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PERSPECTIVE

Habitat, geophysical, and eco-social connectivity: benefits of resilient socio–ecological landscapes

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Abstract
Context Connections among ecosystems and their components are critical to maintaining ecological functions and benefits in human-modified landscapes, including urban areas. However, the literature on connectivity and ecosystem services has been limited by inconsistent terminology and methods, and largely omits human access to nature and its benefits as a form of connectivity.
Objectives In this paper, we build upon previous research and theory to define distinct categories of connectivity, considering both ecological and social dimensions, and identify ecosystem services that are supported by them.
Methods We reviewed the literature to determine socio–ecological benefits that depend on the categories of connectivity.
Results We identified four distinct but interrelated categories of connectivity: landscape, habitat, geophysical, and eco-social connectivity. Each connectivity category directly or indirectly supports many ecosystem services. There are overlaps, conflicts, and synergies among connectivity categories and their associated services and disservices.
Conclusions Identifying the services that arise from these four categories of connectivity, and how they interact, can help build a common understanding of the value of connectivity to maximize its benefits, improve understanding of complex socio–ecological systems across disciplines, and develop more holistic, socially equitable decision-making processes, especially in urban landscapes.

Keywords Ecological connectivity · Environmental benefits · Landscape connectivity · Landscape sustainability · Socio–ecological systems · Urban and regional planning

Introduction

Context: the importance of connectivity

Rapid, disruptive landscape change is one of the most consequential phenomena of the Anthropocene (Crutzen 2002; Millennium Ecosystem Assessment 2005). Processes such as urbanization, extractive land use, agriculture, and road building continue to increase rapidly alongside human population and development, with both intensive and extensive impacts on the landscape (DeFries et al. 2004). Indeed, the widespread loss and fragmentation of ecosystems is a major driver of species decline and extinction from the local

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to global scales (Pimm and Raven 2000; Millennium Ecosystem Assessment 2005; Cardinale et al. 2012; Zambrano et al. 2019). Fragmentation also disrupts geophysical processes, potentially worsening the impacts of natural disturbances, both abrupt (e.g. storms, floods, wildfires) and progressive (e.g. heat waves, droughts, sea-level rise) (Laurance and Williamson 2001; Li et al. 2017), and diminishes the renewable economic and cultural resources in the landscapes people inhabit (DeFries et al. 2004). All of these outcomes, furthermore, are unevenly distributed across demographics and geographies, generating or worsening the systemic inequities experienced by society's most vulnerable and disadvantaged communities (Voelkel et al. 2018; Baró et al. 2019). This fragmentation can be understood, to a large extent, as the loss or degradation of functional connections among landscape elements–which suggests that restoring such connections may be able to mitigate its negative and inequitable consequences (Crooks and Sanjayan 2006; Hilty et al. 2006).

Sustainable landscape stewardship aimed at reducing and mitigating fragmentation requires a holistic approach, including biotic, abiotic, and human elements in management, along with an explicit spatial understanding of how these elements function and interact (Wu 2013). Maintaining connections for species, processes, and socio–ecological relationships is critical to preserve ecological function in landscapes where fragmentation is a given, such as within cities. However, connectivity is not always considered, or effectively implemented if included, in conservation planning in these landscapes (Neeson et al. 2015). Identifying how humans benefit directly and indirectly from ecological connectivity could help increase collaboration and support for efforts to enhance and preserve existing connectivity. Our literature search for these benefits found examples spanning many disciplines and geographies yet also revealed many inconsistencies and gaps in how connectivity and its benefits are understood, discussed, and valued, particularly in the area of social equity and environmental justice. This paper, a general theoretical synthesis illustrated with examples from literature in the natural, social, and applied sciences, is our effort to build a common framework to advance work in these fields.

Landscape ecology strives to be a transdisciplinary science (Bastian 2001; Opdam et al. 2013), which requires collaboration across sectors. Developing shared language and values empowers researchers, practitioners, and community advocates to restore and preserve ecological function and to bring the benefits of functioning habitats to all people. In this paper we seek to structure and further develop the array of concepts around connectivity in landscape ecology, to expand and clarify the related terminology, and to use the ecosystem services (ES) framework to identify the many interrelated, interacting benefits (and risks) associated with connectivity in the landscapes we inhabit. While broadly applicable, this paper is particularly relevant to urbanized landscapes where the intensity of fragmentation, the economic and societal benefits of maintaining multifunctional connectivity, and the opportunity costs of ecological conservation are greatest (McDonald et al. 2009; Kabisch et al. 2018). With this context in mind, many of our examples are from urban settings, particularly Portland, Oregon, USA.

Understanding connectivity

Connectivity has emerged as a key concept in landscape ecology in recent years, particularly as the discipline has increasingly turned its attention to the novel ecosystems, altered geographies, and disrupted human and environmental functions of complex socio–ecological landscapes such as cities and agricultural regions (Bennett 2003). However, there is disagreement over what is meant by connectivity, as well as how to measure it and its ecological functions and benefits. As Fischer and Lindenmayer (2007) point out, the word "connectivity" is used in different disciplines to refer to different phenomena, ranging from gene flows within a metapopulation to the contiguity of protected greenspaces. These phenomena are not always analogous and, in some situations, can even conflict with each other. The confusion has grown with the inconsistent use of associated adjectives such as "ecological", "landscape", and "habitat" (Fischer and Lindenmayer 2007).

In the broadest sense, we define "connectivity" as the coherency of landscape components and processes across three-dimensional space (Box 1). Connectivity spans spatial and hierarchical scales (Spanowicz and Jaeger 2019) and can also be dynamic over time, even periodically appearing and disappearing, as with ephemeral wetlands (Allen et al. 2020). It is both possible and, we argue, necessary to include human needs within the definition of connectivity. Indeed, landscape attributes and dynamics such as connectivity may be crucial to sustaining the benefits humans receive, and require, from functional environments (Wu 2013). A growing body of evidence supports the direct and indirect benefits of human connection to nature (Bratman et al. 2019; Shanahan et al. 2016; Van der Bosch and Bird 2018), and reveals significant inequities in how those benefits are distributed across socioeconomic and demographic dimensions (Shanahan et al. 2014; Rigolon 2016; Cole et al. 2017; Haeffner et al. 2017). Connectivity mitigates the disruptive effects of landscape change by maintaining important processes, ecological resilience, and adaptive capacity, particularly when integrated into multifunctional, landscape-scale networks (Mastrangelo et al. 2014; Beller et al. 2019). However, it can also facilitate unwanted processes or changes, such as biological invasions (Aronson et al. 2017). Perhaps surprisingly, then, relatively little research has been conducted into whether connectivity sustains the social and economic benefits of landscapes in the face of increasing fragmentation, climate change, and other disruptions (Mitchell et al. 2015).

Connectivity is not exactly the antonym of fragmentation, as some kinds of fragmentation (e.g., gaps, edge effects) cannot be properly described in terms of connections, while some processes that disrupt connectivity (e.g., river channelization, increased recreational activity) do not quite fit within the general concept of fragmentation. The term “fragmentation” typically applies to landscape patterns and biotic populations, while “connectivity” can also include abiotic and social processes, as well as teleconnections such as long-distance migrations. However, connectivity is mainly of interest in the context of anthropogenic landscape alteration, as is reflected in much of the theoretical literature discussing connectivity and fragmentation (e.g., Fischer and Lindenmayer 2007; Mitchell et al. 2015).

In their review of fragmentation and connectivity literature, Fischer and Lindenmayer (2007) described three distinct, though related and nonexclusive, categories of connectivity: habitat connectivity, ecological connectivity, and landscape connectivity. Because these categories do not capture the integral place of humans in the landscape and the many social purposes of landscape sustainability, we propose a fourth, complementary category: eco-social connectivity. Although we generally embrace maintaining established terminology, we propose replacing the name “ecological connectivity” with the more precise term “geophysical connectivity” given that habitat, geophysical, and eco-social connectivity are all, in some sense, “ecological”.

