# Geometry of Forest Landscape Connectivity: Pathways for Persistence

**Deanna H. Olson and Kelly M. Burnett**


## Abstract

Streamside areas may be dispersal funnels or runways for a variety of species. For over-ridge dispersal, headwaters offer the shortest distance links among riparian zones in adjacent drainages. We summarize landscape designs for connectivity of habitats using headwater riparian linkage areas as the foundation for a web of landscape-scale links. We developed management considerations for placement of headwater linkage areas including: 1) providing connections between larger basins; 2) maintaining habitat connectivity in the face of climate change; 3) incorporating place-based disturbance regimes such as headwater debris-flow-prone areas; 4) targeting connectivity areas to address sensitive species conservation strongholds; and 5) accounting for geometry at the forest-stand scale of a single project or proposed timber sale, including managing habitats to connect lands on adjacent federal ownerships, by means of connecting corners of checkerboard landscape blocks along diagonals. Although our proposed linkage areas are designed to target headwater species, the resulting web of connections across the landscape is expected to benefit many forest-dependent species.


**Keywords:** watersheds, forest, headwaters, biodiversity, linkage areas, dispersal.

## Introduction

Biodiversity retention and restoration is an emerging priority for global ecosystems. Astounding losses within major taxonomic groups have been reported nationally and internationally (41 percent of amphibians, 25 percent of mammals, 15 percent of bony fishes, 13 percent of birds: Hoffmann et al. 2010; 50–60 percent of turtles: Kiester and Olson 2011). In particular, protection and restoration of forests and forest biodiversity has become a paramount concern worldwide (e.g., Convention on Biological Diversity: *www.cbd.int/forest/*). A toolbox of management approaches has been developed to conserve forest biodiversity, largely through a mixture of fine- and coarse-grained habitat protections (e.g., United States Northwest Forest Plan: USDA and USDI 1993, 1994; Cissel et al. 1998; Lindenmayer and Franklin 2002; Raphael and Molina 2007; Lindenmayer et al. 2007) and site-specific designs to maintain or restore forest structural heterogeneity (McComb 2001; Lindenmayer and Franklin 2002; Brockerhoff et al. 2008).

Development of landscape designs to manage habitat connectivity for multiple species is an especially active research topic in forest biodiversity conservation, due to continuing trends of forest fragmentation and to an upswing

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in world reforestation efforts. Managing forested landscapes for connectivity functions benefiting biodiversity requires incorporating several fundamental conservation concepts. These basic conservation tenets include identifying the critical habitats used throughout species' life histories (breeding, foraging, overwintering, and dispersal habitats), and commensurate habitat protections to ensure that these biotic functions are retained. If an organism uses different habitats through its life cycle, then maintaining connectivity among these habitats is essential to ensure its persistence. Of particular relevance is the characterization and retention or restoration of dispersal habitat. This includes the home ranges of individuals and the broader dispersal of offspring or individuals that tie sub-populations and populations together over larger areas. This broader-scale dispersal function maintains genetic variation within natural populations, which may foster resiliency needed to adapt to changing environmental conditions. The future of species may rely on our careful attention to managing for connectivity now.

Defining the adequacy of dispersal habitat in forests is a complex topic (Noss et al. 1997) and may address a variety of elements, including habitat condition, corridor sizes (length, width), and corridor redundancy (Pinto and Keitt 2008). Redundancy is especially relevant because multiple connectivity pathways can assist dispersal across landscapes by organisms in different locations and increase the probability of movement in the face of many interacting site-specific factors (microsite features, disturbances). Redundancy of habitat connectivity hedges against catastrophe, uncertainty, and stochastic processes that can affect individuals and sub-populations that vary in their movement propensities, possibly related to patch size, habitat quality, and population demography.

Low-mobility species may merit special attention devoted to the placement and redundancy of connectivity corridors, because barriers to dispersal may arise as a result of their basic biology and ecology (Raphael and Molina 2007). These species may move slowly and require refugia along corridors because it may take them years to move between optimum habitat patches. Due to a potentially longer residency time within connectivity corridors, low-mobility species may be particularly vulnerable to sub-optimal corridor conditions and stochastic processes. Hence, redundancy of connections may be critically important to increase their likelihood of successful movement across landscapes for such low-mobility species. Patches of higher-quality habitat within dispersal corridors may be used as stepping stones for such species and may be an essential aspect of their long-term persistence (e.g., Grant et al. 2010). Such stepping stones may function as habitat refugia or "stopover reserves" (Dobson et al. 1999), which promote survival of individual organisms as they move through the environment. Stepping stones may have more suitable physical habitat conditions than the surrounding area, or may allow individuals to forage to replenish energy reserves or survive harsh seasons (summer, winter) in localized refugia, from which they may disperse again later.

Herein, we synthesize our ongoing studies of the utility of headwater riparian areas as proposed connectivity corridors, or linkage areas, for dispersal of riparian-associated and low-mobility species in Pacific Northwest forests. Once designed, such headwater linkage areas may benefit many taxa. Our studies also conceptually integrate aquatic network and upland-forest habitats, functions, and processes. The combination of protections for aquatic and upland systems is providing new insights into forest ecosystem management approaches. We summarize the key considerations for the geometric orientation of connectivity pathways to assist migration of species across watersheds and across webs of connections, to maintain linked aquatic-terrestrial populations at landscape scales. Our goal here is to provide a summary of these conceptual designs, while research continues to address these issues and advance design effectiveness.

## Utility of Watersheds as Redundant Landscape-scale Linkage Units

Watersheds are widely accepted units for monitoring and evaluating the effects of land use on aquatic resources (Omernik and Bailey 1997). Where their boundaries can be clearly mapped, watersheds are increasingly common units for forest management planning and conservation designs. For example, in the U.S., the Aquatic Conservation Objectives of the federal Northwest Forest Plan (USDA and USDI 1994: p. B-11), address connectivity among watersheds:

> *"Maintain and restore spatial and temporal connectivity within and between watersheds. Lateral, longitudinal, and drainage network connections include floodplains, wetlands, upslope areas, headwater tributaries, and intact refugia. These network connections must provide chemically and physically unobstructed routes to areas critical for fulfilling life history requirements of aquatic and riparian-dependent species."*

Hydrologic units (HUs), delineated by the U.S. Geological Survey (Seaber et al. 1987), are also a convenient and widely used basis for forest assessment and planning (e.g., Maxwell et al. 1995; Suring et al. 2011). The HU coding describes a hierarchical system of units nested by drainage area; larger code numbers designate smaller drainage areas. Watersheds or segments of watersheds comprise HUs. Even though the majority of HUs at each level of the hierarchy are not true topographic watersheds, such a perspective can aid biodiversity conservation designs, especially as smaller headwater basins are delineated and used for replicating protected areas (e.g., 6t$^{h}$-code HUs: Suzuki et al. 2008) and creation of redundant connections across landscapes (via 6$^{th}$- and 7$^{th}$-code HUs: Olson and Burnett 2009).

