

Landscape connectivity and conservation prioritization for an old forest species with limited vagility

M. A. Linnell  & D. B. Lesmeister

USDA Forest Service, Pacific Northwest Research Station, Corvallis, OR, USA

Keywords

arboreal rodent; *Arborimus longicaudus*; endangered species; forest patch mosaic; habitat network; red tree vole; multi-generation connectivity; landscape connectivity.

Correspondence

Mark A. Linnell, USDA Forest Service, Pacific Northwest Research Station, 3200 SW Jefferson Way, Corvallis, OR 97331, USA.

Email: marcolinnell@yahoo.com

Editor: Gurutzeta Guillera-Aroita

Associate Editor: María del Mar Delgado

Received 13 June 2018; accepted 19

February 2019

doi:10.1111/acv.12496

Abstract

Old forests are often patchily distributed in contemporary forested landscapes leading to conservation concerns for species dependent on these forest types. In the absence of broad-scale recovery of old forests, conservation initiatives have emphasized connecting forested landscapes to facilitate movement of genes or individuals. We assessed forest connectivity for a low-vagile arboreal rodent (red tree vole; *Arborimus longicaudus*), an obligate of old forests within a distinct population segment that is a candidate for listing under the US Endangered Species Act in the northern Oregon Coast Range (USA). Within the distinct population segment, old forests (>80 years old) have contracted by >80% in the previous century, comprise 10.9% of the contemporary landscape and reside in a matrix of young forests (20–80 years old). We combined complimentary graph and circuit theory metrics into spatial conservation prioritization to provide insights into the composition and function of the contemporary forested landscape and to identify potential conservation and research priorities for this area. Given average distances from patches of old forests (3.4 km), we predicted that connectivity can only be achieved if red tree voles move and settle iteratively through young forest matrix, which is suboptimal habitat. We found that the top 1% conservation priorities were a series of small, spatially central patches and several large patches located where old forest cover was most extensive. Most of these patches were in protected reserves. Up to 30% of the top 10% prioritization were forests outside of reserves, highlighting the potential for these forests to contribute to landscape connectivity for this low-vagile species that is dependent on old forest.

Introduction

Reduction in forests containing large, old trees poses pervasive conservation challenges because many species depend on trees with complex structural characteristics that take decades or centuries to develop (Banks *et al.*, 2013). What remains of forested landscapes, including the distribution and extent of remnant old-forest patches and intervening cover types, is a primary driver of the capacity of these landscapes to support populations of old-forest dependent species (Lindenmayer *et al.*, 1999; Fischer & Lindenmayer, 2006). Thus, conservation of remnant old forests can be complimented by identification of intervening cover types that may facilitate population-level connectivity.

In the absence of broad recovery of old forests, conservation initiatives have emphasized assessments of forest connectivity or the capacity of forested landscapes to facilitate movement by individuals and genes (Beier *et al.*, 2011). Forest connectivity is species and landscape specific, dependent on animal movement potential (vagility) and forest amount and configuration (Taylor *et al.*, 1993; Prugh *et al.*, 2008; Cushman & Landguth, 2012). Matrix, defined as the majority cover type in which old forest resides on the landscape

(Lindenmayer & Franklin, 2002), can affect animal movement depending on its similarity or dissimilarity to old forests (i.e. contrast). The extent of matrix and isolation of remaining old forests can determine whether connectivity is most appropriately a measure of movement of multiple generations through matrix (i.e. as measured by movement of genes) or of individuals (Lindenmayer & Franklin, 2002; Cushman & Landguth, 2012).

Due to a precipitous reduction in old conifer forests (>80 years old) during the 20th century (>80% since 1911) due to timber harvest and large wildfires and subsequent conversion into young, managed forests (<80 years old), a distinct population segment of red tree voles (*Arborimus longicaudus*; hereafter tree vole) at the northern periphery of their range in the northern Oregon Coast Range (USA) were proposed as a candidate for protection under the US Endangered Species Act (USDI Fish and Wildlife Service, 2011; Forsman *et al.*, 2016; Linnell *et al.*, 2017). Tree voles are small (~30 g) canopy-dwelling arboreal rodents endemic to western Oregon and northwest California and are associated with old conifer forests at the local (i.e. containing one to several home ranges) and landscape scales (Linnell *et al.*, 2017). Occurrence of tree voles in young forest matrix is

predicted to depend on matrix contrast which is closely related to forest age and disturbance, and distance from large patches (>20 ha) of old forest (Forsman *et al.*, 2016; Linnell *et al.*, 2017). Dispersal data are scarce, and of nine subadult tree voles radio-tracked, six dispersed (mean = 56 m, max = 75 m, $n = 6$; Swingle, 2005). These distances are much shorter than the estimated mean distance from old-forest patches (3.4 km) in the northern Oregon Coast Range (Linnell *et al.*, 2017). Inter-patch connectivity, therefore, is likely to depend on the capacity of tree voles to occasionally colonize and reproduce in young forest matrix (Swingle, 2005; Linnell *et al.*, 2017).

Assessments of connectivity have broadly depended on two approaches, patch-based connectivity that emphasizes identifications of patches which may disproportionately connect landscapes (Bodin & Saura, 2010; Saura *et al.*, 2011) and inter-patch connectivity, including the contribution of the matrix (McRae *et al.*, 2008; Cushman & Landguth, 2012). Both depend on assumptions about animal vagility to identify the contribution of landscape elements and combining them using spatial conservation prioritization mapping may provide resolution to landscape-scale connectivity analyses, particularly in forested landscapes that contain low-contrast matrix and where old forests are scarce (Rayfield *et al.*, 2016; Albert *et al.*, 2017).

To identify potential research and forest conservation priorities including reserve design for tree voles within the distinct population segment we used spatial conservation prioritization mapping to identify forested areas that contribute disproportionately to connectivity. First, we used graph theory to identify discrete meta-population networks (i.e. network components) using old-forest patches as nodes (Bunn, Urban & Keitt, 2000). Second, we used circuit theory to identify pinch-points in the landscape where movement is likely to be limited to one or few pathways (McRae *et al.*, 2008). Finally, we combined metrics derived from graph and circuit theory to identify areas of conservation priority (Moilanen *et al.*, 2005).

Materials and methods

Study area

The study area was defined as an approximately 16 000 km² forested area containing the distinct population segment of tree voles in the northern Oregon Coast Range (Fig. 1). Most forests were dominated by conifers (*Pseudotsuga menziesii*, *Picea sitchensis*) that at approximately 80 years old, begin to develop copious complex structural features that tree voles and other species use as nest substrates (e.g. cavities, epicormic branches; Spies & Franklin, 1991). Eighty years old has been used as an ecological and management threshold to identify old forests, to include late-successional (80–200 years old) and old-growth (>200 year old) forests (Spies & Franklin, 1991; Molina, Marcot & Leshner, 2006). Old forests in the study area contracted by >80% in the 20th century, primarily due to timber harvest and four large wildfires (1931–1951) north of the Nestucca River comprising

the Tillamook Burn (Highsmith & Beh, 1952). The contemporary landscape comprised 10.9% old-forest cover, below the lower bounds of predicted historical range (25–75%; Wimberly *et al.*, 2000; Linnell *et al.*, 2017). Land ownership was highly correlated with forest cover and age with lower amounts of large (old) conifer forests occurring on private lands (Stanfield, Bliss & Spies, 2002; Wimberly & Ohmann, 2004). Regional patterns of ownership within the study area were characterized by land ownership consolidation. Unconsolidated lands comprised either a ‘checkerboard’ pattern of ownership of alternate 2.59 km² sections in public or private ownership, or consolidated blocks consisting of multiple public or private sections.