Ecosystem services as a framework

For our discussion of the benefits people derive from connectivity, we examined the four categories of ecosystem services (ES) developed and popularized by the United Nations’ Millennium Ecosystem Assessment (2005): Provisioning, Regulating, Cultural, and Supporting Services. Provisioning Services include the material products obtained from ecosystems such as food, fiber, and usable water. Benefits from ecosystem processes such as climate or disease regulation or water purification are Regulating Services. Cultural Services capture non-material benefits from ecosystems such as inspirational or spiritual value, recreation, education, and cultural heritage. Underlying all those services are Supporting Services, such as soil formation, primary production, and nutrient cycling, which are necessary for these direct services to exist (Millennium Ecosystem Assessment 2005). Negative effects, or disservices, also exist for each of these categories, and need to be accounted for in any assessment (Lyytimaki and Sipila 2009).

While the ES framework is not without controversy (Vira and Adams 2009; Dempsey and Robertson 2012), it can make ecology more visible in decision-making, provide compelling arguments and incentives for environmental protection, and provide data to support efforts around environmental equity and justice (Goldman and Tallis 2009; Costanza et al. 2014; Everard 2017). In addition to multiple economic valuation methods for ES, it is possible to bring ecosystem function into the ES framework using societal values determined by stakeholders (e.g., Darvill and Lindo 2016). While useful in many cases, strictly economic valuation of environmental benefits can have numerous limitations and pitfalls (Vira and Adams 2009; Büscher et al. 2012; Olander et al. 2018), and is not accepted in many cultures. Therefore, we advocate for a focus on societal values determined by local communities. However quantified, ES implicitly depend on the functionality, integrity, and resilience of the ecosystems from which they arise. Many human activities can both directly and indirectly diminish the functional integrity of ecosystems, with a corresponding decline in ES from those ecosystems (Rapport et al. 1998). Nevertheless, many ES can still exist, to a surprisingly large extent, in novel ecosystems and highly altered landscapes such as cities (Evers et al. 2018).

The literature on ES tends to examine individual components of ecosystems and their associated services in isolation (but see Mastrangelo et al. 2014). Integrative socio–ecological processes (Liu et al. 2007), such as the spatial relationships of landscape elements, complicate our understanding of ES in important ways, particularly when considering multiple ES, heterogeneous landscapes, and/or large spatial extents (Field and Parrott 2017; Rieb and Bennett 2020). To address this issue, Termorshuizen and Opdam (2009) proposed the term "landscape services" as a more holistic, explicitly spatial alternative or complement. Landscape services are evaluated and categorized the same way as ES and the two are generally interchangeable in valuation and decision models (Bastian et al. 2014). While we embrace both terms, and emphasize spatial and integrative considerations, we use "ES" because it is more widely used in the global ecological literature, and because our focus is on conserving the natural components of socio–ecological landscapes.

Categories and services of connectivity

In this section, we define each of the four categories of connectivity, reviewing its theoretical foundations, representations on the landscape, applications, and relationships to ecosystem services.

Landscape connectivity

Landscape connectivity (sometimes referred to as "structural connectivity") is the spatial contiguity or proximity of related landscape elements, which can include human-defined features, such as ownership parcels or management units, as well as natural features. It is inferred from spatial patterns without necessarily representing real-world ecological functions (Bélisle 2005; Önal et al. 2016). Its origins are in geographic information science (GIS), landscape architecture, and land-use planning, and it has become much more commonly used (and misused: see Kupfer 2012) as FRAGSTATS (McGarigal and Marks 1995), graph-theory (Urban and Keitt 2001) and circuit models (McRae 2008), and other GIS applications have facilitated complex spatial pattern analyses (Gustafson 1998). The term "landscape connectivity" is still sometimes used in the literature to refer to the various types of functional connectivity discussed below (e.g., VanAcker et al. 2019; Brodie et al. 2015; Allen et al. 2020), but we follow the lead of Fischer and Lindenmayer (2007) and recommend its exclusive use for connectivity inferred from landscape pattern.

Landscape connectivity is often deductive, assessed in the landscape using spatial statistical and modeling methods (Goodwin 2003), but also can be inductive, in the form of connectivity-oriented design, engineering, and planning criteria (Nassauer and Opdam 2008). The acquisition of adjacent greenspaces with the intent of building regional trails (Jim and Chen 2003), watershed-oriented conservation and restoration (Allan 2005), the conservation of corridor and/or stepping-stone landscape features for wildlife movement (Baum et al. 2004; Van Rossum and Triest 2012; Saura et al. 2014) (but see Stewart et al. 2019), and residential naturescaping initiatives (Rudd et al. 2002) are all applications of landscape connectivity, since they typically rely on spatial location and pattern rather than detailed measurement and analysis of biotic, abiotic, and/or social processes to drive decision-making.

As landscape connectivity is pattern- rather than process-based, it can only be linked indirectly, if at all, to the ES arising from functional types of connectivity (Forman 1991; Rieb et al. 2017). Landscape connectivity can provide a convenient representation when functional connectivity is difficult to measure, such as in the case of urbanized floodplains (Mason et al. 2007). On the other hand, landscape connectivity can miss cryptic processes, such as groundwater movement or stepping-stone habitats, or teleconnections, such as long-distance migrations (Bennett 2003). Alternatively, it may create an exaggerated impression of functional connectivity from map-apparent features with little actual ecological functionality (Kubeš 1996; Gippoliti and Battisti 2017; Laliberte and St-Laurent 2020). For landscape connectivity to be meaningful, there must be a known, scale-appropriate relationship between the observed landscape pattern and the expected process (Tischendorf and Fahrig 2000;

Goodwin 2003; Lynch 2019) or ES outcome (Syrbe and Walz 2012; Duarte et al. 2019). A combination of clear goals, evidence-based strategies, rigorous research and monitoring, and adaptive management can strengthen the effective relationship between landscape and functional connectivity (Adams and Dove 1989; Tischendorf and Fahrig 2000; Kadoya 2009; Beller et al. 2019).

Habitat connectivity

Habitat connectivity is the ability of organisms and/or their genetic material to move among their populations and potential habitats. Originating in the disciplines of biogeography, natural history, and population ecology, habitat connectivity has long been understood intuitively but it was often not easily quantifiable until the development of techniques such as radiotelemetry, camera traps, and genetic analysis. The modern definition of habitat connectivity was coined by Merriam (1984).

Habitat connectivity is necessarily species-specific, as each species has its own habitat requirements and ability to disperse, although some studies seek to aggregate the habitat connectivities of guilds or even entire communities (Hilty et al. 2006). Habitat connectivity is either measured directly by tracking the movements of individual organisms or their propagules or inferred from the genetic similarity of potentially linked populations (Keogh et al. 2007). This form of connectivity is particularly important in metapopulation theory (Wiens 1997), and has led to several approaches to modeling how organisms move through heterogeneous landscapes (Kadoya 2009; Wey et al. 2008; Jeltsch et al. 2013), although research on the topic is still limited by taxonomic biases and methodological issues (Laliberte and St-Laurent 2020; LaPoint et al. 2015). Its applications include road crossings for wildlife (Clevenger and Waltho 2000; Bliss-Ketchum 2019), the geographical risk assessment and containment of biological invasions (Sharov et al. 2002; Epanchin-Niell and Wilen 2012), and land conservation efforts focused on enabling species and communities to shift their ranges in response to climate change (Heller and Zavaleta 2009; Keeley et al. 2018; Walsworth et al. 2019). It can be disrupted by the anthropogenic fragmentation or degradation of habitats, including the construction of barriers such as roads and dams, increased exposure to environmental hazards such as disease and predation, and wildlife avoidance of human activity (Bennett 2003; Hilty et al. 2006).

Habitat connectivity is most associated with biodiversity and the integrity of natural populations (Bennett 2003; Jeltsch et al. 2013; Damschen et al. 2019). While the extent to which biodiversity and ES are correlated is not entirely clear (Brondizio et al. 2019; Martínez-Jauregui et al. 2019), and probably subject to both great variation and great measurement subjectivity (Ricketts et al. 2016), habitat connectivity has a clear role in sustaining species, some of which provide measurable benefits to people and the landscapes they inhabit (Bennett 2003). Considering biodiversity and ES in tandem when making conservation decisions can optimize return on investment, as well (Watson et al. 2020). Examples of ecosystem services and disservices associated in the literature with habitat connectivity are listed in Table 1. In addition, the habitat connectivity of indicator species is sometimes used, with caveats, as a proxy for other connectivity processes (Simberloff and Cox 1987).

