RESEARCH ARTICLE

Measuring ecological connectivity with ecological distance and dynamic resistant kernels

Katherine A. Zeller · Bradley W. Compton ·
Sean P. Finn · Eric C. Palm

Abstract

Context Species-agnostic connectivity models are often used to inform management over broad spatial scales. The four main approaches to species-agnostic models parameterize resistance to movement based on naturalness, structural features, climate, or geo-diversity variables. Though all four of these factors simultaneously affect species movement and flow of ecological processes, they are rarely combined.

Objectives We built upon an approach that uses all four of these factors to model current and future ecological connectivity for the Crown of the Continent Ecoregion, in Canada and the USA.

Methods We estimated resistance for each pixel on the landscape based on multivariate ecological distances to surrounding pixels. We then modeled connectivity with resistant kernels at different scales, and dynamically in response to future climates from 2020 to 2080.

Results Across the study area, we found median connectivity values decreased by 17–50% from 2020 to 2080 depending on the scale, with broader scales experiencing greater losses in connectivity. Though often considered natural conduits for movement, stream and valley bottoms generally lost connectivity through time. Wilderness areas had significantly higher connectivity values than unprotected lands for all time steps and scales, indicating their importance for maintaining future connectivity of ecological processes.

Conclusions We offer an updated approach for species-agnostic connectivity modeling that combines naturalness, structural features, and topo-climatic layers while considering multiple scales of ecological processes over a large spatial extent and dynamism through time. This approach can be applied to other landscapes to produce products for short- and long-term management of connectivity and ecological resilience.

K. A. Zeller (✉) · E. C. Palm
Aldo Leopold Wilderness Research Institute, USDA Forest Service, Rocky Mountain Research Station, 790 E. Beckwith Ave, Missoula, MT 59801, USA
e-mail: Katherine.zeller@usda.gov; kathyzeller@gmail.com

B. W. Compton
Department of Environmental Conservation, University of Massachusetts, 160 Holdsworth Way, Amherst, MA 01003, USA

S. P. Finn
U.S. Fish and Wildlife Service, Mountain Prairie Region, U.S. Department of the Interior, 230 N Collins Rd., Building 4, Boise, ID 83702, USA

E. C. Palm
Computational Ecology Lab, School of Public and Community Health Sciences, University of Montana, 32 Campus Drive, Skaggs Building, Room 177, Missoula, MT 59812, USA

Introduction

The largest threats to ecosystems and ecosystem functioning are habitat loss and fragmentation resulting from human development (Pereira et al. 2010; Haddad et al. 2015), and climate change (Bellard et al. 2012). An important conservation tool for addressing these threats is maintaining, enhancing, and integrating ecological connectivity (Heller and Zavaleta 2009; Krosby et al. 2010), especially in cooperation with local communities and partners (Bennett et al. 2017). Connecting intact protected areas and habitat patches may reduce inherent vulnerabilities of small, isolated populations such as susceptibility to inbreeding and stochastic events (Frankham 2005; Willi et al. 2006). Connectivity may also provide avenues of movement for species to track preferred climate conditions across the landscape as the climate changes (Heller and Zavaleta 2009). Because of its importance in conservation, connectivity is an increasingly critical component of land management plans. For example, in the U.S., the Forest Service is required to consider connectivity in its forest plans under the 2012 Planning Rule (U.S. Forest Service [USFS], 2012), and the Bureau of Land Management has new policy guidance that also requires the consideration of connectivity (U.S. Bureau of Land Management 2022). In Canada, Parks Canada recently initiated the National Program for Ecological Corridors, which aims to protect and restore ecological connectivity (https://parks.canada.ca/nature/science/conservation/corridors-ecologiques-ecological-corridors). As federal governments ramp up landscape conservation programs like the America the Beautiful Challenge (U.S.) and the Target One Challenge (Canada), empirically based spatial models that identify high value connectivity areas could help managers achieve local and continental conservation objectives.

Connectivity is a catch-all term that can refer to areas that allow for species-specific short-distance movements, long-range dispersal events, structural connectivity of vegetation types (e.g., forest cover), or wildlife crossing structures, among other things. All these interpretations and uses of this term make it difficult to determine the most effective approach for modeling connectivity (Hilty et al. 2020). Further, connectivity estimates are often desired across broad spatial extents. Estimating connectivity for a variety of species with different life history traits and dispersal capabilities across large areas is often prohibitively difficult. Therefore, species-agnostic approaches have been used to model generalized connectivity across large landscape extents (e.g. Belote et al. 2022). However, it is important to note that different species sometimes require very different connectivity strategies (Unnithan Kumar et al. 2022); generalized connectivity may therefore produce connectivity predictions which are suitable for many species, but not suitable for others.

Species-agnostic connectivity modeling approaches have typically used one of four general approaches. The first assumes that human development and associated land-use alterations have negative, yet variable effects on species movement across the landscape. Under this 'naturalness connectivity' approach, measures of human modification are used to parameterize 'costs' or 'resistances' to movement of species or ecological processes and develop a resistance surface (Zeller et al. 2012) where areas of high modification have high resistance and more natural areas have a low resistance. Typically, this approach is applied to natural versus developed areas and no other variables are used, though some estimates of human modification consider factors such as agricultural and forestry practices (Theobald et al. 2020). The second approach is based on the definition of 'structural connectivity' and uses the contiguity of specific landscape features to estimate resistance surfaces and model connectivity. For example, one approach might be to model connectivity of cover types, like forest, where low resistance would be assigned to any forested pixel and higher resistances would be applied to pixels dominated by other cover types (e.g., Williamson et al. 2020). A third approach is based on the concept of geodiversity (Gray 2004), which assumes areas with high geodiversity (diversity of landforms) will have high biodiversity (Lawler et al. 2015), and areas with similar geodiversity that are connected will facilitate persistence of biodiversity regardless of land cover or climate variables (Beier and Brost 2010). In this approach, topographic and edaphic variables are used

to identify spatially-explicit 'facets' of geodiversity and linkages among these facets are identified. Lastly, there is climate connectivity. This approach identifies current climates, projects where those climates might be located in the future, and models whether species might be able to move to track those climates (e.g., McGuire et al. 2016; Schloss et al. 2022; Parks et al. 2023).

Though some of the approaches above can be combined (e.g., climate connectivity and human modification, Parks et al. 2020, 2023), every component used to estimate connectivity in each of the four approaches can influence the way an individual animal responds to and moves through the landscape. As part of their estimation of ecological integrity for the northeastern U.S., McGarigal et al. (2018) used a measure of connectivity based on multivariate ecological distance that incorporates all four approaches described above into one measure of connectivity. Their connectivity measure calculated multivariate space at each pixel on the landscape based on ecological attributes such as human modification, land cover, topographic variables, soils, and climate. Multivariate Euclidean distance from each pixel to surrounding pixels within an ecological neighborhood was then calculated, resulting in a unique resistance surface for every pixel on the landscape. A resistant kernel (Compton et al. 2007) was then calculated across this surface for every pixel, representing the capacity for organisms to move from the focal pixel to surrounding pixels with similar ecological attributes. This resistant kernel was multiplied by the ecological distance to each neighboring cell, thus representing accessibility by ecological similarity. Resistant kernels were summed across cells to estimate the overall connectedness of the system. In this case, connectedness represented the capacity for ecological flow (henceforth 'ecological connectivity') to or from every pixel on the landscape.

