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Landscape Connectivity Planning for Adaptation to Future Climate and Land-Use Change

Jennifer K. Costanza[1] · **Adam J. Terando**[2]

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Abstract

Purpose of Review We examined recent literature on promoting habitat connectivity in the context of climate change (CC) and land-use change (LUC). These two global change forcings have wide-reaching ecological effects that are projected to worsen in the future. Improving connectivity is a common adaptation strategy, but CC and LUC can also degrade planned connections, potentially reducing their effectiveness. We synthesize advances in connectivity design approaches, identify challenges confronted by researchers and practitioners, and offer suggestions for future research.

Recent Findings Recent studies incorporated future CC into connectivity design more often than LUC and rarely considered the two drivers jointly. When considering CC, most studies have focused on relatively broad spatial and temporal extents and have included either species-based targets or coarse-filter targets like geodiversity and climate gradients. High levels of uncertainty about future LUC and lack of consistent, readily available model simulations are likely hindering its inclusion in connectivity modeling. This high degree of uncertainty extends to efforts to jointly consider future CC and LUC.

Summary We argue that successful promotion of connectivity as a means to adapt to CC and LUC will depend on (1) the velocity of CC, (2) the velocity of LUC, and (3) the degree of existing landscape fragmentation. We present a new conceptual framework to assist in identifying connectivity networks given these three factors. Given the high uncertainty associated with future CC and LUC, incorporating insights from decision science into connectivity planning will facilitate the development of more robust adaptation strategies.

Keywords Adaptation · Climate change · Climate velocity · Climate-land-use interaction · Coarse filter · Connectivity · Fine filter · Land-use change · Land-use velocity · Landscape fragmentation · Multiple scales · Uncertainty

Introduction

Anthropogenic climate change (CC) and land-use change (LUC) are two major drivers of habitat loss worldwide and are expected to pose severe threats to the ecological integrity of many systems in the future [1, 2]. The effects of CC have already been wide-reaching, leading to substantial shifts in the ranges of some species [3, 4] and relatedly increases in extinction risk [5]. LUC is causing increased fragmentation, compromising the ability of populations and metapopulations to persist, and leading to concomitant effects on biodiversity [6]. While these drivers each act as threats, they also both interact to cause synergistic effects on species and their habitats [7, 8]. Landscape fragmentation compromises the ability of species to track climatic changes while also causing in situ populations to become less resilient to fluctuating climate and disturbance regimes [7, 9]. Thus, to help species persist into the future, maintaining and improving habitat connectivity is often viewed as an essential component of adaptation to CC and LUC [9, 10] and is the most frequently recommended strategy for reducing the negative effects of CC [11].

Maintaining and enhancing connectivity, most commonly through the identification and provision of habitat corridors, has long been a key concept in conservation biology and

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✉ Jennifer K. Costanza
jennifer_costanza@ncsu.edu

1 Department of Forestry and Environmental Resources, North Carolina State University, 3041 Cornwallis Rd., Research Triangle Park, NC 27709, USA

2 US Geological Survey, Southeast Climate Adaptation Science Center, Raleigh, NC, USA

landscape ecology [12–15]. These traditional efforts to increase connectivity are a response to past LUC brought about by human activities that increase habitat fragmentation and are best described as primarily a reaction to existing land-use conditions rather than acting in an adaptive way to future change [16].

In contrast to traditional connectivity science, recent studies have taken a forward looking and adaptive approach by, for example, identifying corridor networks that could maintain or facilitate movement under CC [17–20]. However, the approaches that have been developed thus far vary considerably, and little information exists on under what conditions and in which places a particular modeling or planning framework is the best approach to use. Furthermore, while improved connectivity is often cited as a strategy for CC adaptation, ways to incorporate the connectivity effects of potential LUC as well as simultaneous changes in climate and land use are just beginning to emerge [21, 22]. Because climate and land-use are changing simultaneously, and because successful conservation efforts under CC and LUC depend on a landscape with connected habitats, strategies that lead to enhanced connectivity for both of these global change forcings will be essential.

Here, we review recent advances in the literature on approaches for identifying (i.e., modeling) and promoting (i.e., maintaining and enhancing) connectivity under future CC or LUC and, as much as possible, those that integrate both. While a formal systematic review or meta-analysis of all published works based on structured bibliographic search terms was beyond the scope of this review, we synthesize knowledge gained from the most salient recent literature, focusing on papers published over the past 6 years (January 2012 through April 2018) to capture the most recent trends at the intersection of connectivity science and global change science. This included 80 published articles with examples relevant to the topic; together, we believe these articles reflect the state of the science. Our review focuses on terrestrial landscapes since most examples in the connectivity literature focus on the terrestrial domain but includes a few illustrative examples from aquatic or marine systems.

General ecological connectivity concepts have been defined and summarized elsewhere [23, 24]. We have not summarized those concepts in full here but have included relevant definitions for clarity (see Table 1). Similarly, the alternative approaches to modeling and mapping connectivity have been reviewed [28, 29]. Conceptual frameworks related to CC and connectivity have also been presented in other papers [10, 16], but a review of the current state of the science for enhancing connectivity under CC and LUC, particularly through corridor identification, has not to our knowledge been conducted.

