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Review

# Toward Best Practices for Developing Regional Connectivity Maps

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**Abstract:** *To conserve ecological connectivity (the ability to support animal movement, gene flow, range shifts, and other ecological and evolutionary processes that require large areas), conservation professionals need coarse-grained maps to serve as decision-support tools or vision statements and fine-grained maps to prescribe site-specific interventions. To date, research has focused primarily on fine-grained maps (linkage designs) covering small areas. In contrast, we devised 7 steps to coarsely map dozens to hundreds of linkages over a large area, such as a nation, province, or ecoregion. We provide recommendations on how to perform each step on the basis of our experiences with 6 projects: California Missing Linkages (2001), Arizona Wildlife Linkage Assessment (2006), California Essential Habitat Connectivity (2010), Two Countries, One Forest (northeastern United States and southeastern Canada) (2010), Washington State Connected Landscapes (2010), and the Bhutan Biological Corridor Complex (2010). The 2 most difficult steps are mapping natural landscape blocks (areas whose conservation value derives from the species and ecological processes within them) and determining which pairs of blocks can feasibly be connected in a way that promotes conservation. Decision rules for mapping natural landscape blocks and determining which pairs of blocks to connect must reflect not only technical criteria, but also the values and priorities of stakeholders. We recommend blocks be mapped on the basis of a combination of naturalness, protection status, linear barriers, and habitat quality for selected species. We describe manual and automated procedures to identify currently functioning or restorable linkages. Once pairs of blocks have been identified, linkage polygons can be mapped by least-cost modeling, other approaches from graph theory, or individual-based movement models. The approaches we outline make assumptions explicit, have outputs that can be improved as underlying data are improved, and help implementers focus strictly on ecological connectivity.*

**Keywords:** connectivity, conservation planning, corridors, focal species, landscape conservation cooperatives, wildlife linkages

Hacia Mejores Prácticas para Desarrollar Mapas de Conectividad Regional

**Resumen:** *Para conservar la conectividad ecológica (la habilidad para soportar movimiento de animales, flujo de genes, cambios de rango de distribución y otros procesos ecológicos y evolutivos que requieren áreas extensas), los profesionales de la conservación necesitan mapas de grano grueso que sirvan como herramientas de soporte para la toma de decisiones y mapas de grano fino para recomendar intervenciones en sitios específicos. A la fecha, la investigación se ha centrado principalmente en mapas de grano fino (diseño de conexiones) que abarcan áreas pequeñas. En contraste, diseñamos 7 pasos para hacer mapas de grano grueso de docenas hasta centenas de conexiones en un área extensa, como un país, provincia o ecorregión. Proporcionamos recomendaciones de cómo llevar a cabo cada paso con base en nuestras*

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*experiencias con 6 proyectos: Conexiones Faltantes en California (2001), Evaluación de la Conexión de Vida Silvestre en Arizona (2006), Conectividad de Hábitat Esencial de California (2010), Dos Países-Un Bosque (noreste de Estados Unidos y sureste de Canadá) (2010), Paisajes Conectados del Estado de Washington (2010), y el Complejo del Corredor Biológico de Bután (2010). Los dos pasos más difíciles son el mapeo de los bloques de paisaje natural (áreas donde el valor de conservación se deriva de las especies y sus procesos ecológicos) y la determinación de los pares de bloques que son factibles de conectarse de manera que promueva la conservación. Las reglas de decisión para el mapeo de bloques de paisaje natural y la determinación de cuales pares de bloques serán conectados debe reflejar no solo criterios técnicos, sino también los valores y prioridades de los actores involucrados. Recomendamos que los bloques sean mapeados con base en una combinación de naturalidad, estatus de protección, barreras lineales, y calidad del hábitat para especies selectas. Describimos procedimientos manuales y automatizados para identificar las conexiones restaurables o funcionales actualmente. Una vez que los pares de bloques han sido identificados, los polígonos de conexión pueden ser mapeados por modelaje de costo mínimo, otros métodos de teoría de grafos o modelos de movimiento basados en individuos. Los métodos que delineamos hacen suposiciones explícitas, tienen resultados que pueden ser mejorados a medida que mejoran los datos subyacentes y ayudan a que los implementadores se concentren estrictamente en la conectividad ecológica.*

**Palabras Clave:** conectividad, conexiones de vida silvestre, cooperativas de conservación del paisaje, especies focales, planificación de la conservación

