Fragmentation and Connectivity Considerations for Larimer County Open Space Lands

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Background

New parcel acquisitions and coordination with City of Fort Collins on northern Larimer county public lands are driving upcoming management plan revisions for Red Mountain Open Space and Horsetooth Mountain Open Space. Intensive recreational use of Horsetooth Mountain Open Space and other open space properties is also increasing concern about the effects of habitat fragmentation, and county staff are in need of information about methods of retaining connectivity in these areas. The following summarizes a literature review of existing methods for identifying and managing fragmentation and maintaining functional habitat patches, with a focus on foothill habitat types that are present in Larimer County.

Fragmentation and connectivity

The study of fragmentation and connectivity are typically part of the field of landscape ecology, which identifies, describes, and analyzes the spatial patterns and processes of ecosystems, and tracks changes in those patterns. The origins of interest in these topics can be traced to several converging lines of investigation in ecology, including the theory of island biogeography (MacArthur and Wilson 1967), metapopulation dynamics (Pulliam 1988, Hanski 1991), and biodiversity conservation (Soulé and Wilcox 1980). Each of these fields concerns itself with the behavior of plant and animal populations in a patchy environment. These several topics were largely pulled together by pioneers in the emerging field of landscape ecology (Wiens et al. 1985, Noss 1990, Turner et al. 1993, Forman and Godron 1996), with the realization that ongoing human impacts and use of the landscape make it important to both understand and quantify the species-specific effects of changing landscape patterns in order to conserve biodiversity (Noss and Cooperrider 1994).

What is fragmentation?

The heterogeneity of different habitat patch types in a natural landscape is not necessarily fragmentation, but simply a characteristic of the environment to which animal and plant species have become adapted. Fragmentation is essentially the result of habitat loss; the removal or alteration of native vegetation produces remnant isolated patches surrounded by agriculture, development, or other changed use (Saunders et al. 1991, Didham 2010). Fragmentation can be considered both a process (change in habitat amount) and a pattern (spatial arrangement of habitat patches), although both are most properly measured at the landscape scale (Fahrig 2003). A transition from one land cover type to another is a patch “edge” in the landscape pattern. Roads and trails, with their zones of influence extending beyond the actual footprint, are also edges. The arrangement of and connections between habitat patches on the landscape can mitigate for loss of habitat to some degree, so this topic is a key factor in protected area design.

Why fragmentation is a problem

Habitat fragmentation can be the result of any barrier to movement in otherwise continuous habitat. Barriers and other habitat changes can reduce or eliminate the foraging, migration, mating, or dispersal of individuals, and lead to decreased individual fitness and reproduction, with eventual impacts on population sizes and genetic variability (Didham 2010). Barriers may include lack of sheltering vegetation, vegetation that is too dense, housing developments, energy extraction activity, and linear features such as fences, canals, railways, roads, and trails. The scale and mobility of an organism and its physical requirements during different parts of its life cycle determine how habitat patchiness or fragmentation affect its ability to persist, thrive, and reproduce. Because species differ in their ability to move across these barriers, each species perceives landscape patchiness differently. Fragmentation isolates patches of suitable habitat, and can change the physical environment of remnant patches by changing patterns of exposure to sunlight, water, and air movement (Harper et al. 2005, Fischer and Lindenmayer 2007). Patch edges may support more species than core areas, but this is not always a good thing. Edges can allow invasion by non-native or aggressive species, or magnify the amount of disturbance experienced by organisms in the vicinity. In general, fragmentation has significant negative effects on biodiversity.

When is a fragmentation analysis useful?

Measures of fragmentation are numerous, and often difficult to interpret in a biological or ecological context. Early indices were derived from information theory (e.g., O'Neill et al. 1988), and measured landscape richness, evenness, patchiness and diversity, similar to indices of species diversity. Additional indices based on patch arrangement (e.g., fractal dimension, contagion, nearest neighbor) were soon developed to describe landscape structure (reviewed by Turner 1989). With the development of the FRAGSTATS spatial pattern analysis software (McGarigal and Marks 1995), the ease of calculation and number of potential metrics increased dramatically, spawning something of an academic cottage industry in theoretical comparisons and development of additional fragmentation metrics. Cushman et al. (2008) eventually identified a subset of components as a minimum set of structure attributes to describe landscape structure (Table 1), but stopped short of recommending specific metrics to measure these components.

Fragmentation analysis describes the arrangement of patches in the analysis area, primarily through the use of statistics. The resulting values are highly scale dependent, results differ according to the size of the analysis area and the grain of analysis (i.e. pixel size), and the values are difficult to link to effects experienced by plants and animals. Fragmentation metrics are most useful for comparisons that ask questions such as:

- Which of two or more otherwise very similar parcels is least fragmented?
- Is a particular management action successful at reducing fragmentation?
- On comparable areas that are managed differently, which management is best for reducing fragmentation?
- Is fragmentation increasing over time in this landscape?

Šimová and Gdulvoá (2012) identify a few relatively easy to interpret indices, including number of patches, patch density, edge density, and mean patch size that have predictable response to changes in scale. Finally, there is increasing acknowledgement that other measures of community structure, such as community composition, and species presence or use patterns may be better descriptions of fragmentation effects biotic communities (Wilson et al. 2016).

Table 1. Universal components of landscape structure (adapted from Cushman et al. 2008).

Component	Description
Contagion/diversity	Degree of aggregation of patch types (or the overall clumpiness of the landscape) and the diversity/evenness of patch types. Contagion and diversity are inversely related; clumped landscapes containing large, compact patches and an uneven distribution of area among patch types have high contagion and low diversity.
Large patch dominance	Degree to which the landscape is dominated by large patches.
Interspersion/juxtaposition	Degree of intermixing of patch types.
Edge contrast	Degree of ‘‘contrast’’ among patches, where contrast is user-defined and represents the magnitude of difference between classes (e.g., vegetation types, etc.) in one or more attributes.
Patch shape variability	Variability in patch shape complexity, where shape is defined by perimeter-area relationships.
Proximity	Degree to which patches are isolated from nearby patches of the same type.
Nearest neighbor distance	Proximity of patches to neighbors of the same type, based on the area-weighted average distance between nearest neighbors.