Geophysical connectivity

Geophysical connectivity describes the permeability or resistance of the landscape to matter and energy flows; it is the connectivity of natural processes and the landscape features that regulate them. Its origins are in the geosciences and physical geography, particularly with hydrologic connectivity and the river continuum concept (Vannote et al. 1980) and, more recently, the integration of biogeochemical cycles (Pataki et al. 2011) and geomorphology (Brierly et al. 2006; Wainwright et al. 2011) with landscape ecology. However, it also encompasses energy fluxes, the movement of pollutants, disturbance processes such as wildfire, and atmospheric and ocean currents, among other features. It even includes connectivity of biota when viewed through a geophysical lens, as with the regulation of environmental processes provided by contiguous vegetation or biogeochemical transport via migratory animals. As with habitat connectivity, the permeability of the landscape to these flows can be greatly affected by land use change and the built environment, such as impermeable surfaces and above and below ground (Frazer 2005). They can also be altered by biological invasions (Donovan et al. 2013).

Table 1 Representative ecosystem services and disservices of different landscape features representing habitat connectivity

Connectivity feature	Service or *disservice*	Examples and notes
Beneficial animal habitat connected to croplands and gardens	Pest regulation (R) (Mitchell et al. 2015)	Larger and more complex fallow habitats adjacent to croplands were associated with increased parasitoid activity and reduced damage from rape pollen beetles (Thies et al. 2003; Thies and Tscharntke 1999). Beneficial spiders are more likely to move into cropland surrounded by non-crop habitat (Schmidt and Tscharntke 2005)
	Pollination (R, S) (Kremen et al. 2007; Mitchell et al. 2015)	Pollination services to agriculture from native bees are much higher adjacent to natural areas (Kremen et al. 2004)
Functional connectivity of actual and potential habitats across environmental gradients	Climate adaptation and resilience by facilitating range and community shifts (P, R, C, S) (Heller and Zavaleta 2009; Keeley et al. 2018; Littlefield et al. 2019)	Habitat connectivity potentially increases species' capacity for rapid evolutionary response to climate change vs. refugia-based conservation (Walsworth et al. 2019). Keeley et al. (2018) provide guidance for incorporating climate assumptions into assessments of habitat connectivity. See Hodgson et al. (2009) for a critique of focusing on connectivity (particularly when defined as corridors or stepping-stones) as opposed to reserve size and quality in this context
Functionally connected habitats in human- inhabited landscapes (Adams and Dove 1989)	*Ecological traps (S)*	Narrow corridors (Weldon 2006) and urban yards accessible from natural habitats (Demeyrier et al. 2016) can be ecological traps for birds. Reconnected urban streams attract spawning coho salmon, which experience high mortality from toxic road runoff (Feist et al. 2017)
	Human-wildlife conflict (C)	Wildlife corridors for potentially destructive animals such as big cats can result in human-wildlife conflict (Malviya and Ramesh 2015); local mitigation can simply redirect these conflicts elsewhere in the landscape (Osipova et al. 2018)
	Inspiration value of wild species where people can see them (C)	Conserving pollinators and their habitats in an urban landscape creates opportunities for city dwellers, particularly in disadvantaged communities, to connect with nature and enjoy the health and social benefits of greenspace (Bellamy et al. 2017), as well as providing those services to urban agriculture (Galhena et al. 2013). Aggregations of bird-friendly yards support native bird biodiversity (Belaire et al. 2014), which people enjoy experiencing (Belaire et al. 2015)

Table 1 continued

Connectivity feature	Service or *disservice*	Examples and notes
Habitat connectivity for species with important (socio–)ecological functions	Foundation, facilitating, and ecosystem engineer species where beneficial (*or harmful*) in landscape (S)	Cavity-creating birds need a certain amount of canopy connectivity in urban landscapes to access habitat patches (Fernández-Juricic 2000). Beavers, a critically important ecosystem engineer in Northern Hemisphere riparian landscapes, require riparian habitat connectivity to naturally repopulate areas from which they were extirpated (Pollock et al. 2017)
	Herbivory: regulation (*or degradation*) of vegetation quality and quantity (R); nutrient cycling (R); *herbivore damage to crops and/or ornamental landscaping (P, C)*	Connectivity between mangrove and coral reef habitats within marine reserves is associated with increased fish grazing on algae, leading to healthier, more resilient coral populations (Olds et al. 2012b). Connectivity tends to promote ES from herbivorous insects with relatively stable populations, but increases the destructive potential of outbreaking species across the landscape (Maguire et al. 2015)
	Nutrient subsidies from organisms and their remains or wastes (R, S)	Brown bears, a highly fragmentation-sensitive species, distribute substantial amounts of salmon-derived nutrients into boreal forests near streams, providing trees with 15%-18% of their total nitrogen (Hildebrand et al. 1999)
	Pollination of ecologically beneficial wild plants; *pollination of invasive plants* (S)	Wild bee species richness and abundance are highest at intermediate levels of functional connectivity in heterogeneous landscapes (Boscolo et al. 2017). Pollination of holly and associated pollinator activity are much higher in connected vs. isolated patches (Tewksbury et al. 2002). Mitchell et al. (2015) summarize the services of pollination from connectivity
	Propagule dispersal of ecologically beneficial wild plants; *propagule dispersal of invasive plants* (S)	Abundance and diversity of native hydrochorous plant seed dispersal along small urban streams decrease as impervious area increases and forest cover decreases in streamside areas and watersheds (von Behren 2018). Dispersal of yaupon holly seeds by birds was higher in connected patches than in isolated patches of the same size (Tewksbury et al. 2002), likely due to facilitation by corridors (Levey et al. 2005a)
	Viable and accessible populations of fish, game, and forage species (P, C)	Anadromous salmonid spp. require both reach-scale stream connectivity for access to side channels and cold-water refugia (Ebersole et al. 2003) and watershed-scale stream connectivity to move between spawning and feeding grounds (Yeakley et al. 2014); removing in-stream barriers has been shown to increase their population performance (Sheer and Steel 2006). Connectivity between mangrove and coral reef ecosystems within reserves was associated with increased fish populations in Australia (Olds et al. 2012a)

Table 1 continued

Connectivity feature	Service or *disservice*	Examples and notes
Habitat connectivity for undesirable organisms	*Facilitated spread of invasive or undesirable species (S)* (Aronson et al. 2017)	Human- and wildlife-vectored dispersal of the invasive grass *Brachypodium sylvaticum* was found to occur primarily along riparian corridors in a suburban landscape (Arredondo 2018). Connected patches had more invasive fire ants and lower native ant diversity than unconnected patches (Resasco et al. 2014)
	Spread of disease organisms and their vectors (R); regulation of disease organisms and vectors (R)	Areas of high habitat connectivity displayed increased tick abundance vs. sites with low habitat connectivity (Estrada-Peña 2003), likely due to increased dispersal of vector animals (Watts et al. 2018). Habitat connectivity for predators such as mesocarnivores can significantly regulate tick abundance (Hofmeester et al. 2017)
Increased or novel connectivity of historically isolated populations	*Exposure of isolation-protected populations to introduced or novel hazards (S)*	Endangered Oregon chub persist in isolated side channels where nonnative predators are absent; reconnecting these waterways to the river system could imperil the species (Scheerer 2002)
	Genetic homogenization and loss of localized diversity (S) (Rhymer and Simberloff 1996)	Displacement and hybridization of spotted owls by barred owls due to the latter's range expansion into western North America (Hamer et al. 1994); genetic contamination of nearby wild tree populations by intensively bred or genetically-modified forestry stock (Brunner et al. 2007)
Multi-species and multi-functional group habitat connectivity (Marczak et al. 2007)	Functional, resilient food webs (S) (Pillai et al. 2011); stability of biological communities and metacommunities (S) (Brodie et al. 2016)	Increased habitat connectivity can decrease food web stability of high trophic levels but increase stability of lower trophic levels (LeCraw et al. 2014). Multi-species corridors appear to be more effective when tailored to guilds of functionally similar species vs. a more general approach (Brodie et al. 2015). Coherent habitat in road verges supports substantial urban invertebrate biodiversity and associated ES (O'Sullivan et al. 2017)
	Increased biodiversity over time by facilitating colonization (S)	Corridor-connected ecosystem fragments in an experimental forest increased in floristic biodiversity faster than isolated fragments in a long-term study (Damschen et al. 2019)

Disservices are listed in italics

The category of each service/disservice is listed as follows: *P* provisioning, *R* regulating, *C* cultural, *S* supporting. Services/disservices are illustrated and elaborated upon with examples from literature

Geophysical connectivity is assessed by measuring matter and energy flows across space and time, using methods ranging from point monitoring to remote sensing analysis and computer modeling (Arnfield 2003; Mimikou et al. 2016). Its applications include such diverse practices as green stormwater infrastructure (Fahy 2018), wildfire management (Wei et al. 2019), and the use of tree canopy to mitigate the stresses of urban environments (Makido et al. 2019).