The value of using headwater basins as the premise for establishing connectivity corridors across forested landscapes is due to their habitat conditions, potential use by a variety of organisms, frequency of occurrence on the landscape, and minimization of dispersal distances (fig. 1). Olson et al. (2007) summarized some of the merits of headwater riparian habitats for species in the northwest, including providing cool, moist microclimates for interior-forest dependent organisms and aquatic-riparian associated species such as amphibians. Some taxa may use these areas due to their habitat suitability; others may respond to streams as movement barriers, and then move along banks parallel to such barriers. Streamside areas may be dispersal funnels or runways for a variety of species. For example, we have seen terrestrial salamanders (species that do not use stream or pond habitats for breeding or other life-history functions) moving predominantly through near-stream areas (D. Olson and M. Kluber, unpubl. data). Additional taxa that use riparian corridors in northwestern forests include a variety of lichens, bryophytes, fungi, vascular plants, mollusks, mammals (e.g., ground-dwelling mammals: Wilk et al. 2010), birds, and general forest-obligates that may occur in legacy forest attributes such as wolf trees along riparian buffer zones. As a minimum estimate across taxonomic groups, over 100 species were identified as likely to benefit by habitat protections of combined intermittent and perennial streams provided by riparian reserves in federal forest lands in the range of the Northern Spotted Owl (*Strix occidentalis caurina*) (table 1) (USDA and USDI 1997). Species with restricted dispersal abilities were identified for special consideration relative to utility of riparian reserves during watershed analyses under the Northwest Forest Plan (USDA and USDI 1997).

Furthermore, the high density of small streams in upland northwest forests has been widely recognized over the last 20 years, as our basic

**Table 1—**Species benefitting from interim riparian reserves developed for the federal Northwest Forest Plan (from table B1 in USDA and USDI 1997). Riparian reserve protection includes a one site-potential tree-height or 30.5 m (100 ft) buffer, whichever is greater, as an interim measure along all intermittent streams, and a two site-potential tree-height buffer as an interim measure along perennial streams (see USDA and USDI 1993, page III-9).

| Taxonomic group | Species |
|---|---|
| **Bryophytes** | *Antitrichia curtipendula, Douinia ovata, Kurzia makinoana, Scouleria marginata, Tritomaria exectiformis* |
| **Fungi** | |
| Rare chanterelles | *Polyozellous multiplex* |
| Rare gilled mushrooms | *Clitocybesubditopoda, C. senilis, Neolentinus adherens, Rhodocybe nitida, Rhodocybe speciosa, Tricholomposis fulvenscens* |
| Rare cup fungi | *Helvella compressa, H. crassitunicata, H. elastica, H. maculata* |
| Jelly mushroom | *Phlogiotis helvelloides* |
| Moss-dwelling mushrooms | *Cyphellostereum leave, Galerina atkinsoniana, G. cerina, G. hetrocysis, G. sphagnicola, G. vittaeformis, Rickenella setipes* |
| **Lichens** | |
| Riparian lichens | *Certelia cetrarioides, Collema nigrescens, Leptogium burnetiae var. hirsutum, L. cyanescens, L. saturninum, L. teretiusculum, Platismatia lacunose, Ramalina thrausta, Usnea longissima* |
| Aquatic lichens | *Dermatocarpon luridum, Hydrothyria venosa, Leptogium rivale* |
| **Vascular plants** | *Bensoniella oregano, Botrychium minganense, B. montanum, Coptis trifolia* |
| **Mollusks** | *Ancotrema voyanum, Crypotmastix devia, C. henersoni, Monadenia fidelis salmonensis, Verspericola depressa, V. sierranus, Fluminicola* spp. nov. 1-20*, F. seminalis, Helisoma newberryi newberryi, Juga (C.) acutifilosa, J. (C.) occata, J (O.)* spp. nov. 2-3, *J. (Oreobasis) orickensis, Lanx alta, Lyogyrus* sp. nov. 1, 3, *Pyrgulopsis intermedia, Vorticifex klamathensis sintsini, V.* sp. nov. 1 |
| **Amphibians** | |
| Riparian | *Aneides flavipunctatus, Rhyacotriton cascadae, R. kezeri, R. variegatus, Dicamptodon copei, Plethodon vandykei, Ascaphus truei* |
| **Fish** | Coho Salmon (*Oncorhynchus kisutch*), fall and spring Chinook Salmon (*O. tshawytscha*), resident and sea-run Cutthroat Trout (*O. clarkii clarkii*), resident Rainbow Trout (*O. mykiss*), summer and winter Steelhead (anadromous *O. mykiss*) |
| **Birds** | Common Merganser (*Mergus merganser*)<br>[Marbled Murrelet, *Brachyramphus marmoratus*; Northern Spotted Owl, *Strix occidentalis caurina*] |
| **Bats** | Fringed, Long-eared, and Long-legged Myotis (*Myotis thysanodes, M. evotis, M. volans*), Hoary Bat (*Lasiurus cinereus*), Pallid Bat (*Antrozous pallidus*), Silver-haired Bat (*Lasionycteris noctivagans*) |
| **Other mammals** | Fisher (*Martes pennanti*), Marten (*Martes americana*), Red Tree Vole (*Arborimus longicaudus*) |

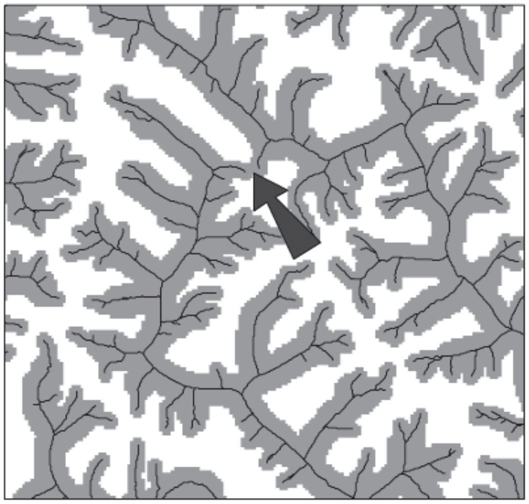

**Figure 1—**Example interim riparian reserve network from the US federal Northwest Forest Plan implemented in the Pacific Northwest, showing frequency of headwater streams on the landscape and the resulting one and two site-potential tree-height buffers along streams (upper left quadrant). Arrow indicates example over-ridge area where the distance between headwater riparian reserves in different watersheds is small and over-ridge connectivity may be more easily achieved. These headwater riparian areas can be used to facilitate landscape linkage area designs for organism dispersal and aquatic-terrestrial habitat connectivity functions.

