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Opinion

Demystifying ecological connectivity for actionable spatial conservation planning

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Connectivity underpins the persistence of life; it needs to inform biodiversity conservation decisions. Yet, when prioritising conservation areas and developing actions, connectivity is not being operationalised in spatial planning. The challenge is the translation of flows associated with connectivity into conservation objectives that lead to actions. Connectivity is nebulous, it can be abstract and mean different things to different people, making it difficult to include in conservation problems. Here, we show how connectivity can be included in mathematically defining conservation planning objectives. We provide a path forward for linking connectivity to high-level conservation goals, such as increasing species' persistence. We propose ways to design spatial management areas that gain biodiversity benefit from connectivity.

The need for integrating connectivity into spatial conservation planning

In a world of dwindling natural resources and increasing human pressures, global conservation goals aim to ensure that habitats and species can persist into the future. Most notably, the United Nations Sustainable Development Goals (SDG) SDG14 (life below the water) and SDG15 (life on land), and the Convention on Biological Diversity's (CBD) post-2020 Global Biodiversity Framework aim to halt loss of biodiversity and associated ecosystem services. A dominant mechanism to achieve these goals will be through area-based conservation and management [1–3], with specific goals of achieving the protection of 'well-connected systems'. **Connectivity** (see Glossary) underpins the **persistence** of populations, species, communities, and ecosystems, and thus needs to play a pivotal role in conservation strategies (e.g., [4–6]). Yet, conceptual advancements and tools to quantitatively integrate connectivity for and across land, freshwater, and marine systems with area-based conservation are still being developed (e.g., [5,7–10]), and are only implemented in a fraction of existing conservation areas [11,12]. In this opinion article, we define connectivity as the flow of energy, materials, and organisms across space. At the species level, this connectivity includes adult and propagule dispersal, species movement and migration, species interactions, and ontogenetic linkages.

Flow processes of energy, materials, and organisms that underpin connectivity are dynamic, variable, and often spatially unconstrained (Box 1), generating a considerable challenge for formulating both suitable metrics and useful objectives for traditional conservation planning approaches [9,13,14]. The variable characteristics and scale of flow processes have led to diverse characterisations of connectivity in environmental conservation, ranging from spatial wetland linkages for amphibians [15] to recent genetic exchange among populations [16] (Table 1). Assessments of the global protected area estate highlight shortfalls in capturing dynamic ecological processes, such as connectivity, where only 9.7% of intact land is protected and connected [12], two thirds of critical areas for the flow of animals on land are not conserved [17], only 17% of

Highlights

There is a disconnect between global high-level conservation goals and on-the-ground actions such as maintaining ecosystem services or persistence and local planning of protected areas.

Dynamic processes such as ecological connectivity underpin species persistence and ecosystem resilience but are difficult to represent in mathematical spatial planning problems for protected areas.

Quantitative and SMART (specific – measurable – action-oriented – realistic – time-bound) conservation objectives can provide a link between high-level conservation goals and local or regional design and implementation of functionally connected protected area networks.

With current implementation gaps of protected area commitments and increasing climate change threats, there is tremendous opportunity to use quantifiable objectives for ecological connectivity as a vehicle to future-proof protected area networks to help achieve global conservation goals.

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the world's free-flowing rivers are protected [18], and 90.5% of marine species have less than 5% of their ranges protected [19]. This implementation gap is often because broad conservation goals for connectivity are difficult to translate into quantitative conservation objectives, data that measure connectivity are difficult to acquire, and there is no scientific consensus on the appropriate metrics to use to assess connectivity retention or improvement [13], especially for multiple species [4].

The shortfalls in implementing connectivity in spatial management can be explained in part by the fact that the concept of connectivity is broad, complex, and means different things to different people at different scales and times. There are many different conceptualisations of ecological connectivity within the conservation community (Table 1). For example, a park manager in Kenya may be most concerned with connectivity that enhances the movement of high-value, charismatic species that bring critical tourism revenues from wildlife experiences. By contrast, a coral reef ecologist assisting with the design of marine protected areas in the Indo-Pacific may value larval connectivity, and focus conservation on reefs linked by propagule dispersal and fish spawning

Box 1. Types and scales of connectivity that hinder its estimation

A key hurdle to including connectivity in spatial planning is its spatial–temporal complexity. The directionality, spatial constraint, and spatial–temporal scales of the flows of energy, materials, and organisms vary with their physical or ecological process, the properties of the environment, and the flowing entity (Figure I). These flows can occur in any medium (e.g., land, river, ocean, air) and across spatial scales ranging from metres to across continents, hemispheres, or ocean basins. Ensuing connectivity may be manifested and relevant over time scales ranging from hours to centuries or even longer (as in the case of evolutionary time scales). Many flows can be either symmetrical (e.g., movement along animal migration corridors) or asymmetrical (e.g., movement across ontogeny, seed or larva dispersal). This variability underpins the measurements of connectivity that are appropriate in each case.

