

Overcoming the disconnect between species interaction networks and biodiversity conservation

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Decision-makers need to act now to halt biodiversity loss, and ecologists must provide them with relevant species interaction indicators to inform about community- and ecosystem-level changes. Yet, the integration of ecological networks into conservation is still virtually non-existent. Here, we argue that existing data and methodologies are sufficient to generate network information usable for conservation, and to begin overcoming existing barriers to the integration of network information and biodiversity decision-making. Interaction network indicators must meet criteria important to decision-makers and be tied to specific conservation goals, which requires academics to better engage with practitioners. We use network robustness as an example of an already applicable indicator, and showcase its potential with a reusable workflow to inform decision-making.

Keywords:
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Highlights

- Practitioners and scientists increasingly need multi-species and whole-ecosystem indicators for biodiversity conservation and management. Species interaction networks hold a promising potential to fill those needs.
- Explicit and quantitative integration of network indicators into conservation is still lacking due to challenges with uncertainty and indicator accessibility to practitioners. The resulting gap between network science and management leads to decisions being made without considering available scientific knowledge.
- We need to start bridging network information into biodiversity management, towards application. We can do this now, building on existing metrics and available data as starting points. We must accept data limitations and uncertainty, and use what we have to establish an oper-

ational framework and then focus on improving it with better data and sampling programs.

1

Can interaction network knowledge be quantitatively used for biodiversity conservation and management?

The need to shift from single-species conservation approaches to multi-species and whole ecosystem approaches has long been recognized [1,2]. Network information can provide a new perspective for whole ecosystem assessments in biodiversity conservation and management. Preserving species interactions can ensure long-term population persistence and maintain ecosystem functions and services [3,4]. Focusing on **species interaction networks** (see [Glossary](#)) as conservation targets promotes the stability of populations and ecosystem functions and minimises negative outcomes regarding species extinctions [5–7]. Recent reviews list specific interaction **network metrics** that decision-makers can use [8]. Implicit network information has already been integrated into conservation planning, which should facilitate the uptake of network-based biodiversity **indicators** in decision-making [2,9,10]. For instance, network information is implicitly integrated through the consideration of keystone species that disproportionately affect local communities (see Box 1).

Despite the potential benefits, conservation practices rarely *explicitly* consider information derived from ecological network metrics, and conservation policy and practice still heavily focus on single species and habitats. This is in part due to uncertainty, and in part due to the choice of indicators. Uncertainty about network structure and responses to human disturbances mirrors concerns in macro-ecological and ecosystem models [11,12]. Additionally, identifying which interaction network metrics are suitable biodiversity indicators with clear interpretation for conservation remains challenging.

Decision- and policy-makers must act now to bend the curve of extinction and accelerate ecosystem recovery [13,14]. Ecologists need to provide them with useful network and ecosystem-wide information. For instance, protected area planning could prioritise regions where mutualistic interaction partners or prey and predators overlap [15], or where there is high trophic diversity and redundancy, enhancing **robustness** to extinctions [16]. Moreover, since interaction network structure is linked to ecosystem functioning and ecosystem service provision, focusing on network metrics changes for conservation targets should ensure ecosystem stability and service delivery [e.g., pollination, pest control, food production, 5,7,17]. Given the global goals to maintain ecosystem services [Goal B of the Kunming-Montreal Global Biodiversity Framework, 18], assessing changes in network structure and stability should help managers and decision-makers prioritise areas to maintain ecosystem functioning and resilience [5,19].

Here, we identify the major challenges and opportunities in incorporating information from species interaction networks into biodiversity conservation and ecosystem management. Despite these challenges, we need to start integrating network concepts into management and conservation in the face of global change, as we have sufficient scientific evidence and tools to do so. Using network robustness as an example, we show how simple approaches and indicators can provide relevant information for managers based on decision-making criteria, available data, and reproducible workflows.

