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Quality matters: stoichiometry of resources modulates spatial feedbacks in aquatic-terrestrial meta-ecosystems

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Abstract

Species dispersal and resource spatial flows greatly affect the dynamics of connected ecosystems. So far, research on meta-ecosystems has mainly focused on the quantitative effect of subsidy flows. Yet, resource exchanges at heterotrophic-autotrophic (*e.g.*, aquatic-terrestrial) ecotones display a stoichiometric asymmetry that likely matters for functioning. Here, we joined ecological stoichiometry and the meta-ecosystem framework to understand how subsidy stoichiometry mediates the response of the meta-ecosystem to subsidy flows. Our model results demonstrate that resource flows between ecosystems can induce a positive spatial feedback loop, leading to higher production at the meta-ecosystem scale by relaxing local ecosystem limitations (“spatial complementarity”). Furthermore, we show that spatial flows can also have an unexpected negative impact on production when accentuating the stoichiometric mismatch between local resources and basal species needs. This study paves the way for studies on the interdependency of ecosystems at the landscape extent.

1 Introduction

2 Flows of organisms, resources, and energy connect communities and ecosystems at the
3 landscape scale (Polis et al., 1997). These spatial connections are key to consider for
4 understanding ecosystem functioning and its response to global changes. As habitats are
5 increasingly fragmented, species indeed often disperse to track more favourable abiotic
6 conditions (Haddad et al., 2015; Thompson & Fronhofer, 2019). In addition, ongoing
7 changes in resource flows between ecosystems greatly affect ecosystem functioning,
8 as exemplified by the consequences of increasing terrestrial organic matter inputs on
9 aquatic ecosystems (Solomon et al., 2015). In this context, the meta-ecosystem framework
10 (*sensu* Loreau et al., 2003) unveils the strong links between local processes and landscape
11 dynamics (Polis et al., 2004; Massol et al., 2011). Meta-ecosystem theory has shown that
12 spatial flows at the landscape scale can affect source-sink dynamics (Gravel et al., 2010),
13 the local coexistence of communities (Marleau & Guichard, 2019; Peller et al., 2021), and
14 both the stability and functioning of ecosystems (Marleau et al., 2014; Gounand et al., 2014).
15 However, this theory has so far been restricted to flows between identical ecosystems
16 mediated by species dispersal. It has focused on flow magnitude, ignoring the importance
17 of flow quality (but see Marleau et al., 2015). While adapted to describe spatial networks
18 of connected forest patches or lakes, these models do not capture the diversity of resource
19 flows crossing ecotones, such as terrestrial-aquatic ecotones (Massol et al., 2017; Gounand
20 et al., 2018a).

21 Indeed, resource flows (*i.e.*, detritus or nutrients) of varying quantity and quality
22 cross ecotones and connect dissimilar ecosystems (*e.g.*, forest and streams), with strong
23 impacts on recipient ecosystems (Bartels et al., 2012). For instance, plant litter fuels stream
24 communities with carbon-rich subsidies (Wallace et al., 1997; Nakano & Murakami, 2001;
25 Bartels et al., 2012) while fish caught from streams by terrestrial predators feed riparian
26 communities with nutrient-rich carcasses, providing as much as 25% of the nitrogen

27 budget in riparian forests (Baxter et al., 2005; Helfield & Naiman, 2006). A recent data
28 synthesis showed that carbon resources commonly flow from net autotroph ecosystems
29 (*i.e.*, where primary production exceeds ecosystem respiration), to net heterotroph ones,
30 where primary production is limited by different factors (*e.g.*, shade, aridity, or water
31 depth in benthic systems; Gounand et al., 2018b). In many lakes and small shaded
32 streams, for instance, more carbon is respired than fixed, making their functioning net-
33 heterotroph and dependent on terrestrial carbon flows (Bartels et al., 2012; Gounand
34 et al., 2018b). By contrast, terrestrial or pelagic net autotrophic systems receive smaller
35 carbon flows, which seem negligible compared with their primary production (Gounand
36 et al., 2018b). This asymmetry in the quantity of resources transferred between autotroph
37 and heterotroph ecosystems can, however, be balanced by a stoichiometric asymmetry.
38 Here we complemented the carbon view of spatial coupling at terrestrial-freshwater
39 ecotones by data on nitrogen spatial flows (Appendix S2): we show that the asymmetry
40 of resource flows is reversed in terms of quality of resources (*i.e.*, N:C ratio), leading to
41 nitrogen spatial flows of the same order of magnitude to aquatic and terrestrial ecosystems
42 (Fig. 1, Box 1). Indeed, organisms produce detritus of different qualities, depending on
43 their stoichiometric composition: resource flows from terrestrial ecosystems are mostly
44 composed of primary producers with low N:C ratios, whereas the resource flows from
45 freshwater ecosystems originate from organisms at higher trophic levels with higher N:C
46 ratios (Fig. 1, Elser et al., 2000; Sitters et al., 2015). Therefore, subsidy stoichiometry likely
47 plays a strong role in the functioning of aquatic-terrestrial meta-ecosystems, as already
48 suggested at the ecosystem level.

49 Differences in stoichiometry and limitations between organisms in local communities
50 are known to strongly impact local ecosystem processes ranging from nutrient recycling
51 by consumers to species coexistence (Daufresne & Loreau, 2001; Cherif & Loreau, 2013;
52 Daufresne, 2021). The stoichiometry of spatial flows exported is thus expected to affect
53 the functioning of connected ecosystems, depending on the limitation of their basal

54 species. Primary producers are mainly limited by nutrients (*i.e.*, phosphorus or nitrogen)
55 in autotrophic systems, while in heterotrophic systems where primary production is low,
56 species at the basis of the food web are decomposers that can also be limited by carbon
57 (Elser et al., 2007; Daufresne et al., 2008; Harpole et al., 2011). Changing the limitation of
58 organisms within an ecosystem can drastically change the interactions and the feedbacks
59 between trophic levels (Zou et al., 2016; Buchkowski et al., 2019). Together, this suggests
60 that the impact of subsidy flows on ecosystem and meta-ecosystem scale production
61 may depend on both (*i*) the stoichiometry of subsidies and (*ii*) the local stoichiometric
62 constraints on communities.

63 Recent experimental and theoretical works suggest a functional complementarity
64 of ecosystems at the landscape scale (Gounand et al., 2017; Harvey et al., 2021). For
65 instance in watersheds, terrestrial ecosystems generally drive autotrophic production at
66 the landscape extent while some aquatic ecosystems, such as rivers with high riparian cover
67 or lakes, could display net heterotrophic functioning and perform intensive decomposition
68 processes (Gounand et al., 2018b). In addition, aquatic ecosystems tend to have higher
69 trophic efficiency (*i.e.*, ratio of consumer to prey production; Shurin et al., 2006), and
70 may boost landscape-scale secondary production using terrestrial carbon resources. Thus,
71 resource flows may optimize different functions in the meta-ecosystem (Harvey et al.,
72 2021). Studies on aquatic-terrestrial meta-ecosystems have so far considered differences
73 in trophic efficiency and primary production (Evans-White & Halvorson, 2017). We
74 hypothesize that similar mechanisms can be expected with stoichiometry. If spatial flows
75 fuel local ecosystems with resources that are limiting producer growth (*e.g.*, carbon-rich
76 subsidies from terrestrial ecosystems relaxing carbon limitation of decomposers in streams),
77 we expect higher production and positive feedbacks to emerge at the meta-ecosystem
78 scale. However, to our knowledge, no theoretical and empirical studies investigated such
79 hypotheses.

