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1           On embedding meta-ecosystems into a socio-ecological framework

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20 **Keywords**

21 Metaecosystem; spatial flows; mental model; ecosystem functioning.

22 Spatial flows of organisms and resources are increasingly recognized as key elements of  
23 ecosystem functioning [1,2]. In a previous article [3], we called for an update of the meta-  
24 ecosystem framework, a key conceptual and theoretical framework regarding spatial dynamics  
25 [4]. Specifically, we identified ways to better integrate different types of flows connecting  
26 ecosystems and their specific spatio-temporal scales in order to improve our understanding of  
27 ecosystem couplings. Building on this article, Roque et al. [5] wrote that, to be more predictive  
28 and operational, the meta-ecosystem framework should also explicitly include the socio-  
29 ecological mechanisms underlying the impacts of human societies on these flows. Their rationale  
30 is that socio-cultural mechanisms govern the way human society interacts with ecosystems and  
31 influence spatial flows connecting ecosystems. Roque et al. provide some case studies of such  
32 influence, for instance with the perception of ivory trade [6].

33 We see some potential value of such a socio-ecological perspective, for example to address  
34 specific questions about dynamical feedbacks between humans and the environment (e.g., on the  
35 environmental sustainability of human practices [7]). However, it is noteworthy that human-  
36 induced effects on meta-ecosystem dynamics are already integrated within the variation in spatial  
37 flow values considered in meta-ecosystem models (e.g., variance and mean quantity/quality of  
38 flows) [4]. Thus, studying the effects of processes acting at different scales on ecosystem  
39 functioning can already be achieved with the existing meta-ecosystem framework while avoiding  
40 additional layers of complexity, which might reduce interpretability and understanding.

41 As we illustrate with a strongly human-shaped landscape in our previous article [3], human  
42 activities influence the spatial flows linking ecosystems in various ways. This includes increasing  
43 some flows (e.g., leaching of agricultural fertilizers to aquatic systems), regulating the species

44 driving other spatial flows, or even modifying the landscape configuration itself. We here explain  
45 one well-known example of the role of human activities in meta-ecosystems including all these  
46 aspects (Fig. 1A): Geese populations in the southern United States massively increased following  
47 agriculture intensification in the 1960's, because the geese shifted their diets from feeding in  
48 wetlands to feeding on the augmented resources in agro-ecosystems [8]. This resource  
49 augmentation was of course triggered by socio-economic changes in farming practices, and also  
50 had effects on local meta-ecosystems (i.e., runoff into waterways). In the context of global meta-  
51 ecosystems, the subsequent increase in flows of migratory birds dramatically affected arctic  
52 tundra ecosystems [8], and this effect was partly modulated by hunting along the geese's  
53 migratory routes, in itself a socio-cultural phenomenon.

54 Thus, along with Roque et al. [5] and others working on socio-ecological linkages [9,10], we  
55 agree that culture and mental models are central to the people-nature relationship, and a crucial  
56 link in the decision pathway leading to environmental regulation of anthropic impacts on nature  
57 (e.g., land use management, hunting rules; see Fig. 1B, arrow 1). However, accounting for these  
58 anthropic impacts can already be done by directly implementing the forcing derived from socio-  
59 cultural processes on flows (e.g., in Fig. 1A adding fields and reducing migratory flow), without  
60 explicitly modelling the socio-cultural processes in the meta-ecosystem framework.

61 Thus, when would the additional complexity brought by integrating mental models into the meta-  
62 ecosystems framework be more useful than the pre-existing implicit consideration of human  
63 influences in meta-ecosystems? We find that this may depend on the questions being addressed,  
64 for example, when the focus is no longer on the meta-ecosystem dynamics themselves, but rather  
65 on the long-term consequences of feedbacks between meta-ecosystem and socio-cultural

66 dynamics. This implies that the ecosystem services provided by meta-ecosystem dynamics ([11],  
67 arrow 2 in Fig. 1B) strongly feed back on mental models (arrow 3); in the geese example, this  
68 would happen if tundra loss is sufficiently important for public opinion to change agricultural or  
69 hunting practices towards “tundra-sustainable” ones. To analyse such scenarios, the meta-  
70 ecosystem framework could be embedded into a socio-ecological perspective in stylized models  
71 explicitly focusing on these feedback links (bold arrows in Fig.1B), similarly to approaches  
72 proposed in the study of biodiversity – human society interactions [7]. In such models, however,  
73 explicit consideration of meta-ecosystem dynamics is not needed, merely the effects that these  
74 meta-ecosystem dynamics produce on ecosystem properties of values for humans.

