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RESEARCH ARTICLE

Focal species and landscape "naturalness" corridor models offer complementary approaches for connectivity conservation planning

Meade Krosby · Ian Breckheimer · D. John Pierce · Peter H. Singleton ·
Sonia A. Hall · Karl C. Halupka · William L. Gaines · Robert A. Long ·
Brad H. McRae · Brian L. Cosentino · Joanne P. Schuett-Hames

Abstract

Context The dual threats of habitat fragmentation and climate change have led to a proliferation of approaches for connectivity conservation planning. Corridor analyses have traditionally taken a focal species approach, but the landscape "naturalness" approach of modeling connectivity among areas of low human modification has gained popularity as a less analytically intensive alternative.

Objectives We compared focal species and naturalness-based corridor networks to ask whether they identify similar areas, whether a naturalness-based approach is in fact more analytically efficient, and whether agreement between the two approaches varies with focal species vagility.

Methods We compared focal-species and naturalness-based connectivity models at two nested spatial extents: greater Washington State, USA, and, within it, the Columbia Plateau ecoregion. We assessed complementarity between the two approaches by examining the spatial overlap of predicted corridors, and regressing organism traits against the amount of modeled corridor overlap.

Results A single naturalness-based corridor network represented connectivity for a large (>10) number of focal species as effectively as a group of between 3 and 4 randomly selected focal species. The naturalness-based approach showed only moderate spatial agreement with composite corridor networks for large numbers of focal species, and better agreed with corridor networks of large-bodied, far-dispersing species in the larger scale analysis.

Conclusions Naturalness-based corridor models may offer an efficient proxy for focal species models,

M. Krosby (✉)
Climate Impacts Group, College of the Environment,
University of Washington, Box 355674, Seattle,
WA 98195, USA
e-mail: mkrosby@uw.edu

I. Breckheimer
Department of Biology, University of Washington,
Box 351800, Seattle, WA 98195-1800, USA

D. John Pierce · B. L. Cosentino · J. P. Schuett-Hames
Washington Department of Fish and Wildlife, 600 Capitol
Way N, Olympia, WA 98516, USA

Present Address:
J. P. Schuett-Hames
5146 Blue Heron Ln NW, Olympia, WA 98502, USA

P. H. Singleton
USDA Forest Service, Pacific Northwest Research
Station, 1133 N. Western Ave., Wenatchee, WA 98801,
USA

S. A. Hall
SAH Ecologia LLC, 669 Crawford Ave, Wenatchee,
WA 98801, USA

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but a multi-focal species approach may better represent the movement needs of diverse taxa. Consideration of trade-offs between the two approaches may enhance the effectiveness of their application to connectivity conservation planning.

Introduction

Maintaining and restoring landscape connectivity has become a central priority for wildlife conservation (Soulé and Orians 2001; Hilty et al. 2006), and is the most frequently proposed climate change adaptation strategy for biodiversity preservation (Heller and Zavaleta 2009; Lawler 2009). Efforts to maintain and restore connected networks of habitat have consequently multiplied in recent years, including numerous large-scale initiatives (e.g., the Yellowstone to Yukon Conservation Initiative). The significant financial investment and technical challenge associated with planning for connectivity at large scales have stimulated debate around the relative utility of fine-filter (e.g., focal species) and coarse-filter (e.g., "naturalness" or "ecological integrity") approaches to modeling connectivity networks (Theobald et al. 2012).

Connectivity-planning efforts have traditionally employed a focal-species approach. This method relies on choosing a limited number of species to serve as surrogates for a larger suite of species (Lambeck 1997), and modeling connectivity networks for these focal species. Expert opinion is often used to guide model parameterization (e.g., assigning values

K. C. Halupka
U.S. Fish and Wildlife Service, Central Washington Field Office, 215 Melody Lane, Suite 103, Wenatchee, WA 98801-8122, USA

W. L. Gaines
Washington Conservation Science Institute, 12725 Wilson St, Leavenworth, WA 98826, USA

R. A. Long
Woodland Park Zoo, 5500 Phinney Ave. N, Seattle, WA 98103, USA

B. H. McRae
The Nature Conservancy, 117 E Mountain Ave, Suite 201, Fort Collins, CO 80524, USA

to the resistance of certain landscape elements, such as roads, to species movement). Focal species methods have been used for decades, and empirical studies suggest that, at least in some cases, they have been successful (Epps et al. 2011). However, focal species connectivity modeling becomes difficult to implement at large scales; the process for conducting a full focal species connectivity analysis can typically require months or years and a large financial investment (Beier et al. 2011), and large-scale analyses may require large numbers of focal species to represent diverse habitat types.

In response to these limitations, there has been growing interest in the application of coarse-filter approaches to large-scale connectivity planning efforts, particularly those that model connectivity based on the degree of landscape "naturalness" or "ecological integrity" (Spencer et al. 2010; Theobald et al. 2012). The benefits of such an approach are that it requires relatively easily-obtained data regarding human land use (e.g., roads, agriculture, dwelling density); parameterization is relatively straight forward (though also expert-based), with resistance directly related to the degree of human modification (Theobald et al. 2012); and it typically yields a single connectivity network, which may avoid uncertainty arising from the interpretation of numerous focal species connectivity networks. However, it also may be difficult to interpret resulting connectivity networks (e.g., understanding which species are best represented), and implementation may be hindered by the species-based mandates of most wildlife management agencies and organizations (Lacher and Wilkerson 2014).

