



**HAL**  
open science

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

Eric Harvey, Isabelle Gounand, Colette Ward, Florian Altermatt

► **To cite this version:**

Eric Harvey, Isabelle Gounand, Colette Ward, Florian Altermatt. Bridging ecology and conservation: from ecological networks to ecosystem function. *Journal of Applied Ecology*, 2017, 54 (2), pp.371-379. 10.1111/1365-2664.12769 . hal-03000348

**HAL Id: hal-03000348**

**<https://hal.science/hal-03000348>**

Submitted on 11 Nov 2020

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

3

4 **Running Head:** From ecological networks to ecosystem function

5

6 **Type of Article:** Forum

7

8 **Authors:** Eric Harvey<sup>1,2</sup>, Isabelle Gounand<sup>1,2</sup>, Colette Ward<sup>3</sup> and Florian Altermatt<sup>1,2</sup>

9

10 **Corresponding Author:** [eric.harvey@eawag.ch](mailto:eric.harvey@eawag.ch)

11

12 **Affiliations:**

13 <sup>1</sup>Department of Evolutionary Biology and Environmental Studies, University of Zurich,  
14 Winterthurerstrasse 190, CH-8057 Zürich, Switzerland.

15 <sup>2</sup>Eawag: Swiss Federal Institute of Aquatic Science and Technology, Department of  
16 Aquatic Ecology, Überlandstrasse 133, CH-8600 Dübendorf, Switzerland

<sup>3</sup> National Center for Ecological Analysis and Synthesis, University of California, Santa  
Barbara, 735 State Street, Suite 300, Santa Barbara, CA, USA 93101-5504

17

18

19

20

21

22 **Word counts:**

23 Summary: 171

24 Main text: 4'013

25 Acknowledgements: 48

26 References: 1'358

27 Figure legends: 476

28 Number of figures: 4

29 Number of references: 55

30

31 **Key words:** Ecological network, conservation biology, ecosystem functioning, global  
32 environmental change, meta-community, meta-ecosystem, spatial ecology, species  
33 interactions.

34

35

36 **Summary**

- 37 1. Current approaches to conservation may be inadequate to maintain ecosystem  
38 integrity because they are mostly based on rarity status of organisms rather  
39 than functional significance. Alternatively, approaches focusing on the  
40 protection of ecological networks lead to more appropriate conservation  
41 targets to maintain ecosystem integrity.
- 42 2. We propose that a shift in focus from species to interaction networks is  
43 necessary to achieve pressing conservation management and restoration  
44 ecology goals of conserving biodiversity, ecosystem processes and ultimately  
45 landscape-scale delivery of ecosystem services.
- 46 3. Using topical examples from the literature, we discuss historical and  
47 conceptual advances, current challenges, and ways to move forward. We also  
48 propose a road map to ecological network conservation, providing a novel  
49 ready to use approach to identify clear conservation targets with flexible data  
50 requirements.

51 **Synthesis and applications.** Integration of how environmental and spatial constraints  
52 affect the nature and strength of local interaction networks will improve our ability to  
53 predict their response to change. This will better protect species, ecosystem processes,  
54 and the resulting ecosystem services we depend on.

55

56 **Introduction - linking conservation science with 21<sup>st</sup> century ecology**

57

58 Conservation biology and restoration ecology are two modern research areas fostered  
59 by national park movements, wildlife conservation, and the broad international  
60 recognition of human impact on the planet that developed during the 20<sup>th</sup> century (e.g.,  
61 1987 Montreal protocol, and 1992 Rio De Janeiro convention on biodiversity). At the  
62 intersection between ecology and social sciences, conservation biology evolved as an  
63 independent science with its own body of scientific journals and communities. As an  
64 unintended consequence, there is now a significant divide between current concepts and  
65 knowledge in the field of ecology and the prescription of conservation measures and  
66 development of new policies. This schism has been noted (Pulliam 1997), and the gap is  
67 widening as the field of ecology has experienced significant conceptual and  
68 methodological paradigm shifts at the onset of the 21<sup>st</sup> century which have yet to be  
69 integrated into conservation and restoration perspectives.

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

79 to ecological network conservation using a novel and ready-to-use tool to identify clear  
80 conservation targets.

81

## 82 **From species to interaction networks**

### 83 *Current state of knowledge*

84 In the context of increasing human population, reduction in habitable land owing to  
85 climate change, and increasing demand for food and goods production, the ‘glass bell’  
86 approach to conservation, involving complete landscape protection through the creation  
87 of national parks, poses important spatial and societal challenges (Millenium Ecosystem  
88 Assessment, 2005). The often-perceived alternative to the more holistic park perspective  
89 is a species-level focus (Fig. 1). Protective legislation for rare or endangered species can  
90 be successful, however ‘Noah's Ark’ approaches are often costly and ineffective  
91 (Laycock *et al.* 2009). Moreover, this approach tends to be reactive and targets species  
92 based on rarity rather than functional significance, which can lead to significant resource  
93 allocation to a specific group of species or even a single species with limited return in  
94 terms of ecosystem integrity and functioning (e.g., Gotelli *et al.* 2012, discussing this in  
95 the context of resource-allocations to the presumably extinct ivory-billed woodpecker).  
96 Frequent lack of resources for conservation management has led to the development of  
97 cost-effective trade-offs in conservation efforts (Weitzman 1998). However, ranking  
98 conservation priorities among species or habitats is a complicated matter because such an  
99 assessment cannot be achieved without considering inter-dependencies among species  
100 owing to complex direct and indirect interactions (Courtois, Figuières & Mulier 2014).  
101 The integration of interdependent survival probabilities within conservation projects

102 prioritization models has shown that taking species interactions into account can  
103 completely reverse conservation priorities (Simianer 2007). However, to accurately rank  
104 conservation priorities, one would need predictions about which species or functional  
105 groups are most likely to respond to future changes, and how these changes would spread  
106 across the interaction network and affect other species (for an example see “a road map to  
107 ecological network conservation” section further below). The net effect of perturbations  
108 is not always intuitive, owing to different types of interactions (e.g., trophic, mutualistic)  
109 and indirect links between species (Tylianakis *et al.* 2010). For instance, the extinction of  
110 the butterfly *Phengaris (Maculinea) arion* in the UK resulted indirectly from the  
111 biocontrol of European rabbits (*Oryctolagus cuniculus*): the butterfly depended on the  
112 nest of the ant *Myrmica sabuleti* for the development of its larvae; *Myrmica*, in turn,  
113 depended on open areas supplied by rabbit grazing to establish their nests (Thomas,  
114 Simcox & Clarke 2009).