75 In conclusion, to our opinion, zooming in the meta-ecosystem box (Fig. 1B), or zooming out on  
76 the socio-ecological feedback loop, relates to different questions, which might be better  
77 addressed with different modelling frameworks (meta-ecosystem *versus* socio-ecological). In that  
78 context, we suggest that the interactions between socio-cultural processes and meta-ecosystem  
79 dynamics should be addressed in an iterative scientific process through planned collaborations, as  
80 has been proposed for coordinating exchanges between theory and empirical work [12]. Thus, the  
81 results of one perspective can inform the other, better hypotheses can be tested, and our  
82 understanding can be bolstered by strong inference, without all processes necessarily being  
83 integrated into one framework.

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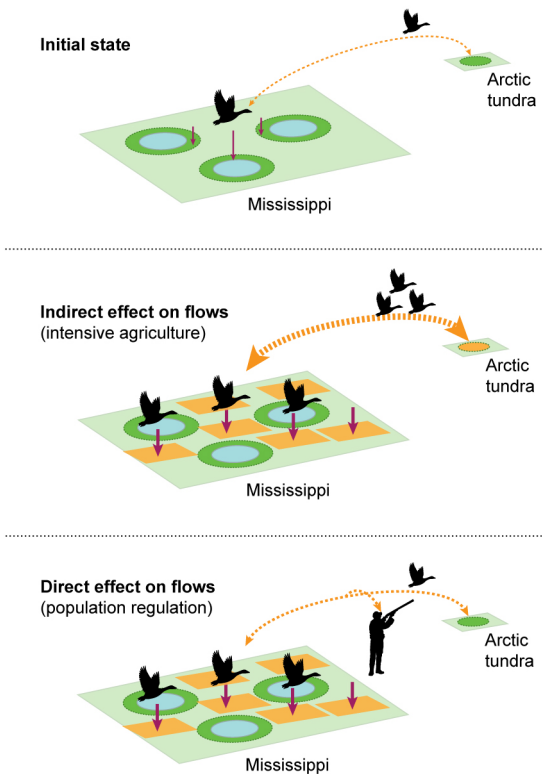
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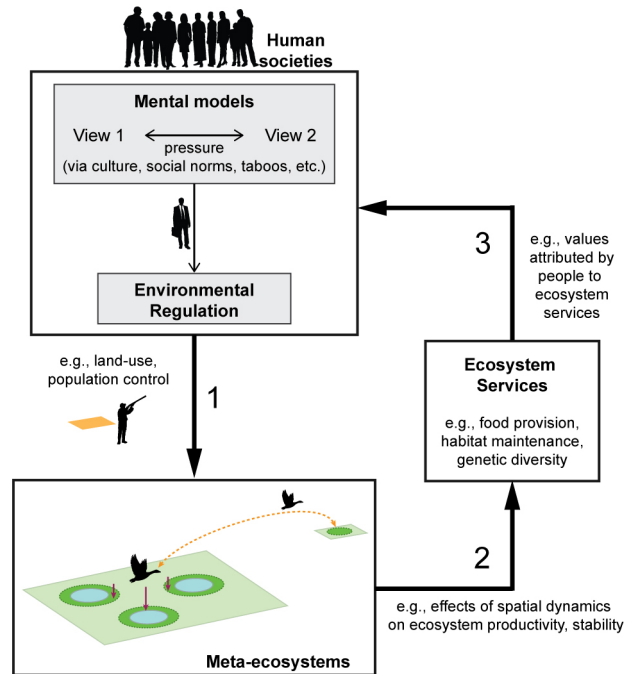
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(A) Human impact on a migration-based meta-ecosystem



(B) Embedding meta-ecosystems into a socio-ecological framework



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116 **Figure 1. Meta-ecosystems in the Anthropocene.** (A) The left panels show an example of

117 human impacts on meta-ecosystem dynamics with the emblematic case-study on migratory geese

118 linking resource flows between the Mississippi basin with the arctic tundra (top panel):

119 agriculture intensification in the Mississippi in the 1960's (fields in yellow) increased geese food

120 supply (foraging arrows in magenta), which resulted in higher abundance of migratory geese and

121 associated nutrient flow to the tundra (dotted yellow arrow), triggering catastrophic shifts of

122 arctic communities ([8]; middle panel); hunting on the migratory road illustrates a direct human

123 impact on spatial flow (flow reduction; bottom panel). (B) Meta-ecosystems can be embedded in

124 a socio-ecological framework. Within human societies, culture and social norms drive the

125 dominance of some views in the public opinion regarding the interaction between humans and



126 nature (e.g., profit versus non-profit views on ivory trade [6]). These mental models influence  
127 environmental regulation, which modulates the impact of human activities on spatial flows and  
128 meta-ecosystem dynamics (e.g., through rules on land-use or hunting; arrow 1). Meta-ecosystem  
129 dynamics affect ecosystem properties, such as productivity, or biodiversity, which provide  
130 services to people (arrow 2). Depending on the value that people attribute to these ecosystem  
131 services, change in meta-ecosystem dynamics might feedback on mental models (arrow 3), for  
132 instance (example panel A) the public opinion might shape hunting practices and regulations.