Title: Bridging ecology and conservation: from ecological networks to ecosystem function

Running Head: From ecological networks to ecosystem function

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Summary

1. Current approaches to conservation may be inadequate to maintain ecosystem integrity because they are mostly based on rarity status of organisms rather than functional significance. Alternatively, approaches focusing on the protection of ecological networks lead to more appropriate conservation targets to maintain ecosystem integrity.

2. We propose that a shift in focus from species to interaction networks is necessary to achieve pressing conservation management and restoration ecology goals of conserving biodiversity, ecosystem processes and ultimately landscape-scale delivery of ecosystem services.

3. Using topical examples from the literature, we discuss historical and conceptual advances, current challenges, and ways to move forward. We also propose a road map to ecological network conservation, providing a novel ready to use approach to identify clear conservation targets with flexible data requirements.

4. *Synthesis and applications.* Integration of how environmental and spatial constraints affect the nature and strength of local interaction networks will improve our ability to predict their response to change and to conserve them. This will better protect

5. species, ecosystem processes, and the resulting ecosystem services we depend on.

Introduction - linking conservation science with 21st century ecology

Conservation biology and restoration ecology are two modern research areas fostered by national park movements, wildlife conservation, and the broad international recognition of human impact on the planet that developed during the 20th century (e.g., 1987 Montreal protocol, and 1992 Rio De Janeiro convention on biodiversity). At the intersection between ecology and

social sciences, conservation biology evolved as an independent science with its own body of scientific journals and communities. As an unintended consequence, there is now a significant divide between current concepts and knowledge in the field of ecology and the prescription of conservation measures and development of new policies. This schism has been noted (Pulliam 1997), and the gap is widening as the field of ecology has experienced significant conceptual and methodological paradigm shifts at the onset of the 21st century which have yet to be integrated into conservation and restoration perspectives.

The objective of our commentary article is to identify major conceptual advances from ecological science that could enhance our capacity to efficiently protect and predict diversity and ecosystem integrity in the face of global change. In light of recent developments in ecology we argue that addressing the gap between conservation management and ecology requires (**i**) a better integration of ecological networks as conservation target, which would, in turn, allow for better conceptual bridging toward (**ii**) the prediction of ecosystem-level supporting processes and emerging services (Fig. 1). For each of these two points we identify challenges, illustrated by current examples, and suggest productive ways to move forward. Finally, we propose a step-by-step road map to ecological network conservation using a novel and ready-to-use tool to identify clear conservation targets.

From species to interaction networks

Current state of knowledge

In the context of increasing human population, reduction in habitable land owing to climate change, and increasing demand for food and goods production, the 'glass bell' approach to conservation, involving complete landscape protection through the creation of national parks,

poses important spatial and societal challenges (Millenium Ecosystem Assessment, 2005). The often-perceived alternative to the more holistic park perspective is a species-level focus (Fig. 1). Protective legislation for rare or endangered species can be successful, however 'Noah's Ark' approaches are often costly and ineffective (Laycock *et al.* 2009). Moreover, this approach tends to be reactive and targets species based on rarity rather than functional significance, which can lead to significant resource allocation to a specific group of species or even a single species with limited return in terms of ecosystem integrity and functioning (e.g., Gotelli *et al.* 2012, discussing this in the context of resource-allocations to the presumably extinct ivory-billed woodpecker). Frequent lack of resources for conservation management has led to the development of cost-effective trade-offs in conservation efforts (Weitzman 1998). However, ranking conservation priorities among species or habitats is a complicated matter because such an assessment cannot be achieved without considering inter-dependencies among species owing to complex direct and indirect interactions (Courtois, Figuieres & Mulier 2014). The integration of interdependent survival probabilities within conservation projects prioritization models has shown that taking species interactions into account can completely reverse conservation priorities (Simianer 2007). However, to accurately rank conservation priorities, one would need predictions about which species or functional groups are most likely to respond to future changes, and how these changes would spread across the interaction network and affect other species (for an example see "a road map to ecological network conservation" section further below). The net effect of perturbations is not always intuitive, owing to different types of interactions (e.g., trophic, mutualistic) and indirect links between species (Tylianakis *et al.* 2010). For instance, the extinction of the butterfly *Phengaris* (*Maculinea) arion* in the UK resulted indirectly from the biocontrol of European rabbits (*Oryctolagus cuniculus*): the butterfly

depended on the nest of the ant *Myrmica sabuleti* for the development of its larvae; *Myrmica,* in turn, depended on open areas supplied by rabbit grazing to establish their nests (Thomas, Simcox & Clarke 2009).