## Introduction

Conservation professionals often conduct spatially explicit analyses to identify areas important for ecological connectivity, which we define as the ability to support animal movement, gene flow, range shifts, and other ecological and evolutionary processes that require large areas. We use the term *map* to encompass these analyses, products, and explanations of how the products can be interpreted and used. These maps can be coarse grained or fine grained, each serving different and complementary needs. Coarse-grained (resolution $\geq$ 100 m), spatially extensive maps (typically > 20,000 km$^2$) depict dozens or hundreds of natural landscape blocks (areas whose conservation value derives from their content; synonymous with core areas or wildland blocks) and connectivity areas (areas whose conservation value derives from their context between landscape blocks and their potential to support movement of plants and animals between those blocks). We refer to these maps as regional connectivity maps; they serve as decision-support tools and concise expressions of desired future connectivity. In contrast, fine-grained (typically $\leq$ 30 m) connectivity maps prescribe site-specific interventions (e.g., conserving individual parcels, building highway-crossing structures in particular locations) needed to conserve or restore connectivity between 2 (rarely 3 or 4) landscape blocks, typically < 100 km apart. We refer to fine-grained maps as linkage designs. To date, connectivity modeling has focused on developing reliable linkage designs (summarized by Beier et al. 2008). Less attention has been paid to procedures for mapping connectivity among numerous natural landscape blocks over large areas, such as a nation, province, or ecoregion (i.e., creating a regional connectivity map).

In the United States, the first statewide connectivity maps were produced for Florida in 1998 (Hoctor 2004) and California in 2001 (Penrod et al. 2001). Bhutan, India, and Tanzania produced nationwide connectivity maps in 1999 (Wildlife Conservation Division 2010), 2005 (Menon et al. 2005 [for elephants, *Elephus maximus*, only]), and 2009 (Jones et al. 2009), respectively. Recent events have sparked more interest in producing statewide connectivity maps in the United States. In 2005 Congress required each state to develop and regularly revise their state wildlife action plans as a condition for receipt of federal funds (i.e., state wildlife grants). Many plans identified connectivity as a major concern and indicated that revised plans would include connectivity maps. Also in 2005, each state's transportation agency was required to coordinate its planning with that state's wildlife agency (Public Law 109–59). In 2008 governors of 19 western states called for connectivity maps to help reduce the undesirable effects of energy development, urbanization, and highway projects (Western Governors' Association 2008). Governors of 6 northeastern states similarly called for statewide maps as a "foundation for regional work on habitat connectivity" (Barringer et al. 2009).

There is also increased interest in connectivity maps that transcend state or national boundaries, such as the Yellowstone to Yukon initiative launched in 1998 (Y2Y 2004). The Freedom to Roam initiative, launched in 2009, encourages businesses and citizens to support corridors for wild plants and animals in North America. In 2009 the U.S. Department of the Interior inaugurated its Landscape Conservation Cooperative program to integrate management actions to address climate change and other landscape stressors and build scientific and technical expertise to do so (Salazar 2009; USFWS 2010).