Despite growing interest in using naturalness-based approaches as relatively fast and less expensive alternatives to focal species approaches to large-scale connectivity planning, no attempt has yet been made to compare the spatial outputs of the two approaches within the same landscape. Yet such comparison is critical for determining whether naturalness-based approaches provide an effective proxy for a focal species-based analysis. We addressed this need by comparing two distinct models of ecological connectivity networks spanning Washington State, USA, and neighboring areas of Idaho, Oregon, and British Columbia, Canada (WHCWG 2010; 2012). One network was based on the habitat requirements and dispersal characteristics of a suite of focal species,

whereas the other was based solely on human land use intensity. Comparing the two networks allowed us to address several important questions regarding the use of naturalness-based and focal species-based approaches to connectivity conservation planning. First, do naturalness-based and species-based connectivity models identify similar areas? Second, are naturalness-based models in fact more analytically efficient than focal species models (i.e., can a single naturalness model represent areas identified by multiple focal species models)? Finally, are areas identified by naturalness-based models biased toward focal species with particular movement traits? In answering these questions, we help clarify the similarities and differences between these alternative approaches to connectivity conservation planning, to better inform their interpretation and implementation.

Methods

Connectivity models

We compared focal-species and naturalness-based corridor networks created by the Washington Wildlife Habitat Connectivity Working Group (WHCWG), a collaborative effort to identify opportunities and priorities for maintaining and restoring wildlife habitat connectivity in Washington State, USA (http://www. waconnected.org). Detailed methods describing the WHCWG's development of the corridor networks are described elsewhere (WHCWG 2010; 2012) and are summarized here. We compared focal-species and naturalness-based (specifically, and henceforth, "landscape integrity") corridor networks modeled by the WHCWG at two nested spatial scales. The first is a 447,000 km^2 rectangular area (henceforth "Statewide," Fig. 1a) spanning Washington State and neighboring areas of Idaho, Oregon, and British Columbia, Canada (WHCWG 2010). The second is the 84,000 km^2 Columbia Plateau ecoregion (henceforth "Columbia Plateau," Fig. 1b, WHCWG 2012).

The WHCWG modeled corridor networks for 22 terrestrial vertebrate species in the study region (Table 1) using a least-cost corridor approach (Singleton et al. 2002; Adriaensen et al. 2003). Species were selected to be geographically representative of major habitat types, vulnerable to the isolating effects

of habitat fragmentation, and analytically tractable (i.e., to have adequate data for modeling). Wildlife biologists with expertise on focal species led the development of habitat and resistance models using expert opinion, literature review, and/or empirical data (when available), to identify suitable conditions for habitat and dispersal. Expert opinion was solicited via workshops and conference calls. GIS data on land cover, roads, and other features were used to map habitat and resistance to movement at a raster resolution of 100 m for the Statewide analysis, and 90 m for the Columbia Plateau. For each focal species, large areas of suitable habitat, referred to as habitat concentration areas (HCAs), were mapped using a variety of methods, including delineation of polygons based on survey data, use of legally-defined recovery areas, and habitat suitability modeling followed by aggregation of high-quality habitat pixels into discrete polygons. For the latter, the HCA Toolkit was used (Shirk 2011). Grid cells outside of HCAs were given species-specific resistance values based on expert opinion, literature review, and/or empirical data, when available. The Linkage Mapper toolbox for ArcGIS (McRae and Kavanagh 2011) was used to map least-cost corridors between HCAs, and to identify networks of core areas and key dispersal corridors between them.

The WHCWG constructed naturalness-based corridor models using the same spatial data and methods as the focal species models, but with resistance values based on the degree of human landscape modification or "landscape integrity." These models were parameterized according to similar efforts (Comer and Hak 2009; 2012; Sanderson et al. 2002; Leu et al. 2008; Theobald 2010), and assigned relatively high resistance values to roads, agricultural, and urban areas. Contiguous areas of low resistance that spanned at least 4047 hectares were delineated as HCAs using the HCA toolkit. To represent landscape linkages for organisms with different sensitivities to human influence, four different resistance models were developed which assigned heavily human-modified lands different resistance values relative to lightly-modified lands. The Linkage Mapper toolbox for ArcGIS (McRae and Kavanagh 2011) was used to map least-cost corridors between HCAs, and to identify networks of core areas and corridors between them.

Habitat and resistance values were mapped at 100 and 30 m resolutions for the Statewide and Columbia
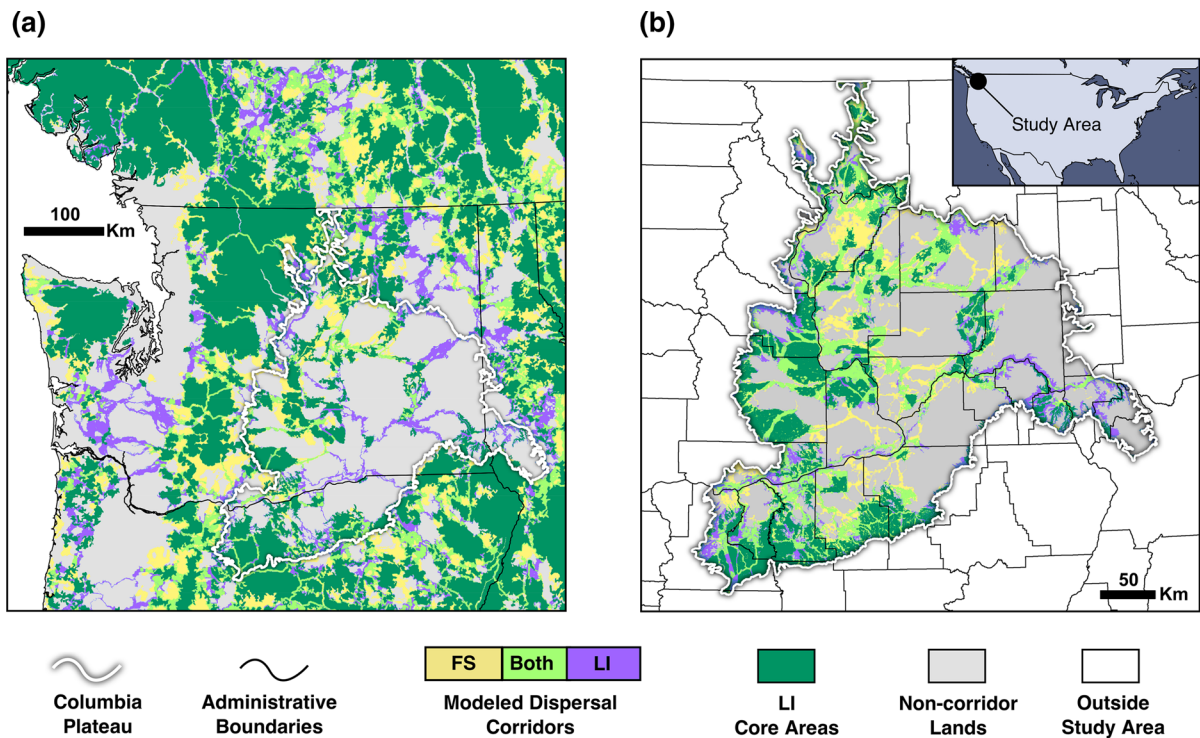
(a)