115       The study of species interactions has greatly improved our appreciation of the  
116 importance of network structure for ecological community stability, sensitivity to  
117 invasion, and extinction. For example, Pearse & Altermatt (2013a) analyzed regional  
118 extinctions in a trophic network of 900 Lepidoptera and 2403 potential host plant species  
119 in Central Europe. They reported that 8 of the 59 observed regional extinctions of  
120 Lepidoptera were associated with host-plant loss. Importantly, all 8 observed regional  
121 extinctions of Lepidoptera associated with host-plant loss occurred before the actual  
122 extinction of the host-plant. Thus, strong declines of host-plants can have cascading  
123 extinction effects on higher trophic levels before the plants actually go extinct,  
124 illustrating that interactions can be lost before any actual decline in species richness

125 (plants persisted at low abundance). This illustrates that preserving keystone interactions,  
126 rather than species, can be a pro-active way to maintain ecosystem integrity in the face of  
127 global change instead of allocating resources to already endangered species. In a  
128 conservation biology context, the network structure, and more specifically the  
129 connectance (number of interactions per node), is also important with respect to which  
130 species are likely to be threatened: monophagous or strictly oligophagous Lepidoptera are  
131 significantly more often listed as “regionally extinct” or “critically endangered” than as  
132 “least concern”, indicating that interaction networks may give a direct causal explanation  
133 for species’ threat status (Pearse & Altermatt 2013a).

134 A possible further contribution of studies of pairwise species interactions for  
135 conservation management is a better understanding of biocontrol failure or potential  
136 indirect effects of novel trophic interactions on community structure, species invasions,  
137 and response to perturbations (Russo *et al.* 2014, Wood *et al.* 2014, Alexander *et al.*  
138 2015). Among-species interactions can also be a powerful tool for predicting potential  
139 novel trophic interactions based on existing interactions in a straightforward manner  
140 (Pearse & Altermatt 2013b). For instance, the integration of 459 non-native plants into  
141 the diet of 900 native, Central European lepidoptera could be accurately predicted by a  
142 simple model based only on the interactions of lepidoptera with their native hosts as well  
143 as a plant phylogeny (Pearse & Altermatt 2013b). Some of the observed, and accurately  
144 predicted, novel trophic interactions between native plant hosts and lepidopteran  
145 herbivores also included species of agricultural or forestry significance, such as  
146 extensions of the Tussock moth (*Calliteara pudibunda*) larval diet to the non-native red  
147 oak (*Quercus rubra*) or sesiid moth *Synanthedon tipuliformis* larval diet to a non-native,

148 introduced gooseberry species (e.g., *Ribes aureum*). If such among-species interactions  
149 are ignored, natural enemies could potentially fail to control important agricultural pests,  
150 for instance the green peach aphid (*Myzus persicae*) has devastated potato fields (Straub  
151 & Snyder 2006), despite efforts to increase natural enemies abundance and diversity.  
152 Moreover, introduced non-native biocontrol agents can have non-target indirect effects  
153 despite high host-specificity. For instance gall flies (*Urophora affinis* and *U.*  
154 *quadrifasciata*), introduced in North America to control the expansion of knapweeds  
155 (*Centaurea maculosa* and *C. diffusa*), failed in their biocontrol role but became  
156 superabundant and subsidized populations of the generalist deer mouse (*Peromyscus*  
157 *maniculatus*), which in turn triggered several declines of native plants, insects and small  
158 mammals (Pearson & Callaway 2003).

159

#### 160 *Caveats and future perspective*

161 Unfortunately, despite these important contributions, early ecological network studies  
162 did not produce general principles for the organization and dynamics of natural  
163 communities, largely because they did not consider the environmental context in which  
164 these interactions occur (McGill *et al.* 2006). However, recent conceptual developments  
165 in community ecology have successfully integrated biotic interactions within both their  
166 local environment and their spatial context (Leibold *et al.* 2004). During the same period,  
167 the field of biogeography began to question the use of species-specific climatic envelopes  
168 for predicting species range-shifts following climate change, acknowledging that species  
169 do not migrate into empty vacuums but rather into established, complex and diverse  
170 biotic communities (Pearson & Dawson 2003). Thus, there is now compelling evidence

171 from both biogeography (Araújo & Luoto 2007) and meta-community research that local  
172 biodiversity strongly depends on interactions occurring at local and regional scales. For  
173 instance Pillai and colleagues (2011) demonstrated that complex food webs can persist in  
174 a structured landscape on a single basal resource, even though local coexistence would be  
175 impossible.

176 One of the greatest impediments to a broader development of ecological network  
177 research in conservation sciences is the challenge to construct accurate and meaningful  
178 interaction networks (Morales-Castilla *et al.* 2015). Complete species networks are rare  
179 and prone to resolution issues because they are often built over many years and integrate  
180 information from many contrasting sources (e.g. expert knowledge, gut contents, co-  
181 occurrence data). The problem with these time- and resource-consuming methods is that  
182 they can lead to false negatives (missing links that are important), overestimation of the  
183 importance of some links, or even – and most importantly – to false positives  
184 (hypothesized links that are not realized) when assuming interactions based on simple co-  
185 occurrences (Morales-Castilla *et al.* 2015). This is problematic because it means that  
186 most species network knowledge has been produced from a small subset of non-  
187 reproducible networks. Moreover, these traditional methods are not amenable to  
188 construction of interaction networks beyond food webs, resulting in historical bias  
189 towards the study of antagonistic interactions (Morales-Castilla *et al.* 2015), despite  
190 increasing awareness of the importance of mutualistic and facilitation interactions for the  
191 maintenance of diversity and ecosystem processes (Bascompte 2009).

192 There is also a need for development of new and more accurate process-based  
193 experimental and empirical knowledge. Recent breakthroughs have shown that the

194 qualitative nature (competitive, predator-prey, mutualistic) and quantitative strength of  
195 species interactions can change in space as a function of local conditions (Poisot *et al.*  
196 2012). For instance, stress gradients can modify the net balance between competition and  
197 facilitation, with competition dominating in low stress habitats and facilitation  
198 dominating in high stress habitats (Lortie & Callaway 2006). This has obvious  
199 implications for the study of species range shifts along environmental degradation  
200 gradients (e.g., climatic, drought) because increasing positive interactions at each end of  
201 the gradient could support better persistence rates than previously predicted. However our  
202 mechanistic understanding of how the nature and strength of these interactions change as  
203 a function of environmental context remains shockingly anemic (Poisot *et al.* 2012). In  
204 the context of increased frequency of perturbations and landscape alterations, we also  
205 need to understand mechanistically how multiple perturbations spread through local  
206 networks (Tylianakis *et al.* 2010). In a recent study, Harvey and MacDougall (2015)  
207 showed how regional landscape fragmentation and local fertilization in grasslands  
208 interact to homogenize insect herbivore regulation. This unfolded because fragmentation  
209 reduced predator abundance, while both fragmentation and fertilization altered host plant  
210 diversity. These effects led to a significant increase in bottom-up constraints, facilitating  
211 a reduction in insect diversity and regional dominance by a few Hemipteran herbivore  
212 generalists (mainly Miridae family). Most importantly, the study demonstrated that these  
213 perturbation effects on insect herbivores were entirely mediated by bottom-up and top-  
214 down trophic interactions, suggesting that herbivores themselves would be the wrong  
215 target to mitigate effects of landscape alteration. For these purposes, accessible methods  
216 have been recently proposed to measure interaction strengths within controlled laboratory

217 experiments (Carrara *et al.* 2015), and the use of molecular toolkits (e.g., stable isotopes,  
218 eDNA) promise an exciting future for the generation of *in situ* new empirical data beyond  
219 species level information (Smith *et al.* 2011).