Although it is possible to detect changes using fragmentation metrics, if the changes are small we have low confidence that change is the result of our actions instead of some other, possibly unknown, factor. In addition, animals and plants on the landscape may not agree with our diagnosis of reduced fragmentation. Finally, good comparisons across time depend on having good baseline data.

What is connectivity?

Structural connectivity is similar to the description of fragmentation, concerned with the pattern of structural elements (habitat patches, topography, barriers, etc.) on the landscape. In contrast, functional connectivity is concerned with how easily organisms can travel or be successfully dispersed from one suitable habitat patch to another across intervening sub-optimal habitat types (Taylor et al 1993). A functional connectivity (or functional patch) analysis is a measure of landscape connectivity or permeability. Individual species have different habitat patch-size and composition requirements, and vary in their ability to travel between habitat patches across intervening unsuitable or dangerous areas. In addition, animal movements on a daily or seasonal basis may require different scales of habitat patches (Chetkiewicz et al. 2006). Patch size requirements can even differ between male and female individuals of the same species.

When is connectivity analysis useful?

As with fragmentation, there are numerous methods for connectivity analysis producing estimates or models of how particular species are moving between core habitat areas on the landscape. This task can be as basic as local experts drawing circles and lines on a map. Expert knowledge can also provide parameters for complex species-movement models. Some type of corridor-delineation method is typically used for connectivity analysis. One common and widely used method is the “least-cost path” analysis (Adriaensen et al. 2003), which calculates *effective distance,* or the actual distance between habitat patches, weighted by the difficulty (cost) of movement between patches. Least-cost paths avoid difficult, dangerous, or unsuitable terrain if possible, while balancing the energy-efficient tendency of an animal to take the shortest path between two patches. Analyses based on graph theory (including networks and circuits) are another popular method for modeling functional landscape connectivity (McRae et al. 2008, Galpern et al. 2011, Rayfield et al. 2011). These analyses generate multiple patch connections, and focus on the *resistance* or difficulty of use for each corridor.

A generalized, or coarse-filter connectivity analysis (i.e., not tied to a particular species) can be used to identify core areas and connecting corridors that are primarily natural habitat, with the assumption that these more natural areas are more likely to support a variety of species. In general, connectivity analyses should be focused on a particular species of management concern, and incorporate everything that is known about its life cycle and habitat requirements. Connectivity analyses are most useful in situations where:

- A species is a clear management concern (populations declining, roadkill problem, etc.) and movement pinch-points need to be identified
- There are multiple alternatives but limited funding for actions to improve connectivity on the landscape; prioritization is needed
- Concerns about changes to the landscape under future climatic conditions are driving a need to identify where movement corridors may be lost or persist

The utility of any connectivity analysis increases with good information about the species using the landscape, but no analysis can guarantee that species will use corridors in the way predicted by the models. As with fragmentation, analysis results are scale-dependent; species may use paths that lie outside the analysis area for at least part of their length. When corridors or links have been identified, prioritization criteria can define relative linkage importance by the number of focal species likely to use it, use by a focal species of regulatory or other concern, known migratory pathways, or greatest permeability. Corridors that are already of an ecologically relevant size and configuration would likely be the focus of conservation efforts, whereas important linkages that are not in an optimal configuration could be prioritized for management and restoration efforts. Barriers and bottlenecks within an important linkage must be addressed to maintain linkage viability, and ownership, easement status, and habitat quality of an area will further focus County efforts on effective strategies.

Managing for connectivity in Larimer County

Larimer County covers the northernmost stretch of eastern mountain front in the state, from the Little Thompson River north to the Wyoming border, and west to the continental divide. In the foothills vicinity, land use and cover include natural vegetation, agriculture, and levels of development ranging from sparse to heavy. Natural habitats transition from shortgrass prairie to montane forest with increasing elevation. Larimer County Department of Natural Resources (LCDNR) lands are imbedded in a largely natural landscape in many areas, and support characteristic habitats of the area. These lands are largely dominated by foothill shrubland and grassland vegetation, with a substantial component of ponderosa pine woodland and shortgrass prairie as well. Riparian habitats are comparatively rare on LCDNR lands, as valley bottoms have historically been largely privately owned throughout the region. Each of these vegetation types supports a different suite of species, with smaller or less mobile species more-or-less confined to a single type, while larger species range across multiple vegetation types in the course of their lives. LCDNR lands are part of a mosaic of public and private lands, but are frequently adjacent to other natural or less disturbed lands, which increases the potential for conserving and managing habitat connectivity. At the same time, however, the proximity of many LCDNR parcels to developed residential areas, especially the cities of Fort Collins and Loveland, also increases the potential for negative impacts from human activities.

Area-sensitive mammal habitat in Larimer County

Natural vegetation of the mountain front in Larimer County provides habitat for a number of larger mammal species (Table 2), and LCDNR lands play a clear role in overall landscape connectivity for these species within the region. In particular, ungulates such as mule deer and elk are present as resident populations in the area, both in and around LCDNR units (Figure 1a and b). The foothills landscape forms an important part of local wintering habitat for both species. Deer populations support mountain lions in the area (Figure 2a), and black bears are also relatively common in the region (Figure 2b). Although these four species are highly mobile, wide-ranging, and dependent on large habitat blocks, many other wide-ranging or area-sensitive mammal species are present as well, both species of management concern (e.g., pronghorn, swift fox, Aberts squirrel) and common (e.g., bobcat, coyote, badger, etc.). In addition, numerous comparatively sedentary species of small patches (e.g., mice, squirrels, rabbits, snakes, lizards, butterflies), as well as highly mobile flying species (birds, bats), each with its particular response to disturbance and habitat fragmentation, are present on LCDNR lands, and can be impacted by habitat fragmentation.

Table 2. Area-sensitive mammal species that may use Larimer County Department of Natural Resources units. The primary focal species are indicated with red Xs.