(b)

Study Area

~~	~~~	FS	Both	LI
Columbia Plateau	**Administrative Boundaries**		**Modeled Dispersal Corridors**	

▉	▉	▉
LI Core Areas	**Non-corridor Lands**	**Outside Study Area**

Fig. 1 Statewide (**a**) and Columbia Plateau (**b**) corridor networks, identified using the landscape integrity (LI) approach (*purple*), and the focal species (FS) approach (*yellow*), and both

approaches (*light green*). Corridor networks represent the highest-value 30 % of the land area outside of the landscape integrity core areas (*dark green*)

Plateau analyses, respectively. For the Columbia Plateau analysis, these values were re-sampled to 90 m prior to HCA and corridor modeling to reduce effects of single-pixel errors in base data derived from satellite image classification (WHCWG 2012). Resistance values for landscape classes and criteria used to delineate HCAs for both focal-species and landscape integrity models are detailed in WHCWG (2010), and WHCWG (2012).

Comparing areas identified as dispersal corridors using each approach

To directly compare focal-species and landscape integrity corridor networks, we standardized and created composites of individual focal-species and landscape integrity models to produce maps representing overall corridor networks for each of the two modeling approaches. Specifically, we linearly rescaled relative cost-distance values for all corridors to vary from 0 to 1, and combined these areas with HCAs to create corridor network maps for individual

focal species (Fig. S1 and S2). In the resulting maps, the HCAs and the least-cost paths between them had a value of 1, with values decreasing to 0 in inverse proportion to their cost distance relative to the least-cost path. We summed individual focal species and landscape integrity sensitivity models to create composite maps representing overall corridor networks for each approach (Fig. S3). Creating these maps by summing reflects the assumption that areas included in a large number of focal species (or landscape integrity sensitivity models) are the most important overall landscape linkages.

To focus the analysis on lands important for connectivity, as opposed to primary habitat, we compared corridor networks in areas that fall outside of the landscape integrity core areas: human-modified lands for which anthropogenic habitat fragmentation is a more pressing concern (Theobald et al. 2012). We measured the spatial overlap of composited focal-species and landscape integrity corridor maps by computing the rank-correlation between the standard scores of the two maps, as well as calculating the

Table 1 Focal species included in the analysis

Code	Common name	Scientific name	Analysis Window	Adult Mass (g)	Max. Natal Dispersal (km)	Max. home range (km^2)	References
ANBO	Western Toad	Anaxyrus boreas	S	35	4	0.17	Rogers (2009); AmphibiaWeb; Jones and Raphael (2000)
CEEL	Elk	Cervus elaphus	S	240,867	100	58.42	Jones et al. (2009); Yott et al. (2011)
CEUR	Greater Sage-Grouse	Centrocercus urophasianus	S, CP	1921	85	3.48	Hupp and Braun (1991); Bradbury et al. (1989)
GLSA	Northern Flying Squirrel	Glaucomys sabrinus	S	138	7	0.11	Jones et al. (2009); Smith et al. (2011)
GUGU	Wolverine	Gulo gulo	S	12,792	82	296	Jones et al. (2009); Vangen et al. (2001)
LECA	Black-tailed Jackrabbit	Lepus californicus	S, CP	2422	57	3	Jones et al. (2009); Grant (1987)
LETO[a]	White-tailed Jackrabbit	Lepus townsendii	S, CP	3372	57	2	Jones et al. (2009)
LYCA	Canada Lynx	Lynx canadensis	S	9683	40	60.4	Jones et al. (2009); Squires and Laurion (2000)
MAAM	American Marten	Martes americana	S	874	61	27.2	Jones et al. (2009); Lofroth (1993)
ODHE	Mule Deer	Odocoileus hemionus	S, CP	84,561	217	34	Jones et al. (2009); Robinette (1966)
ORAM	Mountain Goat	Oreamnos americanus	S	72,105	60	18.17	Jones et al. (2009); Fielde and Keesee (1988)
OVCA	Bighorn Sheep	Ovis canadensis	S	74,645	40	18.94	Jones et al. (2009); Epps et al. (2005)
SCGR	Western Gray Squirrel	Sciurus griseus	S	704	19.2	0.008	Jones et al. 2009; M. Vander Haegen, personal communication in WCWG (2010)
TATA	American Badger	Taxidea taxus	S	7842	110	9	Jones et al. (2009); Messick and Hornocker (1981)
TYPH	Sharp-tailed Grouse	Tympanuchus phasianellus	S, CP	868	21.5	6.41	Boisvert et al. (2005)
URAM	American Black Bear	Ursus americanus	S	110,500	219	21	Jones et al. (2009); Rogers (1987)
AMTI	Tiger Salamander	Ambystoma tigrinum	CP	30	9	0.078	Madison and Farrand (1998); Trenham (2001)
CACA	Beaver	Castor canadensis	CP	18,124	49.6	50.26	Jones et al. (2009); Sun et al. (2000)
CROR	Western Rattlesnake	Crotalus oreganus	CP	380	4	3.01	Macartney et al. (1990); Gomez (2007)
NEMI	Least Chipmunk	Neotamias minimus	CP	43	0.335	0.055	Jones et al. (2009); Martinsen (1968)
URTO[b]	Townsend's Ground Squirrel	Urocitellus townsendii	CP	207	3.52	0.024	Jones et al. (2009); Klein (2005)
URWA	Washington Ground Squirrel	Urocitellus washingtoni	CP	215	3.52	0.077	Jones et al. (2009); Klein (2005)