220

### 221 *From ecological network conservation to ecosystem functioning*

222 Recent evidence that interactions can be lost at a quicker pace than species following  
223 environmental degradation, for instance through the local extinction of host plants  
224 (Pearse & Altermatt 2013a) or through the desynchronization of species activity periods  
225 (Visser & Both 2005), is concerning because it demonstrates that essential functions  
226 performed by species (e.g., pollination, herbivore regulation) can be lost despite species  
227 remaining present in a system (Valiente-Banuet *et al.* 2015). For instance, many  
228 insectivorous birds, such as the great tit (*Parus major*), hatch in synchrony with the  
229 emergence of high-protein insect prey necessary to sustain youngling development (Fig.  
230 2b). Earlier springs and longer growing seasons due to climate change generate a  
231 mismatch between hatching time of the great tit and its prey emergence, leading to a  
232 decrease of the number and fitness of fledged chicks (Visser, Holleman & Gienapp  
233 2005). Despite the presence of both prey and predator, the interaction can be weakened,  
234 and even disappear, with phenological mismatches. This may have cascading negative  
235 effects on ecosystem functions, such as herbivory control, and services, for instance if the  
236 resource of herbivores is of agricultural interest (Figs. 2a, 2c). It also means that the  
237 common practice of monitoring species richness as a surrogate for ecosystem integrity or  
238 functioning is not always relevant, especially under a high level of extinction debt.  
239 Interactions can be lost, but novel interactions can also emerge with equally important

240 consequences for the maintenance of diversity and ecosystem processes (Pearse &  
241 Altermatt 2013b).

242       There is now good evidence that species interactions vary in space independently of  
243 species composition because the same co-occurring species do not always interact, while  
244 different species can all share the same type of interactions (Poisot *et al.* 2012). This  
245 suggests that interactions themselves can trump species identity, and that eventually the  
246 main driver of community structure and ecosystem processes is the spatial build up and  
247 arrangement of interaction diversity, identity, and strength (Pillai, Gonzalez & Loreau  
248 2011). Therefore at the ecosystem process level, what matters are the interactions, rather  
249 than the species, we lose from the system.

250       The main logical implication of spatial variation in biotic interactions is that  
251 ecosystem processes likely vary across the landscape, resulting in spatial variation in the  
252 provision of ecosystem functions and services (Nelson *et al.* 2009; Steffen *et al.* 2015).  
253 The causes of these variations in ecosystem functions are not yet well understood,  
254 however spatial connections between ecosystems through consumer coupling of habitats  
255 and the exchange of living (dispersal) and dead organisms (detritus, resources) certainly  
256 affect local interactions (Loreau, Mouquet & Holt 2003). Indeed, theoretical work using  
257 the meta-ecosystem framework recently demonstrated that structural attributes of a  
258 species interaction network in one ecosystem can have important effects on diversity and  
259 functioning of neighbouring ecosystems through direct dispersal or indirect energy and  
260 material flux (Loreau, Mouquet & Holt 2003). For example, in the Palmyra Atoll, the  
261 translocation of pelagic nutrients to otherwise oligotrophic coastal waters is facilitated by  
262 native trees *Pisonia grandis* and *Tournefortia argentea*, which are preferred nesting and

263 roosting habitat for pelagic-foraging marine birds. This nutrient conveyer belt is thus  
264 disrupted by the replacement of native trees with cultivated coconut palm *Cocos nucifera*  
265 (Mccauley *et al.* 2012). Relative to *Cocos* stands, forest patches dominated by *Pisonia*  
266 and *Tournefortia* have greater marine bird abundance, greater soil and foliar nitrogen  
267 (attributed to bird guano), which are associated with greater nitrogen runoff into coastal  
268 waters, which is in turn associated with enhanced phytoplankton, zooplankton, and  
269 finally planktivorous manta ray (*Manta birostris*) abundance. Taking into account the  
270 potential impacts of reciprocal effects between ecosystems due to spatial flux may help  
271 predict how species interactions change with local environmental variation, possibly  
272 induced by anthropogenic perturbations. This should explain, at least in part, the wide  
273 spatial variation in ecosystem processes observed among naturally connected ecosystems  
274 (Altermatt 2013), or heterogeneous landscapes such as agricultural mosaics. For instance,  
275 in the deciduous boreal forest organic matter is exported to otherwise nutrient-poor, low-  
276 productivity lakes (Tanentzap *et al.* 2014). This subsidy enhances biomass in a food chain  
277 leading from bacteria to zooplankton and ultimately yellow perch (*Perca flavescens*), a  
278 species of commercial and recreational value. The subsidy is disrupted by timber  
279 harvesting as the resultant reduced vegetation and poorly developed soils supply less  
280 organic matter to downstream lakes. Such effect of forest harvesting on riverine  
281 zooplankton may have spatially cascading effects on biotic interactions downstream (see  
282 Fig. 3), which ultimately may cause nutrient loadings and boosts of algal growth,  
283 resulting in loss of important ecosystem services (see Fig. 3).

284 Moving from a species to an interaction network perspective is necessary to  
285 understand how global change will affect biodiversity (McCann 2007) and will also offer

286 a pro-active alternative targeting keystone interactions based on functional significance  
287 rather than the current, necessary, but more reactive approach to conservation. Targeting  
288 keystone interactions will therefore provide a much better proxy and predictor of  
289 ecosystem processes (Tomczak *et al.* 2013; Schleuning, Fründ & García 2015; Creamer  
290 *et al.* 2016).