Unit	Aberts squirrel	Bighorn sheep	Black bear	Black-tailed prairie dog	Elk	Moose	Mountain lion	Mule deer	Pronghorn	River otter	Swift fox	White-tailed deer
Big Thompson Parks	X	X	X		X	X	X	X		X		X
Devil's Backbone/Rimrock			X		X		X	X				X
Flatiron Reservoir			X		X		X	X				X
Carter Lake			X		X		X	X				X
Eagle's Nest	X		X		X	X	X	X	X		X	X
Fossil Creek Reservoir			X	X				X				X
Hermit Park	X		X		X	X	X	X				
Horsetooth Mountain	X		X		X		X	X				X
Pinewood Reservoir			X		X		X	X				
Ramsay-Shockey			X		X		X	X				
Red Mountain	X		X	X	X		X	X	X		X	X
Lions Open Space			X	X			X	X		X		X
River Bluffs				X				X		X		X
Chimney Hollow			X		X		X	X				
Red-tail Ridge			X	X	X		X	X				X

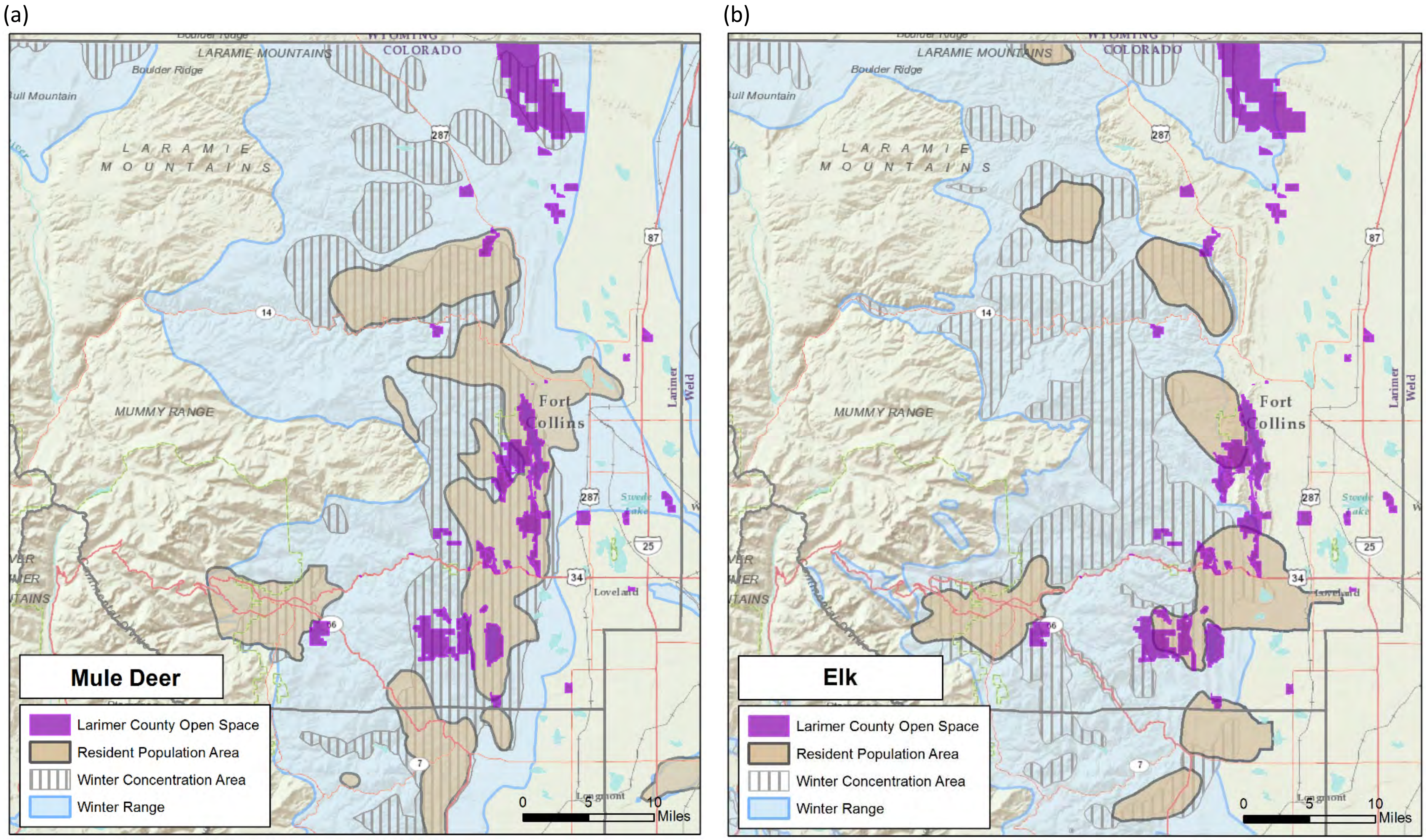

Figure 1. Colorado Parks and Wildlife seasonal activity maps for mule deer (a) and elk (b) in eastern Larimer County.