Box 1 - Network information is already implicitly considered in conservation and decision-making

Explicitly considering interaction networks in conservation and decision-making (i.e. by **monitoring** and managing for network-derived indicators) is not a drastic shift, as they are often implicitly included in conservation decisions and recovery plans. For example, the keystone species concept, frequently mentioned in conservation literature [e.g., 2,20] and highlighted by initiatives focused on rewilding and ecological restoration [21,22], is linked to the disproportionate effects some species have on their (trophic) networks and ecosystem functioning [23, also see 24 for the diverse roles of species identified as keystones]. Similarly, several large carnivores have been associated with trophic cascades, where effects of predator declines propagated across food webs to herbivores, mesopredators, and beyond [25]. This reflects network consideration through species' effects on others, even if network-specific metrics are not explicitly quantified (see **network metrics** in [Glossary](#)) and do not explicitly enter planning or decision-making.

Importantly, keystone species are often tied to quantified conservation targets, highlighting how the concept is both accepted and used by practitioners. For example the Recovery Strategy and Action Plan for the Black-tailed Prairie Dog (*Cynomys ludovicianus*) in Canada identifies it as a conservation priority due to its keystone status – crucial for the recovery of the Black-footed Ferret (*Mustela nigripes*) and a vital food source for several other at-risk species [26]. Conservation targets for Black-tailed Prairie Dogs in Canada include maintaining a minimum area of occupancy of 1,400 ha across 20 colonies and a minimum average population density of 7.5 individuals/ha by 2040, ensuring at least an 80% probability of population persistence over 50 years [26; targets on which recovery of the Black-footed ferret also depend].

The existing implicit consideration of network structure in conservation targets can facilitate the uptake of new network-based indicators by practitioners and decision-makers. Other forms of network-thinking are also part of management considerations, such as spatial ecological networks planning [27] and ecosystem-based management [11]. Explicitly considering indicators of interaction networks will complement these forms of network-thinking and enhance conservation assessments to include ecosystem-wide components.

Challenges & Opportunities

The explicit integration of network information into management and conservation faces several challenges linked to uncertainties and lack of interpretability and relevance of network metrics for practitioners. These challenges will hinder making effective decisions, for example on what biodiversity and network-related metrics need to be measured and monitored, what conservation targets and management actions should be applied, how often to re-evaluate decisions, etc. Hence, we can expect challenges at different stages of management planning and decision-making [e.g. 28], such as the evaluation of current conditions or upon decisions on possible actions (e.g. responsive, preventative, etc.).

2.1. Uncertainty

Network Structure and Composition There is uncertainty in network structure, composition, and variation across space and time, which affects conservation assessments and actions [29,30]. Empirical studies on networks are often spatially disjointed, biased geographically and in the types of interactions, and rarely replicated [31–33]. Sampling biases can distort reported network patterns [34,35]. Terrestrial and freshwater food webs are less studied than marine ones, often with different research objectives [e.g., determining the effect of environmental factors, rather than investigating management-related elements such as sustainability, 31,36]. Such deficits of information are problematic for decision-making, as it may seem impossible to extract hard and transferable (geographically or between ecosystems) guidelines for both scientists and practitioners.

Despite these challenges, existing methodologies and data can help integrate network information into conservation, while empirical data continue to be gathered. Food webs can be constructed from extensive, long-term monitoring datasets to analyse network structure and stability [37,38]. As **binary** interaction data are commonly available, we can start ahead with these to establish operational monitoring frameworks, while later integrating uncertainties and flow-based data for a deeper and error-informed understanding of ecological systems. Building **metawebs** of all potential interactions in a region or species pool, like the pan-European terrestrial tetrapod metaweb [TETRA-EU, 39], can help inform broad-scale assessments of network structure [40,41]. Metawebs have already been used to derive spatially explicit network metrics and generate conservation-relevant information [42–44]. For instance, Albouy *et al.* [42] used a metaweb to examine robustness to extinction scenarios for marine food webs, showing higher robustness in coastal waters compared to open waters and highlighting some potential to absorb perturbations. Moreover, metaweb inference approaches allow us to circumvent the lack of available local interaction data [40] and, when used with **probabilistic networks**, to integrate uncertainty and variation in network structure across space [45]. Network metrics and their uncertainties can therefore be measured for broad-scale assessments of variation in network structure, and to derive network indicators that can be used to inform decisions and planning (Boxes 2-3). As new empirical data becomes available, predictions can be evaluated, refined, and become more informative [46]. We discuss the challenges surrounding their validation in our [Concluding Remarks](#).

