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RESEARCH ARTICLE

A comparison of approaches for including connectivity in systematic conservation planning

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Abstract

1. Plans for expanding protected area systems (prioritizations) often aim to facilitate connectivity. To achieve this, many approaches—based on different assumptions and datasets—have been developed. However, little is known about how such approaches influence prioritizations.
2. We examine eight approaches that aim to promote connectivity in prioritizations. Using Washington State (USA) and its avifauna as a case study, we generated prioritizations that aimed to meet species' representation targets and promote connectivity by (a) maximizing total area; (b) further maximizing species representation; (c) minimizing boundary length; and connecting areas based on (d) minimizing human pressure, (e) minimizing naturalness-based landscape resistance, (f) minimizing focal species landscape resistance, (g) minimizing habitat heterogeneity and (h) maximizing environmental similarity. We controlled for total expenditure, species' representation, and existing land use policies to enable comparisons among prioritizations. We then used a hierarchical cluster analysis to compare prioritizations, based on which areas they selected. We also evaluated how well each approach facilitated connectivity as measured by the other approaches.
3. We found that different approaches for promoting connectivity can lead to very different or very similar prioritizations, depending on their underlying assumptions. In particular, the boundary length approach—which is widely used in systematic conservation planning—resulted in a prioritization that was highly dissimilar to all other prioritizations. Surprisingly, approaches based on very different underlying assumptions produced similar prioritizations, such as maximizing total area and minimizing focal species landscape resistance approaches. Moreover, when comparing the prioritizations based on the level of connectivity they could facilitate, we found that none of the prioritizations facilitated a high level of connectivity for all eight approaches.

4. *Synthesis and applications*. We recommend carefully considering the assumptions and limitations that underpin approaches for promoting connectivity. Our findings demonstrate that different connectivity approaches can produce marked differences in priorities and, in turn, produce trade-offs between different approaches. Indeed, despite the ubiquity of the boundary length approach, practitioners might find that other approaches can better achieve conservation objectives. Practitioners can use our methodology for comparing different connectivity approaches to help to navigate trade-offs among them.

KEYWORDS
conductivity, connectivity, human footprint index, integer programming, landscape resistance, reserve selection, spatial prioritization, systematic conservation planning

1 | INTRODUCTION

Protected areas play an integral role in conserving biodiversity (Brooks et al., 2004). Because funding is limited, plans for expanding protected area systems (hereafter, prioritizations) should maximize conservation objectives for minimum expenditure (Rodewald et al., 2019). In addition to providing adequate habitat to support populations, protected area systems should ideally facilitate the movement of individuals and genes between different populations (hereafter, connectivity; Olds et al., 2012). Indeed, connectivity can help prevent inbreeding, enhance adaptive capacity and increase population sizes (Daigle et al., 2020; Olds et al., 2012). This realization has sparked innovation in the development of methodologies to account for connectivity in prioritizations (Beger et al., 2010; Dwyer et al., 2019; Leonard et al., 2017).

Many approaches have been developed to promote connectivity in prioritizations (reviewed in Kool et al., 2013). These approaches often involve using particular assumptions (e.g. assumed effects of land use or distance on connectivity), because the genetic and movement data needed to quantify connectivity are rarely available at the scales needed to guide prioritizations (for exceptions, see Dwyer et al., 2019; Hanson et al., 2019). For this reason, these approaches often involve using expert opinion or particular assumptions. For instance, some approaches use continuous scores (e.g. derived from land use data; Leonard et al., 2017) to describe the strength of connectivity between different places across a landscape (see Beger et al., 2010). Other approaches are based on spatial configuration, such as the widely used approach of minimizing the total boundary (perimeter) length of protected areas within a prioritization (Choe et al., 2018; Harris et al., 2014; Stralberg et al., 2011). Approaches have also aimed to maximize connectivity based on metapopulation dynamics (Lehtomäki et al., 2009). Although different approaches rely on different assumptions, little is known about how they alter prioritizations.

Here we examine different approaches for promoting connectivity in prioritizations. Using Washington State (USA) and its avifauna as a case study, we generated eight prioritizations for expanding the protected area system based on different approaches for connectivity. Specifically, they were based on the following approaches (see below for details on each): (a) total area, (b) species representation, (c) boundary length, (d) human pressure, (e) naturalness-based landscape resistance, (f) focal species landscape resistance, (g) habitat heterogeneity and (h) environmental similarity. We controlled for total expenditure, species' representation and existing land use policies when generating these prioritizations to facilitate comparisons among them. After generating the prioritizations, we compared them based on which areas they selected and how well each approach facilitated connectivity as measured by the other approaches.

2 | MATERIALS AND METHODS

2.1 | Study system

Our study area was Washington State (USA). Within this region, bird species are facing mounting pressure from climate change and habitat destruction (Northrup et al., 2019). To guide our prioritizations, we obtained data for 261 native bird species (Table S1) from the eBird Status and Trends dataset (using the `ebirdst` `R` package; Auer et al., 2020; Fink, Auer, Johnston, Strimas-Mackey, et al., 2020). These species—spanning 17 taxonomic orders—encompass a diverse range of avian evolutionary history. Furthermore, five of them are globally threatened with extinction (IUCN, 2020). We recognize that additional taxa would be needed to identify priorities for conserving overall biodiversity in this region. Our primary aim here is to examine different approaches for promoting connectivity using birds as an example.