Directed flows involve the movement of an entity along a single, dominant direction (Figure II). These flows can be constrained, with relatively low lateral variation in the path (e.g., upstream or downstream salmon migration, downstream transport of leaf litter,movement along terrestrial migration corridors, annual bird migrations across continents or ocean basins). Directed flows can be unconstrained when lateral variation in the path is high. This variation can result from the movement of the medium or of the moving entity, for example in spread of invasive/range-expanding species along a coast with a boundary current, turtle migration from foraging to spawning grounds, or ungulate migration across seasonal feeding grounds.

In diffuse flows, movement proceeds along a number of directions, and can originate from a single source (e.g., during an oil spill, foraging from a nesting aggregation) or multiple sources (e.g., multiple introductions of non-native species) (Figure III). They can also be either constrained with relatively clear movement corridors or pathways (e.g., detrital dispersal into valleys or basins, foraging within a particular ambit, spread of invasive species or disease within a bounded suitable habitat) or unconstrained with multiple possible pathways such as the movement of propagules that are dispersed by wind or ocean current.

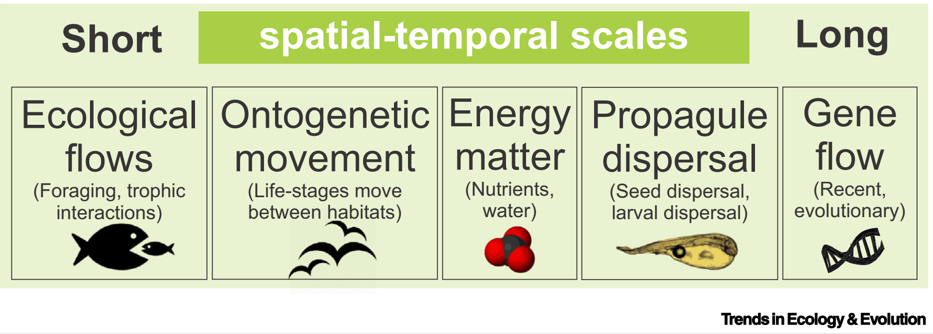

Figure I. Typical spatial–temporal scales of connectivity; all examples may include species or processes that deviate from this conceptualisation.

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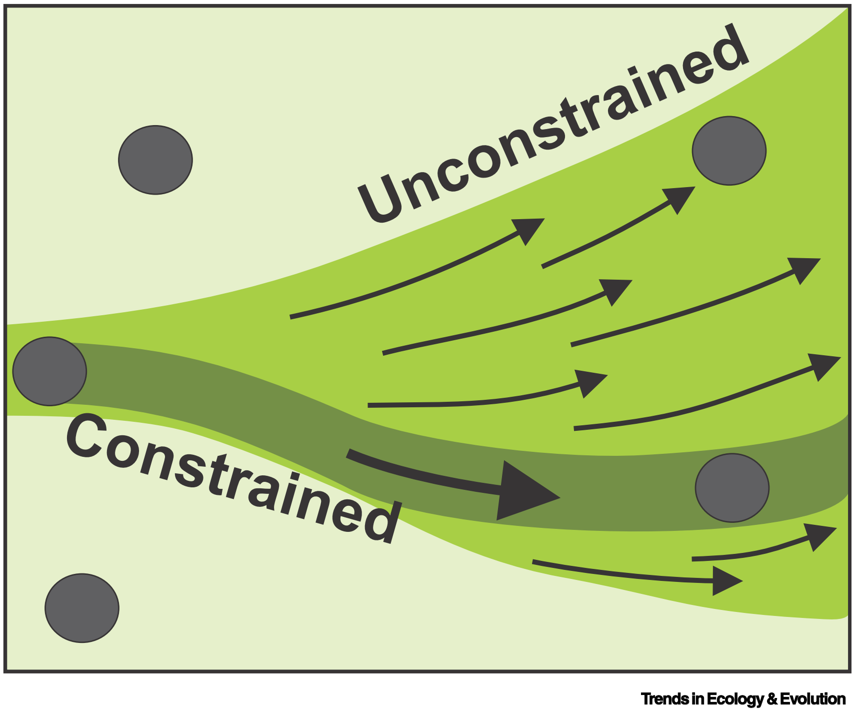

Figure II. Directed connectivity has a dominant direction of movement and is easier to conceptualise.