291

## 292 **A road map to ecological network conservation**

293 Despite the above-discussed conceptual and logistical advances, it remains unclear  
294 how network conservation should take form in practice: which specific metrics should be  
295 measured, and which current management tools could help to restore or protect  
296 ecological networks (Tylianakis *et al.* 2010; Hagen *et al.* 2012)? The use of interaction  
297 networks in management remains in its infancy, hindered by the technical and scientific  
298 caveats highlighted above, frequent lack of localized abundance and interaction data, and  
299 gaps in mechanistic understanding of how interactions change across local contexts.

300 Here, given the state of current knowledge, we demonstrate a novel approach to  
301 ecological network conservation allowing for a direct stability assessment of the  
302 community and the identification of clear conservation targets to maintain it. We address  
303 questions related to the minimum amount of information needed, how to build the  
304 network, which metrics to measure and how, and then briefly discuss possible  
305 management tools. In its simplest implementation the technique is suitable for data-poor  
306 systems; as localized data become available and as mechanistic underpinnings of context  
307 dependencies become better understood, it will become possible to use interaction  
308 networks (or this technique) in management within spatially explicit contexts, integrating

309 local context dependencies and quantitative interactions to accurately predict and prevent  
310 the consequences of perturbations such as species invasion, habitat fragmentation or  
311 climate change.

312 *1. Building ecological networks*

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

321 Simplifying the process of building ecological networks remains a work in progress.  
322 Fortunately, the recent resurgence of interest in interaction networks has triggered new  
323 methodological developments toward this goal. Perhaps most promising and exciting is  
324 the use of inferential methods based on likelihood estimators (i.e. maximum likelihood or  
325 Bayesian) which allow for the flexible integration of prior knowledge and measurement  
326 error estimation (Grace *et al.* 2012; Hooten & Hobbs 2015), and machine learning, which  
327 facilitates the construction and validation of food webs using algorithms (Bohan *et al.*  
328 2011; Tamaddoni-Nezhad *et al.* 2013). These approaches, mixed with available  
329 functional traits, phylogenetic, and co-occurrence data, can generate accurate,  
330 standardized, and highly reproducible networks (for a promising example see Morales-  
331 Castilla *et al.* 2015). Furthermore, publically available platforms already compile

332 ecological network data that can be used to gain essential information to build similar  
333 ecological networks (Poisot *et al.* 2015). For conservation purposes, these new  
334 developments allow access to the “gold mine” that represents the vast collection of  
335 currently available empirical datasets previously considered ill-suited or insufficiently  
336 complete for network studies. The construction of interaction networks using time series  
337 or spatially explicit large datasets will allow direct testing of how interaction networks  
338 are qualitatively and quantitatively affected by land use changes, perturbations, and  
339 which network attributes hold the most important predictive value; all essential and  
340 previously unavailable keys for the implementation of network approaches in  
341 conservation science.

## 342           2. *Identifying conservation targets*

343       Many network metrics are known to be important for ecological community stability,  
344 however it remains unclear how these are affected by sampling effort and perturbations;  
345 furthermore, measuring these metrics often requires extensive knowledge of species  
346 interactions (Martinez 1991; Tylianakis *et al.* 2010). Instead, and until more information  
347 is available, we propose to extend the already well proven and extensively used keystone  
348 species concept (Paine 1995; Jordán 2009) by defining it here as the interactions between  
349 two species with the strongest impacts on community stability following their removal.  
350 The advantage of using keystone interactions is that it provides clear conservation targets,  
351 in contrast to other holistic but more diffused metrics (e.g. protecting network  
352 connectance). Moreover, identifying keystone interactions can be achieved easily with a  
353 directed network without prior knowledge of interaction strengths (see proof of concept  
354 in Fig. 4). Starting with a simple adjacency matrix composed of 1 (interaction) and 0 (no

355 interaction, see Fig. 4b) we use a recently developed bootstrapping method to evaluate  
356 changes in network structural stability after removing each interaction sequentially (with  
357 replacement, based on Tang, Pawar & Allesina 2014 and Sauve *et al.* 2016, see Appendix  
358 1 in Supporting Information for a detailed description and a ready-to-use annotated R  
359 code to perform the analysis). We propose a two-step approach to identify conservation  
360 targets in ecological networks: (i) each pairwise interaction is ranked based on its effect  
361 on network structural stability. This step provides information on which pairwise  
362 interactions need specific attentions from managers (see Fig. 4c). (ii) Sensitive species  
363 that are likely to go extinct following the removal of their prey (e.g. specialist  
364 consumers), potentially leading to cascading extinctions, are identified (Fig. 4c). This  
365 step provides managers with the identity of especially sensitive network nodes.  
366 Therefore, together these two steps lead to clear conservation targets for the holistic  
367 protection of both network structure and stability (Fig. 4d). Importantly, in Fig. 4 we  
368 document an example for consumptive interactions, however the technique is readily  
369 applicable to other types of interactions (e.g. mutualisms, see Appendix 1 for more details  
370 on how to proceed).

### 371 *3. Management tools*

372 Once keystone interactions and sensitive nodes are identified, the main issue is to  
373 efficiently achieve their protection. Based on current knowledge, we suggest that the  
374 main lever to restore or conserve ecological network structure and stability is the  
375 management of spatial configuration. Extensive research on effects of habitat loss and  
376 fragmentation on ecological networks (Hagen *et al.* 2012) suggests that re-thinking the  
377 spatial configuration of reserve networks is paramount to ecological network

378 conservation (Hamilton *et al.* 2010; Spiecker, Gouhier & Guichard 2016). Specific  
379 recommendations on spatial management for ecological network conservation are beyond  
380 the scope of this work, but we believe that despite a growing interest there is still a great  
381 need for research on the subject (for an extensive review see Hagen *et al.* 2012).

382

### 383 **Back to conservation**

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

396 Ecosystems provide benefits to humans via a myriad of provisioning, cultural, and  
397 regulating services, which are all maintained by supporting ecosystem processes. Recent  
398 global indicators suggest that we have likely crossed the ‘safe operating space’ for many  
399 biogeochemical cycles directly related to these services. In light of current knowledge,  
400 global biodiversity loss and associated erosion of ecosystem processes are likely to lead  
401 to sudden collapses in the provision of several essential services. Here, we focus on

402 current challenges to advance ecological sciences. Future research should also focus on  
403 fostering a better integration of social, economic, and ecological sciences, which  
404 constitutes the only way toward a unified framework to maintain ecosystem service  
405 provision (Consortium 2016). The Millennium Ecosystem Assessment (2005) called for a  
406 change of perspective that yet needs to be fully implemented; now is the time to do so.

407

#### 408 **Acknowledgements**

409 We would like to thank C. Lortie, A. Sauve, E. Thébault and the E.M.E.R.Ge research  
410 group for enlightening discussions, and D. Bohan and one anonymous reviewer for  
411 comments that improved our manuscript. EH, IG, and FA acknowledge funding from the  
412 Swiss National Science Foundation Grant PP00P3\_150698, University of Zurich and  
413 Eawag.

