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Abstract

The United States Forest Service promulgated new planning regulations under the National Forest Management Act in 2012 (i.e., the Planning Rule). These new regulations include the first requirements in U.S. public land management history for National Forests to evaluate, protect, and/or restore ecological connectivity as they revise their land management plans. Data and resource limitations make single-species, functional connectivity analyses for the myriad species that occur within the 78 million ha the Forest Service manages implausible. We describe an approach that relies on freely available data and generic species, virtual species whose profile consists of ecological requirements designed to reflect the needs of a group of real species, to address the new Planning Rule requirements. We present high-resolution connectivity estimates for 10 different generic species across a 379,000 ha study area centered on the Custer Gallatin National Forest (CGNF) in Montana and South Dakota under two different movement models. We identify locations important for connectivity for multiple species and characterize the role of the CGNF for regional connectivity. Our results informed the Plan Revision process on the CGNF and could be readily exported to other National Forests currently or planning to revise their land management plans under the new Planning Rule.

KEYWORDS

coarse and fine filter, forest planning, generic species, National Forest Management Act, wildlife connectivity

1 | INTRODUCTION

Ecological connectivity is the degree to which the landscape facilitates or impedes movement among habitat

Target audience: Our target audiences are forest managers, planners, and the researchers that work with them to develop tools for informing decisions.

patches. Connectivity influences key ecological processes such as daily foraging movements, seasonal migrations, gene flow, and range shifts in response to environmental change (Bennett, 1999; Crooks & Sanjayan, 2006; Gilbert-Norton, Wilson, Stevens, & Beard, 2010; Rudnick et al., 2012; Taylor, Fahrig, Henein, & Merriam, 1993). Continuing loss of habitat, fragmentation of existing habitats, and the need for species to shift their ranges in response

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to global climatic changes have spurred a substantial increase in efforts to identify important movement pathways and develop new policies (e.g., land use plans, zoning regulations) and actions (e.g., wildlife overpasses, new protected areas) to enhance, maintain, or restore those pathways (Heller & Zavaleta, 2009; Keeley et al., 2019).

Despite recognition of the importance of connectivity, developing policies and coordinating actions that conserve or restore connectivity remains a challenge for state and federal land managers (Keeley et al., 2018). Planning for daily movements, seasonal migrations, and long-term range expansion often requires different data and analytical methods because these processes operate over different temporal and spatial scales (Crooks & Sanjayan, 2006). Further, information on the features that make a habitat suitable for movement (e.g., vegetation type, predator density, defended territory boundaries, and topographic characteristics) exacerbates these challenges as the data for each of these factors and their relative importance to the species-at-hand is often lacking or limited in spatial extent (Fagan & Calabrese, 2006; Theobald, Crooks, & Norman, 2011). Addressing this complexity often requires more empirical data and other resources than are typically available to resource management agencies. Moreover, landscape-scale conservation planning typically involves habitat patches and movement corridors that span multiple jurisdictions with different mandates and stakeholders, and thus requires multi-stakeholder processes that can be time-intensive and challenging to navigate (Schwartz et al., 2018). Finally, many land management agencies lack specific mandates or policy guidance for considering connectivity among other natural resource objectives, making it difficult to translate connectivity conservation goals into implementable management decisions (Keeley et al., 2018, 2019).

In 2012, the United States Forest Service (USFS) promulgated new planning regulations under the National Forest Management Act (NFMA; 77 FR 21162) that included the first requirements in U.S. public land management history for National Forests (the administrative units comprising the National Forest System) to evaluate, protect, and/or restore ecological connectivity as the Forests revise their land management plans (i.e., Forest Plans). These regulations (collectively the Planning Rule) define connectivity as “...ecological conditions that exist at several spatial and temporal scales that provide landscape linkages that permit the exchange of flow, sediments, and nutrients; the daily and seasonal movements of animals within home ranges; the dispersal and genetic interchange between populations; and the long distance range shifts of species, such as in response to climate

change” (36 C.F.R. § 219.19). With 78 million ha of National Forest System lands comprising 8.5% of US lands and 30.1% of federally owned lands (Vincent, Hanson, & Argueta, 2012), the explicit incorporation of connectivity as a management objective could substantially improve connectivity conservation in the United States. Incorporating connectivity conservation into National Forest management, however, requires an analytical approach that addresses both ecological complexity and limited resources. A standardized method could facilitate uptake by multiple Forests engaged in plan revision.

1.1 | Connectivity and National Forests

The Planning Rule and its associated Directives (available at: <https://www.fs.fed.us/im/directives/>) for National Forest System Land Management Planning explicitly identifies “conserving the biological diversity of the area” (USFS, 2012, p. 124) as an objective of land management plans. The 2012 Rule shifts the focus of the USFS from individual species' viability (as required by the 1982 Planning Rule) to ecological integrity, a strategy that relies more on the management and monitoring of ecosystem and habitat (i.e., coarse-filter) components, but incorporates individual species (i.e., fine-filter) criteria for species whose needs are not adequately captured by the coarse-filter approach (Schultz, Sisk, Noon, & Nie, 2013). Both coarse- and fine-filter assessments of connectivity are common, provide complimentary information, and require different assumptions and data.

Coarse-filter approaches are often species-neutral and characterize structural connectivity—the physical arrangement of habitat patches or land cover types within the landscape. For connectivity assessments that must inform management decisions for large numbers of species within large, ecologically diverse areas, these coarse-filter and structural approaches are a straightforward, low-cost option because they rely on readily available land cover data. Although integral to a comprehensive assessment of connectivity and ecological integrity, they may, however, fail to account for different dispersal abilities, habitat affinities, or life history traits of species (Vuilleumier & Metzger, 2006; With & King, 1997). As such, managing for connectivity based solely on structural connectivity may fail to adequately conserve key components of ecological integrity or biological diversity and thereby fail to meet the USFS' stated objectives.

Fine-filter analyses are typically species-specific and characterize functional connectivity—actual movement of individuals, genes, and species in response to elements of the landscape (Crooks & Sanjayan, 2006). They are

generally believed to provide more biologically informative estimates of movement potential and patterns (Bélisle, 2005). However, for each species of interest they require identification of areas that constitute quality habitat, consideration of landscape elements that deter or promote movement, and explicit identification of the appropriate scale of the analyses based on the species-specific attributes. Biological movement data (e.g., genetic data, occurrence estimates, expert opinion; Zeller, McGarigal, & Whiteley, 2012) for the majority of these species do not currently exist and analyzing connectivity for each species would be cost- and time-prohibitive given that Plan revision must be completed in a timely manner and within a constrained budget.

