in
 257 other derivations (Jansen & Lloyd 2000). Unlike previous work (Marleau *et al.* 2010, 2014,
 258 2015), we do not require \mathbf{C}_k matrices to be symmetric and c_{iik} does not need to equal to the
 259 negative row sum of its other elements (i.e. $c_{iik} \neq \sum_{j=1}^n c_{ij}$). This means that the flows
 260 between ecosystems can be unidirectional or bidirectional (reciprocal) and they can leave the
 261 meta-ecosystem partially or entirely.

262 This meta-ecosystem mathematical model allows for the incorporation of many types of
 263 flows and thus a better application of the theory to empirical meta-ecosystems. First, there can be
 264 different local dynamics (trophic flows) within different ecosystems (or ecosystem patches) for
 265 each ecosystem compartment. For example, a terrestrial herbivore (e.g., grasshopper
 266 (*Trimerotropis verruculata*)) will interact differently in the local river system, where it dies and
 267 becomes detritus, than in the local forest system, where it is a herbivore. This feature of the
 268 model makes it possible to appropriately model spatial flows across different ecosystem types,
 269 because these types of flows often result in the material or organism moving across different

270 compartments in the donor and recipient ecosystem (in our above-mentioned example, the
271 flowing material is a living herbivore in the donor ecosystem while it is dead detritus in the
272 recipient ecosystem). Second, each ecosystem compartment can have unique physical
273 connectedness (see Figure 3d), which is likely to happen for species that differ in preferred
274 habitat or foraging areas (McLeod & Leroux 2021). For example, an aquatic-terrestrial boundary
275 may be more permeable for a terrestrial avian predator (e.g., osprey (*Pandion haliaetus*)) than a
276 small terrestrial herbivore (e.g., snowshoe hare (*Lepus americanus*)). Third, we can separate the
277 effects of physical connectedness among ecosystems from the rate of spatial flows (flow
278 intensity), which are normally measured separately from one another for both organisms and
279 materials. The combination of physical connectedness of ecosystems and movement or flow
280 potential leads to realized connectivity. With this model, we are now able to predict impacts of
281 spatial flows in a simplified watershed meta-ecosystem.

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

283 We apply the model to a simulated watershed composed of two aquatic (i.e., stream and
284 lake) and one riparian forest ecosystem (Figure 3d). Each ecosystem has its own local flows or
285 internal dynamics of material transfer among its inorganic nutrients, autotrophic, and
286 heterotrophic components (Figure 3a-b). The local ecosystem components can potentially flow
287 across boundaries, such that an aquatic herbivore may enter into a terrestrial environment, e.g.,
288 when aquatic insect larvae mature into flying insects on land. The majority of current meta-
289 ecosystem theory models flows among ecosystems as diffusion, and therefore implicitly assume
290 that the material is of the same trophic level and composition in all patches and that it flows with
291 the gradient in resources (i.e., from high to low). Other studies modelled direct flows from one
292 ecosystem to another across trophic levels, i.e. a consumer in an ecosystem consumes a resource

293 in another (McCann *et al.* 2005; García-Callejas *et al.* 2019). However, such a flow implicitly
294 assumes that there is instantaneous movement between ecosystems for either the consumer
295 and/or resource, and therefore tight coupling between consumption and movement. An
296 alternative is to explicitly model the dynamics of a non-local compartment in its non-local
297 ecosystem type (see Figure 3b; Leroux & Loreau 2012). While this approach creates more
298 variables to keep track of, it also helps us generalize our methods to more diverse situations and
299 allows for cleaner mathematical treatment.

300 The model units are stocks expressed in mass of a limiting nutrient, such as nitrogen, in
301 each model compartment (e.g., the mass of nitrogen in autotrophs). Here, vector \mathbf{x} keeps track in
302 each ecosystem patch i of the amount of inorganic nutrients (N_i), detritus (D_i), aquatic and
303 terrestrial autotroph stocks ($A_{A,i}$ and $A_{T,i}$), herbivore stocks ($H_{A,i}$ and $H_{T,i}$) and predator stocks ($P_{A,i}$
304 and $P_{T,i}$) ($m=8$) across a forest, a lake and a stream each composed of a single patch ($n=3$).
305 Vector \mathbf{x} has therefore a size of $mn=24$.