414 **References**

- 415 Alexander, J. M., Diez J. M., and Levine J. M. (2015) Novel competitors shape species'  
416 responses to climate change. *Nature*, **525**, 515-518.
- 417 Altermatt, F. (2013) Diversity in riverine metacommunities: a network perspective.  
418 *Aquatic Ecology*, **47**, 365–377.
- 419 Araújo, M.B. & Luoto, M. (2007) The importance of biotic interactions for modelling  
420 species distributions under climate change. *Global Ecology and Biogeography*,  
421 **16**, 743–753.
- 422 Bascompte, J. (2009) Mutualistic networks. *Frontiers in Ecology and the Environment*, **7**,  
423 429–436.
- 424 Bohan, D.A., Caron-Lormier, G., Muggleton, S., Raybould, A. & Tamaddoni-Nezhad, A.  
425 (2011) Automated discovery of food webs from ecological data using logic-based  
426 machine learning. *PLOS ONE*, **6**, e29028.
- 427 Carrara, F., Giometto, A., Seymour, M., Rinaldo, A. & Altermatt, F. (2015) Inferring  
428 species interactions in ecological communities: a comparison of methods at  
429 different levels of complexity. *Methods in Ecology and Evolution*, **6**, 895–906.
- 430 Consortium, T.Q. (2016) Networking our way to better ecosystem service provision.  
431 *Trends in Ecology & Evolution*, **31**, 105–115.
- 432 Courtois, P., Figuières, C. & Mulier, C. (2014) Conservation priorities when species  
433 interact: the noah's ark metaphor revisited. *PLoS ONE*, **9**, e106073.
- 434 Creamer, R.E., Hannula, S.E., Leeuwen, J.P.V., Stone, D., Rutgers, M., Schmelz, R.M.,  
435 Ruiter, P.C. de, Hendriksen, N.B., Bolger, T., Bouffaud, M.L., Buee, M.,  
436 Carvalho, F., Costa, D., Dirilgen, T., Francisco, R., Griffiths, B.S., Griffiths, R.,  
437 Martin, F., Silva, P.M. da, Mendes, S., Morais, P.V., Pereira, C., Philippot, L.,  
438 Plassart, P., Redecker, D., Römbke, J., Sousa, J.P., Wouterse, M. & Lemanceau,  
439 P. (2016) Ecological network analysis reveals the inter-connection between soil  
440 biodiversity and ecosystem function as affected by land use across Europe.  
441 *Applied Soil Ecology*, **97**, 112–124.
- 442 Gotelli, N.J., Chao, A., Colwell, R.K., Hwang, W.-H. & Graves, G.R. (2012) Specimen-  
443 based modeling, stopping rules, and the extinction of the Ivory-Billed  
444 Woodpecker. *Conservation Biology*, **26**, 47–56.
- 445 Grace, J.B., Schoolmaster, D.R., Guntenspergen, G.R., Little, A.M., Mitchell, B.R.,  
446 Miller, K.M. & Schweiger, E.W. (2012) Guidelines for a graph-theoretic  
447 implementation of structural equation modeling. *Ecosphere*, **3**, art73.
- 448 Hagen, M., Kissling, W.D., Rasmussen, C., De Aguiar, M.A.M., Brown, L.E.,  
449 Carstensen, D.W., Alves-Dos-Santos, I., Dupont, Y.L., Edwards, F.K., Genini, J.,

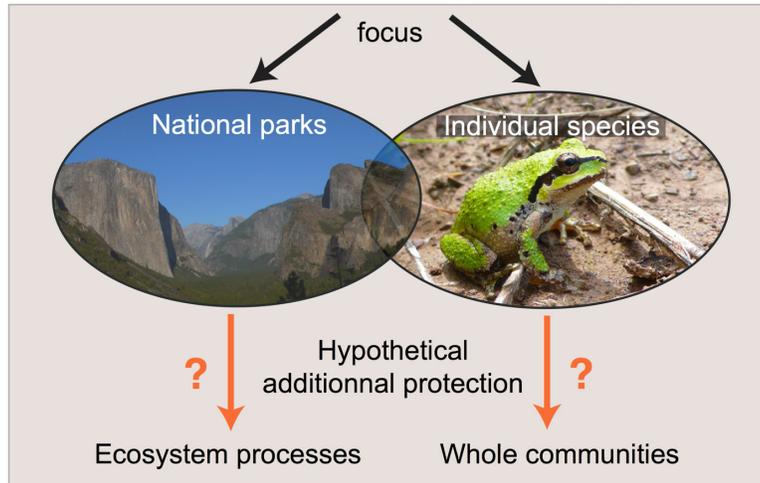
- 450 Guimarães Jr., P.R., Jenkins, G.B., Jordano, P., Kaiser-Bunbury, C.N., Ledger,  
 451 M.E., Maia, K.P., Marquitti, F.M.D., Mclaughlin, Ó., Morellato, L.P.C.,  
 452 O’Gorman, E.J., Trøjelsgaard, K., Tylianakis, J.M., Vidal, M.M., Woodward, G.  
 453 & Olesen, J.M. (2012) 2 - Biodiversity, species interactions and ecological  
 454 networks in a fragmented world. *Advances in Ecological Research* Global Change  
 455 in Multispecies Systems Part 1. (ed U.J. and G. Woodward), pp. 89–210.  
 456 Academic Press.
- 457 Hamilton, S.L., Caselle, J.E., Malone, D.P. & Carr, M.H. (2010) Incorporating  
 458 biogeography into evaluations of the Channel Islands marine reserve network.  
 459 *Proceedings of the National Academy of Sciences of the United States of America*,  
 460 **107**, 18272–18277.
- 461 Harvey, E. & MacDougall, A.S. (2015) Spatially heterogeneous perturbations  
 462 homogenize the regulation of insect herbivores. *The American Naturalist*, **186**,  
 463 623–633.
- 464 Hooten, M.B. & Hobbs, N.T. (2015) A guide to Bayesian model selection for ecologists.  
 465 *Ecological Monographs*, **85**, 3–28.
- 466 Jordán, F. (2009) Keystone species and food webs. *Philosophical Transactions of the*  
 467 *Royal Society B: \dots*, **364**, 1733–1741.
- 468 Laycock, H., Moran, D., Smart, J., Raffaelli, D. & White, P. (2009) Evaluating the cost-  
 469 effectiveness of conservation: The UK Biodiversity Action Plan. *Biological*  
 470 *Conservation*, **142**, 3120–3127.
- 471 Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F.,  
 472 Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M. & Gonzalez, A. (2004)  
 473 The metacommunity concept: a framework for multi-scale community ecology.  
 474 *Ecology Letters*, **7**, 601–613.
- 475 Loreau, M., Mouquet, N. & Holt, R.D. (2003) Meta-ecosystems: a theoretical framework  
 476 for a spatial ecosystem ecology. *Ecology Letters*, **6**, 673–679.
- 477 Lortie, C.J. & Callaway, R.M. (2006) Re-analysis of meta-analysis: support for the stress-  
 478 gradient hypothesis. *Journal of Ecology*, **94**, 7–16.
- 479 Martinez, N. (1991) Artifacts or Attributes ? Effects of resolution on the Little Rock lake  
 480 food web. *Ecological Monographs*, **61**, 367–392.
- 481 McCann, K. (2007) Protecting biostructure. *Nature*, **446**, 29–29.
- 482 Mccauley, D.J., Desalles, P.A., Young, H.S., Dunbar, R.B., Dirzo, R., Mills, M.M. &  
 483 Micheli, F. (2012) Long ecological interaction chains in less-disturbed  
 484 ecosystems. *Scientific Reports*, 10.1038/srep00409.