We review the recent approaches for identifying and promoting connectivity for CC and the emerging studies that have considered LUC. We examine the challenges associated with incorporating future LUC into connectivity planning, review the efforts to jointly consider CC and LUC when modeling connectivity, and examine some strategies for minimizing the often high levels of uncertainty that can accompany a consideration of CC and LUC. Based on ideas in the existing literature, we present a new conceptual framework to assist in identifying connectivity networks that can respond to, and are resilient to, CC and LUC. Finally, we identify important avenues for future research.

Connectivity Networks Explicitly Designed to Address CC

Promoting connectivity as a means to accommodate the migration of populations, species' range shifts, or in situ adaptations means that the vector of salient climatic changes must be considered over both space and time. Given that this could require networks that not only address local connectivity but also span large areas such as regional extents or larger (see definition of "regional extent" in Table 1) [9, 10, 16, 30] while maintaining viability over long time periods, consideration of CC requires approaches that are fundamentally different from traditional insular connectivity studies that focus on a single landscape [16] (see definition of "landscape extent" in Table 1). In response, methods have emerged to identify connectivity networks that can serve as a strategic adaptation response to CC. In this section, we focus on four approaches that are commonly employed: (1) consideration of projected habitat change for species-specific targets (i.e., fine-filter approaches), (2) broadening the spatial extent of the considered network, (3) considering or even promoting temporal dynamism in the connectivity network, and (4) identifying "climate corridors" that connect areas that over time will share similar climatic characteristics.

Approaches based on fine-filter (species-based) targets can be used to incorporate CC information directly and thus model connectivity under CC. We describe these approaches below and summarize them in Table 2. Fine-filter approaches that focus on connectivity for individual species are often driven, either directly or indirectly, by legal mandates or concerns for the long-term viability of the species of interest. Legal mandates such as the Endangered Species Act and State Wildlife Action Plans in the USA can also be leveraged to consider conservation actions under CC [35, 36]. Targeting connectivity for individual species in this way may be particularly beneficial for habitat specialists [37] or when the goal is to draw attention toward conservation of one or more charismatic species [17].

Most studies that have incorporated CC information into connectivity planning for fine-filter targets have explicitly modeled future shifts in habitat via a projection approach. By linking climate model projections with habitat models for a given species or suite of species, a picture of how

Table 1 Definitions of key terms used in this review that are related to connectivity, CC, and LUC

Term	Definition
Climate velocity or CC velocity	The vector of movement as defined by the distance and direction a species would have to travel to keep up with a shifting climate [25]
Connectivity	The extent to which organisms can move among habitat patches
Corridor	A natural or human-designed linear feature that can facilitate connectivity among habitat patches (also called a connection or a linkage)
Functional connectivity	The degree to which individuals can move between habitat patches; depends on the structure of the landscape as well as attributes of the focal species such as dispersal ability
Landscape extent	An area with spatial heterogeneity in both habitat patches and patterns of LUC
LUC velocity	A measure of the amount and direction of change in land use through time across a spatial gradient (referred to as "LUC speed" when no directionality is implied) [26]
Model projection	A simulation of the response to a prescribed set of assumptions that make up a particular scenario of the future; contrasts with model predictions that attempt to forecast the actual future state of the system at some point in time [27]
Regional extent	An area that encompasses multiple landscapes and a gradient of climate conditions and CC
Structural connectivity	The degree to which habitat patches appear connected in the landscape via physical features such as vegetation cover or hydrology; depends only on the landscape itself, not on attributes of species

For additional background on the connectivity terms and concepts referred to here, see Rudnick et al. [23], Cushman et al. [24], and Cross et al. [16]

functional connectivity (see definition in Table 1) may respond to future CC emerges (e.g., [38]), and potential adaptation strategies like habitat corridors can be identified [39]. In areas that are expected to experience rapid CC (an example of high "CC velocity," see Table 1), or for species whose habitat requirements are closely tied to a particular set of climatic conditions, changes in connectivity that are driven directly by CC are important to consider. For instance, in the northern Rocky Mountains, even moderate warming scenarios had substantial effects on models of future available connections and population connectivity for the American marten, a species that is heavily dependent on winter snowpack [40]. Thus, in that case, although changes to the functional connectivity network under CC were considered rather than using connectivity itself as a CC adaptation strategy, including CC projections into models of future connectivity likely improved the realism and reliability of the results [40], and can be used as a first step in the development of adaptation strategies.

While traditional connectivity studies typically focus on smaller extents and assume species distributions are constant, perhaps the most popular way to incorporate CC into connectivity design is to focus on larger spatial extents as a means to facilitate species movements at a scale that matches the magnitude of expected CC [41]. Indeed, most published studies examining priorities for enhancing connectivity as a response to CC have done so at regional or national extents [42]. And, individual corridors that are designed to meet conservation objectives under CC often extend over long distances. For example, McGuire et al. [18], in identifying potential corridors for use under CC, allowed two natural areas to be considered connected if they were separated by up to 100 km. However, we note that because species vary in their dispersal abilities, a combination of longer and shorter corridors may be needed. In addition, shorter corridors or a series of shorter habitat connections acting as "stepping stones" can facilitate local adaptation to CC, including migration of populations within a landscape [43] (see the following section for discussion of cases when larger spatial extents may not be necessary).

