

attention to conservation challenges has had a limited appearance (but see [5,6]). Such limited uptake may reflect the formal nature of the scientific process, but Chapron *et al.* [1] demonstrate that there may be a place for satire in scientific journals after all. Conservation lends itself to satire because it is a value-laden topic full of social, political, and ethical obstacles [6]. We thus applaud Chapron *et al.* [1] for their use of satire and encourage others to do so too where appropriate, even if the views being expressed are sadly closer to reality than exaggeration. After all, the joke is on us. Nature has been around for a few billion years and will be around for a good while longer. Nature needs us a lot less than we need her. With that in mind, and understanding Earth's new and potentially destructive climate, we have, of course, also booked our seats to the 'second planet' along with Chapron and his mates [1], leaving those unwilling to put up with the admittedly rather hefty price tag and terrible interstellar food to stew, roast, bake, or boil on Earth a little longer.

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## Letter

### On Embedding Meta-ecosystems into a Socioecological Framework: A Reply to Renaud *et al.*

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

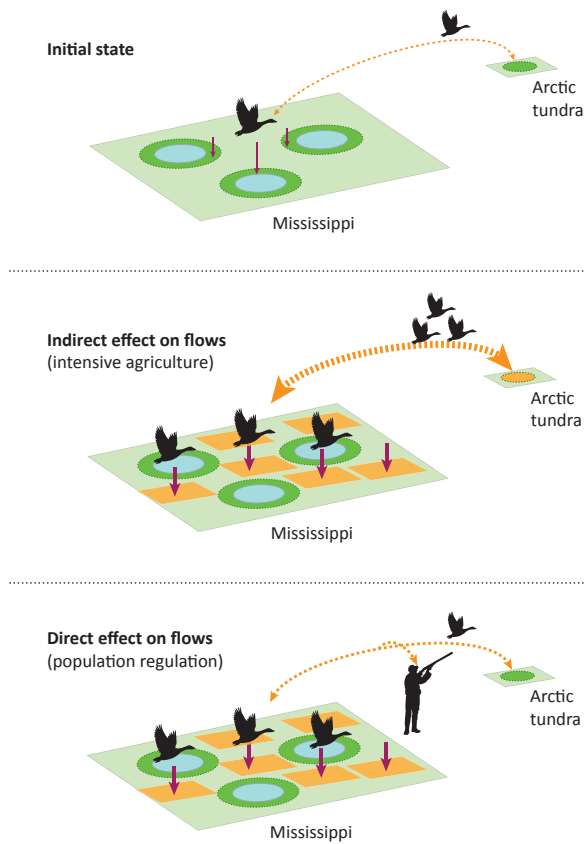
We see some potential value of such a socioecological perspective; for example, to address specific questions about dynamical feedbacks between humans and the environment (e.g., on the environmental sustainability of human practices [7]). However, it is noteworthy that human-induced effects on meta-ecosystem dynamics are already integrated within the variation in spatial flow values

considered in meta-ecosystem models (e.g., variance and mean quantity/quality of flows) [4]. Thus, studying the effects of processes acting at different scales on ecosystem functioning can already be achieved with the existing meta-ecosystem framework while avoiding additional layers of complexity that might reduce interpretability and understanding.

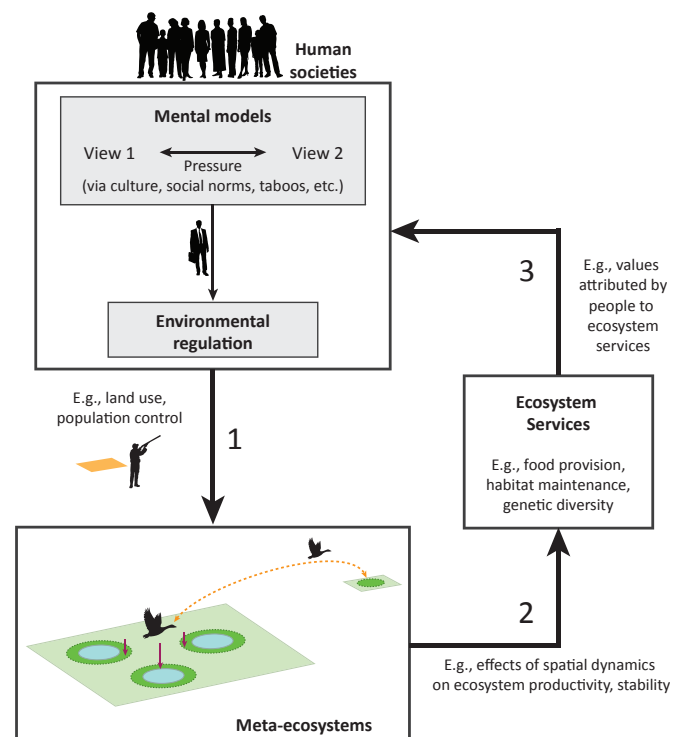
As we illustrate with a strongly human-shaped landscape in our previous article [3], human activities influence the spatial flows linking ecosystems in various ways. This includes increasing some flows (e.g., leaching of agricultural fertilizers to aquatic systems), regulating the species driving other spatial flows, or even modifying the landscape configuration itself. We here explain one well-known example of the role of human activities in meta-ecosystems including all of these aspects (Figure 1A). Goose populations in the southern USA increased massively following agricultural intensification in the 1960s because the geese shifted their diets from feeding in wetlands to feeding on the augmented resources in agroecosystems [8]. This resource augmentation was of course triggered by socioeconomic changes in farming practices and had effects on local meta-ecosystems (i.e., runoff into waterways). In the context of global meta-ecosystems, the subsequent increase in flows of migratory birds dramatically affected arctic tundra ecosystems [8], and this effect was partly modulated by hunting along the geese's migratory routes, in itself a sociocultural phenomenon.