80 Here we integrate ecological stoichiometry and the meta-ecosystem framework to
81 understand (i) how stoichiometry mediates the response of meta-ecosystems to subsidy
82 flows and (ii) whether subsidy flows increase meta-ecosystem production by inducing
83 positive spatial feedback through the relaxation of local limitation in carbon or nutrients.
84 To test our hypotheses, we develop a stoichiometrically explicit meta-ecosystem model,
85 which connects the dynamics of a heterotrophic and an autotrophic ecosystem by carbon
86 and nitrogen fluxes (*e.g.*, aquatic-terrestrial ecotones). To root our narrative in natural
87 systems, and since we focused our empirical data search on terrestrial-freshwater ecotones,
88 we hereafter assign aquatic and terrestrial labels to our modelled ecosystems, but our
89 framework is generic to any autotrophic-heterotrophic meta-ecosystem and could, for
90 example, be applied to benthic-pelagic dynamics. With this model, we explore how flows
91 of carbon and nitrogen subsidies interact with local community dynamics to determine
92 meta-ecosystem functioning under different scenarios of resource limitations. Our results
93 reveal non-linear positive feedbacks between ecosystems under carbon limitation of the
94 aquatic ecosystem, but negative feedbacks under nitrogen limitation. Spatial flows of
95 resources increase or decrease overall production depending on whether they accentuate
96 the stoichiometric complementarity or the mismatch, respectively, between the needs of
97 local communities and the composition of available resources.

98 **Material and methods**

99 **Model description**

100 **Meta-ecosystem model** - We built a meta-ecosystem model with explicit stoichiometry
101 that couples carbon and nitrogen dynamics between two ecosystems with contrasting
102 functioning (Fig. 2): one autotroph, hereafter labelled terrestrial (indexed by \mathcal{T} , *e.g.*, forest
103 or grassland) and one heterotroph, hereafter labelled aquatic (indexed by \mathcal{A} , *e.g.*, stream
104 with a high riparian cover or oligotrophic lake). We focus on the autotrophic-heterotrophic

105 extrema of a gradient in ecosystem functioning, by considering the basal species of the
106 terrestrial ecosystem to be autotrophic plants (P), while the aquatic ecosystem harbours
107 no primary producers, and instead has heterotrophic decomposers (B) as basal species.
108 We assume that each ecosystem consists of two trophic levels to ease the interpretation
109 of our results. While spatial flows exported by aquatic ecosystems mainly originate from
110 higher trophic levels (Fig. 1), this assumption does not affect our results (see Appendix S4
111 for results with an additional trophic level). Therefore, grazers (G) and consumers of
112 decomposers (C) consume basal species in terrestrial and aquatic ecosystems, respectively.
113 Each ecosystem has a detritus (D) and an inorganic nitrogen pool (N). We followed the
114 carbon for the biotic and detritus pools (e.g., B_{C_A} for aquatic decomposers), and we derived
115 the nitrogen content of organisms (e.g., P_N for plants) by assuming a fixed stoichiometry
116 (homeostasis) corresponding to their molar nitrogen to carbon ratio, N:C (α_X , where
117 $X \in \{G, P, C, B\}$; Fig. 2a). This homeostasis involves different mechanisms across trophic
118 levels: contrary to plants that maintain a constant N:C ratio through the control of their
119 uptake (Tilman, 1982), grazers and consumers of decomposers hold their homeostasis
120 through differential assimilation (Grover & Holt, 1998; Sterner & Elser, 2002).

121 **Basal species limitation** - Plants are exclusively limited by nitrogen for growth and
122 maintain their stoichiometric homeostasis by adjusting their carbon intake, such that
123 net photosynthesis equals f_P (Eq 1). Decomposers can either be limited by carbon or
124 nitrogen (Fig. 2b, or by both in Appendix S5). Decomposers feed primarily on detritus.
125 Yet, as the detritus N:C ratio does not always match the decomposer stoichiometry due
126 to different stoichiometry of detritus produced by organisms, decomposers take up or
127 excrete nitrogen to maintain their homeostasis (Daufresne & Loreau, 2001). Decomposers
128 limitation determines whether decomposition (ϕ_D , i.e., consumption of detritus flux) is
129 constrained by nitrogen immobilization (ϕ_I ; N-limitation) or whether decomposition
130 determines nitrogen dynamics (C-limitation). This link between decomposition and

131 immobilization fluxes, which allows decomposers to maintain their homeostasis is detailed
132 in Appendix S3.

133 **Consumer dynamics** - Grazers and consumers of decomposers feed on the basal species
134 in their respective ecosystems at a rate a_G , a_C respectively, which follows the law of mass
135 action (*i.e.*, type I functional response): $f_G = a_G P_{C_T} G_{C_T}$ and $f_C = a_C B_{C_A} C_{C_A}$ (Appendix S6
136 details a donor-controlled version of our model). Due to inefficiencies of assimilation,
137 only fractions e_G and e_C of consumption support consumer growth, while the rest is lost
138 from the meta-ecosystem. In addition, to maintain their homeostasis, consumers excrete
139 the excess nitrogen due to the stoichiometric imbalance between their food and their
140 needs (*e.g.*, $\beta_G f_G$ where $\beta_G = (\alpha_P - e_G \alpha_G)$ for grazers) (Grover & Holt, 1998; Marleau &
141 Guichard, 2019).

142 **Nutrient and resource flows** - Recycling occurs through the production of detritus
143 of each biotic compartment at rate $d_X \in \{G, P, C, B\}$, fuelling the detritus pool, and
144 the mineralization of detritus into nitrogen at a rate m_A , in the aquatic system, which
145 corresponds to decomposer's nitrogen mineralization (Daufresne & Loreau, 2001), and a
146 rate m_T in the terrestrial ecosystem, where the action of decomposers is implicit.

147 Both ecosystems are supplied with autochthonous nitrogen and detritus flows I_{N_Z} and
148 I_{D_Z} respectively, and detritus and nitrogen are lost at rates l_{N_Z} and l_{D_Z} ($Z \in [T, A]$). We
149 assume that inputs of autochthonous detritus do not vary the N:C ratio of detritus.

150 **Meta-ecosystem flows** - Ecosystems are coupled by spatial flows of subsidies (*e.g.*,
151 detritus from leaching or flooding material decomposition), with a fraction Δ of the
152 produced detritus and excreted nitrogen being directly transferred from each biotic
153 compartment in one ecosystem to the detritus and nitrogen pools in the other ecosystem
154 (regional flow) while the remaining fraction being locally recycled ($1 - \Delta$, local flow).

155 Because $P_{N_T} = \alpha_P P_{C_T}$, and $G_{N_T} = \alpha_G G_{C_T}$, the set of equations for the terrestrial

156 ecosystem reduces to (Fig. 2):

$$\left\{ \begin{array}{l}
 \frac{dP_{C_T}}{dt} = f_P - f_G - d_P P_{C_T} \\
 \frac{dG_{C_T}}{dt} = e_G f_G - d_G G_{C_T} \\
 \frac{dD_{N_T}}{dt} = I_{D_T} \frac{D_{N_T}}{D_{C_T}} - l_{D_T} D_{N_T} + \alpha_G d_G G_{C_T} (1 - \Delta) + \alpha_P d_P P_{C_T} (1 - \Delta) + \alpha_C d_C C_{C_A} \Delta \\
 \quad + \alpha_B d_B B_{C_A} \Delta - m_T D_{N_T} \\
 \frac{dD_{C_T}}{dt} = I_{D_T} - l_{D_T} D_{C_T} + d_G G_{C_T} (1 - \Delta) + d_P P_{C_T} (1 - \Delta) + d_C C_{C_A} \Delta + d_B B_{C_A} \Delta_B - m_T D_{C_T} \\
 \frac{dN_T}{dt} = I_{N_T} - l_{N_T} N_T + \beta_G f_G (1 - \Delta) + \beta_C f_C \Delta \\
 \quad - \alpha_P f_P + m_T D_{N_T}
 \end{array} \right. \quad (1)$$