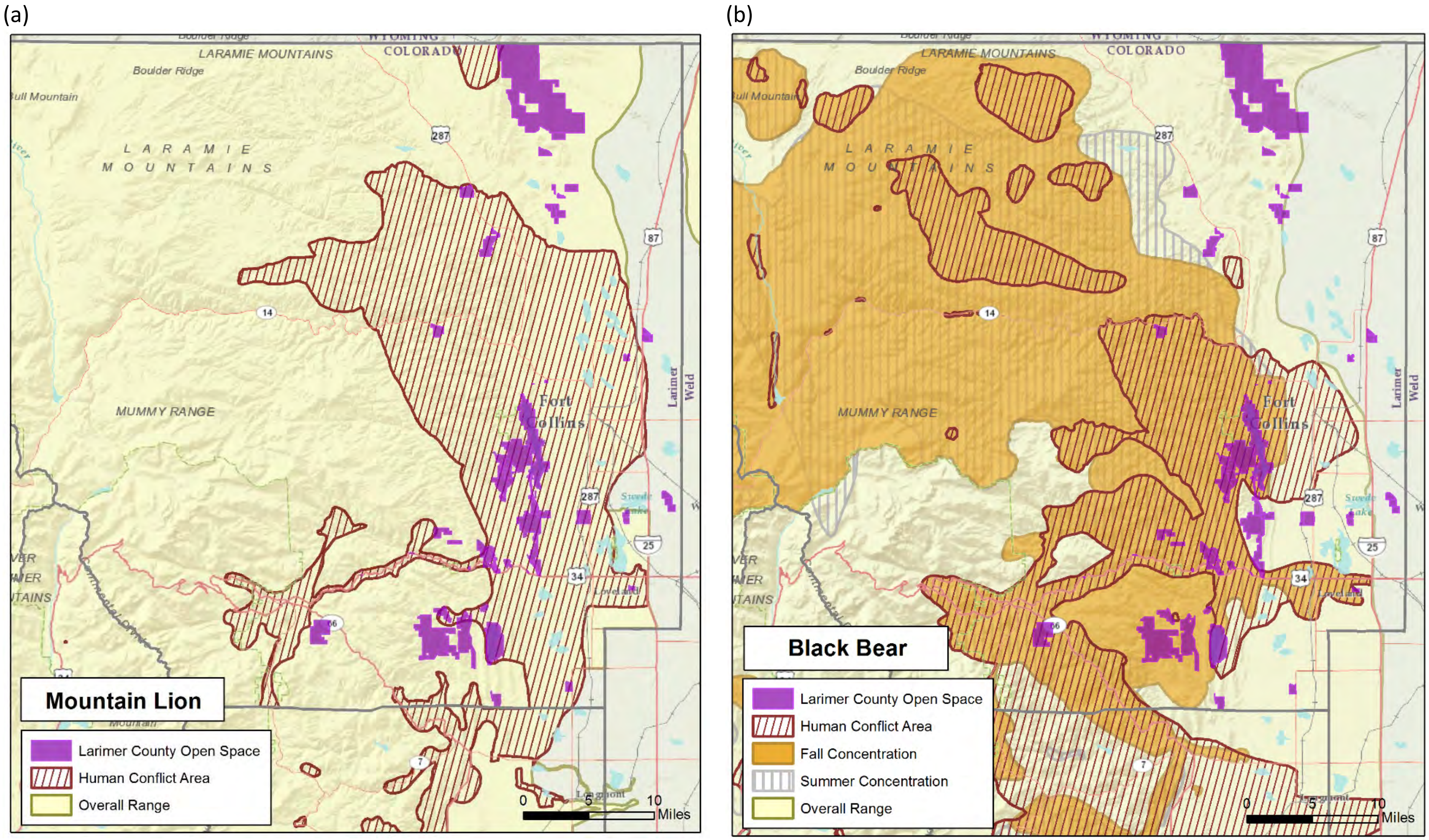

Figure 2. Colorado Parks and Wildlife seasonal activity maps for mountain lion (a) and black bear (b) in eastern Larimer County.

Hierarchy of habitat patch sizes

The multi-scale nature of fragmentation and connectivity considerations should also apply to land management within LCDNR parcels. An area of relatively undisturbed natural vegetation within a LCDNR parcel is also likely to be part of a larger ecosystem patch within either the foothill, montane, or plains zone, and in turn, part of the natural landscape of the mountain front region in northern Colorado and southern Wyoming.

An ecosystem patch in this context refers to an area generally dominated by a particular vegetation type (defined as a recurring group of biological communities found in similar physical environments and influenced by similar dynamic processes, such as fire or flooding), but that is likely to have small inclusions of dissimilar types. A mapping representation that smooths out the small dissimilar inclusions is suitable for determining the approximate extent of large patches. Patches of types that occur in the same local region (e.g., foothill shrublands and foothill grasslands) will often be intermingled, and may therefore in some circumstances be managed as part of the same habitat patch. The patchiness of each type is perceived at different scales by individual species, thus, conservation efforts should focus at appropriate spatial levels.

Although management actions are limited to LCDNR properties, the larger ecological context and effect of these actions should be considered. A hierarchy of potential landscape scales is used in Table 3 to illustrate how patch sizes within LCDNR lands can be tied to the larger landscape context. Vegetation types within LCDNR parcels can be delineated at different levels of the hierarchy, depending on management goals. Whenever possible, higher levels should be used in preference to lower levels in setting connectivity goals.

Table 3. Hierarchy of minimum patch sizes for management targets occurring on LCDNR lands.

Area considered	Habitat evaluated:	Minimum size (acres)	Source
Mountain front region (N. Colo/S. Wyo)	Natural landscape	30,000	Minimum matrix-forming ecosystem occurrence size
	Ecosystem combination patch	10,000	2x large patch best size
Zone (foothill, lower montane, plains)	Natural landscape	16,200	Average of zonal patch sizes > 100 ac in region
	Ecosystem patch	5,000 (3,200)	Large patch best size (if excellent condition)
	Large/highly mobile species (bear, lion)	12,000	Home range size estimates from literature
	Mid-sized, moderate range species	300- 5,000	Home range estimates from literature Highly variable by species
LCDNR unit	Natural landscape	5,000 (2,600)	Large patch best size (if excellent condition)
	Ecosystem patch	1,200	Large patch minimum size
	Mid-sized, moderate range species	unknown	Highly variable by species
	Matrix vegetation community	50	Generalized C-rank min, foothills
	Large patch vegetation community	25	Generalized C-rank min, foothills
	Small patch/sessile/habitat specialist target (butterflies, rare plants, etc.)	3-60	Buffered populations or habitat M2P and EO specs
	Linear ecosystem type	0.5 mi	Minimum linear occurrence size

An area within an LCDNR parcel that is part of a large, relatively undisturbed natural landscape (i.e., an area including all native vegetation cover occurring in a contiguous patch not broken or separated by major barriers such as urban or industrial development, interstate or state highway) can contribute to the overall minimum size of that natural landscape if maintained unfragmented. If zonal vegetation types such as foothills shrubland are targeted, the generalized ecosystem patch minimum size can be used as goals. The ecosystem patch is best defined using a geo-spatial technique to identify contiguous cover of matrix-forming or large patch ecosystem vegetation that may include small patches of other types. CNHP defined patches according to SW Regional GAP vegetation mapping, smoothed by using a focal majority ½ mile radius moving window analysis (Rondeau et al. 2011). For example, Red Mountain Open Space is part of a largely natural landscape between I-25, and Highway 287 south of the Wyoming border that exceeds 150,000 acres (Figure 3). Within the foothill zone of this landscape, Red Mountain Open Space overlaps a patch of foothill shrubland ecosystem larger than 28,000 acres. The portion of this patch that falls within the LCDNR boundary is about 7,900 acres. Because ecosystem patches are delineated at a landscape level using major barriers, it may be more appropriate for LCDNR to modify patch boundaries within their holdings using smaller, more local effect disturbances such as primitive roads and trails.