The study of species interactions has greatly improved our appreciation of the importance of network structure for ecological community stability, sensitivity to invasion, and extinction. For example, Pearse & Altermatt (2013a) analyzed regional extinctions in a trophic network of 900 Lepidoptera and 2403 potential host plant species in Central Europe. They reported that 8 of the 59 observed regional extinctions of Lepidoptera were associated with host-plant loss. Importantly, all 8 observed regional extinctions of Lepidoptera associated with host-plant loss occurred before the actual extinction of the host-plant. Thus, strong declines of host-plants can have cascading extinction effects on higher trophic levels before the plants actually go extinct, illustrating that interactions can be lost before any actual decline in species richness (plants persisted at low abundance). This illustrates that preserving keystone interactions, rather than species, can be a pro-active way to maintain ecosystem integrity in the face of global change instead of allocating resources to already endangered species. In a conservation biology context, the network structure, and more specifically the connectance (number of interactions per node), is also important with respect to which species are likely to be threatened: monophagous or strictly oligophagous Lepidoptera are significantly more often listed as "regionally extinct" or "critically endangered" than as "least concern", indicating that interaction networks may give a direct causal explanation for species' threat status (Pearse & Altermatt 2013a).

A possible further contribution of studies of pairwise species interactions for conservation management is a better understanding of biocontrol failure or potential indirect effects of novel trophic interactions on community structure, species invasions, and response to perturbations (Russo *et al.* 2014, Wood *et al.* 2014, Alexander *et al.* 2015). Among-species interactions can also be a powerful tool for predicting potential novel trophic interactions based on existing interactions in a straightforward manner (Pearse & Altermatt 2013b). For instance, the integration of 459 non-native plants into the diet of 900 native, Central European lepidoptera could be accurately predicted by a simple model based only on the interactions of lepidoptera with their native hosts as well as a plant phylogeny (Pearse & Altermatt 2013b). Some of the observed, and accurately predicted, novel trophic interactions between native plant hosts and lepidopteran herbivores also included species of agricultural or forestry significance, such as extensions of the Tussock moth (*Calliteara pudibunda*) larval diet to the non-native red oak (*Quercus rubra*) or sesiid moth *Synanthedon tipuliformis* larval diet to a non-native, introduced gooseberry species (e.g., *Ribes aureum*). If such among-species interactions are ignored, natural enemies could potentially fail to control important agricultural pests, for instance the green peach aphid (*Myzus persicae*) has devastated potato fields (Straub & Snyder 2006), despite efforts to increase natural enemies abundance and diversity. Moreover, introduced non-native biocontrol agents can have non-target indirect effects despite high host-specificity. For instance gall flies (*Urophora affinis* and *U. quadrifasciata*), introduced in North America to control the expansion of knapweeds (*Centaurea maculosa* and *C. diffusa*), failed in their biocontrol role but became superabundant and subsidized populations of the generalist deer mouse (*Peromyscus maniculatus*), which in turn triggered several declines of native plants, insects and small mammals (Pearson & Callaway 2003).

Caveats and future perspective

Unfortunately, despite these important contributions, early ecological network studies did not produce general principles for the organization and dynamics of natural communities, largely because they did not consider the environmental context in which these interactions occur (McGill *et al.* 2006). However, recent conceptual developments in community ecology have successfully integrated biotic interactions within both their local environment and their spatial context (Leibold *et al.* 2004). During the same period, the field of biogeography began to question the use of species-specific climatic envelopes for predicting species range-shifts following climate change, acknowledging that species do not migrate into empty vacuums but rather into established, complex and diverse biotic communities (Pearson & Dawson 2003). Thus, there is now compelling evidence from both biogeography (Araújo & Luoto 2007) and meta-community research that local biodiversity strongly depends on interactions occurring at local and regional scales. For instance Pillai and colleagues (2011) demonstrated that complex food webs can persist in a structured landscape on a single basal resource, even though local coexistence would be impossible.