In addition to larger spatial extents, promoting connectivity for CC requires consideration of long *temporal* extents to account for changing habitats. This could require consideration of relatively long temporal horizons of years, decades, or centuries, since as the climate changes, some core patches and their connections may become less suitable while others become more suitable. Thus, the design of connectivity networks must account for the temporal impacts of CC on the source and destination habitats *and* the patches or corridors that form the connections. One way to address this potential dynamism in habitat and connectivity networks is to identify connections that can also serve as climate refugia [44, 45]. These stepping stone connections, where suitability may remain high over time, are termed "temporal connections" by Makino et al. [46].

Targeted blocks of core habitat, habitat connections, or an entire connectivity network may also explicitly be designed to shift over time as habitat suitability shifts with CC [47, 48]. In the most extreme case, some locations may even be released from protection status so that others can be conserved when budgets are constrained and the matrix of sites that was

Table 2 A list of recent coarse- and fine-filter targets for maintaining and enhancing connectivity for CC and/or LUC, along with recommendations from the recent literature about when they are appropriate, and an example paper for each

Coarse or fine filter	Target	When or where to use	Example reference
Fine filter	Individual species	When habitat specialists, species with limited dispersal, or charismatic species are of concern; in places with high anticipated CC or LUC	Leonard et al. [31]
	Surrogate species, a species likely to have habitat requirements similar to other species	When information on habitat, movement, or dispersal requirements is lacking for some species	Breckheimer et al. [32]
Coarse filter	Climate corridors, the connectivity of climate conditions	Where habitat fragmentation is low and future land-use change is likely to be minimal	Nuñez et al. [19]
	Intact vegetation	When a group of species that are particularly sensitive to human disturbance is of concern; where climate velocity is low and existing land fragmentation is low	Belote et al. [33]
	Land facets or geodiversity, the diversity of abiotic settings	Where habitat generalists are of concern; where biotic interactions are not important; in places with low climate velocity; where geodiversity is high	Brost and Beier [17]
	Structural connections	When a group of species that are particularly sensitive to human disturbance is of concern; where climate velocity is low and existing land fragmentation is low	Jaeger et al. [34]

expected to maximize connectivity for a species is predicted to change over time [47, 48]. However, it should be noted that protected areas have been shown to be effective for conservation of a wide range of species under climate change, and thus, releasing areas from protection based on benefits to a specific target or targets may risk forgoing those conservation benefits for non-target species [49, 50]. Thus, considering multiple species and CC scenarios in this context would be particularly important in order to limit negative consequences for lower priority species. Although they did not explicitly account for changes in connectivity, Strange et al. [51] developed a conceptual model that accounts for temporal variability in habitat quality and immigration/emigration rates of species and allows conservation priorities to shift from currently protected lands to private lands. This concept could be adapted for use with other recent advances such as the Migratory Flow Network introduced by Taylor et al. [52] to examine shifts in connectivity, and thus conservation priorities, over time; in this case by simulating how bird species (and potentially other migratory taxa) adjust the timing of their migratory routes in response to changes in phenology under CC. Explicitly accounting for shifting habitats over time when planning connectivity networks is expected to lead to connectivity strategies that favor robustness to a wide variety of possible outcomes, rather than a single optimal choice [53].

Finally, the direction and pace of CC along the connections or corridors is itself an important consideration, especially for those strategies targeting slow-moving species. Of particular interest is the climate velocity [25] (see definition in Table 1) or the distance and direction required to travel over a specified time so that a species continues to occupy the historical climate space. For species that are sensitive to CC and where continued population viability may require migration, high climate velocities can make it difficult to track changing conditions for all but the most vagile species [41]. To address this, "climate corridors" have been proposed as a means to increase climate connectivity [18] across landscapes by minimizing the distance traversed across dissimilar climates over space and time. A number of criteria have been suggested for identifying corridors based on climate and CC. In one of the first climate corridor-based approaches, temperature gradients (based on recent historical conditions) were used to identify least-cost paths for dispersal and migration in the Pacific Northwest, USA [19]. Climate corridors can also take advantage of locations where the projected magnitude of CC is small relative to the surrounding region or where the site conditions should result in the persistence of relatively cool microclimates that can serve as long-term refugia or as stepping stones along a corridor route [23, 44, 45]. These approaches to identifying corridors based on climate conditions are likely to be most effective in areas that are not substantially impacted by habitat fragmentation or high rates of land-use change [18] (high "LUC velocity," see Table 1) and thus where regional climate connections are not severely disrupted by fragmentation [54].