Anthropogenic (human-caused) disturbance is a primary source of fragmentation (Cushman et al. 2008). Disturbance effects due to human presence or landscape modification can be assessed as either the distance to a particular disturbance or the density of disturbance within an area of concern. Disturbance types vary in their intensity and distance effects (Figure 4); these variations are probably species-specific, and have not been investigated for most species. However, a generalized landscape disturbance index (LDI, Figure 5) can be used to identify the cumulative effects of a variety of disturbance types (Decker et al. 2017). Best management practice suggests that additional disturbance should avoid previously undisturbed area, and where possible, be concentrated in the influence zone of existing disturbances. Additional disturbance should also be sited in such a way as to avoid breaking a single large patch into one or more much smaller patches. Patches that extend across LCDNR boundaries should also be considered when minimizing fragmentation; disturbance sited along a LCDNR boundary in an effort to maintain the largest within-parcel patch size may have the effect of breaking off a sizeable portion of a much larger cross-boundary patch.

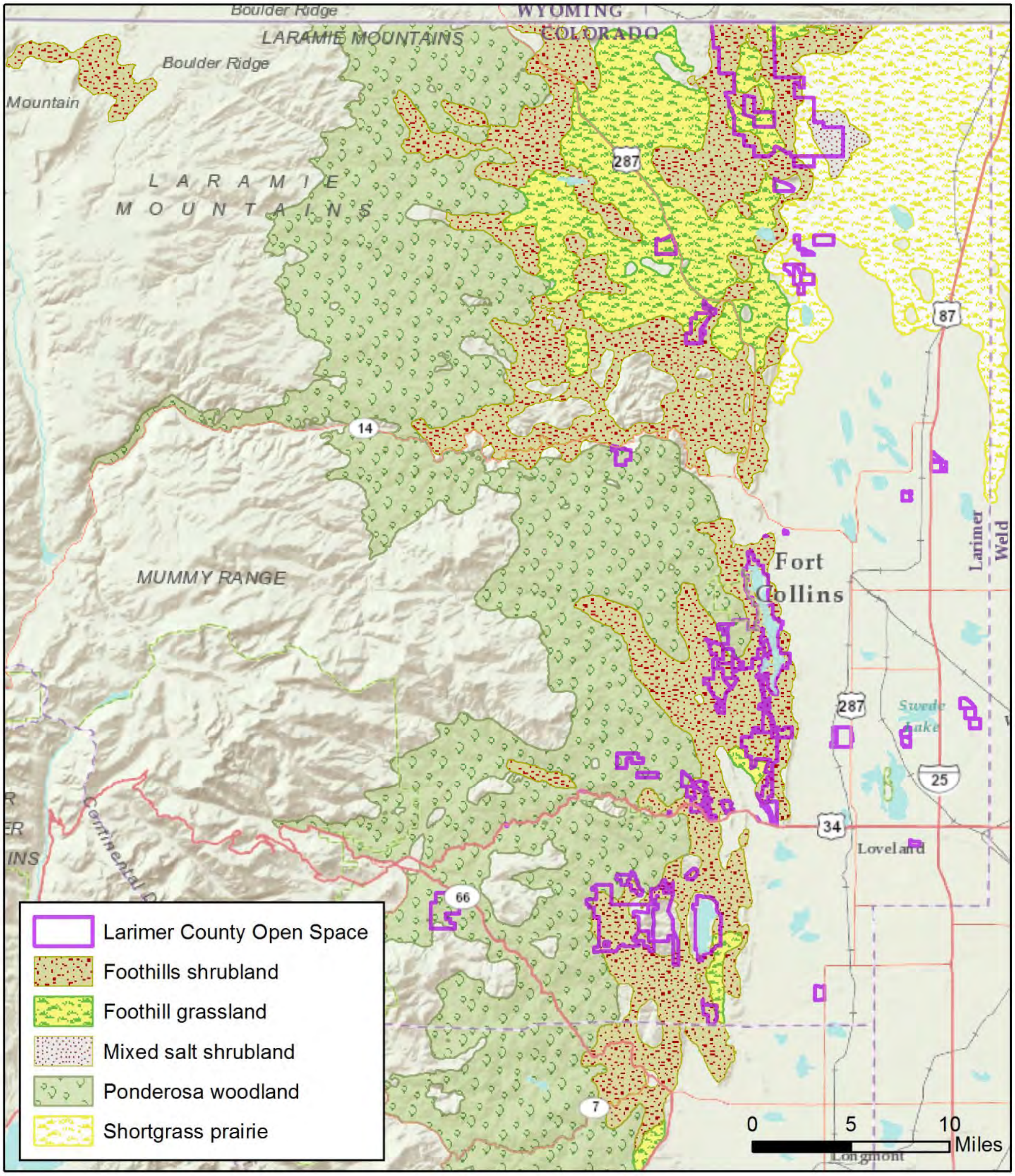

Figure 3. Lower montane, foothill, and plains ecosystem patches in Larimer County.