We used 4 km × 4 km grid cells as land parcels for prioritization (*N* = 10,757; Figure 1). These land parcels (hereafter, planning units; sensu Rodewald et al., 2019) correspond to discrete spatial areas that can potentially be selected for protected area establishment. Analyses described hereafter were completed using the `R` statistical computing environment (version 4.0.3) and the `tidyverse` `R` packages (R Core Team, 2019; Wickham et al., 2019). Spatial processing was completed using the sf and `raster` `R` packages

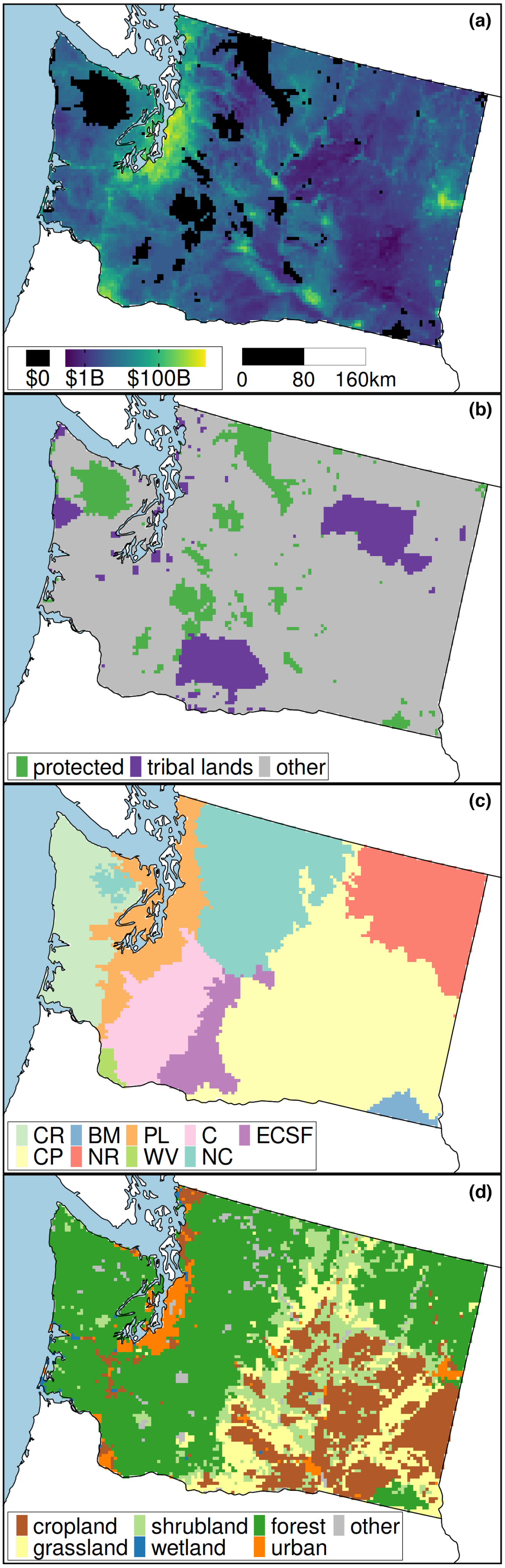

FIGURE 1 Planning units for generating prioritizations. Maps show (a) protected area establishment costs (USD; depicted on the log10 scale), (b) existing land management, (c) ecoregions and (d) dominant land cover. Ecoregions are the Coast Range (CR), Columbia Plateau (CP), Blue Mountains (BM), Northern Rockies (NR), Puget Lowland (PL), Willamette Valley (WV), Cascades (C), North cascades (NC) and Eastern Cascades Slopes and Foothills (ECSF)

(Hijmans, 2020; Pebesma, 2018). Our study did not require ethical approval.

2.2 | Biodiversity, economic and land use data

We developed 822 spatial distribution maps for the 261 study species (e.g. Figure S1). These were derived from the eBird Status and Trends dataset, which contains high resolution maps of the relative abundance modelled for each species during each week of 2018 (Fink, Auer, Johnston, Ruiz-Gutierrez, et al., 2020). It also contains estimates of the beginning and end dates of seasonal stages for many species (i.e. breeding, non-breeding, pre-breeding migration and post-breeding migration stages). For the 214 species with seasonal information, we computed an average relative abundance map for each seasonal stage for each species—based on the beginning and end dates for each stage—to account for seasonal habitat requirements during prioritization. For the 47 species lacking seasonal information, we computed average relative abundance maps based on data for all weeks. All of these maps were then resampled (bilinearly) to match the planning units, and linearly rescaled such that the values for each map summed to a value of 100. They were subsequently used to generate prioritizations.

We estimated protected area establishment costs for the planning units (Figure 1a) using land valuation data based on modelled full market value (Nolte, 2020a, 2020b). The valuation data were aggregated and resampled (bilinearly) to match the planning units. To account for existing protected areas, we obtained protected area boundaries from the World Database on Protected Areas (IUCN & UNEP-WCMC, 2021) and cleaned them following standard practices (via the `wdpar` `R` package; Hanson, 2020). We treated planning units that had at least half their area covered by protected areas as fully protected, and set their costs to $0 USD (Figure 1b).

To describe existing management for the planning units, we obtained and reclassified land cover data (30 m resolution; Commission for Environmental Cooperation, 2020) to seven classes (cropland, forest, grassland, shrubland, urban, wetland and other; Table S2), and then resampled (nearest neighbour) and aggregated these data to match the planning units. Next, we obtained boundaries of ecoregions (US Environmental Protection Agency, 2012) within the study area. After compiling these datasets, we overlaid them with the planning units and associated each planning unit with the dominant ecoregion and the dominant land cover class inside it (Figure 1c,d).

We also obtained boundaries of tribal reservations and trust lands (Washington State Department of Transportation, 2017), and treated planning units that had at least 1% of their area overlapping with these boundaries as fully covered (Figure 1b). This strict threshold was chosen to ensure that prioritizations would not select such lands, because they are governed by Indigenous communities (although the authors recognize tribal boundaries do not capture the full extent of Indigenous land rights).