This multivariate approach for estimating ecological connectivity has numerous advantages. First, it has the capacity to incorporate all four of the above approaches into a single method. Second, no source or destination points are needed since flows are modeled from each pixel in the landscape, producing a continuous connectivity map with values for every landscape pixel. Third, resistant kernels are used as the connectivity algorithm, an approach shown to have high predictive performance for animal movement, often outperforming other algorithms (Unnithan Kumar and Cushman 2022). Fourth, because ecological connectivity is estimated among a focal pixel and its neighboring pixels, it can simultaneously represent connectivity for less vagile species at finer spatial scales and highly mobile species across entire ecosystems. Lastly, this measure of ecological connectivity may be considered one measure of resilience—the ability to absorb stressors while retaining ecological functions (Gunderson 2000). Ecologically connected pixels are those that are connected to other, similar pixels, which should facilitate recovery following a disturbance (McGarigal et al. 2018) and provide resource managers with options as they prioritize and invest in recovery actions.

Here, we expand on the connectivity measure used in McGarigal et al. (2018) by incorporating dynamic resistant kernels to quantify changes in connectivity through space and time. We use the Crown of the Continent Ecoregion (CCE) as our focal landscape—a biologically rich area of the Northern Rocky Mountains spanning the U.S.-Canada border (Fig. 1). The CCE covers over 70,000 km^2 at the convergence of the Great Plains and the Rocky Mountains. The CCE includes a multitude of land management jurisdictions each with specific missions, mandates, and policies, and includes land administered by several Tribes and First Nations, two countries, two provinces and one state, and thousands of private landowners. We identified variables that represent human development, climate and energy, moisture and hydrologic, chemical substrate, and physical disturbance to develop ecological attributes, calculated ecological distances, and modeled ecological connectivity for the years 2020, 2050, and 2080 at three different spatial scales (a.k.a., ecological neighborhood sizes) to represent different ecological processes. We estimated connectivity dynamically through time by using the ecological attributes at a pixel for the current time step and estimating ecological distance to surrounding pixels at future time steps. We also evaluated the importance of protected areas in this system for maintaining ecological connectivity into the future.

Methods

Study area

The study was conducted in the CCE, a 72,843 km^2 area that covers parts of the provinces of British

Fig. 1 The crown of the continent ecoregion study area

Columbia and Alberta and the state of Montana. It is bounded approximately by Elk Lakes Provincial Park and Elbow-Sheep Wildland Provincial Park to the north, Interstate 90 to the south, the Rocky Mountain Trench to the west, and the prairie foothills to the east (Fig. 1). The region is topographically complex, and elevations range from 729 m near Dixon, Montana to 3351 m at Mt. Harrison, British Columbia. Habitats range from lowland floodplains and grasslands to glaciers and alpine meadows. To the west of the Continental Divide, climate is dominated by Pacific Northwest Maritime weather; to the east, climate is drier and dominated by continental weather patterns.

Biophysical variables

Through consultation with the Crown Manager's Partnership (https://www.crownmanagers.org/) Technical Team and following McGarigal et al. (2018), we identified six broad categories to represent the biophysical characteristics of the landscape and 15 geospatial layers, which included variables for naturalness connectivity, geodiversity, and

climate (Table 1). Each layer was selected for its unique effect on ecological systems (Table 1, ecological influence). Layers were resampled to a 30 m pixel size and then range rescaled from 0 to 1.

Calculating connectedness

Connectedness was measured through the following process, for which more detail is provided below.

1) Resistance weights were estimated for each biophysical variable in terms of its importance in influencing ecological flow. The range-rescaled variables described above were multiplied by these weights.
2) For each pixel, multivariate Euclidean distance was calculated to all surrounding pixels, based on the environmental variables and weights selected for those variables. This multivariate Euclidean distance served as a resistance surface for each location on the landscape.
3) A resistant kernel was then calculated from each pixel on the landscape across the unique resistance surface for that pixel. Three ecological neighborhoods were used as the bandwidths of the resistant kernels to capture variation in dispersal distances across species and scales of ecological flows (500, 2000, and 8,000 m; Bowman et al. 2002).
4) Ecological distance weights were selected for each variable. These weights indicated the importance of a variable for ecological similarity, and represented how closely related pixels are, with the assumption that areas that are more ecologically similar to a species' habitat are better able to meet its resource needs. See below for more details on ecological distance weights.
5) The resistant kernel was multiplied by the ecological distance weights for each pixel, yielding a kernel representing both accessibility and ecological similarity to the focal pixel.
6) The ecologically weighted kernels were summed across the landscape to create a raw connectedness surface.
7) The raw connectedness surface was quantile rescaled by cover type to rank the most important areas for connectivity within each cover type.

Because there is no approach for empirically quantifying the resistance and ecological distance weights of each variable, we used the weights from McGarigal et al. (2018) as a starting point (Table 1). McGarigal et al. (2018) reasoned that not all biophysical variables would contribute equally to resistance or ecological distance. For example, human development variables were weighted higher than other variables since moving across an impervious surface or a road with high traffic rate is expected to disrupt ecological flow to a greater degree than moving from one soil type to another. Therefore, resistance weights were applied that reflected the relative contribution of each variable in creating resistance to movement. The same approach was used for the ecological distance weights. Though hard development had a very high weight, that weight was only considered in areas where hard development was present since it is very different ecologically than any other changes in natural features. We adjusted the weights used in McGarigal et al. (2018) to account for the wider ranges in topography and climate in our study area.

Although conceptually a resistance surface and resistant kernel would be built for every pixel on the landscape, for computational reasons we built kernels for sampled pixels (every 5th pixel for the 500 m scale, every 10th pixel for the 2,000 m scale, and every 100th pixel for the 8,000 m scale). At these pixels, resistance was calculated as the weighted multivariate Euclidean distance to each neighboring cell. Then, we divided the distance surface by the maximum resistance weight. This resulted in a surface where two pixels with the same environmental attributes had a value of 0, and maximally dissimilar values had a value of 1. We then multiplied the Euclidean distance surface by 50 and added a 1 to ensure the minimum resistance value was not less than 1, as required by the resistant kernel algorithm. Fifty is the theoretical maximum resistance among pixels and was determined based on iterative testing. Please see McGarigal et al. (2018) for more information.