Following adoption of the Northwest Forest Plan, most old forests on federal lands were protected as late-successional reserves for the northern spotted owl *Strix occidentalis caurina* and its habitat (old conifer forests), and by extension what were assumed to be reserves for a broad suite of organisms associated with old forests including the marbled murrelet *Brachyramphus marmoratus*, and many non-vertebrate species (USDA Forest Service & USDI Bureau of Land Management, 1994). On federal lands many species, including the tree vole, were required to be surveyed for before management actions could occur on non-reserve forests >80 years old (Molina *et al.*, 2006). Some state forest lands were managed for old-forest structure within a shifting mosaic over time but contained relatively few set-aside reserves (Oregon Department of Forestry 2010).

Across ownerships, most young forests (<80 years old) were managed as plantations of native conifers for timber production, primarily Douglas-fir *P. menziesii*. Partial removal harvests (thinning) predominated on federal lands and total removal harvests (i.e. clear-cuts) on private and state owned lands. Harvest rotation periods ranged 40–50 years on private lands and up to 80 years on state and non-reserve federal lands (Adams *et al.*, 2002; Oregon Department of Forestry 2006). Fire return intervals in these temperate forests were estimated to be 230 ± 30 years (mean $\pm$ sd) during the previous millennium, exceeding the contemporary 40–50 year harvest rotation periods (Long *et al.*, 1998).

Study organism and habitat suitability map

Tree voles consume a diet of conifer needles and build their nests and forage almost exclusively in the forest canopy (Forsman *et al.*, 2016). Several factors have been hypothesized to contribute to their close association with old forests (e.g. predation, lack of nest substrates), and a recent study found evidence that availability of nest substrates in the canopy limited abundance of tree voles in young forests 22–44 years old (Linnell *et al.*, 2018). In addition to supporting the ecological conditions that tree voles require, many old forests were protected in federal reserves and were most likely to remain on the landscape assuming timber harvesting continued to be the most prevalent disturbance.

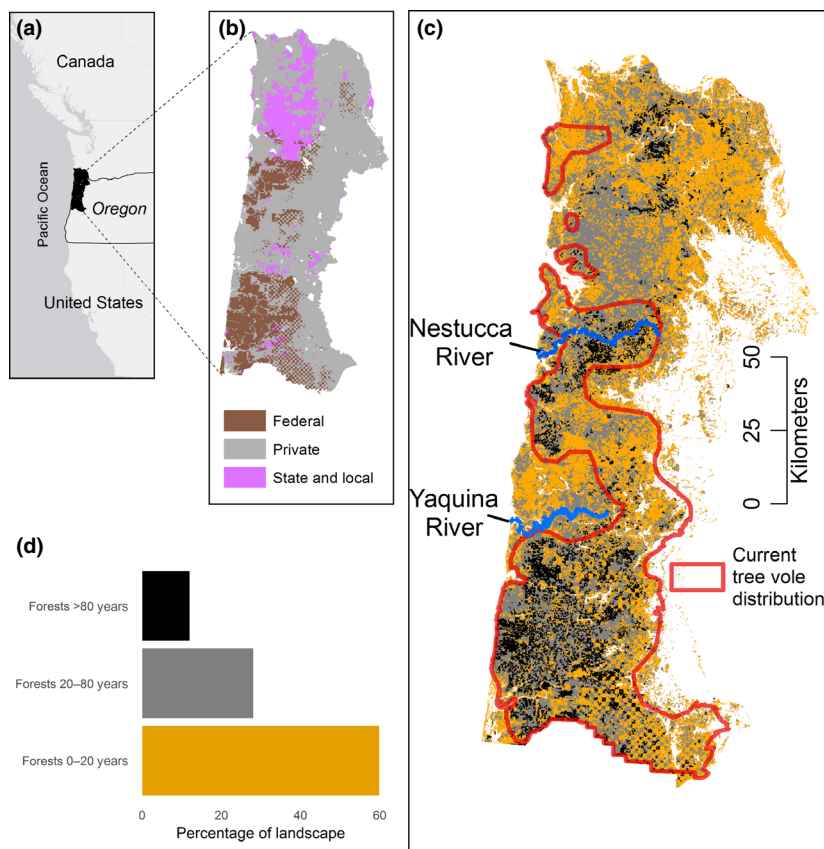


Figure 1 Map of the study area in the northern Coast Range of western Oregon (USA) within the area of the distinct population segment of red tree voles (a), land ownership (b), current distribution of red tree voles (Forsman *et al.*, 2016) and forest age classes with non-forest depicted in white (c,d). Area was bounded by the Columbia River (north), the primarily un-forested Willamette Valley (east), Pacific Ocean (west) and the Siuslaw River (south).

Minimum patch size requirements for tree voles, and other temperate forest-dwelling vertebrates, are frequently unknown (Bunnell *et al.*, 1999). Linnell *et al.* (2017) identified >20 ha as a biologically relevant old-forest patch size estimated to support a small tree vole population of ~30 animals based on indices of tree vole abundance: 1.0 (Maser, 1966) and 1.9 ± 1.0 (mean $\pm$ 1 SE; Marks-Fife, 2016) tree voles per ha. Although 30 animals is well below suggestions for viable populations in isolation over multiple generations (Frankham, Bradshaw & Brook, 2014), we assumed that 20 ha was sufficient in size to remain occupied for several years if isolated and thus considered it a conservative estimate of minimum patch size. We used >20 ha old-forest patches as nodes in network analysis and our study area comprised 1274 nodes.

We used the habitat suitability index (HSI) map (30×30 m resolution) produced by Linnell *et al.* (2017) to create a resistance surface to assess movement connectivity using circuit theory. The HSI map was produced using a presence-only model trained and tested using machine learning in program Maxent (Phillips, Anderson & Schapire, 2006) and forest cover covariates derived from light detection and ranging (lidar) and Landsat data collected 2006–2016. Model fit for the four-covariate final model (percentage old forest, recent disturbance, distance from old-forest patch >20 ha and hardwood cover) was estimated to be high with a continuous Boyce index (based on Spearman rank) of 0.95 ± 0.03 .

Graph analytical approaches

Graph theory analyses can assess inter-patch connectivity by conceptualizing the landscape as a series of nodes (patches) and links. Graphs are sensitive to assumptions about dispersal distances of focal species (Bunn *et al.*, 2000; Urban & Keitt, 2001). Dispersal and recruitment, however, are difficult to estimate and this information is lacking for many species (Baguette & Van Dyck, 2007; Le Galliard *et al.*, 2012). For low-vagile species inter-patch connectivity is further complicated because it may take multiple generations to link neighbouring patches if patches are dispersed many times further than individual dispersal distances (Barrows, Fleming & Allen, 2011).