2.3 | Connectivity approaches

We examined eight approaches for parameterizing connectivity. Each approach aims to promote connectivity based on different assumptions and data (Figures S2 and S3). By encoding these assumptions and data into mathematical optimization problems (Appendices S1–S6), we generated prioritizations that—in addition to other considerations (e.g. species' representation, existing protected areas; see below for details)—were based on connectivity approaches. The first two approaches are based on assumptions about population size and dispersal success, and the latter six approaches involve selecting planning units that are adjacent (neighbouring) each other, mainly using scores to parameterize the level of connectivity between adjacent planning units. These scores were produced by (a) obtaining data (e.g. human pressure data), (b) transforming them (e.g. calculating inverse values) to generate maps describing the relative degree that landscape attributes facilitate movement (termed conductance maps; Figures S4 and S5) and (c) using these maps to compute connectivity scores for optimization (see Appendix S1; Beger et al., 2010). Because these latter six approaches only parameterize connectivity between adjacent planning units—neglecting landscape properties and potential movements between distant planning units—they aimed to enhance connectivity within potential protected areas (Spanowicz & Jaeger, 2019).

2.3.1 | Total area

This approach aims to promote connectivity by increasing the amount of land inside protected areas. It is based on the following assumptions: (a) all natural area outside of protected areas is vulnerable to habitat destruction (per the scorched Earth assumption; Edwards et al., 2010); (b) on average, habitat isolation—mean distances between habitat areas—declines with increasing total habitat, which increases connectivity (per percolation thresholds; With & King, 1999); (c) the total abundance of each species depends on the extent of natural areas; and (d) the number of potential dispersing individuals for a given species increases with its total abundance. Given these assumptions, it follows that establishing protected areas to prevent habitat destruction increases connectivity by reducing habitat isolation and limiting declines in the total abundance of each species which, in turn, limits declines in dispersing individuals. Thus, establishing more protected areas will promote connectivity (Synes et al., 2020). Note that focusing only on the total amount of natural area protected does not fully account for the environmental conditions inside protected areas which, in turn, could potentially affect the total abundance of particular species. This can be somewhat alleviated by the species' representation targets. Although this approach does not explicitly account for environmental conditions outside natural areas that could influence species' movements, many species can easily disperse through areas containing marginal or unsuitable environmental conditions (Fahrig et al., 2021).

2.3.2 | Species representation

This approach aims to promote connectivity by maximizing the amount of habitat for each species in protected areas. It is based on a similar set of assumptions to the total area approach. However, while the total area approach does not incorporate species information, the species representation approach explicitly accounts for species-specific habitat requirements using species' spatial distribution maps. Greater representation of a species' distribution by a prioritization is assumed to result in less habitat destruction and, in turn, limit increases in habitat isolation and declines in total abundance and number of dispersing individuals for that species. Although all prioritizations were generated to improve species' representation by protected areas using target thresholds (see below), this approach is distinct because it aims to promote connectivity by further maximizing species' representation as much as possible—above the targets—instead of considering other criteria.

2.3.3 | Boundary length

This widely used approach aims to promote connectivity by creating prioritizations that contain large, compact protected areas (Choe et al., 2018; Harris et al., 2014; Stralberg et al., 2011). It involves minimizing the total boundary (perimeter) length of reserves (i.e. spatially contiguous sets of selected planning units within a prioritization). This approach assumes that places outside of protected areas impede species' movements (Edwards et al., 2010), and so aims to promote connectivity by creating protected areas that encompass the movements of dispersing individuals.

2.3.4 | Human pressure

This approach aims to promote connectivity by prioritizing adjacent planning units with low human pressure. It is based on the assumption that areas under greater human pressure present a greater impediment to species' movements (Tucker et al., 2018). To parameterize this approach, we used the human footprint index dataset for 2013 (1 km resolution; Williams et al., 2020) to compute connectivity scores (see Appendix S1). Briefly, the dataset was developed using human population density, land use, infrastructure and accessibility data, all assigned weights based on expert opinion (Williams et al., 2020).

2.3.5 | Naturalness-based landscape resistance

This approach aims to promote connectivity by prioritizing adjacent planning units with natural conditions. To parameterize this approach, we used a landscape resistance map produced by The Nature Conservancy (180 m resolution; McRae et al., 2016) to compute connectivity scores (see Appendix S1). The map was assembled to quantify the relative amount that anthropogenic activities impede movements of terrestrial species that rely on natural landscapes to persist. It was produced by combining land cover, roads, railroads, energy infrastructure and housing density datasets through expert weights. Although both this approach and the human pressure approach are based on land use data, the spatial datasets that underpin these two approaches were produced using different weights that, in turn, led to differences in where they predict high levels of connectivity (Figure S4).

2.3.6 | Focal species landscape resistance

This approach aims to promote connectivity by prioritizing adjacent planning units that can strongly facilitate movements of a single focal species. It assumes that the movement capabilities of a particular species encompass the connectivity requirements of all species of interest. Because estimating the movement capabilities of multiple species requires additional funding, the use of a landscape resistance map for a single (focal) species as a representative for multiple species has been suggested as a cost-effective strategy (Breckheimer et al., 2014). To parameterize this approach, we used a resistance map developed for one of the study species to compute connectivity scores (see Appendix S1). We selected the greater sage-grouse (*Centrocercus urophasianus*; Figure S6) because it (a) is recognized as globally imperilled and under Washington State legislation, (b) is considered an umbrella species and (c) requires management to enhance connectivity (IUCN, 2020; Washington Department of Fish and Wildlife, 2020; Wisdom et al., 2005). Also, its spatial distribution overlaps with grassland areas that contain a relatively high number of rare study species (Figure S7). Briefly, the resistance data were produced using land cover, forest structure, roads, housing density, elevation and slope data and weights—per expert judgement and literature review—to estimate how much different places impede movements of this species (Washington Wildlife Habitat Connectivity Working Group, 2010).