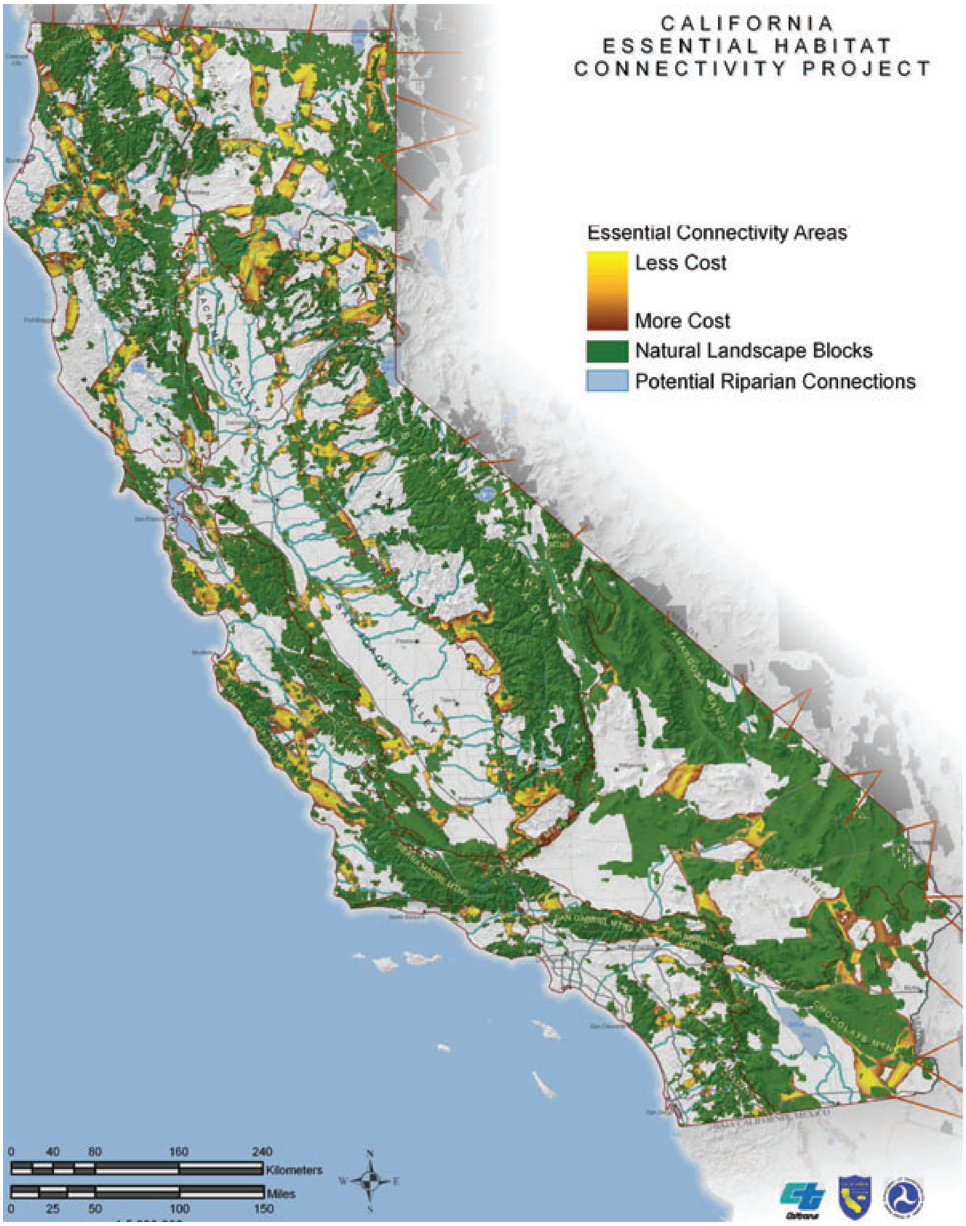


*Figure 1. The 2010 California Essential Habitat Connectivity map (Spencer et al. 2010), developed on the basis of rule-based procedures. It depicts 850 natural landscape blocks (green), connectivity polygons (yellow and brown tones) across gaps between 630 pairs of neighboring polygons, and major riverine connections (blue). An additional 522 connectivity areas where a highway is the only barrier between natural landscape blocks are not displayed. Red lines (sticks) are placeholders for connections to adjacent states. Figure credit: California Department of Transportation, California Department of Fish & Game, Federal Highways Administration.*

Here we provide guidance for developing regional connectivity maps on the basis of our experiences in recent efforts to map connectivity for the states of California (Fig. 1), Arizona, and Washington; Two Countries, One Forest (northeastern United States and southeastern Canada [Fig. 2]); the Western Governors' Wildlife Council (19 western states and territories), Bhutan, 3 ecoregions in California, and 4 counties in Arizona. This paper is organized around 7 logical steps in developing a statewide or regional map.

Several of these steps require choices of models, thresholds, and decision rules for which there is no clear best option. In these cases, we recommend showing stakeholders and collaborators draft results of different choices because these choices often produce nonintuitive outcomes. We have found several cycles of draft products and feedback improve the final products and stakeholder satisfaction with them.

Although increasing connectivity is the most frequently cited recommendation to conserve the ability of species and ecosystems to adapt to climate change (Heller & Zavaleta 2009), we found no regional connectivity map specifically designed to conserve connectivity as climate changes. Accordingly, after describing current practices related to the 7 steps, we describe 3 approaches to identify areas that might maintain connectivity as climate changes. We close with an estimate of financial costs of producing regional connectivity maps and a description of the effect of the mapping efforts in which we participated.