Geophysical connectivity underlies many regulating and supporting services, among others (Table 2).

Table 2 Representative ecosystem services and disservices of different landscape features representing geophysical connectivity

Connectivity feature	Service or *disservice*	Examples and notes
Contiguity of wildfire fuel loads with built environments	*Spread of wildfire into populated areas (R)* (Ager et al. 2017)	Rapid expansion of cities and exurbs into fire-prone landscapes connects fuel loads with housing and makes fuel load management a high priority for land stewards (Lafortezza et al. 2015). Strategic planting arrangements (MacLeod et al. 2019) and defensible space such as firebreaks and waterbodies (Penman et al. 2019), coupled with compact development (Braziunas et al. 2021), are effective strategies for mitigating this fire risk while maintaining the benefits of vegetation
Contiguous patches/strips of vegetation retained in erosion-prone landforms	Soil retention and geological stability (R)	Large areas of disturbed soils (e.g., from wildfires) increase runoff and erosion on hillslopes (Williams et al. 2016). Connectivity of soil conservation measures can mitigate this erosion: continuous woody riparian vegetation > 5 m tall has been shown to substantially reduce riverbank erosion during flood events (McMahon et al. 2020)
Functional coastal buffers, floodplains, windrows	Landscape-scale physical protection against major disturbances and disasters (R, S)	Functioning (i.e., minimally fragmented) floodplains provide direct ES from reduced loss of life and property damage (Watson et al. 2016) and indirect ES from diverse ecosystem functions (Ward and Stanford 1995)
Hydrologic connectivity	Biological and geological filtration of water (R, S) (Brauman et al. 2007; McMillan & Noe 2017)	The spatial scale of hydrologic connectivity matters: models suggest that green stormwater infrastructure is far more effective in urban watersheds when more, smaller installations are hydrologically connected to more, smaller drainage areas, rather than fewer, larger installations hydrologically connected to fewer, larger drainage areas (Fahy 2018). The effectiveness of urban floodplains in capturing sediments and nutrients tends to increase over time following hydrologic reconnection as the systems mature (McMillan and Noe 2017)
	Groundwater recharge and recycling (S)	Complex, braided river systems have more connections to the surrounding landscape and thus greater and more extensive groundwater recharge than channelized streams (Rodgers et al. 2004). Hyporheic discharge into streams tends to buffer short-term fluctuations in water temperature (Arrigoni et al. 2008)
	Mosaics of aquatic and riparian habitats supporting high biodiversity (S) (Ward et al. 1999)	Complex hydrologic connectivity in floodplains creates spatiotemporal diversity of aquatic, terrestrial, and transitional niches and ecotones facilitating biologically and structurally diverse vegetation (Amoros and Bornette 1999; Leyer 2006). Conversely, some aquatic habitats (e.g., ponds, impoundments) can have greater wildlife value with artificially restricted hydrologic connectivity in highly modified river or wetland systems (Jackson and Pringle 2010)
	Release and dispersal of pollutants from point and nonpoint sources (R) (Jackson and Pringle 2010)	Urban catchments with numerous stormwater outfalls show considerable and unpredictably distributed heavy metal contamination (Chang et al. 2019)
	Reliability of fresh water quantity and supply (P) (Brauman et al. 2007)	Intact upland forest ecosystems can play a critical role in fresh water provisioning by intercepting, retaining, and recycling precipitation (Brauman et al. 2007)
	Sediment discharge into and through stream systems (R) (Jackson and Pringle 2010; Liu et al. 2020)	Features of continuous stream systems functionally connected to floodplains, such as riparian vegetation (Gurnell 2014), beaver dams (Pollock et al. 2017), and coarse woody debris (Seixas et al. 2020; Stevens 1997), can trap suspended sediments. By contrast, anthropogenic features which disconnect stream systems from floodplains, such as road and rail grades, culverts, and ditches, can increase erosion effects and amplify sediment loads (Boardman et al. 2019)
	Transportation routes and water trails (C) (Kondolf and Pinto 2017)	Ferries along water routes serve as important, sometimes development-driving public transit in cities in several countries (Burke et al. 2020; Tanko et al. 2018)

Table 2 continued

Connectivity feature	Service or *disservice*	Examples and notes
Urban tree canopy	Air filtration (R) (Escobedo et al. 2011); *decreased local air quality from VOC or pollen release* (R) (Leung et al. 2011)	Dense aggregations of trees near pollution sources such as busy roads may reduce the dispersion of air pollutants, concentrating them on-site (Tong et al. 2015). Taxonomic and structural diversity may increase the air-quality benefits of urban trees (Manes et al. 2012)
	Interception of stormwater, resulting in decreased surface runoff and pollution into streams (R)	While it is evident that urban tree canopy is important for stormwater interception and infiltration (Xiao & McPherson 2002), a network of trees is likely even more important. However, the role of connectivity of the urban tree canopy is a research gap for stormwater (Kuehler et al. 2017)
	Positive and *negative* impacts of trees to built infrastructure (R, C, S)	Street trees can damage sidewalks with their root systems, and be damaged by pavement replacement (North et al. 2017), but also protect paved surfaces from solar damage (McPherson & Muchnick 2005). Appropriate species selection (North et al. 2017) and design approaches (Dupey et al. 2019) can proactively reduce conflict between trees and infrastructure
	Positive and *negative* outcomes in regulation of biogeochemical processes (R)	Tree cover over pervious surfaces typically results in nutrients being retained by soils and plants, whereas tree cover over impervious surfaces is more likely to increase nutrient loads in waterways through stormwater runoff (Decina et al. 2018)
	Zones of cooling around canopy areas (R) (Vieira et al. 2018)	Greater vegetation structural complexity (Vieira et al. 2018) and areal coverage (Deilami et al. 2018) increase the extent and magnitude of local climate regulation effects
Vegetated riparian buffer areas	Ecological values (habitat structure, productivity, biogeochemical cycling, biodiversity) of increased coarse woody debris (Stevens 1997) and leafy material (Marcarelli et al. 2011) in streams (S)	These processes are often deficient and overwhelmed by hydrologic disruptions in urbanized watersheds (Imberger et al. 2011). The importance of woody debris in riparian systems is still under-recognized in many regions after decades of intentional removal for purported ecological benefit (Wohl 2019)
	Interception and filtration of potential water contaminants (R)	Contiguous vegetated buffers as narrow as 1 m between livestock pastures and waterways can greatly reduce in-stream fecal coliform bacteria concentrations (Sullivan et al. 2007)
	Mitigation of sediment and nutrient runoff into streams (R) (Barling and Moore 1994; Hill 1996)	Spatial gaps in riparian vegetation create points of failure in this protection (Weller et al. 1998)
	Seasonal temperature regulation of waterways by canopy shade (R) (Blann et al. 2002)	Riparian revegetation has been used in a local ES market to offset thermal pollution from municipal wastewater discharge (Smith and Ory 2005). Vegetated riparian areas are expected to be more resilient to future temperature increases than surrounding upland habitats in many landscapes (Keeley et al. 2018)

Disservices are listed in italics

The category of each service/disservice is listed as follows: *P* provisioning, *R* regulating, *C* cultural, *S* supporting. Services/disservices are illustrated and elaborated upon with examples from literature