One method for dealing with resource limitation is to use an umbrella species—one whose conservation indirectly protects a large number of naturally co-occurring species (Roberge & Angelstam, 2004). Umbrella species are typically large-bodied, wide-ranging organisms with large area requirements; for instance, the grizzly bear (*Ursus arctos horribilis*) is a common umbrella species for conservation efforts in the northern Rocky Mountains (Carroll, Noss, & Paquet, 2001; Proctor, Nielsen, & Kasworm, 2015). However, evidence that umbrella species are representative of connectivity requirements for groups of species is mixed, and using the typical wide-ranging generalist predator as an umbrella species may not provide connectivity for species with specialized movement needs (Breckheimer et al., 2014; Meurant, Gonzalez, Doxa, & Albert, 2018; Roberge & Angelstam, 2004). Further, without species-specific comparisons of the effectiveness of a species as an umbrella (i.e., evaluations of the amount of connectivity that management for a selected species provides to a broader community of species), the selection of umbrella species may appear to the public as arbitrary, thereby risking the acceptability or validity of plans built around those species.

The generic species approach is an alternative to comprehensive modeling of species-specific functional connectivity or selection of umbrella species (i.e., fine filter approaches; Watts et al., 2008) that may also overcome many of the limitations of coarse-filter approaches for assessing connectivity on National Forests. A generic species is a virtual species whose profile consists of a set of ecological requirements designed to reflect the needs of a group of real species. This approach requires developing a set of profiles of characteristics (e.g., habitat preference, perceptual range, and vagility) for each species group of interest. Generic species have been used for connectivity conservation planning in several other instances (Foster, Love, Rader, Reid, & Drielsma, 2017; Lechner, Sprod, Carter, & Lefroy, 2017; Watts et al., 2010). Because

generic species provide a means of incorporating attributes of multiple species' life histories without requiring species-specific movement data, they represent an intermediate approach between coarse-filter structural connectivity analyses and fine-filter functional connectivity analyses that is both biologically defensible and logistically feasible (Lechner et al., 2017).

The Custer Gallatin National Forest (CGNF) is revising its Forest Plan under regulations set forth in the 2012 Planning Rule. Here we describe an analytical approach developed in conjunction with the CGNF designed to leverage existing, freely-available data to generate relatively fine-grained estimates of connectivity for a suite of species across a broad spatial extent. We used a generic species approach to characterize connectivity across multiple habitat types and jurisdictions while adhering to the resource constraints imposed by limited data and a compressed timeline for land management planning under the National Forest Management Act. We then discuss how our results are informing the current CGNF Plan revision process and consider how this approach might inform similar efforts.

2 | METHODS

2.1 | Study area

The CGNF encompasses more than 1.2 million ha of southern Montana and northwestern South Dakota (Figure 1) and provides habitat for more than 700 wildlife species (Montana Natural Heritage Program: <http://mtnhp.org/>). The CGNF is situated between the Greater Yellowstone and Northern Continental Divide Ecosystems, making it a key area for landscape connectivity conservation. As such, we buffered each of the CGNF administrative units by ~161 km thereby allowing us to assess connectivity within the region rather than just between administrative units. This resulted in a study area of over 379,000 ha comprised of multiple federal, state, and private jurisdictions.

2.2 | Defining generic species

We modeled connectivity for terrestrial generic species that represent combinations of five vegetation type preferences (forest specialist, alpine specialist, grassland specialist, shrubland specialist, or habitat generalist that prefers any of the preceding vegetation types) and two body sizes (large or small). Body size is positively correlated with both dispersal ability (Jenkins et al., 2007) and perceptual range (the distance at which an animal can

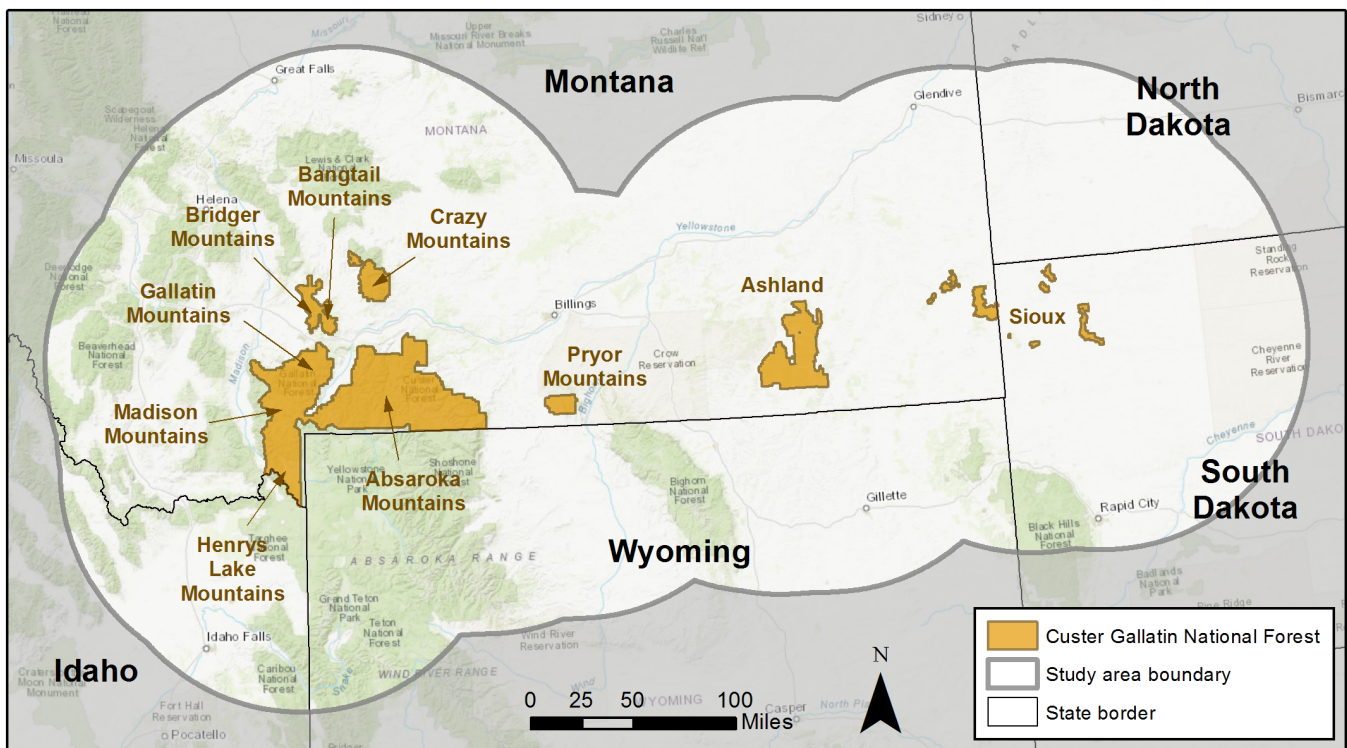


FIGURE 1 Study extent for connectivity analysis, including all lands within 100 miles (160.9 km) of Custer Gallatin National Forest (CGNF). CGNF geographic areas used for forest planning purposes are labeled

perceive landscape elements; Mech & Zollner, 2002), which influence connectivity and habitat selection. While dispersal ability defines the limits of an animal's movements across the landscape, perceptual range determines the immediately surrounding area that an animal's habitat selection and movement decisions are based upon.