2.3.7 | Habitat heterogeneity

This approach aims to promote connectivity by prioritizing adjacent planning units with low habitat heterogeneity. It assumes that places with greater habitat heterogeneity have reduced species' movements (Tucker et al., 2019). To parameterize this approach, we used a spatial dissimilarity dataset (1 km resolution) produced by Tuanmu and Jetz (2015) to compute connectivity scores (see Appendix S1). The dataset was produced using remotely sensed vegetation data, and assigns higher dissimilarity values to places that break up contiguous areas containing similar vegetation characteristics (e.g., rivers, forest boundaries).

2.3.8 | Environmental similarity

This approach aims to promote connectivity by prioritizing adjacent planning units with similar environmental conditions (based on Alagador et al., 2012). It assumes that steep environmental gradients impede species' movements. To parameterize this approach, we used 26 bioclimatic variables for North America (Table S3; AdaptWest Project, 2015; Wang et al., 2016). We then computed connectivity scores for pairs of adjacent planning units based on inverse distances derived from the bioclimatic variables (using the `RStoolbox R` and `PCDimension R` packages; Coombes & Wang, 2019; Leutner et al., 2019) (see Appendix S7 and Figure S8).

2.4 | Prioritizations

We identified a suitable budget to control for total expenditure when generating prioritizations based on the eight connectivity approaches. To achieve this, we performed a sensitivity analysis. The first step in the sensitivity analysis involved generating a baseline prioritization that did not explicitly account for connectivity (Figure S9; see Appendix S2). This involved minimizing protected area establishment costs and included targets to ensure that solutions covered (represented) at least 10% of each spatial distribution for each species. Although such targets are somewhat arbitrary, they were based on protected area policies (Brooks et al., 2004). The formulation also included constraints to lock in planning units covered by existing protected areas, and lock out those covered by urban areas (per land cover data) or tribal lands. After solving the formulation to generate the baseline prioritization (see below for details), we computed its total cost (i.e. $6,626.57B USD). The next step in the sensitivity analysis involved generating a series of prioritizations based on different connectivity approaches and different budgets (described below and in Appendices S3–S6). For each connectivity approach, we generated prioritizations under budgets that constituted a 1%, 5%, 10%, 15%, 20%, 30% and 40% increase above the total cost of the baseline prioritization (see Figures S10–S18 and Table S4). The last step in the sensitivity analysis involved selecting a budget. Based on the results of the previous step, we selected a budget of $7,620.55B USD (i.e. total cost of baseline prioritization plus an extra 15%) because it revealed the main differences between the connectivity approaches and constituted a reasonable increase in cost.

We generated prioritizations using each of the eight approaches (described in the previous section) for parameterizing connectivity. To accomplish this, we updated the problem formulation for the baseline prioritization with a different objective function to parameterize a given approach (see below for details), and an additional constraint to ensure that total costs did not exceed the budget. By modifying the objective function, we generated (a) a single prioritization by maximizing the total area of selected planning units (Appendix S3), (b) a single prioritization by maximizing species representation (Appendix S4), (c) a single prioritization by minimizing total boundary length (Appendix S5), and a further five prioritizations by maximizing (separately) connectivity scores for the human pressure, naturalness-based landscape resistance, focal species landscape resistance, habitat heterogeneity and environmental similarity (Appendix S6; Beger et al., 2010). Prior to optimization, we standardized boundary lengths and connectivity scores (separately) by linearly rescaling non-zero values to values between 0.01 and 10.

Our methodology produced prioritizations based on different connectivity approaches that can be compared with each other, because they were all generated using the same economic data, biodiversity data, representation targets, land use constraints and budgets. All of the prioritizations were generated using the `prioritizr` and `gurobi` R packages (Gurobi Optimization LLC, 2020; Hanson et al., 2021). All prioritizations—except the boundary length approach—were solved to within 1% of optimality. Since the boundary length approach was more computationally demanding, the prioritization generated following this approach was solved to within 10% of optimality. Note that a smaller optimality gap for the boundary length approach would result in a slightly more spatially clustered prioritization.

2.5 | Statistical analysis

We performed a hierarchical clustering analysis to compare the selection of planning units among prioritizations (Harris et al., 2014). To achieve this, we used Jaccard distances (via the `vegan` R package; Oksanen et al., 2020) to describe how different the prioritizations were to each other (Table S5). These distances were computed using binary values indicating if each planning unit was selected (or not) within a given prioritization. We then constructed a dendrogram (via UPGMA algorithm) to describe differences among prioritizations and applied the silhouette method to identify the best supported clusters (using the `factoextra` R package; Kassambara & Mundt, 2020).

We computed the level of connectivity each prioritization could facilitate as measured by each of the approaches (see Appendix S8). These measures were computed as percentages, relative to the prioritization generated using each approach. We also calculated summary statistics to describe the spatial distribution, costs, reserves and species' representation associated with the prioritizations (Tables S6–S9). To help understand the spatial distribution of the prioritizations, we calculated summary statistics to describe the ecological and economic conditions within each ecoregion (Tables S10 and S11). We also calculated pairwise Pearson correlation coefficients between connectivity scores for different approaches (Table S12).

3 | RESULTS

The prioritization generated using the boundary length approach was the most dissimilar to every other prioritization (Figures 2c and 3). It selected the smallest total area, and comprised a relatively small number of reserves (i.e. spatially contiguous sets of planning units; Table 1 and Table S6). These reserves were sited farther apart than reserves in other prioritizations and were, on average, the largest among all the prioritizations (30.13% greater, on average, among all prioritizations; Table 1 and Table S6). To achieve this, it selected planning units that were, on average, the most expensive among all prioritizations (32.56% more expensive, on average, than those selected among all prioritizations; Table S6), and therefore protected less total area for the given budget (Table 1).

