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.

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

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 4 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 6 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 8 ecosystem functions and minimises negative outcomes regarding species extinctions [5–7]. Recent reviews list 9 specific interaction **network metrics** that decision-makers can use [8]. Implicit network information has 10 already been integrated into conservation planning, which should facilitate the uptake of network-based 11 biodiversity **indicators** in decision-making [2,9,10]. For instance, network information is implicitly integrated 12 through the consideration of keystone species that disproportionately affect local communities (see Box 1). 13 Despite the potential benefits, conservation practices rarely *explicitly* consider information derived from 14 ecological network metrics, and conservation policy and practice still heavily focus on single species and 15

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 20 [13,14]. Ecologists need to provide them with useful network and ecosystem-wide information. For instance, 21 protected area planning could prioritise regions where mutualistic interaction partners or prey and predators 22 overlap [15], or where there is high trophic diversity and redundancy, enhancing **robustness** to extinctions [16]. 23 Moreover, since interaction network structure is linked to ecosystem functioning and ecosystem service 24 provision, focusing on network metrics changes for conservation targets should ensure ecosystem stability and 25 service delivery [e.g., pollination, pest control, food production, 5,7,17]. Given the global goals to maintain 26 ecosystem services [Goal B of the Kunming-Montreal Global Biodiversity Framework, 18], assessing changes 27 in network structure and stability should help managers and decision-makers prioritise areas to maintain 28 ecosystem functioning and resilience [5,19]. 29

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.

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38 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 ⁴⁵ actions (e.g. responsive, preventative, etc.).

46 Uncertainty

47 Network Structure and Composition

There is uncertainty in network structure, composition, and variation across space and time, which affects 48 conservation assessments and actions [29,30]. Empirical studies on networks are often spatially disjointed, 49 biased geographically and in the types of interactions, and rarely replicated [31-33]. Sampling biases can 50 distort reported network patterns [34,35]. Terrestrial and freshwater food webs are less studied than marine 51 ones, often with different research objectives [e.g., determining the effect of environmental factors, rather than 52 investigating management-related elements such as sustainability, 31,36]. Such deficits of information are 53 problematic for decision-making, as it may seem impossible to extract hard and transferable (geographically or 54 between ecosystems) guidelines for both scientists and practitioners. 55

Despite these challenges, existing methodologies and data can help integrate network information into 56 conservation, while empirical data continue to be gathered. Food webs can be constructed from extensive, 57 long-term monitoring datasets to analyse network structure and stability [37,38]. As **binary** interaction data are 58 commonly available, we can start ahead with these to establish operational monitoring frameworks, while later 59 integrating uncertainties and flow-based data for a deeper and error-informed understanding of ecological 60 systems. Building **metawebs** of all potential interactions in a region or species pool, like the pan-European 61 terrestrial tetrapod metaweb [TETRA-EU, 39], can help inform broad-scale assessments of network structure 62 [40,41]. Metawebs have already been used to derive spatially explicit network metrics and generate 63 conservation-relevant information [42–44]. For instance, Albouy et al. [42] used a metaweb to examine 64 robustness to extinction scenarios for marine food webs, showing higher robustness in coastal waters compared 65 to open waters and highlighting some potential to absorb perturbations. Moreover, metaweb inference 66 approaches allow us to circumvent the lack of available local interaction data [40] and, when used with 67 **probabilistic networks**, to integrate uncertainty and variation in network structure across space [45]. Network 68 metrics and their uncertainties can therefore be measured for broad-scale assessments of variation in network 69 structure, and to derive network indicators that can be used to inform decisions and planning (Boxes 2-3). As 70 new empirical data becomes available, predictions can be evaluated, refined, and become more informative 71 [46]. We discuss the challenges surrounding their validation in our Concluding Remarks. 72

73 Network Responses to Environmental Change

⁷⁴ Uncertainty exists in how networks will respond to environmental changes and disturbances, particularly for
 ⁷⁵ interaction **rewiring** and changes in interaction strength. Questions remain on the extent of rewiring due to
 ⁷⁶ species turnover versus prey switching and behavioural adaptation, and how these changes will propagate across
 ⁷⁷ trophic levels.

