Spatial ecological networks: planning for sustainability in the long-term

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Humans are producing complex and often undesirable social and ecological outcomes in many landscapes around the world. To sustain biodiversity and ecosystem services in fragmented landscapes conservation planning has turned to the identification and protection of large-scale spatial ecological networks (SEN). Now widely adopted, this approach typically focuses on static connectivity, and ignores the feedbacks between changes to the network's topology and the eco-evolutionary dynamics on the network. We review theory showing that diversity, stability, ecosystem functioning and evolutionary adaptation all vary nonlinearly with connectivity. Measuring and modelling an SEN's long-term dynamics is immensely challenging but necessary if our goal is sustainability. We show an example where the robustness of an SEN's ecological properties to node and link loss depends on the centrality of the nodes targeted. The design and protection of sustainable SENs requires scenarios of how landscape change affects network structure and the feedback this will have on dynamics. Once established, SEN must be monitored if their design is to be adapted to keep their dynamics within a safe and socially just operating space. When SEN are co-designed with a broad array of stakeholders and actors they can be a powerful means of creating a more positive relationship between people and nature.

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Introduction

Globalization of human society has created a spatially embedded and expansive ecological footprint [1], characterized by interdependent networks of transport, energy, trade and information that crisscross the planet. The strengthening coupling between human and ecological systems is produced a network of networks with complex social and ecological outcomes at different spatial scales [2••]. For example, urban-land telecoupling is reconfiguring landscapes through road building and land clearing for agriculture [2••], the effects of which have led to widespread ecosystem fragmentation and changes to local and regional biodiversity [3–6,7,8•,9] and ecosystem functioning [9]. The isolation and fragmentation of ecosystems is a particularly pervasive indicator of the human ecological footprint (e.g. 20% of all forest is within 100 m of natural and human-made edges; [9]) that is impacting ecological connectivity from local to continental scales [10]. Sustainability science is now focused on understanding and mitigating the risks to biodiversity, ecosystems and human wellbeing arising from the feedbacks between social and ecological networks.

The spatial ecological network as conservation strategy

Pressed by the severity and scale of the problem of eroding ecological connectivity, conservation science has developed the science [11] and policy support (i.e. a IUCN connectivity conservation specialist group) for implementing spatial ecological networks as an integrated conservation strategy [11,12]. A spatial ecological network (SEN) is *a system of natural and/or semi natural ecosystem elements, or patches, that are configured and managed with the objective of maintaining, or restoring, ecological function as a means of conserving biodiversity and ecosystem functioning and services, while also providing appropriate opportunities for sustainable use of natural resources from the network* (modified from [13], Figure 1). This definition makes clear that SEN are multidimensional in terms of the number of properties (or criteria) to be protected and the management of human demand placed on the resources it produces (e.g. timber). This approach to landscape conservation integrates people and aims to understand the feedbacks between the social and the ecological process occurring within the SEN. The application of SEN involves methods from network science and decision theory to identify functionally connected networks embedded in land and seascapes that encompass natural spatial and temporal scales of heterogeneity [11,12]. The aim of SENs has been to meet multiple criteria, such as

Figure 1
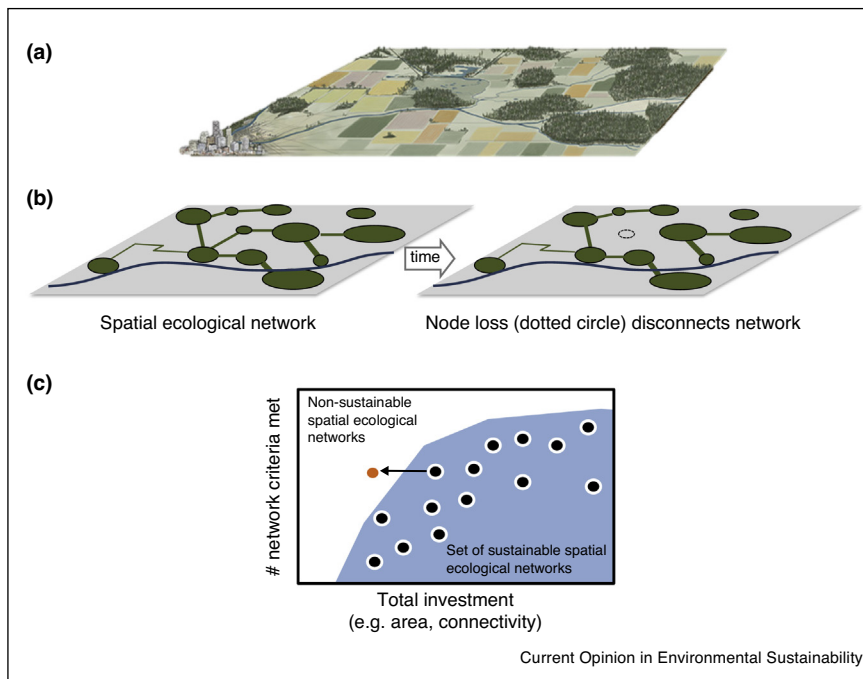
(a) A graphical representation of a landscape showing a network of forest patches embedded in other networks of human land covers: landscapes are networks of networks (image from Encyclopedia Britannica 2013). (b) The network of the forest patches (nodes) is connected by weighted links defining flows of resources, energy, information or organisms among forest patches, but also to flows with other networks (e.g. fields, or rivers). Analysis can be used to assess the robustness of important variables, like total network flow, to node loss. Here the loss of a single node (dotted circle) leads to the fragmentation of the network. (c) Typically, a spatial ecological network (SEN, see main text for definition) is identified for protection based on a set of objective conservation criteria. Criteria for investment include the number, quality and configuration of forest nodes and the spatial extent of the network that best meets the criteria for sustainability of the species set and ecosystem services offered by the SEN (e.g. support for wild pollinators valuable to fruit production). An SEN can move from a sustainable to a non-sustainable region (arrow) of performance space through changes in key structural features, such as network area and connectivity. Many networks (black dots) could conceivably be sustainable and meet some or all of the conservation criteria. In most instances the spatial dynamics of the SEN network are not modelled or used to inform conservation planning. Without models of the eco-evolutionary dynamics of the SEN and how human intervention in the landscape mediates the feedback between network topology and dynamics it is impossible to assess the long-term sustainability of the network.