306 In this simulation, we consider a forest that surrounds a lake and a stream that flows out of
307 the lake (Figure 3) and common flows among these ecosystems (see Figure 2). Live plant
308 biomass (e.g., leaves, branches), dead organic matter (e.g., dead leaves, top soil) and inorganic
309 nutrients can fall into and runoff in the lake, while aquatic insect herbivores (e.g., caddisfly
310 (*Trichoptera sp.*)) can emerge and enter the forest (Figure 3d). Nutrients, dead organic matter
311 (detritus), alive terrestrial plant biomass (e.g., white birch (*Betula papyrifera*)) and
312 phytoplankton flow passively downstream from the lake to the stream, while aquatic herbivores
313 and carnivores (e.g., dragonfly (*Odonata sp.*)) can move actively between the stream and lake
314 based on diffusive movements (Figure 3). Thus, while the ecosystems are all physically
315 connected, the realized biotic connectivity (as defined by the **QC** matrix) is limited and much of

316 the abiotic connectivity is unidirectional. We simulated our system in this way to highlight the
317 effects of meta-ecosystem connectivity.

318 To model flows in local ecosystems, we assumed a linear food chain for the biotic
319 ecosystem compartments with Lotka-Volterra functional responses when they are in their local
320 or donor ecosystem type (Figure 3). When biotic compartments flow from terrestrial to aquatic
321 or from aquatic to terrestrial ecosystems, the biotic compartments considered here simply
322 become dead organic material at a given rate as they can only survive a limited time in the
323 recipient ecosystems (Figure 3).

324 *Simulation scenarios*

325 We chose parameters to produce realistic local flow hierarchy, such that the forest
326 ecosystem has the greatest primary production, while the aquatic ecosystems are more efficient
327 in the transfer of biomass between trophic levels and have faster mineralization (Gounand *et al.*
328 2020). We used empirical parameter ranges for spatial flow rates to explore relevant parameter
329 space as examples (see Table S1). Furthermore, our analysis focused on functions and
330 parameters that ensured a stable equilibrium in all ecosystems over the range of parameter values
331 investigated. For this study, we ran one thousand simulations where we varied the nutrient inputs
332 to the local ecosystems to examine the impacts of nutrient supply on relative ecosystem
333 functioning (see Supplementary materials for full case study model equations and details on
334 model parameterization).

335 To highlight the importance of spatial flows across different ecosystems, we developed
336 four scenarios where (i) the meta-ecosystem had no spatial flows at all, (ii) the meta-ecosystem
337 was fully connected (bidirectional flows of biotic and abiotic material between terrestrial and

338 aquatic ecosystems), (iii) scenario without a biotic terrestrial to aquatic flow, and (iv) scenario
339 without a biotic aquatic to terrestrial flow.

340 Scenario (i) can be viewed as a baseline for compartment stocks (i.e. N, D, A, H, P) and
341 ecosystem function (primary, herbivore and predator production) through local processes only at
342 the meta-ecosystem and local levels (Figures 4 and S1). As this scenario has less nutrient losses
343 given the reduced flow out of the meta-ecosystem, we see higher nutrient stocks (Figure S1) and
344 higher primary production (Figure 4D) than the scenarios that consider spatial flows, though this
345 effect is reduced or absent for secondary production for spatial flow scenarios (ii) and (iv)
346 (Figures 4H and 4L). The key spatial flow to understanding these phenomena is the terrestrial
347 primary producer flow to the lake. Without the terrestrial primary producer flow (scenario (iii)),
348 nutrient stocks are relatively high in the meta-ecosystem as terrestrial primary producers keep
349 their stocks 'on land', leading to higher forest primary and secondary productivity (Figures 4A, E
350 and I). The spatial flow from the terrestrial to the aquatic ecosystems is then solely composed of
351 inorganic nutrients and detritus. The detritus and inorganic nutrient flows are relatively small
352 compared to potential primary producer spatial flows, and the flux into the lake is less than the
353 flux out of the lake, leading to a decline in lake productivity (Figures 4B, F and J), while the
354 stream benefits from the larger flows into it compared to those out of it (Figures 4C, G and K).

355 When nutrients were released by the terrestrial primary producers into the aquatic
356 ecosystems, however, they stimulated aquatic primary producers significantly, which led to
357 higher secondary production in the stream (Figure 4). This aquatic secondary production is high
358 enough to compensate for the losses in the terrestrial ecosystem, despite significant losses of
359 nutrients out of the meta-ecosystem (Figure S1). Furthermore, if aquatic herbivores do not send
360 individuals to the terrestrial ecosystem, thus breaking reciprocal links between the terrestrial and

361 aquatic ecosystems, predator production greatly increases in the lake, leading to greater meta-
362 ecosystem predator production overall (Figures 4I-L).