Tree voles are low-vagile and old-forest specialists; therefore, we assumed that connectivity (to include gene flow and demographic connectivity) across relevant distances would be a multi-generational process occurring at the population-level, whereby tree voles would need to iteratively move, settle and reproduce within low-contrast matrix to connect old-forest patches. This assumes that matrix supports movement and occasional reproduction, as has been shown for tree voles (Forsman *et al.*, 2016) and for birds in agro-ecosystems (Manning, Lindenmayer & Barry, 2004), but that lack of nest substrates or other factors limit suitability of matrix compared to old-forest patches (Linnell *et al.*, 2018). The limited information regarding tree vole dispersal

suggests natal dispersal distances of up to 75 m (Swingle, 2005), although Biswell (1994) reported a single instance of a subadult male located 340 m from his natal tree. To incorporate uncertainty of dispersal distance into assumptions of inter-patch connectivity we assessed graph metrics at two distances: (1) 2 km from old-forest patches which was the distance threshold identified in the Linnell *et al.* (2017) model where HSI transitioned from suitable to unsuitable, and (2) 7 km which represents a maximum expansion scenario.

Although multi-generation connectivity via gene flow has rarely been empirically tested for small mammals, a model of gene flow for a generalist mouse species *Peromyscus leucopus* suggested that several generations of successful dispersal of at least 80 m facilitated gene flow (Marrotte, Gonzalez & Millien, 2017). Given limited information about dispersal and settlement by tree voles, a plausible first step in assessing connectivity may be to assume a similar scenario: that multiple successive dispersal events facilitate connectivity. In this scenario (maximum expansion scenario), we assumed (1) that tree voles move in a stepwise pattern whereby each generational step was equal to the observed straight-line natal dispersal distance of 75 m (Swingle, 2005), (2) tree voles breed year-round and can produce an estimated 3 litters/generations per year (Forsman, Swingle & Hatch, 2009) and (3) young forest matrix provides habitat for up to 30 years (forest age: 20–50 years old) at the local and landscape scales (continuous forest cover) through 50-year timber harvest rotations. Using these assumptions, tree voles could move a maximum of $75 \text{ m} \times 3 \text{ generations/year} \times 30 \text{ years of forest cover} = 6750 \text{ m}$ in 30 years, which we then rounded to 7 km.

Spatial graphs

Because the forested matrix between old-forest patches was highly variable and dynamic, we used an unweighted (i.e. patches were not expected to contribute to flow/connectivity differently) minimum planar graph (Fall *et al.*, 2007) to represent discrete old-forest patches, assuming that intervening linkages would form and contract as young forests that comprised the matrix aged and then were harvested. We further assumed that tree vole populations would expand directly between patches *i* and *j* such that pairwise inter-patch distances could be represented as the Euclidean distance from the edge of patch *i* to the edge of patch *j*. This represents a conservative estimate of inter-patch distance as it is unlikely that tree voles would have expanded across the shortest linkage between patches or that forest cover was likely to form such direct linkages. To examine the sensitivity of the network to assumed dispersal distances and estimate the number of potential discrete meta-populations, we estimated the number of network components (connected networks) at 1 km intervals formed at each distance threshold and present this area curve (Bunn *et al.*, 2000). Finally, we estimated the connectivity distance at which the slope tangent of the curve approached -1 which indicated the point where the landscape becomes only marginally more connected with longer assumed inter-patch dispersal (Appendix S1).

Graph metrics

We estimated two network metrics, equivalent connected area index (ECA; Saura *et al.*, 2011) and weighted betweenness connectivity (BC) that are predicted to provide complementary information in network mapping (Estrada & Bodin, 2008; Baranyi *et al.*, 2011). ECA explicitly weights the size, in our case more extensive patches have higher weight, and ECA was the total forested area consisting of old forests within the largest connected network in the landscape. To evaluate the contribution of each node to inter- and intra-patch connectivity, we estimated the decrease in habitat area within the network if that node was removed (dECA). Following Rayfield *et al.* (2016), we set the distance-decay constant, which characterizes the probability of dispersal beyond our assumed dispersal distances (2 km, 7 km), to -0.01 representing a 0.05 probability of tree vole dispersal beyond 2 km or 7 km (see Rayfield *et al.*, 2016). All analyses were performed in program R using the *igraph* v 1.1.2 and raster 2.6-7 packages (Csárdi & Nepusz, 2006; Hijmans *et al.*, 2015; R Core Team 2018). We used code provided by Rayfield *et al.* (2016) to estimate dECA.

BC estimates provide information on centrality of node *i* within the network as the proportion of the weighted shortest paths between *j* and *k* that pass through *i* (Freeman, 1978; Bodin & Saura, 2010). Old-forest patches were included in only one network each, and networks were defined by our distance thresholds.

Movement connectivity using circuit theory

We used circuit theory, implemented by program Circuitscape 4.0, to evaluate the potential for inter-patch connectivity within the contemporary landscape (McRae *et al.*, 2008). Circuitscape uses current passed through a landscape to identify paths of least resistance represented by a raster grid whereby each pixel has a conductance value corresponding to ease of movement of the modelled organism. For tree voles, we assumed that circuit flow maps needed to represent the process of multi-generational expansion to link disjunct patches of old forest, including movement, settlement and reproduction, and therefore we used a HSI map (Linnell *et al.*, 2017) to estimate conductance at each pixel. Higher conductance values represent pixels that are hypothesized to provide habitat for tree voles. Conductance and habitat suitability values in our analysis should therefore be highly correlated because they are based on the same underlying values. Circuit flow, however, provides a metric of least resistance connectivity for the entire landscape, providing information unique to HSI values at the pixel-level. To estimate circuit flow across the study area we used the tiling approach outlined by Pelletier *et al.* (2014) to create an omnidirectional circuit flow map (Appendix S2). To evaluate correlations between HSI and circuit flow as well as the other metrics used in analysis (dECA, BC), we estimated Pearson correlation for all pairs of metrics (Appendix S3).

Spatial conservation prioritization in ZONATION

We used spatial conservation prioritization software (ZONATION v 4.0; Moilanen *et al.*, 2005) to identify spatial conservation priorities using four metrics represented spatially as raster maps (HSI, dECA, BC, circuit flow; Fig. 2). We considered each raster map as plausibly contributing unique and equal information to the analysis and so used equal weights for each in our analysis (Lehtomäki & Moilanen, 2013). Each pixel was ranked using the additive benefit function that prioritizes pixels that contribute highly to all four connectivity metrics (features), and lowest ranked pixels were iteratively removed to produce spatial priorities. We compared the performance and sensitivity of the product of spatial prioritization, which we henceforth refer to as prioritization maps, to the assumptions we made for each metric (Appendix S4).

Results

Values for HSI and circuit flow had a Pearson correlation coefficient 0.69, indicating that these two features contributed similar information to the conservation prioritization analysis. Graph metrics (dECA, BC) were moderately correlated with Pearson correlations of 0.49 (Appendix S3) with BC more pronounced where old-forest patches were more sparsely distributed between the Yaquina and Nestucca Rivers (Figs 1 and 2). Circuit flow primarily occurred on federal lands with some linkages forming on private and state lands south of the Nestucca river albeit temporarily (Figs 2b and 4d). Most circuit flow north of the Nestucca River occurred on the flanks of state forest lands in the area of the historic Tillamook Burn (Fig. 2b).