knowledge of stream and forest ecology has expanded. In some areas, headwaters comprise 80 percent of a stream network (Gomi et al. 2002). This realization intersected with forest management practices when mapping of Northwest Forest Plan scenarios revealed that large percentages of watersheds were being incorporated into interim riparian reserves due to the high density of headwater stream networks (fig. 1). An additional value of using headwater drainages to plan landscape connectivity designs is that the distance from headwater streams to ridgelines is the shortest within a watershed, hence reducing travel distances for overland dispersal to neighboring stream-riparian areas or forest reserve blocks. Distance analysis tools, such as for "least-cost path" in landscape modeling (e.g., ArcGIS, Environmental Systems Research Institute, Inc., Redlands, CA), have been developed to assess distances between habitat patches. These tools would be useful for designing least-distance headwater linkage areas. Least "cost" path is a relevant term applied to the economics of animal movements, to minimize the distance moved—especially for mobility-restricted organisms. This term may also apply to the economics of forest management if identification of a dispersal corridor results in a financial cost for on-the-ground implementation or affects revenue from resource extraction in a managed forest context.

Northwest Forest Plan riparian reserves were intended as major contributors to the maintenance and restoration of aquatic conservation objectives, including aquatic network connectivity (USDA and USDI 1994). The importance of linking headwater stream functions and processes to those of downstream stream networks has been a focus of much work in the last two decades. Welsh (2011) captured many elements of the developing history of stream network theory and the role of aquatic connectivity in summarizing the conceptual frameworks of geomorphic channel processes (transfer and depositional zones), nutrient cycling (upstream marine influence via salmonid migration, downstream nutrient spiraling via down wood movements), aquatic-riparian linkages via reciprocal subsidies, and the intersection of herpetofaunal distributions with the classic stream continuum concept of taxonomic patterns that vary with stream order. As we look up the aquatic network into headwater streams and beyond, we summarize how extending riparian buffers up drainages and connecting them over ridgelines can both maintain terrestrial connectivity and functionally link aquatic-terrestrial systems.

Several conceptual designs of riparian buffer widths and patch reserves have been proposed to assist over-ridge migration of organisms within forests (fig. 2; Olson et al. 2007). Over-ridge connectivity considerations were further developed by Olson and Burnett (2009), and modeled for the Oregon Coastal Province. This model of connectivity linked every 6$^{th}$- and 7$^{th}$-code HU to each neighboring HU. Focusing on the Siuslaw River basin, a 4$^{th}$-code HU within that area, the linkage design illustrated where one over-ridge link could connect each adjacent HU (fig. 3). At the 7th-code HU scale, one link between each adjacent 7th-code watershed resulted in roughly 15 percent of headwater streams being extended and connected For the Oregon Coastal Province, this resulted in over 5,000 links, with about one link per 4.6 km$^2$. This is an example of redundant connectivity, essentially creating a web of connections across the landscape. Using the 6th-code HU scale, the amount of connectivity created is approximately halved, with one link per 9.3 km$^2$ for the Oregon Coastal Province.

There are no defined guidelines for how many links or how much habitat connectivity is necessary to maintain populations. The amount of dispersal habitat that might be needed to sustain even highly researched species, such as

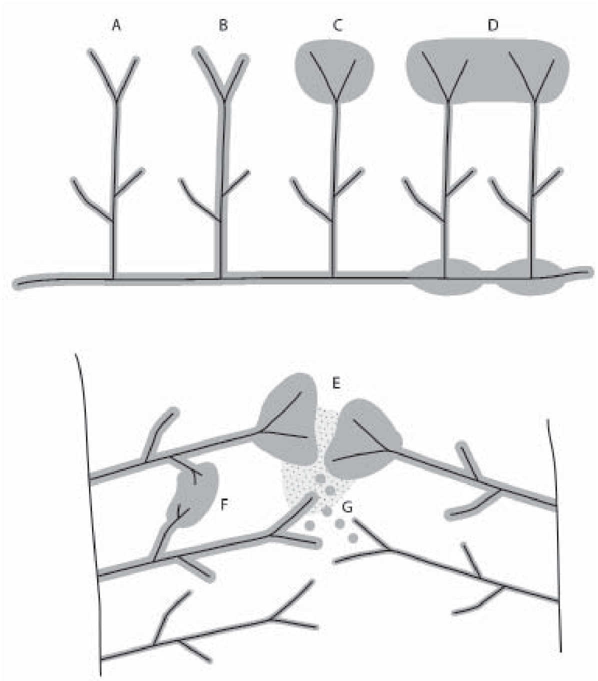


**Figure 2—**Headwater management considerations to retain aquatic-riparian biodiversity by stream buffers of different widths (A, B) and provide linkage areas between adjacent basins (C-G) using alternative forest management practices including uncut blocks (C, D, F), thinning (E), and leave islands (E, G) (from Olson et al. 2007).