157 Similarly, with $C_{N_A} = \alpha_C C_{C_A}$, we get the following equations for the aquatic ecosystem

158 dynamics:

$$\left\{ \begin{array}{l}
 \frac{dB_{C_A}}{dt} = \phi_D - d_B B_{C_A} - f_C - m_A B_{C_A} \\
 \frac{dB_{N_A}}{dt} = \phi_I \alpha_B + \phi_D \frac{D_{N_A}}{D_{C_A}} - f_C \alpha_B - d_B B_{C_A} \alpha_B - \alpha_B m_A B_{C_A} \\
 \frac{dC_{C_A}}{dt} = e_C f_C - d_C C_{C_A} \\
 \frac{dD_{N_A}}{dt} = I_{D_A} \frac{D_{N_A}}{D_{C_A}} - l_{D_A} D_{N_A} + \alpha_C d_C C_{C_A} (1 - \Delta) + \alpha_B d_B B_{C_A} (1 - \Delta) + \alpha_G d_G G_{C_T} \Delta + \\
 \quad \alpha_P d_P P_{C_T} \Delta - \phi_D \frac{D_{N_A}}{D_{C_A}} \\
 \frac{dD_{C_A}}{dt} = I_{D_A} - l_{D_A} D_{C_A} + d_C C_{C_A} (1 - \Delta) + d_B B_{C_A} (1 - \Delta) + d_G G_{C_T} \Delta + d_P P_{C_T} \Delta - \phi_D \\
 \frac{dN_A}{dt} = I_{N_A} - l_{N_A} N_A + \beta_C f_C (1 - \Delta) + \beta_G f_G \Delta \\
 \quad - \phi_I \alpha_B + m_A B_{C_A} \alpha_B
 \end{array} \right. \quad (2)$$

159 A fully annotated system of equations is available in Appendix S3.

160 **Ecosystem & meta-ecosystem metrics**

161 To test our hypotheses on the effect of subsidy stoichiometry on meta-ecosystem functioning,
162 we compared the following ecosystem and meta-ecosystem metrics for two different
163 scenarios of decomposer limitation: nitrogen versus carbon limitation (see parameters
164 in Appendix S3). Under each scenario, we made sure decomposer limitation remained
165 unchanged by the studied variations in decomposer and plant stoichiometry.

166 **Production and spatial subsidy flows -** We measured the basal and secondary productions
167 (in carbon units) at the ecosystem and meta-ecosystem scales, defined as the flow at
168 equilibrium to basal species (plants and decomposers) and to consumers, respectively.
169 When decomposer growth is limited by nitrogen, basal production corresponds to immobilization
170 flux of nitrogen (ϕ_I), while it is the decomposition flux (ϕ_D) under carbon limitation. We
171 compared the production of the meta-ecosystem when ecosystems are connected versus
172 isolated (*i.e.*, local recycling of detritus) while varying the stoichiometry of plants and
173 decomposers, using a log ratio response (LRR) defined as:

$$\log\left(\frac{Prod_{j, \Delta=1}}{Prod_{j, \Delta=0}}\right) \quad (3)$$

174 , where $Prod_j$ is the production of the trophic level j from both ecosystems (meta-ecosystem
175 scale). A positive LRR value means that production benefits from subsidy flows relative to
176 a scenario where all subsidies are locally recycled (no spatial flows).

177 **Measuring the feedback between ecosystems -** We measured the spatial effects (hereafter
178 feedbacks) of subsidy flows as the difference in production between scenarios where
179 ecosystems are bidirectionally versus unidirectionally connected by subsidy flows. In the
180 latter, the focal ecosystem receives subsidies from the connected ecosystem but its own
181 exported flows are lost from the meta-ecosystem. For instance, for the case of the terrestrial
182 ecosystem, we aim to quantify how resources it exports impact its own production through

183 the effect of spatial flows exported to the aquatic ecosystem and the quantity of aquatic
 184 subsidies exported back (see Fig. S1.1). We interpret this measure as the strength of the
 185 spatial feedback \mathcal{F} induced by the subsidy flow:

$$\begin{aligned}\mathcal{F}_{\mathcal{T}_j} &= \mathcal{P}_{\mathcal{T}_j, \Delta \neq 0} - \mathcal{P}_{\mathcal{T}_j, \text{terrestrial subsidies lost}} \\ \mathcal{F}_{\mathcal{A}_j} &= \mathcal{P}_{\mathcal{A}_j, \Delta \neq 0} - \mathcal{P}_{\mathcal{A}_j, \text{aquatic subsidies lost}}\end{aligned}\tag{4}$$

186 , where $\mathcal{P}_{\mathcal{Z}_j}$ is the production of the trophic level $j, j \in [1, 2]$ in ecosystem $\mathcal{Z}, \mathcal{Z} \in [\mathcal{T}, \mathcal{A}]$.
 187 In addition, because this metric evaluates the long-term impact of spatial flows on each
 188 ecosystem production, we also measured the short-term response of each trophic level
 189 density to a transient increase in the fraction of subsidies received by the other ecosystem
 190 (Appendix S1).

191 **Parameters and sensitivity analysis** - We parameterized the model to account for
 192 differences of functioning between aquatic and terrestrial ecosystems, and of stoichiometry
 193 between plants and decomposers, while staying generic and covering the different qualitative
 194 behaviours that might be observed in different systems (see Appendix S3, and Table S3.3).
 195 In addition to the sensitivity analyses on the shape of the functional responses, and the
 196 number of trophic levels, we performed one on the parameter values (Appendices S6-S7).
 197 As the model is not analytically tractable, we performed simulations using *DifferentialEquation*
 198 package in Julia (version 1.7.3), and analysed them in R (version 4.1.0). Details about the
 199 simulation method are given in Appendix S3.

200 **Results**

201 The following results hold qualitatively when changing the type of functional response,
 202 adding a third trophic level, modifying the asymmetry of flows between ecosystems, and
 203 varying the parameter values (Appendices S4, S6-8).

204 **Spatial complementarity under carbon limitation**

205 Under the scenario of carbon limitation for aquatic decomposers, resource spatial flows
206 maximize both primary and secondary production in each local ecosystem when decomposers
207 have high nitrogen content (α_B) and plants have low nitrogen content (α_P) (Fig. 3a).
208 In addition, spatial flows also increase the densities of grazers and aquatic consumers
209 (Fig. S1.2).

210 As decomposers need more nitrogen to maintain their homeostasis (α_B increases), both the
211 nitrogen content of decomposer-produced detritus and the quantity of nitrogen excreted
212 by aquatic consumers through stoichiometric imbalance ($\beta_C = \alpha_B - e_C \alpha_C$) increase. When
213 ecosystems are connected, this flow of nitrogen fuels the terrestrial nitrogen pool, and
214 supports higher plant production (Fig. 3a-(iii) to (i)) and higher density of grazers (Fig. S1.2).
215 These mechanisms contribute to higher carbon and nitrogen flows exported back to the
216 aquatic ecosystem. In addition, we observe that the aquatic ecosystem is a net source for
217 nitrogen and a net sink for carbon at the meta-ecosystem scale (Fig. 3a (i)-(iii)).

218 Production in both ecosystems is maximized for plants with a low N:C ratio (low α_P ,
219 Fig. 3a). When plant N:C decreases (e.g., from Fig. 3a-(ii) to (i)), basal plant production
220 increases due to lower needs of nitrogen for the same growth, and consequently leads
221 to a higher grazer density (Figs S1.2, 3a-(ii)). Thus, the quantity of detritus produced by
222 plants and grazers, and then exported, increases (Fig. S1.3). Consequently, it supports
223 higher production in the aquatic ecosystem (Fig. S1.2). Additionally, because resources
224 exported from the terrestrial ecosystem have on average a lower N:C ratio compared with
225 the ones produced by the aquatic ecosystem, the N:C ratio of aquatic detritus decreases
226 (Fig. S1.4b), which relaxes the decomposer limitation for carbon (Fig. S1.4c) and could,
227 in specific conditions, induce a change in the limitation of decomposers (from carbon to
228 nitrogen, Fig. S1.5).

229 Besides, at the meta-ecosystem scale, spatial coupling between ecosystems mainly lead
230 to higher primary and secondary production than the sum of the production of isolated

231 systems (Fig. 4a). Positive effects result from a stoichiometric matching between the
232 local community needs and the spatial flows (*e.g.*, plants need nitrogen that is brought by
233 nitrogen-rich aquatic subsidies), suggesting a spatial complementarity of ecosystems.