Prioritization maps produced at 2 and 7 km distances had high overlap of conservation rankings (Appendix S4). This indicates broad agreement in prioritization despite the difference in assumptions about tree vole movement capacity. Given overall conservation prioritization results were similar between the two distance thresholds (Appendix S4), we mainly reported results from the 7 km distance.

Spatial rankings on the top 1%, assuming 7 km dispersal capability, indicated conservation priorities consisted primarily of large patches comprising extensive reserve areas near the Nestucca River and south of the Yaquina River and small, highly central patches between those rivers (Fig. 3). At 5%, maps incorporated some young forests primarily located north of the Yaquina River. For 2 km dispersal, ranking of small, central patches was slightly lower (top 5%) compared to the 7 km prioritization. Circuit flow was highly concentrated through consolidated private lands forming impermanent forested corridors whereas in unconsolidated checkerboard flow was concentrated at corners of 2.59 km² sections (Fig. 4b).

Although overall prioritization results were similar at our two dispersal distances, the spatial graph network demonstrated a rapid increase in connectivity (decrease in number of network components) as assumed dispersal distances

increased between 1 and 4 km (Appendix S1). At 1 km the spatial graph was composed of 1170 network components and at 5 km, 29 components. The tangent of the slope curve approached -1 between 3 and 4 km, indicating that at >4 km, the number of network components decreased much more slowly (Fig. S1 in Appendix S1).

Discussion

Herein, we identified three conservation and research priorities: (1) small, highly central old-forest patches between the Nestucca and Yaquina Rivers, (2) large patches within the two largest clusters of extensive old forests on federal lands and (3) linkages provided by young forests. Of these, linkages were dynamic, likely only to provide spatial connectivity on brief time-scales (i.e. <30 years) due to the highly dynamic landscape that results from short-rotation timber harvests (Fig. 4c,d). Assuming that maintaining gene flow is a priority and that tree voles can traverse young forests at relevant distances, small patches south of the Nestucca River appear to be central nodes with high spatial priority value, potentially able to maintain connectivity in a highly dynamic portion of the landscape.

Spatial aggregation of patches affects individual- and population-level processes such as connectivity and involves conservation trade-offs when a limited area can be set aside in reserves (Lindenmayer & Fischer, 2006). Highly clustered large forest patches provide extensive refugium for imperiled forest specialists but large, severe, stochastic (and contagious) threats, such as wildfires or disease, can eliminate populations and habitat in highly connected refugia (Turner, 1989; Hess, 1994). The existence of multiple large refugium may therefore be required to mitigate risk of extirpations, especially in forests with regimes of infrequent but severe wildfires that can potentially eliminate extensive reserve areas, such as in the northern Oregon Coast Range (Long *et al.*, 1998). Small, isolated patches, in contrast, may disperse risk from severe and contagious threats, but limited gene flow caused by isolation may limit both genetic diversity and population viability (Mills & Allendorf, 1996). In general, the top 5% of spatial prioritization of our analysis identified patches at the extreme: moderately clustered and large, or isolated and small. Given that tree voles move and occasionally breed in young forest matrix, moderate clustering with short inter-patch distances (i.e. short enough for occasional multi-generational immigration) may be sufficient to maintain gene flow and potentially allow for recolonization of areas suffering patch-level extirpation. Many portions of the landscape, however, are outside a single-generation dispersal step, below minimum recommended tolerances to maintain genetic diversity (Mills & Allendorf, 1996). Ultimately, retention of large patches may need to be complemented by moderate and small patches that provide functional connections among more extensive old-forest refugium (Lindenmayer & Fischer, 2006).

Reserve design and connectivity-based conservation are often constrained by land ownership and economic trade-offs therein (e.g. Murphy & Noon, 1992). In the distinct

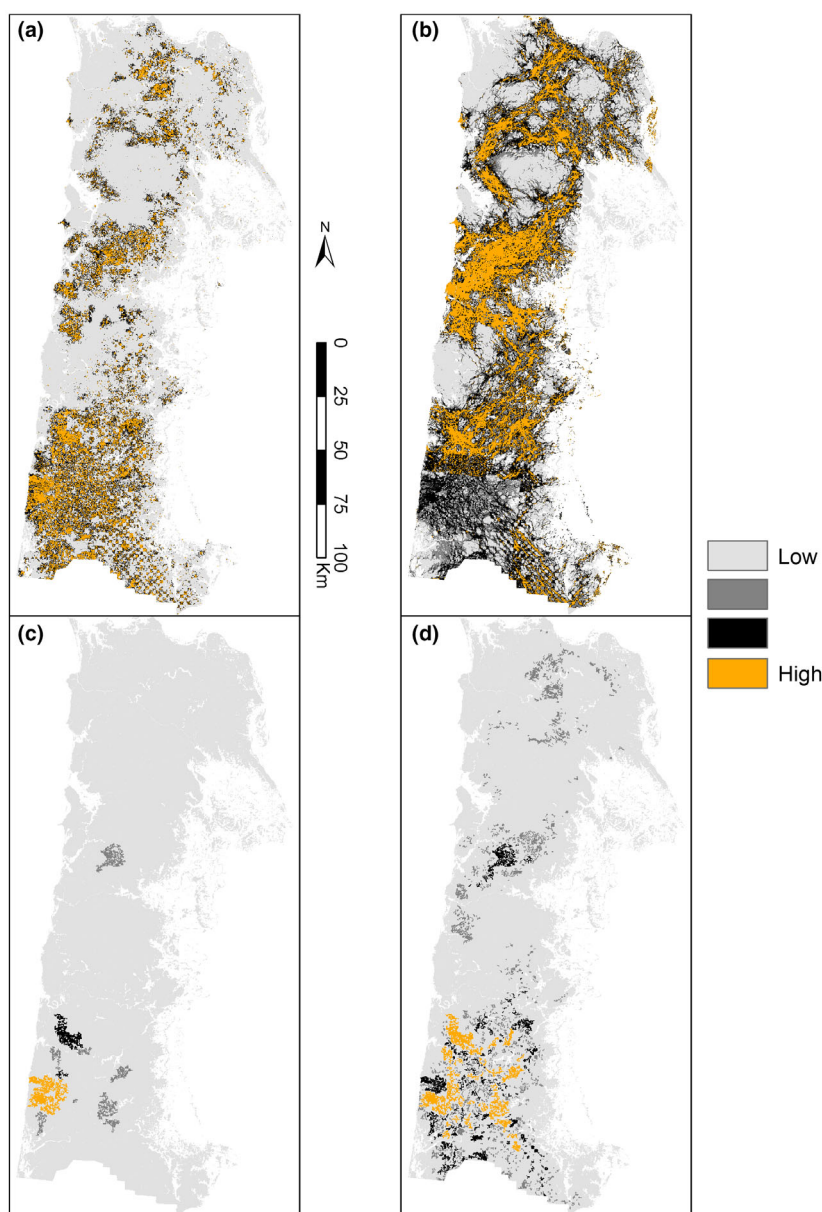


Figure 2 Raster maps of the study area in the northern Coast Range of western Oregon (USA) that comprised the spatial prioritization analysis for red tree voles: (a) habitat suitability index from model produced by Linnell *et al.* (2017), (b) omnidirectional circuit flow map, (c) relative variation in equivalent connected area: old-forest patches that if removed would disproportionately reduce the connected habitat area within the connected network and (d) betweenness connectivity represented by old-forest patches that if removed would result in linkage loss in connected network.