S Statewide, *CP* Columbia Plateau

[a] Dispersal value taken from mean of congener

[b] All values taken from mean of congeners

amount of spatially coincident corridor area at various equal-area thresholds (e.g. the highest-value 30 % of the landscape identified using each approach). We compared these values to null criteria that estimate the proportion of cells that would be jointly selected if the two networks were independent of each other at that percentile. For a given proportion of the landscape, p, the null criterion for two overlapping maps is simply p^2.

Comparing the analytical efficiency of each approach

To test the hypothesis that naturalness-based models are more analytically efficient than focal species models, we compared the correlation of random subsets of focal-species composites to the full 16- or 11-species composite at each spatial scale (Statewide or Columbia Plateau, respectively) and compared these values to the correlation between the landscape integrity composite and the full focal species composite. We sampled between 1 and 15 species (Statewide) or 1 and 10 species (Columbia Plateau) without replacement and combined these networks using the procedure described above. We then computed the Spearman rank correlation coefficient between the randomly sampled composite and the composite representing the full suite of focal species at each scale. To reduce the computational demands of this analysis, we resampled the composites to a 1 km (Statewide) and 900 m (Columbia Plateau) grid size and computed correlations based on a random sample of 10,000 raster cells for each comparison. To test the sensitivity of our results to resampling resolution, we repeated the Columbia Plateau analysis at 450 and 1800 m resolutions (higher resolution analysis of Statewide composites was computationally prohibitive).

Testing whether landscape integrity networks better represent certain types of focal species

To test whether landscape-integrity networks better agree with the networks of certain types of focal species, particularly in regards to traits relevant to sensitivity to habitat fragmentation, we assembled life-history and dispersal data from the PanTHERIA database (mammals; Jones et al. 2009) and primary literature (non-mammals), including adult body mass,

home range size, and maximum natal dispersal distance (Table 1). If reported values varied between sexes, we averaged the two values for each species. Natal dispersal distances for the white-tailed jackrabbit, Townsend's ground squirrel, and sharp-tailed grouse were not available, and were estimated as the average dispersal distance of congeneric species for which estimates were available.

Because these traits strongly co-vary (Pearson correlation coefficients between log-transformed traits were 0.50–0.83) and our sample size was small, we performed a principal components analysis to arrange species on a single axis (PC1) representing a continuum from small-bodied, short-dispersing species with small home ranges to large-bodied far-dispersing species with large home ranges, which we refer to as a "vagility index" (Fig. S4). The vagility index represented 85.8 % of the variation in log-transformed adult mass, maximum natal dispersal distance, and home range size with loadings of 0.59, 0.58, and 0.57, respectively. We then regressed this vagility index against the rank correlation between each focal species and the landscape integrity composite. Because focal species geographic ranges differ, we measured correlation only within the minimum convex hull enclosing each focal-species' geographic range. All geographical and statistical analyses were performed in R 3.0.2 (R Core Team 2013).

Results

Comparing habitat concentration areas identified using each approach

Habitat concentration areas defined in the landscape integrity and focal species analyses were largely congruent (Fig. S5); at the statewide scale, 95 % of the area in landscape integrity HCAs contained blocks of primary habitat for at least one focal species, and in the Columbia Plateau, this proportion was 99 %. Fifty-three percent of the area in focal species HCAs fell within landscape integrity HCAs in the statewide analysis, including 73 % of the area in HCAs for more than one focal species. This supported the decision to use landscape integrity HCAs as a proxy for focal species HCAs, and to focus the analysis on intervening lands.

Comparing dispersal corridors identified using each approach

Overall, we found moderately strong correlations between focal-species and landscape integrity composite standard scores (rank correlation 0.62 for the Statewide analysis, and 0.65 for the Columbia Plateau). We also found that high-value corridor networks identified using each approach (Fig. 1) are more congruent than would be expected by chance alone at both spatial scales, independent of which threshold was considered. For example, if we examine the 30 % of the landscape with the highest corridor standard score using the landscape integrity approach, we find that it overlaps with 53 % of the Statewide composite focal species network, and 66 % of the Columbia Plateau composite network using the same threshold (Fig. S6).