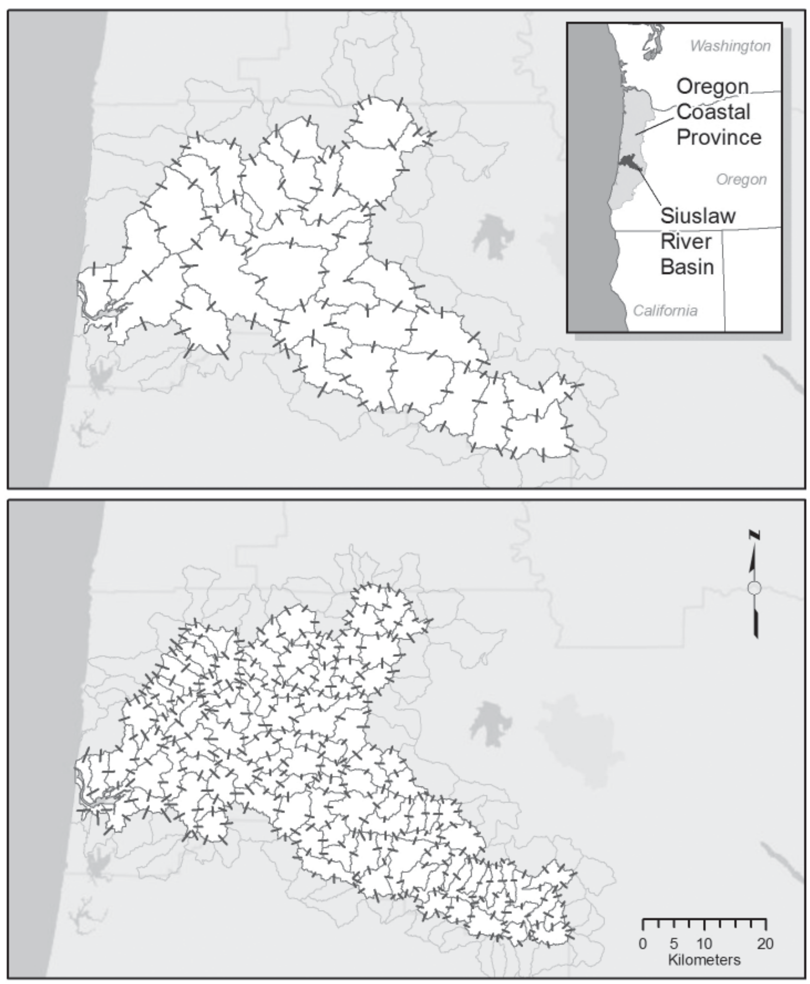


**Figure 3**—Linkage areas between watersheds can provide connectivity of headwater habitats across landscapes. In the Oregon Coast Range Province, the Siuslaw River basin, a 4th-code Hydrologic Unit (HU), is used to illustrate: A) a single connection between adjacent 6th-code HUs; and B) a single connection between adjacent 7th-code HUs, which results in 376 connections across the basin and if expanded to the entire province, about 5000 links within 23 000 km$^2$ (from Olson and Burnett 2009).

the northern spotted owl, is unknown; a "more is better" attitude prevails in the face of this uncertainty. Nevertheless, research is accruing about how much dispersal may be needed to maintain genetic diversity within and among populations. The "one migrant per generation" rule has been offered as a minimum level to reduce genetic isolation, inbreeding, and bottlenecks (e.g., Mills and Allendorf 1996). However, such a rule has many underlying assumptions that may not be supported when the complexities of natural systems are considered (e.g., Wang 2004).

Furthermore, relating effective migration rates to habitat protections in managed systems is not a straightforward exercise: if we build corridors, will they be used? Ongoing mark-recapture, radio tracking, and genetic studies are helping us to answer this question. For example, genetic connectivity analyses of stream-associated Rocky Mountain Tailed Frogs (*Ascaphus montanus*) in Idaho supported this species' affiliation with intact forested habitats: their path of connectivity followed riparian corridors in managed forests (Spear and Storfer 2010). This pattern supports the "riparian corridors as funnels" concept, but it contrasted with Coastal Tailed Frog (*A. truei*) genetic connectivity pathways in the Olympic Peninsula, Washington, which were primarily overland in areas that had timber harvest activities (Spear and Storfer 2008). Precipitation and population differences between these areas were hypothesized as accounting for these differences, as the more mesic conditions that prevail in northwestern Washington may facilitate the upland dispersal of moisture-reliant tailed frogs. Other studies (Wahbe et al. 2004; Johnston and Frid 2002; Dupuis and Steventon 1999; Nauman and Olson 2004) also found differences in riparian-corridor associations of various amphibian species in response to climate and forest conditions, generally supporting their ability to respond to microsite gradients with an apparent affiliation to cool, moist local conditions (e.g., riparian "funnels") (Olson et al. 2007). Furthermore, Spear et al. (2012) reported that Coastal Tailed Frogs track remnant tree patches in their migration pathways after the volcanic blast at Mount St. Helens, Washington. So, if we build it, will they come? The early answer is "yes, but…" —meaning that a variety of organisms appear to be occurring in or moving along pathways of retained habitats, but with geographic, taxonomic, and population-specific contexts being important considerations. A similar conclusion has recently been supported for hedgerows as corridors between woodland fragments (Davies and Pullin 2007). More research on the design of effective linkage areas will be needed. In the interim, conceptual priorities for landscape connectivity designs can be identified, and these relate directly to emerging research priorities.

## Priority Areas for Habitat Connectivity

Prioritizing linkage area placement may be important to address connectivity objectives under economic constraints, and to advance research into the effective design of linkage areas. Because linking all adjoining watersheds at small HU scales may be difficult for land managers to plan and implement in the face of myriad conflicting resource objectives, priorities may guide the first steps in connecting habitats. Olson and Burnett (2009) itemized linkage area considerations at two spatial scales, landscape and drainage area (table 2). Here, we further develop five of these priority considerations:

1. "Triads," where three large basins, with limited or no aquatic connectivity, converge at their headwaters;
2. Climate change considerations including north-south, east-west, and altitudinal linkages;
3. Landslide-prone areas;
4. Species conservation strongholds; and
5. Diagonal considerations.

**Table 2—**Design considerations for placement of headwater linkage areas to assist migration of forest-dependent species in the Pacific Northwest (Olson and Burnett 2009). **Bold-face type** indicates new concepts discussed further in text.

| Linkage Area Design Considerations | Priorities |
|---|---|
| ***Landscape scale*** | |
| 1. Connections across large basins | **"Triads"** – headwater locations that link three adjoining basins having no aquatic connectivity. |
| 2. Climate change migration corridors | North-south (latitudinal) dispersal routes.<br>Altitudinal dispersal routes.<br>Migration across ecoregion boundaries.<br>**East-west dispersal routes.** |
| 3. Linking landscape fragments | Connecting remnant late-successional and old-growth (LSOG) forest patches to other patches or restored habitats may aid dispersal of LSOG-associated species, especially those with dispersal limitations such as lichens, bryophytes, and mollusks; creation of connected archipelagos of patches. |
| 4. Disturbance frequency | Correlating frequency of connections with rates of landscape-scale disturbances, natural or anthropogenic; i.e., more linkage areas in more-disturbed places. |
| 5. **Redundancy** | Planning for multiple paths across landscapes will improve dispersal probabilities. |
| ***Drainage-basin scale*** | |
| 6. Known sites for target species | Low-mobility species.<br>LSOG-associated species.<br>Species with status of concern.<br>**Biodiversity hotspots** – communities.<br>**Species "strongholds"** – priority species management areas such as key watersheds |
| 7. Existing protections | Co-location of linkages on current set-asides (e.g., federal late-successional reserves, owl "cores", Survey and Manage species sites, botanical set asides, landslide-prone areas included in riparian reserves) |
| 8. Short connections | For economy of space, with economic and ecological benefits, shorter connectivity corridors are preferred; ecologically, shorter distances for dispersal may reduce energetic costs for individual movements and time needed for propagules to disperse. |
| 9. Paths of least resistance | Easier dispersal routes may be lower-gradient or lower-elevation "saddles" across ridgelines.<br>Wind-dispersers may have least resistance in paths that follow wind directions during seasons of dispersal. |
| 10. Risk of disturbance | Use hazard models for disturbances such as landslides, debris flows, ice/wind damage, and fire in placement of linkage areas, or in decisions about the need for redundant linkages. For example, debris-flow-prone areas may be headwater set-asides during riparian reserve delineation, and such areas may be co-located with dispersal corridors; redundant links may be considered in fire-prone areas. Mapped overlays of roads, recreation areas, human development, and mining might be avoided during linkage area delineation, when alternative locations exist. |
| 11. Land ownership patterns | Co-location of links on federal and state lands, where possible.<br>**Diagonal linkage areas across checkerboard ownerships.** |

Each of these five considerations results in a geometric view of how connectivity webs may be arranged across landscapes.