Climate Change as One Consideration Among Many—Leveraging Coarse-Filter Approaches to Connectivity

While the development of approaches that integrate CC directly into connectivity studies could be of great utility to decision makers, there is some debate about whether those new approaches are necessary. Some have argued that framing connectivity for the purpose of responding to CC as fundamentally different from traditional connectivity problems could actually be harmful to conservation efforts. For example, conserving habitat corridors across long distances is likely to be difficult to accomplish [55]. Furthermore, these types of corridors would not help species that cannot disperse over long distances [42], and species with limited dispersal may be precisely the ones most challenged by CC [41]. A series of short corridors across a landscape can promote population connectivity and thus increase resilience to the negative impacts of CC. Therefore, maintaining and enhancing connectivity to facilitate range shifts may be a matter of designing corridors to promote a series of movements over short distances (e.g., [52]), which could be considered as being no different from designing corridors for fragmented landscapes without CC [55]. Approaching the problem in this way, where the design of connectivity networks gives consideration to but is not explicitly tied to a CC-determined objective (i.e., niche or climate tracking), suggests that other approaches could be leveraged and potentially adapted for use in a CC context.

Most prominent among the existing approaches that could be used as a means to adapt to CC is to identify coarse-filter (habitat or environmental facet-based, summarized in Table 2) connectivity targets that include a broad suite of landscape characteristics but need not explicitly consider network-specific climatic changes [23, 42, 55]. The one notable exception to this is the use of climate gradients in the identification of the previously mentioned "climate corridors," which could also be classified as a coarse-filter approach [56] (see Table 2). The methods to identify networks based on non-climate coarse-filter targets generally fall into one of two categories: (1) connectivity network designs that maximize variation in geophysical or abiotic settings and (2) connectivity networks based on structural connectivity, including minimizing human modification or maximizing naturalness.

Preserving geodiversity, or the diversity of abiotic landscape attributes such as elevation, landform, or lithology, is also known as "conserving nature's stage" [57, 58]. A geodiversity-based approach to connectivity planning relies on the assumption that landscapes with diverse abiotic conditions also support high levels of biodiversity and will continue to do so as the climate changes, even if the assemblage of species that is supported differs from historical conditions [55, 58]. The idea, based on earlier coarse-filter and geodiversity concepts [59–62], has become a popular strategy for prioritizing places to conserve for CC adaptation. Specifically, identifying corridors based on "land facets," which are unique combinations of elevation and soils that occur in a given landscape, has been the focus of several recent studies [17, 55, 63, 64]. Land facets in a landscape can be connected by linkages in which either the continuity or interspersion of unique conditions is maximized [65].

CC has also been a consideration in coarse-filter approaches that seek to identify networks that maximize the structural connectivity (as opposed to functional connectivity, see definition in Table 1) of landscape features, whether riparian corridors, relatively natural vegetation, or aquatic habitat [33, 66]. The idea behind such a focus is that by conserving relatively intact habitat features of interest, species that are sensitive to human disturbance will benefit [33, 67]. In some cases, projections of structural connectivity can provide useful information about functional connectivity (see definition in Table 1) for a large number of species. For example in the US Southwest, hydrologic connectivity is critical for a number of endemic fish species and thus simulations of future hydrology provided important information about the implications of habitat connectivity for those species [34]. However, in other cases, the link between structural connectivity and functional connectivity may be weak or unknown, particularly for data-poor species [68].

Coarse-filter approaches are attractive because they avoid the need for detailed habitat or life history data and may lead to more constrained solutions with less uncertainty compared to species-specific approaches. They are likely to be most effective for conserving habitat generalists or species that use relatively common habitats [17] or in regions where abiotic conditions are the most important determinants of species distributions [69]. To ensure conservation of rare species or habitat specialists, or where geophysical settings are not the only drivers of species distributions and diversity (for example, where biotic interactions are important), fine-filter species-based approaches may be more appropriate to address CC [17, 69].

Maximizing Connectivity under LUC—a Challenging Mix of Rapid Change and Deep Uncertainty

While studies aiming to identify corridors and connections to directly or indirectly mitigate the effects of climate change are rapidly emerging, efforts to explicitly consider future landscape change or interactions between LUC and CC are less common. Furthermore, omitting LUC can be a common methodological choice in studies that seek to identify climate-resilient corridors, under the assumption that any effects from changes in the landscape will be avoided through a rapid conservation of those corridors [19]. This (often implicit) assumption of partial controllability over the system through corridor creation is common in connectivity studies regardless of whether CC is explicitly considered (e.g., [70]). Aside from this, the omission of future LUC in connectivity studies is likely related to the overall paucity of LUC simulations, especially at relatively fine spatial resolutions (~ 500 m × 500 m or finer) and limited data-access infrastructure compared to the amount of publicly available climate model datasets and tools for use in connectivity analyses. This situation is improving however, especially as spatially explicit projections of human population and land use for national and global extents become more widely available [71–73]. Other potential reasons for the seemingly slower pace of inclusion of LUC into connectivity planning include the large uncertainties associated with projecting LUC [72, 74] or choosing to consider CC and LUC jointly rather than solely considering LUC [22].

Despite the challenges of incorporating future LUC, simply assuming a static landscape over time risks communicating to stakeholders a false level of precision and accuracy, and at worst, erroneous predictions of future habitat distributions [75]. In reality, conservation plans are carried out over many years or decades. During that time, substantial LUC can occur, resulting in degradation of habitat and connectivity that existed when the plan was made, thus rendering the plan less effective or obsolete even for CC adaptation. And, even if parcels within corridors are purchased quickly, changes in the surrounding land uses can lead to increased isolation of habitat within corridors, resulting in "spillover" effects on both the intended structure and functionality [76]. Consequently, omitting the potential effects of future LUC may result in a significant overestimate of the predicted utility of a proposed CC connectivity network.