363 These simulation results show how spatial flows between different ecosystems can lead to
364 complex responses at both local and meta-ecosystem scales. Spatial flows, even the ones that
365 significantly reduce the overall amount of nutrients in the meta-ecosystem, can reallocate
366 nutrients to more efficient ecosystems, leading to greater levels of productivity at local and even
367 regional scales. In other words, cross-ecosystem flows maximize the realization of multiple
368 functions at landscape extent. We termed this finding the ‘*cross-ecosystem efficiency*
369 *hypothesis*’. This general hypothesis emphasizes the complementarity and interconnectedness
370 among ecosystems in the landscape and the importance of addressing ecosystem diversity for
371 meta-ecosystem function. Therefore, while the application of our model is relatively simple, it
372 provides a realistic scenario as it generated predictions that were not possible with previous
373 meta-ecosystem theory. Thus, by utilizing tools to better integrate real world ecosystems into
374 theory, we have expanded the possibilities of theory and can motivate empirical tests in the
375 future.

376 **Perspectives for predicting ecosystem functions across landscapes**

377 **Landscape function(s)**

378 The meta-ecosystem framework we developed highlights the interdependence among the
379 different ecosystems that can be found alongside one another at the landscape scale. Terrestrial
380 ecosystems drive primary production but are less efficient than aquatic at transferring the energy
381 produced up the food chain, which leads to higher nutrient stock accumulation. Conversely,
382 aquatic systems tend to be more heterotrophic with higher trophic efficiency, which leads to

383 higher secondary production. This ‘spatial trade-off’ can lead to co-dependencies between
384 systems that share limiting resources through spatial flows (Gounand *et al.* 2017). With our
385 model, we showed that this trade-off also means that accounting for spatial flows across different
386 ecosystem types can maximize multiple functions related to biomass accumulation versus
387 production at the landscape scale (Figures 4 and S1). When flows are accounted for, the energy
388 lost by the terrestrial to the aquatic system is well compensated at the meta-ecosystem level by
389 the increase in herbivore and predator production in the aquatic system (Figure 4). Thus, the
390 landscape can be perceived as an assembly line where each ecosystem type has its own
391 ‘expertise’ (e.g., biomass accumulation vs. production at different levels) and only by accounting
392 for energy flows across those systems can we maximize the landscape of functions (hence the
393 ‘cross-ecosystem efficiency hypothesis’, Figure 5).

394 By pairing our model with realistic landscape perturbation scenarios, we surmise that the
395 conceptual approach we developed can be used to predict how ecosystem functions may be
396 altered by different types of perturbations (Figure 5). Watersheds not only constitute relatively
397 good enclosed functional ecological units, but they also correspond to a human functional unit.
398 In that sense, watersheds include where we find and manage natural resources (wood, mine),
399 where we grow our food, where we go for recreational purposes (camping, fishing) and where
400 we live (urban centers) (Dudgeon *et al.* 2006; Abell *et al.* 2007). The spatial configuration of
401 these land-use patterns is essential to understanding feedback effects between local ecosystems
402 and the whole landscape. The conceptual approach we developed here, emphasizes the
403 importance of considering the mesoscale (watershed, landscape) as a scale of reference for
404 understanding changes in ecosystem functions that are relevant for human societies.

405 The flow perturbation results also suggest that those cross-scale interactions generally
406 maximize functions at the landscape scale whereas each of the three ecosystems tend to be more
407 dynamic in production. Those dynamical variations in production at each ecosystem scale tend to
408 cancel or compensate each other out at higher spatial scales. Indeed, one could imagine that
409 some scenarios could lead to the amplification of perturbations in space (across the three
410 connected ecosystems) and across spatial scales (see McCann *et al.* 2021). In a context where
411 conservation and restoration sciences are increasingly concerned with landscape management (as
412 opposed to local-scale habitat management), our approach could lend a direct contribution to
413 understanding and predicting how a particular perturbation in a given location of the landscape
414 might affect the whole landscape function in terms of production and standing stocks.