These five considerations are not mutually exclusive; how they may interact during prioritization exercises also is developed briefly here. Although they were derived for northwest forest landscapes, these concepts may have broader utility worldwide.

## 1. "Triads"

In the Oregon Coastal Province, Olson and Burnett (2009) highlighted the potential importance of linking larger river basins, which have no freshwater connectivity, through existing riparian buffer networks. Over-ridge forest habitat linkages may be absent unless reserves are placed in the area. Streams in such basins may flow directly to the Pacific Ocean or into a much larger river without a forested riparian area, and so have headwaters that are functionally disconnected. Here, we examined 4th-code HUs for the Oregon Coastal province, the scale of the Siuslaw River basin highlighted above. We then looked for locations where three of these 4th-code HUs joined at their headwaters: we call this a "triad" location. For example, headwaters of the Siuslaw River, Yaquina River, and Marys River converge at Marys Peak (between Corvallis, Newport, and Waldport, OR), which would be one such triad. Only 18 of these headwater triads exist for the Oregon Coastal Province (fig. 4). We suggest that such triads be considered priorities for habitat linkage areas because these would be spatially economical for land managers to implement and potentially ecologically efficient as connections across three watershed boundaries simultaneously.

A current research priority is to empirically assess the proposed linkage-area function of landscape locations such as headwater triads. Using a genetic approach, we have sampled northwestern amphibians from headwater streams of adjacent drainages that are potentially connected across ridgelines in the Oregon Coast Range, including three adjoining headwaters in triads (such as Marys Peak). Preliminary genetic analyses of the Coastal Giant Salamander, *Dicamptodon tenebrosus*, generally support our contention of over-ridge connectivity among drainages (L. Knowles and M.R. Marchán-Rivadeneira, Univ. Michigan, unpubl. data). Previous studies have supported overland connectivity of stream-breeding amphibians (e.g., Spear and Storfer 2008, 2010), and such animals have been found up to 400 m from streams (Olson et al. 2007), but no previous published study has designed

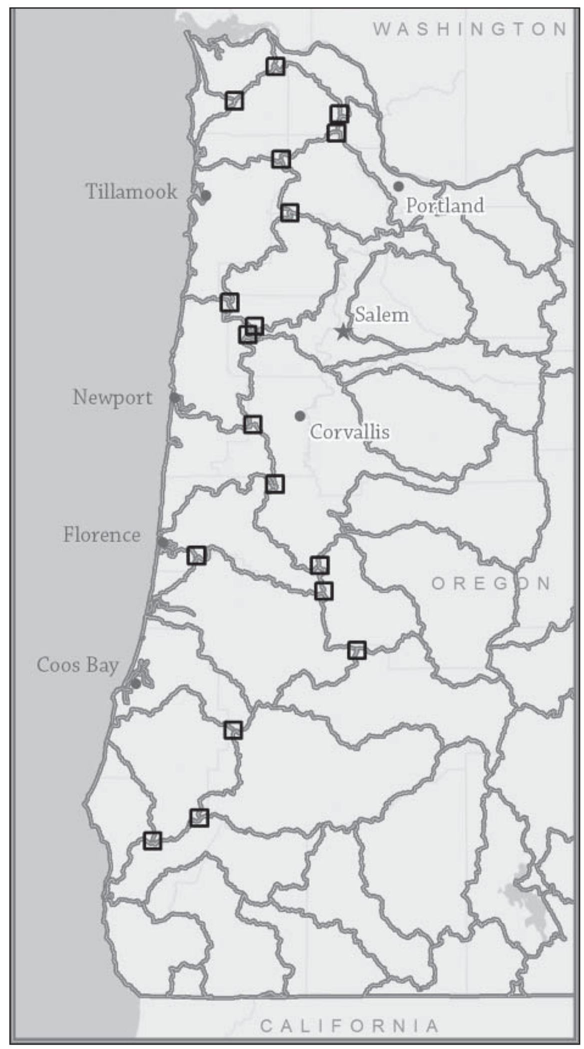


**Figure 4**—"Triads" are indicated (squares) where three 4th-code Hydrologic Units in the Oregon Coast Range Province meet at their headwaters. Triads are priority locations for linkage area or 'species stronghold' placement to effectively manage for species dispersal simultaneously across three distinct watershed boundaries.

sampling to specifically address headwater over-ridge connectivity among discrete drainages. This remains an information gap that could be addressed for all forest taxonomic groups, and would aid the adaptive management of the triad connectivity concept.

## 2. Climate Change

A second priority consideration for northwest forest connectivity is assisting migration in the face of climate change (Olson and Burnett 2009). Predicted climate change effects on northwest forest habitats include drought, insect, and fire effects on forest stands, with large conifers and high-elevation trees being vulnerable to losses (Spies et al. 2010). Aquatic habitat changes in forested landscapes are anticipated in cold-water mountain streams (Spies et al. 2010) and in headwaters (Olson and Burnett 2009). Increasing stream temperatures, with negative implications for cold-water fauna, are already apparent across the northwest (Isaak et al. 2011). Given uncertainty in the geographic specificity of climate change trajectories due to complex El Niño and Pacific Decadal Oscillation cycles, "dynamic and adaptive thinking" (Spies et al. 2010) is needed. A prudent course for linkage area placement may be to consider connected routes in north-south, east-west, and altitudinal directions within and among watersheds (fig. 5). Such consideration may allow multiple potential pathways of movement for species facing changing conditions. Pockets of suitable microhabitats for species persistence may be related to local conditions, and may occur as "stepping stones" along these linear trajectories, like beads along a string. Providing connectivity paths adjoining both riparian areas and north-facing slopes is one such example, with both near-stream areas and hill shading resulting from topographic relief providing cool, moist conditions for target species such as some late-successional and old-growth (LSOG)-associated salamanders (e.g., Suzuki et al. 2008). Landscape-scale monitoring of forest conditions and species distributions may inform adaptive management of likely climate change refugia for different taxa.