population segment, reserves on federal lands provide primary habitat for tree voles. Additions to those reserves could be informed by spatial prioritization mapping. For example, several small patches are highly central but isolated; increasing the extent of these patches could increase their potential value as population refugia in a highly dynamic portion of the landscape. This could be achieved by allowing young forests to age on non-reserve federal lands. Conservation on private timber lands is constrained to a greater degree than federal or state lands by economic considerations as harvest rotation periods are driven by market forces and yield targets. Young forests on private lands are likely limited to providing short-term linkages consisting of low-contrast young forest matrix (Calkin *et al.*, 2002; Franklin &

Lindenmayer, 2009). Highest prioritization on these lands were late rotation (i.e. >20 year-old) forests that provide structural linkages between reserves on federal lands. Increasing harvest rotation period and implementing landscape-scale planning of harvests could extend linkage duration and extent. For example, focused conservation efforts at the corners of checkerboard ownership would likely have a disproportionately positive effect on connectivity of the landscape for old-forest species. The current management of young forests on federal lands (i.e. thinning) has short-term negative effects at the stand-level and uncertain long-term effects on arboreal rodent populations although landscape context may mitigate short-term stand-level effects if sufficient suitable habitat is located adjacent (Wilson & Forsman,

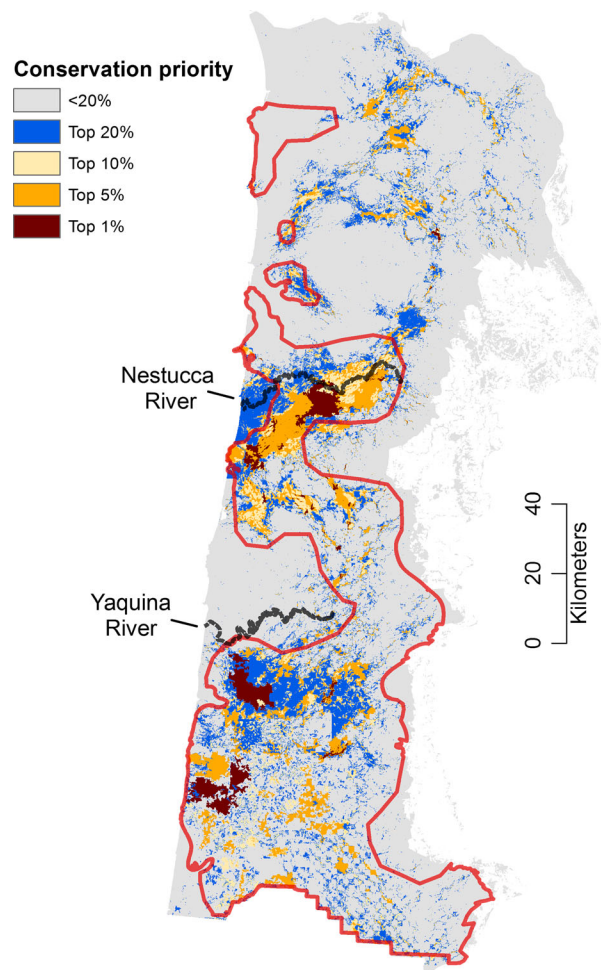


Figure 3 Final map showing red tree vole conservation priorities consisting of the top 1, 5, 10 and 20% of pixels within the northern Coast Range of western Oregon (USA). Map shown includes all connectivity metrics assuming that connectivity occurred between patches up to 7 km apart. Red polygons indicate the current distribution of tree voles in the northern Oregon Coast Range.

2013; Sollmann *et al.*, 2016). Altering forest management or adding to current reserves would involve comprehensive land management plans, and substantial coordination and participation from a wide range of forest managers (Brodie *et al.*, 2015). Nevertheless, extending current reserves could be complimented by reducing contrast within young-forest matrix to maintain connectivity for tree voles and other old-forest associates (Franklin & Lindenmayer, 2009).

Maintaining suitable conditions outside of the current distribution may be necessary to reduce risk of substantial loss of the population and habitat due to future large-scale disturbances or shifts in environmental conditions. High intensity disturbances (fires and timber harvest) eliminated most forests in the northern range of tree voles in the late 1800s to mid-1900s. The tree vole subpopulations occurring in the northernmost distribution polygon (Fig. 1c), may be functionally extirpated, unable to persist in isolation, as very few

tree voles have been detected there (Kuussaari *et al.*, 2009; Forsman *et al.*, 2016). Although many forests have recovered north of the current distribution (Forsman *et al.*, 2016), including 16% of the top 10% of conservation priorities (Fig. 3), tree voles remain absent. If inter-patch distances are too great for natural recolonization, assisted dispersal (translocations), although economically expensive and uncertain to succeed (Perez *et al.*, 2012), could provide the only alternative for tree voles to once again inhabit much of the northern extent of the distinct population segment. Ideally assisted dispersal would occur concomitant with managing for linkages to facilitate movement outside of the current distribution. Maintaining short inter-patch distances and connectivity could help preclude future translocations in the inevitable event of additional large wildfires where tree voles are most common south of the Nestucca River. Conservation of extant populations may therefore need to be complimented by actions that provide broader resiliency to relatively short- (e.g. timber harvest) and long-term (e.g. climate change) shifts in habitat suitability.

We recognize several caveats that can affect potential conservation decisions based on our findings. First, matrix contrast, and by extension conductance through the landscape, can shift spatially over relatively short time frames because young forests are primarily managed for timber production. This highlights the need to implement conservation actions soon after analyses because linkages are unlikely to remain static in dynamic landscapes. Second, we conceptualized connectivity as a population-level process through low-contrast matrix. Most studies consider connectivity as an individual-level process or as a structural feature of landscapes (see review in Wade, McKelvey & Schwartz, 2015). The outcome of connectivity for small mammals may better be conceptualized as occurring over multiple generations of successful dispersers (Marrotte *et al.*, 2017). Although tree voles are occasionally observed in young forests (Forsman *et al.*, 2016; Linnell *et al.*, 2017) no empirical evidence of gene flow occurring through matrix for the species currently exists. Validating the structural connectivity models presented here using gene flow rather than individual movements may be warranted to ensure conservation decisions are appropriate to enhance functional connectivity for tree voles (Baguette *et al.*, 2013).