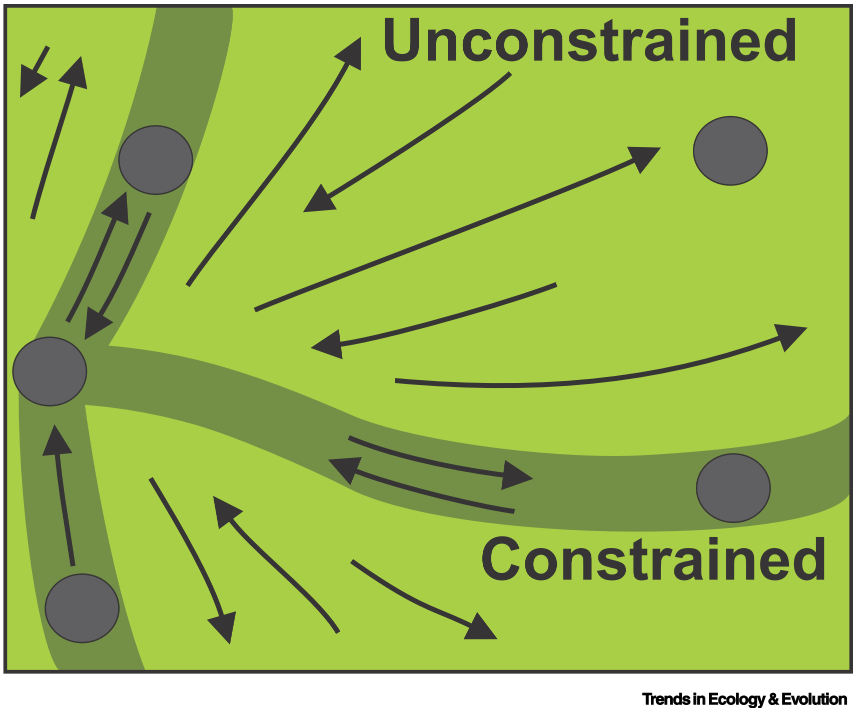

Figure III. Diffuse connectivity is mixed in direction and strength and is extremely difficult to estimate.

Glossary

Adequacy: adequacy in spatial conservation planning requires that all factors that enable species persistence are captured in conservation area systems and networks. These factors include sufficient area, habitat quality, genetic diversity, and processes underpinning persistence (connectivity, species interactions).

Connectivity: the flow of materials, energy, and/or organisms, genes, etc. among habitat patches or regions of interests. Specifically, ecological connectivity can include propagule dispersal, adult movement, species migrations, species interactions, and ontogenetic linkages, with the associated flows of energy and matter.

Conservation area networks: systems of conservation areas that are connected, that is, were designed with connectivity as an explicit goal.

Conservation feature: species, habitat, or natural feature that we aim to conserve.

Conservation target: the amount of a conservation feature to be conserved, often expressed as a percentage of the total amount of the conservation feature within a spatial planning region.

Flow matrix: the amount of movement of individuals or particles among sites, assuming that larger values represent greater movement and that there are no limits imposed on these values. The sum of individuals or particles leaving sources may be larger than the sum of those arriving at destinations where they are lost to mortality or exit the system [9].

Flow processes: movement of materials, energy and/or organisms/genes, akin to functional connectivity.

Functional connectivity: the effective movement of agents across a structurally connected ecosystem.

Migration matrix: the proportion of individuals or particles arriving at a receiving site that originated from a source site for all pairs of sites, where all elements of the matrix are relative to the destination [9], conceptually linked to the migration matrix in metapopulation modelling [82].

Persistence: the continued survival of a species or population over time.

Probability matrix: the proportion of individuals or particles originating from a source site which arrive at a receiving site, where the proportion arriving can be interpreted as the arrival probability. The elements of the matrix are relative to the aggregations [20], or climate-resilient areas [21]. As is often the case in applied conservation, accounting for value-laden perspectives of different stakeholders will have trade-offs, and may hinder a unified approach to operationalise connectivity in the context of global conservation goals.

One of the most widely recognised, prioritised, and historically implemented forms of connectivity on land is wildlife corridors, which connect fragmented habitats across landscapes that have been impacted by conversion or land-use change [13,22]. Habitat fragmentation affects the movement of individuals, and often, but not always [e.g., 23], reduces persistence probabilities, mostly due to edge and isolation effects [24] and by changing species interactions [25]. However, corridor conservation, whilst important, addresses a form of **structural connectivity** that may serve only a few focal species, miss important and unknown barriers to movement [26], and ignore essential attributes needed to retain **functional connectivity**, such as dynamic flows of matter and energy. By contrast, marine and freshwater conservation often focus on the functional conservation value of preserving dynamic flows in these systems [27–29], but implementation in conservation plans is historically lacking [11,18].

Despite challenges, connectivity is a focal component of the CBD's Global Biodiversity Framework and government policies for area-based **conservation targets**. Spatial planning as a means to achieve these targets also features prominently in ongoing discussions. Our aim is to highlight the challenges facing 'connectivity' as a global policy ambition and propose how high-level goals for connectivity can become quantitatively integrated into conservation plans to deliver connected **conservation area networks**.

We recognise much progress has been made in academic research for incorporating connectivity into spatial conservation planning [8,30–33]. However, the transferability and uptake of these

number of individuals or particles leaving from the source site.
Structural connectivity: habitat or physical features or processes that may form a platform for the movement of agents (organisms, pollutants, pathogens).