maximizing the persistence of a set of target species, for a given investment in land area allocated to the SEN. Recently the stated goals of SEN have been broadened to social–ecological criteria, that include the sustainability of ecosystem services and their resilience to environmental change [13–18].

However, this approach is not without its critics. Concern has been raised about overly simplistic landscape planning where connectivity is a panacea [19,20]. This criticism is often relevant because: (1) links in the SEN defining connectivity are taken as spatially fixed and static through time and (2) relevant measures are not in place to assess the SEN's dynamics as the topology changes, or as new demands are placed on it through resource exploitation. Without these measures it is impossible to establish whether a proposed SEN is the right option in the long-term given available investment and anticipated risks [19,20]. The next generation of SEN models and planning must assess, model and manage the

feedbacks between the network's structure and dynamics and how these determine resilience to perturbations within the network and due to links with other networks.

The spatial network and the interplay between structure and dynamics

A spatial network is defined formally as a graph, composed of nodes (or vertices) and edges, where the nodes represent individual spatial units (e.g. a patch of habitat or ecosystem type) and the edges represent connections or interactions between the nodes (e.g. via movement between them), which are often weighted, directional and fluctuating in strength [21]. Methods for network planning are now built on a powerful array of tools for identifying the nodes and links of an SEN, and for ranking the importance of these nodes and links to network's structure, such as connectivity at multiple scales [21–23]. In many cases, the configuration of the network's nodes and links are considered static, where nodes and links defining connectivity are fixed and

unchanging through time [11,19,20]. However, although this representation might be valid in the short term this is unlikely in the long term. The importance of nodes and link varies through time because of fluctuations in the biotic and abiotic environment. A clear example is the time and space varying connectivity of a dendritic network during alternating periods of flooding and drought. Organisms occupying these networks will experience a highly dynamic network structure. Another example is range expansion by a population under climate change, where individuals move across spatial networks reflecting gradients in biotic and abiotic conditions [24]. Plans for SEN rarely use models of the dynamics (gain and loss) of the network's node and link structure, even though these maybe out of steady-state due to large scale anthropogenic drivers.

An SEN is also dynamic because the ecological and evolutionary states of its nodes change over time (e.g. population abundance, network productivity, species or genetic diversity). Node state changes over time because the dynamics depend not only on past states, but also on the state of the nodes with which it is interacting and the flow of information through the links (node degree) connecting them [25–27]. Predicting the dynamics of the network's nodes from the flows of information through the network's topology is very challenging. However, recently significant progress has been made, and it is now possible to explore the interplay between network topology and dynamics and even to separate the contribution of topology and dynamics to the network's response to perturbations and its resilience to them [25–27].

In principle, from [26] an SEN's spatial structure could be designed to protect and manage the information flow mediating the dynamics of biodiversity and ecosystem functioning. In most instances, we do not possess quantitative estimates of species' movements in conjunction with the flows of energy, resources and information across a SEN. Dynamic models of SEN are data hungry, and the data sets required are costly to assemble because they involve monitoring on the ground and by earth observation systems. But, if we are to manage SEN for time and space varying risks we need to understand how changes to the network's topology affects its dynamics and vice versa [25–27].