One of the greatest impediments to a broader development of ecological network research in conservation sciences is the challenge to construct accurate and meaningful interaction networks (Morales-Castilla *et al.* 2015). Complete species networks are rare and prone to resolution issues because they are often built over many years and integrate information from many contrasting sources (e.g. expert knowledge, gut contents, co-occurrence data). The problem with these time- and resource-consuming methods is that they can lead to false negatives (missing links that are

important), overestimation of the importance of some links, or even – and most importantly – to false positives (hypothesized links that are not realized) when assuming interactions based on simple co-occurrences (Morales-Castilla *et al.* 2015). This is problematic because it means that most species network knowledge has been produced from a small subset of non-reproducible networks. Moreover, these traditional methods are not amenable to construction of interaction networks beyond food webs, resulting in historical bias towards the study of antagonistic interactions (Morales-Castilla *et al.* 2015), despite increasing awareness of the importance of mutualistic and facilitation interactions for the maintenance of diversity and ecosystem processes (Bascompte 2009).

There is also a need for development of new and more accurate process-based experimental and empirical knowledge. Recent breakthroughs have shown that the qualitative nature (competitive, predator-prey, mutualistic) and quantitative strength of species interactions can change in space as a function of local conditions (Poisot *et al.* 2012). For instance, stress gradients can modify the net balance between competition and facilitation, with competition dominating in low stress habitats and facilitation dominating in high stress habitats (Lortie & Callaway 2006). This has obvious implications for the study of species range shifts along environmental degradation gradients (e.g., climatic, drought) because increasing positive interactions at each end of the gradient could support better persistence rates than previously predicted. However our mechanistic understanding of how the nature and strength of these interactions change as a function of environmental context remains shockingly anemic (Poisot *et al.* 2012). In the context of increased frequency of perturbations and landscape alterations, we also need to understand mechanistically how multiple perturbations spread through local

networks (Tylianakis *et al.* 2010). In a recent study, Harvey and MacDougall (2015) showed how regional landscape fragmentation and local fertilization in grasslands interact to homogenize insect herbivore regulation. This unfolded because fragmentation reduced predator abundance, while both fragmentation and fertilization altered host plant diversity. These effects led to a significant increase in bottom-up constraints, facilitating a reduction in insect diversity and regional dominance by a few Hemipteran herbivore generalists (mainly Miridae family). Most importantly, the study demonstrated that these perturbation effects on insect herbivores were entirely mediated by bottom-up and top-down trophic interactions, suggesting that herbivores themselves would be the wrong target to mitigate effects of landscape alteration. For these purposes, accessible methods have been recently proposed to measure interaction strengths within controlled laboratory experiments (Carrara *et al.* 2015), and the use of molecular toolkits (e.g., stable isotopes, eDNA) promise an exciting future for the generation of *in situ* new empirical data beyond species level information (Smith *et al.* 2011).

From ecological network conservation to ecosystem functioning

Recent evidence that interactions can be lost at a quicker pace than species following environmental degradation, for instance through the local extinction of host plants (Pearse & Altermatt 2013a) or through the desynchronization of species activity periods (Visser & Both 2005), is concerning because it demonstrates that essential functions performed by species (e.g., pollination, herbivore regulation) can be lost despite species remaining present in a system (Valiente-Banuet *et al.* 2015). For instance, many insectivorous birds, such as the great tit (*Parus major*), hatch in synchrony with the emergence of high-protein insect prey necessary to sustain youngling development (Fig. 2b). Earlier springs and longer growing seasons due to climate

change generate a mismatch between hatching time of the great tit and its prey emergence, leading to a decrease of the number and fitness of fledged chicks (Visser, Holleman & Gienapp 2005). Despite the presence of both prey and predator, the interaction can be weakened, and even disappear, with phenological mismatches. This may have cascading negative effects on ecosystem functions, such as herbivory control, and services, for instance if the resource of herbivores is of agricultural interest (Figs. 2a, 2c). It also means that the common practice of monitoring species richness as a surrogate for ecosystem integrity or functioning is not always relevant, especially under a high level of extinction debt. Interactions can be lost, but novel interactions can also emerge with equally important consequences for the maintenance of diversity and ecosystem processes (Pearse & Altermatt 2013b).