Comparing the analytical efficiency of each approach

The landscape integrity networks represent connectivity for the full suite of focal species as effectively as a median of between 3 and 4 species selected at random from the species included in both the Statewide and Columbia Plateau analyses. All focal species combinations that include more than 9 species (Statewide) or 6 species (Columbia Plateau) outperform the landscape integrity networks at representing the full composite of focal species. At each spatial scale, composites based on half of the focal species (8 for the Statewide, and 5 for the Columbia Plateau) have rank correlations of greater than 0.8 with the composite corridor network that includes the full suite of focal species. In addition, at the Statewide scale, corridor networks for mule deer, elk, and American black bear, alone, have approximately the same rank correlation with the full focal-species network as the composite landscape integrity corridor network. For the Columbia Plateau, only mule deer matches the performance of the landscape integrity network at representing corridors for the full suite of focal species (Fig. 2).

The similarity of results across the three resampling resolutions used for the Columbia Plateau (450, 900, and 1800 m) indicates that analysis results are relatively insensitive to resampling resolution (Fig. 2 and Fig. S7).

Testing whether landscape integrity networks better represent certain types of focal species

Accounting for differences in geographic range size between focal species (see methods), we found a significant positive relationship between a focal species' vagility index and the correspondence of its Statewide corridor network with the Statewide landscape integrity network (n = 16, $r^2 = 0.31$, F = 10.60, p = 0.024). This indicates that, all things being equal, corridor networks for large-bodied, far-dispersing focal species were more congruent with the landscape integrity corridor network than small-bodied species with short dispersal distances. This relationship was not significant for the Columbia Plateau (n = 12, $r^2 = 0.026$, F = 0.49, p = 0.631).

Discussion

We compared focal species and landscape integrity analyses in part to evaluate the latter's ability to identify connectivity areas that would also be identified by a comprehensive focal species approach, while investing fewer resources. The substantial spatial overlap exhibited between landscape integrity networks and the focal species composite networks (Fig. 1) suggests that naturalness-based models may indeed offer at least a partial proxy for a focal species-based approach. The naturalness-based approach was also more analytically efficient, as the single landscape integrity model represented connectivity networks for a large (>10) number of focal species as effectively as a group of between 3 and 4 randomly selected focal species. The landscape integrity model is more efficient despite the fact that it is a composite of 4 underlying models; these models differed only in the amount of resistance applied to landscape features (to account for a range of potential movement sensitivities to human land use), and thus the total analytical investment for the landscape integrity model was similar to that of a single focal species model. The efficiency advantage of the landscape integrity model was consistent across the two spatial scales in our study (Fig. 2).

However, our results also suggest that naturalness-based models better represent the movement needs of larger, more vagile species than those of smaller, more locally-dispersing species, at least at larger scales

Fig. 2 Performance of the landscape integrity approach at representing the full focal-species composite corridor network (*dotted horizontal line*) compared to increasing numbers of randomly selected focal species in the Statewide analysis (**a**) and Columbia Plateau ecoregion (**b**)
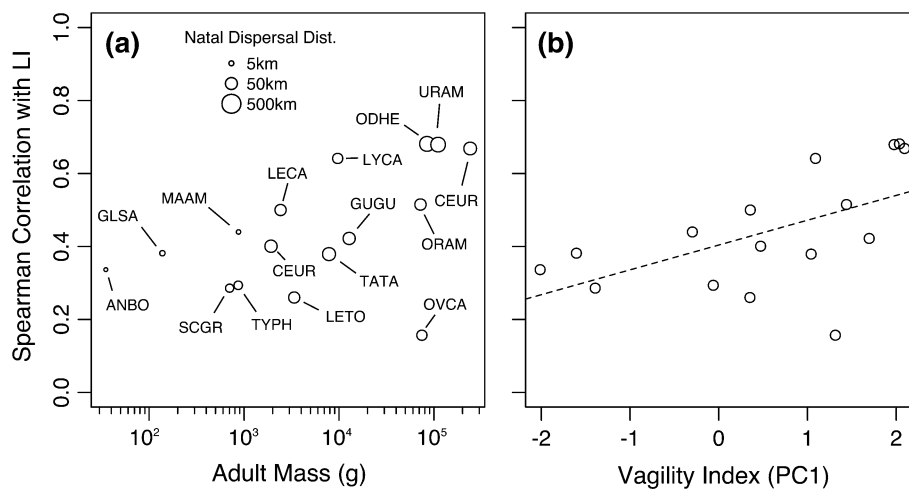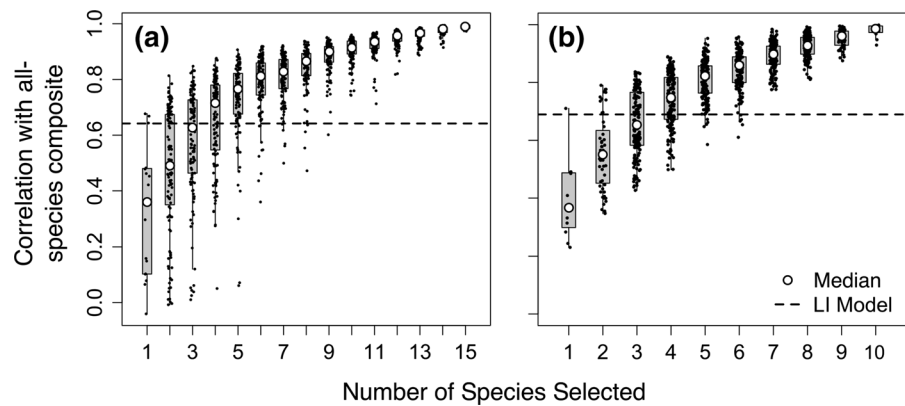