Our main point is that if we are to manage landscapes as SEN to mitigate the effects of ecosystem fragmentation we must understand which features of the network's topology can be managed to maintain desirable system properties (e.g. biodiversity, adaptive capacity, ecosystem functioning) within trajectories that are bounded away from irreversible degradation or collapse. This focus links SEN design to the burgeoning theory of network controllability [e.g. 28] and the idea that an SEN's topology can

be managed to remain within a range of ecological and socially desirable conditions.

Linking structure to dynamics: theoretical expectations

With the aim of informing the next generation of policies focused on establishing SEN, we now summarize findings from metacommunity models that identify the nonlinear and threshold effects of changing network structure on SEN dynamics.

Diversity as networks of networks

Extensions of network theory to metacommunity ecology have revealed how diversity and stability emerge from processes operating at different scales across an SEN [29–36]. For example, Pillai et al. [33] showed that the branching structure and diversity in a spatial embedded food web is maximized at intermediate colonization rates and constrained scales of dispersal. Increased food web complexity and species diversity are made possible by the structural role played by food web branches that are supported by omnivore and generalist feeding links. Thus, in contrast to traditional food web theory, which emphasizes the destabilizing effect of omnivory feeding in closed systems, metacommunity theory predicts that these feeding links, which are commonly observed in empirical food webs, play a critical structural role as food webs assemble and persist across the SEN.

Ecological sustainability via spatial insurance effects arising from connectivity

Theory predicts that the degree of spatial connectivity, governed by the rate of movement of individuals and resources, mediates the dynamics of a SEN. We formalized the conditions leading to the long-term persistence of diversity and ecosystem functioning as the *spatial insurance effects* of connectivity in a network [37]. Central to this theory is the hierarchical character of production and stability; stability of production at the network level is based on asynchronous variability in population dynamics across the nodes. Across the SEN, diversity *and* production change nonlinearly with connectivity, and aggregate variability of ecosystem processes across the network is reduced (stabilized) by asynchronous fluctuations in the relative biomass of different species through time and across nodes in the network [37].

Many theoretical models show that connectivity has a nonlinear (unimodal) effect on diversity, functioning and stability. This nonlinearity appears as strong sensitivity of the network's properties to small changes in dispersal rate (functional connectivity). Analyses of metacommunity models have shown that diversity and stability arise at different scales in the network [e.g. 37,38]. At very low rates of connectivity ecosystems are too isolated, species cannot move from node to node to keep track of shifting environmental conditions and diversity cannot be

maintained (e.g. due to local competitive exclusion or overconsumption). This occurs because we assumed no local coexistence mechanism (only one species persists in each patch without dispersal), but spatial insurance does not depend on this assumption. Intermediate rates of movement promote species persistence as they move to keep track of shifting environmental conditions. This spatial sorting of species enhances biomass production locally and regionally [38], even though significant turnover in species dominance occurs through time. Intermediate rates of movement also maintain local diversity by mass effects, which allow species to persist in suboptimal nodes [38]. In many cases, although this is not universal [39], at very high rates of connectivity a few species come to dominate the network because of competitive exclusion by species that have the greatest fitness for the average conditions across the network. Intermediate rates of connectivity are strongly stabilizing because the maintenance of asynchronous species fluctuations reduces temporal and spatial variance across the network [37].

All properties of SEN are therefore a nonlinear function of rates of dispersal. Small changes in connectivity can lead to large losses or gains of diversity and functioning depending on where an ecosystem lies on this gradient of connectivity (Figure 2). In general, we do not know the rates or patterns of connectivity for SEN, or how much connectivity change will result in substantial loss of diversity and functioning. The implementation of SEN for conservation must put in place the means to monitor connectivity. These efforts should include tracking the dispersal of organisms, but also the spatial fluxes of resources, (genetic) information and nutrients arising from the network dynamics.

At regional scales, spatial variation in environmental conditions (natural and anthropogenic) is often much greater than local variation, so regional sustainability places greater emphasis on connectivity at larger scales. The insurance effects tend to be stronger at larger spatial scales because differences in beta diversity (differences in species composition from node to node in the spatial network) desynchronize fluctuations in ecosystem processes at different locations [40]. The maintenance of asynchronous fluctuations across the network mean ecosystem functions and services are less variable and more predictable at larger spatial scales [41]. Examples of insurance effects due to species and genetic diversity include the greater resistance of grassland productivity to droughts [42] and the recovery of seagrass ecosystems after climate extremes [43•]. Anthropogenic drivers such as land use intensification could, however, lead to a loss of response diversity [44] and greater reduction in ecosystem stability at larger spatial scales than at smaller scales if they not only drive local species loss, but also synchronize fluctuations in species by homogenizing biota, abiotic conditions, or harvesting across the network [45••]. For

example, commercial exploitation of cod stocks in the North Atlantic drove synchronous population variability [46] and declines [47] at very large scales.