While data gaps exist, modelling and inference can explore the limits of network rewiring under current or 78 future conditions (Box 3). Rewiring potential is likely captured in existing and inferred metawebs [47], which 79 can be combined with simulations to anticipate network changes. For instance, Dansereau et al.'s [45] approach 80 can be extended to explore climate change impacts on network structure, given the dual uncertainty in species 81 interactions and future species ranges. Importantly, network models (and information) do not need 82 well-constrained or low uncertainty predictions before they can inform management decisions on interventions 83 like species eradication, especially if they tend to correctly identify whether effects on other species will be 84 positive or negative [48]. Model uncertainty can also be high despite high quality data [48]. Regardless of its 85 generality, this suggests that the performance of a model should be monitored whenever new data are added. 86 Similar trends of model change in performance with additional data have been reported in the study of species 87 distributions [49]. 88

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.

96 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.

Interpretability and relevance

Network metrics are often not intuitive or deemed relevant for practitioners and decision-makers; many are 117 complex and may not show clear relationships with ecosystem- and species-level responses, particularly in 118 applied contexts. For instance, omnivory and network motifs are tied to food web robustness and extinction 119 risks [59,60], highlighting their ecological relevance. On the other hand, while network nestedness indicates a 120 buffer against extinctions and fluctuations in mutualistic networks, this is less clear in antagonistic networks [7]. 121 Connectance has also been tied in contrasting ways to network stability, with higher connectance leading to 122 increases or decreases of invasion success rates given invader trophic levels [61], or linked to higher robustness 123 to extinction, but larger extinction cascades [62]. 124

¹²⁵ Moreover, not all network metrics are suitable as conservation indicators, nor do they need to be. Several have ¹²⁶ been reviewed for their relevance and limitations in achieving conservation goals [63, see Table 1 therein]. For ¹²⁷ example, prioritising trophic networks with stabilising motifs when selecting protected areas can help achieve ¹²⁸ ecological resilience goals [63]. This information can already be used towards conservation planning but it ¹²⁹ needs to be both accepted by and available to decision-makers and managers.

¹³⁰ 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 138 tools, theory and theoretical validation, to involving decision-makers and meeting their needs [64]. Consensus 139 for conservation goals can be achieved through mixed methodology, such as iterative and anonymous Delphi 140 panels [see 65 for applications in ecology]. Engaging stakeholders in this way would ultimately provide 141 valuable guidance to prioritise new fundamental research questions and methodological development. Although 142 they do not ultimately make the decisions, network ecologists must be proactive in this process, especially given 143 the limited time and staffing resources across many institutions where decisions are made. This process takes 144 time and co-production effort, and needs to be promoted by academics who can guide and support practitioners 145 in designing management strategies and making conservation decisions using network information. Academics 146 place a strong focus on the development of tools and knowledge, but ensuring their adoption (particularly for 147 non-academics) will require delivering them in a form that can instantly be used with minimal additional work 148 [66]. 149

Finally, network ecologists can take concrete steps to ensure that network-based measures are perceived as 150 relevant by decision-makers. Workshops and stakeholder involvement are essential to bridge the gap between 151 science and practice [66] and can facilitate choosing appropriate metrics [8]. Involving a wide-range of 152 ecosystem-management players, and creating new opportunities to actively involve stakeholders in deciding 153 how network information can be applied, will be key to ensure receptiveness and a speedy uptake of indicators 154 for management planning and actions. Forecasting changes in network structure under environmental and 155 management scenarios (Box 3) and linking network indicators to ecosystem services [17] can enhance 156 receptiveness, especially if we clearly demonstrate that forecasts work well. This will provide essential 157 information on risks, on boundaries of change given environmental conditions, and on the effectiveness of 158

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

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:

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

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.