234 **Ecosystem spatial competition under nitrogen limitation**

235 Conversely, under nitrogen limitation of decomposers, we observe opposite patterns
236 between ecosystems: spatial flows maximize production in one ecosystem when minimizing
237 it in the other. Basal production in the aquatic ecosystem peaks for high α_P (*i.e.*, nitrogen-
238 rich plants), when plants produce nitrogen-rich detritus, while it peaks for low α_P in
239 the terrestrial ecosystem, when plant demand for nitrogen is low (Fig. 3b). When α_B
240 increases, it exacerbates the stoichiometric mismatches between decomposers and both
241 their consumers and their detrital resources (*i.e.*, $\alpha_B - \frac{D_{N_A}}{D_{C_A}}$ increases; Fig. S1.4). The
242 stoichiometric mismatch with consumers reduces secondary production (Fig. S1.2b). The
243 stoichiometric mismatch with detritus reduces the nitrogen pool in the aquatic ecosystem
244 (because decomposers need more nitrogen to maintain their homeostasis) and limits the
245 decomposition of detritus (Fig. 3b). In these conditions (high α_B), the aquatic ecosystem
246 acts as a net sink receiving on average more carbon and nitrogen flows than it exports
247 (Fig. 3b). We find the same pattern in empirical data on terrestrial-freshwater exchanges
248 (Fig. 1c; Box 1). Additionally, we observe that meta-ecosystem primary and secondary
249 production generally decrease when both ecosystems are connected (Fig. 4b), which
250 denotes a spatial competition rather than complementarity effect between ecosystems:
251 the resources exported by the terrestrial ecosystem do not match the aquatic community
252 needs.

253 **Cross-ecosystem feedbacks**

254 Lastly, we measured how the subsidies exported by a donor ecosystem, feedback on
255 its production through the subsidies exported by the recipient (Figs. 5, S1.1). Under
256 carbon limitation of decomposers, feedbacks on basal and secondary production in both
257 ecosystems are always positive and scale non-linearly with the fraction of subsidies
258 regionally exported (Figs. 5a, S1.7a). This means that exports of resources from the
259 donor ecosystem, compared with when being lost, always increase production of the
260 recipient ecosystem, which further increases the fraction of subsidies exported back. The
261 strength of this positive feedback is highly and positively modulated by the stoichiometry
262 of decomposers, while plant stoichiometry only slightly changes the feedback (Fig. 5a).
263 Conversely, feedbacks reach negative values under nitrogen limitation of decomposers,
264 meaning that production is lower with bidirectional flows than with a unidirectional flow
265 leaving the meta-ecosystem (Figs 5b, S1.7b). Indeed, we found a U-shape relationship
266 crossing 0 between the fraction of subsidies being transferred regionally and the strength
267 of the feedback in the terrestrial ecosystem.

268 At first, the feedback decreases with increasing connectedness of ecosystems (for $\Delta \in$
269 $[0, 0.25]$ and $\Delta \in [0, 0.9]$ in aquatic and terrestrial ecosystems, respectively) due to an
270 amplification of the stoichiometric mismatch between decomposers and their detritus
271 following carbon-rich terrestrial subsidies inputs. However, at higher regional flows, the
272 terrestrial ecosystem exports more detritus regionally due to higher levels of nitrogen-rich
273 subsidies from the aquatic ecosystem. The mass effect of abundant terrestrial subsidies
274 overcomes the negative saturating effect of stoichiometric mismatch between detritus and
275 decomposers (Fig. S1.7c), thus allowing the terrestrial system to sustain higher aquatic
276 production compared with a scenario where subsidies from the aquatic ecosystem are lost.
277 We summarized the mechanisms driving spatial feedbacks at terrestrial-aquatic ecotones
278 in Fig. S1.8.

279 **Discussion**

280 By analysing a stoichiometrically explicit meta-ecosystem model, we reveal how local
281 ecosystem limitations and basal species stoichiometry drive meta-ecosystem functioning,
282 by leading either to stoichiometric complementarity or competition between spatial flows
283 and local demand. Our results highlight the potential for complementarity in resource use
284 among ecosystems at the landscape scale, but also show that resource flows can induce
285 negative spatial feedback between terrestrial and freshwater ecosystems, depending on
286 local nutrient limitations. We discuss the implications of these findings and provide
287 perspectives for spatial ecology.

288 **Spatial complementarity vs competition through subsidy flows**

289 Under carbon limitation of aquatic decomposers, spatial flows maximize production in
290 both ecosystems for basal species with complementary needs (low-N plants and high-N
291 decomposers). Terrestrial subsidies alleviate carbon limitation and sustain production in
292 the aquatic ecosystem, while nitrogen-rich subsidies from the aquatic ecosystem allow
293 plants of the terrestrial ecosystem to fix more carbon, together leading to higher meta-
294 ecosystem production. Both recent experimental works and reviews have stressed the
295 importance of spatial flow quality for local ecosystem functioning (Sitters *et al.*, 2015;
296 Gounand *et al.*, 2017). Using two-patch microcosms, Gounand *et al.* showed that detritus
297 exchange between autotrophic and heterotrophic communities can maximize densities in
298 both communities compared with isolated ones (Gounand *et al.*, 2017). In a recent meta-
299 ecosystem modelling work, (Harvey *et al.*, 2021) propose the cross-ecosystem efficiency
300 hypothesis to describe how spatial flows might foster higher functions at the landscape
301 scale by redistributing resources among ecosystems differing in the functions they optimize
302 (primary production in terrestrial ecosystems versus higher trophic efficiency in aquatic
303 ecosystems). We further propose that complementarity between ecosystem can arise from

304 the match between the stoichiometry of spatial flows and local community needs, leading
305 to higher production when ecosystems are connected. Indeed, the complementarity
306 of ecosystems creates a spatial positive feedback loop: on the one hand, autotrophic
307 ecosystems, export carbon-rich organic matter that fuels heterotrophic ecosystems and
308 fosters local production. In return, more nutrient-rich subsidies are exported back,
309 promoting primary production and closing the meta-ecosystem loop. Therefore, we
310 propose that cross-ecosystem flows bound ecosystems into a spatial auto-catalytic loop
311 (*sensu* Veldhuis et al., 2018), maximizing the production of the whole.

312 However, cross-ecosystem effects are highly modulated by local ecosystem limitations.
313 While we find that connectedness leads to complementarity when the aquatic ecosystem
314 is limited by carbon, a mismatch arises between aquatic community needs and resources
315 exported by the terrestrial ecosystem under nitrogen limitation. In this case, plants and
316 decomposers indirectly compete at the meta-ecosystem scale for nitrogen: high nitrogen
317 demand and low-quality terrestrial subsidies lower decomposition and production in the
318 aquatic ecosystem, leading to negative spatial feedback on terrestrial primary production.
319 Then, both consumers of decomposers and grazers shrink in densities due to reduced
320 basal production. In non-spatial experiments, decomposers often evolves toward co-
321 limitation as a mechanism to avoid competitive exclusion when competing for nutrients
322 with autotrophs (Daufresne & Loreau, 2001; Danger et al., 2008; Daufresne et al., 2008). In
323 our meta-ecosystem model, N-C co-limitations in decomposers always trigger positive
324 spatial feedbacks (see Appendix S5), suggesting that if such evolution was to occur in a
325 spatial context, it would maximize production at the meta-ecosystem scale.