Recent studies that have included future LUC scenarios illustrate the need to consider this global change forcing when identifying connectivity networks. From a methodological perspective, Bishop-Taylor et al. [77] used a long-term remotely sensed dataset to demonstrate that connectivity networks identified through static modeling approaches may substantially differ from those identified using dynamic modeling approach, particularly in regions with high land cover variability (such as seasonally dry wetlands). Two studies focusing on LUC in the southeastern USA modeled future urbanization, showing that the potential to degrade network connectivity was high for a range of species with varying habitat requirements [31, 78]. Piquer-Rodríguez et al. [79] examined the effect of policy choices on future LUC by modeling how changes to Argentina's Forest Law could impact landscape connectivity. This scenario approach revealed the importance of stepping stones to the robustness of the entire network, even under a maximum deforestation scenario.

CC-LUC Interactions and Joint Consideration of CC and LUC

Synergies or interacting effects between land-use change and climate change are important global drivers of shifting species distributions and future biodiversity levels [7, 30, 80]. In some cases, greater human modification of the landscape may prevent species from tracking changes in climate over time [81]. Highly vagile organisms have been shown to be particularly at risk because fragmentation and human land uses often cause high mortality during long dispersal events [82, 83]. Changing land use can also alter microclimates and thus may interact directly with CC to affect biologically important climate variables [84, 85]. Moreover, CC-LUC synergies can exacerbate the effects of extreme events like large disturbances and drought [54]. Antagonistic effects are possible between CC and LUC too. For example, Nogués and Cabarga-Varona [86] found that under certain conditions, adding forest plantations to the landscape increased overall network connectivity and robustness. A scenario could also develop in which CC renders environmental conditions less favorable for targeted species but allows for new land uses that can be leveraged within an adaptation strategy to promote a more resilient climate connectivity network.

Thus, explicitly considering both CC and LUC in connectivity studies in regions where (1) species or systems of interest are sensitive to both drivers, (2) both are likely to have high rates of change, or (3) the two may interact is a critical consideration in the design of robust connectivity networks. However, jointly considering both drivers is challenging, in part due to the limited availability of LUC models, the large projection uncertainty associated with LUC and CC, the different scales at which CC and LUC are expected to affect connectivity, and because robust estimates of the joint and marginal effects of these drivers on species and their habitats rarely exist.

Despite existing challenges, a small number of studies have integrated information on both drivers of environmental change into connectivity planning. In one recent study, habitat connectivity for the Mohave ground squirrel in the western USA was simulated under future CC and LUC, as well as scenarios that incorporated both of those drivers [21]. By using least-cost paths, graph theory, and circuit theory, movement routes within the landscape of currently occupied habitat as well as potential areas for range expansion were identified. Leonard et al. [87] combined models of future energy development, urbanization, and climate change to identify an optimized and connected network of conservation lands in the Appalachian Mountains region of the USA. Another study near Montreal, Canada combined graph-theoretic and circuit analyses to find a network of habitat patches for a suite of species that promoted both short- and long-range connectivity under multiple scenarios of CC and LUC [22], thus addressing the multiple scales at which CC and LUC affect connectivity. Multiscale approaches such as these are a promising way forward to incorporate the effects of both CC and LUC on connectivity.

Beyond the direct effects of CC and LUC, in some cases, human responses to CC will have effects on LUC that may be important to consider. For example, changes in land management and LUC resulting from human migrations and movements are likely to interact with climate change to affect natural habitats [88]. In addition, climate change can affect land values, which in turn can affect land use and the availability of lands for conservation [53]. Some of these indirect CC effects on LUC will be difficult to predict or model, such as the effect of greenhouse gas abatement policies that promote the use of biomass, which in turn could affect regional deforestation rates [89]. Future work examining these and other synergistic effects among land use and climate change on habitat and connectivity will be critical. Such advancements should make it more feasible to incorporate and model the effects of future land-use change and dynamics on habitat connectivity.

Alternative Approaches for Connectivity Planning: Taming the Uncertainty Beast

Model projection approaches [27] for CC or LUC allow consideration of many potential futures, leading to a high degree of dimensionality in terms of the future scenarios considered. Evaluating a range of potential futures is important, but it also widens the uncertainty bounds that decision makers must consider [90]. For example, integrating downscaled climate projections and habitat models under one or more future climate scenarios propagates the uncertainty inherent in climate projections through habitat and connectivity models, which can have their own uncertainty [91]. For kelp and sea urchins off the eastern coast of Australia, uncertainty about connectivity within a single climate scenario was greater than the variation among scenarios [92], illustrating the need for improved information regarding the temporal variability of connectivity. And yet, large amounts of uncertainty can be burdensome for land managers who must decide how to enhance connectivity under CC and LUC. Moreover, decisions regarding management and conservation made under models that depict deep uncertainty can be difficult to defend in the judicial system, at least by federal agencies in the USA, should a negative consequence occur [93].