Network Responses to Environmental Change Uncertainty exists in how networks will respond to environmental changes and disturbances, particularly for interaction **rewiring** and changes in interaction strength. Questions remain on the extent of rewiring due to species turnover versus prey switching and behavioural adaptation, and how these changes will propagate across trophic levels.

While data gaps exist, modelling and inference can explore the limits of network rewiring under current or future conditions (Box 3). Rewiring potential is likely captured in existing and inferred metawebs [47], which can be combined with simulations to anticipate network changes. For instance, Dansereau *et al.*'s [45] approach can be extended to explore climate change impacts on network structure, given the dual uncertainty in species interactions and future species ranges. Importantly, network models (and information) do not need well-constrained or low uncertainty predictions before they can inform management decisions on interventions like species eradication, especially if they tend to correctly identify whether effects on other species will be positive or negative [48]. Model uncertainty can also be high despite high quality data [48]. Regardless of its generality, this suggests that the performance of a model should be monitored whenever new data are added. Similar trends of model change in performance with additional data have been reported in the study of species distributions [49].

Approaches to include specific types of network response uncertainty in conservation and management have also been proposed. Van Kleunen *et al.* [50] suggested a multi-step framework for decision-making under uncertainty for species introduction into ecological networks, based on conservation decision theory. This framework includes: the identification of management objectives, the evaluation of outcomes for management (including multiple outcomes, evaluation of trade-offs, and assessment of uncertainty), and the improvement of future predictions through an adaptive management framework. Van Kleunen *et al.*'s [50] decision-making approach can be applied now, despite uncertainties, to guide management of species introductions.

Compounding Uncertainty in Change Types There is compounding uncertainty in the type and strength of change applied to a network. Climate uncertainty, for instance, results from uncertainty in future greenhouse gases emissions (i.e. emission scenario uncertainty), in climate processes (general circulation model uncertainty) and their stochasticity (model run uncertainty). For networks, we add uncertainty in changes resulting from disturbance regimes (e.g. fire, drought, pests) and in species distribution predictions [which can result from direct impacts of abiotic change, of disturbance regimes and of biotic changes that may be linked to network structure itself, 51,52]. If accounted for simultaneously, these uncertainties will inevitably lead to high variance in predicted network responses.

We can estimate some uncertainty through **hindcasting**: past environmental changes are used to predict changes in network metrics that are cross-validated against observed past or current networks. Fisheries data, for instance, allow reconstructing well-resolved networks over time, which can be related to known environmental changes [53–55] and be used to calibrate predictive network models, like Bayesian networks [56]. Hindcasting models, used as ex-ante scenarios of change, have been successfully used to simulate and assess the effectiveness of conservation actions on ecosystem services [57].

Simulating scenarios of change can also help delimit the possible changes in network structure [Box 3, 58]. When combined with metrics of network change and sensitivity to disturbance, these **projections** can be used to identify target areas that show fragility to an array of scenarios and are of special concern, or that show less fragility and could be considered refugia. They can also highlight problematic or incomplete sampling. Projections will also serve to perform validation and assess indicator behaviour in an empirical setting, whether through existing data or hindcasting exercises, which could lead to network-specific monitoring programs.

2.2. Interpretability and relevance Network metrics are often not intuitive or deemed relevant for practitioners and decision-makers; many are complex and may not show clear relationships with ecosystem- and species-level responses, particularly in applied contexts. For instance, omnivory and network motifs are tied to food web robustness and extinction risks [59,60], highlighting their ecological relevance. On the other hand, while network nestedness indicates a buffer against extinctions and fluctuations in mutualistic networks, this is less clear in antagonistic networks [7]. Connectance has also been tied in contrasting ways to network stability, with higher connectance leading to increases or decreases of invasion success rates given invader trophic levels [61], or linked to higher robustness to extinction, but larger extinction cascades [62].

Moreover, not all network metrics are suitable as conservation indicators, nor do they need to be. Several have been reviewed for their relevance and limitations in achieving conservation goals [63, see Table 1 therein]. For example, prioritising trophic networks with stabilising motifs when selecting protected areas can help

achieve ecological resilience goals [63]. This information can already be used towards conservation planning but it needs to be both accepted by and available to decision-makers and managers.

