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# Perspectives in modelling ecological interaction networks for sustainable ecosystem management

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## Abstract

1. The concept of ecological interaction networks has been widely used in fundamental ecology in the last two decades, and has progressively infused in a diverse array of applied studies. Classical studies represented species interactions as static interaction webs to identify generalities in the structure of ecological networks and understand the propagation of indirect effects of species on each other and the environment.
2. More recent research demonstrates that ecological networks are emerging features of community and interaction processes. Understanding the determinants of interaction variability in space and time and its consequences for biodiversity dynamics and ecosystem functioning constitute current frontiers in ecological network science. Although these frontiers meet a variety of applied ecological questions, many network models have been developed without clear applied perspectives.
3. We detail how we could build on them to advance three main topics. First, the spatial dimension of ecological networks has direct implications for the design of sustainable landscapes and fisheries, for agroecology and for lake management. Second, the temporal dimension of ecological networks provides important insights for projecting biodiversity changes and adapting human actions. Third, the interactions between the abiotic and biotic components of ecosystems constitute key drivers of biogeochemical cycles, thereby providing important levers for sustainable management.
4. *Synthesis and applications:* Collaborative work between empirical and theoretical network ecologists could accelerate the delivery of realistic models to inform applied practices across disciplines.

## Introduction

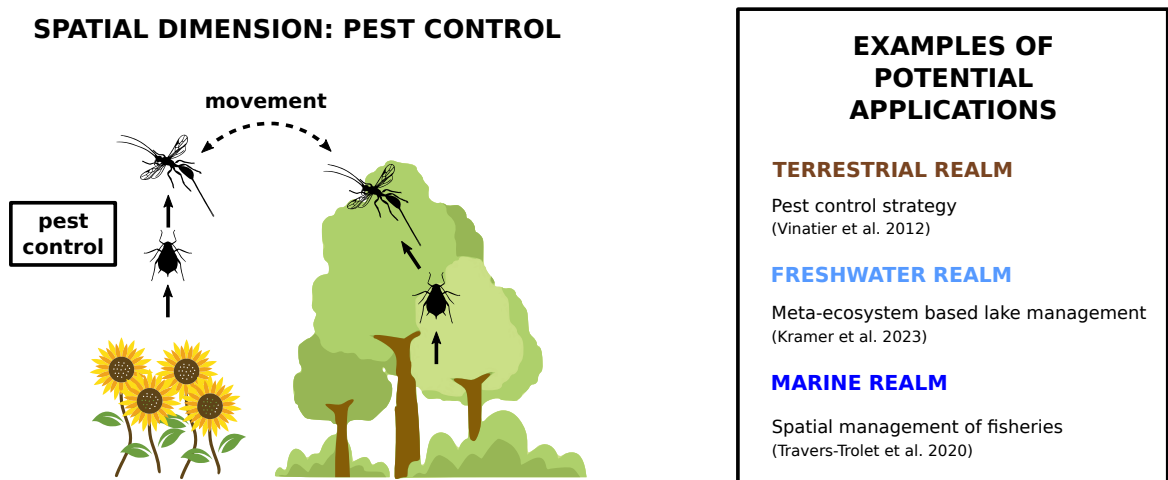
Applied questions in ecology have usually been addressed by simple population models, which consider one or two species at a time. Ecological systems are more complex and their functioning emerges from the multitude of direct and indirect interactions linking dozens of species. Memmott (2009) highlighted the value of network approaches to describe positive or negative interactions among species. This approach for instance enables us to identify keystone species and to reveal the underlying mechanics of apparent competition, apparent mutualism or trophic cascades (Lopezaraiza-Mikel et al. 2007, Carvalheiro et al. 2008). These early applications considered “static” ecological networks without any spatio-temporal variation in species interactions.

Since then, evidence has accumulated about the dynamics of ecological interactions, both in time (Sauve & Barraquand 2020, Glaum et al. 2021) and space (Carstensen et al. 2016, Arantes et al. 2019). These findings invite approaching interaction networks as emerging features of dynamic community processes (Tylianakis & Morris 2017). This modifies the way ecological networks might be mobilised for applications from purely network-based approaches (Memmott 2009), toward process-based modelling. We will here focus on three recent and ongoing developments of network studies, namely 1) the study of the spatial dimension of ecological interactions, 2) the study of the temporal dimension of ecological interactions, and 3) the coupling of food webs with biogeochemical cycles. For each of these developments, we will highlight the linked perspectives for ecological applications.