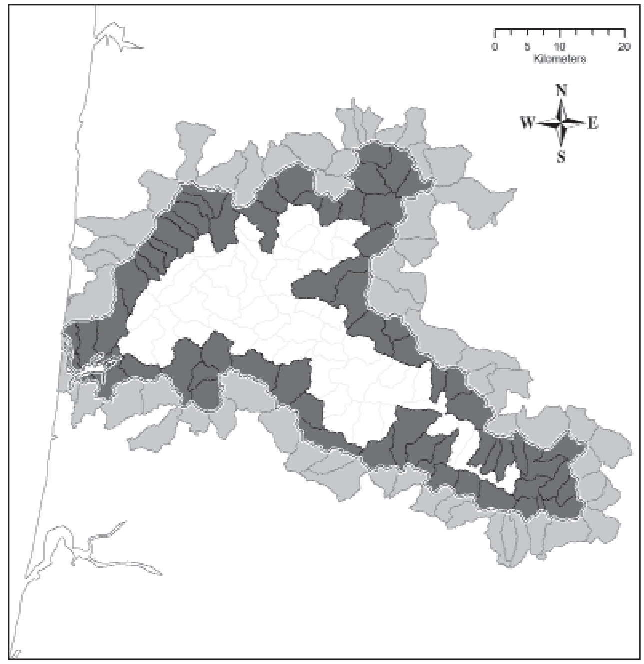


**Figure 5**—Designs for assisted migration of species in the face of climate change might include prioritizing headwater linkage area placement across north-south and east-west watershed boundaries. The Siuslaw River basin, a 4th-code Hydrologic Unit in the Oregon Coast Range Province, is shown highlighting perimeter sub-drainages (dark grey) where linkage areas could be made to discrete drainages to the north, south, and east.

## 3. Managing Disturbances: Landslide-Prone Areas

A third priority consideration for the design of linkage areas is to integrate their placement with local disturbance regimes. Landslides and debris flows can be dominant disturbance processes affecting headwater streams in forested, mountainous regions (e.g., Benda 1990; Iverson et al. 1997). The Northwest Forest Plan directs that riparian reserves incorporate landslide-prone areas to reduce the probability that activities associated with timber harvest will alter wood and sediment inputs to streams by changing the rate, magnitude, composition, or timing of debris flows. Co-locating linkage areas with existing riparian reserves, where these include steep areas prone to landsliding, can provide economic efficiency and conservation synergy for land and resource managers. Burnett and Miller (2007) modeled differences among hill slopes and headwater channels in probabilities of initiating and transporting debris flows that deliver to fish-bearing channels for the Oregon Coastal Province (fig. 6). Those headwaters with the highest likelihood of affecting downstream areas important for fish might be high priorities for extending riparian reserves over ridgelines. Because debris flows can be important sources of large wood (May and Gresswell 2003; Hassan et al. 2005), a fundamental component of stream habitat complexity (Bilby and Bisson 1998; Gregory et al. 2003), managing these expanded riparian reserve areas to accelerate tree growth could be an additional consideration. Redundancy of connections would be important when planning ground-disturbing activities for linkage areas with a high probability of landsliding. To aid identification and adaptive management of landslide-prone areas, these areas have been mapped for many northwest forests by the NetMap interactive web-tool developed by Earth Systems Institute (*http://netmaptools.org/*).

## 4. Species Strongholds

"Species strongholds" are areas where biodiversity conservation is a priority, and where thriving populations can occur to anchor species persistence in the region. Retaining connectivity among species strongholds enhances the likelihood of persistence under the uncertainty of stochastic events (catastrophic fire, disease outbreaks) or emerging patterns of disturbance (climate change) that may affect any particular stronghold. Managing stronghold-to-stronghold connectivity is a fourth priority to consider in developing linkage area designs across forest landscapes. Species strongholds may be created for communities of diverse taxa at larger spatial scales by land-use allocations such as

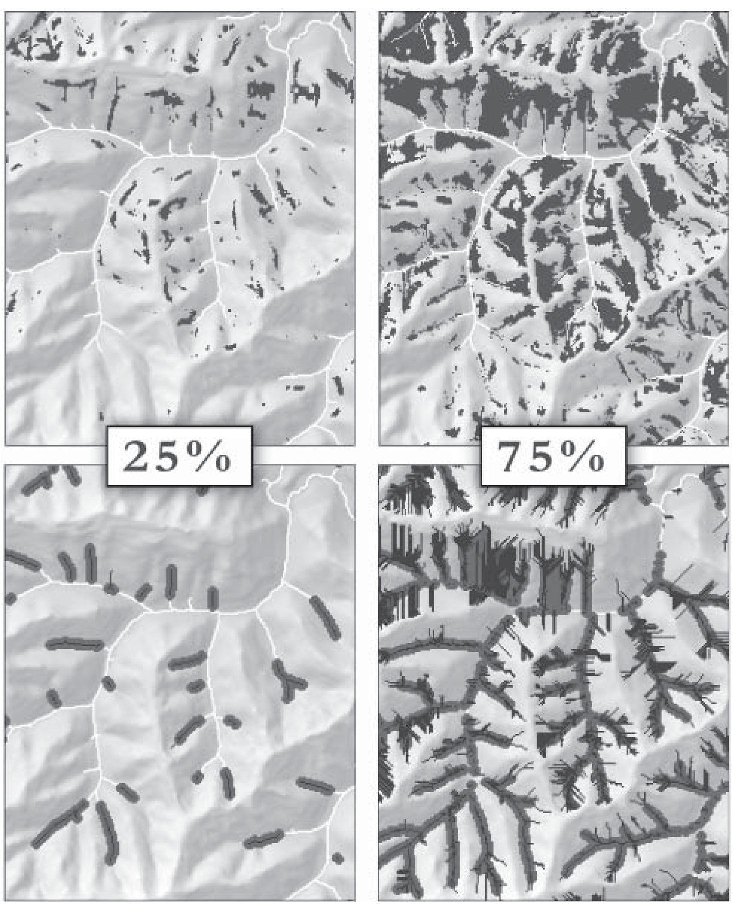


**Figure 6**—Placement of between-drainage links might consider other landscape-scale provisions such as management scenarios to retain the natural disturbance regime, including landslide-prone areas managed to deliver wood and sediment to streams. Top figures show models of 25 percent and 75 percent of the landslide-prone hillslopes in an example forest landscape, and bottom figures show their likely traversal paths to streams (Burnett and Miller 2007). Headwater riparian buffers of these areas provide long-term wood and sediment inputs for stream biota. From Olson and Burnett 2009.