- 485 McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006) Rebuilding community  
486 ecology from functional traits. *Trends in Ecology & Evolution*, **21**, 178–185.
- 487 Millenium Ecosystem Assessment, Ecosystems and Human Well-Being : Synthesis.  
488 (2005) Island Press, Washington, DC.
- 489 Morales-Castilla, I., Matias, M.G., Gravel, D. & Araújo, M.B. (2015) Inferring biotic  
490 interactions from proxies. *Trends in Ecology & Evolution*, **30**, 347–356.
- 491 Nelson, E., Mendoza, G., Regetz, J., Polasky, S., Tallis, H., Cameron, Dr., Chan, K.M.,  
492 Daily, G.C., Goldstein, J., Kareiva, P.M., Lonsdorf, E., Naidoo, R., Ricketts, T.H.  
493 & Shaw, Mr. (2009) Modeling multiple ecosystem services, biodiversity  
494 conservation, commodity production, and tradeoffs at landscape scales. *Frontiers  
495 in Ecology and the Environment*, **7**, 4–11.
- 496 Paine, R. (1995) A conversation on refining the concept of keystone species. , **9**, 962–  
497 964.
- 498 Pearse, I.S. & Altermatt, F. (2013a) Extinction cascades partially estimate herbivore  
499 losses in a complete Lepidoptera--plant food web. *Ecology*, **94**, 1785–1794.
- 500 Pearse, I.S. & Altermatt, F. (2013b) Predicting novel trophic interactions in a non-native  
501 world. *Ecology Letters*, **16**, 1088–1094.
- 502 Pearson, D.E. & Callaway, R.M. (2003) Indirect effects of host-specific biological  
503 control agents. *Trends in Ecology & Evolution*, **18**, 456–461.
- 504 Pearson, R.G. & Dawson, T.P. (2003) Predicting the impacts of climate change on the  
505 distribution of species: are bioclimate envelope models useful? *Global Ecology  
506 and Biogeography*, **12**, 361–371.
- 507 Pillai, P., Gonzalez, A. & Loreau, M. (2011) Metacommunity theory explains the  
508 emergence of food web complexity. *Proceedings of the National Academy of  
509 Sciences of the United States of America*, **108**, 19293–8.
- 510 Poisot, T., Baiser, B., Dunne, J.A., Kéfi, S., Massol, F., Mouquet, N., Romanuk, T.N.,  
511 Stouffer, D.B., Wood, S.A. & Gravel, D. (2015) mangal – making ecological  
512 network analysis simple. *Ecography*, **39**, 384-390.
- 513 Poisot, T., Canard, E., Mouillot, D., Mouquet, N., Gravel, D. & Jordan, F. (2012) The  
514 dissimilarity of species interaction networks. *Ecology letters*, **15**, 1353–61.
- 515 Pulliam, H. (1997) Conservation ecology: bridging the gap between ecology and resource  
516 management, <http://www.ecologyandsociety.org/vol1/iss1/art14/>
- 517 Russo, Laura, Memmott J., Montoya D., Shea K., and Buckley Y. M. (2014) Patterns of  
518 introduced species interactions affect multiple aspects of network structure in  
519 plant–pollinator communities. *Ecology*, **95**, 2953–63.

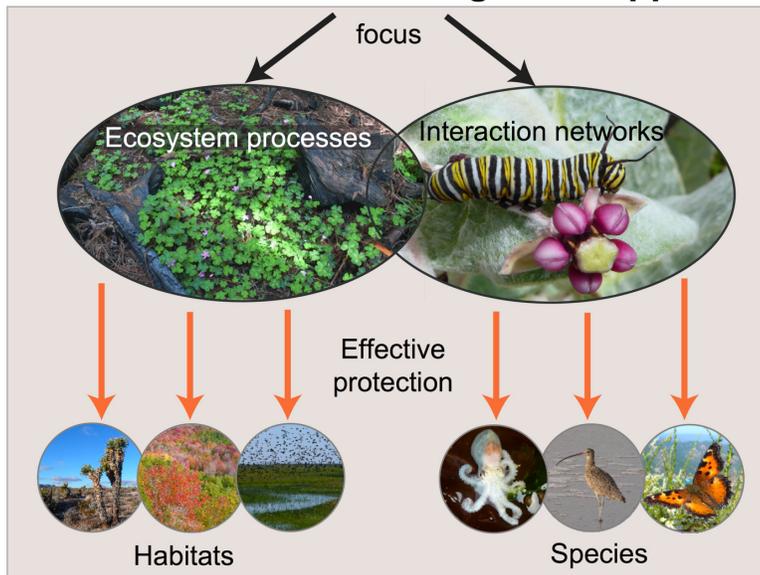
- 520  
521 Sauve, A.M.C., Thébault, E., Poccock, M.J.O. & Fontaine, C. (2016) How plants connect  
522 pollination and herbivory networks and their contribution to community stability.  
523 *Ecology*, **97**, 908–917.
- 524 Schleuning, M., Fründ, J. & García, D. (2015) Predicting ecosystem functions from  
525 biodiversity and mutualistic networks: an extension of trait-based concepts to  
526 plant–animal interactions. *Ecography*, **38**, 380–392.
- 527 Simianer, H. (2007) Accounting for non-independence of extinction probabilities in the  
528 derivation of conservation priorities based on Weitzman’s diversity concept.  
529 *Conservation Genetics*, **9**, 171–179.
- 530 Smith, M.A., Eveleigh, E.S., McCann, K.S., Merilo, M.T., McCarthy, P.C. & Van  
531 Rooyen, K.I. (2011) Barcoding a quantified food web: crypsis, concepts, ecology  
532 and hypotheses. *PLoS ONE*, **6**, e14424.
- 533 Spiecker, B., Gouhier, T.C. & Guichard, F. (2016) Reciprocal feedbacks between spatial  
534 subsidies and reserve networks in coral reef meta-ecosystems. *Ecological*  
535 *Applications*, **26**, 264–278.
- 536 Steffen, W., Richardson, K., Rockström, J., Cornell, S.E., Fetzer, I., Bennett, E.M.,  
537 Biggs, R., Carpenter, S.R., Vries, W. de, Wit, C.A. de, Folke, C., Gerten, D.,  
538 Heinke, J., Mace, G.M., Persson, L.M., Ramanathan, V., Reyers, B. & Sörlin, S.  
539 (2015) Planetary boundaries: Guiding human development on a changing planet.  
540 *Science*, **347**, 1259855.
- 541 Straub, C.S. & Snyder, W.E. (2006) Species identity dominates the relationship between  
542 predator biodiversity and herbivore suppression. *Ecology*, **87**, 277–282.
- 543 Tamaddoni-Nezhad, A., Milani, G.A., Raybould, A., Muggleton, S. & Bohan, D.A.  
544 (2013) Chapter Four - Construction and validation of food webs using logic-based  
545 machine learning and text mining. *Advances in Ecological Research Ecological*  
546 *Networks in an Agricultural World*. (ed G.W. and D.A. Bohan), pp. 225–289.  
547 Academic Press.
- 548 Tanentzap, A.J., Szkokan-Emilson, E.J., Kielstra, B.W., Arts, M.T., Yan, N.D. & Gunn,  
549 J.M. (2014) Forests fuel fish growth in freshwater deltas. *Nature*  
550 *Communications*, **5**.
- 551 Tang, S., Pawar, S. & Allesina, S. (2014) Correlation between interaction strengths drives  
552 stability in large ecological networks. *Ecology Letters*, **17**, 1094–1100.
- 553 Thomas, J.A., Simcox, D.J. & Clarke, R.T. (2009) Successful conservation of a  
554 threatened *Maculinea* butterfly. *Science*, **325**, 80–83.