First, metrics must meet decision-makers' criteria. The ROARS (Relevant, Objective, Available, Realistic, Specific) and SMART (Specific, Measurable, Achievable, Replicable, Time-bound) criteria [8, see Table 3 therein] focus on the decision-makers' receptiveness to suggested indicators during the selection, paving a way to communicate network information with stakeholders and embed network indicators in ecological monitoring and ecosystem health assessments. Network indicators will therefore need to be evaluated in terms of usefulness to achieve conservation goals [63] and decision-maker receptiveness [as in 8], as we move towards developing ecosystem management and monitoring frameworks that quantitatively and explicitly embed network indicators (see example in Box 2).

Second, network ecologists have the opportunity to expand their focus from the development of mathematical tools, theory and theoretical validation, to involving decision-makers and meeting their needs [64]. Consensus for conservation goals can be achieved through mixed methodology, such as iterative and anonymous Delphi panels [see 65 for applications in ecology]. Engaging stakeholders in this way would ultimately provide valuable guidance to prioritise new fundamental research questions and methodological development. Although they do not ultimately make the decisions, network ecologists must be proactive in this process, especially given the limited time and staffing resources across many institutions where decisions are made. This process takes time and co-production effort, and needs to be promoted by academics who can guide and support practitioners in designing management strategies and making conservation decisions using network information. Academics place a strong focus on the development of tools and knowledge, but ensuring their adoption (particularly for non-academics) will require delivering them in a form that can instantly be used with minimal additional work [66].

Finally, network ecologists can take concrete steps to ensure that network-based measures are perceived as relevant by decision-makers. Workshops and stakeholder involvement are essential to bridge the gap between science and practice [66] and can facilitate choosing appropriate metrics [8]. Involving a wide-range of ecosystem-management players, and creating new opportunities to actively involve stakeholders in deciding how network information can be applied, will be key to ensure receptiveness and a speedy uptake of indicators for management planning and actions. **Forecasting** changes in network structure under environmental and management scenarios (Box 3) and linking network indicators to ecosystem services [17] can enhance receptiveness, especially if we clearly demonstrate that forecasts work well. This will provide essential information on risks, on boundaries of change given environmental conditions, and on the effectiveness of certain management actions in achieving conservation targets [67].

Box 2 - Assessing the relevance of a potential network indicator for decision-making

Network metrics should be evaluated using criteria important to decision-makers to ensure their relevance as indicators and encourage adoption. In addition to the ROARS and SMART criteria, Fath *et al.* [8] suggest that effective indicators should also “*describ[e] directional change [of ecosystems], [be] easily communicable to managers and policy makers, [be] integrative and indicative to a known response to a disturbance*” [as per 68], and provide insight to ecosystem functioning and services.

Table I illustrates the process of detailing how a potential network indicator meets the criteria mentioned previously, using trophic network robustness to species extinctions (hereafter robustness) as an example. Evaluating network metrics in this way is crucial for making them more relevant and acceptable to decision-makers, as it demonstrates why and how the indicator can be used effectively. We emphasize that such evaluation should be done with other network metrics to facilitate uptake by practitioners and decision-makers.

We chose robustness as it can be a useful indicator of ecosystem integrity and stability to environmental change given data we already have. The structural stability of trophic networks is closely linked to the stability of ecosystem functioning [see review by 69], with trophic interactions considered as ecosystem functions and services (e.g., top-down pest control by predators). Here we show a formulation of robustness derived from earlier work [70–72] that reflects the capacity of a network (or the ecosystem it represents) to withstand cascading extinctions:

$$Robustness = 1 - \frac{\text{no. secondary extinctions}}{\text{initial no. secondary consumers}}$$

where ‘no. **secondary extinctions**’ are extinctions due to the loss of prey species and ‘**secondary consumers**’ are species that consume other species in the network (calculated as network species richness minus the number of **basal species**). ‘Initial’ refers to before extinctions took place.

Robustness is easy to interpret (see *Specific* in Tbl. 1) and to calculate using binary trophic networks, which are more commonly available and can be constructed from existing trophic metawebs – this allows us to derive initial (even if coarse) estimates of robustness at large, regional and local scales (see references in Tbl. 1). It also relates to ecological issues that have a firm place in ecosystem management and conservation, and resonate with decision-makers – numerous directives, policies and management frameworks focus on avoiding species extinctions (see examples in Tbl. 1). By showing here how robustness meets decision-making criteria, we highlight a process transferable to other network metrics to identify the most applicable ones for biodiversity conservation and management.