A Gaussian resistant kernel was applied to this resistance surface at each focal pixel. The resistant kernel accumulated cost and distance as it moved away from the focal pixel. These cost distances were transformed to probabilities weighted by the Gaussian distribution so that probabilities summed to one. The extent of the kernel was governed by the bandwidth (e.g., 500, 2000, or 8000 m). Resistant

Table 1 Six biophysical categories and associated geospatial variables used in the ecological connectivity analysis

Variable	Ecological influence	Resistance weight	Ecological distance weight	Spatial data source
Anthropogenic				
Hard development	Impervious surfaces interrupt ecological flows, comprised of a 'developed' land cover class, building footprints, and roads	10	1000	Crown Managers Partnership (2016); Microsoft (2019); Canada Centre for Remote Sensing (CCRS) et al. (2020)
Traffic rate	All roads act as at least partial barriers for many species; Higher traffic roads pose greater mortality risks for species movement	40	0	Crown Managers Partnership (2016)
Agriculture	Affects natural ecological processes	3	3	Canada Centre for Remote Sensing (CCRS) et al. (2020)
Moisture and hydrology				
Wetness	Amount of moisture at any location. Affects species habitat, soils, and nutrient cycling	1	4	Derived from NASA 30 m SRTM; Farr et al. (2007)
Flow accumulation (ln)	Amount of water in rivers, streams, and wetlands. Affects species habitat and sediment transport	4	4	Derived from NASA 30 m SRTM; Farr et al. (2007) and stream lines from Jones et al. (2017)
Flow gradient	Stream slope (percent). Affects sediment and nutrient transport and species habitat	1	2	Derived from NASA 30 m SRTM; Farr et al. (2007) and stream lines from Jones et al. (2017)
Winter precipitation	Affects annual water recharge and aquifer replenishment	2	3	Wang et al. (2016); ClimateNA; AdaptWest Project (2021)
Climatic moisture deficit	Measure of aridity. Affects moisture stress and water deficit for plants	2	3	Wang et al. (2016); ClimateNA; AdaptWest Project (2021)
Climate/Energy				
Mean temperature warmest month	May indicate southern range limits of species	2	3	Wang et al. (2016); ClimateNA; AdaptWest Project (2021)
Mean summer stream temperature	Several native fish species in this system can only survive in coldwater streams and may be limited by warmer temperatures	1	2	Jones et al. (2017)
Growing degree days	Integrates heat availability throughout the season. Degree days can estimate plant growth and may indicate northern range limits of species	2	3	Wang et al. (2016); ClimateNA; AdaptWest Project (2021)
Chemical substrate				
Soil pH	Affects nutrient uptake of plants	0.5	1	OpenLandMap; Hengl (2018a, b)
Percent Clay	Affects nutrient uptake of plants	0.5	1	OpenLandMap; Hengl (2018b)
Soil moisture	Affects water availability to plants and species habitat	0.5	1	OpenLandMap; Hengl and Gupta (2019)
Physical disturbance				
Percent Slope	Affects gravity-induced disturbance which can limit plant development	1	1	Derived from NASA 30 m SRTM; Farr et al. (2007)

kernels were equivalent to a standard Gaussian kernel when resistance was minimal (i.e., in a landscape where biophysical variables are identical across all pixels), but spread of the kernel was reduced in areas where biophysical variables differ from those of the focal pixel. The resistant kernel was then multiplied by the ecological distance weights (Table 1), thereby reducing the value at neighboring pixels that are dissimilar to the focal pixel. The result was a modified resistant kernel that measured both accessibility from and similarity to the focal pixel.

Overlapping weighted kernels were summed for each pixel, resulting in a raw connectedness value at each pixel. This resulted in one of two measures of connectivity that we considered, raw connectedness and scaled connectedness. Raw connectedness was used to quantify changes in absolute connectivity among the time steps. Scaled connectedness incorporated structural cover types and was used as our final mapped products. To obtain scaled connectedness, we quantile rescaled the raw connectedness values by cover type to obtain ecological connectedness values at each pixel. We performed this rescaling for two reasons. First, quantile rescaling ranked cells within a cover type against one another allowed us to identify pixels with the greatest connectivity within that particular cover type. Second, many cover types are inherently less connected ecologically with the surrounding landscape because they are very ecologically different. For example, wetlands would have large ecological distances with their surrounding environment and typically have consistently lower connectedness than forests. By quantile rescaling in this manner, the value of each pixel represented its connectivity relative to all other pixels in that cover type and incorporates structural connectivity into the final surfaces. We used the following cover type bins from the Commission for Environmental Cooperation North American Land Cover Product (Centre for Remote Sensing et al. 2020) to rescale the connectivity surface; coniferous forest, deciduous forest, mixed forest, shrub, grassland, wetland, open water, snow, and streams.

The process outlined above resulted in connectivity surfaces for three ecological neighborhoods, 500, 2000, 8000 m. To evaluate multi-scale connectivity and areas important at all scales, we then averaged the surfaces across the neighborhoods.

Future predictions

To evaluate potential climate influences on ecological connectivity, we modeled connectivity in a dynamic framework across time steps (Ash et al. 2020). We implemented this for the 2050 time step by using the 2020 climate layers (in addition to the other layers) at each source pixel in the landscape and calculating ecological distance to the surrounding pixels with the 2050 layers. For the 2080 time step, we considered the 2050 environment at the source pixels and calculated ecological distance to the surrounding pixels with the 2080 layers. These time steps were chosen to be consistent with the future stream temperature data source (more below; Jones et al. 2017).