The generic species defined for this analysis were based on the dispersal characteristics of local wildlife species. We developed generic species profiles for larger-bodied and/or wide-ranging species based on the dispersal characteristics of: elk (*Cervus elaphus*), gray wolf (*Canis lupus*), Canada lynx (*Lynx canadensis*), and wolverine (*Gulo gulo*). Similarly, we developed generic species profiles for smaller-bodied and/or shorter-ranging species based on the dispersal attributes of: bobcat (*Lynx rufus*), red fox (*Vulpes vulpes*), and marten (*Martes americana*). We relied on expert opinion of CGNF biologists and published literature (e.g., Schaefer, Morellet, Pépin, & Verheyden, 2008; Zollner, 2000) to define the dispersal, movement, and habitat selection attributes of each generic species based on habitat preference, tolerance of human impacts on the landscape, perceptual range, and dispersal distance (Table S1).

We identified potential habitat based on 30-m resolution LANDFIRE Existing Vegetation Type (EVT) version 1.4 geospatial data (U.S. Geological Survey, 2014) to

classify landscapes pixels into dominant habitat types based on the "EVT Lifeform" attribute in the dataset (Table S1; Figure 2). We then used an index of human modification (Theobald, 2013) as a complementary indicator of habitat suitability that is available for North America (available at DataBasin: <https://databasin.org/datasets/110a8b7e238444e2ad95b7c17e889b66>). The human modification index (HMI) quantifies overall modification on a scale ranging from 0 (low modification) to 1 (high modification) and integrates the effects of a wide variety of anthropogenic stressors for which spatial data are widely available (e.g., development, agriculture, energy production, mining, and roads).

We defined specialists as those species that required 80% of the area within their perceptual range to be comprised of one of four dominant vegetation types in the region (alpine, forest, grassland, or shrubland) and relatively un-modified by human activities (see Table S2 for a complete description of the thresholds used here). In contrast, generalists were those that required 80% of the area within their perceptual range to be any combination of the dominant vegetation types with a greater tolerance for human impacts. All other cover types (e.g., residential/commercial/urban development, agriculture, open water) were considered nonhabitat.

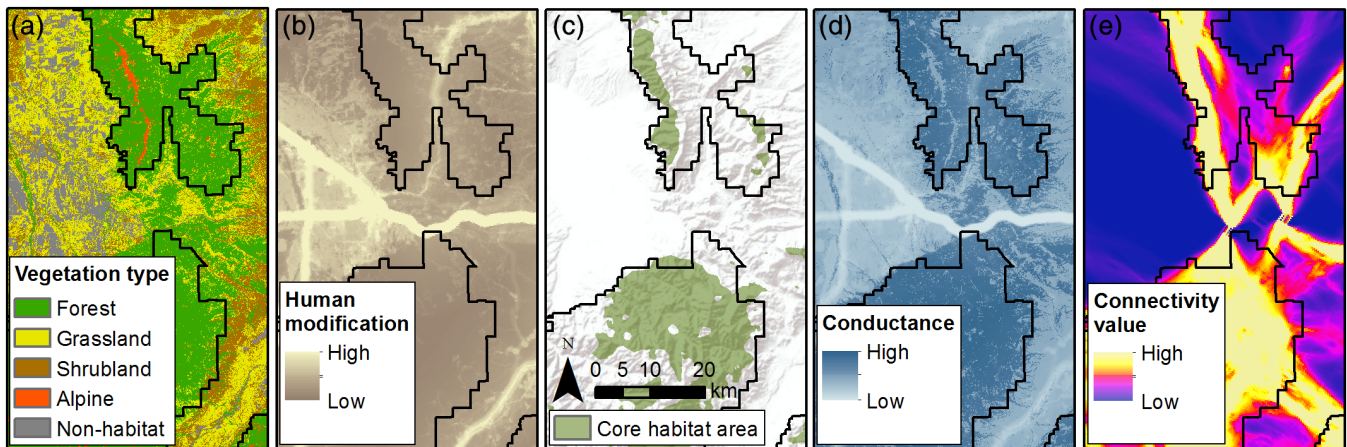


FIGURE 2 Examples of data inputs, intermediate analysis products, and connectivity model outputs for the large forest specialist generic species within a small portion of the study area surrounding Bozeman, Montana. (a) Dominant vegetation type derived from LANDFIRE Existing Vegetation Type “Lifeform” attribute. (b) Human modification index from Theobald (2013). (c) Core habitat areas (i.e., patches of relatively homogeneous, minimally impacted forest) derived from a moving-window algorithm. (d) Landscape conductance surface based on human modification and vegetation type. (e) Connectivity model output assuming optimal movement behavior. Borders of Custer Gallatin National Forest (CGNF) units are shown with black lines. CGNF geographic areas included in figure extent are the Bridger and Bangtail Mountains to the north and Gallatin Mountains to the south (see Figure 1)

2.3 | Identifying core areas

Connectivity analyses generally begin by identifying specific areas to be connected (Sawyer, Epps, & Brashares, 2011). We developed a novel approach that incorporates vegetation type, degree of human modification, and an organism’s perceptual range to define core areas of highest-quality habitat for generic species. We resampled 270-m resolution HMI geospatial data to 30-m resolution using bilinear interpolation to align it with the EVT layer. We then created a moving-window algorithm that identified each pixel in the landscape as core habitat or not for a particular generic species by: (a) defining a circular neighborhood around the focal pixel with radius equal to the perceptual range of the generic species; (b) calculating the proportion of the pixels within this neighborhood that had HMI below a given value (the “modification threshold,” Table S2) and were the preferred vegetation type(s) for the generic species; and (c) classifying the focal pixel as core habitat if that proportion met or exceeded a given value (the “habitat threshold,” Table S2).

We identified threshold values for both modification level and vegetation type homogeneity for core areas by iterating combinations of each threshold value and assessing the degree to which the subsequently identified core areas matched with CGNF staff expertise regarding the location and extent of high-quality habitat. This approach was designed to identify those areas that have relatively continuous cover of a particular vegetation type (or combination of vegetation types for generalists) and minimal human impacts (including impacts that do not result in a change in

cover type but reduce habitat suitability, such as light pollution or road noise; based on the HMI). We recognize that the core habitat areas identified in our analysis are by no means the only areas utilized by wildlife, particularly generalist species. However, they are the areas believed by local managers to exhibit the highest habitat quality in the region, and therefore are considered the highest priority locations among which we desire to maintain connectivity.