Table 1 Relevance of a network indicator for decision-making. Dale & Beyler’s [68], ROARS (Relevant, Objective, Available, Realistic, Specific) and SMART (Specific, Measurable, Achievable, Replicable, Time-bound) criteria for good ecological network indicators, as described by Fath *et al.* [8], and how they apply to robustness of trophic (binary) networks.

Criteria	Description [as in Fath <i>et al.</i> , 8]	How it applies to robustness
Dale & Beyler [68]		
	Describe directional change	Robustness measures loss of species with respect to a given (pre-disturbance) species composition.
	Easily communicable to managers and policy makers	The relationship between robustness and species extinctions is intuitive and easy to understand. See also entry for “Relevant” below.
	Integrative and indicative to a known response to a disturbance	Trophic networks summarise the energy flows in an ecosystem; their structural stability is linked to stability of ecosystem functioning [69]. Robustness measures trophic network responses to disturbances that lead to cascading species extinctions.
ROARS		
Relevant	It relates to an important part of an objective or output	Preventing species extinctions is at the heart of numerous conservation policies, directives and frameworks [e.g., 73,74–76].
Objective	Based on facts, rather than feelings or impressions and thus measurable	Robustness is based on assessments of species composition pre- and post- disturbance.
Available	Data should be readily available or reasonably measurable	At the regional scale, available metawebs [e.g., 39,53] can be combined with species range data (e.g., IUCN ⁱⁱ and GBIF ⁱⁱⁱ) and scenarios of change to assess robustness (see Box 3). Sub-regional/local scale assessments are possible in locations with monitoring data [e.g., 37,38].

Realistic	It should not be too difficult or too expensive to collect the information	Marine and freshwater network data are already being collected as part of monitoring programs and fisheries activities; Terrestrial metawebs exist [39] or can be inferred [77] Methodology to calculate robustness is not overly complex and can be pipelined (see Box 3).
Specific	The measured changes should be expressed in precise terms	Robustness is calculated as 1 minus the ratio of secondary extinctions to the initial number of secondary consumers. It is scaled from 0-1, with 1 indicating maximum robustness (no secondary extinctions) and 0 indicating no robustness (all secondary consumers went secondarily extinct due to loss of feeding resources).
SMART		
Specific	Measured changes should be expressed in precise terms and suggest the direction of actions	See entry for “Specific” above. Maps of robustness can indicate hotspots and priority areas for conservation. Networks with high robustness will indicate ecosystems whose structure is more stable and that could be managed as “safety nets” and/or with more liberal use. Those with low robustness should be further assessed for their uniqueness (e.g., uniqueness of species composition and interactions, of habitat type, etc.) to plan conservation actions.
Measurable	Indicators should be related to things that can be measured in an unambiguous way	In an empirical setting, there may be ambiguity in determining whether an extinction was secondary (due to loss of other species in the network) or primary (due to, e.g., loss of climate suitability). In a modelling setting secondary and primary extinctions can be determined. Null models can be used to test whether projected extinctions significantly deviate from random. Uncertainty in both network species composition and structure will need to be recognised and accounted for explicitly whenever possible [e.g., 45]
Achievable	Indicators should be reasonable and possible to reach, and therefore sensitive to changes	See entry for “Available” above. Hindcasting and historical observational data can be used to gauge the sensitivity of robustness to past environmental change. Forecasting data can be used to assess robustness boundaries to expected changes and complemented with monitoring data to verify how networks are responding to change.
Replicable	Measurements should be the same when made by different people using the same method	Transparent and freely accessible pipelines can be developed and automated to ensure repeatability.

Time-bound	There should be a time limit within which changes are expected and measured	This likely depends on the species and type of environmental changes considered, given different life cycle histories and species' sensitivities to change.
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Box 3 - Illustration of an accessible and reproducible workflow to inform decision-making using network robustness

Effective decision-making requires indicators based on accessible and reproducible workflows that evaluate a range of scenarios. Keeping trophic network robustness as our example, we demonstrate how such a workflow can be built using different network disturbance scenarios and open-access data (Fig. 1). By using extreme scenarios, we can explore the boundaries of robustness to projected environmental change. The framework can be applied spatially to identify target areas for management and conservation action (Fig. 2), or to single well-resolved networks (e.g. local scale).