## Considering the spatial dimension of ecological interactions

Ecological interactions are spatially variable and influenced by multiple drivers. Dispersal limitation and differences in species’ environmental niches constrain the local assemblage of co-occurring species, leading to species spatial turnover and consequently to interaction turnover. Additionally, foraging choices within the local pool of co-occurring species can also be variable across environmental gradients (Tylianakis & Morris 2017) or due to historical contingency (Waser 1986), leading to interaction turnover per se (sensu Poisot et al. 2012). The other way around, ecological interactions influence species’ spatial distributions by affecting their local fitness and subsequently community assembly (Jabot & Bascompte 2012, Wisz et al. 2013). This feedback between ecological interactions and spatial dynamics has been the focus of a number of theoretical studies that provide insightful predictions for the conservation of biodiversity and biological control in the context of agroecology (Tixier et al, 2013, Vinatier et al. 2012, Fig. 1).

For instance, Fortuna et al. (2013) demonstrated that habitat loss could lead to the sudden disassembly of animal-plant mutualistic networks after a critical threshold of lost habitat. This new body of knowledge may advance conservation actions by helping develop early-warning indicators of catastrophic shifts taking into account ecological interactions (Dakos & Bascompte 2014). More generally, the dependence of network structure to area and connectivity is increasingly documented and understood (Galana et al. 2018) and reveals that ecological complexity is likely to increase in larger and well-connected habitat patches with potential beneficial effects for ecosystem functionality (Li et al. 2022).



**Fig. 1:** Spatial dimension of ecological interactions in an agroecological context. Predators control pest populations thriving on crops (e.g. parasitoid wasps and aphids) and find refuge in the natural vegetation surrounding the field.

Spatially-explicit ecological network models have proposed several mechanisms linked to spatial heterogeneity to explain these patterns. For instance, connectivity in environmentally heterogeneous landscapes may benefit biodiversity thanks to two complementary mechanisms: rescue effects in less productive habitats and drainage effects in productive ones (Ryser et al. 2021). Such spatial food web models have potential implications for landscape planning with the development of software tools to design sustainable agricultural systems maximising ecological functions such as biological control or pollination (e.g., Malard et al. 2020). Focusing on the spatial flow of nutrients rather than organisms, Kramer et al. (2023) demonstrated interesting feedback between local food web processes and landscape-scale nutrient flows between connected lakes.

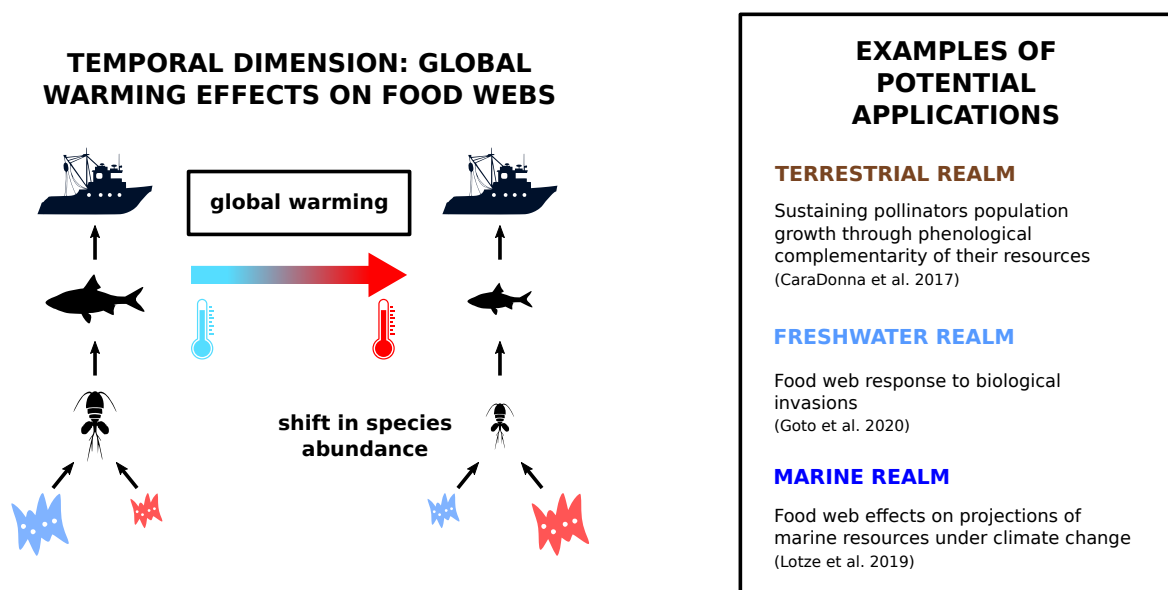
Spatial heterogeneity can be extended to the spatial coupling of ecosystems through widespread cross-ecosystem subsidies between habitats, e.g. litterfall from forest to stream ecosystems or the emergence of insects from aquatic to terrestrial ecosystems (Gounand et al. 2018). Investigating how the effect of these subsidies propagate in food webs and may alter associated ecosystem services such as pest control, pollination or nutrient regulation constitute important applied perspectives (McCann et al., 2020, Osakpolor et al. 2021).