2.4 | Developing the resistance surface

Connectivity models simulate movement of individuals across spatially heterogeneous landscapes represented as resistance surfaces: gridded spatial data in which the value of each pixel is an estimate of the willingness, physiological cost, and/or reduction in survival of an organism moving through the pixel as a function of the environmental characteristics encountered there (Zeller et al., 2012). Typically, the effects of multiple factors that influence movement (e.g., cover type, topography, proximity to human development) are incorporated into resistance surfaces, and the final resistance surface is a pixel-by-pixel map of the landscape’s relative resistance (i.e., unsuitability) to animal movement, with larger pixel values indicating greater resistance. A variety of information sources can be utilized to assign resistance values to the landscape, including expert opinion, relocation or detection data, movement path data, and genetic data (Sawyer et al., 2011; Zeller et al., 2012).

Because we modeled generic species, detailed empirical data (e.g., genetic data or point locations from GPS telemetry studies) were not available to develop appropriate resistance surfaces. Instead, we used an estimate of “naturalness”—the degree to which the landscape is influenced by human activities and modification to land cover—as a predictor of the permeability to ecological flows. This approach assumes that areas of greater naturalness are more likely to support ecological processes and function as animal movement routes and has been used in previous connectivity studies (e.g., Belote et al., 2016; Dickson et al., 2016; Theobald, Reed, Fields, & Soulé, 2012).

We modified this “naturalness” value to reflect our generic species by assuming that (a) specialists are more sensitive than generalists to human modification, and (b) nonpreferred vegetation types have additional resistance for specialist species regardless of level of human modification (Table S2). The connectivity algorithm we used (see description of “Modelling connectivity” below) relies on a conductance surface (i.e., the inverse of a resistance surface) wherein higher values represent areas more conducive to movement. We transformed Theobald’s (2013) HMI into conductance by assuming a negative linear relationship between the two, which implies that animals are more likely to move through areas that are less modified by humans. We then modified the conductance surface for each specialist species by multiplying conductance values by 0.5 for all pixels with vegetation type other than the preferred vegetation type to reflect that specialists are less likely to move through nonpreferred vegetation types. Real specialist species likely do not perceive all nonpreferred vegetation types as equally unsuitable for movement, but given the generic nature of our modeled species, we chose to penalize all nonpreferred vegetation types equally. For generalist generic species, we assumed that all four vegetation types (forest, grassland, shrubland, or alpine) were preferred, and we applied this penalty to all other cover types (e.g., developed, barren, agriculture, open water). Finally, we aggregated conductance surfaces to 300-m resolution to reduce computational requirements.

2.5 | Modeling connectivity

A variety of approaches have been used to model landscape connectivity, but the most commonly used are least-cost path analysis (Adriaensen et al., 2003) and circuit theory (McRae, Dickson, Keitt, & Shah, 2008). These two approaches represent opposite ends of a spectrum of animal movement behaviors. Least-cost path models assume that individuals have perfect knowledge of the

landscape and are able to travel between an origin and destination along the single path that minimizes the total cost of movement, which is a function of both the actual distance traveled and resistance encountered along the way. In contrast, circuit theory models assume that individuals are moving stochastically as random walkers, with no knowledge of the landscape beyond what they perceive from their immediate surroundings. Both approaches are frequently used to assess landscape connectivity and design conservation strategies despite relying on assumptions about animal dispersal behavior that are unrealistic for most species.

We modeled connectivity within and around CGNF using randomized shortest paths (RSP; Saerens, Achbany, Fouss, & Yen, 2009), which incorporates elements of both least-cost paths and circuit theory and has been used to model movements of grizzly bears (*Ursus arctos horribilis*) and elk in the study extent (Brennan et al., 2018; Peck et al., 2017). Randomized shortest paths are least-cost paths modified by introducing random deviations that simulate exploratory movements away from the optimal route, which may more accurately reflect movement behavior of many species in real landscapes. The degree of random deviation is controlled by a parameter, θ , that ranges from 0 (analogous to a purely random walk) to 20 (analogous to a deterministic LCP). We tested a series of θ values within this range for a 1.5 million ha subset of the study extent and identified two values (0.1 and 10) that we believe bracket an appropriate range of variation in dispersal behavior of wildlife species.

RSP models require a set of point locations among which to simulate movement of individuals (i.e., source and destination points, or “nodes”). We established these node locations by (a) defining distinct core habitat patches in the landscape as groups of core habitat pixels connected by an edge or corner (i.e., the 8-neighbor rule), (b) randomly selecting one pixel within each distinct core habitat patch ≥ 100 ha area for large species and ≥ 25 ha for small species, (c) continuing to randomly select core habitat pixels within the landscape until a desired overall density of nodes within core habitat across the study extent had been achieved, and (d) establishing a node at the center of each randomly selected pixel. We used this procedure because we wanted to ensure that all core habitat patches of significant size (i.e., large enough to accommodate the perceptual range for a given size class) were represented as starting and ending points, but we could not achieve this via purely random sampling without increasing the overall node density to a level that made it computationally infeasible. For large specialists, a density of 1 node per 2,000 ha of core habitat best met our dual objectives of comprehensive sampling of core areas and computational feasibility. For small specialists,

a much higher density of 1 node per 500 ha of core habitat was required to generate a reasonable number of node pairs separated by the much smaller maximum dispersal distance. Given the much larger core area extent for generalists, we used densities of 1 node per 15,000 ha of core habitat for large generalists and 1 node per 2,000 ha of core habitat for small generalists to keep computation time reasonable.

We used the **passage** function in the *gdistance* package (van Etten, 2012) for R (R Development Core Team, 2018) to implement RSP analyses for each generic species. For every pair of nodes separated by a Euclidean distance less than the maximum dispersal distance (150 km for large species or 10 km for small species), we ran the RSP algorithm to simulate movement between the source node i and destination node j . To make this computationally feasible, we reduced the study area for each node pair (i, j) by drawing a bounding box around the node pair and buffering this box by 50 km (large species) and 10 km (small species). We then ran the passage function within this buffered bounding box (rather than across the entire study area). Although landscape boundaries can have an impact on connectivity model outputs, the buffer distances we used would require the species to travel at least a third of its maximum dispersal distance in the wrong direction before reaching the destination node. As such, our method of reducing the study area for node pairs should have minimal impact on our results. We calculated the net number of passages through each pixel in the landscape as an indicator of the contribution of that pixel to connectivity from node i to node j . We then summed these passage values across all node pairs to determine the overall importance of each pixel for connectivity among all core areas within the landscape. We ran a total of 20 models: five vegetation type preferences (alpine, forest, grassland, shrubland, and generalist) \times two animal sizes (large and small) \times two movement behaviors (random and optimal movement).