Eco-social connectivity

Research on anthropogenic landscape change often focuses on impacts to biodiversity and natural systems (Fischer and Lindenmayer 2007), and frames management decisions through that lens (Newbold et al. 2015), overlooking the integral interrelationship of humans with the landscapes they use and inhabit. Eco-social connectivity [partially introduced as "social connectivity" in Kondolf and Pinto (2017)] captures how the spatial features and properties, both natural and built, of landscapes facilitate people's access to nature and its benefits. While such access has been well-studied in numerous disciplines (e.g., ecopsychology, environmental sociology, environmental economics, environmental medicine, human geography, environmental education) (Thompson 2011), and although landscape sustainability science (Wu 2013) emphasizes the need to study access to nature in a geographical/landscape context (e.g., Weber and

Sultana 2013), the literature rarely frames such access as a form of "connectivity" (Kondolf and Pinto 2017). Social connectivity has mostly been used for human-to-human connections, and has been defined as the communication and movement of people, goods, ideas, and culture (Kondolf and Pinto 2017). The study and modeling of social networks (Scott 1988) has made social connectivity, linking humans to humans, a widespread concept in the social sciences, but one not often explored in ecology. In addition, the concept of social connectivity does not fully capture the magnitude and importance of human access to nature's benefits and the interrelationship between landscape and society. Thus, eco-social connectivity bridges the gap between ecological and social connectivity.

Eco-social connectivity overlaps with a number of other current ideas in landscape sustainability, such as inclusive (Imrie and Hall 2001) and biophilic (Beatley 2011) design philosophies, political ecology (Turner and Robbins 2008), nature-based learning (Jordan and Chawla 2019), and recreation ecology (Monz et al. 2010). As eco-social connectivity is fundamentally human-centered, it is best assessed by active stakeholder engagement, such as through surveys, interviews, workshops, and public participation/process equity in planning and implementation (Matsuoka and Kaplan 2008; Stringer et al. 2006; Rall et al. 2019). Passive measurements typically do not provide valuable data on eco-social connectivity, although some methods, such as trail counts, can (Reynolds et al. 2007). Eco-social connectivity is closely tied to environmental equity and justice. There is strong and growing evidence linking access to nature with human wellbeing (Van der Bosch and Bird 2018). In many landscapes, particularly urban areas where total greenspace is relatively scarce, profound disparities in this access reflect deeply embedded social inequities along lines such as race, ethnicity, ability, and socioeconomic class (Shanahan et al. 2014; Kowarik 2018; Nesbitt et al. 2019). Efforts to increase eco-social connectivity in disadvantaged communities can backfire, however, if increased access to natural amenities fuels gentrification, helping to displace the communities it is meant to serve (Dooling 2009; Cole et al. 2017). Planning for eco-social connectivity thus needs to occur alongside policies and practices to address the underlying causes of gentrification, and to integrate strong community input throughout the process (Wolch et al. 2014).

Eco-social connectivity can be disrupted by lack of natural resources integrated into communities, insufficient quantity and quality of reachable greenspace, inadequate accessibility infrastructure, and cultural barriers such as safety concerns and discrimination in parks (Gobster 2002; Williams et al. 2020). Discriminatory policies and practices such as red-lining have created enduring unequal access to quality natural resources and greenspace (Shanahan et al. 2014; Nesbitt et al. 2019). These policies have perpetuated localized disparities in green infrastructure benefits such as shade trees and stormwater management (Hoffman et al. 2020), and even have evolutionary and ecological implications (Schell et al. 2020). Applications of eco-social connectivity are diverse and widespread, ranging from biocultural restoration (Morishige et al. 2018) to inclusive design in outdoor recreational areas (Doick et al. 2013), community gardens (Glover et al. 2005), and tree-planting initiatives in under-resourced neighborhoods (Stone et al. 2015).

Eco-social connectivity is particularly associated with provisioning and cultural services (Table 3).

Discussion

Overlaps and interactions

The four types of connectivity are not mutually exclusive. Fully connected watersheds that allow stream passage for anadromous salmonids, for instance, represents habitat (the movement of organisms among feeding, transitional, and spawning waters), geophysical (the delivery of nutrient subsidies from the ocean to headwater streams), eco-social (access to fishing and associated cultural and economic activities), and landscape (planning and design practices to remove or mitigate barriers) connectivities (Smith 1994; Yeakley et al. 2014). Another example is extensive urban tree canopy, which makes the urban matrix more permeable to wildlife (habitat) (Baum et al. 2004); regulates stormwater, air quality, and local climate (geophysical) (Escobedo et al. 2011; Nyelele et al. 2019); increases the value and vibrancy of local communities (eco-social) (Bolitzer and Netusil 2000; Stone et al. 2015); and requires spatial

Table 3 Representative ecosystem services and disservices of different landscape features representing eco-social connectivity

Connectivity feature	Service or *disservice*	Examples and notes
Accessible greenspaces in human-inhabited landscapes	Educational outcomes (C); awareness of and concern for the environment (C) (Wells and Lekies 2006)	Individuals who were more involved in nature as children tend to become more active in environmental advocacy as adults (Wells and Lekies 2006), particularly regarding wildlife (Zhang et al. 2014). Childhood access to biophilic experiences is significantly lower in urban vs. rural schools in much of the world (Zhang et al. 2014)
	Formation and cohesion of communities around nature and greenspaces (C) (Dinnie et al. 2013; Jennings and Bamkole 2019)	The interpersonal aspects of access to nature and biophilic experiences have received relatively little study (Dinnie et al. 2013). Social interaction with peers has been cited as important to community scientists participating in wildlife monitoring (Ng et al. 2018)
	Human health benefits from time spent in nature (R, C) (Mao et al. 2012; Shanahan et al. 2016)	Human health and wellbeing benefits of urban forest patches are amplified when forests are relatively undisturbed and well-connected to exurban natural areas (Pirnat and Hladnik 2018). Wildlife sightings, street trees, and viewsheds have been identified as particularly relevant to human mental health within urban spaces (McEwan et al. 2020), as has biodiversity of vegetation and birds (Fuller et al. 2007; Luck et al. 2011), though the latter depends on people's ecological literacy (Dallimer et al. 2012)
	Increased human exposure to pathogens and their vectors (R)	Human exposure risk to Lyme disease in urban landscapes may be higher than previously thought due to extensive interfaces between built environments and fragmented greenspaces (VanAcker et al. 2019)
	Restoration/enhancement of populated ecosystems as economic, social, and ecological stimulus (C) (Standish et al. 2012)	The U.S. "restoration economy" is estimated to directly support 126,000 jobs and $9.6 billion in output, and indirectly support an additional 95,000 jobs and $15 billion in output (BenDor et al. 2015), though primarily in rural areas (Nielsen-Pincus and Moseley 2013). Ecological restoration in urban landscapes has potential to reconnect communities with nature and provide highly accessible cultural, educational, and economic amenities to residents (Standish et al. 2012)
	Retention and transmission of local and/or traditional ecological knowledge (C) (Berkes et al. 2000)	Some public urban gardens (Waldroupe 2018) and natural areas (Eldridge 2018) are managed for "first foods" and associated Indigenous cultural practices in the Portland, OR metro area, sometimes with limited access to protect cultural resources
	Social resilience during times of crisis (C)	Accessible public spaces, including parks and greenspaces, provide critical infrastructure for maintaining community ties during disaster recovery (Caughman 2017) and facilitating political engagement through civil protest (Schwartzstein 2020)
Accessible greenspaces in socioeconomically disadvantaged urban areas (Rigolon 2016)	*Gentrification and economic displacement (C)* (Dooling 2009; Wolch et al. 2014)	The causal relationships between accessible greenspace and gentrification are complex and likely context-specific (Cole et al. 2017). While creating access to greenspace without addressing underlying socioeconomic inequities can undercut intended outcomes (Cole et al. 2017), responsive, scale-flexible governance systems, based on a recognition of social capital, have the potential to help ensure environmental and economic justice in connectivity planning (Brondizio et al. 2009)
	Increased community vibrance and value (C) (Stone et al. 2015)	A strong inverse relationship was found between crime and tree canopy or other vegetation in Philadelphia (Wolfe and Mennis 2012) and most parts of Baltimore (Troy et al. 2012)
Access to resource gathering areas	Opportunities for food and materials gathering (P, C)	Huckleberry picking in the Cascades (Richards and Alexander 2006); urban food foraging (Fischer and Kowarik 2020; Sardeshpande and Shackleton 2020)