The prioritizations generated using total area, species representation, focal species landscape resistance, habitat heterogeneity and environmental similarity selected a similar set of planning units (Figures 2a,b,f–h and 3). Broadly speaking, they selected a large amount of croplands and grasslands within the Columbia Plateau ecoregion (Figure 1c,d, Table 1). Indeed, these five prioritizations selected the greatest overall area among all prioritizations, with the total area approach selecting the largest area as expected. Over half of the selected planning units for these five approaches were located inside the Columbia Plateau (Table 1, Tables S6 and S7). Furthermore, the prioritizations generated using focal species landscape resistance, habitat heterogeneity and environmental similarity had, on average, larger reserves than the other prioritizations, except for the prioritization generated using the boundary length approach (Table S6).

The prioritizations based on total area, species representation, focal species landscape resistance, habitat heterogeneity and environmental similarity likely selected similar set of planning units due to spatial congruences between land cost and their parameterizations of connectivity. The Columbia Plateau contained, on average, the largest percentage of the species' distributions (Table S10) and—with the greatest number of planning units and the second lowest median land costs (Table S10)—it contained many planning units with low protected area establishment costs. Thus it is not surprising that the prioritizations based on total area and species representation emphasized the Columbia Plateau. Additionally, the Columbia Plateau contained connectivity scores for the focal species landscape resistance, habitat heterogeneity and environmental similarity approaches that were, on average, among the highest of all ecoregions (511.64%, 12.69% and 19.52% higher, on average, among all ecoregions respectively; Table S11). As such, prioritizations based on these connectivity scores could rapidly maximize

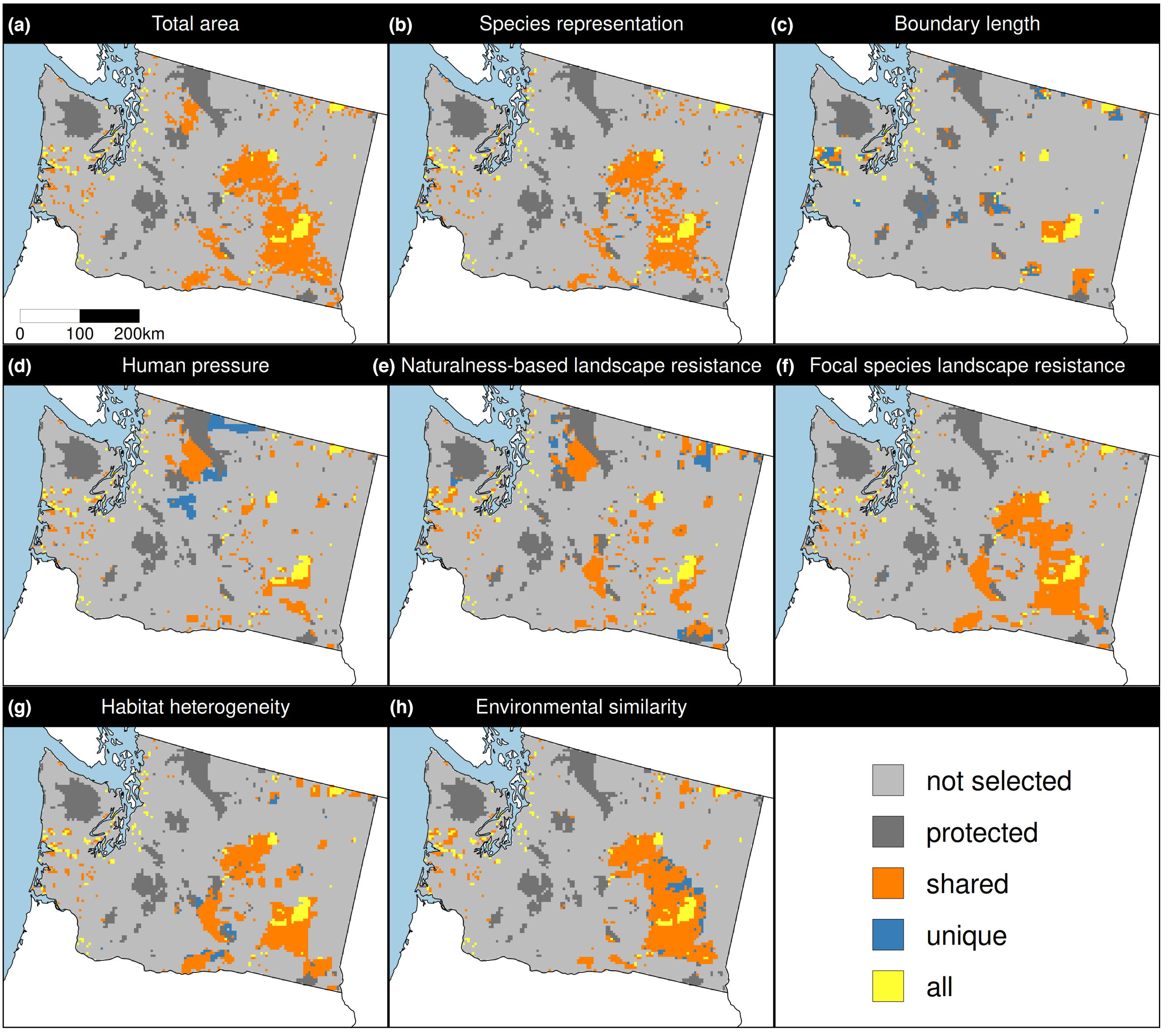

FIGURE 2 Prioritizations generated to account for connectivity using eight approaches: (a) total area, (b) species representation, (c) boundary length, (d) human pressure, (e) naturalness-based landscape resistance, (f) focal species landscape resistance, (g) habitat heterogeneity and (h) environmental similarity. Within each panel, grid cells correspond to planning units and their colours indicate those selected by (unique) only the single prioritization, (shared) multiple prioritizations, (all) all prioritizations and (protected) existing protected areas

FIGURE 3 Dendrogram depicts hierarchical cluster analysis comparing prioritizations based on selected planning units. Rectangles denote the best supported clusters