Replicable, Time-bound) criteria for good ecological network indicators, as described by Fath <i>et al.</i> [8], and how they apply to robustness of trophic (binary) networks.				
Critorio	Description	How it applies to robustness		
Dale &				
Beyler [68]				
	Describe directional	Robustness measures loss of species with respect to a given		
	change	(pre-disturbance) species composition.		
	Easily communicable	The relationship between robustness and species extinctions is		
	Lashy communication	The relationship between robustness and species extinctions is		
	to managers and	intuitive and easy to understand.		
	policy makers	See also entry for "Relevant" below.		
	Integrative and	Trophic networks summarise the energy flows in an		
	indicative to a known	ecosystem; their structural stability is linked to stability of		
	response to a	ecosystem functioning [69].		
	disturbance	Robustness measures trophic network responses to		
		disturbances that lead to cascading species extinctions.		

Table 1: Relevance of a network indicator for decision-making. Dale & Beyler's [68], ROARS

ROARS

Relevant	It relates to an	Preventing species extinctions is at the heart of numerous
	important part of an	conservation policies, directives and frameworks [e.g.,
	objective or output	73,74–76].
Objective	Based on facts, rather	Robustness is based on assessments of species composition
	than feelings or	pre- and post- disturbance.
	impressions and thus	
	measurable	
Available	Data should be readily	At the regional scale, available metawebs [e.g., 39,53] can be
	available or	combined with species range data (e.g., IUCN ⁱⁱ and GBIF ⁱⁱⁱ)
	reasonably measurable	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	Marine and freshwater network data are already being
	difficult or too	collected as part of monitoring programs and fisheries
	expensive to collect	activities;
	the information	Terrestrial metawebs exist [39] or can be inferred [77]
		Methodology to calculate robustness is not overly complex and
		can be pipelined (see Box 3).

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Specific SMART	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).
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	See entry for "Available" above.
	reasonable and	Hindcasting and historical observational data can be used to
	possible to reach, and	gauge the sensitivity of robustness to past environmental
	therefore sensitive to	change.
	changes	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	Transparent and freely accessible pipelines can be developed
	be the same when	and automated to ensure repeatability.
	made by different	
	people using the same	
	method	
Time-bound	There should be a time	This likely depends on the species and type of environmental
	limit within which	changes considered, given different life cycle histories and
	changes are expected	species' sensitivities to change.
	and measured	

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:

- 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;
- For each baseline network, calculate the number of secondary consumers and other relevant network metrics (e.g., species and average trophic level, connectance, etc.);
- 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 networks. 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,



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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 175 robustness) to environmental change can refrain academics from providing guidance to practitioners. 176 Robustness and extinction studies usually rely on simulations to investigate effects of species loss (rather than 177 observations or experimental removals) and predictions remain mostly untested in the field [83, see Table 1 178 therein for some empirical validation examples]. Overcoming this barrier will require setting up programs that 179 go beyond documenting networks and towards empirical measurements of network responses to realistic 180 disturbances. Moreover, empirical and monitoring programs will need to collect and integrate network 181 information across multiple scales, as management actions and policy-making differ between regional and local 182 levels. Yet, despite this and other limitations (i.e., data, uncertainty, and interpretability challenges highlighted 183 above), we believe the field is sufficiently mature to make recommendations for ecosystem management and 184 conservation as these programs are implemented. 185

We envision five important aspects for future directions (see also Outstanding Questions). First, developments 186 addressing evaluation, propagation, and communication of uncertainty in network structure and metrics are 187 needed. These will be key to a) integrate uncertainty into management frameworks and move towards more 188 transparent and informed decisions, but also to b) use existing tools and data to compare known network and 189 ecosystem changes with predictions (e.g. hindcasting), estimate boundaries of future network changes (e.g. 190 forecasting), and assess the usefulness of network metrics as indicators of future change. Second, network 191 considerations will need to be explicit in future sampling and monitoring designs, and in ecosystem 192 conservation regulations and decisions. Third, current data, network models and indicators need to be more 193 widely assessed for their usefulness for ecosystem management, which should actively involve stakeholders. 194 Fourth, empirical programs focused on testing and measuring network (metrics') responses to change, and 195 across scales, will need to be set up. Finally, incorporating network information explicitly into conservation will 196 require developing network-based targets—specific, quantified metric values to aim for or avoid (thresholds) 197

¹⁹⁸ 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?

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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 composition, 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.

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212 Resources
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<sup>1</sup> https://www.iucnredlist.org/resources/spatial-data-download
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ii https://www.gbif.org/what-is-gbif
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