Table 1. Connectivity as a value-laden concept. Selected contexts of connectivity and potential audiences applying these concepts for spatial conservation area network planning

Type of connectivity	Definition/examples	Reference for definition	Example user group
Land–sea connectivity	Flows of sediment and pollutants from rivers into the sea, and movement of animals between land, rivers, and the sea	[70]	Ecologist, environmental scientist, engineer
Ontogenetic connectivity	Movement of individuals occurring as part of life cycles (metres to thousands of km), e.g., amphibians	[15,48]	Ecologist, park manager
Corridors	Distinct habitant patches are linked such that movement of animals can be facilitated. Disruption of corridors often occurs due to fragmentation	[36]	Environmental scientist, wildlife biologist, park manager, tourism operator
Pathogen dispersal	Airborne dispersal of fungal spores (regional and continental scale, 50–5000 km)	[46]	Epidemiologist
Pollutant advection and diffusion	Transport of pollutants in a medium (e.g., oil spill, sewage transport in water)	[54]	Engineer, geophysicist
Dispersal connectivity	The movement of propagules or juveniles among spatially distinct habitat patches. Scale highly variable, dependent on medium and species	[55,57,58,79]	Modeller, hydrodynamics engineer, oceanographer, ecologist
Migration	The scheduled movement of individuals	[47,83]	Wildlife biologist, ornithologist, park manager, tourism operator
Genetic connectivity	The movement of genetic material between nearby or distant habitat regions over multiple generations	[16]	Geneticist, evolutionary ecologist
Temporal connectivity	Linkages among sites as species shift their ranges over time	[51,84]	Climate scientist, global change ecologist
Energy flow	Transport of nutrients as part of animal movement	[39]	Ecologist, chemist

methods to the real-world remains limited given that these explorations often ignore objectives that are important to decision-makers on the ground (e.g., social–economic considerations, equity, political realities) [34]. As a consequence, the integration of connectivity into conservation decisions by practitioners has not been fully realised even though the importance of connectivity for management goals is widely recognised, particularly for addressing threats of climate change to biodiversity and livelihoods [28]. Here, we provide a conceptual overview of how flows of energy, materials, and organisms, or connectivity, can support the achievement of global conservation goals. With specific examples, we illustrate how to link objectives of high-level conservation goals with local and regional connectivity objectives.

Conservation area networks need to capture ecological connectivity

Planning for area-based conservation actions (e.g., protection, restoration, or management of harvesting) that support the long-term persistence of species and ecosystem processes relates to the foundational conservation planning principle of **adequacy** [20,35]. This principle ensures that the coverage and intensity of conservation actions is enough to maintain functional and adaptive structured populations or communities so they persist through time [25,36,37]. Achieving persistence requires continued functional integrity of biological communities through species interactions [38] and energy flow [39,40]. Flows of energy (e.g., carbon) and matter (e.g., detrital subsidies) that are critical for the persistence of ecosystems can be achieved by connectivity via animal movement and habitat linkages [41,42]. The flow of genes amongst populations enhances their persistence by promoting genetic diversity that often underpins adaptive potential [6,43,44]. It is important to note that connectivity can also impede conservation goals through the flow of pollutants or the spread of invasive species. For example, strong pathways for vector exchange can enhance the exposure of populations to disease [45,46].

Ensuring that conservation actions maintain or restore connectivity of species and their habitats is crucial for persistence [22,30,36]. Conservation area networks must include adequate amounts of habitats that support all life-history stages and the maintenance of movement across those habitats or ecosystems [13,47]. For example, we must protect the movement corridors between nesting beaches on land and foraging areas at sea to conserve sea turtles [20,48] or stopover sites for migratory birds moving across borders [49]. Further, dispersal of propagules depends largely on maintaining vectors (e.g., seed dispersing animals [50]), and ensuring seasonal animal movement is explicitly prioritised when designing conservation networks [47]. Lastly, connected habitat patches enable range shifting across multiple species due to global climate change on land [51], whilst a combination of static and dynamic protected areas can support range shifts and should be considered in network designs and updates [27,28]. In areas primarily used for natural resource management, persistence is subject to balancing growth and mortality of populations during stochastic and scheduled (e.g., harvest) biophysical and socioeconomic fluctuations across their ranges [52].

Connectivity varies in both space and time (Box 1), rendering its measurement or modelling at the relevant spatial scales a major challenge for conservation planning [6]. Yet, only if we understand where, when, how far, and how frequently organisms move is it useful to consider such connectivity in spatial planning. Greater computing power, new models, and technology have facilitated a much-improved quantification of dynamic flows. For example, telemetry technology can track the movement of species through corridors and across land, fresh water, and seascapes [29,48,53], whereas the spread of oil-spill plumes can now be observed by satellite [54]. Further, the measurement of short-distance larval dispersal amongst coastal marine habitats has proliferated in the past decade, by the use of chemical tags [55] or parentage analysis [56]. Over larger spatial scales, scientists rely on individual-based biophysical models that predict the likely movement of entities [57,58]. Such biophysical models can predict the likely movement of pollutants in the atmosphere [59], the dispersal of airborne seeds [57] and pathogens [46], and the dispersal of pelagic larvae [58] or fragments [60] of organisms. Whilst biophysical model outputs are difficult to ground-truth with measurements at the relevant spatial scales (but see [56]), they provide the spatial coverage required for conservation planning most easily compared to other methods.