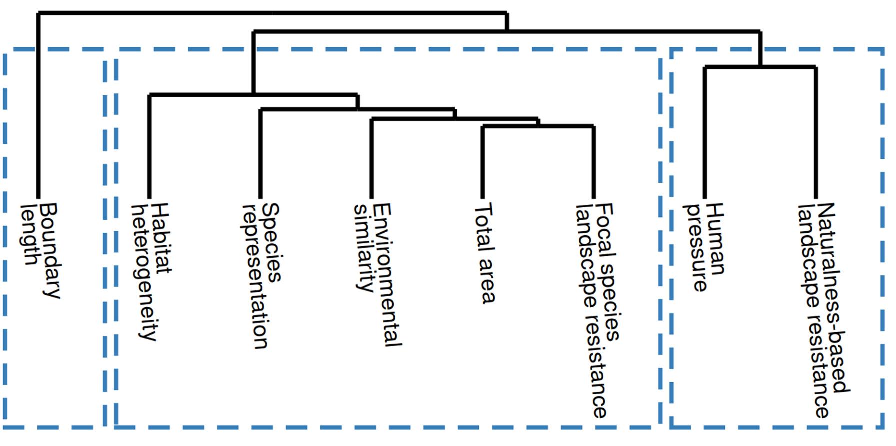

TABLE 1 Summary of prioritizations. Data show the approaches used to generate prioritizations and their total acquisition cost (USD), total size (km^2) and the percentage of the prioritization sited within each ecoregion (see Figure 1 caption for conventions)

Approach	Cost (USD)	Size (km^2)	Ecoregions BM	C	CP	CR	ECSF	NC	NR	PL	WV
Total area	$7,620.2B	42,352	1.74%	7.91%	53.29%	9.27%	1.25%	19.49%	3.82%	2.95%	0.26%
Species representation	$7,620.52B	37,120	1.43%	9%	51.43%	10.86%	1.38%	18.17%	3.89%	3.55%	0.3%
Boundary length	$7,619.26B	27,184	3.48%	13.33%	27.85%	16.05%	2.24%	26.78%	5.19%	4.66%	0.41%
Human pressure	$7,620.52B	32,032	2.15%	10.47%	25.49%	12.22%	1.6%	39.36%	4.56%	3.81%	0.35%
Naturalness-based landscape resistance	$7,620.49B	35,248	4.68%	9.73%	30.1%	11.87%	1.64%	29.38%	8.78%	3.5%	0.32%
Focal species landscape resistance	$7,620.41B	40,672	1.62%	8.24%	55.97%	9.66%	1.22%	16.48%	3.51%	3.04%	0.28%
Habitat heterogeneity	$7,620.53B	38,496	3.12%	8.7%	51.35%	10.25%	1.29%	17.33%	4.5%	3.17%	0.29%
Environmental similarity	$7,620.55B	40,832	1.37%	8.16%	55.53%	10.09%	1.22%	16.44%	3.89%	3.02%	0.27%

their parameterization of connectivity by selecting combinations of adjacent planning units with relatively low land costs and high connectivity scores.

The prioritizations generated using human pressure and naturalness-based landscape resistance selected a similar set of planning units (Figures 2d,e and 3). They selected a large group of planning units that ended up connecting two existing protected areas in the North Cascades ecoregion (Table 1 and Table S7; see Appendix S9 for discussion of the few differences between them). This result is likely due to the fact that the North Cascades ecoregion contained connectivity scores for human pressure and naturalness-based landscape resistance that were, on average, the highest and second highest among all ecoregions (195.44% and 47.24% greater, on average, among all ecoregions respectively; Table S11). These approaches also selected planning units within the Columbia Plateau, although far fewer than the prioritizations generated using total area, species representation, focal species landscape resistance, habitat heterogeneity and environmental similarity (Table 1 and Table S7). Since the Columbia Plateau has, on average, low connectivity scores for human pressure and naturalness-based landscape resistance (55.9% and 62.83% lower, on average, among all ecoregions respectively; Table S11), it seems likely that the low land costs of planning units within this ecoregion played a role in their selection.

None of the prioritizations promoted a high level of connectivity as measured by all eight of the connectivity approaches (e.g. over 80%; Figure 4). Although some of the prioritizations promoted, on average, a higher level of connectivity across all eight approaches compared with other prioritizations, none of the prioritizations outperformed all other prioritizations according to each and every connectivity approach. For example, although the prioritization generated using the environmental similarity approach had, on average, a relatively high performance as measured by all eight of the approaches, it did not promote high connectivity (e.g. over 80%) as measured by the boundary length, habitat heterogeneity, human pressure and naturalness-based landscape resistance approaches. These results also reveal stark trade-offs, with prioritizations generated using the boundary length and human pressure approaches promoting a low level of connectivity (e.g. under 30%) as measured by the focal species landscape resistance approach.

4 | DISCUSSION

We found that different approaches for promoting connectivity can lead to very similar or very different conservation plans. In particular, we found that the boundary length approach produced a distinctly different prioritization and selected a much smaller total area than the other connectivity approaches. Although we lack data to evaluate functional connectivity, this prioritization does exhibit characteristics—such as a relatively small total conserved area and relatively large distances among reserves (Table 1 and Table S6)—that can indicate low functional connectivity (Fahrig, 2017). This