2.6 | Characterizing the contribution of current land-use designations to connectivity

Forest Planning may result in the development of new land use designations and direction for management. To determine the degree to which existing conservation designations (e.g., wilderness areas, wilderness study areas, and inventoried roadless areas) within the CGNF and across the broader study area align with important movement pathways, we first created binary maps of high-value connectivity pixels (those with a passage value in the Top 5 percentile for at least one of the 20 connectivity

models run) and very high-value connectivity pixels (Top 1 percentile for at least one model) for the regional study area ("TOP PERCENTILE" approach described below). We then calculated the percentage of regional high-value and very high-value pixels contained within each conservation designation and compared this to the percentage of the full study area comprised by each designation as a measure of the degree to which connectivity value was over- or under-represented within a given designation.

2.7 | Characterizing connectivity across models

Forest Plans are intended to guide land use patterns and habitat management needs for a wide range of species. As such, we developed several approaches to integrate the 20 different models into a single map that could be used to help identify locations within CGNF that could be managed to benefit connectivity for species from multiple generic species groups. Those locations benefitting multiple species outside of existing designations (see above) could then be considered for new designations or connectivity-specific plan components. We used three approaches for integrating information across models that reflected different assumptions about habitat affinity, conductance values, dispersal distance, and perceptual range in order to identify areas of model overlap within CGNF: (a) normalizing all passage values to a common 0–1 scale and then summing values across all models as a measure of each pixel's total contribution to regional connectivity for all generic species and movement behaviors (NORMALIZED SUM); (b) calculating the Top 1 percentile (i.e., very high connectivity value) or Top 5 percentile (i.e., high connectivity value) of passage values for each model and identifying pixels that meet this threshold for at least one model (TOP PERCENTILE); and (c) counting the number of models for which each pixel had a passage value in the top percentile (MODEL COUNT).

3 | RESULTS

3.1 | Effects of animal size

Core areas identified using the moving-window algorithm had broadly similar spatial distributions for large and small generic species of the same preferred vegetation type, although small species core areas tended to include more numerous but smaller habitat patches while large species core areas tended to include fewer but larger habitat patches (Figure S1). This pattern likely resulted from differences in perceptual ranges for large

and small species, whereby smaller species were assumed to perceive habitat quality over a finer spatial extent.

Although the spatial distribution of core areas was similar for large and small species, landscape-level patterns of connectivity for the two sizes of generic species tended to be quite distinct (Figures 3 and 4). Large species connectivity model outputs highlighted long-distance connections that included significant portions of the landscape outside of core areas (i.e., inter-patch connections). In contrast, connectivity model outputs for small

species indicated that high-value connectivity areas were located almost exclusively within core areas (i.e., intrapatch connections). The large difference in maximum dispersal distance for large and small species (150 and 10 km, respectively) accounts for this pattern, as connectivity models for large species allowed for connections between distant core areas, while relatively few core areas for small species were separated by a distance smaller than their maximum dispersal range, generally resulting in movements concentrated within individual

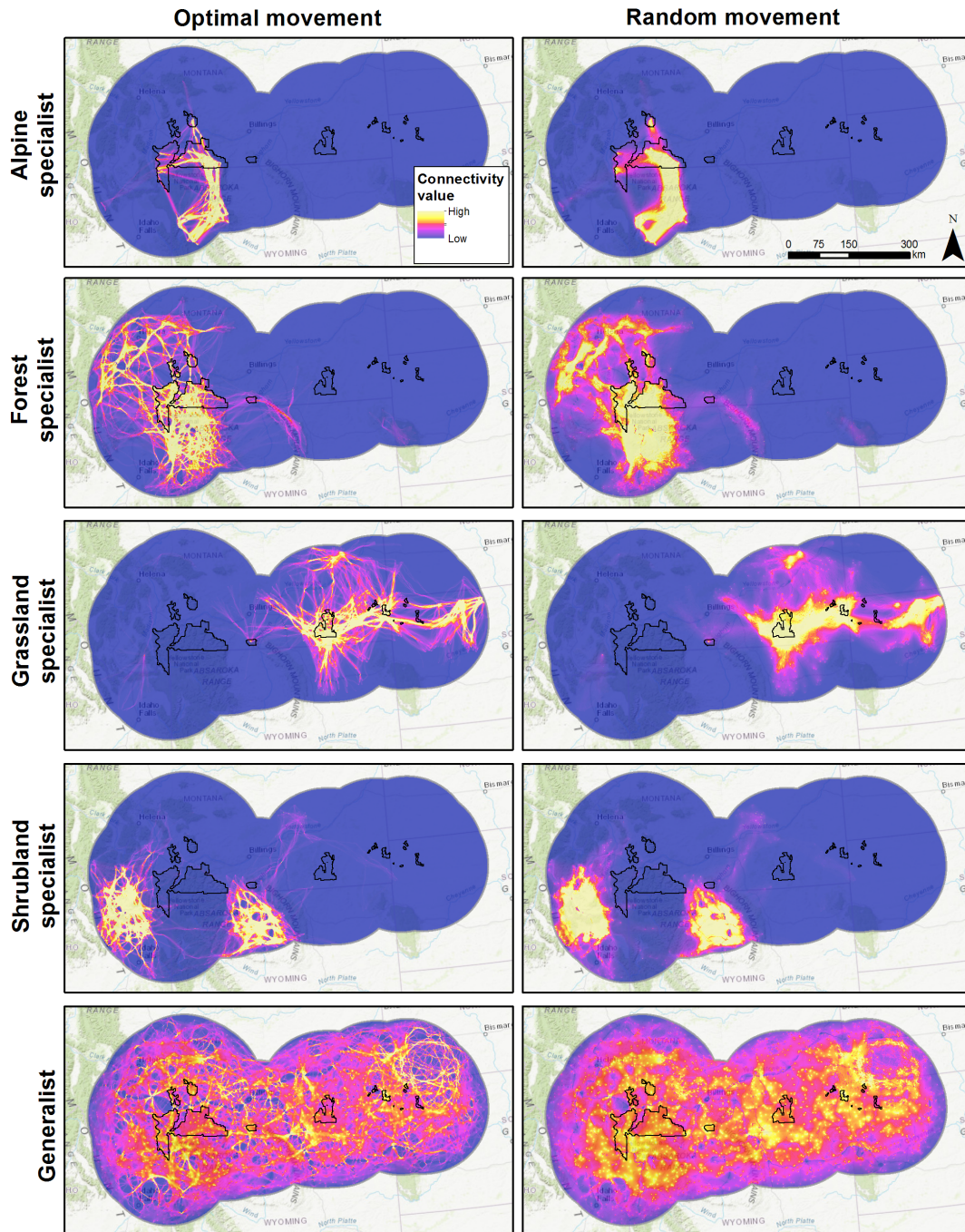


FIGURE 3 Connectivity model outputs for large generic species (rows) assuming different movement behaviors (columns). Custer Gallatin National Forest boundaries are shown with black lines