One way to avoid some of the false precision associated with projecting future habitat networks and reduce the risk of overconfident decision-making is to use ensemble methods to integrate information from multiple climate models, emission scenarios, habitat, and/or connectivity models [94] (hereafter, "projection-ensemble approach"). A projection-ensemble approach can better represent the range of future uncertainty, as has been shown increasingly in species distribution modeling [95]. For example, Meller et al. [96] tested alternative ways in which an ensemble of predicted species distributions could be integrated in conservation prioritization modeling. Retaining all species distributions then averaging final prioritization model outputs, rather than averaging species distributions before prioritization modeling, resulted in a network of reserves that better represented the variability in habitat distributions across all species [96]. These results suggest that if a projection-ensemble approach is used for integrating future CC and LUC into connectivity studies, it may be best to model connectivity under a wide range of alternative futures before integrating those results into an ensemble plan for future connectivity.

An alternative way to manage some of the uncertainty associated with projections of future CC or LUC effects on habitat connectivity is via an assessment of future threats to existing connectivity. In an assessment approach, the aim is not necessarily to show precisely how connections will change but to point to places that are vulnerable to change (similar to a vulnerability analysis [97]). Often, the existing connectivity network is overlaid on layers that include information about future change, and core habitat and connections are scored based on their expected degree of change in connectivity [16]. For example, in the East Asian-Australasian Flyway, an assessment of potential sea-level rise effects on existing connectivity of migratory habitat for shorebird species revealed increased vulnerability of those species to CC and pointed to key places where changes in connectivity could be investigated further [98].

Irrespective of whether an assessment or projection-ensemble approach is used, any plan focused on species can be subject to additional uncertainty because information about habitat requirements for dispersal or actual movement data for many species is lacking [9, 16]. One way to address this challenge is to identify species for which data are available that can act as surrogates for species that use similar habitat. While no study to our knowledge has examined the efficacy of using surrogate species' connectivity networks for other species in an explicit CC or LUC context, some studies have examined the representativeness of surrogate species in traditional connectivity studies. In the Sandhills region of North Carolina, there were substantial overlaps in habitat that could maintain and restore connectivity for three at-risk species [32]. In a similar vein to the surrogate species idea, the generic focal species approach, wherein profiles of conceptual species are developed by experts to represent groups of species with similar habitat needs, has shown promise for modeling functional habitat networks in woodlands in the UK [99]. However, while surrogate species may obviate some uncertainty associated with explicitly modeling connectivity for species that lack habitat or movement data, the use of surrogates inherently introduces other sources of uncertainty associated with how well such species' requirements are correlated with those of other species. Thus, more work is needed to determine how connectivity networks based on a surrogate species may represent other species needs, especially in a CC and LUC context. Nonetheless, approaches based on surrogates are promising and may overcome some challenges and uncertainties associated with developing species-by-species connectivity plans.

Which Approach, Where?

The complexity and large uncertainty involved in modeling CC-LUC connectivity networks is daunting and leaves no obvious best methodological choice (for example, Table 2) for identifying corridors and connections that are adaptive to future change. Nevertheless, based on our synthesis of results from the growing body of research and applications in connectivity science, we present a conceptual framework for better understanding which methodological approach for a given set of CC and LUC conditions may be most appropriate for use by practitioners and researchers. Specifically, building from the velocity of CC concept [25], we suggest that three state variables can help determine which approach to take for identifying corridors that will maintain and enhance connectivity in a given landscape: (1) CC velocity, (2) the expected rate of human modification of the landscape, termed "LUC velocity" (or "LUC speed" when no directionality is implied) [26], and (3) the initial landscape state in terms of the degree of existing fragmentation or human modification [100] (see Fig. 1). The first two variables, CC velocity and LUC velocity, form two axes in Fig. 1 that translate to four qualitative landscape "states," i.e., (1) high CC and LUC velocities, (2) high CC velocity, low LUC velocity, (3) low CC velocity, high LUC velocity, and (4) low CC and LUC velocities. The third variable informs which connectivity approaches are still feasible given the likelihood that increased human modification of the landscape will constrain options, increase costs, or both.

While not specifically a climate connectivity concept, climate velocity (see definition in Table 1), can be thought of as a set of CC metrics that can inform conservation planning and priorities [56, 101, 102]. For example, where climate velocities are smallest, such as in mountainous areas, species that are sensitive to changes in the climate variables of interest can travel shorter distances to experience a similar climate, but as climate velocities increase, longer distances are required to keep pace with the changing climate, and thus long, corridors may be necessary. LUC velocity is analogous to CC velocity (see definition in Table 1) and can be used to determine the rate at which habitat loss, spatial isolation, and dispersal barriers may occur in a given landscape [26].

Notably, areas with low climate or land-use velocity do not necessarily have low absolute rates of change but may have a high degree of local spatial heterogeneity in climate or land use that buffers against the expected rate of change. Optimal adaptation strategies will also vary somewhat depending on the specific landscape characteristics and conservation targets (e.g., life history traits and species' responses to the landscape), along with data availability and governance structures in the landscape or region of interest. Nevertheless, knowledge of the projected CC and LUC velocities for a landscape can be a starting point for discerning where and when alternative connectivity approaches may be most suitable.