326 **Understanding cross-ecosystem interactions through resource feedbacks**

327 Cross-ecosystem facilitation (*i.e.*, complementarity mechanism) and competition (*i.e.*,
328 mismatch mechanism) occur through spatial feedback, which sign is modulated by
329 the limitation of decomposers and the stoichiometry of basal species. In particular, we

330 emphasize that feedbacks on terrestrial production could reach negative values under
331 nitrogen limitation of the aquatic ecosystem while they are always positive and scale
332 non-linearly with the connectedness of ecosystems under carbon limitation. In addition,
333 feedbacks on the production of both ecosystems increase with the N:C ratio of decomposers.
334 While our model is spatial, recent models connecting brown and green food chains in non-
335 spatial contexts also emphasized the importance of microbial stoichiometry in determining
336 the interaction between decomposers and plants (Zou et al., 2016; Buchkowski et al., 2019).
337 Zou et al. (2016) showed how the impact of the green food web on the brown one was
338 highly determined by their resource limitation of decomposers: the effect was either
339 positive or negative when decomposers were C- or N-limited respectively. In a meta-
340 ecosystem perspective, we found that feedbacks between autotrophic and heterotrophic
341 food-webs reach negative values under nitrogen limitation: spatial flows of terrestrial
342 subsidies negatively impact aquatic ecosystem production through a direct stoichiometric
343 mismatch effect, and may indirectly decrease terrestrial ecosystem production compared
344 with a scenario where terrestrial resources exported are lost from the system. This
345 finding questions the term "subsidies" (*sensu* Polis et al., 1997; but see Subalusky &
346 Post, 2019), defined as a positive effect on production in the recipient ecosystem. This
347 stoichiometric mechanism contrasts with previous theoretical works, which suggested
348 that cross-ecosystem flows always increase landscape production (*e.g.*, Marleau et al.,
349 2014). In fact, stoichiometric mismatch is an important constraint upon consumer growth
350 (Hillebrand et al., 2009). In an experimental context, several authors stressed that lower
351 food quality can decrease consumer assimilation efficiency and population growth rates,
352 and further lead to population decrease in aquatic systems (*e.g.*, Anderson et al., 2005;
353 Brett et al., 2009; Hillebrand et al., 2009). For instance, Kelly et al. (2014) showed a negative
354 association between zooplankton production and inputs of terrestrial organic carbon in
355 lakes caused by shading and low quality of terrestrial inflows (Kelly et al., 2014).

356 By contrast, Pacific salmon that annually migrate to freshwater ecosystems can relax

357 nitrogen limitation of heterotrophic bacteria, leading to higher aquatic production (Rüegg
358 et al., 2011). Salmons can further be eaten by bears, increasing both their excretion
359 rates and the carcass deposition and contributing to a nitrogen flow positively affecting
360 riparian forests (Helfield & Naiman, 2006 ; Box 1). Besides, empirical studies support our
361 results that cross-ecosystem material flows can shape the functioning within recipient
362 ecosystems by modulating nutrient limitation (see Sitters et al., 2015 for a review). Thus,
363 empirical observations support our results that cross-ecosystem material flows can shape
364 the production of recipient ecosystems by relaxing or exacerbating nutrient limitation
365 (Montagano et al., 2018).

366 **Relaxing some model assumptions**

367 As for any modelling studies, we derived mechanisms and predictions at the cost of
368 simplifying hypotheses on processes. First, we assumed that each organism was held at a
369 constant stoichiometry. Recent experiments or meta-analyses suggest that decomposers
370 and their consumers can deviate from strict homeostasis (Cross et al., 2003; Persson
371 et al., 2010; Scott et al., 2012) Similarly, plant stoichiometry often changes depending
372 on the dominance of species and their traits (*e.g.* Yu et al., 2010), and nutrient inputs
373 into terrestrial ecosystems. We would expect this plasticity mechanism to reduce the
374 stoichiometric mismatch between terrestrial exports and aquatic needs as the nitrogen
375 content of plants would increase in response to nitrogen-rich aquatic subsidies and the
376 decomposers would have reduced N:C ratio following carbon-rich terrestrial inputs. In
377 the example of salmon, nitrogen actively transferred to terrestrial ecosystems by bears
378 increases the N:C ratio of plant foliage (Hilderbrand et al., 1999). Additionally, we ignored
379 compensatory feeding mechanisms that consumers can develop when facing low-quality
380 food (Cebrian & Lartigue, 2004; Hillebrand et al., 2009). Yet, these mechanisms can promote
381 extinction of producers through consumer overfeeding (Marx et al., 2021) and decrease
382 trophic efficiency of terrestrial and aquatic ecosystems (Frost et al., 2006; Hillebrand et al.,

383 2009). In addition, at the ecosystem level, a balance between top-down and bottom-up
384 control also emerges depending on whether subsidies are direct resources or not (as
385 reviewed by Allen & Wesner, 2016). For instance, using models (McCary et al., 2021) and
386 (Leroux & Loreau, 2008) showed that the net control induced by subsidy flow depends
387 on the trophic position of the species consuming the subsidy in the recipient ecosystem
388 as well as its preference for this subsidy. Accounting for both top-down and bottom-up
389 effects at both physiological (compensatory feeding and deviation from strict homeostasis)
390 and ecosystem level (net control) may help to better predict community response to spatial
391 subsidies.

392 Secondly, the impact of subsidy quality can be explored using a different framework
393 than ecological stoichiometry such as nutritional ecology (Raubenheimer et al., 2009;
394 Schindler & Smits, 2017; Osakpolor et al., 2023). At the terrestrial-aquatic ecotone, if
395 carbon-rich subsidies exported by the terrestrial ecosystem decrease decomposer growth-
396 efficiency due to carbon being recalcitrant, the strength of the positive feedback emerging
397 at the landscape level would decrease (Fig. S7.4).

398 **Perspectives at the landscape scale**

399 We stress that future models should go beyond spatially implicit models to account for
400 landscape structure and its heterogeneity. A promising future path would be to link
401 the spatial distribution of resources and foraging behaviour of consumers. Consumers
402 often avoid areas with low-quality resources (*e.g.*, Duparc et al., 2020; Rizzuto et al., 2021).
403 By doing so, they limit important stoichiometric mismatch with their food and avoid
404 nutrient limitations. Modelling studies integrating such processes would help for instance
405 understanding how animal foraging movements interact with predation avoidance to
406 determine the distribution of nutrients at the landscape scale (Anderson et al., 2010;
407 Schmitz et al., 2018; Ferraro et al., 2022). This may highlight further emergent patterns
408 such as nutrient co-limitation induced by spatial processes (Marleau et al., 2015) or patchy

409 distribution of resources (Johnson-Bice et al., 2022). Our study sets bases to understand
410 fundamental mechanisms by which spatial flow stoichiometry modulates cross-ecosystem
411 interactions and the functioning of communities at different scales. Integrating perspectives
412 of movement ecology and ecological stoichiometry should help building a more integrative
413 spatial ecology better accounting for the interplay between biogeochemical cycles and
414 community dynamics at the landscape extent.

415 **Figure 1: Empirical data on stoichiometry and magnitude differences between**
416 **resources exchanged at freshwater-terrestrial ecotone.**

417 (a): Distribution of the number of observations of cross-ecosystem flows at terrestrial-
418 freshwater ecotone according to their magnitude (in $gDW.m^{-2}.yr^1$, see Appendix S2 for
419 data extraction). The surface (in m^{-2}) corresponds to the area of the ecosystem receiving
420 the resource flow. (b): Nitrogen to carbon ratio (molar) of materials exported by terrestrial
421 (forests and grasslands in green) and freshwater (streams and lakes in blue) ecosystems.
422 The shape of the points indicates the type of materials being exported by ecosystems. Fresh.
423 = Freshwater, Terr. = Terrestrial, amphib. = amphibians and inverteb. = invertebrates.
424 Terrestrial or aquatic labels indicate the donor ecosystem. (c): Cross-ecosystem flows of
425 resources (carbon (left) and nitrogen (right)) crossing freshwater-terrestrial ecotone. The
426 units of flows are $gC.m^{-2}.yr^1$ and $gN.m^{-2}.yr^1$ for carbon and nitrogen respectively. Fresh.
427 = Freshwater, Terr. = Terrestrial. Boxplots present the median surrounded by the first and
428 third quartiles, and whiskers are not shown. Mean flows are indicated on the top of each
429 boxplot. Note that, panel (b) shows the stoichiometry of material **exported** by each type of
430 ecosystem, while panel (c) represents the quantity of C and N fluxes fuelling each type of
431 ecosystem. The number of observations, n , is indicated in each panel.