- 555 Tomczak, M.T., Heymans, J.J., Yletyinen, J., Niiranen, S., Otto, S.A. & Blenckner, T.  
556 (2013) Ecological network indicators of ecosystem status and change in the baltic  
557 sea. *PLOS ONE*, **8**, e75439.
- 558 Tylianakis, J.M., Laliberté, E., Nielsen, A. & Bascompte, J. (2010) Conservation of  
559 species interaction networks. *Biological Conservation*, **143**, 2270–2279.
- 560 Valiente-Banuet, A., Aizen, M.A., Alcántara, J.M., Arroyo, J., Cocucci, A., Galetti, M.,  
561 García, M.B., García, D., Gómez, J.M., Jordano, P., Medel, R., Navarro, L.,  
562 Obeso, J.R., Oviedo, R., Ramírez, N., Rey, P.J., Traveset, A., Verdú, M. &  
563 Zamora, R. (2015) Beyond species loss: the extinction of ecological interactions  
564 in a changing world. *Functional Ecology*, **29**, 299–307.
- 565 Visser, M.E. & Both, C. (2005) Shifts in phenology due to global climate change: the  
566 need for a yardstick. *Proceedings of the Royal Society of London B: Biological  
567 Sciences*, **272**, 2561–2569.
- 568 Visser, M.E., Holleman, L.J.M. & Gienapp, P. (2005) Shifts in caterpillar biomass  
569 phenology due to climate change and its impact on the breeding biology of an  
570 insectivorous bird. *Oecologia*, **147**, 164–172.
- 571 Weitzman, M.L. (1998) The Noah’s Ark problem. *Econometrica*, **66**, 1279–1298.
- 572 Wood, J. R., Dickie I., Moeller H., Peltzer D. A., Bonner K. I., Rattray G., and  
573 Wilmshurst J.M. (2014) Novel interactions between non-native mammals and  
574 fungi facilitate establishment of invasive pines. *Journal of Ecology* **103**: 121–29.  
575  
576  
577  
578

**(a) Past conservation management approach**



**(b) Future conservation management approach**



581

582

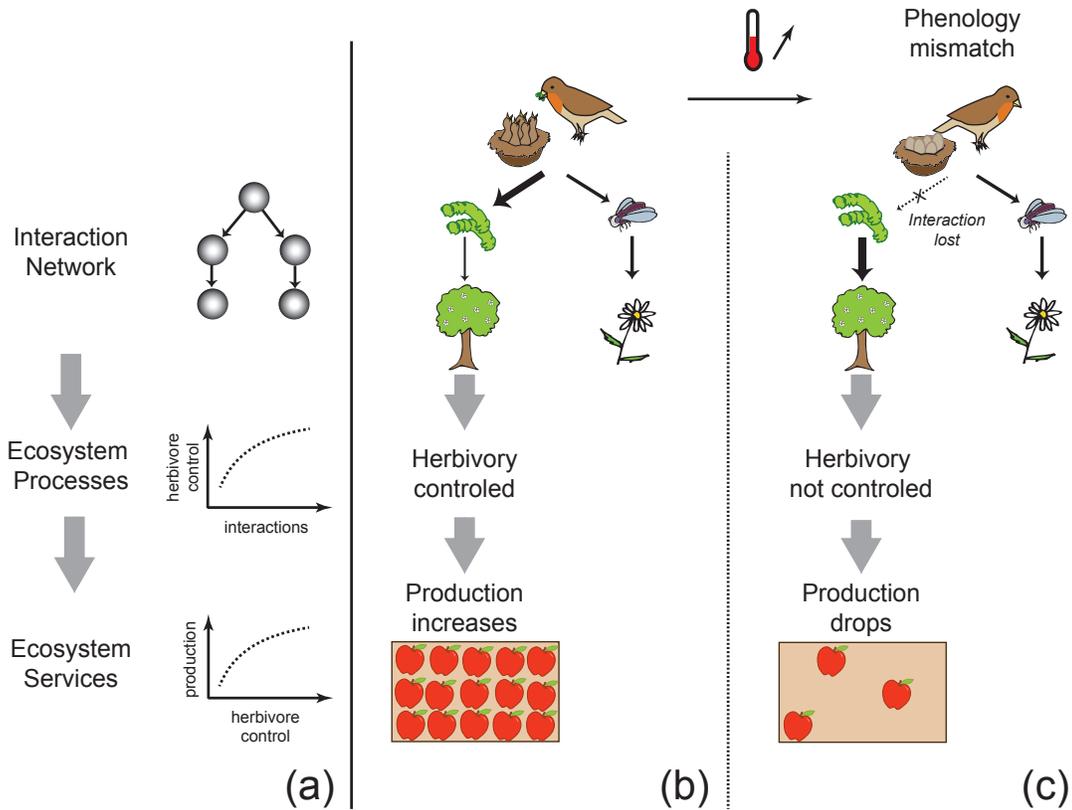
Figure 1. A New focus in conservation biology.