Where spatial insurance effects cannot buffer systemic risks, such as strong system-wide pulse or press events, an evolutionary process of rapid adaptation and diversification will be needed for recovery. Genetic rescue is a fairly common strategy used to overcome inbreeding depression and boost the heterozygosity and fitness of declining metapopulations [48]. Evolutionary rescue occurs when genetic adaptation occurs *in situ*, due to the appearance of beneficial mutations or relevant standing genetic variation, that allows populations to recover from rapid demographic decline initiated by persistent environmental change that would otherwise cause extinction [48]. Spatial structure is known to affect rates of adaptation and probability of evolutionary rescue at node and network levels in response to severe environmental stress. For example, connectivity in an evolving microbial metacommunity allowed the evolutionary rescue of many species, resulting in the recovery of diversity and productivity despite sustained lethal stress from a pesticide [49]. Maintaining the potential for rapid adaptation in ecological networks is essential for their long-term sustainability, especially where threats are unknown. We know of no planned SEN that has designed its structure for evolutionary rescue. Much more work on the eco-evolutionary dynamics of SEN is needed.

Network robustness

Resilience is an important property of SEN [50,51] and is increasingly seen as a target for policies [15], but it has proven challenging to define, measure and implement resilience as an operational management strategy for multi-dimensional systems with many components interacting through a network [15,27,51].

Here we focus on network robustness, one dimension of resilience, which is a quantifiable measure of the ability of a network to withstand failures and perturbations and still function; it is a critical attribute of many networked systems [52]. Research on network robustness (usually for food webs) assesses how a network disconnects during the removal of nodes or links through time [29,53]. SEN are also potentially vulnerable to node and link loss via land use intensification and sprawl, and node specific perturbations, such as harvesting or climate events.

In a recent study [38], the robustness of the spatial insurance effects of connectivity was assessed by simulating sequences of node loss by removing habitat patches based on their betweenness centrality (i.e. the degree to which a patch serves as a connection between other patches in the metacommunity). In this analysis, habitat loss had a large, non-linear impact on diversity, ecosystem functioning and stability especially when patches of high

Figure 2
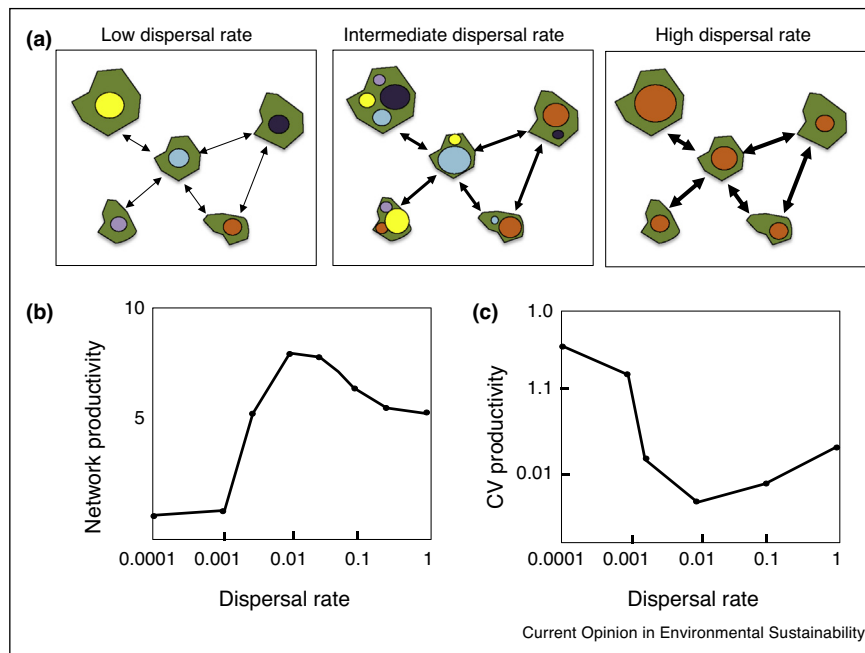
The spatial insurance hypothesis [see 37] connects the spatial structure of a network the dynamics of the communities embedded within the metacommunity and to the emergent diversity and ecosystem functioning at node and network levels. **(a)** Node and network diversity vary with dispersal rate: at very low dispersal rates (thin arrows) each habitat patch maintains a single species (colored circles correspond to the presence and abundance of different species) that is best adapted to the local conditions in each patch. At intermediate dispersal rates the number of species per patch is maximal because of source–sink effects. Note that each patch maintains several species but that only one species is dominant (large colored circle) whereas the others are of low abundance (small colored circle). Ecosystem productivity **(b)** is greatest, and **(c)** the variability of productivity, measured by the coefficient of variation, (CV) is lowest at intermediate rates of dispersal ($d = 0.01$) because of the insurance effects of biodiversity and the spatial-averaging of environmental heterogeneity allowed by dispersal (see text for explanation). At high dispersal rates only one species is present throughout the metacommunity. This species is the best competitor under the average conditions across all patches and excludes all other species. Biodiversity has been lost and ecosystem productivity and stability are maintained only by spatial-averaging. In general, we do not know where SEN lie on this spectrum of connectivity, so we do not know how changes to connectivity will alter the spatial insurance effects present in a landscape.