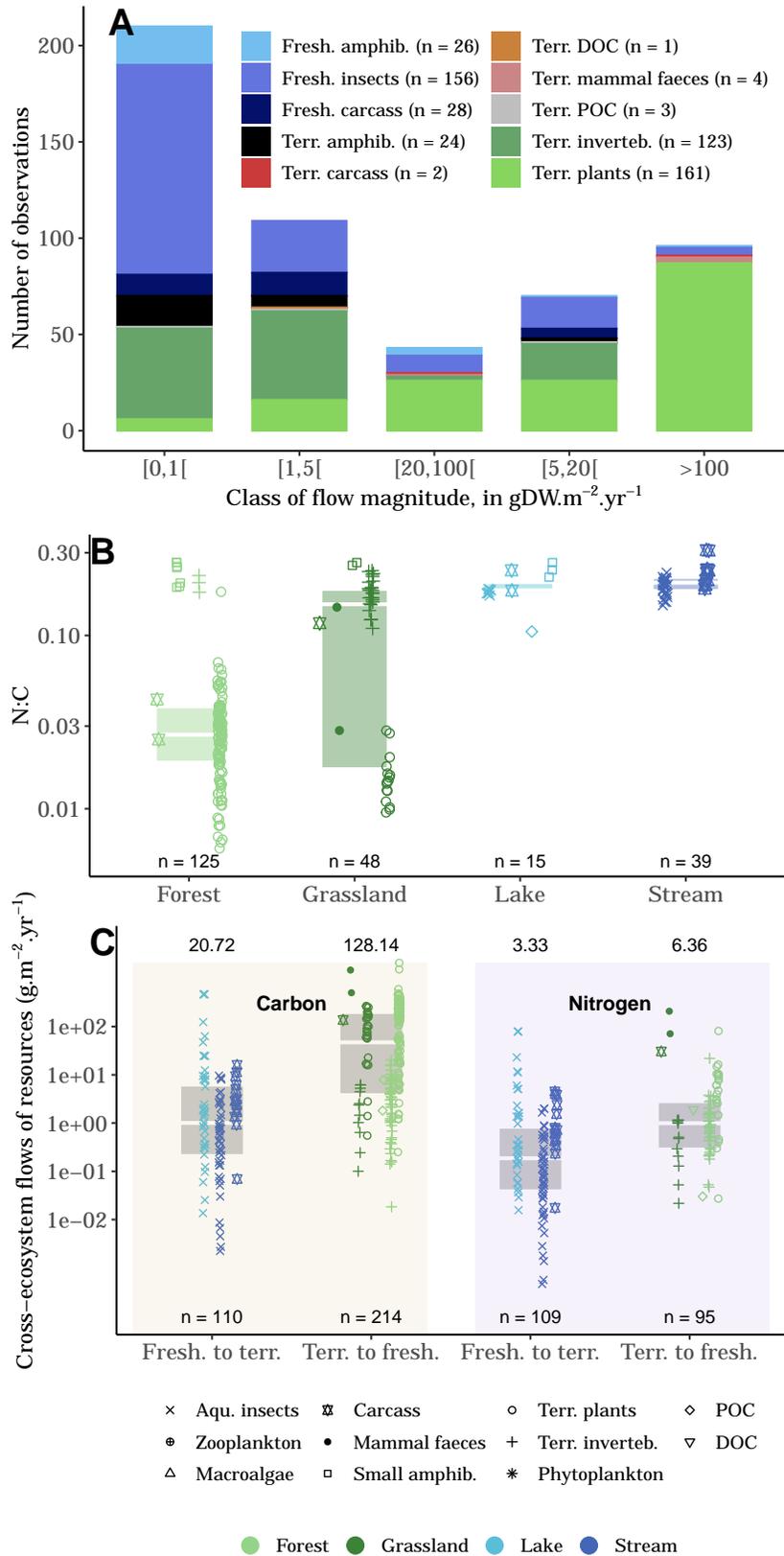


Figure 1

432 **Figure 2: Stoichiometric meta-ecosystem model - hierarchy of processes and scales.**
433 Basal species and consumers are held at a fixed stoichiometry (homeostasis). (a): Stoichiometric
434 imbalance (β_G) results from the differences between producer stoichiometry and consumer
435 needs and lead to nitrogen excretion. A similar mechanism occurs for the interaction
436 between decomposers and their consumers. (b): Decomposers from the freshwater
437 heterotrophic ecosystem have two possible limitations: nitrogen or carbon. Their limitation
438 sets which flow (decomposition of detritus (ϕ_D) or immobilization of nitrogen (ϕ_I))
439 constrains the other so that decomposers maintain a constant stoichiometry. (c): Two
440 ecosystems, one heterotrophic (freshwater) with decomposers as basal species and the
441 other autotrophic (terrestrial) with plants as primary producers, are linked at the landscape
442 level by subsidy flows (dead organic matter and nitrogen flows due to stoichiometric
443 imbalance). Symbols are used in the model equations: mineralization rates in ecosystems
444 (m_T, m_A), immobilization flow (ϕ_I), decomposition flow (ϕ_D), plant net photosynthesis
445 (f_P) and nitrogen uptake ($\alpha_P f_P$), attack rates of consumers of decomposers and grazers
446 (f_C, f_G respectively), decay rates of organisms (d_G, d_P, d_B, d_C), the stoichiometric imbalance
447 between producers and consumers (β_G, β_C), the fraction of subsidies recycled regionally (Δ ,
448 assumed constant across ecosystems and trophic levels, see Appendix S8 for heterogeneous
449 rates) and nitrogen to carbon ratio of organisms ($\alpha_G, \alpha_C, \alpha_P, \alpha_B$) Black thick arrows describe
450 trophic interactions while grey dashed arrows correspond to recycling paths.

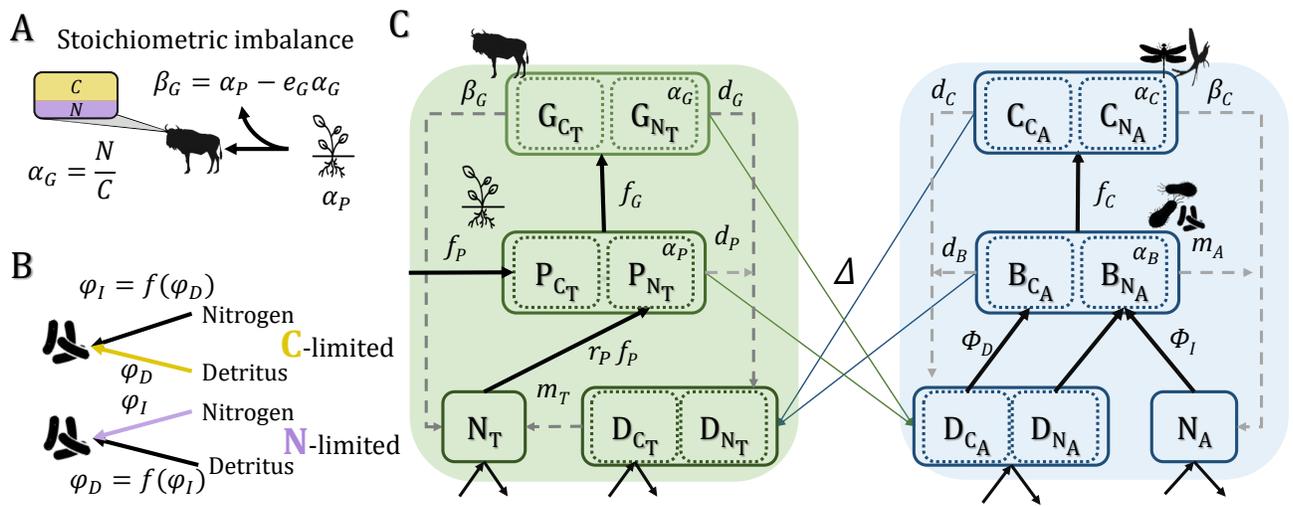


Figure 2

451 **Figure 3: Effects of basal species limitation and stoichiometry on ecosystem production**