Congressionally reserved lands (wilderness areas, national parks), or the Northwest Forest Plan late-successional reserves or key watersheds (USDA and USDI 1993, 1994). At smaller spatial scales, strongholds for a targeted species of concern may be critical habitat areas, such as caves, ponds, meadows, botanical set-asides, or areas managed for Survey and Manage species under the federal Northwest Forest Plan (USDA and USDI 1993, 1994). Riparian buffers themselves might be considered as strongholds, but here, we expand that perspective to other areas.

Developing new species strongholds is particularly important when considering connectivity issues. Three examples follow. First, areas with high "intrinsic potential," the capacity to support high-quality habitats for salmon (Burnett et al. 2007), may serve as nuclei for designing linkage areas. Intrinsic potential models have been developed and broadly applied for salmonids in the Pacific Northwest and elsewhere (e.g., Mollot and Bilby 2008; Sheer et al. 2009; Busch et al. 2011; Barnett and Spence 2011). Streams with high intrinsic potential can be identified and then targeted, as appropriate, for salmon conservation across a landscape. Such areas of high intrinsic potential are essentially "species strongholds" from which aquatic-terrestrial linkage areas can originate. Areas of high intrinsic potential for some salmonid species may occur in larger streams, but tools exist to easily identify headwater streams that feed into these both laterally and from upstream (Clarke et al. 2008).

Second, criteria for Priority Amphibian and Reptile Conservation Areas (PARCAs) are under development for nationwide application (Riley et al. 2011). PARCAs are being discussed for integration into the landscape planning processes of other entities, such as the U.S. Department of Interior Landscape Conservation Cooperatives (*http://www.doi.gov/lcc/index.cfm*), which is a partnership network to sustain America's land, water, wildlife, and cultural resources. Once established, PARCAs would function as species strongholds. Similarly, the International Union for the Conservation of Nature (IUCN) is developing criteria to identify sites of global significance for biodiversity conservation, called Key Biodiversity Areas. Such areas are synonymous with the concept of species strongholds. The additional element that we suggest is to provide connectivity among such areas.

Third, triads, as we previously described, could be ideal locations for species strongholds, as these occur at the ridgeline junction of three large basins. However, we note that triads are not established biodiversity hotspots, and are proposed here as a conceptual design.

Development of landscape-scale linkage webs from either new or existing species strongholds is needed to reduce isolation of those areas, and as possible to allow them to function as potential "source" habitats with optimal conditions that can anchor species over time and also connect to adjoining areas, in a metapopulation context. Linking dispersal pathways from strongholds up and over ridgelines to adjacent watersheds and neighboring strongholds is a direct approach that may offer a least-cost path. Relevant to our proposed headwater linkage areas concept, connecting such species strongholds to headwaters which then extend and connect over ridgelines is another consideration. Additionally, strongholds may be linked to protected riparian areas along larger streams that are subsequently extended upstream into headwaters and connected over ridgelines. Multiple connectivity pathways may be conceived. As a web of connections is considered relative to species stronghold connectivity, the previous priorities discussed above and outlined in table 2 can be overlain, including large basins and triads, linear trajectories to address for climate change gradients, and occurrence of landslide-prone areas.

Adaptive management of strongholds may need to be addressed over the long term as future conditions unfold. As applied here, the concept of a stronghold evokes less of an immovable fortress than an anchor. A species stronghold intended to anchor habitat may need to function as do real anchors on occasion, and be repositioned or "drag" across landscapes in response to changing conditions or management priorities (Olson et al. 2007). The temporal scale of strongholds can be addressed at the time of their development, and interact with the spatial scale of stronghold designs and the frequency of strongholds. For example, habitat anchors designed to drag across landscapes may be implemented more easily if they are smaller and more numerous. Olson et al. (2007) suggested considering 6th-code watersheds (HUs) as a spatial scale for amphibian habitat anchors. The anchor concept warrants testing, with a sufficient timeframe to weigh success at the landscape scale, in addition to replication. It may have greater success if it were to be implemented in areas with more resilient ecosystems.

## 5. Thinking Diagonally: Funnels and Chains

The geometry and land-management context of land-use and land-ownership parcels on the landscape is a final set of priority considerations for linkage-area placements that we will develop briefly here. The northwest forest landscape is a patchwork of land ownerships and land-use allocations, each with differing management priorities, which creates a complex challenge for biodiversity conservation (Suzuki and Olson 2007). During planning for large blocks of forest land, and during planning of individual projects at smaller spatial scales, managing for connectivity within and among ownership areas can be difficult due to differing priorities across boundaries. To diminish the dilemma of achieving effective biodiversity conservation in such a multi-ownership landscape, it may help to think of streams as dispersal "funnels" that serve to channel organisms along protected riparian areas, and connectivity corridors or linkage areas as "chains" functionally moving animals up and over ridgelines (Olson and Kluber, unpubl. data). Overlaying many of the previously discussed priorities can provide an integrated perspective for addressing the challenges of land-ownership/allocation geometries.

Diagonal linkage areas are of specific relevance in a landscape with a checkerboard ownership pattern (fig. 7), and in other landscape geometries that abut at corners or other edge types (Olson and Kluber, unpubl. data). Species dispersal along such diagonals might be promoted by forest management actions that retain habitat elements toward the corners of such lands. For example, weighted green-tree retention, leave islands, and directional felling of down wood (recruitment of large logs, in particular) from corners may assist migration of species along the diagonal by providing chains or stepping stones of suitable microhabitats for species refugia. Linking chains of habitat elements from corners to stream- and riparian-protected areas, especially headwaters (fig. 7B), may functionally extend and connect riparian buffers. Organisms that are funneled along riparian areas may venture through corners via these habitat chains. A chain of habitat need not extend from headwaters, but could extend from any part of a riparian buffer, or from a species stronghold, as discussed above.

It may be neither feasible nor desirable to address habitat connectivity at all corners of adjacent lands within an ownership. Similarly, when land parcels are in close proximity but do not adjoin, it may not be possible to consider linkage areas along their entire boundaries. Several additional design concepts arise and interface with ideas presented above.