Fig. 3 Correlation between organism traits and the performance of the landscape integrity approach at representing dispersal corridors for that species in the Statewide analysis. Relationships in the raw data are shown in (**a**) with labels corresponding to species codes in Table 1. Because organism traits are correlated and our sample size is small, we used PCA to reduce these traits to a single axis, the vagility index (*see text*). The relationship between landscape integrity performance and the vagility index is shown in (**b**). The *dotted best-fit line* in (**b**) is statistically significant (n = 16, r^2 = 0.32, F = 10.6, p = 0.024)

(Fig. 3). This is not surprising, as the landscape integrity model is similar to that of a habitat generalist whose movements are sensitive to human-modification of the landscape. In addition, the use of a relatively large moving window to identify large blocks of natural lands to act as core areas for landscape integrity linkage modeling (WHCWG 2010; 2012) would tend to exclude small, patchily distributed lands in natural condition that could support smaller bodied, smaller ranging species. Our analysis suggests that patch size (Galpern et al. 2011) can have a particularly strong influence on how well naturalness-based connectivity analyses represent diverse focal species. For example, naturalness-based

models may do a better job of capturing connectivity networks of smaller-bodied species if they incorporate a range of minimum-patch sizes.

Our results also offer insight into the efficiency of focal species-based approaches. A relatively modest number of focal species captured a relatively large percentage of the variation in the total focal species composite (Fig. 2), suggesting broad spatial overlap of movement corridors for diverse taxa (Breckheimer et al. 2014). Yet, our results indicate that there are decreasing returns to the new information provided by increasing numbers of focal species; for example, just half of the focal species modeled had a correlation of greater than 0.8 with the full composite network at

Fig. 4 Decision-tree for using focal species and landscape "naturalness" connectivity models in conservation planning. While this tree reflects the technical and financial considerations involved in model selection, the appropriate model will also depend on the conservation goals and mandates of individual planning entities
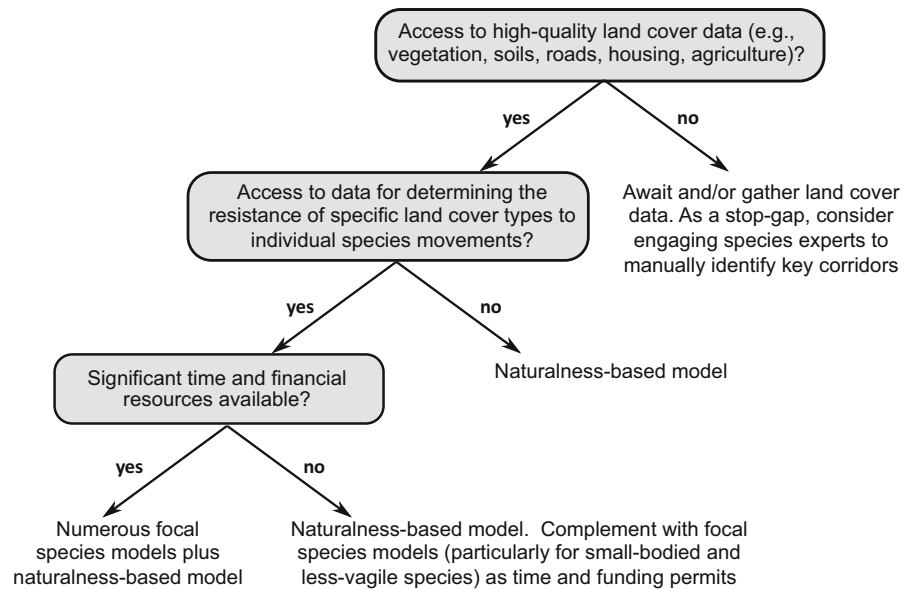
each scale of analysis. Furthermore, at both scales, there were individual focal species networks (e.g., mule deer) that captured a large proportion of the total focal species composite, approximately the same proportion as the landscape integrity model. This suggests that a single focal species model could provide as good a proxy for a larger suite of focal species as a naturalness-based model; in our analysis, such species were large-bodied and highly vagile (Fig. 3). However, not all large-bodied, highly vagile species were good surrogates (e.g., bighorn sheep). Thus, using such characteristics to guide a priori selection of a single focal species would not appear to offer as robust an approach as using a naturalness-based model alone.

Much remains to be done to improve the evidence base for connectivity conservation decision-making. Our analysis compares the outputs of two widely-used connectivity modeling approaches, but does not evaluate either approach's ability to represent functional connectivity (Tischendorf and Fahrig 2000); extensive empirical analysis will be required to determine the relative performance of these two proxies for meeting connectivity conservation targets. Both approaches used here are also patch-based (i.e., feature core areas connected by corridors) and an increasingly important question in connectivity planning is how the results of such models compare to more recent approaches that do not distinguish between core areas and corridors

(Carroll et al. 2012; Theobald et al. 2012). Additionally, both approaches employed least-cost corridor modeling, and it will be important to see whether similar results are found when other modeling methods are used (e.g., circuit theory; McRae et al. 2008). The underlying corridor models used in our analysis are also relatively coarse grained (100 m for Statewide and 90 m for Columbia Plateau); this is consistent with resolutions typically employed in connectivity modeling and planning across large landscapes, and reflects the computational demands associated with processing raster datasets over large geographic extents. However, increased access to high performance and throughput computing facilities may soon make finer grain analysis feasible for most users (Leonard et al. 2014), allowing higher resolution corridor modeling and facilitating rapid sensitivity-testing of analysis resolution. Higher resolution modeling may also improve corridor results for smaller-bodied, patchily distributed species. Finally, it remains an important task to integrate connectivity analyses into more general conservation planning processes, which typically balance connectivity with a broader suite of management objectives (Kukkala and Moilanen 2013; Pouzols and Moilanen 2014).