We used climate and stream temperature projections in a dynamic connectivity framework to predict how the connectivity of ecological processes changes through time. For the climate data, we used Climatic Moisture Deficit (CMD), Growing Degree Days (GDD), Mean Temperature of the Warmest Month (MTWM), and Winter Precipitation (WTPP) from the ClimateNA database (AdaptWest Project 2021; Wang et al. 2016). We used data from the ensemble models which averaged the following eight Global Climate Models (GCMs), as recommended by Mahony et al., (2022); ACCESS-ESM1.5, CNRM-ESM2-1, EC-Earth3, GFDL-ESM4, GISS-E2-1-G, MIROC6, MPI-ESM1.2-HR, and MRI-ESM2.0. We used two projected future time periods, 2041–2070 (hereafter 2050), and 2071–2100 (hereafter 2080). For the stream temperature data, we used projected stream temperatures developed by Jones et al. (2017). Stream temperatures were predicted for 2035 and 2075 with RCP 4.5 and 8.5 emissions using the CAN ESM2 Global Climate Model. To match years with our other climate variables, we took the average stream temperature of the 2035 and 2075 projections to obtain a 2055 projection, and used the 2075 projection for the 2071–2100 time period. To determine how connectivity was changing through time, we also calculated the per-pixel differences in raw connectedness (unscaled by cover type) between the 2020 and 2080 time steps as percent difference. To help assess drivers of changes in connectivity through time we calculated the Pearson correlation coefficient between the 2020
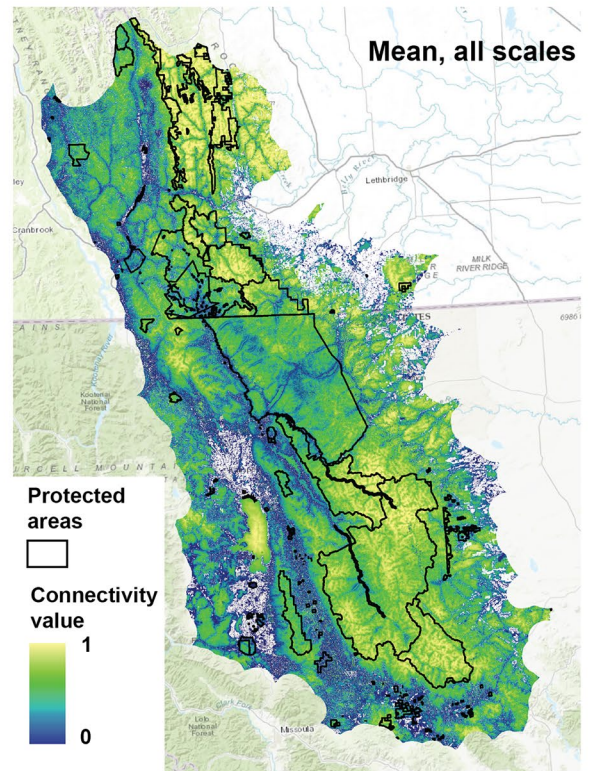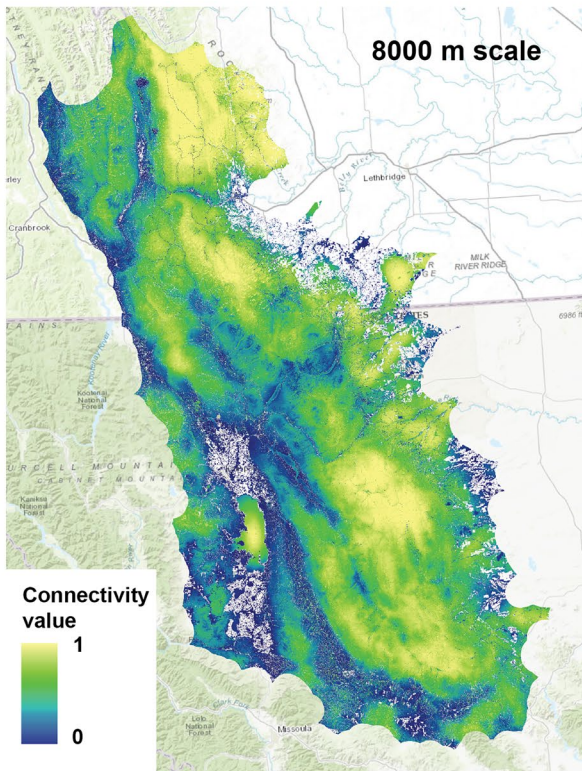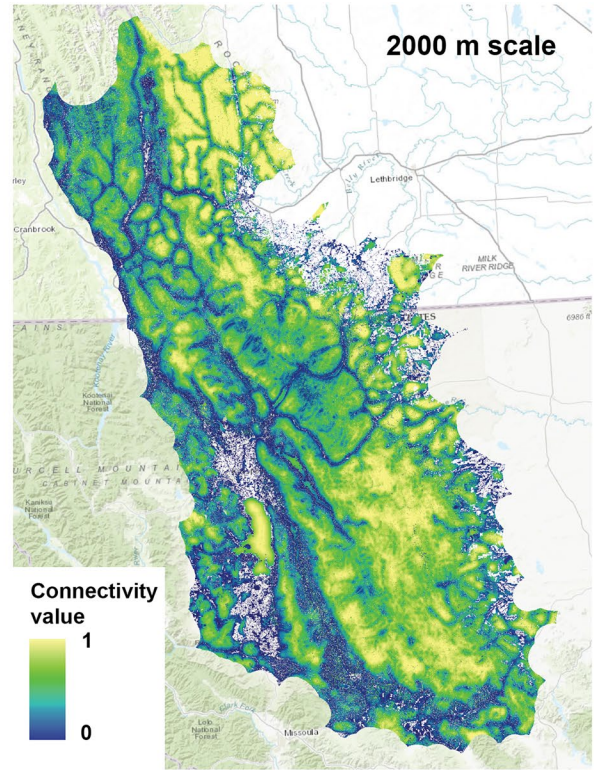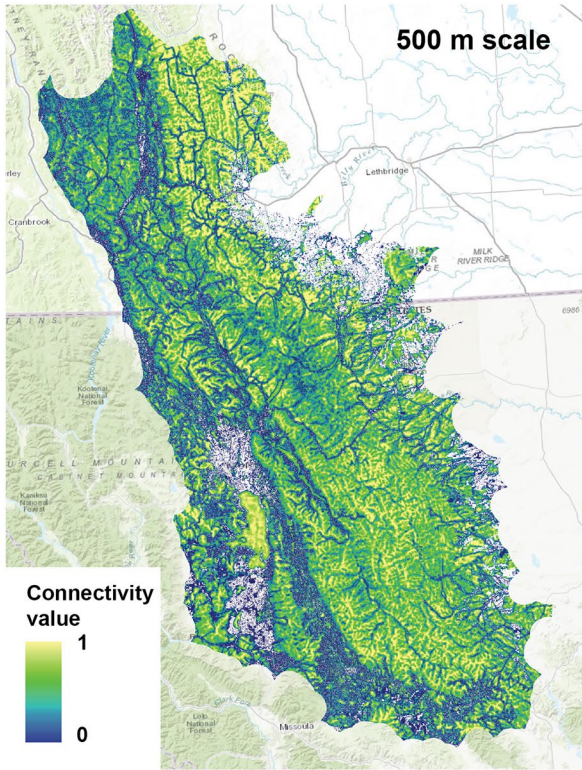
◄**Fig. 2** Connectivity surfaces from using the **a** 500 m, **b** 2,000 m, and **c** 8,000 m bandwidths for the year 2020. Mean connectivity surface across scales, **d** is shown with protected area boundaries. White areas within the study area boundary indicate developed pixels with no associated connectivity value

to 2080 difference in raw connectedness and the 2020 to 2080 difference for each of the climate variables.

Protected area effectiveness

To determine current protected area effectiveness at providing for ecological connectivity and resilience across the entire CCE landscape we obtained protected area information from PAD-US v 3.0 for the U.S (U.S.G.S. 2022) and CPCAD for Canada (CPCAD 2021) and grouped these protected areas by IUCN classifications into three categories, all IUCN I levels (e.g., preserves and wilderness areas), all IUCN II areas (e.g., National Parks), and all other IUCN categories (e.g., National Forests). We first converted the CCE connectivity rasters to points and identified the autocorrelation distance of the points for each spatial scale, indicated by the sill of a spatial variogram fit using the *gstat* package in R (Pebesma 2004; Graler et al. 2016). We then subsampled the points at these distances and extracted the following information at each point: connectivity value, elevation, and protection (i.e., protected or not, category of protection).