452 We show the basal production in terrestrial (left) and freshwater (right) ecosystems
453 with spatial coupling ($\Delta = 1$, see Fig. S7.5 in appendix S5 for varying values) according
454 to the N:C ratio of basal species. In (a), decomposers are carbon limited, while they are
455 limited by nitrogen in (b). Production in both ecosystems is expressed in carbon units.
456 The results for secondary production are depicted in Fig. S1.6. We also represent the
457 meta-ecosystem compartments at equilibrium when ecosystems are connected $\Delta = 1$
458 (terrestrial ecosystem in green and freshwater one in blue) for the four corners of the heat
459 map ((i): $\alpha_B = 0.25, \alpha_P = 0.025$, (ii): $\alpha_B = 0.25, \alpha_P = 0.1$, (iii): $\alpha_B = 0.12, \alpha_P = 0.025$,
460 (iv): $\alpha_B = 0.12, \alpha_P = 0.1$). Black arrows correspond to trophic interaction while grey
461 arrows correspond to recycling paths. The two trophic levels are represented in pink
462 for primary consumers and green for basal species. Nitrogen and detritus pools are
463 respectively in blue and brown. For detritus, we only represent the carbon content. The
464 size of each compartment is set relative to the other same compartment to allow direct size
465 comparison across the stoichiometric conditions. We also represent the net flow of carbon
466 (orange arrow) and nitrogen (purple arrow) at the meta-ecosystem scale. Their width is
467 proportional to the flow.

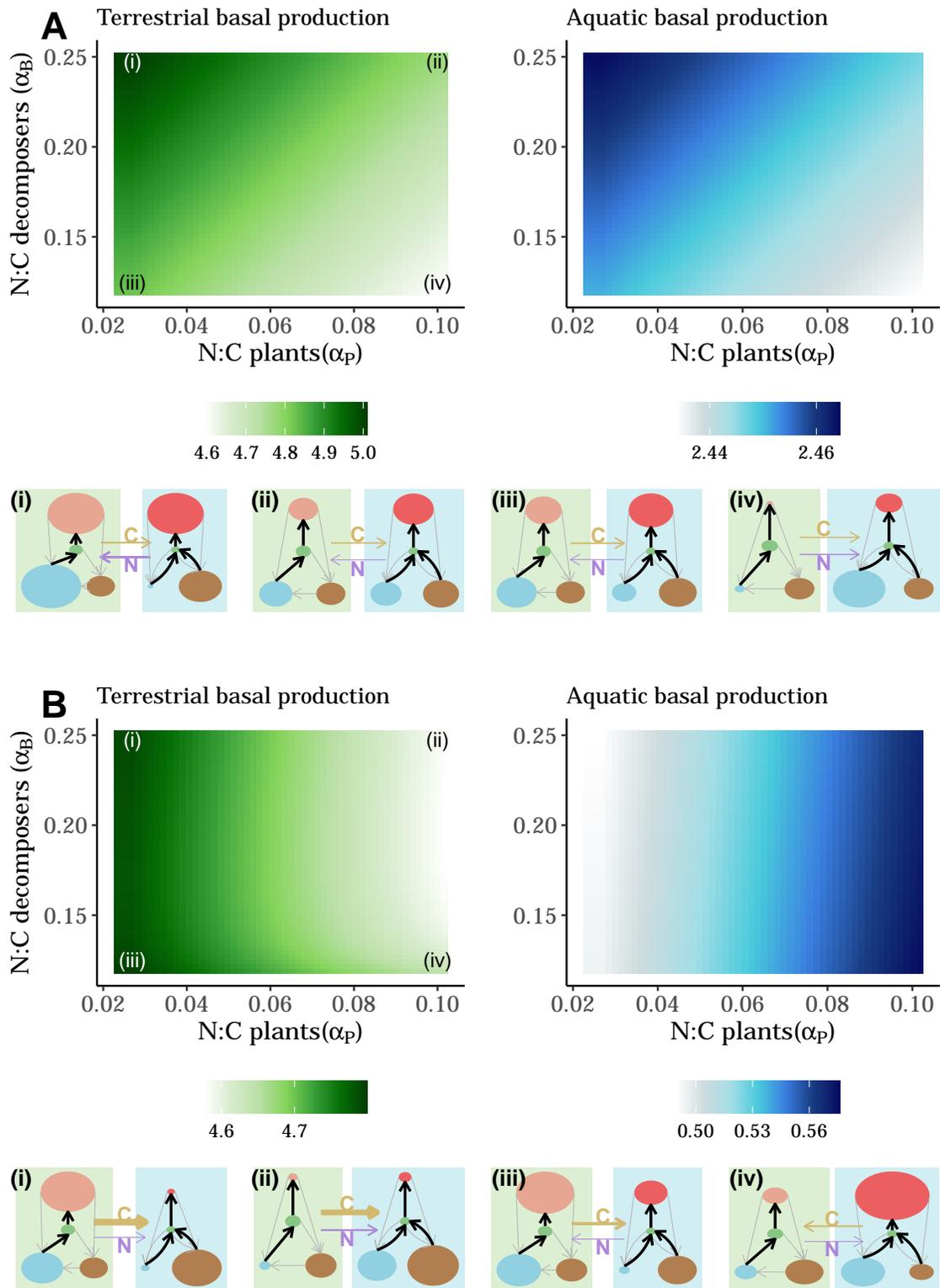


Figure 3

468 **Figure 4: Effect of spatial flows on meta-ecosystem production.** We compare the log
469 ratio-response of basal production (plants + decomposers) in left panels, and secondary
470 production (grazers + consumers of decomposers) in right panels, at the meta-ecosystem
471 scale when ecosystems are connected versus isolated. (a): Decomposers are carbon limited.
472 (b) Decomposers are nitrogen limited. The black line indicates the isocline delimiting
473 positive and negative effects of spatial subsidies. We provide in Fig. S1.8 a scheme that
474 summarizes the mechanism.