Table 3 continued

Connectivity feature	Service or *disservice*	Examples and notes
Aesthetic values of intact greenspace and natural resources (Barendse et al. 2016)	*Aesthetic preferences incompatible with biodiversity and/or ecosystem function (C)*	Many residents of urban settings, particularly in lower-income neighborhoods, have negative perceptions of some types of natural vegetation and wildlife (Rega-Brodsky et al. 2018). By contrast, many visitors to South Africa's Cape Floristic Region appreciate the aesthetic qualities of invasive trees in the landscape, despite their negative impacts to the region's biodiversity and ecological function, which may be unknown to visitors (Barendse et al. 2016)
	Increased community vibrance and value (C) (Stone et al. 2015)	Real estate values are higher in locations overlooking a natural viewshed even in urban or peri-urban landscapes (Joly et al. 2009)
	Noise mitigation by vegetation (R)	Individuals who reside in homes that have a "quiet" side due to natural landscape elements had lower physiological stress than those who live in homes without a "quiet" side (Gildof-Gunnarsson and Ohrstrom 2007)
	Sense of place (C) (Hausmann et al. 2016)	Access was a key factor in community members developing place attachment to and helping to restore shoreline areas in Puget Sound, WA (Poe et al. 2016)
Human access to natural waterways	*Conflict between aesthetic and ecological values of accessible waterways* (C)	People view downed trees and logs in waterways as undesirable, even though they provide important ecological functions in waterways (Wantzen et al. 2016; Wohl 2019)
	Recreation, sense of place, relaxing environment (C)	Residents were more likely to use and appreciate urban waterways when public access points were near their neighborhoods (Haeffner et al. 2017)
	Social health benefits of river access (C)	Increased access to culturally and socially important natural river areas decreases social stress and conflict (Wantzen et al. 2016)
	Waterways as avenues for communication and commerce (C)	Many of the large and historically important cities in the US built before the modern era were situated near waterways due to transportation and resource availability, which enabled commerce and communication via ships (Kondolf and Pinto 2017)
Human access to wildlife habitat	*Fragmentation of wildlife habitat and movement corridors by trails and other infrastructure (S)*	Recreational uses of trails in natural areas result in a variety of ecological impacts, including stress effects on wildlife and degradation of wildlife habitat (Hennings 2017)
	Humans as vectors for invasive species, pollutants, and litter (R, S)	Both formal and informal trails are associated with the dispersal of invasive plants in urban forests (Van Winkle 2014)
	Human-wildlife conflict (P, R, C, S) (Soulsbury and White 2015)	Off-leash dogs are a particular hazard to both wildlife and human visitors in natural areas (Wilson et al. 2018)
	Inspiration value of wildlife viewing (C) (Miller 2005)	Urban wildlife spectacles such as the Congress Avenue Bridge free-tailed bat colony in Austin, TX (Murphy 2020) or the Chapman School Vaux's swift roost in Portland, OR (Houck 2011) have become major community attractions and even tourist draws
Regional greenspace trail systems	Opportunities for exercise, social engagement, and other healthy activity (C) (Schultz et al. 2016)	Children who live within 0.5 mile of a trail system were found to have lower BMI than those who do not (Kim et al. 2020)
	Transportation alternatives reducing deleterious effects of automobile traffic (R)	Aesthetically pleasing cycling routes separated from motor traffic are safer than on-road routes in terms of injury rates (Lusk et al. 2011), increase commuter usage (Hirsch et al. 2017), and are important to cyclists (Winters et al. 2011). The regional trail system in Portland, OR, is estimated to save commuters $1.1 billion/year in transportation costs (Spurlock 2016)

Table 3 continued

Connectivity feature	Service or *disservice*	Examples and notes
Urban gardens as accessible greenspace	Access to biophilic and eusocial experiences in disadvantaged communities (C) (Glover et al. 2005)	Space for small-scale polycultural gardens, at or a short walk from home, in both urban and rural areas provides multiple cultural services (Galhena et al. 2013)
	Decreased food insecurity and malnutrition, increased economic opportunity from micro-agriculture (P)	Space for small-scale polycultural gardens, at or a short walk from home, in both urban and rural areas leads to nutritional security, health benefits, an uplift to women's status, and economic growth (Galhena et al. 2013)
	Environmental health and pollution hazards of gardens (R)	In some areas public use of urban gardens increases exposure to insect-borne and/or fecal-related diseases, while still bringing many societal benefits (Hamilton et al. 2014). Urban agriculture can be a locally significant source of nutrient pollution from excessive use of fertilizer, compost, and irrigation (Harada et al. 2018; Nelson 2018; Wielemaker et al. 2019)
Urban tree canopy	Cognitive, psychological, and eusocial benefits to urban residents (R, C) (Bratman et al. 2019)	A study of elementary school students in California found a strong positive influence of neighborhood-scale urban tree canopy on test scores, when controlled for common demographic variables (Tallis et al. 2018). Increased tree canopy in urban neighborhoods in Baltimore was a strong predictor of increased social capital among residents (Holtan et al. 2016)
	Facilitation of public use of outdoor spaces (C)	A study of urban areas in Wisconsin found a strong positive correlation between street tree cover and active transportation activity, whereas other kinds of vegetation cover had neutral or negative effects (Tsai et al. 2019)
	Provision of air quality and climate regulation services to underserved communities (R) (Baró et al. 2019)	Landscape-scale urban heat island assessment during a 2014 heat wave in Portland, OR found that the most vulnerable socioeconomic and demographic groups were most exposed to extreme heat, in part due to lack of continuous, functional tree canopy in their neighborhoods (Voelkel et al. 2018). Excessive urban heat has broad negative effects on physical and mental wellbeing, ranging from morbidity and mortality (Kravchenko et al. 2013) to diminished learning outcomes (Park et al. 2020; Zivin et al. 2020)

Disservices are listed in italics

The category of each service/disservice is listed as follows: *P* provisioning, *R* regulating, *C* cultural, *S* supporting. Services/disservices are illustrated and elaborated upon with examples from literature

analysis, modeling, and planning standards to be effective and equitable (landscape) (Gatrell and Jensen 2008; Ordonez and Duinker 2013).

Such overlaps frequently interact, resulting in both synergies and tradeoffs. These interactions can vary by location, time, and scale (Termorshuizen and Opdam 2009). The field of recreation ecology, for instance, is concerned with quantifying the many impacts human visitors have on natural areas and weighing them against the social benefits and conservation incentives of human access to nature (Monz et al. 2010). Here, the roads and trails that support eco-social connectivity can fragment habitats, deter wildlife, and impact watersheds, but at broader scales can justify and incentivize the protection of large, well-connected natural landscapes. Such overlaps and synergies, commonly termed "ecosystem multifunctionality" (Manning et al. 2018), provide opportunities to optimize landscape-scale conservation and planning efforts and maximize their return on investment (Conrad et al. 2012; Önal et al. 2016).