We modeled connectivity as a linear function of protected status while controlling for the effect of elevation for all models using the *lm* function in R. We first modeled connectivity as a function of elevation and protected area status (protected or unprotected). We then modeled connectivity as a function of elevation and protected area category.
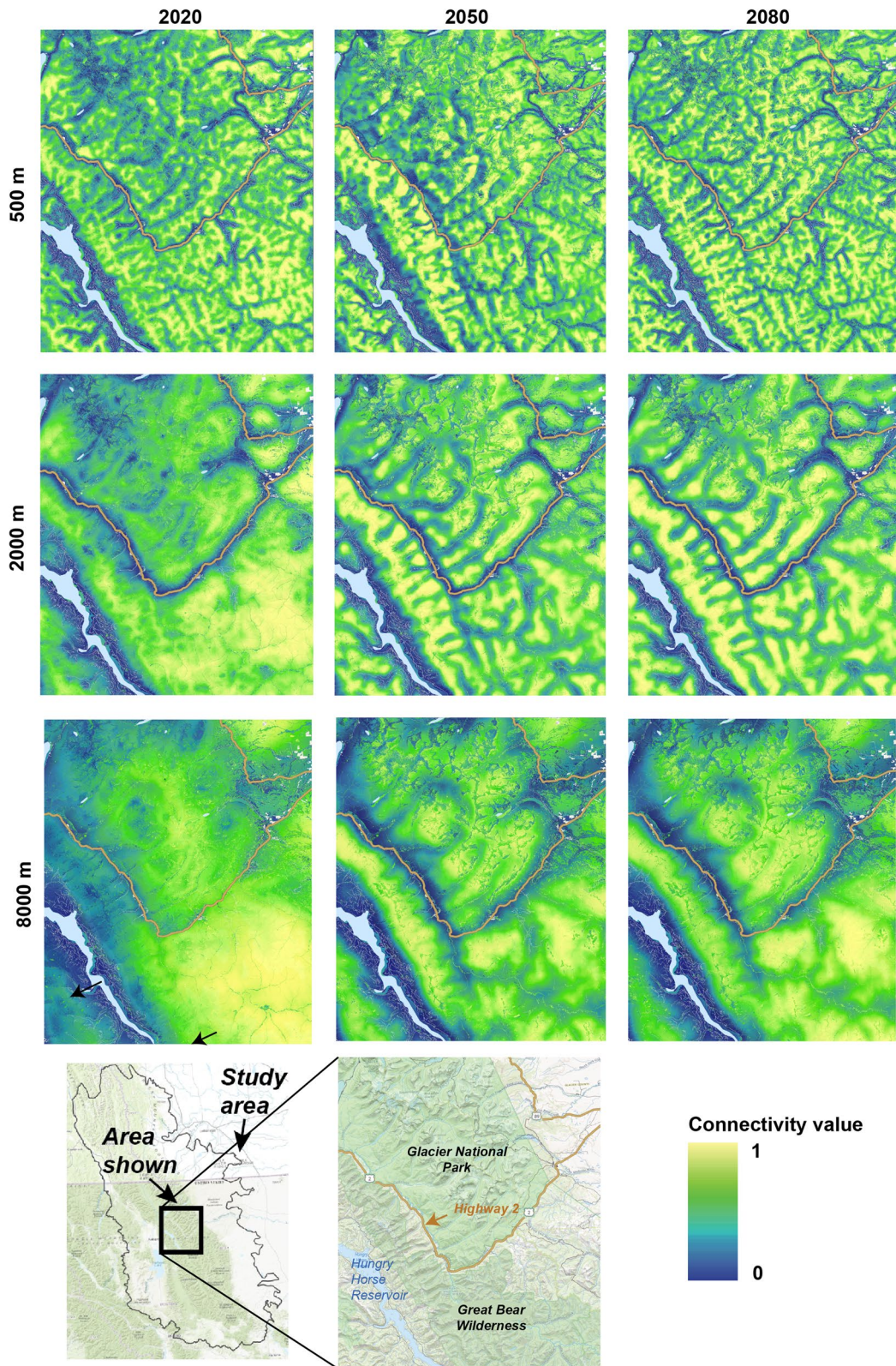
Results

For the 2020 time step, and regardless of spatial scale, ecological connectivity was higher in the northeastern corner of the study area, on both sides of Highway 22 in Alberta, between Route 3 to the south and Route 40 to the north. Higher connectedness was also present in and around Castle Provincial Park and in the foothill grasslands around the Ross Lake Natural Area in Alberta, and the Bob-Marshall Wilderness Complex in Montana (Fig. 2). As expected,

ecological connectivity values were more heterogeneous at the 500 m scale and more smoothed at the 8000 m scale. At this broadest scale, ecological connectivity was lower for areas like the Mission Mountains Wilderness and Mission Mountains Tribal Wilderness due to development in the valleys on either side of this mountain range.

Though future ecological connectivity values increased for some patches, areas around streams tended toward lower connectivity in future time steps, resulting in higher connectivity patches being surrounded by lower connectivity linear features (Fig. 3).

Because rescaling by cover type quantile rescales the connectivity values for each type, overall changes in connectivity among the time steps were assessed with the raw connectivity values. The raw median connectivity values of the 2020 surfaces were 0.82, 0.72, and 0.42 for the 500 m, 2,000 m, and 8,000 m scales respectively. For the 2080 surfaces, these values were 0.68, 0.58, and 0.21 respectively, indicating reduced connectivity in the future for all scales and a reduction in connectivity values from 17 to 50%. To better highlight differences in raw ecological connectivity among the time steps and scales, we estimated the percent difference in connectivity values between 2020 and 2080 (Fig. 4; Appendix B). Losses in connectivity increased with scale, with the 8000 m scale having the largest losses in future connectivity. These losses were especially evident on the eastern side of the Rocky Mountains in grassland areas.

For the 2020 time step and both emissions scenarios, protected areas had higher ecological connectivity than unprotected areas (Fig. 5; Appendix C). This was also true for the 2080 time step, but to a lesser degree than the current time step, indicating that protected areas overlapped with lower connectivity values in future time steps. For all scales and for the 2020 and 2080 time steps, IUCN category I protected areas had significantly higher ecological connectivity compared with unprotected areas. For only the 500 m scale, and for the 2020 and 2080 time steps and the RCP 8.5 emissions scenario, IUCN category II protected areas had significantly higher ecological connectivity compared with unprotected areas (Appendix C). For all other IUCN categories, only the 2000 m and 8000 m scales were significant for 2020 (Fig. 5; Appendix C). There was no significant difference from unprotected of the 'other' IUCN category for 2080 for any scale.

Discussion

We predicted ecological connectivity by accounting for the composition and configuration of anthropogenic development, moisture and hydrology, soil attributes, physical disturbance, and climate and energy under current conditions and under future scenarios. This approach incorporated multiple species-agnostic connectivity methods that are often applied separately (e.g., naturalness, topographic and soil variables, and climate) into a single framework. An additional strength of this approach is the ability to model connectivity for different scales of ecological processes. We extended the methods of McGarigal et al., (2018) to model dynamic ecological connectivity into the future with projected climate variables. Through this process, we were able to identify important differences among spatial scales, time steps, and the efficacy of the current protected area system for maintaining ecological connectivity in the CCE.

Ecological processes like dispersal, gene flow, and connectivity occur at multiple spatial scales and one of the challenges of ecology is to identify the appropriate scale for the process of interest (Levin 1992; Noss 1992). We examined three spatial scales to capture connectivity for species with different movement capabilities and observed different scaling patterns. Raw connectivity across the study area was higher at finer spatial scales than coarser ones, likely due to inherent spatial autocorrelation in natural landscapes and lower ecological dissimilarities at fine scales. Species that move shorter distances likely encounter similar environments over these distances and may not be as constrained by environmental dissimilarities than species that move longer distances. However, as distances increase and environments become more dissimilar, constraints in movement may be encountered—especially for specialist species with particular environmental niches. Across all scales, we found an overall decrease in raw connectivity values across the study area for future time steps, suggesting reduced ecological connectivity in this system's future. This change in connectivity was driven by changes in the values of the climate layers through time, especially

for growing degree days and climatic moisture deficit, and to a slightly lesser degree, winter precipitation (Appendix D). Our coarse-scale evaluations project larger losses of raw connectivity through time, which again is likely a result of lower spatial autocorrelation. Therefore, connectivity for ecological processes occurring at fine scales in our study area may be less sensitive to climatic changes in the near term, though more research is needed (Collins et al. 2012).