## Considering the temporal dimension of ecological interactions

Interaction networks experience temporal changes, which can be random due to stochastic events, or directed due to

environmental or anthropogenic forcing. We focus on the latter category, a good example being the study of seasonal interaction rewiring in plant-pollinator networks (CaraDonna et al. 2017). Generalisation of such studies, however, requires understanding of the drivers of temporal changes in interaction networks, notably related to global changes. This will require developing mechanistic models to understand how temporal environmental variation and/or perturbations 1) affect each species and in turn propagate through the network, and 2) affect interspecific interactions (Tylianakis et al. 2008, Schleuning et al. 2020). Such advances are important for developing reliable projections of biodiversity changes (Wisz et al. 2013) and adapting human actions accordingly.

Theoretical works have investigated how perturbations propagate in ecological networks (e.g. Quévieux and Loreau 2022). They have shown that the effect of perturbations depends on the biomass distribution among species and the trophic position of interacting species. One major dimension of global change is temperature alteration, whose effect on ecological networks is particularly challenging since it simultaneously affects various components of food web dynamics. This includes the demographic rates of individuals, their behaviour, phenology, but also their interaction rates and temporal mismatches (Bideault et al. 2021). These effects eventually translate into altered network structure and dynamical parameters, which can propagate to changes in ecosystem functioning (Raatz et al. 2019). For instance, Wollrab et al. (2021) demonstrated that gradual changes in seasonal forcing can lead to abrupt transitions between food web dynamical regimes. Ecological interaction networks thus constitute important improvement pathways for projecting changes in



**Fig. 2:** Temporal dimension of ecological interactions in the context of fisheries. Global warming shifts the relative abundance of phytoplankton species, which alters resource availability for zooplankton and fish, and ultimately alters yields. Models enable us to project the future abundance of harvested species and improve the sustainable management of fisheries.

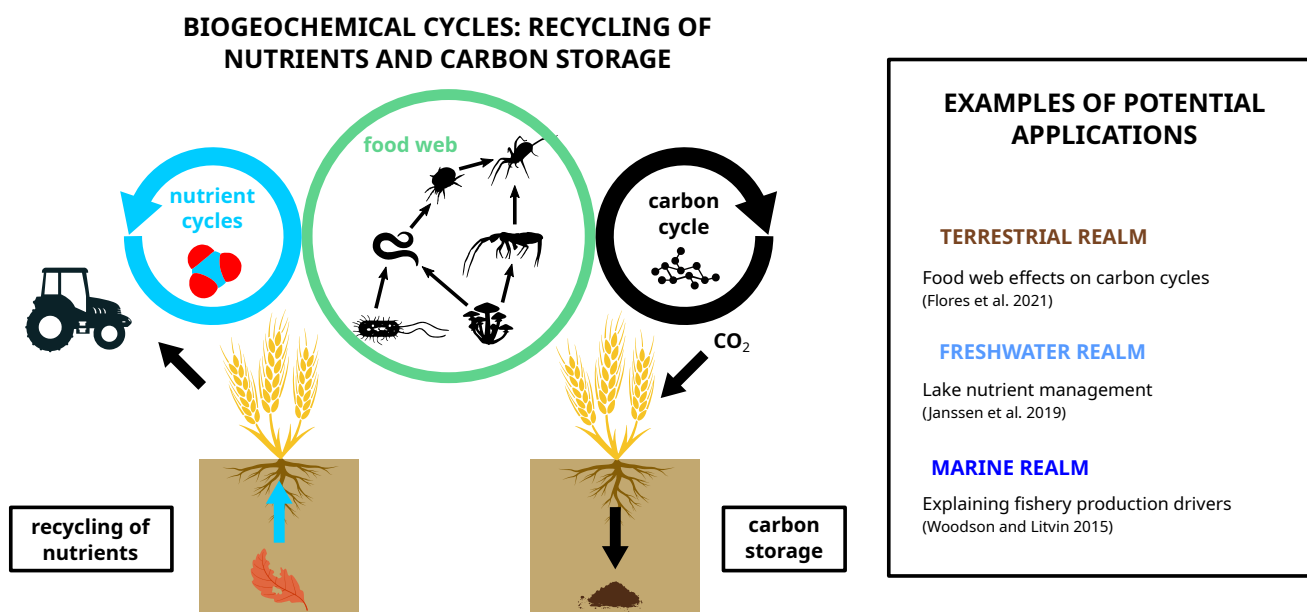
biodiversity and ecosystem functioning in response to global change, with the difficulty to keep model complexity tractable (Mouquet et al. 2015). In this regard, trait-based models of species interactions constitute interesting trade-offs by offering the possibility to summarise complicated interspecific interactions with a limited set of parameters (Schleuning et al. 2020, Bauer et al. 2021) and indications for possible adaptations (Klauschies et al. 2016, Ehrlich & Gaedke 2020).