*Figure 2. Regional connectivity map for the Northern Appalachian Ecoregion, as defined by The Nature Conservancy and Nature Conservancy Canada, and a 20-km planning-area buffer. Last of the Wild are patches of high ecological integrity (the inverse of the human footprint [Woolmer et al. 2008]) among which least-cost corridors were modeled.*

## Mapping Steps

### Step 1: State the Goal of the Map

The goal should be clearly stated and measurable, so that success of implementation can be assessed (Beazley et al. 2010). Most connectivity maps have 2 goals, although a map may emphasize only one. One goal is to identify areas where conservation of connectivity can be addressed by linkage designs and decisions to forego or mitigate projects that would likely reduce connectivity. This was the main goal of connectivity maps for Bhutan, India, Tanzania, and most statewide maps in the United States. The Western Governors' Association (2008) refers to these as decision-support maps. Another goal is to express a vision of future ecological connectivity and inspire potential partners to achieve that vision, such as the maps produced by Yellowstone to Yukon (Y2Y 2004), Subtropical Thicket Ecosystem Planning in the Cape Floristic Region (Rouget et al. 2006), and Two Countries, One Forest (Trombulak et al. 2008) initiatives. Importantly, the coarse-grained, spatially extensive map is not meant to be an implementable conservation plan or linkage design. Rather, it depicts areas where linkage designs can be developed.

Stakeholders (see step 2) include entities whose primary mission is not conservation. These include transportation, land-use planning, and water agencies; energy and real-estate developers; and resource-extraction interests. We caution, however, that allowing stakeholders to broaden the goal beyond conservation to include facilitating development, resource extraction, or agricultural production rarely produces a plan that conserves or restores ecological elements, functions, and processes (Layzer 2008). A single-goal connectivity map provides a benchmark against which decision makers can evaluate trade-offs among connectivity and other goals.