These challenges of quantifying ecological connectivity pose hurdles for selecting spatial conservation areas or actions within them. It is particularly difficult for planners and practitioners to access technical advances in estimating or measuring dynamic processes, as the approaches and terminology of modellers and analysts are highly topic-specific. This introduces challenges for linking high-level conservation goals (e.g., planning for species or ecosystem persistence or maintaining ecosystem services), to connectivity objectives, because high-level goals need to correspond to relevant monitoring and evaluation measures [1].

Challenges in conservation area network planning with connectivity

Best practice for spatial conservation planning uses a problem-based and quantitative approach to achieve area-based conservation goals across land, freshwater, and seascapes; it is used by many countries to meet global conservation agreements [2,3] (Figure 1). This process identifies sets of candidate conservation and management areas that together realise an objective-driven suite of conservation goals, whilst minimising the cost to and conflict with resource users [35,61]. It is referred to as 'problem-based' planning because the goals, constraints, and actions are formulated into a mathematical expression; this approach ensures transparency and repeatability through the universal language of mathematics. Doing so rigorously structures conservation planning to avoid common prioritisation mistakes made by non-government organisations (NGOs) and governments – for example, hidden value judgements, arbitrariness (such as weighted scoring systems), and not deliberately planning for specific actions – which may undermine conservation efforts and misallocate resources [62]. Typically, conservation prioritisations in spatial planning are achieved by subscribing to foundational ecological principles that relate to nature-based outcomes (e.g., adequacy and representation of the different facets of biodiversity we aim to conserve) [30,37,51,61] and people-based considerations (e.g., cost-effectiveness, stakeholder buy-in) [35].

Connectivity plays directly or indirectly into contemporary spatial planning approaches and can be operationalised in a variety of ways depending on how the problem is structured (Box 2).

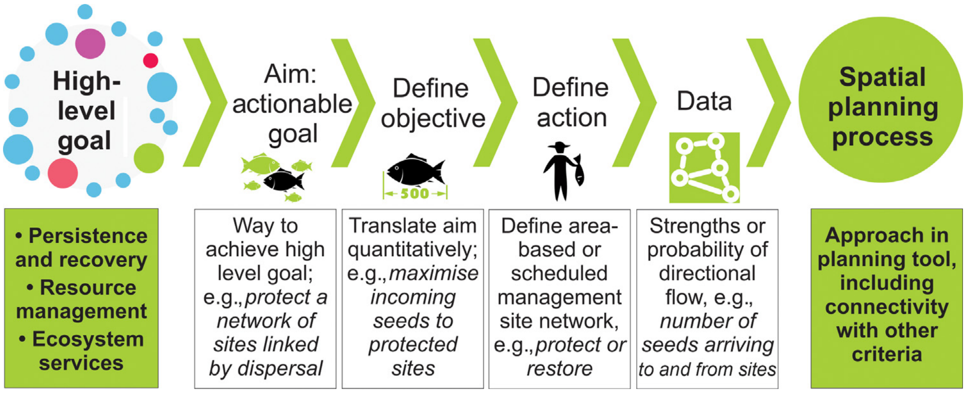

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Figure 1. Flowchart conceptualising the steps from high-level conservation goals to area-based spatial planning with connectivity.

Box 2. Ways to incorporate connectivity into spatial conservation planning

All methods apply to both supporting useful connectivity (e.g., animal movement) and disrupting harmful connectivity (e.g., disease, invasive species [85]).

Minimum set conservation problem

The minimum set problem identifies sets of sites that together contain adequate amounts of conservation features whilst minimising the overall cost. Direct flow can be considered explicitly by targeting habitat adjacency across a continuous landscape [75,84], or applying connectivity among sites as a cost to maximise spatial [20,32], or temporal [84] connectivity. Alternatively, multidirectional flows can be converted into site-specific attributes representing connectivity (e.g., centrality, Google Page Rank) for which a target is set [5,9,31,74].

Budget-constrained conservation problem

Flows can inform site selection in a maximum gain framework that meets the conservation objectives within a defined budget constraint. For example, integer programming optimisations may find the optimal set of fully connected sites satisfying a budget constraint [14], with low relative climate risk [21], or capturing generation-wise movement [47].

Maximising mean metapopulation capacity or population growth

Metapopulation models describe the probability of a species' persistence in terms of its extinction risk, given survival, reproduction, and movement. This approach can identify best protected area configurations [58] and proxy parameters for connected protected areas [86], and assess the potential persistence arising from a protected area configuration [5]. The framework also supports prioritising linkages to benefit both biodiversity and harvesting [87]. Metapopulation models require extensive demographic data for the target species and hence pertain to few species.

Rules of thumb

In the absence of data on connectivity, prioritisations of sites can rely on rule-of-thumb decision criteria based on life history (e.g., length of propagule stage) and structural connectivity characteristics (e.g., habitat quality). Typically, they inform the size of or the minimum/maximum distances between protected areas [88], and can be species-specific or regionally specific (e.g., [89]).