415 **Linking meta-ecosystem theory and empirical studies**

416 We propose a meta-ecosystem model with three major components. First, the model
417 integrates flows in local ecosystems, spatial flows within the same ecosystem, and spatial flows
418 across different ecosystems. Empirical studies showed that flows at all three levels are common
419 (Figure 2, Table S1; see reviews in Allen & Wesner 2016; Gounand *et al.* 2018a; Montagano *et*
420 *al.* 2019). Yet, existing theory usually focuses on only one of these components. Second, the
421 framework we propose is flexible enough to incorporate abiotic and biotic flows at different
422 scales. Empirical studies highlight that the spatial and temporal scales of abiotic and biotic flows
423 may differ and that there are important interactions between abiotic and biotic flows (see review
424 in McLeod & Leroux 2021), yet existing theory rarely captures these dynamics - especially in
425 multi-patch models (Table S1, Figure 1). Third, our framework partitions the physical
426 connectedness of ecosystems from the movement or flow potential (rate) of a compartment. For
427 a flow to occur, there needs to be both physical connection and movement potential. This

428 partitioning has three benefits; (i) it allows for a mathematically tractable way to model complex
429 connectivity scenarios (i.e., K tensor product), (ii) it makes it possible to allow for variable flow
430 scenarios across different local compartments, for instance in terms of directionality and
431 differences of connectivity among trophic levels depending on species mobility, and this
432 flexibility matches with empirical variability in ecosystem connections, and (iii) it provides a
433 model framework to make predictions based on metrics that are often empirically measured or
434 can be measured - for example landscape permeability (e.g., terrain ruggedness, Chetkiewicz &
435 Boyce 200) and animal movement (e.g., movebank, Kranstauber *et al.* 2011). The model could
436 also be used to determine most important fluxes in and across ecosystems to focus future
437 monitoring and research efforts. With a case study, we illustrate how this model can be fit to a
438 specific meta-ecosystem and how it can be used to provide testable predictions in specific
439 systems. In our forest-lake-stream meta-ecosystem case study, we predict that removing key
440 flows (e.g., terrestrial plants via forest harvesting) can cascade to impact stocks and productions
441 at local and landscape scales (Figures 1, 4 and 5), while emphasizing how complementarity in
442 functions among ecosystem types can maximize ecosystem function in the landscape (*'cross-*
443 *ecosystem efficiency hypothesis'*).

444 Overall, we anticipate that our framework could be used to develop a suite of predictions
445 for different ecosystems pertaining to how different flows mediate diverse ecosystem functions.
446 For example, the model could explore how the demonstrated decline in Pacific salmon
447 (*Onchorynchus spp.*, e.g. Oke *et al.* 2020) can impact primary and secondary production of natal
448 streams and riparian forests in the Pacific Northwest of North America. More broadly, habitat
449 fragmentation and land-use changes are the main factors contributing to the current global
450 biodiversity loss (IPBES 2019). In that context, we need to better integrate connectivity loss

451 across trophic levels to make testable predictions about the effects of reduced connectivity on
452 ecosystem function at the mesoscale.

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

468 The three-patch implementation of the model we propose here illustrates how to make
469 predictions on cross-ecosystem exchanges and their regional scale impacts, but it assumes that
470 each ecosystem is homogeneous in resource distribution. Future use of our framework could also
471 include multiple patches within each ecosystem so that flows within the same ecosystem and
472 among different ecosystems would be fully included. This would lead to a more precise

473 quantification of heterogeneity in ecosystem functions (as shown in Figure 1), for instance
474 allowing for spatial gradients in ecosystem functions to emerge from ecotones.

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

485 Finally, our framework can also be parametrized with empirical data which could help to
486 address questions about the functioning of natural systems in the face of perturbations. For
487 instance, our approach could potentially shed new light on carbon sequestration at the landscape
488 scale. Most carbon sequestration models assume homogeneous landscapes and ignore animals
489 (Schmitz *et al.* 2018), but it is not clear how accounting for abiotic and biotic spatial flows in
490 carbon might affect those predictions. Previous work has shown that carbon exchanges between
491 ecosystems at large spatial scales can be highly significant (Gounand *et al.* 2018b). In that
492 context, human induced perturbations such as climate change, but also land use change and
493 habitat fragmentation could potentially alter carbon flows among ecosystems (Leroux *et al.*
494 2017), thus influencing carbon sequestration at regional and landscape extents. Yet, much
495 research is needed to make the link between different types of perturbations and their impacts on

496 spatial flows, and the cumulative effects of different types of perturbations on ecosystem
497 functions in the landscape.