centrality were targeted (Figure 3). Spatial insurance was lost when node deletion fragmented the network into small clusters, impeding the movement of resident species. Loss of connectivity prevented the ability of species to track shifting environmental conditions across the network. Spatial insurance effects in an SEN are most robust to random sequences of node deletion, and sequences prioritizing nodes of low centrality. Spatial insurance effects can collapse quickly when nodes of high centrality are targeted because this quickly fragments the network; as local and regional diversity is eroded, biomass production collapses and becomes more variable and less predictable. These findings argue for a careful monitoring of SEN dynamics as node and link structure is altered.

Early warning signals for spatial ecological networks
Considerable attention has been focused on the possibility of early warning signals of ecological failure (i.e. local extinctions) or resource collapse events. Early warning statistics, such as the variance and autocorrelation, of the

stochastic trajectory of the ecosystem as it approaches a tipping point are only reliable for certain types of dynamical attractor estimated over long time series [54]. In general, the underlying dynamical attractor is not known for any protected SEN, in part because long time series are not available [54,55]. In the case of SEN, desirable early warning indicators would be spatial and employ network measures [31]. A useful indicator of collapse in metapopulations is the change in spatial coherence of ecological variables, such as biomass fluctuations in food webs, which signal a destabilization of the metacommunity network [47]. Spatial coherence can presage the synchronous collapse of a resource or species across the network. Another promising indicator is the 'recovery length', which is the distance necessary for connected populations to recover from spatial perturbations. This recovery length tends to increase before network collapse, suggesting this metric may provide an adequate early warning indicator before tipping points occur in an SEN [56•]. There is much more research to be done to move these ideas from the laboratory to the field. The

Figure 3
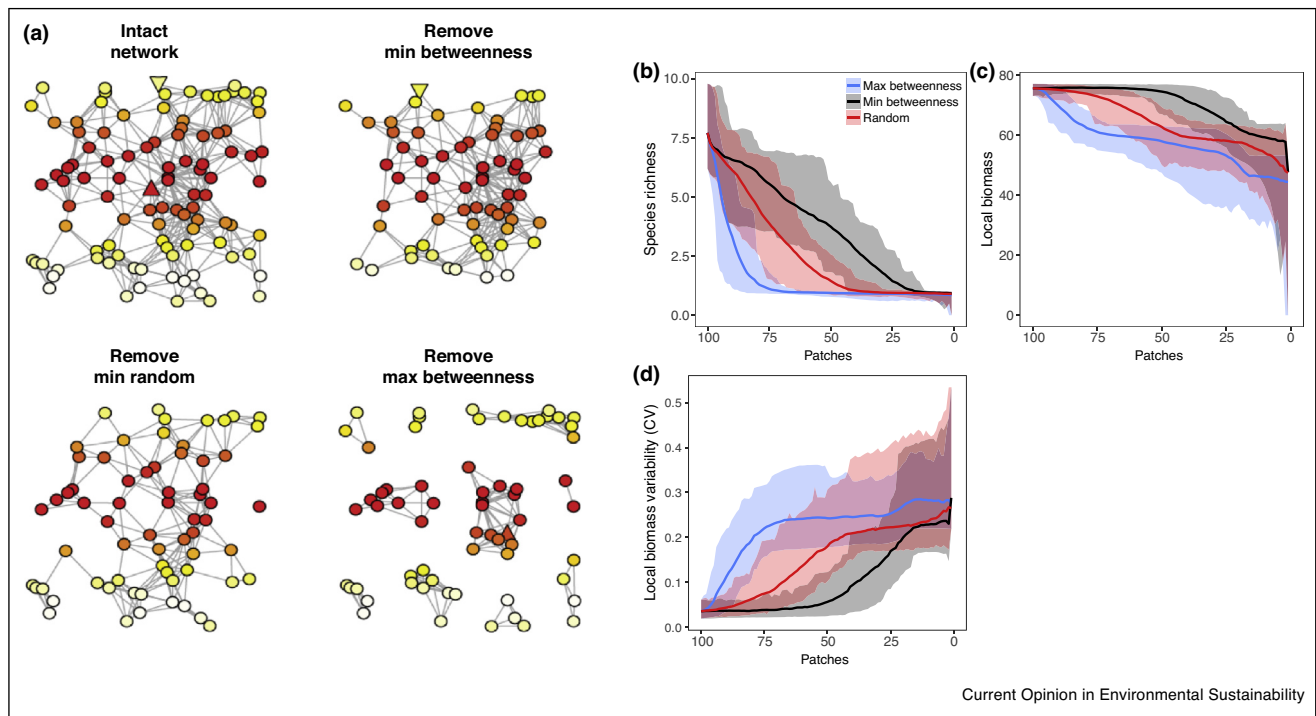
Impact of habitat loss on SEN diversity, ecosystem functioning and stability (adapted from [38]). A metacommunity (dispersal rate = 0.015) on an environmentally heterogeneous network (node color indicates environmental condition at one point in time). **(a)** An intact network, and a fragmented network after 14 patches have been removed based on three removal sequences: removing the patch with the minimum betweenness centrality (yellow triangle) — betweeness centrality is the value of an individual habitat patch in adding to the connectivity of the metacommunity by being a stepping-stone for dispersing individuals — removing a random patch and removing the patch with the maximum betweenness centrality (red triangle). The impact of each patch removal sequence on **(b)** mean local species richness, **(c)** mean local biomass and d) mean local biomass variability (CV = coefficient of variation). Lines are mean values from 100 replicate simulations and ribbons show the range between the 2.5th and 97.5th percentiles of the data. Metacommunities are not robust to the loss of habitat nodes of maximum betweeness centrality.