For places that are expected to experience relatively high velocities of both CC and LUC (Fig. 1, upper right corner), maintaining both landscape and regional connectivity will be important [23]. Regions with little topography but still

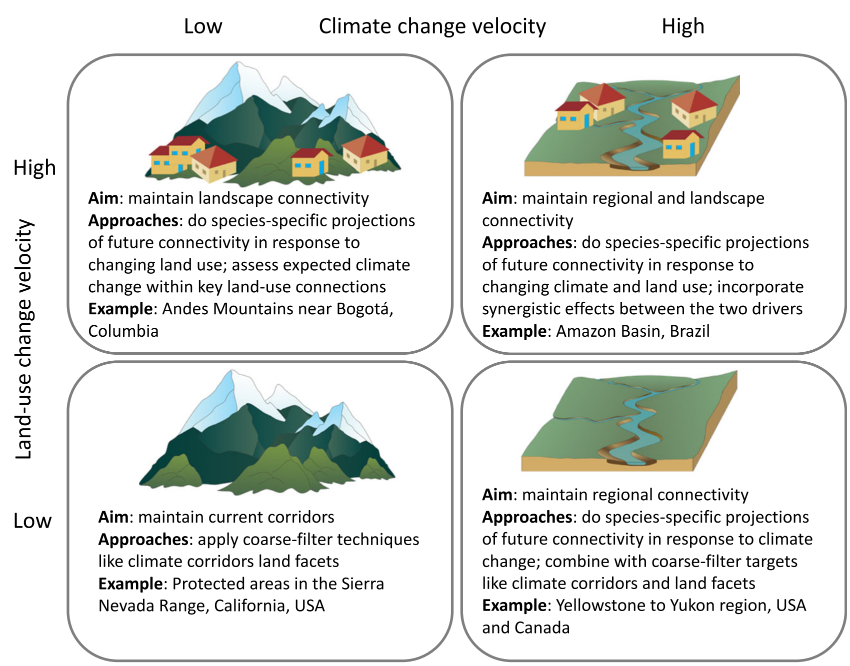

Fig. 1 Suggested approaches for identifying a corridor network that promotes connectivity for both CC and LUC adaptation, given the CC and LUC velocities in a location. See Table 2 for more information on the approaches listed. Images courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/)

relatively intact natural ecosystems, such as the Amazon River Basin, are examples of these types of places [6, 25, 56]. Here, species-specific targets for connectivity may be useful because coarse-filter approaches are not well-suited for places experiencing rapid changes (i.e., velocities) in climate and land use [55, 69]. Despite the increased uncertainty, species-specific models and projections of habitat and connectivity shifts that incorporate both CC and LUC, such as in [21], would be particularly appropriate to account for the impacts of both of those forcings. The potential for feedbacks, synergies, and complex interactions between LUC and CC effects on connectivity should be considered in these places too.

In places where the expected velocity of CC is high but the velocity of LUC is relatively low (Fig. 1, lower right corner), a focus on regional connections to allow species to track their climate niches over long distances is likely to be more important than investments in local connectivity. Specifically, because LUC velocity is expected to be low in these areas, promoting connectivity between currently suitable habitat and currently unsuitable locations that may become suitable in the future would be feasible in these landscapes. In addition, in these locations where abiotic settings are also important for structuring diversity, coarse-filter approaches such as those based on geodiversity may also be most effective for identifying climate refugia but should be coupled with species-specific projections of connectivity, especially where geodiversity is inherently low, species are restricted to rare habitats, or species are poor dispersers [69, 103]. Once key regional connections for adapting to potential CC have been identified, they can then be prioritized based on an assessment of their degree of expected LUC, if any.

In contrast, in places where the expected LUC velocity is high but CC velocity is low (Fig. 1, upper left corner), strategies that focus on establishing or maintaining local connections to ensure that species can track CC through fragmented and changing landscapes are likely to be more effective (see upper left corner of Fig. 1). Such a focus should include projections of habitat connectivity that explicitly incorporate LUC information coupled with an assessment of expected climatic change within connections that are important under LUC. An example of such a place might be the Andes Mountains near Bogotá, Colombia, where urban growth is moving up the mountainsides. The first step in connectivity planning there could involve identifying corridors that can enhance connectivity in the face of urbanization, followed by an assessment of the vulnerability of those corridors to CC. As stated above, we are not implying that mountainous regions such as this one have low absolute rates of CC but that the spatial heterogeneity in their abiotic conditions could provide some buffering against the expected velocity of change.

Finally, in places where the expected velocities of both CC and LUC are relatively low, coarse-filter approaches may be most appropriate (Fig. 1, lower left corner), [104]. Because the climatic gradients are strong in this case, climate corridors that identify linkages of similar climate, such as those modeled by Nuñez et al. [19], would be feasible. Prioritizing abiotic diversity and designing corridors based on land facets would also likely be an effective adaptation strategy in these places [69, 103]. One example of a place with low CC and LUC velocities is the Sierra Nevada mountain range, California. Maher et al. [104] found that such a coarse-filter approach was useful for identifying connected climate refugia (sites that were projected to experience minimal future CC) in meadow ecosystems in the Sierra Nevadas.