Together, our results suggest several recommendations regarding the use of naturalness- and focal species-based approaches in connectivity planning (Fig. 4). First, if working with limited analytical

capacity or information regarding the movement biology of local taxa, or if desiring only an initial indication of landscape connectivity patterns in an area, a naturalness-based model may offer a relatively efficient means of identifying many of the movement corridors that would also be identified by a comprehensive focal species-based approach. Second, a multi-focal species approach may ultimately be the more robust strategy for representing the movement needs of a region's broader biota, as naturalness-based approaches can be biased toward the movement needs of relatively large-bodied, highly vagile species. Finally, there may be decreasing returns to the new information provided by increasing numbers of focal species. Thus, determining the ideal number of focal species will depend on trade-offs between information needs and analytical investments (Grantham et al. 2009). Ultimately, additional research comparing the two approaches across diverse geographies will be needed to generate more general and robust recommendations. Including both naturalness and focal species models in regional connectivity modeling efforts, when possible, would allow us to better understand whether and how agreement between the two approaches varies with regional differences in features such as species diversity, land use, and topography. Formal optimization modeling comparing trade-offs between the two approaches may further improve recommendations regarding their application. With rates of habitat fragmentation and climate change rapidly increasing, choosing our methods wisely will be critical for guiding effective biodiversity conservation.

References

Adriaensen F, Chardon JP, De Blust G, Swinnen E, Villalba S, Gulinck H, Matthysen E (2003) The application of 'least-cost' modeling as a functional landscape model. Landsc Urban Plan 64:233

AmphibiaWeb: Information on amphibian biology and conservation (2015) Berkeley, California: AmphibiaWeb. Available:http://amphibiaweb.org/

Beier P, Spencer WD, Baldwin RF, McRae BH (2011) Toward best practices for developing regional connectivity maps. Conserv Biol 25:879–892

Boisvert JH, Hoffman RW, Reese KP (2005) Home range and seasonal movements of Columbian sharp-tailed grouse associated with conservation reserve program and mine reclamation. West N Am Nat 65:36–44

Bradbury JW, Gibson RM, McCarthy CE, Vehrencamp SL (1989) Dispersion of displaying male sage grouse. II. The role of female dispersion. Behav Ecol Sociobiol 24:15–24

Breckheimer I, Haddad N, Morris W, Trainor A, Fields W, Jobe RT, Hudgens B, Moody A, Walters J (2014) Defining and evaluating the umbrella species concept for conserving and restoring landscape connectivity. Conserv Biol 28:1584–1593

Carroll C, McRae B, Brookes A (2012) Use of linkage mapping and centrality analysis across habitat gradients to conserve connectivity of gray wolf populations in western North America. Conserv Biol 26:78–87

Comer PJ, Hak J (2009) NatureServe Landscape Condition Model. Internal documentation for NatureServe Vista decision support software engineering, prepared by NatureServe, Boulder CO

Comer PJ, Hak J (2012) Landscape condition in the conterminous United States. Spatial Model Summary. NatureServe, BoulderCO

Epps CW, Palsboll PJ, Wehausen JD, Roderick GK, Ramey RR, McCullough DR (2005) Highways block gene flow and cause a rapid decline in genetic diversity of desert bighorn sheep. Ecol Lett 8:1029–1038

Epps CW, Mutayoba BM, Gwin LE, Brashares JS (2011) An empirical evaluation of the African elephant as a focal species for connectivity planning East Africa. Divers Distrib 17:603–612

Fielder PC, Keesee BG (1988) Results of a mountain goat transplant along Lake Chelan, Washington. Northw Sci 62:218–222

Galpern P, Manseau M, Fall A (2011) Patch-based graphs of landscape connectivity: a guide to construction, analysis and application for conservation. Biol Conserv 144:44–55

Gomez LM (2007) Habitat use and movement patterns of the Northern Pacific Rattlesnake (*Crotalus o. oreganus*) in British Columbia. Master's thesis. University of Victoria, Victoria, British Columbia

Grant JC (1987) Ecology of the black-tailed jackrabbit near a solid radioactive waste disposal site in southeastern Idaho. Master's thesis. University of Montana, Missoula, Montana

Grantham HS, Wilson KA, Moilanen A, Rebelo T, Possingham HP (2009) Delaying conservation actions for improved knowledge: how long should we wait? Ecol Lett 12:293–301

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

Hilty JA, Lidicker WZ, Merenlender AM (2006) Corridor ecology: The science and practice of linking landscapes for biodiversity conservation. Island Press, Washington, DC

Hupp JW, Braun CE (1991) Geographic variation among sage grouse in Colorado. Wilson Bull 103:255–261

Jones LLC, Raphael MG (2000) Diel patterns of surface activity and microhabitat use by stream-dwelling amphibians in the Olympic Peninsula. Northwest Nat 81:78

Jones KE, Bielby J, Cardillo M, Fritz SA, O'Dell J, Orme CDL, Safi K (2009) PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. Ecology 90:2648

Klein KJ (2005) Dispersal patterns of Washington ground squirrels in Oregon. M.S. thesis, Oregon State University, Corvallis, Oregon

Kukkala AS, Moilanen A (2013) Core concepts of spatial prioritisation in systematic conservation planning. Biol Rev 88(2):443–464

Lacher L, Wilkerson ML (2014) Wildlife connectivity approaches and best practices in U.S. state wildlife action plans. Conserv Biol 28:13–21