Can we define a safe operating space for spatial ecological networks?

Given the significant investment in land area, resource and governance required to establish and maintain an SEN, and the likely difficulty of identifying early warning signals, a risk-mitigation approach to management is appropriate. Risk-based approaches require developing threat scenarios, evaluating network vulnerabilities and quantifying the consequences, both ecological and social, of the 'failure' (i.e. extinction or resource collapse) of nodes, or the entire network [57**,58,59]. In the context of SEN, risk (risk = hazard × vulnerability) is the expected loss of ecological structure and functioning and human wellbeing when natural and human hazards propagate through the network. We can identify risks to the SEN as perturbations to its node and link structure that affect the persistence of populations and move the

existence of early warning indicators for the loss of network stability and robustness should be a strong motivation for SEN monitoring in the long-term.

system's dynamics outside of a reference safe operating space (SOS) [60•]. The propagation of impacts due to the network's connectivity can result in systemic risk and periods of crisis or collapse [57••]. New metrics of connectedness and system risk are being developed in the finance and insurance sectors that may be of value for SEN monitoring [57••,59].

In system science, the SOS is a multivariate space that circumscribes the region of dynamic persistence, while remaining within an envelope of tolerable variability in the ecological and social conditions required for human wellbeing [60•,61]. Recently, efforts have focused on downscaling the SOS concept from global, to regional [60•] and local [61] social–ecological systems. By downscaling we mean identifying and modelling the network's structure and its dynamics at landscape, or regional, spatial scales (see section 'Co-designing spatial ecological networks with stakeholders' for an example). This effort to downscale the SOS concept is needed if we are to operationalize it for SEN embedded in real world

Figure 4
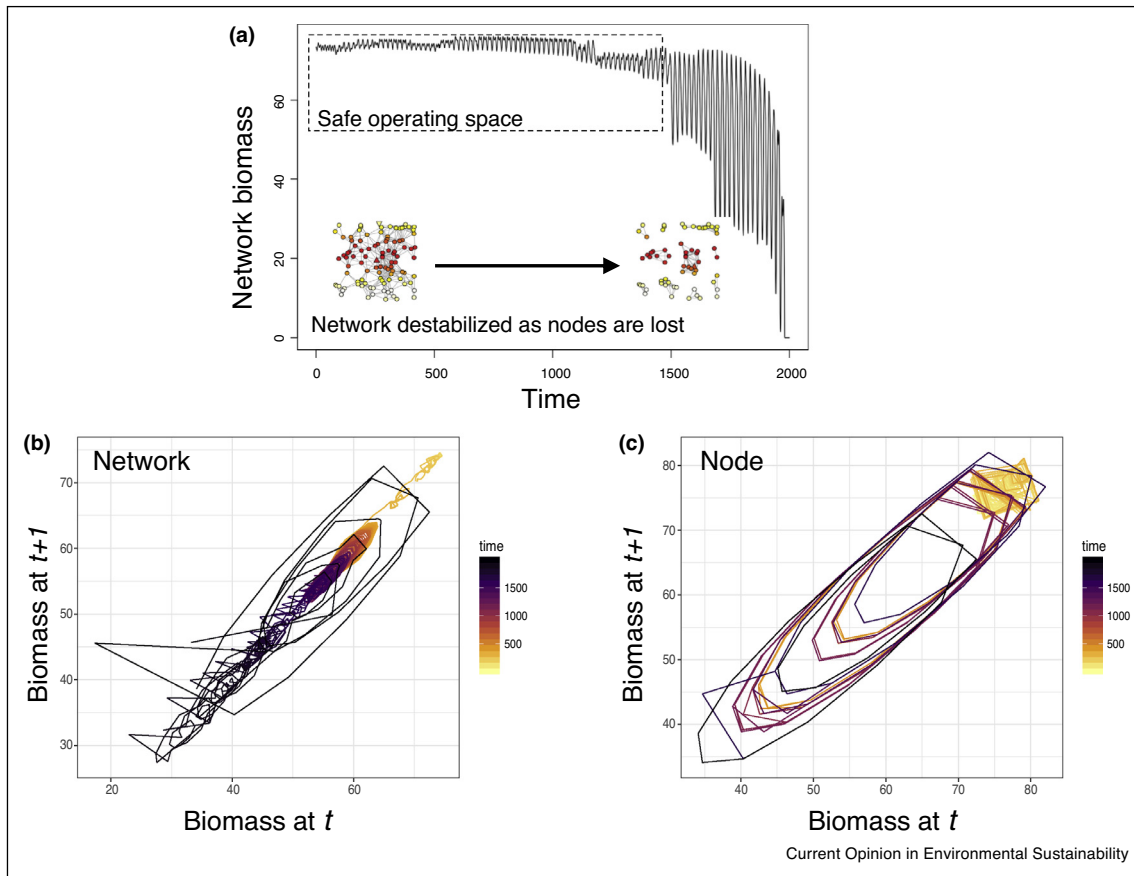
The safe operating space (SOS) for an SEN defined as a region of dynamic multivariate space that depends on the structural and functional properties of the network. Here we show the SOS for a single variable, community biomass. **(a)** The fluctuations of the SEN are initially bounded, but as nodes are lost the fluctuations increase in variance and leave the SOS. The dotted box indicates the period over which the SEN is within the SOS. At a critical level of node and link loss the variance increases through time, the network is no longer functionally connected, and so the SEN leaves the SOS and biomass collapses. The SOS can be defined non-arbitrarily based on the SEN structure that ensures long-term persistence. The degree of network erosion/protection will depend on how risk adverse society is with respect to the fluctuations, and the SEN's robustness to node deletion. **(b)** and **(c)** show the biomass fluctuations as increasing orbits in phase space at the network-level and the node-level respectively. The dynamics are taken from the model described in Figure 3, where patches of min betweenness centrality are targeted for removal from the network.