583

(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.

589

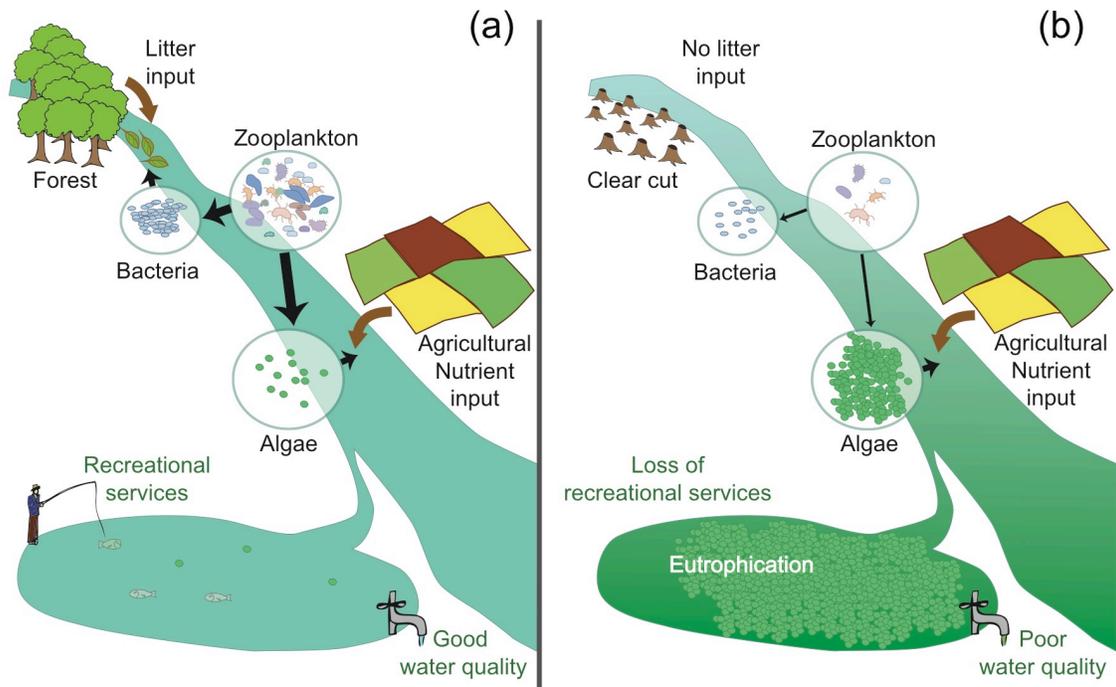
590



591  
 592  
 593  
 594  
 595  
 596  
 597  
 598  
 599  
 600

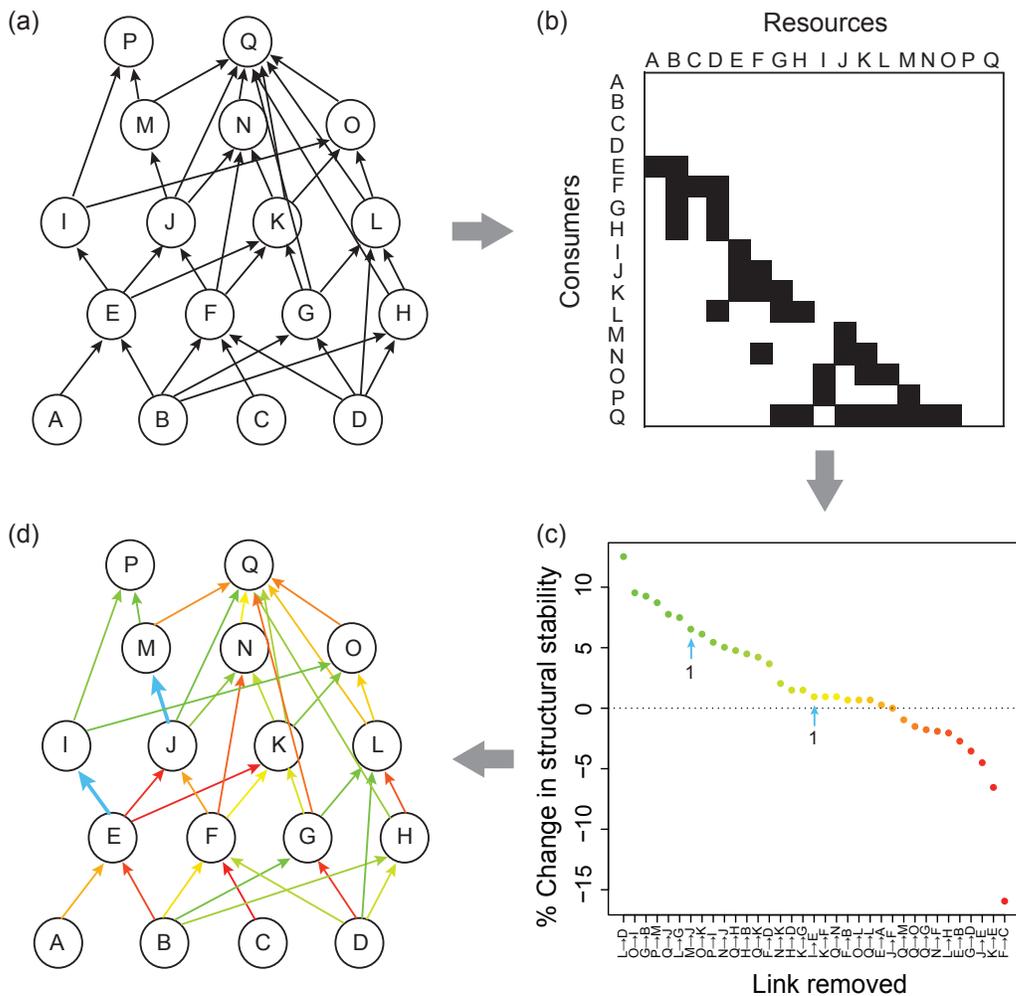
Figure 2. From interactions to ecosystem services.

(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.



601  
 602  
 603  
 604  
 605  
 606  
 607  
 608  
 609  
 610  
 611  
 612  
 613

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.



615  
 616  
 617  
 618  
 619  
 620  
 621  
 622  
 623  
 624  
 625  
 626  
 627  
 628  
 629  
 630  
 631  
 632

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.