First, linkage areas among land parcels might be "stream-lined" if streams align through corners (fig. 8), or connect nearby land blocks. When streams follow diagonals in a checkerboard landscape, riparian protection may more effectively promote multi-species diagonal dispersal: funnels without the added chains linking across diagonals. Streams that loosely follow diagonals, not intersecting exactly at corners, could be quite functional to assist species

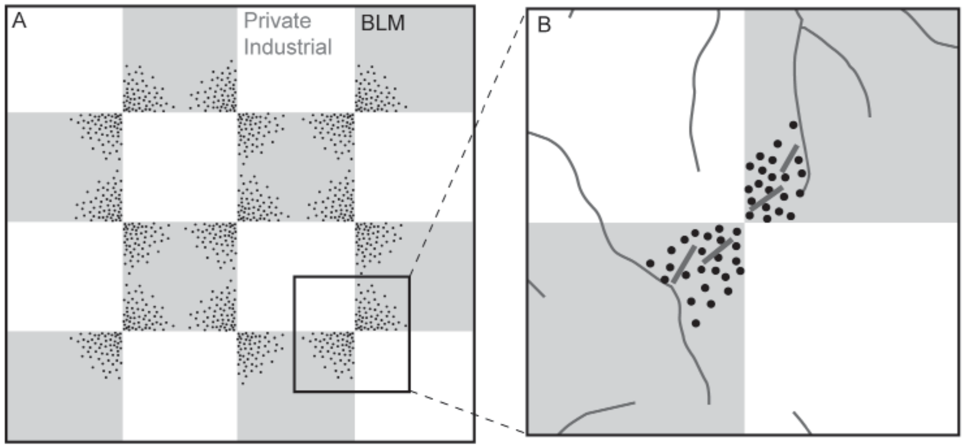


**Figure 7—**In a checkerboard ownership pattern, such as that created by the Oregon and California Lands Act (1937) where US Bureau of Land Management (BLM) and private industrial forestlands are intermixed, management for connectivity along diagonals may improve likelihood of species dispersal within ownerships. A: Corners are shaded to show linkage area considerations. However, routes along selected diagonals to species strongholds, reserves, or triads might be used to prioritize which corners are chosen for connectivity emphasis. B: Forest management options to facilitate species dispersal from stream corridors (which may serve to funnel species movements) to corners might include chains of habitat structures provided by green tree retention, directional log placement from corners to streams, or both. Concepts could be applied to other ownership geometries with corners or edges in proximity.


**Figure 8—**Connectivity designs to aid species dispersal among ownership blocks may overlay on streamside riparian management zones. This US Bureau of Land Management study site for the Density Management and Riparian Buffer Study of western Oregon (Cissel et al. 2006) shows riparian buffers extending along the full diagonal (A) as well as laterally toward an opposing corner (B), with leave islands and dispersed tree retention aiding habitat connectivity, and to a neighboring private land block (C). "Stream-lined" connectivity (A) may aid within-watershed dispersal, but overland connectivity designs (B and C) may warrant consideration to link or "chain" habitats overland between watersheds. Photo provided by Oregon Bureau of Land Management.

migration, in this regard. Streams that link disconnected parcels may similarly function to funnel organisms' movements. The context of the adjoining lands may need to be assessed, however. Managing such a stream-line to promote its potential connectivity function is a consideration, but such stream-lined connectivity does not address overland dispersal. Chains from streams to ridgelines are needed to fully integrate aquatic and terrestrial landscape connectivity functions. Collaborative management of such stream-lines and overland chains among ownerships and across land-use allocations within ownerships, remains a challenge.

Second, in multi-ownership landscapes, road densities may be higher than in single owner landscapes. An assessment of the effects of roads on species connectivity designs may be particularly important in these landscapes. In particular, paved roads or high-use unpaved roads may be barriers to low-mobility species. As roads intersect streams, aquatic organism passage may be affected, with consequences for overland connectivity. Site-specific designs can include these considerations.

Third, as hazard models of disturbances are developed for a landscape, it may be helpful to ask how hazards align with land-ownership boundaries, land-use allocations, and existing connectivity webs. For example, how are landslide-prone areas arranged relative to the geometry of lands by ownership and land-use allocation? As discussed above, can priority linkage areas be designed to overlay on landslide-prone areas that are already set-asides for riparian reserve management, and now also serve "to chain" habitats to adjoin land-ownership blocks?

Fourth, in a larger landscape context, it may be useful to know how larger basins, climate change projections, and species strongholds are arranged and whether these be used to prioritize connectivity area pathways. Can dispersal routes be conceived from streams and then through land-ownership diagonals or between ownership blocks to foster connections relative to these issues?

Multiple overlapping considerations are emerging, and a stepwise process may be needed to integrate them. Limitations may emerge due to topography, geometry of land configurations at local scales, or pre-existing conditions. For example, a dispersal barrier such as a road may need to be considered first. The existence of under-road culverts may create spatially explicit bottlenecks for connectivity planning. Routing linkage area pathways to those stream corridors and culverts may be needed to increase the odds of dispersal across the road. Culverts that act as dispersal nodes in this way could be prioritized for enhancement to provide passage for non-aquatic species. Similarly, triads and species strongholds, as discussed above, are essentially dispersal nodes. Routing dispersal routes via headwater linkage area pathways to triads and strongholds could increase the overall effectiveness of these conservation measures.

## Conclusions

Forest biodiversity conservation is an ecosystem service that will continue to be addressed at local-to-landscape scales in the coming century. Retaining organisms across managed forest landscapes requires a toolbox of approaches including fine- and coarse-scale habitat protections and restoration practices, retaining or creating structural elements that are critical habitats for species, and development and management of connectivity pathways to allow gene flow. Renewed efforts to address communities of organisms as well as species of concern are called for as emerging stressors need evaluation, new knowledge is accrued, and adaptive management of existing forest plans are needed.

We review the numerous benefits of forest connectivity designs that rely on headwater linkage areas, and emphasize priorities for their placement at landscape scales. The benefits of headwater linkage areas include their likely functional role in integrating aquatic and terrestrial systems, their potential use by multiple taxonomic groups, their utility for creating webs of connections across forested lands to increase their effectiveness for biodiversity conservation, and their efficiency in minimizing both the distances that animals must move overland and the financial burdens of forest manager.

Placement of headwater linkage areas may include consideration of a variety of factors (table 2). Prioritizing linkage areas can provide a starting point for managing connectivity among critical habitat areas, suggest directional routes for dispersal among areas, or identify dispersal nodes as anchors for connectivity webs. The five priority considerations that we developed include triads that effectively link three larger basins, north-south and east-west directional routes to address climate change scenarios, linkages overlaid on management of disturbances such as landslide-prone areas, links among species strongholds, and diagonal links that route dispersal across management boundaries. These five concepts can be integrated into an overall geometry of landscape connectivity designs. Our conceptualization of headwater linkage area utility and these priority considerations are posed as hypotheses warranting further study and development. We offer these ideas with the caveat that they will not benefit all taxa in forested landscapes. Extremely rare or patchily distributed organisms with low mobility may need a finer-grained, site-by-site conservation approach (Raphael and Molina 2007).

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