landscapes with multiple levels of governance. We define the SOS for an SEN to be a region of dynamic persistence of the network in multivariate space, where the variables of interest relate to critical factors defining network persistence (e.g. dispersal) and robustness, and the social and ecological variables related to the target criteria for conservation and management (e.g. biodiversity and ecosystem services). Figure 4a shows the SOS over the fluctuations in the dynamics of total biomass of the network presented in Figure 3. As nodes are deleted the trajectory departs from the persistent region and the variance of the fluctuations widen as biomass approaches zero. Figure 4b,c shows these biomass dynamics in phase space for the network and node level dynamics respectively. The size of the ellipse reflects the change in the variance of biomass as the network is eroded;

biomass reaches low values when the network is small and fragmented. In this manner, we link the concept of network robustness to the SOS; the loss of habitat and environmental heterogeneity drives extinction and renders the network less productive and more variable. Much more research is needed to assess whether an SOS can be identified for an SEN and figure out how SEN reach socially and ecologically undesirable trajectories. Ultimately, SEN management will require spatial decision support systems supplied with time series of environmental, economic and social data (surveys and remote sensing) from across the SEN.

Some network properties could be managed to reduce system risks to an SEN. A practical example of this [62] found that an urban–rural SEN was robust to random

Figure 5
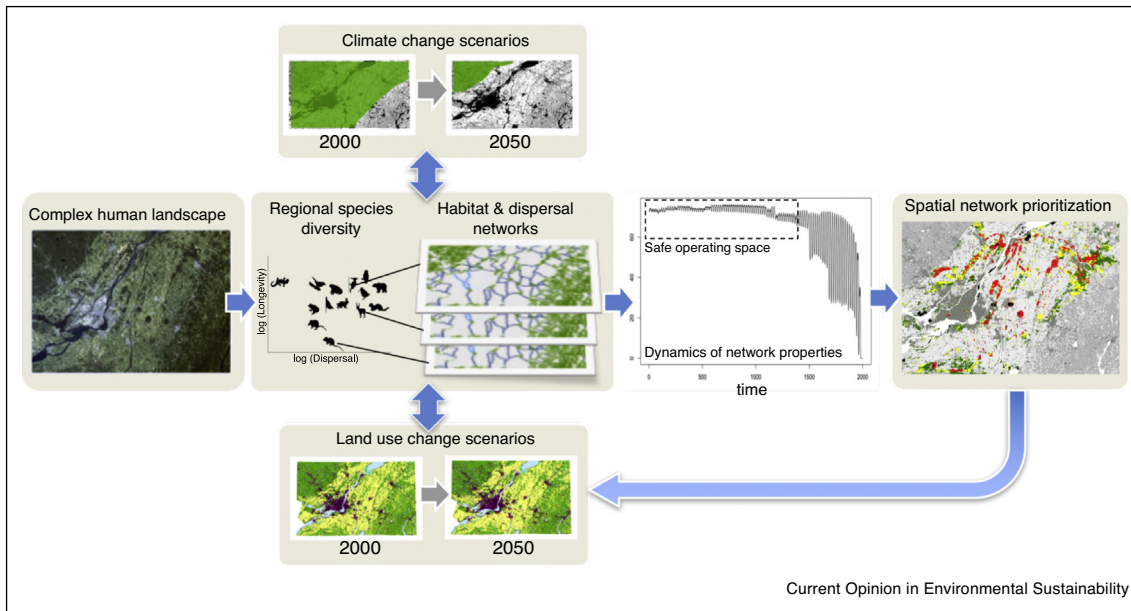
The cycle of steps involved in identifying an SEN. This cycle of analysis expands on [69] by including the dynamics of the network's properties as a criterion for node and link prioritization. For a given landscape six steps are structured within a loop to identify priorities for node and link protection: (1) identify focal criteria, in this case species with a range of life-history characteristics and habitat preferences; (2) identify habitat and dispersal networks of each species from monitoring data and expert opinion; (3) analyse the connectivity of species-specific habitat networks and quantify the resistance of the landscape and the contributions of each habitat pixel to short-range and long-range connectivity; (4) project the eco-evolutionary dynamics of the species occupying the SEN; (5) identify the spatial prioritization of habitat patches for conservation action based on the network criteria, such as short and long distance connectivity, that maintain the dynamics within the safe operating space. Additional criteria may include ecosystem services supplied by these species or the habitat nodes they occupy (e.g. carbon stored in forest); (6) establish the effectiveness of different prioritization schemes into the future based on climate change projections and spatially explicit dynamic land-use change simulations.

patch removal but vulnerable to preferential node (high centrality) removal. Dynamic SEN models would allow an evaluation of the short and long-term impacts of losing an ecosystem node due, for example, to land cover change. Network modularity is another network property that could be the focus for management. For example, increasing spatial modularity may be a viable strategy for mitigating the spread of perturbations to particular nodes [63]. Using a laboratory model system, Gilarranz *et al.* [64] found that modularity was beneficial to population networks in the presence of perturbations, but it hindered population productivity in the absence of perturbations. This finding reinforces our general point that connectivity management can be a double-edged sword; network design must be adaptive and consider the type of risk, and the changing distribution of risks affecting the SEN in the future.