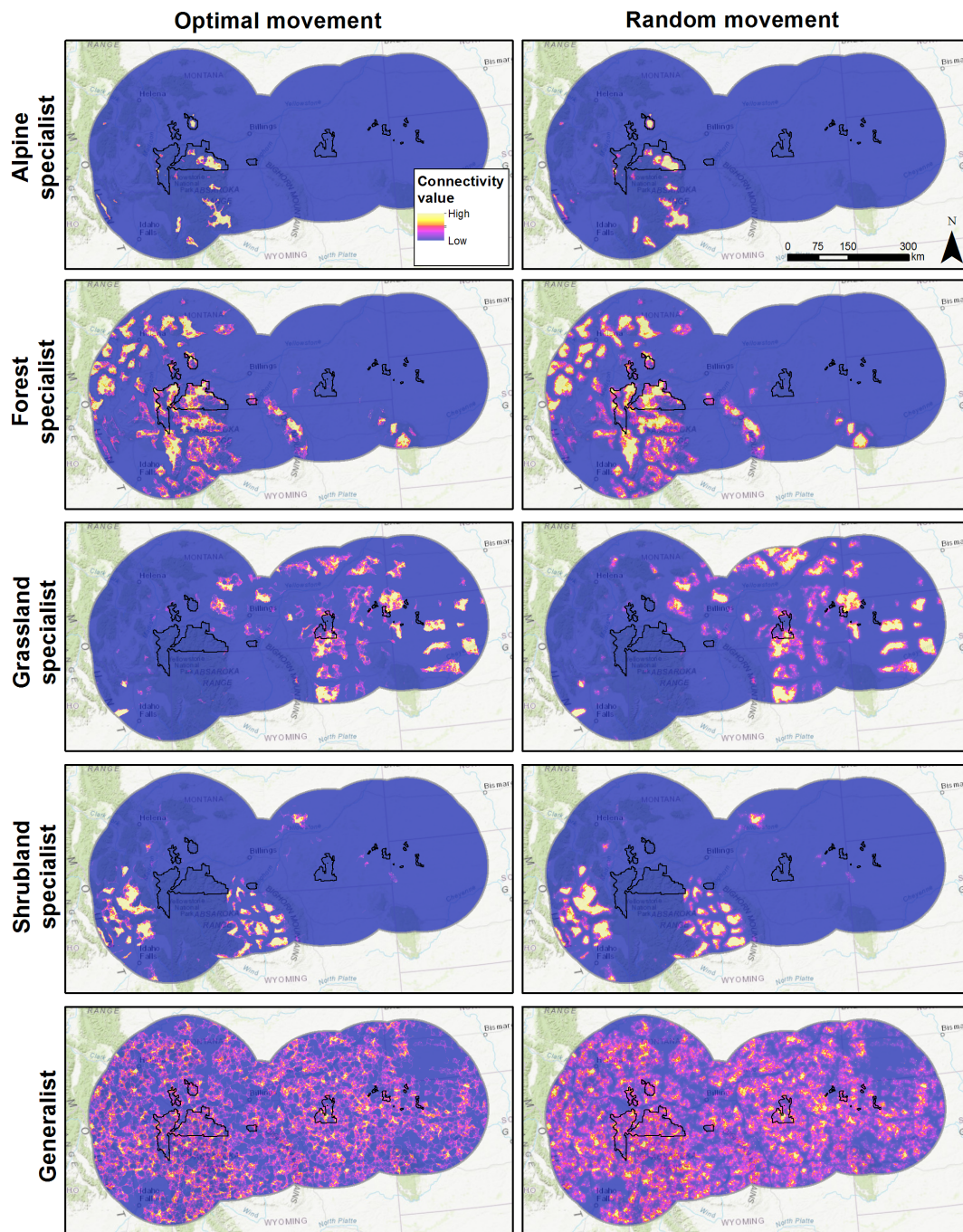


FIGURE 4 Connectivity model outputs for small generic species (rows) assuming different movement behaviors (columns). Custer Gallatin National Forest boundaries are shown with black lines

core areas. Locations of core habitat areas for small species exhibited strong overlap with high-value connectivity areas for larger-bodied species of the same preferred vegetation type (Table S3; Figures S2-S5).

3.2 | Effects of movement behavior

Connectivity models assuming random movement behavior and optimal movement behavior for large species

tended to highlight similar locations within the study extent as important for regional connectivity for a given preferred vegetation type. However, optimal movement models identified narrower corridors, while random movement models identified more diffuse corridors (Figures 3 and 4).

For small species, connectivity models assuming random movement and optimal movement behaviors produced very similar outputs. We believe this was because of the relatively large pixel size (300 m) used in the model

relative to the maximum dispersal distance assumed for small species (10 km), which limited the potential for the two movement types to produce different movement paths.

3.3 | Multi-species connectivity

Our different approaches for identifying areas important for connectivity for multiple species provided complementary results, and each suggested that a major portion of CGNF lands has high connectivity value for at least some generic species. The NORMALIZED SUM approach indicated that nearly all of CGNF, particularly the western portion, is of moderate or higher value when considering all models simultaneously (Figure 5a). The TOP PERCENTILE approach identified a number of coherent pathways that may serve to connect generic species' core areas, but the location and extent of those pathways depended on the percentile threshold (Figure 5b). Using the Top 5 percentile, nearly all of CGNF was identified as high value for at least one generic species, while using the Top 1 percentile resulted in a smaller and less contiguous set of very-high connectivity value areas. The MODEL COUNT provided more nuanced information on multi-species connectivity value, indicating that nearly all high-value pixels identified in the previous approaches were supported by four or fewer out of 20 models. (Figure 5c). Thus, although most of CGNF (and much of the regional study area) was important for connectivity according to at least one model, very little of it was identified as important by more than a small fraction of the models. Because results tended to be most similar among models for generic species of the same habitat preference but assuming different movement behavior or animal size, pixels with support from multiple models do not necessarily represent areas important for animals with different habitat preferences.