Connectivity analyses often lack biological rationales or are considered an individual-level process using high-vagile species (e.g. northern spotted owls) as model organisms that in many cases are not well suited as umbrella species (Carroll, Dunk & Moilanen, 2009; Wade *et al.*, 2015). The Northwest Forest Plan provides protection for many species with extremely short dispersal distances that can occupy low-contrast young forest matrix (e.g. lichens; Sillett *et al.*, 2000). Our analysis, therefore, represents a first step for evaluating connectivity in the region of the Northwest Forest Plan under the assumption that matrix could facilitate connectivity as a population-level process extending up to several thousands of meters, particularly if 'keystone' elements such as large old trees are available to reduce matrix contrast (Sillett *et al.*, 2000; Manning *et al.*, 2004; Doerr, Doerr &

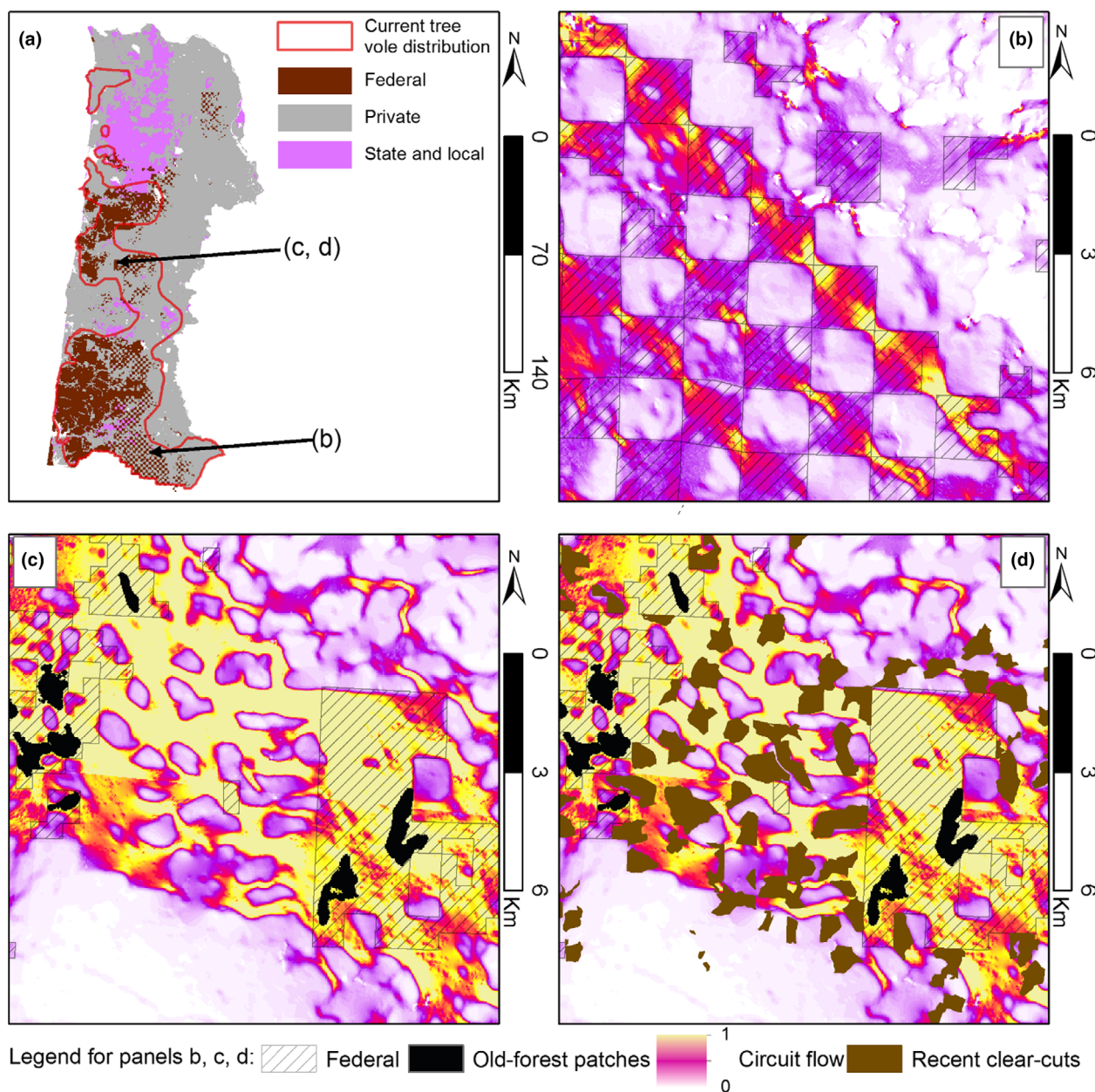


Figure 4 Examples of multi-ownership landscape connectivity, as depicted by a circuit flow map, within matrix in areas containing different levels of consolidation in the northern Coast Range of western Oregon (USA). (a) shows landscape ownership patterns within the distinct population segment of red tree voles, (b) concentrated flow through unconsolidated checkerboard with alternating federal and privately managed lands where flow is concentrated through 1 mile² (2.59 km²) section corners, (c) mostly consolidated private lands where flow is concentrated around non-forest forming temporary forested corridors whereby connectivity was estimated using data layers from 2012, (d) updated panel showing recent forest disturbances (clear-cuts) digitized from a more recent aerial photo (August 2016) demonstrating the short-term duration of forested corridors through consolidated private lands in our study area (Aerial photo image data: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community).

Davies, 2011). Additional connectivity analyses of species (e.g. lichens) where dispersal is even further limited (i.e. tens of meters), but may be able to use old trees as stepping stones (Sillett *et al.*, 2000) would complement work already done for high-vagile (e.g. northern spotted owls; Carroll *et al.*, 2009) and low-vagile species (this study).

Maintaining population-level processes, such as gene flow, depends on connecting landscapes at multiple scales relevant to target species. Forest management, however, often occurs at much finer scales than those relevant to landscape-scale connectivity. For tree voles, connectivity depended on forest age, inter-patch distances and spatial aggregation of patches.

These landscape-scale characteristics could provide connectivity for other terrestrial species that evolved in old forests (Doerr *et al.*, 2011), including several low-vagile species. Landscape-scale connectivity across relevant distances, therefore, may provide finer-scale resolution to regional reserve design and connectivity, including assessment of the efficacy of broader conservation initiatives (Carroll *et al.*, 2009). Finally, by identifying specific areas where fine-scale restoration can complement broader recovery of old forests our connectivity analysis can contribute to multi-scale conservation planning.

Acknowledgements

Funding for this research was provided by the USDA Forest Service, Pacific Northwest Research Station. We thank the many agencies and field biologists that made nest location data available, and land management agencies that provided access to lidar data. We appreciate the thoughtful comments of three anonymous reviewers that greatly improved the manuscript. This publication represents the views of the authors, and any use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