Lambeck RJ (1997) Focal species: a multi-species umbrella for nature conservation. Conserv Biol 11:849–856

Lawler JJ (2009) Climate change adaptation strategies for resource management and conservation planning. Ann NY Acad Sci 1162:79–98

Leonard PB, Baldwin RF, Duffy EB, Lipscomb DJ, Rose AM (2014) High-throughput computing provides substantial time savings for landscape and conservation planning. Landscape Urban Plan 125:156–165

Leu M, Hanser SE, Knick ST (2008) The human footprint in the West: a large-scale analysis of anthropogenic impacts. Ecol Appl 18:1119–1139

Lofroth EC (1993) Scale dependent analyses of habitat selection by marten in the sub-boreal spruce biogeoclimatic zone, British Columbia. Thesis. Simon Fraser University, Burnaby, British Columbia

Macartney JM, Gregory PT, Charland MB (1990) Growth and sexual maturity of the western rattlesnake, Crotalus viridis, in British Columbia. Copeia 1990:528–542

Madison DM, Farrand L III (1998) Habitat use during breeding and emigration in radio-implanted tiger salamanders. Ambystoma tigrinum. Copeia 2:402–410

Martinsen DL (1968) Temporal patterns in the home ranges of chipmunks (Eutamias). Journ Mamm 49:83–91

McRae BH, Kavanagh DM (2011) Linkage mapper connectivity analysis software. The Nature Conservancy, Seattle WA. Available at: https://code.google.com/p/linkage-mapper/

McRae BH, Dickson BG, Keitt TH, Shah VB (2008) Using circuit theory to model connectivity in ecology and conservation. Ecology 10:2712–2724

Messick JP, Hornocker MG (1981) Ecology of the badger in southwestern Idaho. Wildl Mono N-76

Pouzols FM, Moilanen A (2014) A method for building corridors in spatial conservation prioritization. Landsc Ecol 29:789–801

R Development Core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from http://www.R-project.org

Robinette WL (1966) Mule deer home range and dispersal in Utah. J Wildlife Manag 30:335–349

Rogers LL (1987) Factors influencing dispersal in the black bear. Mammalian dispersal patterns: the effects of social structure on population genetics. University of Chicago Press, Chicago, pp 75–84

Rogers KB (2009) Gape Width: an alternative to snout-vent length for characterizing anuran size. Herpetol Rev 40:416–418

Sanderson EW, Jaiteh M, Levy MA, Redford KH, Wannebo AV, Woolmer G (2002) The human footprint and the last of the wild. Bioscience 52:891–904

Shirk A (2011) HCA toolkit user guide. Available from http://waconnected.org/habitat-connectivity-mapping-tools/

Singleton PH, Gaines WL, Lehmkuhl JF (2002) Landscape permeability for large carnivores in Washington: a geographic information system weighted-distance and least-cost corridor assessment. Research Paper N-549. U. S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland

Smith WP, Person DK, Pyare S, Liu J, Hill V, Morzillo AT, Wiens, JA (2011) Source-sinks, metapopulations, and forest reserves: conserving northern flying squirrels in the temperate rainforests of Southeast Alaska. Sources, sinks and sustainability. Cambridge University Press, Cambridge, pp 399–422

Soulé ME, Orians GE (2001) Conservation biology: research priorities for the next decade. Island Press, Washington, D.C.

Spencer WD, Beier P, Penrod K, Winters K, Paulman C, Rustigian-Romsos H, Strittholt J, Parisi M, Pettler A (2010) California essential habitat connectivity project: a strategy for conserving a connected California. Prepared for California Department of Transportation, California Department of Fish and Game, and Federal Highways Administration. Statewide Analysis. Washington Departments of Fish and Wildlife, and Transportation, Olympia

Squires JR, Laurion T. (2000) Lynx home range and movements in Montana and Wyoming: preliminary results. Pages 337–349 in Ecology and Conservation of Lynx in the United States. General Technical Report N-30WWW. USDA Forest Service, Rocky Mountain Research Station, Fort Collins

Sun L, Müller-Schwarze D, Schulte BA (2000) Dispersal pattern and effective population size of the beaver. Can Journ Zoo 78:393–398

Theobald DM (2010) Estimating natural landscape changes from 1992 to 2030 in the conterminous US. Landsc Ecol 25:999–1011

Theobald DM, Reed SE, Fields K, Soulé M (2012) Connecting natural landscapes using a landscape permeability model to prioritize conservation activities in the United States. Conserv Lett 5:123–133

Tischendorf L, Fahrig L (2000) On the usage and measurement of landscape connectivity. Oikos 90:7–19

Trenham PC (2001) Terrestrial habitat use by adult Ambystoma californiense. J Herpetol 35:343–346

Vangen KM, Persson J, Landa A, Andersen R, Segerström P (2001) Characteristics of dispersal in wolverines. Can Journ Zoo 79:1641–1649

WHCWG (Washington Wildlife Habitat Connectivity Working Group) (2010) Washington Connected Landscapes Project: statewide Analysis. Washington Departments of Fish and Wildlife, and Transportation, Olympia, Washington. Available at http://waconnected.org/statewide-analysis/

WHCWG (Washington Wildlife Habitat Connectivity Working Group) (2012) Washington Connected Landscapes Project: analysis of the Columbia Plateau Ecoregion. Washington Departments of Fish and Wildlife, and Transportation. Olympia. Available at http://waconnected.org/columbia-plateau-ecoregion/

Yott A, Rosatte R, Schaefer JA, Hamr J, Fryxell J (2011) Movement and spread of a founding population of reintroduced elk (Cervus elaphus) in Ontario, Canada. Restoration Ecology 19(101):70–77