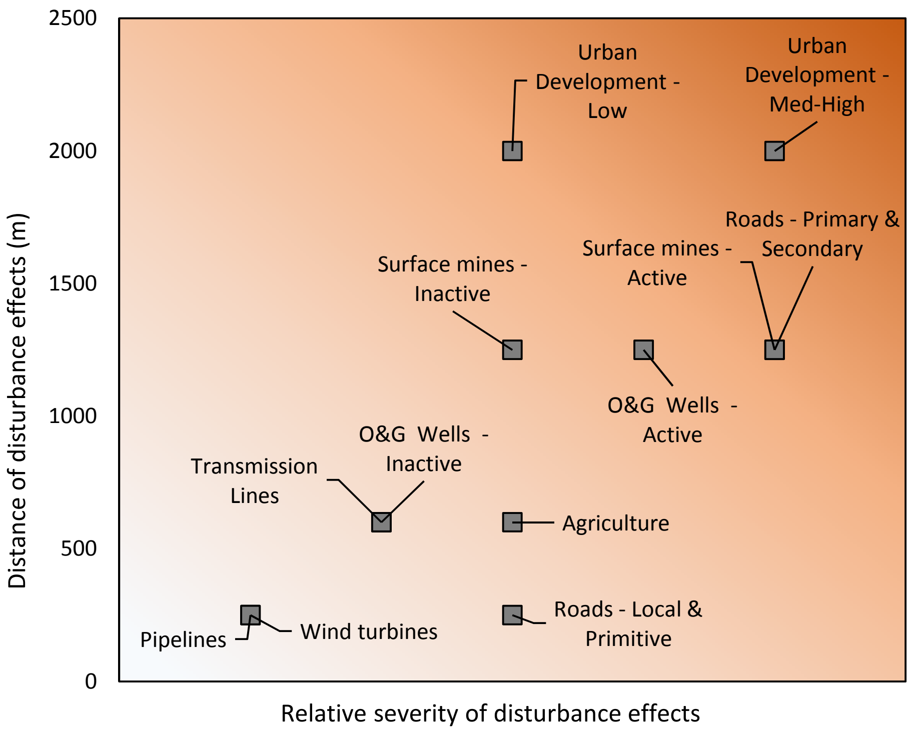

Figure 4. Comparative effects of anthropogenic disturbances included in statewide landscape disturbance index for Colorado.

The Colorado LDI incorporated only anthropogenic disturbance types for which reasonable mapping was available on a complete statewide basis. For individual LCDNR parcels, it may be feasible to map smaller and more localized disturbances, and their effect zones. In particular, recreational trails, which are not a major disturbance on a statewide basis, are an important disturbance source on open space lands in general.

Similar to roads, trails can act as patch edges, facilitating potentially negative human interactions with animals, allowing the spread of invasive species, and gradually degrade the overall quality of the adjacent plant community. If non-native species are already pervasive in an area (e.g., in former pasture areas), trail effects may be minimal (Tyser and Worley 1992), but disturbance tends to favor non-native plant species over natives in most situations (Jauni et al. 2015). The fragmenting effect of recreational trails is tied to use type and frequency; some species will be quite tolerant of disturbance and able to move between patch types, while others will gradually be lost from the area if disturbance increases. Although some highly adaptive species groups respond positively to human disturbance, the majority of documented effects of recreational use are negative (Larson et al. 2016), especially for smaller more sedentary species such as reptiles, amphibians, and invertebrates. Sensitive species or habitat should be buffered by a surrounding landscape composed of natural vegetation in good condition. Development that avoids fragmenting large patches will also protect migration corridors for important species, and intact patches can serve as refugia for sensitive species in case of widespread disturbance.

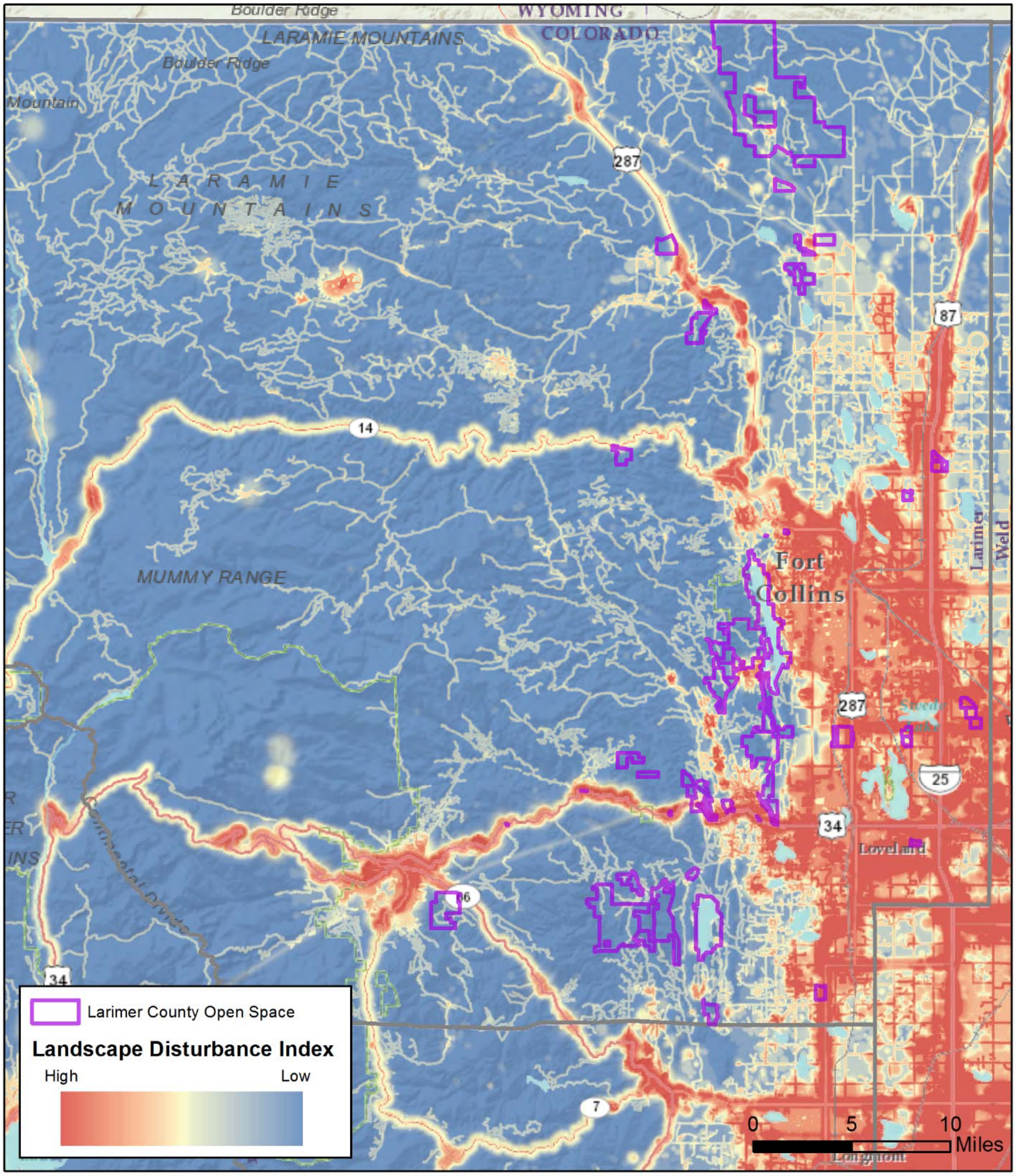

Figure 5. Modeled landscape disturbance intensity in Larimer County.