498

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502

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647 **Figure Legends**

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

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

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

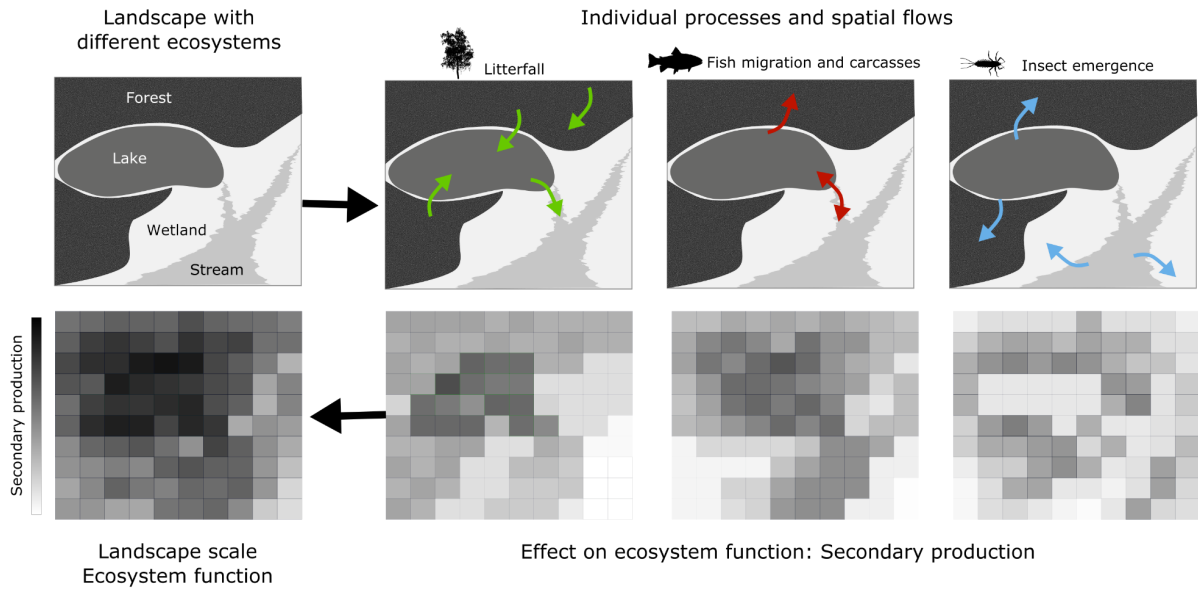
670 boreal watershed used as a case-study in our simulations (see Fig. 4). **(a)** All eight ecosystem
671 compartments included in the landscape, consisting of five trophic levels (detritus (D), inorganic
672 nutrients (N), autotrophs (A), herbivores (H), and predators (P), with terrestrial and aquatic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

683 **Figure 4.** Effects of meta-ecosystem spatial flows on primary production (**A, B, C** and **D**),
684 herbivore production (**E, F, G** and **H**) and predator production (**I, J, K** and **L**) in the forest (**A, E**
685 and **I**), lake (**B, F, and J**), stream (**C, G** and **K**) ecosystems and in the whole meta-ecosystem (**D,**
686 **H** and **L**). The ‘no flows’ scenario is a baseline result with no spatial flows between ecosystems.
687 The ‘all flows’ scenario is the meta-ecosystem with all the flows specified in Figure 3. The ‘no
688 P_T flow’ and ‘no H_A flow’ scenarios have the same spatial flows as the ‘all flows’ scenario,
689 except for the terrestrial primary producer flow and the aquatic herbivore flow, respectively.
690 Lines in the middle of the boxes represent median values of 1000 simulations, with the top and
691 bottom of the boxes representing 75th and 25th percentiles, the whiskers approximate the
692 expected non-outlier maximum and minimum values. Outliers are defined as being more than the

693 interquartile range multiplied by 1.5, and are represented by red crosses (see Supplementary
694 Material for parameters and fuller description of the model).