Alterations of food web dynamics due to global change may further inform decisions by modifying the exploitation potential of these multi-trophic communities (Fig.2). Using a fish food web model coupled to a biogeochemical model, Travers-Trolet et al. (2020) evidenced that climate change projections were likely to induce a modification of the maximum sustainable yield of various commercial fish species. This work therefore enlightens ways to adapt human actions in response to climate change, and to document how these altered human actions feedback to ecosystem dynamics. Another example in a terrestrial system is the work of Barychka et al. (2021) that used a general ecosystem model to assess bushmeat harvesting sustainability in the Congo Basin together with its broader ecosystem impacts. The use of such ecosystem models for decision support, however, faces several obstacles, including credibility issues, associated uncertainties, and the difficulty to communicate model results to decision-makers (Lehuta et al. 2016). The rapid ongoing advances to monitor entire ecosystems with DNA-based and remote sensing technologies (e.g. satellite imagery) should enable us to build credibility and decrease uncertainties of ecological forecasts, thereby favouring their wider use for decision support (Dietze et al. 2018).

## Food webs and biogeochemical cycles

Animals represent a very tiny proportion of the Earth's biomass (less than 0.5% according to Bar-On et al. 2018), so most carbon cycle models neglect their contribution (Schmitz et al. 2018). However, despite this low biomass, they can importantly alter ecosystem functioning through their controlling role in energetic and nutrient fluxes (Barnes et al. 2018, Bianchi et al. 2021) and in the spatial coupling of ecosystems (Gounand et al. 2018, Fig.3). For instance, the consumer-driven recycling theory demonstrates how animal consumers may alter the nutrient limitation of primary producers (Daufresne 2021), while experimental studies estimated that animal consumers account for dozens of percent of litter and deadwood decomposition globally (Seibold et al. 2021; García-Palacios et al. 2013). Understanding how ecological interactions in food webs impact biogeochemical cycles is therefore of potentially great importance for a number of sustainability issues. For instance, de Ruiter et al., (1994) estimated the contribution of soil organisms to nitrogen mineralisation by using a food web model taking field biomasses as inputs.

To advance on these applications, a new generation of ecosystem models is required to couple food web and nutrient dynamics (Grimm et al. 2017; Filser et al. 2016). These models will benefit from recent advances on a number of complementary issues. Scaling theories based on body-mass and other functional traits provide ways to scale up nutrient fluxes from organisms to ecosystem levels (Schramski et al. 2015, Barnes et al. 2018). Recent findings on the general architecture of soil food webs are further advancing our understanding of the multiple channels of energy flows in the soil (Potapov 2022). Besides, the aboveground food web, notably large herbivores, has a



**Fig. 3:** Coupling between food webs dynamics and biogeochemical cycles in an agroecological context. Trophic interactions govern nutrient mineralisation and soil organic matter decomposition, which reduces fertiliser use and promotes carbon storage in soil.

likely strong impact on biogeochemical fluxes due to consumer-driven recycling (Daufresne 2021). From a methodological standpoint, novel databases emerge to document food web interaction potential and organism stoichiometry (e.g., Andrieux et al. 2021, Bloor et al. 2021), as well as tools to ease the computation of fluxes (Gauzens et al. 2019). Taken together, these advances should feed applications of innovative ecosystem models for carbon and nutrient management.

## Conclusion

While theoretical works have prevailed for long in ecological network research due to data scarcity, next generation monitoring tools are progressively changing the picture. We have identified the spatial and temporal dynamics of networks and their links with biogeochemical cycles as important frontiers for contemporary ecological network research. Here, special attention can be paid to food webs in landscape mosaics, above-belowground interactions, and the inclusion of abiotic components to mechanistically link organismic interaction networks to biogeochemistry. These frontiers are central to many applied challenges for reaching sustainability and we believe that our perspective paper will inspire more communication among theoretical and empirical ecologists to push this field of research forward.

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## Conflict of Interest

We have no conflict of interest to disclose.

## Author contributions

Pierre Quévieux and Franck Jabot wrote the first draft of the manuscript. Ulrich Brose, Núria Galiana, Anton Potapov, Élisabeth Thébault, Morgane Travers-Trolet and Sabine Wollrab equally contributed to the editing of the manuscript.

## Data availability

No data were used in this article.

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