Managing LCDNR lands in ways that will prevent or decrease fragmentation and promote functional connectivity will depend on maintaining a clear intent to prevent habitat loss, while balancing the needs of different management perspectives (Table 4). Although construction and management costs are an important driver of open space development, ecological considerations are equally significant. The presence of federally regulated species (e.g., Preble's Meadow Jumping Mouse) or habitat types (e.g., wetlands, designated critical habitat) is an inescapable consideration in public land management. If knowledge of potential sensitive species and other wildlife on an area is inadequate, consider conducting surveys to identify species presence and habitat. Other ecological considerations include state or local species of concern, habitat quality, wildlife-human conflicts, landscape connectivity, and natural ecological processes such as fire, erosion, drought, and so forth. Presumably these factors also impact the quality of open space visitor experience to some extent, and should be considered in prioritization of management alternatives.

Lacher and Wilkerson (2013), in a review of state wildlife action plans, identified a handful of best practices for wildlife connectivity planning: 1) Collect ecologically meaningful background data on species and their habitats; 2) Be specific in stating goals, and prioritize actions and strategies; 3) Establish community-wide partnerships and foster collaboration; 4) Include monitoring and adaptive management, maintain information regarding wildlife presence in area 5) Account for climate change, recognizing that habitat conditions are likely to change in the future; 6) Incorporate sociopolitical and socioeconomic information that may influence the feasibility of management implementation.

Table 4. Overall goals and methods, with example actions for managing to preserve connectivity.

Goals	Methods	Actions
Preserve and maintain high-quality wildlife areas	Regulate land use	• Enforce open space regulations • Monitor impacts and adjust management • Use area closures as needed • Target additional parcel acquisition to provide buffers
Improve degraded areas where appropriate	Manage to reduce impacts	• Trail routing to avoid increasing fragmentation (trails are edges) • Access control (access points, use types and levels) to reduce wildlife disturbance
	Restore vegetation and natural processes	• Seeding/planting native species • Control of invasives • Restore natural hydrology
Connect natural areas	Improve overall landscape permeability	• Protect riparian corridors everywhere • Identify target species and their habitat requirements for connectivity management • Consider connectivity modeling • Don’t break up existing large patches • Collaborate with other land managing agencies for larger-area connectivity planning
	Reconnect broken corridors	• Target additional parcel acquisition to connect with other high-quality areas • Collaborate with other land managing agencies for larger-area connectivity planning
Educate	Transparency and communication about natural values and conflict areas	• Intra-agency communication (other county departments) • Collaboration with local and regional conservation groups / individuals • Strive for public buy-in for connectivity measures • Educational materials • Public outreach programs

Key points

- **Scale:** measurements of fragmentation change as analysis scale changes. Choose scales that reflect the way in which target species perceive the landscape.
- **Species-specific considerations:** Not only does each species perceive the landscape at a different scale, each species has different abilities to move within the landscape, and different requirements to successfully complete its life-cycle. Be aware that one size does not fit all in connectivity design.
- **Goals for biodiversity conservation:** Knowing what is being managed for and why are key considerations for reducing fragmentation and improving connectivity. Corridor design and anti-fragmentation actions will be most effective when focused on specific targets.
- **Thinking ahead:** Management for connectivity and biodiversity conservation is on-going, and future conditions may be different. Consider potential future costs of today's decisions.

References & Resources

General background

Decker, K. L., A. Pocewicz, S. Harju, M. Holloran, M. M. Fink, T. P. Toombs, and D. B. Johnston. 2017. Landscape disturbance models consistently explain variation in ecological integrity across large landscapes. Ecosphere 8(4):e01775. 10.1002/ecs2.1775

Didham, R.K. 2010. Ecological consequences of habitat fragmentation. In: Encyclopedia of Life Sciences (ELS). John Wiley & Sons, Ltd: Chichester. DOI: 10.1002/9780470015902.a0021904

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annu. Rev. Ecol. Evol. Syst. 34:487-515.

Fischer, J. and D.B. Lindenmayer. 2007. Landscape modification and habitat fragmentation: a synthesis. Global Ecology and Biogeography 16:265-280.

Forman, R.T.T. 1995. Some general principles of landscape and regional ecology. Landscape Ecology 10:133-142. Conservation Biology 19:768-782.

Forman, R.T.T. and Godron, M. 1986. *Landscape ecology*. John Wiley, New York.

Hanski, I. 1991. Single species metapopulation dynamics: concepts, models and observations. Biological Journal of the Linnean Society 42: 17-38.

Harper, K.A., E. MacDonald, P.J. Burton, J. Chen, K.D. Brosofske, S.C. Saunders, E.S. Euskirchen, D. Roberts, M.S. Jaiteh, and P-A. Esseen. 2005. Edge influence on forest structure and composition in fragmented landscapes.

Jauni, M., S. Gripenberg, and S. Ramula. 2015. Non-native plant species benefit from disturbance: a meta-analysis. Oikos 124:122-129.

Larson C.L., S.E. Reed, A.M. Merenlender, and K.R. Crooks. 2016. Effects of Recreation on Animals Revealed as Widespread through a Global Systematic Review. PLoS ONE 11(12): e0167259. doi:10.1371/journal.pone.0167259

MacArthur, R.H., and E.O. Wilson. 1967. *The Theory* of *Island Biogeography*. Princeton University Press, Princeton, NJ.

Noss, R.F. 1990. Indicators for monitoring biodiversity: a hierarchical approach. Conservation Biology 4:255-264.

Noss, R.F. and A.Y. Cooperrider. 1994. *Saving Nature's Legacy: Protecting and Restoring Biodiversity.* Island Press.