Integrating dynamic flow optimisation into the objective function

Adding sites to a protected area network immediately changes the flow patterns within that network. Therefore, the best approach to meeting connectivity objectives is to directly evaluate them within the planning objective function, based on a dynamic term to optimise solutions for a connectivity criterion. The high computational power required to conduct such dynamic flow optimisations has so far prevented tests of this approach.

Typically, spatial planning processes that identify conservation priorities for connectivity use decision-support tools such as Marxan [9] or Zonation [34,63]. In these approaches, connectivity can be treated as either **conservation features** or spatial dependencies that interact with the mathematical conservation problem [9]. As such, setting quantifiable objectives for connectivity requires its expression in different site-specific metrics [5,13,21], or treating flows as spatial dependencies among sites [9]. Where no socioeconomic information is incorporated in planning, site-specific flow metrics can also directly input into the objective function [32]. These approaches conceptualise flow processes as pathways into sites and their strengths or probabilities of occurring between pairs of sites. For each site, it can also be important to consider the probabilities of flowing matter remaining in or being released from a location. For example, in the context of propagule dispersal, these can be expressed as retention or migration probabilities. It is important to caution that the chosen approach drastically changes how connectivity can be integrated and achieved.

When conceptualising connectivity as conservation features, the approach typically applies common graph-theoretic metrics that assign values to sites based on their networkwide position (e.g., centrality, Google page-rank) [5,31]. These values are continuous variables representing site-specific network properties (though some discrete metrics exist). However, the data need to be converted to categorial variables in order to serve as conservation features for which to set a target [9]. Because these values are not additive, this treatment can lead to a disconnected network, where highly connected sites are chosen in isolation but they are not connected to each other. Further, converting connectivity to conservation features can include connectivity for several species types at once [5], effectively averaging their connectivity patterns while losing the needs of individual species.

Connectivity is treated as a constraint when integrated within decision-support tools as spatial dependencies (e.g., a design rule on patch size and minimum distance through boundary parameters, or penalty costs [8,20]). This approach can manipulate and maximise spatial dependencies, but cannot directly target a certain level of connectivity, as may be required by truly quantitative connectivity objectives. Further, these spatial dependency approaches can only use one species at a time (as only one penalty can be integrated in decision support tools, e.g., in Marxan), and the connectivity matrices need to be averaged multiple species. Therefore, even though most spatial planning targets multiple species – and thus multispecies connectivity [4] – a key restriction to designing conservation area networks for multiple species is that, regardless of method, different connectivities require scenario planning. Here, scenarios would examine different network options for different types of connectivity, and compare those with prioritisations arising from averaged connectivity. Ideally, connectivity would be built into the objective function (e.g., mathematical problem) in its own right, which would be maximised through optimisation. However, these mathematical formulations are nascent [9,34] and computationally demanding (Box 2).

Lastly, networks are built up incrementally over time, and are often anchored in existing protected area estates that were not designed with ecological criteria, let alone connectivity, in mind. Spatial planning for connectivity needs to also account for real-world considerations such as staggered financial resourcing, paced implementation in zoning plans, time lags, and differences in management effectiveness and stakeholder priorities, all of which can be integrated into spatial planning frameworks [7,64].

Meeting high-level conservation goals for dynamic flows

Effective decision science demands that we quantify the consequences of actions for delivering conservation objectives. Deriving actionable spatial prioritisations from high-level conservation goals, such as those outlined in the SDG’s and post-2020 targets, requires the development of consistent, transparent, and scientifically rigorous approaches that connect the overarching goal to quantifiable conservation objectives achievable with specific actions [1,30,65,66]. Including flow processes into quantifiable objectives is hindered by difficulties in conceptualising how specific temporal, directional, and spatial dynamics (Box 1) can best represent the processes we aim to conserve. A particular challenge is clearly defining the relevance of these objectives to *in situ* management needs. High-level conservation goals should link to conservation objectives that directly aim to disrupt, maintain, or enhance ecological connectivity (Figure 1).

Quantitative conservation objectives for dynamic processes, such as flows, are essential to meeting ecological and societal conservation planning needs (Table 2). For example, when designing marine protected area networks, objectives will differ for localised versus long-distance dispersal goals [67], or range shifts as a response to climate change [28]. Articulating different objectives for planning enables transparency, scenario development, and measuring the success of implemented conservation actions through monitoring [30,68], as well as establishing trigger points for adaptive management [69]. For example, an objective to reduce flows would apply to threatening processes, such as the dispersion of land-based sediment in nearshore marine environments

Table 2. Examples of linking objectives for meeting high-level persistence goals with objectives for connectivity in conservation planning