Using connectivity services in planning

We include Tables 1, 2, 3 with the intent that articulating the ES of these categories of ecological connectivity will help managers and communities gain support for connectivity projects. In Table 4 below, we illustrate the relationships between management actions, connectivity features, and socio–ecological outcomes. However, harnessing the synergies among the different connectivity categories and their services,

Table 4 Links between management actions, functional connectivity features, and outcomes providing ecosystem services and disservices

Management actions	Connectivity features (proxy for)	Management outcomes (services, *disservices*)	Examples and notes
Acquire greenspaces and rights-of-way for regional trails (Jim and Chen 2003), and use accessible trail design and construction	Regional greenspace trail systems (E)	Exercise and recreation (C); alternative transportation (C); sense of place and community (C); higher property values (C); *cost of land acquisition and construction (C)* (Hammons 2015; Spurlock 2016)	A caveat: trail systems are not guaranteed to be used by local populations (Evenson et al. 2005). Trail system use can depend on spatial design principles such as viewshed aesthetics and segment lengths (Lindsey et al. 2008)
Analyze the geographical accessibility of greenspaces to local communities and build infrastructure to address gaps	Accessible greenspaces in human-inhabited landscapes (E)	Mental and physical health benefits of time spent in nature (P, C); *recreation impacts to biodiversity and natural resources (S)* (Monz et al. 2010)	The Trust for Public Land's ParkServe database and analysis tool models the population percentage of each US census block within a 10 min walk of a public park or natural area (Trust for Public Land 2017)
Designate no-take or limited-take areas within or adjacent to important fisheries; reroute shipping lanes around sensitive habitats	Habitat connectivity for species with important (socio–)ecological functions (H)	Productive and sustainable fisheries (P, C); biodiversity (S); *localized economic displacement (C)* (Stewart and Possingham 2005)	Marine reserves are more effective at conserving fish when they protect contiguous feeding and rearing areas (Olds et al. 2012a)
Empower Indigenous ecological land management where possible (Winter et al. 2020)	Accessible greenspaces in human-inhabited landscapes (E); access to resource gathering areas (E); beneficial animal habitat connected to croplands and gardens (H); functionally connected habitats in human- inhabited landscapes (H); multi-species and multi-functional group habitat connectivity (H)	Access to biophilic and eusocial experiences in disadvantaged communities (C); awareness of and concern for the environment (C); decreased food insecurity and malnutrition, increased economic opportunity from micro-agriculture (P); formation and cohesion of communities around nature and greenspaces (C); functional, resilient food webs (S); landscape-scale physical protection against major disturbances and disasters (R, S); mosaics of aquatic and riparian habitats supporting high biodiversity (S); opportunities for food and materials gathering (P, C); retention and transmission of local and/or traditional ecological knowledge (C); sense of place (C); viable and accessible populations of fish, game, and forage species (P, C); *human-wildlife conflict* (C)	Winter et al. (2020) review a suite of Indigenous "ecomimicry" strategies which maintain biodiversity and maximize synergistic ES in extensive socio–ecological landscapes

Table 4 continued

Management actions	Connectivity features (proxy for)	Management outcomes (services, *disservices*)	Examples and notes
Identify and mitigate or remove hydrologic barriers such as dams or culverts	Habitat connectivity for species with important (socio–)ecological functions (H); hydrologic connectivity (G)	Increased fish populations (P, S); water quality and quantity (P, R); *cost of remediation (C); loss of infrastructure functions such as hydropower or flood regulation (P, R, S); disturbance impact of removal process (S)* (Whitelaw and MacMullen 2003)	Long-term research at the former Elwha River dam sites in Olympic National Park is adding to knowledge about ecological and hydrological recovery after dam removal (Duda et al. 2011)
Implement control and/or mitigation features for transmissible hazards	Contiguity of wildfire fuel loads with built environments (G); functional coastal buffers, floodplains, windrows (G); habitat connectivity for undesirable organisms (H); urban tree canopy (G, E)	More effective hazard management and lower loss of life, wellbeing, and property across scales (R, C, S)	Identification of potential control points and risk corridors for wildfires using remote sensing data (Wei et al. 2019); habitat connectivity modeling for invasive species to support more effective management strategies (Drake et al. 2017)
Implement ecological enhancement and management of vegetated buffers along road and highway verges (Säumel et al. 2016; O'Sullivan et al. 2017)	Accessible greenspaces in human-inhabited landscapes (E); contiguous patches/ strips of vegetation retained in erosion-prone landforms (G); functionally connected habitats in human-inhabited landscapes (H)	Local mitigation of climate, pollution, and aesthetic impacts (R, C, S); biodiversity (S); *cost of upkeep (C); ecological traps (S); fuel loading in fire-prone landscapes (R, S)*	Road and highway verges represent one of the largest stocks of open space in many cities (O'Sullivan et al. 2017)
Implement strategic land acquisition and conservation within and between core natural areas at local to continental scales	Functional connectivity of actual and potential habitats across environmental gradients (H); habitat connectivity for species with important (socio–)ecological functions (H); functional coastal buffers, floodplains, windrows (G); hydrologic connectivity (G); regional greenspace trail systems (E)	Ecosystem functions, biodiversity, and landscape resilience (S) (Opdam and Wascher 2004)	Yellowstone-to- Yukon Conservation Initiative (continental) (Levesque 2001); Territorial System of Ecological Stability (regional) (Kubeš 1996); Resilient Silicon Valley project (local) (Beller et al. 2019)
Increase quality, quantity, and connectivity of naturescaped yards (Rudd et al. 2002; Dearborn and Kark 2010) and agricultural habitat enhancements (Donald and Evans 2006)	Accessible greenspaces in human-inhabited landscapes (E); functionally connected habitats in human-inhabited landscapes (H); urban gardens as accessible greenspace (E)	Wildlife viewing (C); pollination and pest regulation (R, S); local climate regulation (R); neighborhood character and property values (C); *economic displacement (C); maintenance costs (C)*	Residential yards provide 65% of the total urban tree canopy cover in Boston, MA, but this coverage is unequally distributed and more fragmented than in protected greenspaces (Ossola et al. 2019)
Integrate cover crops, fallow strips, wind- and hedgerows, and organic farming techniques into agricultural settings (Holzschuh et al. 2010)	Beneficial animal habitat connected to croplands and gardens (H)	Increased pollination and predation services (P, R, S) (Holzschuh et al. 2010); *increased impacts from some herbivores and pathogens (P, R, S)*	"Beetle banks" (patches of unmowed perennial grasses) incorporated into farmlands support predatory ground beetles (MacLeod et al. 2004)

Table 4 continued

Management actions	Connectivity features (proxy for)	Management outcomes (services, *disservices*)	Examples and notes
Integrate infrastructural greenery into buildings and the built environment	Accessible greenspaces in human-inhabited landscapes (E); aesthetic values of intact greenspace and natural resources (E); urban tree canopy (G, E)	Air filtration (R); ecological traps (S); foundation, facilitating, and ecosystem engineer species where beneficial (*or harmful*) in landscape (S); local climate regulation (R); neighborhood character and property values (C); *economic displacement (C); maintenance costs (C); fuel loading in fire-prone landscapes (R, S)*	A primary benefit of urban vegetation is mitigation of the heat-island effect; the effectiveness of different greening strategies for local climate regulation depends a lot on site context (Deilami et al. 2018; Makido et al. 2019)
Integrate multiple contiguous habitat types within and across landscapes into conservation and restoration plans	Functional connectivity of actual and potential habitats across environmental gradients (H); habitat connectivity for species with important (socio–)ecological functions (H); functional coastal buffers, floodplains, windrows (G)	Ecosystem functions,biodiversity, and landscape resilience (S)	The Resilient Silicon Valley project aims to reconnect oak and estuarine habitats across the urban landscape (Beller et al. 2019)
Maintain and expand contiguous urban tree canopy, particularly in tree-deficient areas	Functionally connected habitats in human-inhabited landscapes (H); urban tree canopy (G, E)	Local mitigation of climate, pollution, and aesthetic impacts (R, C, S); biodiversity (S); *cost of upkeep (C); nuisance effects of some trees (R, C, S)*	Important elements of urban forest plans include geographic and socioeconomic equity, genetic and taxonomic diversity, climate resilience, and collaborative governance (Portland Parks and Recreation 2004). Ensuring tree survival is crucial: as little as 7% mortality can negate the local benefits of tree-planting efforts over time (Widney et al. 2016). When supported by effective training, institutional knowledge, and mission alignment, community-driven stewardship can help ensure the long-term success of neighborhood afforestation (Jack-Scott et al. 2013)
Preserve visually important areas	Aesthetic values of intact greenspace and natural resources (E)	Sense of place and community (C); property values (C); *regulatory burden on growth and development (C); economic displacement (C)*	Deeply considered viewshed design and management in Yosemite National Park help build a sense of identity, buy-in, and public attention to an iconic landscape (National Park Service 2012). Research on how to value and manage for landscape aesthetics tends to lag behind planning emphasis on this topic (Barendse et al. 2016)