Co-designing spatial ecological networks with stakeholders

Multi-criteria decision methods and sustained stakeholder engagement are essential if the SEN approach is to be used for integrative conservation planning [65]. Broad engagement with stakeholders is required to

balance the various social, economic and ecological needs in the region especially where resources for land protection are scare [65–68]. For example, Albert *et al.* [69] used a multi-criteria approach to prioritize an SEN for Montreal based on scenarios of land use and climate change out to 2050 (Figure 5). This analysis identified the networks that best met multiple metrics of connectivity (short and long-distance) and the divergent habitat and resource needs of fourteen vertebrate species. The nodes in the network were prioritized for their contribution to the connectivity of the SEN; this was done for the landscape today and into the future under the different scenarios of land use and climate change and compared with a business-as-usual baseline. The aim of this prioritization analysis was to guide decision-making so that the most robust SEN can be protected now and built up through time through addition of protected nodes (via forest planting and restoration) and links (forest corridors).

The SEN for Montreal was founded on a sustained, multi-year, engagement with regional stakeholders [70] — including governments, NGOs and farmers — that had broadly discussed scenarios of environmental

risk and addressed different options for managing connectivity for biodiversity and ecosystem services. SEN identification and prioritization based on multiscale and multi-criteria connectivity analyses have great potential to inform land planning. The co-design of a SEN is an essential part of establishing the trust and cooperation needed for its social acceptability across different sectors of society, and the polycentric modes of governance that must be applied to adaptively monitor network dynamics and manage them in the long-term.

Conclusions

The Anthropocene is characterized by changes in the connectivity of social and ecological systems at all spatial scales. The multi-scale nature of changing connectivity is creating outcomes with impacts large enough to threaten local and regional biodiversity and the long-term sustainability of the ecosystem processes, and benefits we obtain from them. We have stressed the importance of understanding the feedbacks between the spatial structure of SEN and the eco-evolutionary dynamics that together define robustness and resilience of the network's properties. If SENs are to contribute to regional sustainability their design, monitoring and governance must focus on the long-term dynamics crucial to keeping them within a safe and socially just operating space. The co-design of SEN with a diverse array of actors and stakeholders can be an effective means for reframing and forming a more positive relationship between people and nature at large spatial scales.

Conflict of interest statement

The authors confirm that they have no conflict of interest to declare.

Acknowledgements

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Papers of particular interest, published within the period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest

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