Actionable goal	Quantitative objective	Action	Information required	Implementation in decision support tools
High-level goal: species persistence and recovery				
Ensure population viability for X (a given number of) years	Provide X habitat patches for stable metapopulation or metacommunity growth	Protect an ecologically defined number and distribution of functionally connected suitable habitat patches	Habitat quality and distribution; flow relationships; socioeconomic impact of protecting	Represent a set proportion of a species' range/habitat; ensure a minimum distance apart; capture most connected AND highest quality areas
		Restore key patches of habitat as needed for connectivity	Habitat quality and distribution, feasibility (socioeconomics, species traits for restoration)	Least cost analysis of flows; balance the benefit of protecting versus restoring for different sites while considering future threats
		Protect patches with strongest flows to many other patches	Number of connections and the weight of those connections in a network of patches	Maximise flows among patches; corridors as management unit; post-hoc analysis (e.g., population viability analysis)
	Protect top X% of gene flow that balances local adaptation with diversity (immigration)	Protect a defined number and local distribution of patches and habitats	Effective population size (N_e); gene flow from coalescent approaches or parentage analysis	Maximise flows from upstream adapted patches; protect diverse isolated sites specifically; protect larger populations preferentially
Provide corridors for connectivity	Achieve a threshold of amount of energy or materials transferred across ecosystems	Protect adjacent ecosystems responsible for the flow	Trophic pathways, food web analysis; **flow matrix**	Protect a proportion of patches with high centrality [64]; maximise flow among patches; account for uncertainty of flow estimation
	Achieve a threshold of (or maximise) proportion of individuals in a population that survive one stage and enter the next stage in life cycle	Protect the range of habitats used through ontogeny; protect corridors that allow flow across these habitats	Movement frequency; residency time, direction, pathway, and rate of movement of individuals	Represent a set proportion of an ontogenetic habitat types; protect a proportion of patches with high centrality; maximise flows among patches
	Enable migratory movement (e.g., foraging) of X% of individuals or species	Protect corridors known or presumed to aid migration	Direction, pathway, and rate of movement of individuals	Protect a proportion of patches with high centrality
Ensure self-persistence of key patches	Protect X% of sites with high local retention and self-recruitment to sustain or grow populations	Protect X (a sufficient number of) self-recruiting patches	Proportion of individuals released from the patch that recruit back to the patch, i.e., the diagonal of **probability matrix**	Set as individual features and set higher targets for populations with higher local retention; set population as a focus area; post hoc population viability analysis
Reduce risk of flow of harmful entities (e.g., disease, pollutants, invasive species)	Block X% of corridors or patches that allow flow of disease, pollutants, invasive species	Remove patches or corridors that facilitate flow to a large number of other patches	Probability matrix/ flow matrix of harmful entities	Lock out patches with high out degree; minimise flows among patches; avoid high centrality patches
High-level goal: managing sustainable harvesting				
Ensure population viability for X years, see above				
Maximise supply to patches	Achieve a threshold of (or maximise) export production from source patches	Protect X (a sufficient number of) source populations	Dispersal rate of propagules; tracking data; **migration matrix**	Protect patches which are sources to key fisheries sites; identify high 'in degree' sites; maximise outflow from protected patches to fished sites
	Achieve a threshold of (or maximise) import of recruits to destination patches	Protect patches that receive input from many other patches		Protect patches with high 'in flow'

(continued on next page)

Table 2. (continued)

Actionable goal	Quantitative objective	Action	Information required	Implementation in decision support tools
	Promote spill-over from X% of sites	Protect patches that provide input to a large number of other patches		Protect patches with high ‘out flow’
Maximise flow of energy, materials and organisms to sustain fisheries/scheduled extraction events	Achieve a threshold of flow into fishing areas (perspective of the fishing area)	Select fished patches and protected area networks to maximise arrivals to into fished patches	Probability of arriving at each patch from surrounding areas, from the perspective of the destination patch	Locking in focus areas for fishing as features; set as individual feature with a higher target
	Enhance flow from X patches to fishing areas (perspective of the areas)	Select protected area networks to maximise arrivals into a fished patch	Import to pre-identified fishing area; number of individuals that leave a site and successfully settle at a different site; export from surrounding areas to the pre-identified fishing area	Protect patches with high ‘out flow’
Ensure self-persistence of fished patches	Ensure that retention and self-recruitment can replenish population subject to fishing (i.e., scheduled mortality)	Protect sufficient parts of these patches; constrain scheduled mortality	Proportion of individuals released from a patch that recruit back to the same patch; scheduled mortality rates	Set as individual features and set higher targets for populations with higher local retention; set population as a focus area; post hoc population viability analysis

[70], or the input of agricultural nutrients into freshwater bodies [71] or marine systems [40]. In most cases, however, connectivity objectives will relate to enhancing or maintaining beneficial dynamic flow processes in accordance with overarching conservation goals. Such high-level goals may include (i) enhancing persistence and recovery dynamics; (ii) maintaining populations for hunting, fishing, and forestry, and (iii) maintaining ecosystem services and relevant co-benefits. High-level objectives to achieve these goals should be SMART (specific – measurable – action-oriented – realistic – time-bound) [72]. For example, an objective for persistence goals could be to deliver actions that ensure a 90% probability that functional grasslands exist in the year 2060. Here, we provide some key examples (Table 2) to illustrate how to tackle the challenge of defining a nebulous and complex concept in enough detail to operationalise it in planning; the actual quantifiable objectives should be based on local context.