References

- Adams, D.M., Schillinger, R.R., Latta, G. & Nalts, A.V. (2002). *Timber harvest projections for private land in western Oregon*. Research Contribution 37. Corvallis: Forest Research Laboratory, Oregon State University.
- Albert, C.H., Rayfield, B., Dumitru, M. & Gonzalez, A. (2017). Applying network theory to prioritize multispecies habitat networks that are robust to climate and land-use change. *Conserv. Biol.* **31**, 1383–1396.
- Baguette, M. & Van Dyck, H. (2007). Landscape connectivity and animal behavior: functional grain as a key determinant for dispersal. *Landsc. Ecol.* **22**, 1117–1129.
- Baguette, M., Blanchet, S., Legrand, D., Stevens, V.M. & Turlure, C. (2013). Individual dispersal, landscape connectivity and ecological networks. *Biol. Rev.* **88**, 310–326.
- Banks, S.C., Lindenmayer, D.B., Wood, J.T., McBurney, L., Blair, D. & Blyton, M.D.J. (2013). Can individual and social patterns of resource use buffer animal populations against resource decline? *PLoS ONE* **8**, e53672.
- Baranyi, G., Saura, S., Podani, J. & Jordán, F. (2011). Contribution of habitat patches to network connectivity: redundancy and uniqueness of topological indices. *Ecol. Indic.* **11**, 1301–1310.
- Barrows, C.W., Fleming, K.D. & Allen, M.F. (2011). Identifying habitat linkages to maintain connectivity for corridor dwellers in a fragmented landscape. *J. Wildl. Mgmt.* **75**, 682–691.
- Beier, P., Spencer, W., Baldwin, R.F. & McRae, B.H. (2011). Toward best practices for developing regional connectivity maps. *Conserv. Biol.* **25**, 879–892.
- Bodin, Ö. & Saura, S. (2010). Ranking individual habitat patches as connectivity providers: integrating network analysis and patch removal experiments. *Ecol. Modell.* **221**, 2393–2405.
- Biswell, B.L. (1994). Intertree movement and spatial distribution of nest trees occupied by individual red tree voles: implications for conservation [Poster]. In *75th anniversary meeting of the Society of Mammalogists*: Washington, DC.
- Brodie, J.F., Paxton, M., Nagulendran, K., Balamurugan, G., Clements Gopalasamy, R., Reynolds, G., Jain, A., *et al.* (2015). Connecting science, policy, and implementation for landscape-scale habitat connectivity. *Conserv. Biol.* **30**, 950–961.
- Bunn, A.G., Urban, D.L. & Keitt, T.H. (2000). Landscape connectivity: a conservation application of graph theory. *J. Environ. Manage.* **59**, 265–278.
- Bunnell, F.L., Wells, R.W., Nelson, J.D. & Kremsater, L.L. (1999). Patch sizes, vertebrates, and effects of harvest policy in southeastern British Columbia. In *Forest fragmentation: wildlife and management implications*: 271–293. Rochelle, J.A., Lehmann, L.A. & Wisniewski, J. (Eds). Leiden: Koninklijke Brill NV.
- Calkin, D.E., Montgomery, C.A., Schumaker, N.H., Polasky, S., Arthur, J.L. & Nalle, D.J. (2002). Developing a production possibility set of wildlife species persistence and timber harvest value. *Can. J. For. Res.* **32**, 1329–1342.
- Carroll, C., Dunk, J.R. & Moilanen, A. (2009). Optimizing resiliency of reserve networks to climate change: multispecies conservation planning in the Pacific Northwest, USA. *Glob. Change Biol.* **16**, 891–904.
- Csárdi, G. & Nepusz, T. (2006). The igraph software package for complex network research. *InterJ. Complex Syst.* **1695**, 1–9.
- Cushman, S.A. & Landguth, E.L. (2012). Multi-taxa population connectivity in the Northern Rocky Mountains. *Ecol. Modell.* **231**, 101–112.
- Doerr, V.A.J., Doerr, E.D. & Davies, M.J. (2011). Dispersal behaviour of Brown Treecreepers predicts functional connectivity for several other woodland birds. *Emu-Austral Ornithol.* **111**, 71–83.
- Estrada, E. & Bodin, Ö. (2008). Using network centrality measures to manage landscape connectivity. *Ecol. Appl.* **18**, 1810–1825.
- Fall, A., Fortin, M.-J., Manseau, M. & O'Brien, D. (2007). Spatial graphs: principles and applications for habitat connectivity. *Ecosystems* **10**, 448–461.
- Fischer, J. & Lindenmayer, D.B. (2006). Beyond fragmentation: the continuum model for fauna research and conservation in human-modified landscapes. *Oikos* **112**, 473–480.
- Forsman, E.D., Swingle, J.K. & Hatch, N.R. (2009). Behavior of red tree voles (*Arborimus longicaudus*) based on continuous video monitoring of nests. *Northwest Sci.* **83**, 262–272.

- Forsman, E.D., Swingle, J.K., Davis, R.J., Biswell, B.L. & Andrews, L.S. (2016). *Tree voles: an evaluation of their distribution and habitat relationships based on recent and historical studies, habitat models, and vegetation change*. Gen. Tech. Rep. PNW-GTR-948. Portland: USDA Forest Service Pacific Northwest Research Station.
- Frankham, R., Bradshaw, C.J.A. & Brook, B.W. (2014). Genetics in conservation management: revised recommendations for the 50/500 rules, Red List criteria and population viability analyses. *Biol. Conserv.* **170**, 56–63.
- Franklin, J.F. & Lindenmayer, D.B. (2009). Importance of matrix habitats in maintaining biological diversity. *Proc. Natl Acad. Sci. USA* **106**, 349–350.
- Freeman, L.C. (1978). Centrality in social networks conceptual clarification. *Soc. Networks* **1**, 215–239.
- Hess, G.R. (1994). Conservation corridors and contagious disease: a cautionary note. *Conserv. Biol.* **8**, 256–262.
- Highsmith, R.M. & Beh, J.L. (1952). Tillamook burn: the regeneration of a forest. *Scientific Monthly* **75**, 139–148.
- Hijmans, R.J., Etten, J.V., Cheng, J., Sumner, M., Mattiuzzi, M., Greenberg, J.A. & Lamigueiro, O.P., *et al.* (2015). Package 'raster'. *R package version 2.5-8*. Available at <https://cran.r-project.org/web/packages/raster/index.html>
- Kuussaari, M., Bommarco, R., Heikkinen, R.K., Helm, A., Krauss, J., Lindborg, R., Öckinger, E., *et al.* (2009). Extinction debt: a challenge for biodiversity conservation. *Trends Ecol. Evol.* **24**, 564–571.
- Le Galliard, J.-F., Rémy, A., Ims, R.A. & Lambin, X. (2012). Patterns and processes of dispersal behaviour in arvicoline rodents. *Mol. Ecol.* **21**, 505–523.
- Lehtomäki, J. & Moilanen, A. (2013). Methods and workflow for spatial conservation prioritization using Zonation. *Environ. Model. Softw.* **47**, 128–137.
- Lindenmayer, D.B. & Fischer, J. (2006). *Habitat fragmentation and landscape change: an ecological and conservation synthesis*. Washington: Island Press.
- Lindenmayer, D.B. & Franklin, J.F. (2002). *Conserving forest biodiversity: a comprehensive multiscaled approach*. Washington: Island Press.
- Lindenmayer, D.B., Cunningham, R.B., Pope, M.L. & Donnelly, C.F. (1999). The response of arboreal marsupials to landscape context: a large-scale fragmentation study. *Ecol. Appl.* **9**, 594–611.
- Linnell, M.A., Davis, R.J., Lesmeister, D.B. & Swingle, J.K. (2017). Conservation and relative habitat suitability for an arboreal mammal associated with old forest. *For. Ecol. Manage.* **402**, 1–11.
- Linnell, M.A., Lesmeister, D.B., Bailey, J.D., Forsman, E.D. & Swingle, J.K. (2018). Response of arboreal rodents to increased availability of nest substrates in young forests. *J. Mammal.* **99**, 1174–1182.
- Long, C.J., Whitlock, C., Bartlein, P.J. & Millsaugh, S.H. (1998). A 9000-year fire history from the Oregon Coast Range, based on a high-resolution charcoal study. *Can. J. For. Res.* **28**, 774–787.
- Manning, A.D., Lindenmayer, D.B. & Barry, S.C. (2004). The conservation implications of bird reproduction in the agricultural 'matrix': a case study of the vulnerable superb parrot of south-eastern Australia. *Biol. Conserv.* **120**, 363–374.
- Marks-Fife, C.A. (2016). *Estimation of population age structure, detection probability, and density of red tree voles in Oregon*. MS thesis, Oregon State University.
- Marrotte, R.R., Gonzalez, A. & Millien, V. (2017). Functional connectivity of the white-footed mouse in Southern Quebec, Canada. *Landsc. Ecol.* **32**, 1987–1998.
- Maser, C. (1966). *Life histories and ecology of Phenacomys albigipes, Phenacomys longicaudus, Phenacomys silvicola*. MS thesis, Oregon State University.
- McRae, B.H., Dickson, B.G., Keitt, T.H. & Shah, V.B. (2008). Using circuit theory to model connectivity in ecology, evolution, and conservation. *Ecology* **89**, 2712–2724.
- Mills, L.S. & Allendorf, F.W. (1996). The one-migrant-per-generation rule in conservation and management. *Conserv. Biol.* **10**, 1509–1518.
- Moilanen, A., Franco, A.M.A., Early, R.I., Fox, R., Wintle, B. & Thomas, C.D. (2005). Prioritizing multiple-use landscapes for conservation: methods for large multi-species planning problems. *Proc. Roy. Soc. B: Biol. Sci.* **272**, 1885–1891.
- Molina, R., Marcot, B.G. & Leshner, R. (2006). Protecting rare, old-growth, forest-associated species under the survey and manage program guidelines of the Northwest Forest Plan. *Conserv. Biol.* **20**, 306–318.
- Murphy, D.D. & Noon, B.R. (1992). Integrating scientific methods with habitat conservation planning: reserve design for northern spotted owls. *Ecol. Appl.* **2**, 4–17.
- Oregon Department of Forestry. (2006). *Harvest and habitat model project final report presented to the Oregon Board of Forestry March 8, 2006*. Salem: Oregon Department of Forestry.
- Oregon Department of Forestry. (2010). *Northwest oregon state forests management plan revised April 2010*. Salem: Oregon Department of Forestry.
- Pelletier, D., Clark, M., Anderson, M.G., Rayfield, B., Wulder, M.A. & Cardille, J.A. (2014). Applying circuit theory for corridor expansion and management at regional scales: tiling, pinch points, and omnidirectional connectivity. *PLoS ONE* **9**, e84135.
- Perez, I., Anadon, J.D., Diaz, M., Nicola, G.G., Tella, J.L. & Gimenez, A. (2012). What is wrong with current translocations? A review and a decision-making proposal. *Front. Ecol. Environ.* **10**, 494–501.
- Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006). Maximum entropy modeling of species geographic distributions. *Ecol. Modell.* **190**, 231–259.
- Prugh, L.R., Hodges, K.E., Sinclair, A.R.E. & Brashares, J.S. (2008). Effect of habitat area and isolation on fragmented