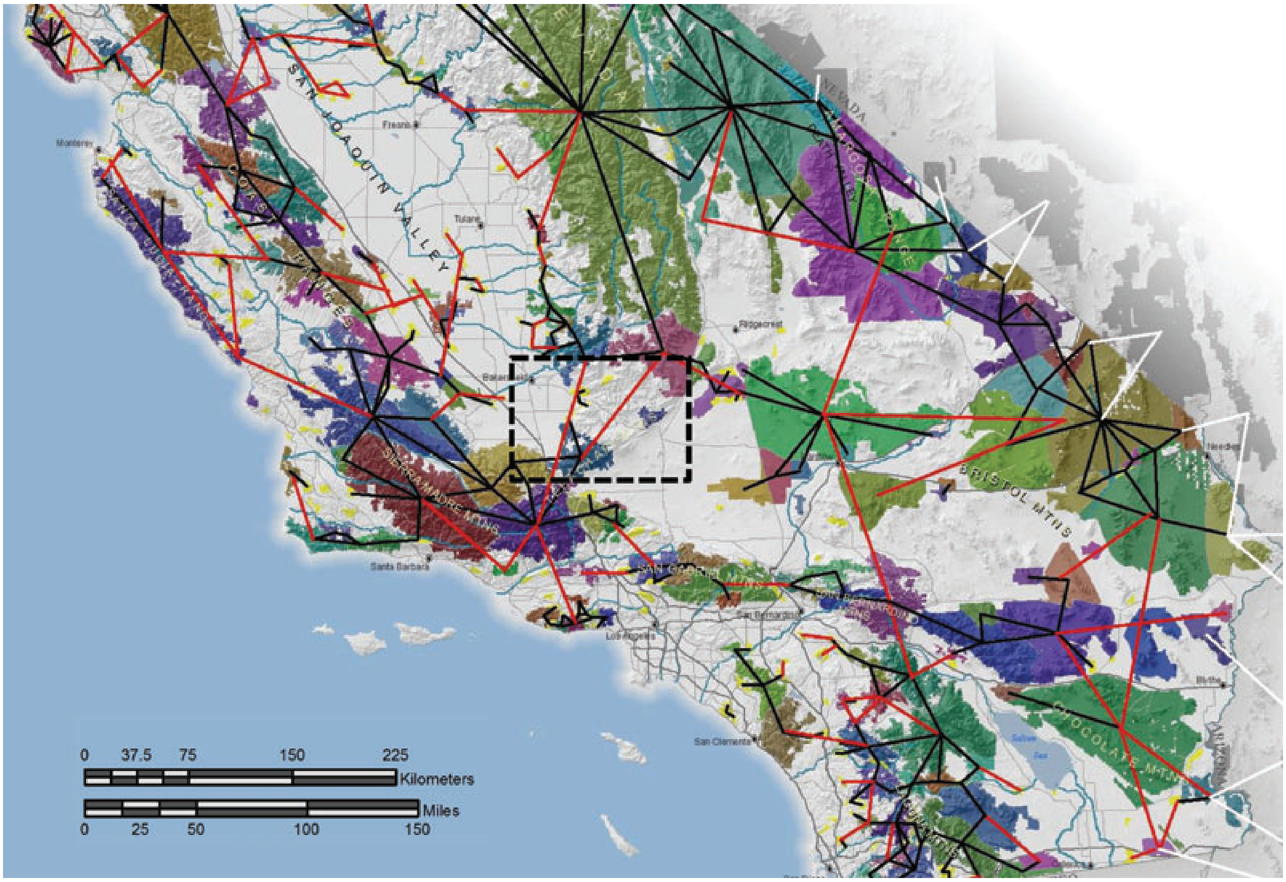


*Figure 3. The "stick map" for southern California (Spencer et al. 2010). Each stick represents a potential connectivity area between a pair of natural landscape blocks. Stick colors distinguish 3 types of connectivity areas: black, connectivity can be achieved by mitigating only for the barrier effect of the highway separating natural landscape blocks; red, conserving connectivity will require land protection and restoration in addition to highway mitigation (replaced by brown and yellow polygons in Fig. 1); white, connectivity area that spans the state boundary (same as red sticks in Fig. 1). Dashed box indicates area depicted in Fig. 4.*

### Step 2: Establish Collaborations

To improve the chances of eventual implementation, we think stakeholders should be involved throughout each step of the planning process (Theobald et al. 2000; Knight et al. 2006; Beazley et al. 2010). Eventual users of the regional connectivity map should define the region (step 3), decide what types of areas they want to connect (step 4), and approve the work plans for steps 5 and 6. For example, the California Essential Habitat Connectivity project (Spencer et al. 2010) was guided by 3 nested groups of stakeholders. There were 200 anticipated map users from 62 federal, state, tribal, regional, and local agencies. A subgroup of 44 technical advisors participated in workshops that made decisions on data sources, models, and mapping criteria. Finally, a steering committee representing 4 agencies conferred with the analysts to make project management decisions.

### Step 3: Define the Region

In many cases, a mapping region is defined on the basis of political boundaries (e.g., a nation, state, county, or transportation district) or ecoregional boundaries. A regional connectivity map of a state or other large extent often inspires maps for subareas. For instance, the statewide 2006 Arizona Wildlife Linkage Assessment stimulated efforts to map linkages in 6 of Arizona's 15 counties. This advances conservation because in the United States, counties and towns rather than states make most land-use decisions. Similarly, the 2001 California Missing Linkages Map stimulated a regional connectivity map for the South Coast Ecoregion (as defined by The Nature Conservancy) and 11 parcel-level linkage designs (e.g., Fig. 4).

On the one hand, defining a large region is advantageous because, on average, a high proportion of connectivity areas will lie within the region rather than along the