There is now good evidence that species interactions vary in space independently of species composition because the same co-occurring species do not always interact, while different species can all share the same type of interactions (Poisot *et al.* 2012). This suggests that interactions themselves can trump species identity, and that eventually the main driver of community structure and ecosystem processes is the spatial build up and arrangement of interaction diversity, identity, and strength (Pillai, Gonzalez & Loreau 2011). Therefore at the ecosystem process level, what matters are the interactions, rather than the species, we lose from the system.

The main logical implication of spatial variation in biotic interactions is that ecosystem processes likely vary across the landscape, resulting in spatial variation in the provision of ecosystem functions and services (Nelson *et al.* 2009; Steffen *et al.* 2015). The causes of these

variations in ecosystem functions are not yet well understood, however spatial connections between ecosystems through consumer coupling of habitats and the exchange of living (dispersal) and dead organisms (detritus, resources) certainly affect local interactions (Loreau, Mouquet & Holt 2003). Indeed, theoretical work using the meta-ecosystem framework recently demonstrated that structural attributes of a species interaction network in one ecosystem can have important effects on diversity and functioning of neighbouring ecosystems through direct dispersal or indirect energy and material flux (Loreau, Mouquet & Holt 2003). For example, in the Palmyra Atoll, the translocation of pelagic nutrients to otherwise oligotrophic coastal waters is facilitated by native trees *Pisonia grandis* and *Tournefortia argentea*, which are preferred nesting and roosting habitat for pelagic-foraging marine birds. This nutrient conveyer belt is thus disrupted by the replacement of native trees with cultivated coconut palm *Cocos nucifera* (Mccauley *et al.* 2012). Relative to *Cocos* stands, forest patches dominated by *Pisonia* and *Tournefortia* have greater marine bird abundance, greater soil and foliar nitrogen (attributed to bird guano), which are associated with greater nitrogen runoff into coastal waters, which is in turn associated with enhanced phytoplankton, zooplankton, and finally planktivorous manta ray (*Manta birostris*) abundance. Taking into account the potential impacts of reciprocal effects between ecosystems due to spatial flux may help predict how species interactions change with local environmental variation, possibly induced by anthropogenic perturbations. This should explain, at least in part, the wide spatial variation in ecosystem processes observed among naturally connected ecosystems (Altermatt 2013), or heterogeneous landscapes such as agricultural mosaics. For instance, in the deciduous boreal forest organic matter is exported to otherwise nutrient-poor, low-productivity lakes (Tanentzap *et al.* 2014). This subsidy enhances biomass in a food chain leading from bacteria to zooplankton and ultimately yellow perch (*Perca*

flavescens), a species of commercial and recreational value. The subsidy is disrupted by timber harvesting as the resultant reduced vegetation and poorly developed soils supply less organic matter to downstream lakes. Such effect of forest harvesting on riverine zooplankton may have spatially cascading effects on biotic interactions downstream (see Fig. 3), which ultimately may cause nutrient loadings and boosts of algal growth, resulting in loss of important ecosystem services (see Fig. 3).

Moving from a species to an interaction network perspective is necessary to understand how global change will affect biodiversity (McCann 2007) and will also offer a pro-active alternative targeting keystone interactions based on functional significance rather than the current, necessary, but more reactive approach to conservation. Targeting keystone interactions will therefore provide a much better proxy and predictor of ecosystem processes (Tomczak *et al.* 2013; Schleuning, Fründ & García 2015; Creamer *et al.* 2016).