3.4 | Contribution of land use designations to connectivity

A greater proportion of lands with high and very high connectivity value occurred within each designation category than would be expected based on these designations' respective areas. This discrepancy was most notable within CGNF lands, which comprise 3.6% of the regional study area but contain 7.7 and 10.3% of the high-value and very high-value pixels, respectively, for regional connectivity (Table 1). We also computed the fraction of pixels within each designation that were classified as high or very high value for connectivity. This metric

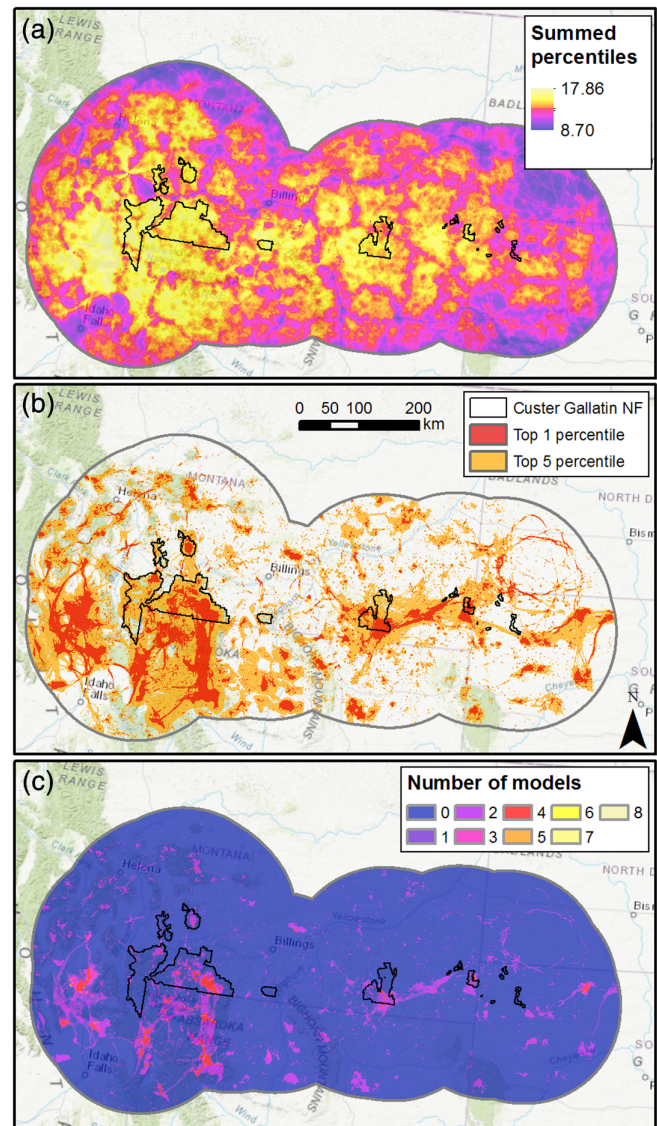


FIGURE 5 Examples of approaches for integrating connectivity results across models. (a) Pixel-wise sum of normalized passage values across all 20 models (i.e., NORMALIZED SUM). (b) Pixels with passage values in the Top 1 percentile or Top 5 percentile for at least one model (i.e., TOP PERCENTILE). (c) Pixel-wise count of number of models with passage values in the Top 1 percentile (i.e., MODEL COUNT)

suggests that pixels of greatest connectivity value tend to be over-represented within CGNF and other protected lands; for instance, 84.4% of CGNF lands were classified as high value for connectivity (compared to 39.7% of lands throughout the study area), and 31.7% of CGNF lands were classified as very high value (compared to 11.15% of lands throughout the study area). Conservation-based designations (e.g., Wilderness Areas, Wilderness Study Areas, and Inventoried Roadless Areas) on the CGNF are largely situated in areas of high and very high connectivity values (Table 1), suggesting that

TABLE 1 Contribution of different designations to connectivity conservation across the study area

Land category	Percentage of regional study area within designation	Percentage of regional HIGH ^a connectivity value pixels within designation	Percentage of regional VERY HIGH ^b connectivity value pixels within designation	Percentage of designation classified as HIGH ^c connectivity value	Percentage of designation classified as VERY HIGH ^d connectivity value
Custer Gallatin National Forest (CGNF)	3.6	7.7	10.3	84.4	31.7
Wilderness area (WA)	3.8	8.8	14.7	92.8	43.4
WA within CGNF	1.1	2.7	5.1	99.1	51.4
Wilderness study area (WSA)	1.1	1.9	1.7	71.7	17.5
WSA within CGNF	0.2	0.4	0.3	97.9	24.1
Inventoried Roadless area (IRA)	7.0	12.0	11.9	67.6	18.8
IRA within CGNF	0.9	2.0	1.9	87.4	23.7

^aHigh connectivity value pixels are those with a passage value in the Top 5 percentile for at least one of the 20 connectivity models run.

^bVery high connectivity value pixels are those with a passage value in the Top 1 percentile for at least one of the 20 connectivity models run.

^cFor reference, 39.7% of the full study area was classified as high connectivity value (Top 5 percentile for ≥ 1 model).

^dFor reference, 11.2% of the full study area was classified as very high connectivity value (Top 1 percentile for ≥ 1 model).

despite their rarity within the study area they contribute substantially to connectivity for the generic species considered here. Further, these areas encompass more connectivity value than similar designations outside of the CGNF. Collectively, these results highlight the critical role that CGNF lands play in facilitating regional connectivity, in concert with other lands managed for conservation purposes.

4 | DISCUSSION

We developed a novel, intermediate-filter approach for assessing connectivity across the CGNF based on generic species. Our approach provided a means of characterizing connectivity both within and between large core areas without being restricted to political or jurisdictional boundaries. Our approach also provided a means of analyzing functional connectivity at an intermediate level of detail and data requirements (compared with structural connectivity assessments or species-specific functional connectivity analyses). Perhaps most importantly, our approach was designed to fit within the existing Forest

Service plan revision process and could be applied by other national forests undergoing revision of their Land Management Plan.

Our method for defining starting and ending points contrasts with other approaches used in large-scale connectivity studies, which either consider each habitat patch or protected area as a single node (Belote et al., 2016; Dickson et al., 2016; Theobald et al., 2012) or model connectivity between nodes situated along opposite boundaries of the study extent (Gray & Dickson, 2015; Koen, Bowman, Sadowski, & Walpole, 2014; Pelletier et al., 2014). The first approach was not well suited to our analysis because we were interested in characterizing connectivity *within* large core areas (which requires multiple nodes within a core) as well as *between* core areas. The second approach was also not ideal because we were interested in omnidirectional movements between any starting and ending locations within the study extent. Our method overcomes these limitations, although at the cost of a considerable increase in computation time.