Poiani, K.A., B.D. Richter, M.G. Anderson, and H.E. Richter. 2000. Biodiversity conservation at multiple scales: functional sites, landscapes, and networks. BioScience 50:133-146.

Pulliam, H.R. 1988. Sources, sinks and population regulation. The American Naturalist 132:652-661.

Rondeau, R., K. Decker, J. Handwerk, J. Siemers, L. Grunau, and C. Pague. 2011. The state of Colorado's biodiversity 2011. Prepared for The Nature Conservancy. Colorado Natural Heritage Program, Colorado State University, Fort Collins, Colorado. https://cnhp.colostate.edu/wp-content/uploads/download/documents/the_state_of_colorados_biodiversity.pdf

Saunders, D.A., Hobbs, R.J., and C.R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biology 5:18-32.

Taylor, P.D., L. Fahrig, K. Henein, and G. Merriam. 1993. Connectivity is a vital element of landscape structure. Oikos 68:571-573.

Tyser, R.W. and C.A. Worley. 1992. Alien flora in grasslands adjacent to road and trail corridors in Glacier National Park, Montana (U.S.A.). Conservation Biology 6:253-262.

Wiens, J.A., C.S. Crawford, J.R. Gosz. 1985. Boundary dynamics: a conceptual framework for studying landscape ecosystems. Oikos 45:421-427.

Soulé, M.E. and B.A. Wilcox, eds. 1980. Conservation Biology: an evolutionary-ecological perspective. Sunderland, Mass: Sinauer Associates.

Fragmentation metrics

Calabrese, J.M., and W.F. Fagan. 2004. A comparison-shopper's guide to connectivity metrics. Frontiers in Ecology and the Environment 2:529-536.

Cushman, S.A., K. McGarigal, and M.C. Neel. 2008. Parsimony in landscape metrics: Strength, universality, and consistency. Ecological Indicators 8:691-703.

Dramstad, W.E. 2009. Spatial metrics – useful indicators for society of mainly fun tools for landscape ecologists? Norwegian Journal of Geography 63:246-254.

McGarigal, K. and B.J. Marks. 1995. Fragstats spatial pattern analysis program for quantifying landscape structure. https://www.umass.edu/landeco/research/fragstats/fragstats.html

McGarigal K., S.A. Cushman, M.C. Neel, E. Ene. 2002. FRAGSTATS: Spatial pattern analysis program for categorical maps. Comp. software prog. Univ. Mass., Amherst.

O'Neill, R.V., J.R. Krummel, R.H. Gardner, G. Sugihara, B. Jackson, D.L. DeAngelis, B.T. Milne, M.G. Turner, B. Zugmunt, S.W. Christensen, V.H. Dale, and R.L. Graham. 1988. Indices of landscape pattern. Landscape Ecology 1:153-162.

Rayfield, B., M. Fortin, and A. Fall. 2011. Connectivity for conservation: a framework to classify network measures. Ecology 92:847-858.

Šímová, P. and K. Gdulová. 2012. Landscape indices behavior: a review of scale effects. Applied Geography 34:385-394.

Turner, M.G. 1989. Landscape ecology: the effect of pattern on process. Annu. Rev. Ecol. Syst. 20:171-197.

Connectivity

Adriaensen, F., J.P. Chardon, G. De Blust, E. Swinnen, S. Villalba, H. Gulinck, and E. Matthysen. 2003. The application of 'least-cost' modelling as a functional landscape model. Landscape and Urban Planning 64:233-247.

Beier, P. 2012. Conceptualizing and designing corridors for climate change. Ecological Restoration 30:312-319.

Chetkiewicz, C-L.B., C.C. St. Clair, and M.S. Boyce. 2006. Corridors for conservation: integrating pattern and process. Annu. Rev. Ecol. Evol. Syst. 37:317-342.

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

Krosby, M. J. Tewksbury, N.M. Haddad, and J. Hoekstra. 2010. Ecological connectivity for a changing climate. Conservation Biology 24:1686-1689.

McRae, B.H., B.G. Dickson, T.H. Keitt, and V.B. Shah. 2008. Using circuit theory to model connectivity in ecology, evolution, and conservation. Ecology 89:2712-2724.

McRae, B.H., S.A. Hall, P. Beier, and D.T. Theobald. 2012. Where to restore ecological connectivity? Detecting barriers and quantifying restoration benefits. PLoSONE 7: e52604. doi:10.1371/journal.pone.0052604

Nunez, T.A., J.J. Lawler, B.H. McRae, D.J. Pierce, M.B. Krosby, D.M. Kavanagh, P.H. Singleton, and J.J. Tewksbury. 2014. Connectivity planning to address climate change.

Practical application

Ament, R., R. Callahan, M. McClure, M. Reuling, and G. Tabor. 2014. Wildlife Connectivity: Fundamentals for conservation action. Center for Large Landscape Conservation: Bozeman, Montana. http://largelandscapes.org/media/publications/Wildlife-Connectivity-Fundamentals-for-Conservation-Action.pdf

Aune, K., P. Beier, J. Hilty, and F. Shilling. 2011. Assessment & Planning for Ecological Connectivity: A Practical Guide. Wildlife Conservation Society, Bozeman, MT. http://www.wcsnorthamerica.com/

Beier, P., D. Majka, and J. Jenness. 2007. Conceptual steps for designing wildlife corridors. Available: http://corridordesign.org/dl/docs/ConceptualStepsForDesigningCorridors.pdf

Circuitscape Project. Free, open source connectivity modeling software http://www.circuitscape.org

Lacher, I., and M.L. Wilkerson. 2013. Wildlife connectivity approaches and best practices in U.S. state wildlife action plans. Conservation Biology 28:13-21.

Majka, D., J. Jenness, and P. Beier. 2007. CorridorDesigner: ArcGIS tools for designing and evaluating corridors. Available at http://corridordesign.org.

Trails and Wildlife Task Force, Colorado State Parks, Hellmund Associates. 1998. Planning Trails with Wildlife in Mind. Available as pdf files: http://cpw.state.co.us/Documents/Trails/TrailsPlanningPrimer.pdf or as a website hosted by American Trails: http://www.americantrails.org/wild/primer-wildlife-trails.html