A road map to ecological network conservation

Despite the above-discussed conceptual and logistical advances, it remains unclear how network conservation should take form in practice: which specific metrics should be measured, and which current management tools could help to restore or protect ecological networks (Tylianakis *et al.* 2010; Hagen *et al.* 2012)? The use of interaction networks in management remains in its infancy, hindered by the technical and scientific caveats highlighted above, frequent lack of localized abundance and interaction data, and gaps in mechanistic understanding of how interactions change across local contexts. Here, given the state of current knowledge, we demonstrate a novel approach to ecological network conservation allowing for a direct stability

assessment of the community and the identification of clear conservation targets to maintain it. We address questions related to the minimum amount of information needed, how to build the network, which metrics to measure and how, and then briefly discuss possible management tools. In its simplest implementation the technique is suitable for data-poor systems; as localized data become available and as mechanistic underpinnings of context dependencies become better understood, it will become possible to use interaction networks (or this technique) in management within spatially explicit contexts, integrating local context dependencies and quantitative interactions to accurately predict and prevent the consequences of perturbations such as species invasion, habitat fragmentation or climate change.

1. *Building ecological networks*

Quantifying interaction strength between each pair of species in an ecological network is too laborious and costly for most managers. Thus, the general ecology motto "the more the better" does not agree well with time and resource constraints associated with conservation management. It is, however, reasonable to assume that most conservation plans already include some kind of biodiversity survey. Therefore, a species list associated with qualitative or quantitative functional trait information as well as information on each species' overall occurrence, is often readily available at low cost, and constitutes the minimum information necessary to build an ecological network.

Simplifying the process of building ecological networks remains a work in progress. Fortunately, the recent resurgence of interest in interaction networks has triggered new methodological developments toward this goal. Perhaps most promising and exciting is the use

of inferential methods based on likelihood estimators (i.e. maximum likelihood or Bayesian) which allow for the flexible integration of prior knowledge and measurement error estimation (Grace *et al.* 2012; Hooten & Hobbs 2015), and machine learning, which facilitates the construction and validation of food webs using algorithms (Bohan *et al.* 2011; Tamaddoni-Nezhad *et al.* 2013). These approaches, mixed with available functional traits, phylogenetic, and co-occurrence data, can generate accurate, standardized, and highly reproducible networks (for a promising example see Morales-Castilla *et al.* 2015). Furthermore, publically available platforms already compile ecological network data that can be used to gain essential information to build similar ecological networks (Poisot *et al.* 2015). For conservation purposes, these new developments allow access to the "gold mine" that represents the vast collection of currently available empirical datasets previously considered ill-suited or insufficiently complete for network studies. The construction of interaction networks using time series or spatially explicit large datasets will allow direct testing of how interaction networks are qualitatively and quantitatively affected by land use changes, perturbations, and which network attributes hold the most important predictive value; all essential and previously unavailable keys for the implementation of network approaches in conservation science.

2. *Identifying conservation targets*

Many network metrics are known to be important for ecological community stability, however it remains unclear how these are affected by sampling effort and perturbations; furthermore, measuring these metrics often requires extensive knowledge of species interactions (Martinez 1991; Tylianakis *et al.* 2010). Instead, and until more information is available, we propose to extend the already well proven and extensively used keystone species concept (Paine

1995; Jordán 2009) by defining it here as the interactions between two species with the strongest impacts on community stability following their removal. The advantage of using keystone interactions is that it provides clear conservation targets, in contrast to other holistic but more diffused metrics (e.g. protecting network connectance). Moreover, identifying keystone interactions can be achieved easily with a directed network without prior knowledge of interaction strengths (see proof of concept in Fig. 4). Starting with a simple adjacency matrix composed of 1 (interaction) and 0 (no interaction, see Fig. 4b) we use a recently developed bootstrapping method to evaluate changes in network structural stability after removing each interaction sequentially (with replacement, based on Tang, Pawar & Allesina 2014 and Sauve *et al.* 2016, see Appendix 1 in Supporting Information for a detailed description and a ready-to-use annotated R code to perform the analysis). We propose a two-step approach to identify conservation targets in ecological networks: (i) each pairwise interaction is ranked based on its effect on network structural stability. This step provides information on which pairwise interactions need specific attentions from managers (see Fig. 4c). (ii) Sensitive species that are likely to go extinct following the removal of their prey (e.g. specialist consumers), potentially leading to cascading extinctions, are identified (Fig. 4c). This step provides managers with the identity of especially sensitive network nodes. Therefore, together these two steps lead to clear conservation targets for the holistic protection of both network structure and stability (Fig. 4d). Importantly, in Fig. 4 we document an example for consumptive interactions, however the technique is readily applicable to other types of interactions (e.g. mutualisms, see Appendix 1 for more details on how to proceed).