Workflow steps:

- 1) Build local 'baseline networks' by combining a regional metaweb of interactions with 'baseline' local species presence/absence information ('baseline' on Fig. 1 referring to any reference period) – species that interact in the metaweb and are locally present will appear and interact in the local network;
- 2) For each baseline network, calculate the number of secondary consumers and other relevant network metrics (e.g., species and average trophic level, connectance, etc.);
- 3) Build local 'disturbed networks' by combining the regional metaweb with species ranges projected under different scenarios;
- 4) Calculate and map robustness and other network metrics (Fig. 2).

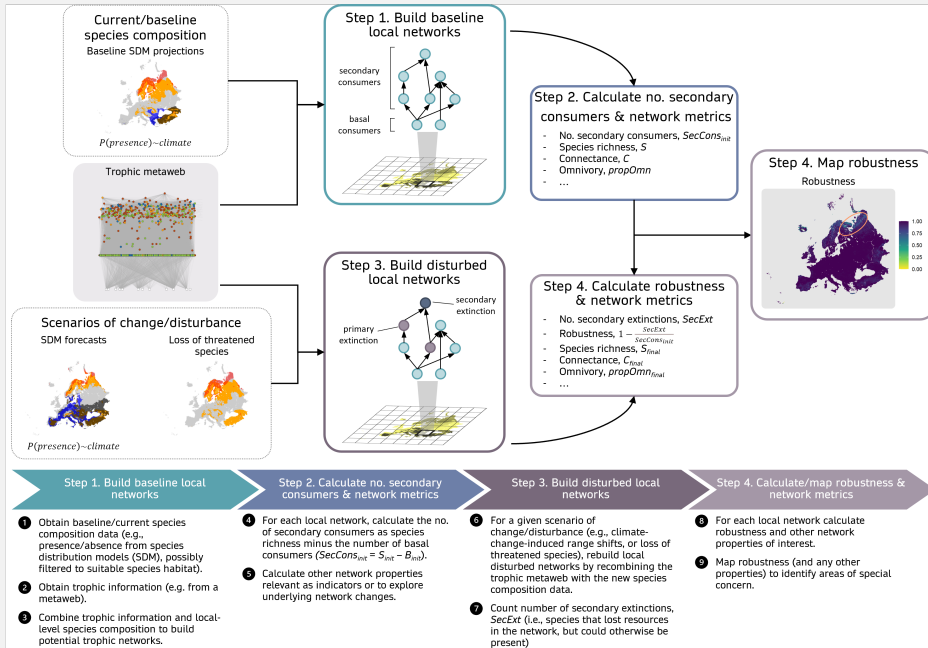


Figure 1 Workflow to calculate robustness. Simple network metrics like robustness can be incorporated into workflows to assess potential ecosystem fragility to scenarios of disturbance and inform management and decision-making at large scales.

Here we illustrate this workflow using a worked example with pan-European tetrapod trophic net-

works. We explore the boundaries of network robustness by using two extreme scenarios: worst-case climate change (CMIP5 RCP 8.5, equivalent to CMIP6 SSP5-8.5), and failure to protect endangered species (loss of all species with IUCN status of Critically Endangered, Endangered, and Vulnerable, across their entire range). The scenarios caused changes in species composition due to climate-driven range shifts ('climate change' in Fig. 2) or to targeted species removals ('IUCN extinctions'). Two extinction outcomes were possible: species became primarily extinct when predicted to be absent from a pixel due to future climatic conditions or due to targeted removal, or secondarily extinct when the pixel was climatically suitable but had too few prey items. Following the workflow above, we used a metaweb adapted from TETRA-EU [78] build baseline and disturbed local networks [using projected species distributions based on habitat preferences and presence-absence data from 79], calculate the number of secondary consumers (from baseline networks) and secondary extinctions (from disturbed networks), then calculate and map robustness (see Supplemental Information online for full workflow details).