Changing dynamics of flows from rapid human expansion and climate change both pose additional challenges and opportunities for integrating connectivity into planning to support ecosystems [20,21,28]. These changes can underpin species and ecosystem persistence and productivity when (i) maintaining appropriate terrestrial corridors by reducing fragmentation through strategically placing protection and restoration areas [73], (ii) representing species across the thermal regime of rivers [69], and (iii) assessing changes in connectivity itself [74]. Similarly, changing flow dynamics are crucial when conservation scientists and managers ponder how to (iv) support or suppress range expansion [28,75], and (v) account for recovery potential provided to degraded areas by linked climate refugia [21]. The detrimental forces of the climate crisis on biodiversity render flow processes even more important to achieving many high-level conservation goals, because changing conditions render habitat representation alone ineffective [28,76]. Increasing habitat declines and patchiness require careful consideration of how flows underpin recovery processes, system productivity, and ecosystem services.

Aligning current practice with upscaling quantitative conservation objectives to high-level goals will require linking context-specific information to the specific objectives (Table 2). This may be very challenging as the analysts developing connectivity data and practitioners using data for value-laden planning may have very different technical skills and understanding of connectivity as a concept (note, this is one of our primary reasons for writing this opinion article). Traditional approaches (Box 2), and new tools, such as Marxan Connect [9], Condatis [75], and RangeShifter [77], are likely to facilitate a better nexus between scientific advances and implementation, but co-learning and interdisciplinary planning is an institutional bottleneck that we must overcome if connectivity, as a global policy ambition and requisite component of safeguarding biodiversity, can be delivered.

Connectivity objectives often apply to multispecies communities or ecosystems, whereas connectivity measurements and models typically focus on single life histories or species [4,48,53,74]. Similarly, the complexity of flows and their interactions with biodiversity results in current conservation planning case studies being limited to testing a single aspect of connectivity. For example, studies that incorporate linkages across realms can be considerably more effective at meeting conservation goals (e.g., [78]), but still omit other ecological flows such as ontogenetic movement. An important challenge occurs when we want to include conservation objectives for multiple dynamic flow processes, be it for multiple types of flows, several species, or different dispersal events over time. For example, variability in connectivity across years or seasons can create a portfolio effect of marine protected area networks [79], where the contributions of each conservation area together balance potential losses during low connectivity times. Similarly, diverse life histories point to highly divergent connectivity patterns across the tree of life: what a lizard needs is very different from an elephant's needs. Thus, conservation decisions assuming that a narrow range of life histories can represent the possible connectivity space in a landscape or seascape (i.e., almost all current examples in conservation planning) are almost certainly wrong if persistence is envisaged for a multispecies assemblage.

Connectivity remains challenging to operationalise because of these network dependencies, as the attributes of any single site for improving connectivity depends on which other sites are also conserved in the network. Unlike other objectives or co-benefits – such as carbon or some ecosystem services – biodiversity benefits and flow processes do not accumulate linearly. This complexity requires thoughtful and deliberate crafting of the problem definition, objectives, and treatment of the data.

Concluding remarks

Smart spatial planning of how management, development, and conservation actions are allocated in space helps to better achieve outcomes for biodiversity and people. Ecological connectivity shapes the responses of populations and species to disturbances, but also to management. Connectivity can be broadly defined, but has many conceptualisations ranging from the adjacency of habitat patches to the annually variable movement of individuals across land and seascapes. Ecological connectivity therefore is a key process to integrate into conservation objectives for spatial planning [3,6,80], but conceptual, practical, and spatial planning challenges still remain (see Outstanding questions). These challenges include planning across multiple connectivity objectives and species, closing the implementation gap through accessible guidelines and quantifiable metrics, and determining appropriate methods and their conservation implications of incorporating connectivity into decision support tools. As with all conservation efforts, the implementation of connectivity conservation plans depends on ongoing stakeholder and policy support, transparency, adequate funding, and strong leadership [81]; these factors require widespread awareness of the importance of connectivity. Representing habitat types or species

Outstanding questions

What are the impacts of including multiple connectivity objectives (e.g., multitype, multispecies, multiscale) on spatial conservation priorities?

Given variability of connectivity over time, can we design protected area networks that buffer the effect of such variability on the network performance?

What are effective and feasible approaches to measuring and monitoring conservation actions that were designed for connectivity goals and objectives?

How can connectivity objectives be mathematically and practically integrated and incorporated into the objective function of decision support tools?

Do different methods and metrics to incorporating connectivity into spatial planning (e.g., representing connectivity with various graph-theoretic metrics, spatial dependency, cost) generate the same priority sites for conservation for a given objective?

and reducing habitat fragmentation are only the first steps towards a comprehensive integration of ecological connectivity for the persistence of biodiversity. Connectivity flows need to be integrated into conservation action [9,10]. Herein we show a pathway towards achieving this goal.

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Declaration of interests

No interests are declared.

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