- animal populations. *Proc. Natl Acad. Sci. USA* **105**, 20770–20775.
- R Core Team. (2018). *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.
- Rayfield, B., Pelletier, D., Dumitru, M., Cardille, J.A. & Gonzalez, A. (2016). Multipurpose habitat networks for short-range and long-range connectivity: a new method combining graph and circuit connectivity. *Meth. Ecol. Evol.* **7**, 222–231.
- Saura, S., Estreguil, C., Mouton, C. & Rodríguez-Freire, M. (2011). Network analysis to assess landscape connectivity trends: application to European forests (1990–2000). *Ecol. Indic.* **11**, 407–416.
- Sillett, S.C., McCune, B., Peck, J.E., Rambo, T.R. & Ruchty, A. (2000). Dispersal limitations of epiphytic lichens result in species dependent on old-growth forests. *Ecol. Appl.* **10**, 789–799.
- Sollmann, R., White, A.M., Tarbill, G.L., Manley, P.N. & Knapp, E.E. (2016). Landscape heterogeneity compensates for fuel reduction treatment effects on Northern flying squirrel populations. *For. Ecol. Manage.* **373**, 100–107.
- Spies, T. & Franklin, J. (1991). The structure of natural young, mature, and old-growth Douglas-fir forests in Oregon and Washington. In *Wildlife and vegetation of unmanaged Douglas-fir forests*: 91–109. Ruggiero, L.F., Aubry, K.B., Carey, A.B. & Huff, M.H. (Eds). Gen. Tech. Rep. PNW-GTR-285. Portland: USDA Forest Service, Pacific Northwest Research Station.
- Stanfield, B.J., Bliss, J.C. & Spies, T.A. (2002). Land ownership and landscape structure: a spatial analysis of sixty-six Oregon (USA) Coast Range watersheds. *Landsc. Ecol.* **17**, 685–697.
- Swingle, J.K. (2005). *Daily activity patterns, survival, and movements of red tree voles (Arborimus longicaudus) in western Oregon*. MS thesis, Oregon State University.
- Taylor, P.D., Fahrig, L., Henein, K. & Merriam, G. (1993). Connectivity is a vital element of landscape structure. *Oikos* **63**, 571–574.
- Turner, M.G. (1989). Landscape ecology: the effect of pattern on process. *Annu. Rev. Ecol. Syst.* **20**, 171–197.
- Urban, D.L. & Keitt, T.H. (2001). Landscape connectivity: a graph-theoretic perspective. *Ecology* **82**, 1205–1218.
- USDA Forest Service & USDI Bureau of Land Management. (1994). *Final supplemental environmental impact statement on management of habitat for late-successional and old-growth related species within the range of the northern spotted owl*. Portland: USDA Forest Service & USDI Bureau of Land Management.
- USDI Fish and Wildlife Service. (2011). Endangered and threatened wildlife and plants; 12-month petition to list a distinct population segment of the red tree vole as endangered or threatened. *Fed. Reg.* **76**, 63720–63762.
- Wade, A.A., McKelvey, K.S. & Schwartz, M.K. (2015). *Resistance-surface-based wildlife conservation connectivity modeling: summary of efforts in the United States and guide for practitioners*. Gen. Tech. Rep. RMRS-GTR-333. Fort Collins: USDA Forest Service Rocky Mountain Research Station.
- Wilson, T.M. & Forsman, E.D. (2013). Thinning effects on spotted owl prey and other forest-dwelling mammals. In *Density management in the 21st century: west side story*: 79–90. Anderson, P.D. & Ronnenberg, K.L. (Eds). Gen. Tech. Rep. PNW-GTR-880. Corvallis: USDA Forest Service Pacific Northwest Research Station.
- Wimberly, M.C. & Ohmann, J.L. (2004). A multi-scale assessment of human and environmental constraints on forest land cover change on the Oregon (USA) Coast Range. *Landsc. Ecol.* **19**, 631–646.
- Wimberly, M.C., Spies, T.A., Long, C.J. & Whitlock, C. (2000). Simulating historical variability in the amount of old forests in the Oregon Coast Range. *Conserv. Biol.* **14**, 167–180.

Supporting information

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

Appendix S1. Number of connected networks at different distance thresholds.

Appendix S2. Omnidirectional circuit flow map.

Appendix S3. Correlations between raster layers used in analysis.

Appendix S4. Comparison of two different dispersal assumptions.