In this example, most networks were very robust to extinctions driven by a) climate change or b) the removal of endangered species listed in IUCN, but several networks in Northern Europe, Crete and in the Canary Islands show lower robustness to targeted IUCN extinctions (Fig. 2 b). For the purpose of this illustration, we show median robustness values per ecoregion [defined by 80], which represent geographically meaningful boundaries for species and interaction composition [81] and simultaneously highlight a regional-level at which robustness can be used to inform policy-making (see Supplemental Information, Figure S2 for pixel values). We note that this is a conceptual illustration to present robustness as an example of a readily applicable indicator given the data we already have. Yet, further analyses could be focused on investigating which species are projected to be lost, their roles in the networks and best strategies to protect these networks from a multispecies perspective.

Antunes *et al.* [17] proposed a similar workflow to calculate network-provided Nature's contributions to people, but our framework involves methodological approaches that are less sophisticated and data-hungry. We emphasize that presenting a fully worked example for potential network indicators, as we do here with an accessible automated pipeline [82], is a transparent and practical way to not only encourage the development and sharing of reusable analyses, but also to facilitate and accelerate uptake by practitioners, managers and decision-makers.

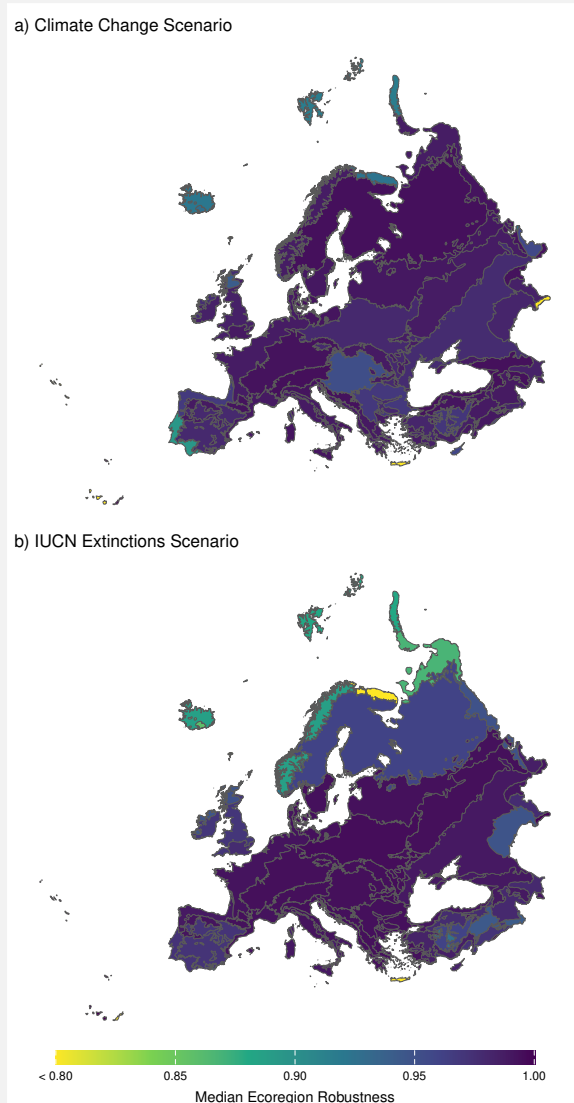


Figure 2 Robustness of European vertebrate networks to disturbance scenarios per ecoregion. Extreme scenarios of climate change and of species extinctions can be used to explore (lower) boundaries of network robustness and identify areas where we may expect a high number of cascading (secondary) extinctions and, consequently, larger disruptions to ecosystem functioning and services. Lower limit was set to 0.80 for illustration purposes.

Concluding remarks

Ecological networks already can and should be used as indicators in biodiversity conservation and ecosystem management. Sufficient data is available for initial assessments of network structure and responses to change. Additionally, we have relevant network indicators for ecosystem management and conservation that can be weaved into management frameworks and monitoring programs. Starting now ensures that future data will be useful to detect network changes and to address current knowledge gaps.

We recognize that the lack of empirical support for theory and scenarios of network responses (including robustness) to environmental change can refrain academics from providing guidance to practitioners. Robustness and extinction studies usually rely on simulations to investigate effects of species loss (rather than

observations or experimental removals) and predictions remain mostly untested in the field [83, see Table 1 therein for some empirical validation examples]. Overcoming this barrier will require setting up programs that go beyond documenting networks and towards empirical measurements of network responses to realistic disturbances. Moreover, empirical and monitoring programs will need to collect and integrate network information across multiple scales, as management actions and policy-making differ between regional and local levels. Yet, despite this and other limitations (i.e., data, uncertainty, and interpretability challenges highlighted above), we believe the field is sufficiently mature to make recommendations for ecosystem management and conservation as these programs are implemented.