695 **Figure 5.** Landscape-matrix representation of secondary production for the different
696 scenarios of spatial flows shown on the left column, in our simulated boreal watershed. From top
697 to bottom: (i) scenario with no spatial flows, (ii) all spatial flows, (iii) only aquatic herbivores
698 crossing the forest-lake interface, or (iv) only leaf litter. The grey values are proportional to the
699 median values (opacity of black is median value * 10) provided in Figure 4 of herbivore and
700 predator productions (middle columns) in each ecosystem type, which contrasts spatial
701 distributions of the production among spatial flow scenarios. The right column provides total
702 secondary production by superimposing the two landscapes. The numbers on the right are the
703 sum of productions of the three ecosystems, giving total nitrogen used for annual secondary
704 production at the landscape-scale. Note that here, cases of the matrix are not individual patches
705 within ecosystems but just a coarse-grain way to represent the landscape.

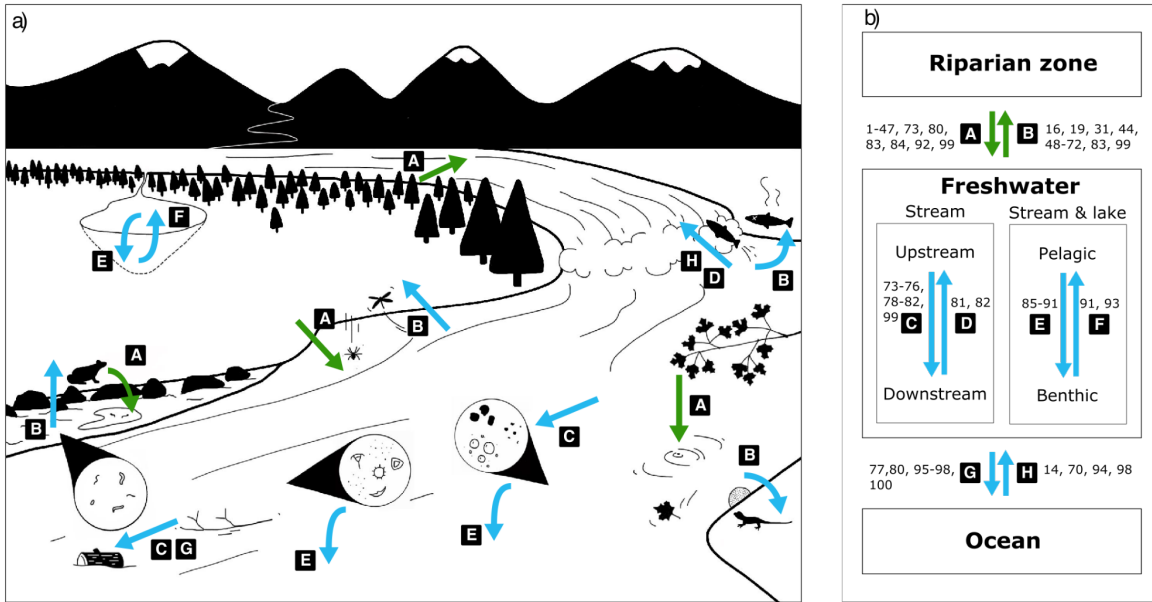
706 **Figure 1**



707

708

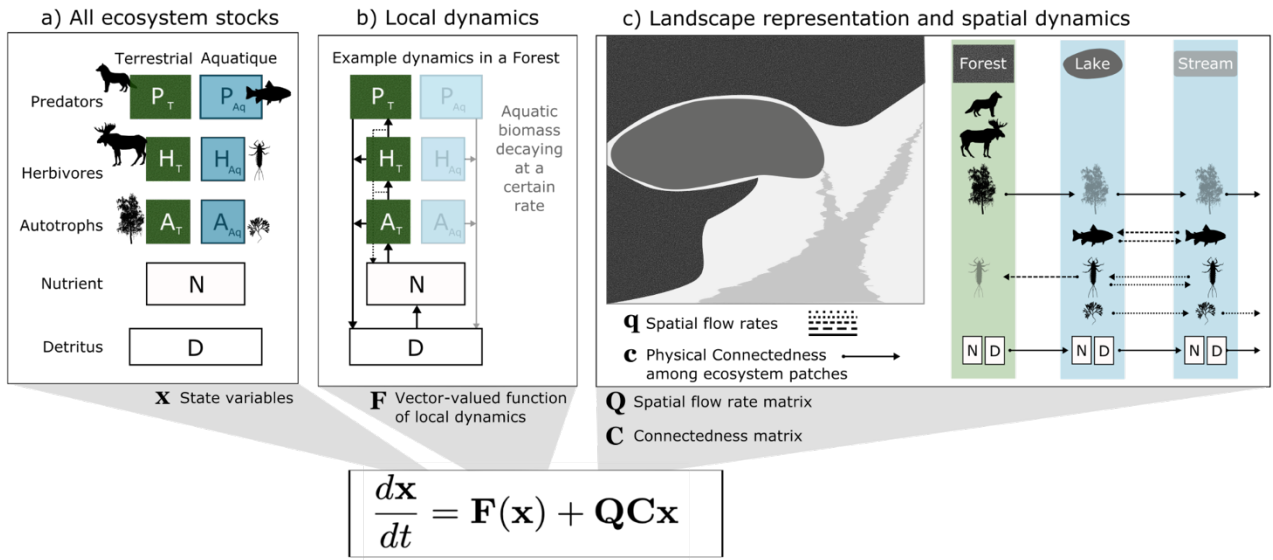
709 **Figure 2**



710

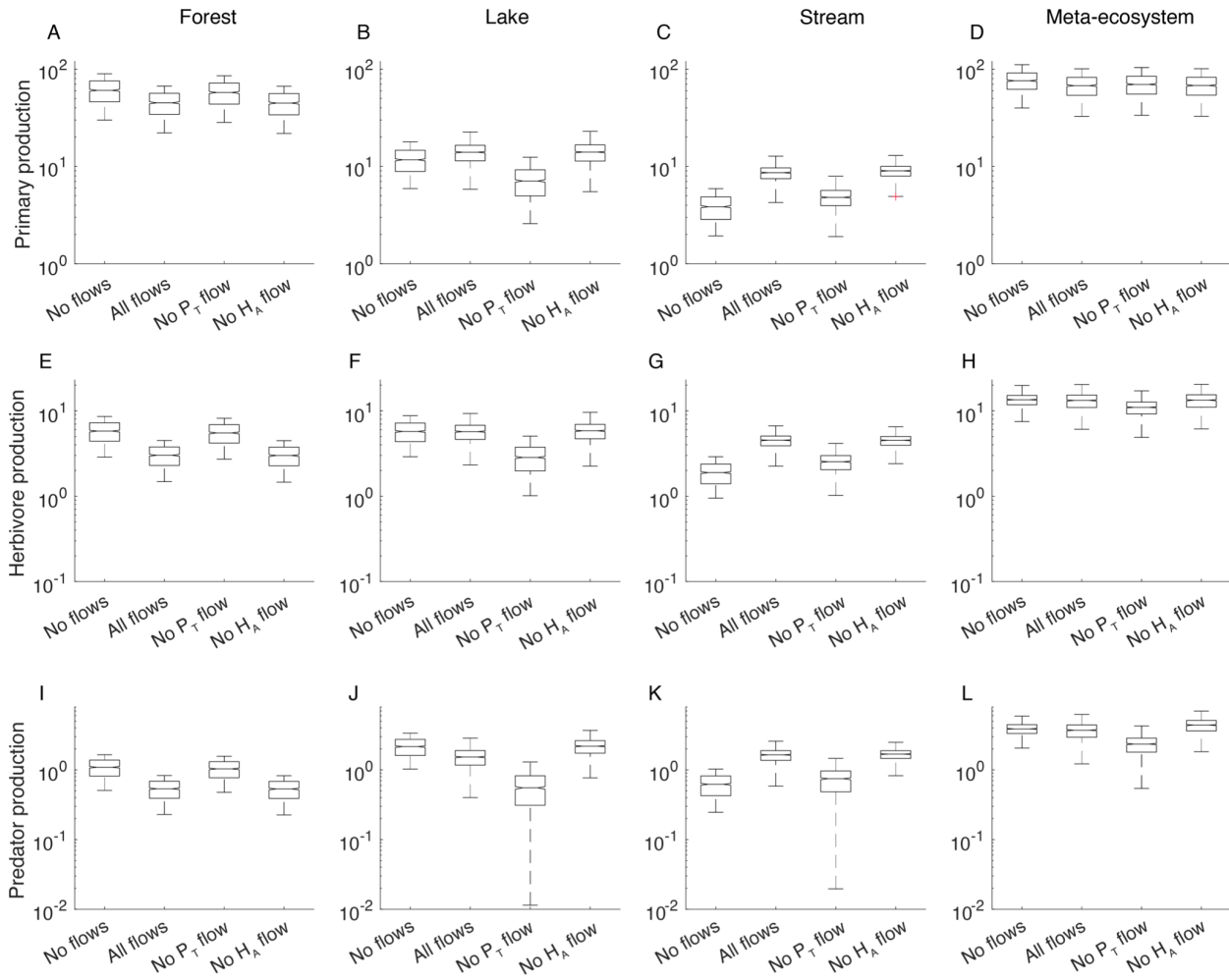
711

712 **Figure 3**



713

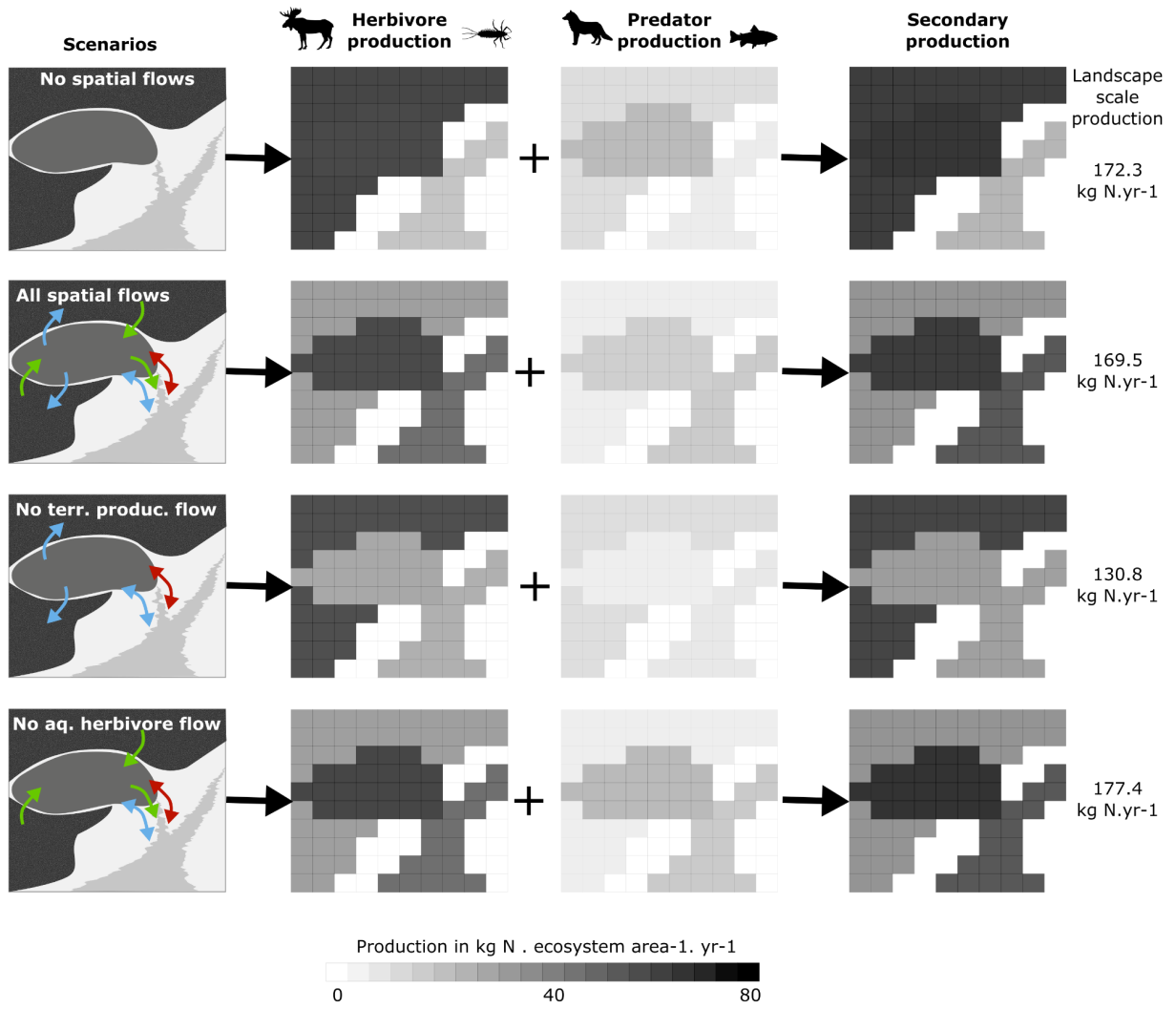
714 **Figure 4**



715

716

717 **Figure 5**



718