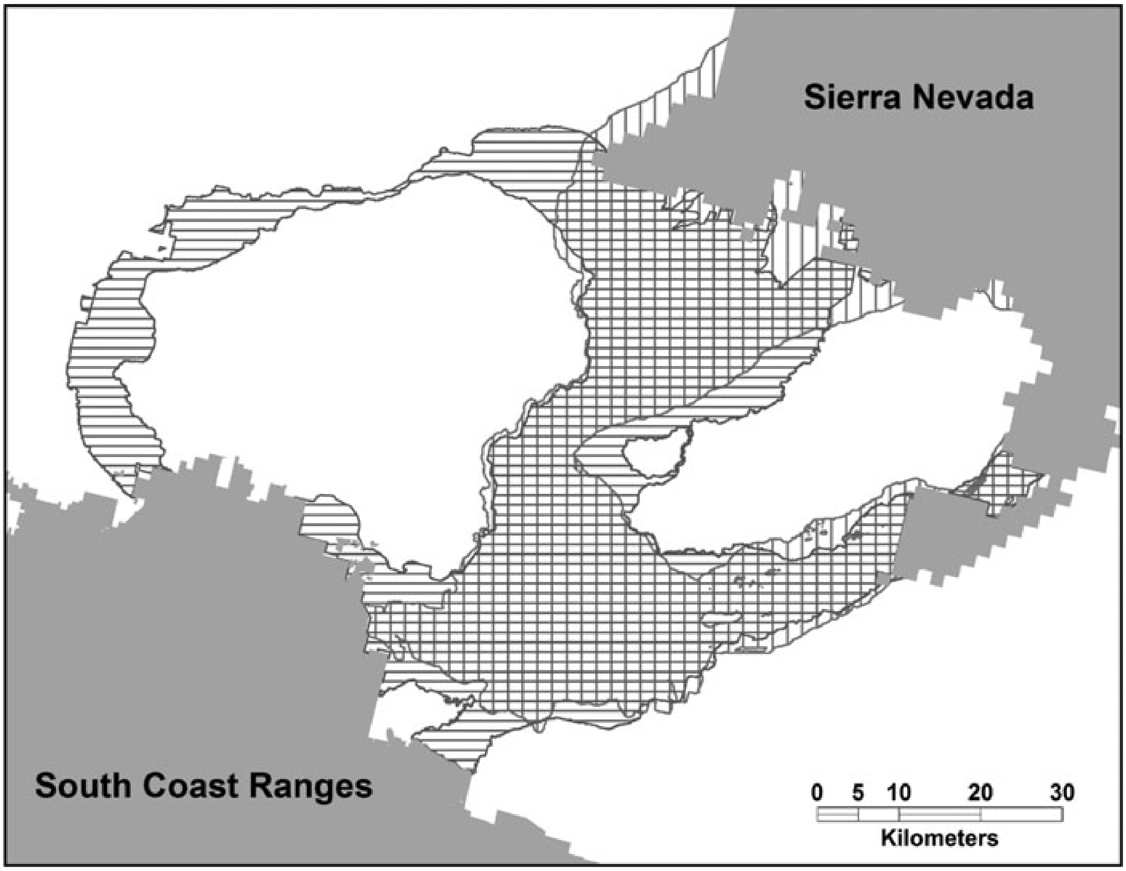


*Figure 4. Spencer et al. (2010) identified a connectivity area (vertical hatching) as the most permeable 5% of the analysis area (dashed box in Fig. 3), using naturalness as a proxy for permeability. This connectivity area delineated on the basis of naturalness captures 87% of the detailed linkage design for 34 focal species (horizontal hatching) (linkage design by South Coast Wildlands 2008) and overlapped all or almost all of the corridors for all but 1 of the 34 focal species.*

margins, where trans-boundary connectivity is depicted with greater uncertainty (e.g., red lines in Fig. 1). On the other hand, as extent increases, environmental and planning contexts become more heterogeneous (Woolmer et al. 2008). Environmental heterogeneity can be addressed by modifying strategies for particular subregions. For instance, Spencer et al. (2010) applied different thresholds of naturalness for delineating natural landscape blocks in subregions of California that differed in land-use intensities.

We recommend that the analysis area extend beyond the state or ecoregion of interest so that linkages to adjacent natural landscape blocks can be included on the map. For example, Spencer et al. (2010) analyzed the state of California plus an 80-km buffer, and Washington's assessment extended up to 200 km beyond the state's boundaries (Fig. 5) (WHCWG 2010).

### Step 4: Delineate Natural Landscape Blocks

A crucial step in any connectivity analysis is defining the entities to be connected. Seven approaches can be used to define natural landscape blocks: invite ecologists to draw polygons by hand; select areas of high ecological integrity; select all or a subset of protected areas; use optimization algorithms to identify areas that meet quantitative conservation targets; use previously developed conservation maps; develop maps of modeled or known habitat for a suite of species; and use highways or other linear barriers to modify preliminary natural landscape blocks.