Table 4 continued

Management actions	Connectivity features (proxy for)	Management outcomes (services, *disservices*)	Examples and notes
Remove or mitigate barriers; plan habitat corridors to reduce human-wildlife conflict (Haddad 1999)	Functional connectivity of actual and potential habitats across environmental gradients (H); habitat connectivity for species with important (socio–)ecological functions (H)	Wildlife viewing (C); functional ecosystems (R, S); reduced vehicle- wildlife collisions (C, S); biodiversity (S); *human-wildlife conflict from range expansion (P, R, C, S); ecological traps (S)*	Research from Banff National Park finds that wildlife use of road-crossing structures by large mammals varies depending on both structure design and landscape context (Clevenger and Waltho 2000, 2005), suggesting the need for a variety of approaches in a given setting
Remove or mitigate water control structures and vulnerable infrastructure in floodplain areas (Ward and Stanford 1995); use protective acquisition or development restriction of land parcels in floodplains (Johnson et al., 2020)	Habitat connectivity for species with important (socio–)ecological functions (H); functional floodplains (G); hydrologic connectivity (G)	Mitigation of flood hazards (R); increased water quantity and quality (P, R); habitat creation (S); *disease risk (R); human displacement (C); loss of developable land (P, C)*	Strategic land acquisition in 100-year floodplains in the US, particularly focused on large contiguous areas, is estimated to produce up to a 5:1 return on investment in avoided costs from flooding disasters, which are predicted to increase in coming decades (Johnson et al. 2020)
Restore suitable habitat in gaps between artificially isolated populations (Bennett 2003)	Habitat connectivity for species with important (socio–)ecological functions (H)	Increased population resilience of valuable species (S); *spread of undesirable species (S)*	Afforestation and reforestation in landscape gaps in the Eastern Usambara Mountains, Tanzania (Bennett 2003); habitat restoration in vacant lots along potential urban greenspace corridors (Newman et al. 2017)

Disservices are listed in italics

The category of each service/disservice associated with a management outcome is listed as follows: *P* provisioning, *R* regulating, *C* cultural, *S* supporting. The category of each related connectivity feature, referring to the corresponding table, is listed as follows: *H* habitat, *G* geophysical, *E* eco-social. Actions and outcomes are illustrated and elaborated upon with examples from literature

and minimizing the disservices that also arise from connectivity, requires a decision framework that can integrate and leverage them together. The basic elements are those proposed by Termorshuizen and Opdam (2009): features linked to functions linked to values. While this suggests a simple, linear chain, real examples exist in a web of interrelated features, multiple function-value combinations, and even feedbacks from supporting ES. Connectivity may function differently at different scales of space, time, or systems organization, as well. Effective frameworks incorporate these complexities; we will propose such an approach in a future paper.

Using this kind of assessment requires appropriate scope, effective goal-setting, accessible high-quality data (both baseline and monitoring), broad multi-sector collaboration both among and between decision-makers and community stakeholders, and the capacity to adapt to unexpected outcomes or changing circumstances (Rieb et al. 2017). Indeed, the complexity and situational uniqueness of socio–ecological landscapes demand an approach that is experimental, adaptive, scale-aware, and inclusive (Cumming et al. 2013). Naturally, it is generally simplest and least expensive to conserve existing connectivity first, and to take advantage of existing landscape elements to restore or enhance what has been diminished (Roni et al. 2002). The socio–ecological perspective is essential, as the conservation of ecological connectivity without regard to the social, economic, and political concerns of those living in its path can result in the displacement and fragmentation of human communities (Rantalla et al. 2013), in much the same way that the infrastructure of human connectivity can displace and fragment ecosystems.

Future directions

Several aspects of connectivity and ES are underresearched. The literature on habitat connectivity, for example, displays strong taxonomic biases towards charismatic organisms such as birds, pollinators, and megafauna (Mitchell et al. 2015). Though invasive species are frequently considered a risk in habitat connectivity, overall evidence for this risk is inconclusive, in many cases perhaps more related to edge vulnerability in narrow corridors (Haddad et al. 2014). Some invasive species, too, can have offsetting benefits such as food, timber, and erosion control (e.g., Dickie et al. 2014), and, in the absence of a specific invasion threat, the benefit of spreading desirable species generally appears to outweigh the risk of spreading undesirable species (Levey et al. 2005b). Geophysical connectivity of soils and the ecological features that regulate them seems to have been studied much less than other areas such as hydrology or biogeochemistry (Liu et al. 2020). Also, while there is much research on the air quality benefits of trees in a landscape context, these studies are often based on empirically limited modeling assumptions (Escobedo et al. 2011). Research on eco-social connectivity to date has been infrequent and, prior to Kondolf and Pinto (2017), we found no framework proposed to bring together ideas scattered across several disciplines; developing the concept of eco-social connectivity is a key motivation and contribution of our work.

We briefly review the translation of connectivity and ES into principles for environmental stewardship in Table 4. Nevertheless, there remains much work to be done in evaluating and improving modeling methodologies, planning strategies, design standards, and best management practices–i.e., bridging the gap between functional and landscape connectivity (Gippoliti and Battisti 2017). Progress here will require intentional collaboration at local to regional scales between researchers, practitioners, and community stakeholders in an iterative, adaptive-management approach, in which research, application, and equitable public inclusion each inform and support each other (Opdam et al. 2013).

Successful collaboration on connectivity and ES depends on having information which is plentiful, rigorous, diverse, and accessible. The long-term ecological research (LTER) framework (National Science Foundation 2018) provides a powerful, integrative approach to understanding landscapes across space and time, and has been applied to explicitly socio–ecological settings such as the Gwynns Falls Watershed in Baltimore, Maryland. Similarly, the "smart cities" movement, with its integrated networks of local and remote sensors collecting and sharing diverse types of data in built environments (Batty et al. 2012), has immense, if largely untapped, potential to support ecological research and natural resource valuation in inhabited landscapes (Gatrell and Jensen 2008; Colding and Barthel 2017). An equally necessary component is the cultural knowledge of communities, including traditional ecological knowledge (Berkes et al. 2000; Charnley et al. 2007), community science (Balazs and Morello-Frosch 2013), and public-participation mapping (Rall et al. 2019), which both challenges and complements quantitative scientific approaches. Local knowledge is crucial to bridging gaps between researchers, practitioners, and the public, and empowers responsive, equitable outcomes (Brondizio et al. 2009). The efficacy of these data, in turn, depends on having open access, open standards, and appropriate precautions or restrictions for sensitive information (Zuiderwijk and Janssen 2014). And, of course, landscape data can only attain their greatest value when effectively visualized and communicated, particularly to the public (Vervoort et al. 2012).

The final challenge is to develop innovative valuation and financing approaches to effectively prioritize and support connectivity conservation and to incorporate connectivity into conservation planning. We will discuss this in detail in a future paper.

Conclusions

Connectivity is the spatial glue that holds the elements of landscapes together, allowing them to interact, move, renew themselves, and adapt to changes over space and time. The ecosystem services concept provides a general framework for assigning values to the many benefits and costs of maintaining connectivity, including those of the greatest direct interest to the human communities within landscapes. These two concepts are typically viewed through separate lenses but are integrated, which presents a need to expand established definitions of ecological connectivity to include connectivity between people and their environment. Indeed, highlighting categories of connectivity, and the distinctions and relationships between them, can help broaden thinking about connectivity and remind ecologists and planners of the importance of including people as part of connectivity planning and research. Moreover, such approaches can help center equity and thus lead to more equitable outcomes. In identifying the four categories of connectivity we also aim to improve consistency of terminology for these different species-specific, process-specific, and pattern-specific concepts. Importantly, the many benefits of all categories of connectivity, highlighted by this discussion on ecosystem services, can be used to garner support for connectivity projects, identify synergies and tradeoffs among connectivity-related goals, and promote holistic thinking. With the shared language proposed in this paper, we aim to enable coordination and collaboration across goals, institutions, and communities. The ES framework creates an opportunity to incorporate connectivity of all kinds more effectively into planning, decision-making, and management of socio–ecological landscapes. Using ES to make connectivity-related decisions, however, requires effective, informed evaluation of landscape elements, connectivity goals, and their benefits and risks. A framework for such an evaluation process is the subject of a future paper.

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Declarations

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