3. Management tools

Once keystone interactions and sensitive nodes are identified, the main issue is to efficiently achieve their protection. Based on current knowledge, we suggest that the main lever to restore or conserve ecological network structure and stability is the management of spatial configuration. Extensive research on effects of habitat loss and fragmentation on ecological networks (Hagen *et al.* 2012) suggests that re-thinking the spatial configuration of reserve networks is paramount to ecological network conservation (Hamilton *et al.* 2010; Spiecker, Gouhier & Guichard 2016). Specific recommendations on spatial management for ecological network conservation are beyond the scope of this work, but we believe that despite a growing interest there is still a great need for research on the subject (for an extensive review see Hagen *et al.* 2012).

Back to conservation

Protecting ecosystem integrity and species diversity is at the core of all conservation or restoration management actions. However, current rates of biodiversity loss speak volumes to the current failures and future challenges in targeting appropriate conservation priorities. In this context, it is important to question some of our basic assumptions about classical conservation approaches. Here we argue that the maintenance of biodiversity and ecosystem integrity are hypothesized rather than realized by species-specific and integral land conservation approaches (Fig. 1a). Instead, evidence suggests that changes in the nature and diversity of biotic interactions directly explain patterns of diversity and ecosystem function. In this context, we propose that a shift in focus from species to interaction networks is necessary to achieve pressing conservation management and restoration ecology goals of conserving biodiversity and the delivery of ecosystem services (Fig. 1b).

Ecosystems provide benefits to humans via a myriad of provisioning, cultural, and regulating services, which are all maintained by supporting ecosystem processes. Recent global indicators suggest that we have likely crossed the 'safe operating space' for many biogeochemical cycles directly related to these services. In light of current knowledge, global biodiversity loss and associated erosion of ecosystem processes are likely to lead to sudden collapses in the provision of several essential services. Here, we focus on current challenges to advance ecological sciences. Future research should also focus on fostering a better integration of social, economic, and ecological sciences, which constitutes the only way toward a unified framework to maintain ecosystem service provision (Consortium 2016). The Millennium Ecosystem Assessment (2005) called for a change of perspective that yet needs to be fully implemented; now is the time to do so.

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Data accessibility

Data have not been archived because this article does not contain data.

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Supporting Information

Appendix S1. Practical assessment of species interactions and their effect on the stability of ecological networks

Figure legends

Figure 1. A New focus in conservation biology.
(a) Current conservation approaches focus on protecting lands (national parks) or individual species of iconic value or hypothesized key role (umbrella species). These approaches assume implicit protection of ecosystem processes or biological communities, which may or may not be realized. (b) We propose that future conservation efforts focus on protecting ecosystem processes and interaction networks *per se*, with explicit positive effects on habitats and biodiversity. Thereby, both ecosystem services (ultimate value) and the diversity of habitats and species (proximate values) are maintained.

Figure 2. From interactions to ecosystem services
(a) Interaction networks drive ecosystem processes, which in turn determine the provision of ecosystem services. For instance, (b) some bird species feed on insects, while caterpillars supply protein-rich food for their offspring; this regulation of herbivores ensures good fruit production. However, (c) global warming may shift species phenology and caterpillar abundances may peak before eggs hatch. Although all species would remain present (no change in species richness), birds would no longer regulate caterpillars. This interaction loss may impact fruit production.