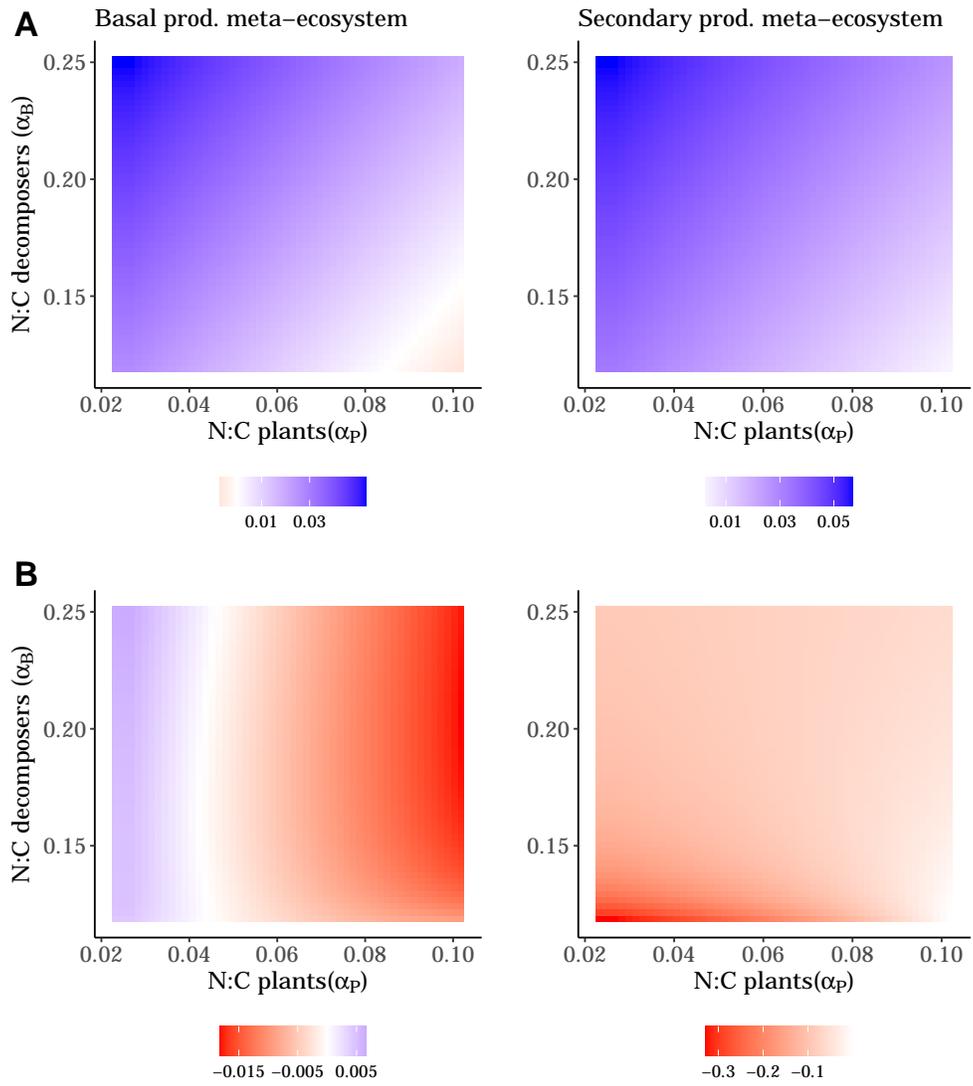


Figure 4

475 **Figure 5: Feedback between ecosystems depends both on decomposer limitation and**
 476 **basal species stoichiometry.**

477 In order to understand how resources exported by an ecosystem feedback on its
 478 own production through the effect on the recipient ecosystem, we compared for each
 479 trophic level and both ecosystems the production of the recipient ecosystem for scenarios
 480 of bidirectional and unidirectional flows of subsidies along a gradient of connectivity
 481 between ecosystems (Δ ; see methods and Fig. S1.1 for formulas). Shapes correspond to
 482 the four extreme scenarios of basal species stoichiometry defined in Fig. 3. of plants and
 483 decomposers (see Fig. 3). (a): C-limited decomposers and (b): N-limited decomposers.
 484 Some inserts are displayed for some curves to zoom in and better visualize the interplay
 485 between stoichiometric mismatch and mass-effect mechanisms (*i.e.*, the sign of the feedback).

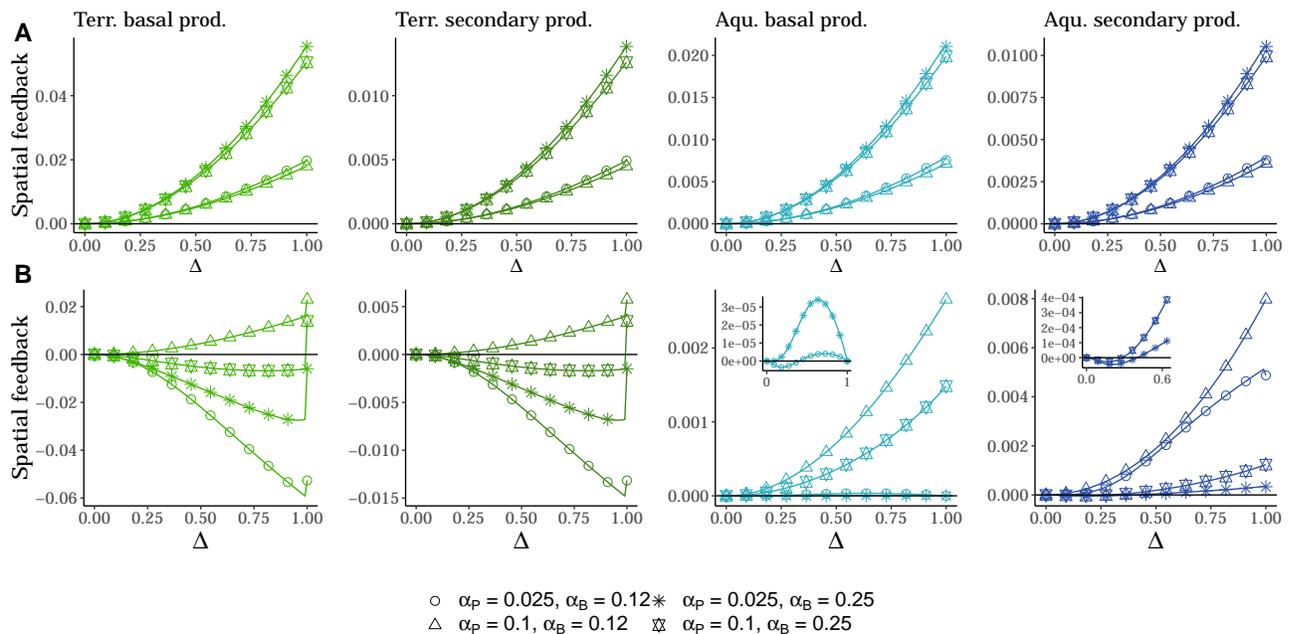


Figure 5

BOX 1: EMPIRICAL CROSS-ECOSYSTEM SUBSIDY FLOWS BETWEEN FRESHWATER AND TERRESTRIAL ECOSYSTEMS

We gathered data from the literature on cross-ecosystem flows between freshwater (streams, lakes) and terrestrial (forests, grasslands) ecosystems and provide here orders of magnitudes and stoichiometric characteristics of these fluxes (see Appendix S1 for details on data extraction). First, at the freshwater-terrestrial ecotone, subsidies are mostly represented by plant litter exported by terrestrial ecosystem and invertebrates exported by both ecosystems (Fig. 1a). Interestingly, exported materials by terrestrial *versus* freshwater ecosystems vary in quantity (Fig. 1c) and quality (carbon and nitrogen content; (Fig. 1b, Table S2.2)). While the exports of terrestrial ecosystems, mainly characterized by plant litter, are of poor quality (*i.e.*, carbon-rich), resources from freshwater ecosystems are richer in nitrogen. Aside from quality, these cross-ecosystem flows also vary in quantity. When comparing the carbon and nitrogen flows at terrestrial-freshwater ecotone, we observe a strong asymmetry of carbon flows crossing ecotones ($20 \text{ gC.m}^{-2}.\text{yr}^{-1}$ exported in average by freshwater ecosystems *versus* $128 \text{ gC.m}^{-2}.\text{yr}^{-1}$ from terrestrial ones; Fig. 1c & Table S2.3). However, this quantitative asymmetry of exported resources is partially compensated by their stoichiometric asymmetry (see Appendix S8). Consequently, while there is one order of magnitude of difference for carbon flows, we only observe a slight difference for nitrogen flows.

Thus, we observe two types of asymmetries in resource flows at freshwater-terrestrial ecotone. First, there is an asymmetry in flow quantity that may originate from differences in convexity of ecosystem profiles (*e.g.* forest *versus* stream ; see Polis et al., 1997; Shurin et al., 2006; Leroux & Loreau, 2008). Second, there is an asymmetry in quality, which originates from stoichiometric differences of organisms (Elser et al., 2000) and can impact local ecosystem functioning. In fact, high quantity but low quality of terrestrial subsidies can limit freshwater ecosystem production by various mechanisms ranging from shading of lakes, increase in stoichiometric mismatch or reduction in freshwater production (*e.g.*, (Kelly et al., 2014)). Similarly, high quality subsidies can considerably impact terrestrial plant communities in both richness and production (Helfield & Naiman, 2006; Rüegg et al., 2011; Hocking & Reynolds, 2011; Bultman et al., 2014). Together, it emphasizes the need to move toward a stoichiometric theory at the landscape extent (Leroux et al., 2017).

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489 **Author contribution:** All authors conceived the study. B.P performed research and wrote
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491 All authors read and approved the final manuscript.

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