For raw connectivity and for ecological connectivity (quantile rescaled by cover type), we observed reduced connectivity along stream and valley bottoms compared with the rest of the landscape for the current time step, and further loss of connectivity in these areas in the future, especially at broad spatial scales. This change in connectivity was also driven by large changes in values of our climate layers particularly along valley bottoms, which aligns with other studies on climate projections in the CCE. For example, currently, much of the precipitation in the CCE falls as snow in the winter, which feeds streams and rivers throughout the summer months. However, that snowpack, which has already declined by 15–30% from historic levels (Mote et al. 2005), is projected to decline further. Winter precipitation in mid to low elevations is also projected to fall more as rain than snow, thereby increasing stream flows during winter, but reducing the overall snowpack and leading to lower summer stream flows, which are already being observed (Leppi et al. 2011). These changes can affect water temperatures, species occupancy and abundance in stream reaches, riparian species compositions, and connectivity to upland habitat. The decrease in connectivity we modeled along riparian areas is concerning since these areas are typically natural conduits for movement. For example, riparian networks not only allow for movement between high and low elevation areas (Beier 2012) and among protected areas (Fremier et al. 2015), but also allow for many species to move through otherwise inhospitable areas (Lees and Peres 2008).

We also found a decrease in predicted future connectivity in many of the eastern Rocky Mountain Front grasslands. This aligns with previous research showing that increasing temperatures and aridity will change grassland ecosystems in the CCE through species turnover, decreasing productivity, and increasing soil erosion (Clark et al. 2002). These changes also have the potential to increase invasion by noxious
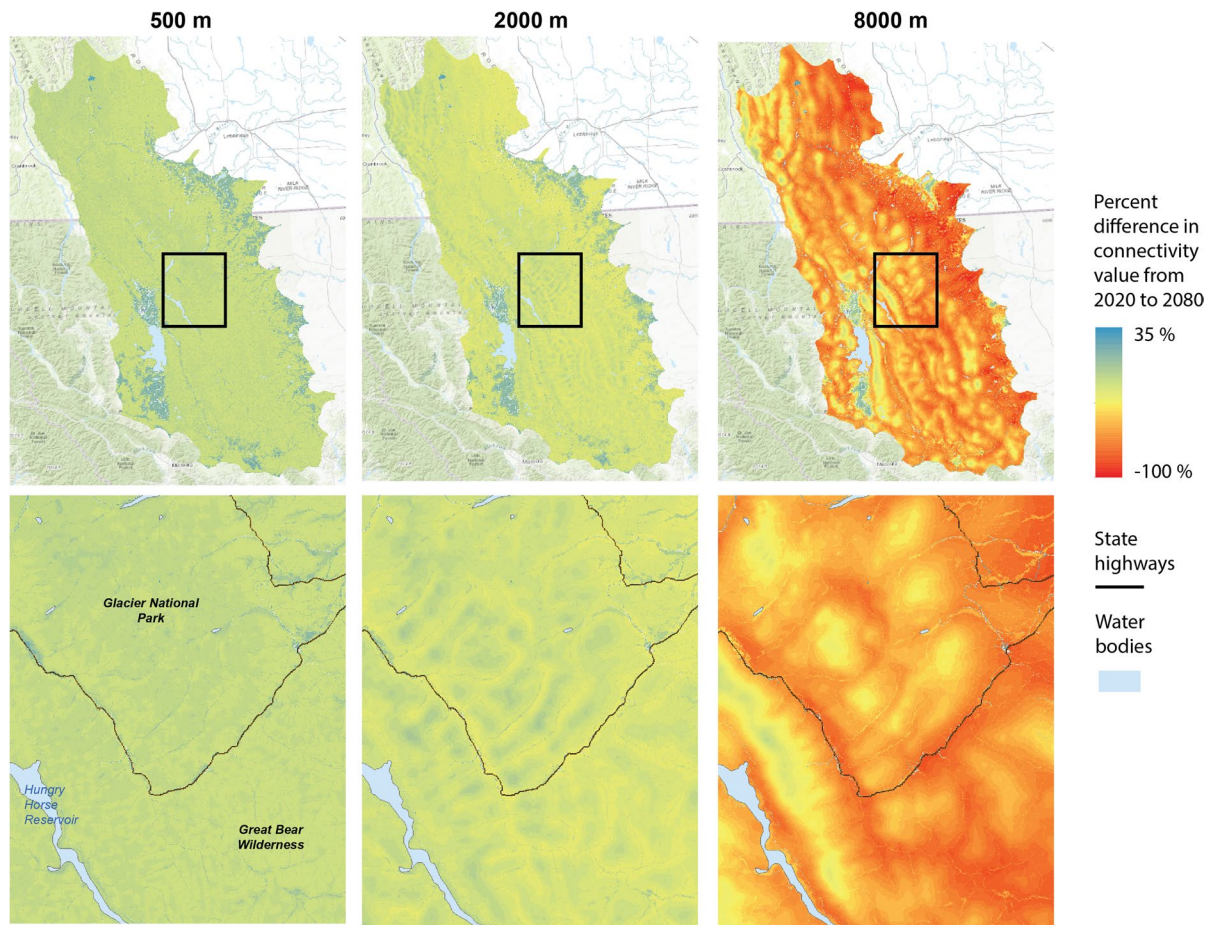
Fig. 4 Percent difference in connectivity values between the 2020 and 2080 time steps for the RCP 8.5 emissions scenario. Cooler colors indicate higher connectivity values in the future and warmer colors indicate lower connectivity values in the future. Results for the RCP 4.5 emissions scenario are provided in Appendix B

weeds and woody shrubs and increase disturbances in grassland areas by increasing the frequency and extent of wildfires (Bradley 2009). All these changes can contribute to ecological dissimilarity across the grassland system and cause an associated decrease in ecological connectivity.

As expected, for the current time step, protected areas had higher ecological connectivity values compared with unprotected areas. However, the strength of this relationship decreased in future time steps. These results may point towards protected areas being slightly less effective at protecting ecological connectivity in this landscape in the future. IUCN category I protected areas had significantly higher connectivity values compared to unprotected lands for all scales and for all time steps, indicating the importance of these areas for maintaining connectivity of future ecological processes. Future development may have large negative effects on ecological connectivity, which could further lower connectivity values in unprotected areas and raise the importance of protected areas. However, we were unable to project development into the future. Therefore, our results may be overestimating predicted future connectivity across the study area.