Figure 3. Resource flows and spatial feedbacks.
Interaction networks (circles and black arrows) are influenced by spatial flows of resources (brown arrows). For instance, (a) litter inputs from riverine forest supply food for bacteria, supporting high zooplankton abundance. This, in turn, enables zooplankton to regulate fast-growing algae (in green), whose abundance is boosted by agricultural fertilizer leachate. In this scenario, ecosystem services are maintained via spatial feedbacks of resource flows on species interactions. However, (b) if the forest is cut, algae escape zooplankton regulation owing to low bacterial density (attributable to disruption of litter input), potentially leading to eutrophication and ecosystem service loss.

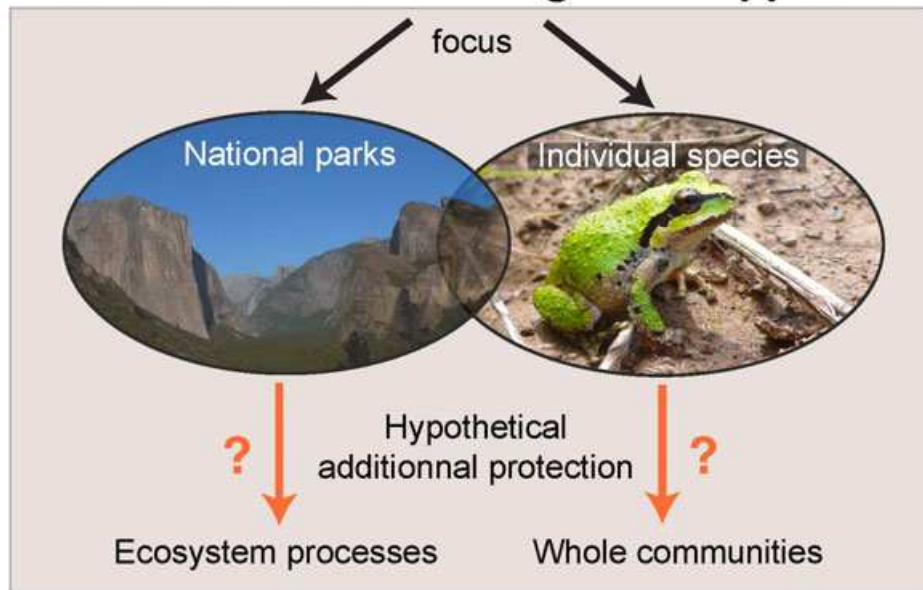Figure 4. Identifying conservation targets in networks.
Based on a hypothetical food web we describe how the loss of interactions affects stability of communities, and give a workflow of how conservation can identify and target such key interactions. Panel (a) illustrates a hypothetical food web composed of species A to Q, with arrows representing consumption links going from the resource to the consumer species. Panel (b) shows the corresponding adjacency matrix, with black squares representing interactions with species in rows consuming species in columns. Panel (c) shows the change in structural community stability (resilience to perturbation) which occurs when each interaction is set to 0. Interactions are ranked on the X-axis from those having the largest positive effect (green colours)

to those having the largest negative effect (red colours) on structural stability when removed. The blue arrows indicate ultra specialist species, which would go extinct following the loss of their prey (i.e., cascading extinctions). The number below each arrow represents the number of species expected to go extinct. In panel (d) we illustrate the interaction ranking from panel (c) with each arrow's colour giving the expected change in network stability following a loss of an interaction.

(a) **Past conservation management approach**

focus

National parks   Individual species

?   Hypothetical additionnal protection   ?

Ecosystem processes   Whole communities

(b) **Future conservation management approach**

focus

Ecosystem processes   Interaction networks

Effective protection

Habitats   Species

Interaction Network

Ecosystem Processes

Ecosystem Services

(a)

Phenology mismatch

Herbivory controled

Production increases

(b)

Herbivory not controled

Production drops

(c)

(a)

Litter input

Forest

Zooplankton

Bacteria

Algae

Agricultural Nutrient input

Recreational services

Good water quality

(b)

No litter input

Clear cut

Zooplankton

Bacteria

Algae

Agricultural Nutrient input

Loss of recreational services

Eutrophication

Poor water quality

(a)

(b) Resources
A B C D E F G H I J K L M N O P Q

Consumers

(c)
% Change in structural stability

Link removed

(d)