We envision five important aspects for future directions (see also [Outstanding Questions](#)). First, developments addressing evaluation, propagation, and communication of uncertainty in network structure and metrics are needed. These will be key to a) integrate uncertainty into management frameworks and move towards more transparent and informed decisions, but also to b) use existing tools and data to compare known network and ecosystem changes with predictions (e.g. hindcasting), estimate boundaries of future network changes (e.g. forecasting), and assess the usefulness of network metrics as indicators of future change. Second, network considerations will need to be explicit in future sampling and monitoring designs, and in ecosystem conservation regulations and decisions. Third, current data, network models and indicators need to be more widely assessed for their usefulness for ecosystem management, which should actively involve stakeholders. Fourth, empirical programs focused on testing and measuring network (metrics') responses to change, and across scales, will need to be set up. Finally, incorporating network information explicitly into conservation will require developing network-based targets—specific, quantified metric values to aim for or avoid (thresholds) based on whole network characteristics.

Outstanding questions

- How variable is network structure across space and time and does it influence the usefulness of network metrics as indicators of ecosystem functioning and stability?
- What network metrics are ubiquitous, reliable and applicable indicators of ecosystem functioning and stability?
- How much can we expect networks to change given uncertainty in future environmental conditions?
- How can current and future monitoring programs be improved to sample network information relevant for management?
- How can we put in place a strong empirical program to validate network indicators, which for now heavily rely on simulations?
- How should we implement coordinated monitoring of network indicators across multiple scales? Can the same indicators be used to inform at broad, regional and local scales?

Glossary

Basal species: species that do not feed on other species in a trophic network; e.g. primary producers.

Binary and probabilistic networks: networks where links represent either the presence or absence of an interaction between species, or its probability.

Forecasting: using current (known) conditions to predict future conditions of a system or events.

Hindcasting: using current (known) conditions to predict past conditions of a system or events.

Metaweb: all potential interactions in a region or species pool. Metawebs can be either binary or probabilistic, and are mostly common for trophic, mutualistic and parasitism networks. Due to their potential nature, they provide an “upper ceiling” of species interactions.

Monitoring programs: established long-term programs to track biodiversity status and changes. Data collected *in situ* through sampling or using remote sensing can be used in the calculation of biodiversity indicators and support decision-making.

Network indicators: network metrics with a clear interpretation and potential use for biodiversity conservation and management. This includes meeting criteria important for decision-making (e.g. ROARS, SMART). Here, we use trophic network robustness as an example of a useful indicator.

Network metrics: measurements made on networks, their nodes and links, regarding their com-

position, structure or properties pertaining to node or link importance. Common examples include number of links (interactions) and nodes (species), connectance, nestedness, trophic level, centrality, omnivory and network motifs.

Primary extinctions: extinctions directly due to disturbances. In our scenarios disturbances were changes in species climate suitability or the failure to protect endangered species.

Projection: a model prediction based on novel data (data beyond the fitting dataset) or scenarios, not necessarily tied to future or past conditions. For instance, a network prediction in a new location or with a different set of species.

Rewiring: changes in the interaction structure of a network. For instance, disturbances, environmental change, and addition or loss of species can lead to gain, loss, and reorganization of interactions.

Robustness: capacity of a network (or the ecosystem it represents) to withstand species extinctions following a disturbance. Robustness can be measured in multiple ways. Here we measure robustness as 1 minus the ratio of secondary extinctions to the initial number of secondary consumers, following concepts of robustness by Dunne *et al.* [70].

Secondary consumers: species that consume other species in the network (calculated as network species richness minus the number of basal species).

Secondary extinctions: extinctions due to the loss of prey species.

Species interaction networks: networks assessing the ecological links and relationships between species, highlighting how they are interconnected and influence each other. Links can be trophic (representing feeding links), flow-based (representing transfers of energy, matter, or resources), and mutualistic (e.g. pollination), among others.

5

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6

Resources

ⁱ <https://www.iucnredlist.org/resources/spatial-data-download>

ⁱⁱ <https://www.gbif.org/what-is-gbif>

7

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