Conclusions

Our analysis provides multiple estimates of ecological connectivity for the CCE, which can also be interpreted as measures of resilience—the ability to
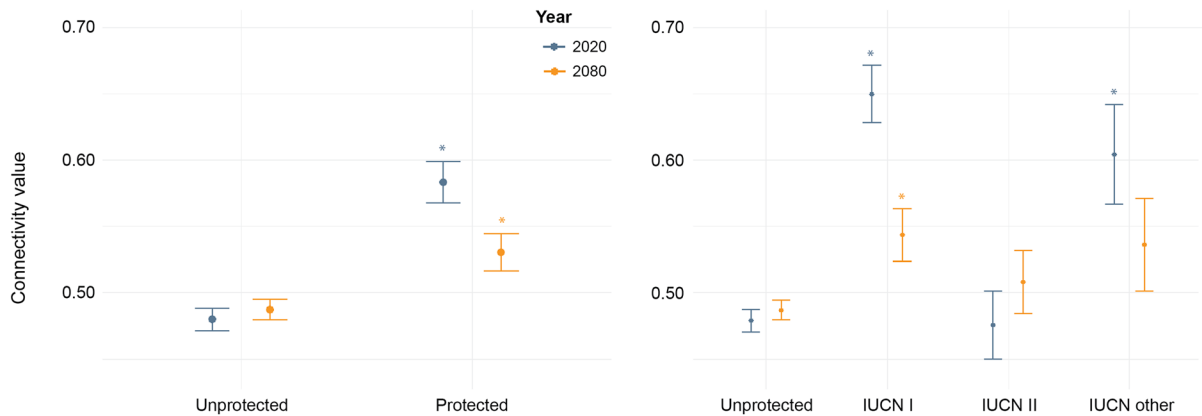
Fig. 5 Mean predicted connectivity values and standard error bars from the 2000 m scale connectivity surfaces in protected and unprotected lands from linear models. The left panel compares connectivity values among unprotected and protected areas for 2020 and 2080 with a RCP 8.5 emissions scenario. The right panel compares connectivity values among unprotected areas and each of 3 IUCN classes, IUCN I (Wilderness areas and Nature Reserves), II (National Parks), and all remaining classes, for 2020 and 2080 with a RCP 8.5 emissions scenario. Significant differences from unprotected areas are indicated with asterisks. Results from the 500 m and 8000 m scales and the RCP 4.5 emissions scenario are provided in Appendix C

absorb stressors while retaining ecological functions (McGarigal et al. 2018). This set of models can help inform management in this diverse ecosystem. For example, the Crown Manager Partnership, led by 16 resource management entities including three First Nations across our study area, identifies six conservation priorities in the most recent strategic plan: five-needle pines, wildfire management, fish and wildlife habitat integrity, ecological connectivity, watershed integrity and resilience and invasive species, insect and disease risk. Our analysis not only speaks to the ecological connectivity priority, but also relates to other priorities and can serve an important role in adaptive management cycles. For example, the Crown Manager's Partnership is partnering with the Confederated Salish and Kootenai Tribes and 20 other partners to implement restoration for the whitebark pine (*Pinus albicaulis*), recently listed as Threatened in the US. This species is adapted to high elevation subalpine zones throughout the CCE and dispersal among mountaintops is accomplished by its ecological companion, the Clark's nutcracker (*Nucifraga columbiana*). Although these species are ecologically co-dependent, changes in ecological connectivity may affect each independently and differently. Our array of models will serve to inform both silvicultural and wildlife managers across the multi-jurisdictional landscape. Since the pine and nutcracker are both most abundant in high-elevation protected areas, our models—which suggest that even our most protected areas may not be as effective at protecting connectivity in the future—can provide information to managers as they make decisions with future consequences.

By identifying areas of high ecological connectivity and resilience, both today and into the future, management can be targeted to maintain these areas, thus buoying the ecological integrity of the system. Furthermore, our observed loss of ecological connectivity in stream bottoms and eastern grasslands, along with a projected decrease in the efficacy of protected areas in conserving connectivity may require short-term interventions to stem long-term ecological losses. Our method takes advantage of many advances in modeling species-agnostic connectivity, adds dynamism through time, and can be applied to other systems and study areas.

Data availability No datasets were generated or analysed during the current study.

Declarations

Competing interest The authors declare no competing interests.

References

AdaptWest Project (2021) Gridded current and projected climate data for North America at 1 km resolution, generated using the ClimateNA v7.01 software

Ash E, Cushman SA, Macdonald DW, Redford T, Kaszta Ż (2020) How important are resistance, dispersal ability, population density and mortality in temporally dynamic simulations of population connectivity? A case study of tigers in Southeast Asia. Land 9:415

Beier P (2012) Conceptualizing and designing corridors for climate change. Ecol Rest 30:312–319

Beier P, Brost B (2010) Use of land facets to plan for climate change: conserving the arenas, not the actors. Conserv Biol 24:701–710

Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F (2012) Impacts of climate change on the future of biodiversity. Ecol Lett 15:365–377

Belote RT, Barnett K, Zeller K, Brennan A, Gage J (2022) Examining local and regional ecological connectivity throughout North America. Landsc Ecol 37:2977–2990

Bennett NJ, Roth R, Klain SC, Chan K, Christie P, Clark DA, Cullman G, Curran D, Durbin TJ, Epstein G, Greenberg A, Nelson MP, Sandlos J, Stedman R, Teel TL, Thomas R, Veríssimo D, Wyborn C (2017) Conservation social science: understanding and integrating human dimensions to improve conservation. Biol Cons 205:93–108

Bowman J, Jaeger JAG, Fahrig L (2002) Dispersal distance of mammals is proportional to home range size. Ecology 83:2049–2055

Bradley BA (2009) Regional analysis of the impacts of climate change on cheatgrass invasion shows potential risk and opportunity. Glob Change Biol 15:196–208

Canada Centre for Remote Sensing (CCRS), Canada Center for Mapping and Earth Observation (CCMEO), Natural Resources Canada (NRCan), Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO), Comisión Nacional Forestal (CONAFOR), Instituto Nacional de Estadística y Geografía (INEGI), U.S. Geological Survey (USGS), 2020. 2015 Land Cover of North America at 30 meters, 2nd edition

Clark JS, Grimm EC, Donovan JJ, Fritz SC, Engstrom DR, Almendinger JE (2002) Drought cycles and landscape responses to past aridity on prairies of the Northern Great Plains, USA. Ecology 83:595–601

Collins M, Chandler RE, Cox PM, Huthnance JM, Rougier J, Stephenson DB (2012) Quantifying future climate change. Nat Clim Chang 2:403–409

Compton BW, McGARIGAL K, Cushman SA, Gamble LR (2007) A Resistant-kernel model of connectivity for amphibians that breed in vernal pools. Conserv Biol 21:788–799

CPCAD (2021) Canadian Protected and Conserved Areas Database (CPCAD)

Crown Managers Partnership (2016) Roads c2011 in the crown of the continent ecosystem

Farr TG, Rosen PA, Caro E, Crippen R, Duren R, Hensley S, Kobrick M, Paller M, Rodriguez E, Roth L, Seal D, Shaffer S, Shimada J, Umland J, Werner M, Oskin M, Burbank D, Alsdorf D (2007) The shuttle radar topography mission. Rev Geophys. https://doi.org/10.1029/2005RG000183