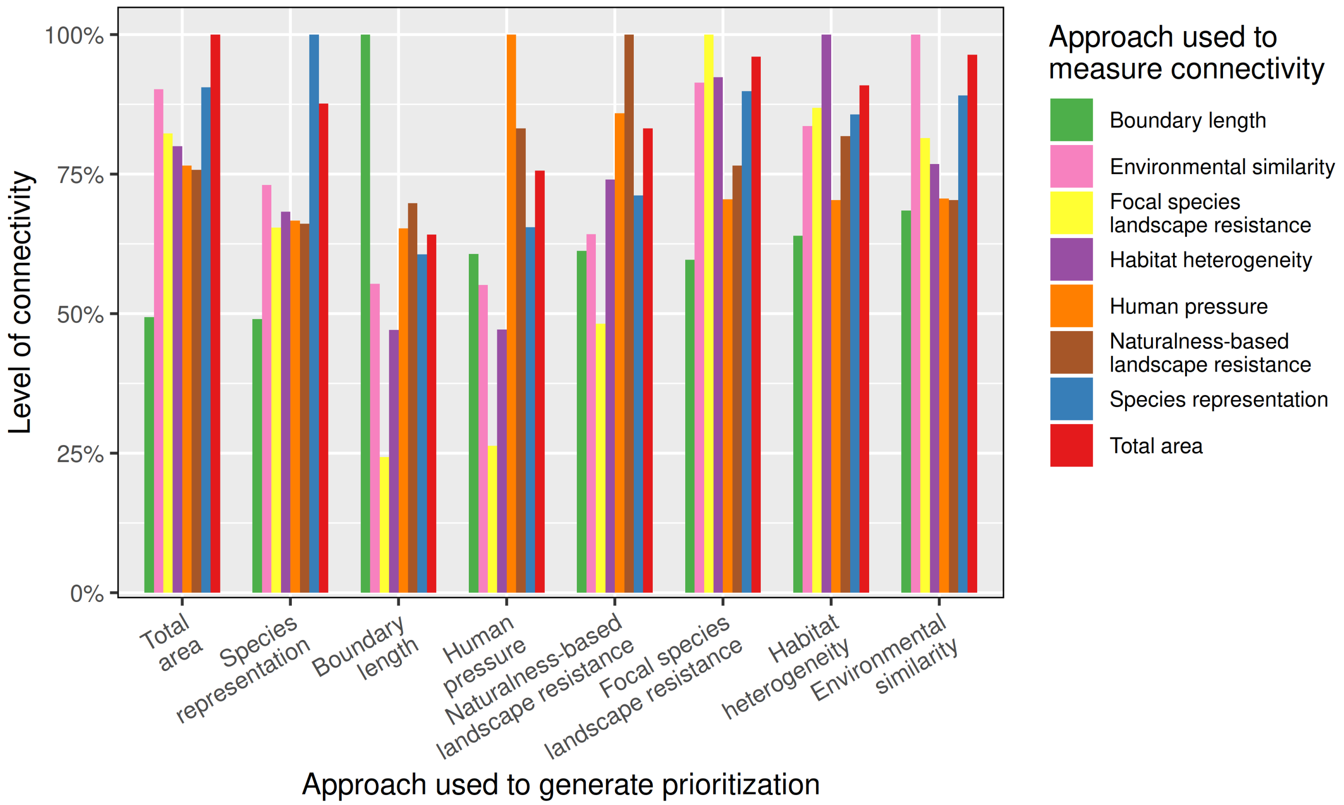

FIGURE 4 Level of connectivity facilitated by each prioritization as measured by the different connectivity approaches (see Appendix S8). Each group of bars corresponds to a different prioritization, and each bar denotes the level of connectivity facilitated by the prioritization as measured by one of the eight approaches. Note that data are percentages, relative to the prioritizations generated using each approach (e.g. level of connectivity as measured by the total area approach is shown relative to the total area of the prioritization generated using the total area approach).

result is especially pertinent because the boundary length approach is widely used (e.g. Choe et al., 2018; Harris et al., 2014; Stralberg et al., 2011). Moving forward, we advise conservation planners to carefully consider if the boundary length approach is most appropriate, and weigh potential alternatives that might better achieve conservation objectives. The boundary length approach may indeed be the most appropriate approach in certain situations, but we urge caution in applying it as a general method to promote connectivity.

Our analysis revealed trade-offs between the different connectivity approaches. This is because none of the prioritizations promoted a high level of connectivity under all eight of the approaches. For instance, prioritizing habitat area can be important for conserving biodiversity (Fahrig, 2013), although we note that simply adding area may not be sufficient to achieve conservation goals (Barnes et al., 2018). Indeed, similar trade-offs have also been observed for different facets of biodiversity (Kling et al., 2019). Thus conservation practitioners will need to decide which approach is most suitable for a particular planning exercise. This will vary among different planning exercises, depending on the underlying goals, region under consideration and biodiversity features of interest (e.g. species) (Keeley et al., 2021). To help conservation practitioners navigate such trade-offs, we detail advantages and disadvantages associated with each approach (see Table 2). We also note that the optimization procedures used in our study could be extended using hierarchical multi-objective techniques to generate a single prioritization based on multiple connectivity approaches (Gurobi Optimization LLC, 2020). Additionally, our methodology could serve as a framework that practitioners could use to compare different connectivity approaches in their own exercises.

Although differences between the prioritizations can be simply explained by differences in their underlying assumptions, similarities between some of the prioritizations could be explained several by factors. First, spatial congruences among the assumptions that underpin the different connectivity approaches could contribute to similarities among the prioritizations. For example, several of the approaches assigned relatively high connectivity scores to planning units in the Columbia Plateau, and so (unsurprisingly) the prioritizations based on these approaches selected many planning units there. Second, approaches that accounted for spatial proximity of planning units produced relatively similar prioritizations. This could be due to spatial clumping or autocorrelation in the distribution of natural areas. Third, spatial correlations between anthropogenic impact and land costs could contribute to similarities among the prioritizations. Indeed, such correlations are often strong enough such that anthropogenic impact data (e.g. human footprint index) are used as a surrogate for cost data (e.g. Leonard et al., 2017). In situations where low

TABLE 2 Advantages and disadvantages of the connectivity approaches examined in the study