Thus, along with Renaud *et al.* [5] and others working on socioecological linkages [9,10], we agree that culture and mental models are central to the people–nature relationship and a crucial link in the decision pathway leading to environmental regulation of anthropic impacts on nature (e.g., land use management, hunting rules; Figure 1B, arrow 1). However, these

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



## (B) Embedding meta-ecosystems into a socioecological framework



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**Figure 1. Meta-ecosystems in the Anthropocene.** (A) The left panels show an example of human impacts on meta-ecosystem dynamics with the emblematic case study on migratory geese linking resource flows between the Mississippi basin and the arctic tundra (top panel). Agricultural intensification in Mississippi in the 1960s (fields in yellow) increased goose food supply (foraging arrows in magenta), which resulted in higher abundance of migratory geese and associated nutrient flow to the tundra (broken yellow arrow), triggering catastrophic shifts of arctic communities [8] (middle panel); hunting on the migratory road illustrates a direct human impact on spatial flow (flow reduction; bottom panel). (B) Meta-ecosystems can be embedded in a socioecological framework. In human societies, culture and social norms drive the dominance of some views in public opinion regarding the interaction between humans and nature (e.g., profit versus non-profit views on the ivory trade [6]). These mental models influence environmental regulation, which modulates the impact of human activities on spatial flows and meta-ecosystem dynamics (e.g., through rules on land use or hunting; arrow 1). Meta-ecosystem dynamics affect ecosystem properties, such as productivity or biodiversity, that provide services to people (arrow 2). Depending on the value that people attribute to these ecosystem services, changes in meta-ecosystem dynamics might feed back on mental models (arrow 3); for instance (A), public opinion might shape hunting practices and regulations.

anthropic impacts can already be accounted for by directly implementing the forcing derived from sociocultural processes on flows (e.g., in Figure 1A adding fields and reducing migratory flow) without explicitly modelling the sociocultural processes in the meta-ecosystem framework.

Thus, when would the additional complexity brought by integrating mental models into the meta-ecosystem framework be

more useful than the pre-existing implicit consideration of human influences in meta-ecosystems? We find that this may depend on the questions being addressed; for example, when the focus is no longer on the meta-ecosystem dynamics themselves but rather on the long-term consequences of feedback between meta-ecosystem and sociocultural dynamics. This implies that the ecosystem services provided by meta-ecosystem dynamics

[11] (arrow 2 in Figure 1B) strongly feed back on mental models (arrow 3); in the goose example, this would happen if tundra loss is sufficiently important for public opinion to change agricultural or hunting practices towards ‘tundra-sustainable’ ones. To analyze such scenarios, the meta-ecosystem framework could be embedded into a socioecological perspective in stylized models explicitly focusing on these feedback links (bold arrows in

Figure 1B), similarly to approaches proposed in the study of biodiversity–human society interactions [7]. In such models, however, explicit consideration of meta-ecosystem dynamics is not needed, merely the effects that these meta-ecosystem dynamics produce on ecosystem properties of values for humans.

In conclusion, in our opinion, zooming in on the meta-ecosystem box (Figure 1B) and zooming out on the socioecological feedback loop relate to different questions that might be better addressed with different modeling frameworks (meta-ecosystem versus socioecological). In that context, we suggest that the interactions between sociocultural processes and meta-ecosystem dynamics should be addressed in an iterative scientific process through planned collaborations, as has been proposed for coordinating exchanges between theory and empirical work [12]. Thus, the results of one perspective can inform the other, better hypotheses can be tested, and our understanding can be bolstered by strong inference, without all processes necessarily being integrated into one framework.

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## Spotlight Lessons in Lateralisation from the Insects

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**The behavioural lateralisation of a species is thought to be influenced by social organisation. However, recent studies of insect species with different social structures suggest that traits showing both population-level and individual-level lateralisation can be found in single species. This has broad implications for our understanding of how lateralisation and handedness evolves.**

Behavioural lateralisation is now recognised to be widespread in the vertebrates [1] and arthropods [2] alike, a marked change from the prevailing view ~50 years ago when humans were thought to be unique in possessing

handedness [1]. However, the direction and the type of lateralisation is neither consistent across lineages nor is it likely to be derived from a common ancestor. This suggests that lateralisation is the result of widespread recurrence, evolving independently as a consequence of lineages being exposed to similar selective regimes. Within the vertebrates, species from numerous lineages have been shown to possess behavioural lateralisation such as turning tendencies or handedness, though this is not consistent across the phylogeny (reviewed in [1]). Within the arthropods, lineages as disparate as spitting spiders, bees, and fruit flies show preferences for limb use, sense organs, or for turning tendencies (reviewed in [2]). Thus, it seems probable that these different forms of lateralisation in such distinct lineages have evolved separately, although it is important to recognise that evidence of lateralisation is sparse in comparison to the number of species within the arthropods. Dense mapping of lateralisation across species level phylogenies will, no doubt, provide new insights into the causes of behavioural lateralisation within particular lineages.

### What Causes the Recurrent Evolution of Lateralisation?

Numerous hypotheses have been proposed to explain that the evolution of lateralisation may relate to specific animal lineages, such as handedness in humans (reviewed in [1]). A more general hypothesis however, suggests that individual-level lateralisation, in which the strength and direction of lateralisation differs among individuals within a population, evolves initially. This might be advantageous because it can permit the specialisation of limb use or ensure that deadlock is not reached during decision making. In such cases, the advantage is conferred irrespective of the direction of lateralisation. Subsequently, population-level lateralisation, in which