Frankham R (2005) Genetics and extinction. Biol Cons 126:131–140

Fremier AK, Kiparsky M, Gmur S, Aycrigg J, Craig RK, Svancara LK, Goble DD, Cosens B, Davis FW, Scott JM (2015) A riparian conservation network for ecological resilience. Biol Cons 191:29–37

Graler B, Pebesma EJ, Heuvelink G (2016) Spatio-temporal interpolation using gstat. R J 8:204–218

Gray M (2004) Geodiversity: valuing and conserving abiotic nature. Wiley, Hoboken

Gunderson LH (2000) Ecological resilience–in theory and application. Annu Rev Ecol Syst 31:425–439

Haddad NM, Brudvig LA, Clobert J, Davies KF, Gonzalez A, Holt RD, Lovejoy TE, Sexton JO, Austin MP, Collins CD, Cook WM, Damschen EI, Ewers RM, Foster BL, Jenkins CN, King AJ, Laurance WF, Levey DJ, Margules CR, Melbourne BA, Nicholls AO, Orrock JL, Song D-X, Townshend JR (2015) Habitat fragmentation and its lasting impact on earth's ecosystems. Sci Adv 1:e1500052

Heller NE, Zavaleta ES (2009) Biodiversity management in the face of climate change: a review of 22 years of recommendations. Biol Cons 142:14–32

Hengl T (2018a) Soil pH in H2O at 6 standard depths (0, 10, 30, 60, 100 and 200 cm) at 250 m resolution

Hengl T (2018b) Clay content in % (kg / kg) at 6 standard depths (0, 10, 30, 60, 100 and 200 cm) at 250 m resolution

Hengl T, Gupta S (2019) Soil water content (volumetric %) for 33kPa and 1500kPa suctions predicted at 6 standard depths (0, 10, 30, 60, 100 and 200 cm) at 250 m resolution

Hilty J, Worboys GL, Keeley A, Woodley S, Lausche BJ, Locke H, Carr M, Pulsford I, Pittock J, White JW, Theobald DM, Levine J, Reuling M, Watson JEM, Ament R, Tabor GM (2020) Guidelines for conserving connectivity through ecological networks and corridors. Int Union Conserv Nat. https://doi.org/10.2305/IUCN.CH.2020.PAG.30.en

Jones LA, Muhlfeld CC, Marshall LA (2017) Projected warming portends seasonal shifts of stream temperatures in the crown of the continent ecosystem, USA and Canada. Clim Change 144:641–655

Krosby M, Tewksbury J, Haddad NM, Hoekstra J (2010) Ecological connectivity for a changing climate. Conserv Biol 24:1686–1689

Lawler JJ, Ackerly DD, Albano CM, Anderson MG, Dobrowski SZ, Gill JL, Heller NE, Pressey RL, Sanderson EW, Weiss SB (2015) The theory behind, and the challenges of, conserving nature's stage in a time of rapid change. Conserv Biol 29:618–629

Lees AC, Peres CA (2008) Conservation value of remnant riparian forest corridors of varying quality for Amazonian birds and mammals. Conserv Biol 22:439–449

Leppi JC, Deluca TH, Harrar SW, Running SW (2011) Impacts of climate change on August stream discharge in the Central-Rocky Mountains. Clim Change 112:997–1014

Levin SA (1992) The Problem of pattern and scale in ecology: The Robert H. MacArthur Award lecture. Ecology 73:1943–1967

Mahony CR, Wang T, Hamann A, Cannon AJ (2022) A global climate model ensemble for downscaled monthly climate normals over North America. Int J Climatol 42:5871–5891

McGarigal K, Compton BW, Plunkett EB, DeLuca WV, Grand J, Ene E, Jackson SD (2018) A landscape index of ecological integrity to inform landscape conservation. Landsc Ecol 33:1029–1048

McGuire JL, Lawler JJ, McRae BH, Nuñez TA, Theobald DM (2016) Achieving climate connectivity in a fragmented landscape. PNAS 113:7195–7200

Microsoft (2019) Microsoft building footprints

Mote PW, Hamlet AF, Clark MP, Lettenmaier DP (2005) Declining mountain snowpack in Western North America*. Bull Am Meteor Soc 86:39–50

Noss RF (1992) Issues of scale in conservation biology. In: Fiedler PL, Jain SK (eds) Conservation biology: the theory and practice of nature conservation preservation and management. Springer, Boston, pp 239–250

Parks SA, Carroll C, Dobrowski SZ, Allred BW (2020) Human land uses reduce climate connectivity across North America. Glob Change Biol. https://doi.org/10.1111/gcb.15009

Parks SA, Holsinger LM, Abatzoglou JT, Littlefield CE, Zeller KA (2023) Protected areas not likely to serve as stepping-stones for species undergoing climate-induced range shifts. Glob Change Biol 29:2681–2696

Pebesma EJ (2004) Multivariable geostatistics in S: the gstat package. Comput Geosci 30:683–691

Pereira HM, Leadley PW, Proença V, Alkemade R, Scharlemann JPW, Fernandez-Manjarrés JF, Araújo MB, Balvanera P, Biggs R, Cheung WWL, Chini L, Cooper HD, Gilman EL, Guénette S, Hurtt GC, Huntington HP, Mace GM, Oberdorff T, Revenga C, Rodrigues P, Scholes RJ, Sumaila UR, Walpole M (2010) Scenarios for global biodiversity in the 21st century. Science 330:1496–1501

Schloss CA, Cameron DR, McRae BH, Theobald DM, Jones A (2022) "No-regrets" pathways for navigating climate change: planning for connectivity with land use, topography, and climate. Ecol Appl 32:e02468

Theobald DM, Kennedy C, Chen B, Oakleaf J, Baruch-Mordo S, Kiesecker J (2020) Earth transformed: detailed mapping of global human modification from 1990 to 2017. Earth Syst Sci Data 12:1953–1972

U.S. Bureau of Land Management (2022) Habitat Connectivity on Public Lands

U.S. Forest Service [USFS] (2012) Final programmatic environmental impact statement: national forest system land management planning. USFS, Washington, DC, USA

U.S. Geological Survey (USGS) Gap Analysis Project (GAP) (2022) Protected areas database of the United States (PAD-US) 3.0

Unnithan Kumar S, Cushman SA (2022) Connectivity modelling in conservation science: a comparative evaluation. Sci Rep 12:16680

Unnithan Kumar S, Turnbull J, Davies OH, Hodgetts T, Cushman SA (2022) Moving beyond landscape resistance: considerations for the future of connectivity modelling and conservation science. Landsc Ecol 37:2465–2480

Wang T, Hamann A, Spittlehouse D, Carroll C (2016) Locally downscaled and spatially customizable climate data for historical and future periods for North America. PLoS ONE 11:e0156720

Willi Y, van Buskirk J, Hoffmann AA (2006) Limits to the adaptive potential of small populations. Annu Rev Ecol Evol Syst 37:433–458

Williamson MA, Creech TG, Carnwath G, Dixon B, Kelly V (2020) Incorporating wildlife connectivity into forest plan revision under the United States Forest Service's 2012 planning rule. Conserv Sci Pract 2:e155

Zeller KA, McGarigal K, Whiteley AR (2012) Estimating landscape resistance to movement: a review. Landsc Ecol 27:777–797