The above recommendations apply to locations that have relatively low or moderate levels of existing fragmentation and human modification; for places that already have high levels of human modification or are already highly fragmented, we propose that the same strategies would generally apply but with a few exceptions. First, coarse-filter approaches such as conserving the stage may not work in any landscape that already has a high degree of land conversion or land-use intensity since many of the important abiotic features may have already been lost [105]. In highly fragmented landscapes, successful adaptation strategies will not only need to conserve remaining habitat but will also likely need to prioritize actions that improve or restore habitat and remove existing barriers to dispersal [106, 107]. Implementation will be challenging, since it will take place across relatively large extents and in complex socio-ecological systems [108]. In addition, because establishing functional connections with suitable future habitat may not be possible in highly modified or fragmented landscapes, other strategies that are not specifically connectivity-related, such as assisted migration or translocation, may be appropriate for some species [109].

Promising New Approaches and Next Steps

Several exciting new frontiers of research promise to improve our ability to effectively integrate connectivity into conservation adaptation strategies in response to ever-increasing CC and LUC and to ensure that any resulting corridors can contribute to the persistence of species and their habitats. As reviewed above, considering complex, synergistic, or even antagonistic interactions between CC and LUC will be a critical step toward fully integrating those drivers into connectivity models. Cross-scale connectivity approaches that focus on both LUC at a local or landscape scale and CC at a regional extent may be particularly well-suited for integrating effects of both drivers [21, 22, 110].

Another research frontier is the development and use of more rigorous biological models when identifying connectivity networks. This could be accomplished with spatially explicit dynamic population or metapopulation models that consider how the interacting effects of CC and LUC affect ecosystem function, dispersal, and species emigration into or immigration out of particular landscapes. Population models are able to incorporate a variety of fine-scale dynamic processes over time, while connectivity models are simpler but more practical to implement, especially across regions [111]. A complimentary approach is to incorporate insights from landscape genetics [112] and population genetics models as a means to understand multi-generational adaptive capacity and niche preferences across taxa (see [29] for a review). Therefore, notwithstanding potential increases in uncertainty and low cross-region applicability (cf. [102]), these are promising avenues for investigating the effects of CC and LUC on connectivity at multiple scales [111].

Identifying optimal networks that satisfy multiple objectives will also be critical. Optimization frameworks that consider multiple connectivity objectives as well as constraints are a set of promising approaches that can facilitate implementation. While multi-objective optimization of conservation actions in general has been addressed, applying optimization methods within a connectivity framework is still in its infancy, primarily due to the significant computational challenges [113, 114]. In a novel approach to optimization for connectivity, Dilkina et al. [113] showed that jointly considering the connectivity needs of two species under a budget constraint could produce a single network that was nearly optimal for each species, at substantial cost savings over the optimal solutions for each species alone. This type of approach has the potential to lead to more efficient, effective, and feasible conservation actions and could be used in a framework that accounts for LUC and CC.

Finally, the large degree of uncertainty that often exists regarding the possible effects of future CC and LUC, and thus designing an optimal connectivity network that satisfies conservation objectives under those future conditions is perhaps the most daunting challenge. While we have already discussed ways to minimize uncertainty, finding ways to identify a connectivity network that will be useful even under a high amount of uncertainty is critical [53]. One promising response is to take advantage of recent developments in decision science in the field of decision-making under deep uncertainty (DMDU). Through associated methods such as robust decision-making (RDM), decisions that do "well enough" to manage risk under a range of scenarios are explored in a collaborative way with stakeholders [115]. This approach has been applied in other CC adaptation settings [116] and could potentially be applied to test the robustness of different connectivity networks. Kujala et al. [90] for example demonstrated the use of a conservation prioritization approach that identifies robust conservation decisions by more fully accounting for uncertainty about future CC and species habitat distributions. Similarly, when prioritizing land for conservation, Albert et al. [22] assigned higher priority to portions of habitat networks that remained suitable over time across a range of future climates; that is, where future suitability was more certain. A full examination of how DMDU approaches could be integrated into connectivity modeling and planning for CC and LUC is a critical path forward for addressing uncertainty.

Conclusions

CC and LUC are likely to affect habitat connectivity for many different types of species nearly everywhere in the world, jeopardizing society's ability to meet conservation objectives. Therefore, for effective adaptation, it is critical to continue building a body of knowledge of best practices for the incorporation of CC and LUC into connectivity planning. We have identified the key recent and novel approaches for identifying connectivity networks in the context of changing climate and land use. The joint effects of these two global change forcings on habitat and connectivity are likely to be complex and highly uncertain and require integration of information across spatial and temporal scales. We also presented a framework for choosing the most appropriate approach for modeling and prioritizing landscape connections given the CC and LUC change velocities, along with the existing degree of human modification. As a caveat, we note that in certain species-specific conservation contexts, choosing the best approach will first and foremost be contingent on the organism's biological response to CC and LUC, inasmuch as that response is known, and could be independent of CC and LUC velocity. The current framework lacks consideration of these additional factors and should be updated to do so in the future. Finally, new approaches and insights from other disciplines that better address the deep uncertainty faced by decision makers are emerging, and overcoming the scientific challenges posed by this complexity will be crucial for ensuring successful adaptation and resilience of species and ecosystems.

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Compliance with Ethical Standards

Conflict of Interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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