Approach	Advantages	Disadvantages
Total area	• Well-suited for species where local conditions have little influence on species' dispersal (e.g. bird species that can fly over highly modified areas) • Well-suited for species with large dispersal ranges (e.g. migratory bird species that can fly large distances), such that they can reach distant reserves • Readily applicable, because no additional data required	• Neglects species-specific dispersal capabilities • Neglects effects of local conditions on species' dispersal • Neglects effects of local conditions on population sizes and number of dispersing individuals • Does not explicitly promote spatial clustering in prioritizations, which can be important when dispersal is limited outside of reserves
Species representation	• Well-suited for species with large dispersal ranges • Well-suited for species where local conditions have little influence on species' dispersal • Readily applicable, because it re-uses species distribution data required for prioritizations	• Neglects species-specific dispersal capabilities • Neglects effects of local conditions on species' dispersal • Does not explicitly promote spatial clustering in prioritizations
Boundary length	• Well-suited for systems where species have limited dispersal abilities outside of reserves (e.g. species that cannot survive outside of well-managed reserves) • Well-suited for species that benefit from large reserves (e.g. species that require pest eradication efforts inside reserves to persist) • Readily applicable, because no additional data required	• Assumes all species can disperse within individual reserves, regardless of local conditions which could potentially impede dispersal • Neglects species-specific dispersal capabilities • Neglects effects of local conditions on species' dispersal • Neglects effects of local conditions on population sizes and number of dispersing individuals
Human pressure	• Well-suited for species with dispersal patterns that are negatively influenced by anthropogenic impacts • Readily applicable to terrestrial systems, because high resolution data are available worldwide (e.g. Williams et al., 2020)	• Neglects species-specific dispersal capabilities • Pressure data are generally assumed to scale linearly with effects of local conditions on species' dispersal (e.g. human footprint index assumes roads impede dispersal twice as much as pasture areas; Williams et al., 2020) • May not be appropriate for exercises where human pressure data are also used as surrogate of land cost data or to model threats • Poorly suited for species which can easily disperse through heavily modified areas
Naturalness-based landscape resistance	• Well-suited for species with dispersal patterns that are strongly influenced by anthropogenic impacts • Landscape resistance data can be tailored for particular taxa, depending on available information	• Poorly suited for species which can easily disperse through heavily modified areas • Neglects species-specific dispersal capabilities • Expert knowledge or species-specific, spatially explicit data—such as individual movement or genetic data—are recommended to generate landscape resistance data
Focal species landscape resistance	• Well-suited for exercises focused on a single species • Well-suited for systems wherein the connectivity requirements for a focal species are representative of a wide variety of taxa (e.g. exercises focused on species with similar dispersal abilities and movement behaviours)	• Poorly suited for systems with diverse taxa, wherein a single species is unlikely to be representative for many other species (e.g. systems spanning multiple biomes that contain a variety of habitat-specialist species) • Expert knowledge or species-specific, spatially explicit data are required to generate landscape resistance data
Habitat heterogeneity	• Well-suited for species that are sensitive to discontinuities in vegetation (e.g. low gap crossing abilities) • Well-suited for systems where species' dispersal is strongly influenced by vegetation characteristics • Readily applicable to terrestrial systems, because high resolution data are available worldwide (e.g. Tuanmu & Jetz, 2015)	• Poorly suited for species that can easily disperse through discontinuities in vegetation • Neglects species-specific dispersal capabilities • Poorly suited for systems where species' dispersal is strongly influenced by abiotic factors (e.g. climate) or human activities (e.g. different land uses could have different impacts on species' connectivity, despite having similar vegetation characteristics)
Environmental similarity	• Well-suited for specialist species that can only disperse through a narrow range of environmental conditions • Readily applicable to terrestrial systems, because high resolution data are available worldwide (e.g. Wang et al., 2016)	• Poorly suited for species that can disperse through a broad range of environmental conditions • Neglects species-specific dispersal capabilities • By avoiding environmental gradients, prioritizations may fail to promote adaptive evolutionary processes (Rouget et al., 2003)

cost does not coincide with high connectivity according to multiple approaches, we might expect greater differences among prioritizations produced by different approaches. These explanations suggest that, in other planning regions with different relationships between land costs and connectivity criteria, these same approaches may result in very different prioritizations.

Our study has notable limitations. First, we limited our analysis to connectivity approaches that—given the scale of our case study—are tractable for mixed integer programming. Although many other approaches have been developed (reviewed in Keeley et al., 2021), they involve nonlinear computations that present challenges for optimization. Second, we did not examine connectivity approaches based on graph theory or meta-population dynamics (e.g. Daigle et al., 2020; Lehtomäki et al., 2009). This is because we lacked data to parameterize species' dispersal (c.f., Donaldson et al., 2021) and because assumptions associated with simple meta-population approaches generally do not hold for migratory species (Taylor & Hall, 2012). Assessing the implications of alternative connectivity approaches based on meta-population dynamics would be an interesting topic for future research where data are available to parameterize species-specific meta-population models. Finally, most of the approaches (all except for the total area and species representation approaches) only considered connectivity within reserves (Spanowicz & Jaeger, 2019). Since they did not consider connectivity between planning units located further apart than immediate neighbours, they lacked information to parametrize connectivity between reserves. Future work could extend the approaches to consider connectivity both within and between reserves (Beger et al., 2010).

Protected area systems must promote connectivity to safeguard biodiversity (Kool et al., 2013; Olds et al., 2012). Our findings demonstrate that different approaches that aim to promote connectivity in a protected area system can produce marked differences in the selection of priority areas. These differences, in turn, influence the level of connectivity facilitated by conservation plans. As such, we urge conservation practitioners to carefully consider the assumptions and limitations that underpin approaches for parameterizing connectivity. We particularly highlight that some of these approaches may lead to substantial trade-offs.

AUTHOR CONTRIBUTIONS

All authors conceived the study. Jeffrey O. Hanson and Jaimie Vincent performed the analyses. All authors contributed critically to writing the manuscript and gave final approval for publication.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Code and data are available via the Zenodo Digital Repository https://doi.org/10.5281/zenodo.4437627 (Hanson et al., 2022).

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