We used a generic species approach because the connectivity conservation mandate of the U.S. Forest Service is very broad and encompasses an enormous variety of species

and ecological elements. This species-agnostic approach overlooks the variability that exists among species with respect to relationships between landscape characteristics and movement behaviors. For instance, we assumed that roads were an impediment to animal movement, but some species have been shown to use roads as travel corridors (Forman et al., 2003). We assumed that developed areas were not suitable habitat, but some species are well adapted to living in and/or moving through urban settings (e.g., deer). We did not account for effects of topography on resistance to movement because these effects are highly variable among species, but topography may be an important determinant of resistance to movement for individual species (e.g., bighorn sheep [*Ovis canadensis*], which prefer to move through steep terrain to avoid predators; Geist, 1971). These assumptions may reduce the ability of our connectivity models to identify all of the important movement pathways for wildlife, but avoid challenges associated with single-species models and the selection of appropriate umbrella species (Meurant et al., 2018). Our approach improves upon coarse-filter habitat-based approaches by explicitly considering habitat requirements, sensitivity to human modification, and dispersal distance, thereby bridging the gap between coarse-filter approaches and data-intensive fine filter approaches. Indeed, our results agree with several species-specific analyses conducted in portions of the study area (e.g., Cushman, McKelvey, & Schwartz, 2009; Peck et al., 2017).

We were able to identify important locations for facilitating movements for a variety of different species across a large landscape containing multiple private, state, and federal jurisdictions. Similar to previous studies (e.g., Cushman & Landguth, 2012), however, our efforts to develop an integrated approach highlighting key areas for multiple species also illustrate the challenges associated with consolidating multiple aspects of species biology into a single map. For example, the NORMALIZED SUM approach is relatively straightforward to implement, but makes it difficult to distinguish between connectivity scenarios that result in similar values but have different management implications (e.g., high connectivity value according to model x and low value according to model y OR low value according to model x and high value according to model y OR moderate value according to both models). The TOP PERCENTILE approach identifies portions of the landscape with exceptionally high connectivity value for any one of the generic species, but it may overlook areas with moderate-to-high connectivity value for multiple generic species that could be useful management targets. The MODEL COUNT approach provides a nonbinary map of the degree of support across models for each pixel as having high connectivity value. However, this and other percentile-based approaches are

sensitive to the threshold value used to define high connectivity value and can result in discrete maps of important vs. not-important areas for connectivity that do not convey the spatial uncertainty associated with boundaries of key movement pathways.

Although this limits our ability to identify movement pathways across generic species groups, it is worth noting that generic species are, by definition, intended to represent the needs of multiple species that may share the same general habitat affinity and dispersal ability. In addition, our approach allowed explicit characterization of the degree to which connectivity conservation actions designed to benefit large specialist generic species might provide additional benefits for additional species (similar to an umbrella species, but based on multiple species' characteristics). Our results indicated that the majority of high-value connectivity areas for small species are largely contained within core areas identified for large species. Because most connectivity for small-bodied species occurs within these core areas due to their limited dispersal range, managing the landscape in a manner that protects connectivity for larger-bodied species should simultaneously protect many of the highest quality habitat patches (and connections within these patches) utilized by smaller-bodied species. Lastly, the results of our generalist models suggest that there are multiple large areas that provide connectivity for species with less restrictive habitat requirements, which represent the bulk of species on the CGNF. Although these results did not identify obvious "corridors" (because large portions of the landscape are generalist habitat), they did highlight optimal locations for crossing major linear barriers that affect all species in the region.

The 2012 Planning Rule emphasizes the importance of an "all lands" approach that reflects the fact that ecological processes are rarely circumscribed by jurisdictional boundaries. With respect to connectivity, our analyses highlight the importance of the CGNF within the context of conserving regional connectivity. They also highlight the critical role of focusing conservation efforts on private lands to maintain regional connectivity. The units administered by the CGNF are in some cases small and separated by large expanses of private or other state/federal lands. Managing (or modeling) connectivity only within the borders of the National Forest System (NFS) would lead to very different outcomes and conclusions. For example, if our nodes were only placed within CGNF units, we would potentially overlook important corridors linking non-NFS habitats. By predicating our analyses on generic species' requirements rather than jurisdictional boundaries, our analyses highlight the importance of collaborating with other entities for achieving regional connectivity objectives, especially for grassland and shrubland species.

The analyses described here were used in conjunction with structural connectivity assessments conducted by CGNF staff to help identify locations on the landscape where managing for connectivity is particularly important and may require trade-offs with other multiple use objectives (Custer Gallatin National Forest (CGNF), 2019). In doing so, our analyses facilitated the development of potential connectivity-related plan components and also provided CGNF staff with spatially explicit information on connectivity throughout the region that can be incorporated into the various effects analyses conducted to fulfill the United States' National Environmental Policy Act (NEPA; 42 U.S.C. § 4,321 et seq.) requirements for Forest Plan revision.

As importantly, developing a team comprised of university and NGO scientists along with CGNF resource specialists enabled us to ensure that our approach addressed agency mandates and a variety of stakeholder objectives (*sensu* Hallett et al., 2017). In addition, we were able to leverage resources from a variety of sources to reduce the impact of resource limitations. Finally, regular communication between the research team and CGNF decision makers helped ensure that the analyses were compatible with the time constraints imposed by the planning process. This ensured that the analyses presented here could be considered within the NEPA process and helped facilitate the identification of Key Linkage Areas, a potential new land use designation for the CGNF, within several alternatives contained in the recently issued Draft Environmental Impact Statement (CGNF, 2019). These alternatives also contain proposed plan components to guide forest management in these areas designed to reduce potential negative impact on connectivity. We suggest that our approach provides an efficient, biologically meaningful approach for incorporating connectivity into the Forest Plan revision process under the 2012 Planning Rule and could be readily exported to the over 78 million ha currently managed by the USFS. Moreover, our approach could be useful for any land management agency attempting to incorporate connectivity information into planning documents in situations where time, data, and monetary resources may be limited.

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CONFLICT OF INTEREST

The authors report no conflicts of interest in this research.

AUTHOR CONTRIBUTIONS

M.W., T.C., G.C., B.D., and V.K. conceived and designed the research. G.C., B.D., and V.K. collated information from Custer Gallatin National Forest staff. M.W. and T.C. conducted the analyses. M.W. and T.C. drafted the manuscript. M.W., T.C., G.C., and B.D. contributed revisions to the manuscript.

ETHICS STATEMENT

No formal university ethics approval was required for this research.

DATA AVAILABILITY STATEMENT

All underlying datasets for the analysis conducted here are freely available at the locations noted in their citations. Code for reproducing the analysis is available from the authors upon request. Please note that code was designed for HPC application and may require some modification to fit new users' specifications.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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