Although most stakeholders in California, Washington, and the northern Appalachians initially argued for focal-species, habitat-based approaches, each group eventually used some combination of these 7 approaches. Washington conducted parallel analyses that defined blocks on the basis of core habitats for 16 focal species and areas of high ecological integrity. Stakeholders in the other efforts decided that maps of modeled habitat for focal species over large heterogeneous areas would likely be inaccurate and no better than basing the analysis on ecological integrity. California stakeholders adopted a hybrid approach that identified preliminary natural landscape blocks as areas of high ecological integrity or

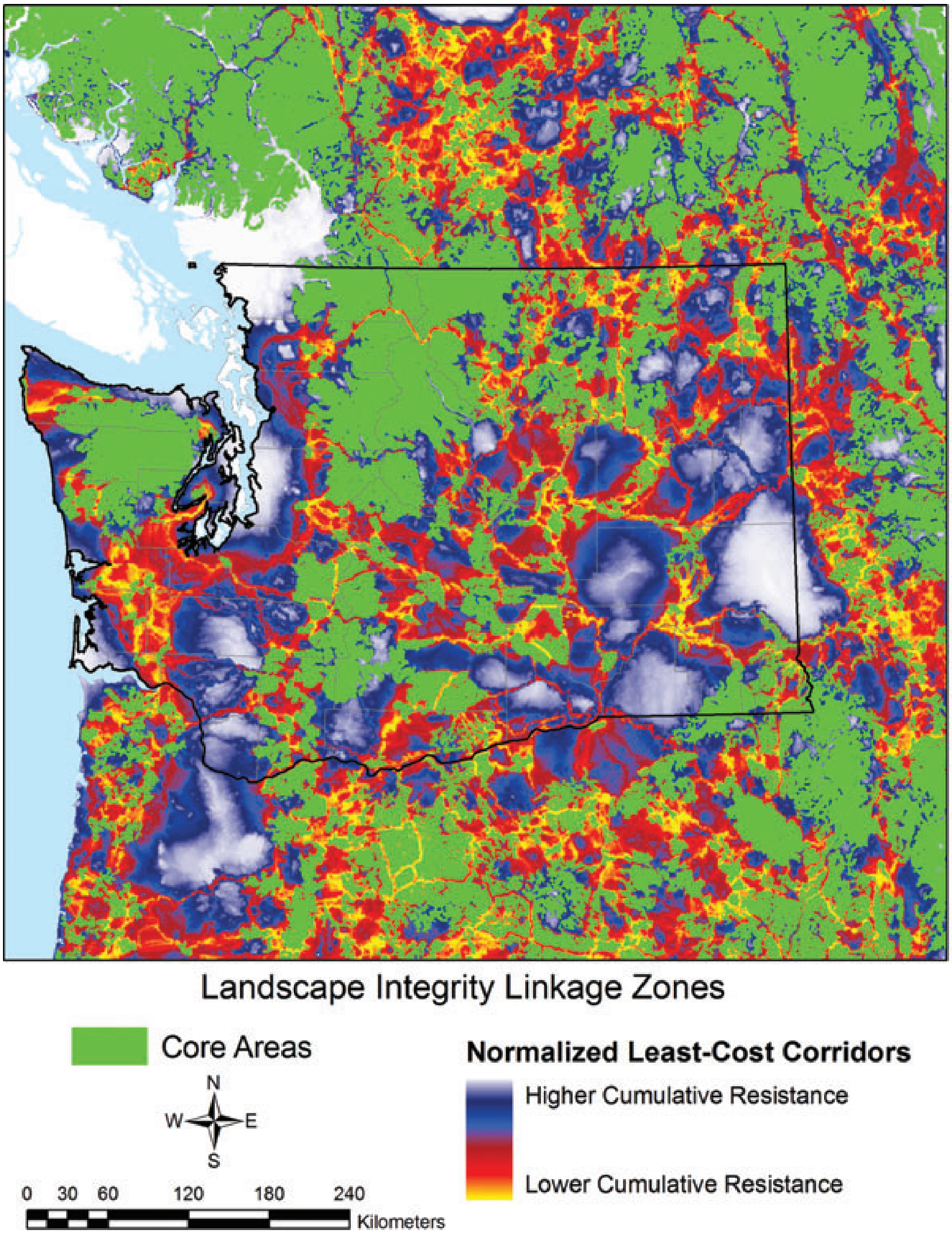


*Figure 5. Composite of 4 integrity-based connectivity maps for the state of Washington depicting linkages between 349 areas of high ecological integrity (WHCWG 2010). These maps complement similar maps for 16 focal species across the same project area.*

areas of high protection status, with higher weight given to mapped conservation areas. They further modified the preliminary blocks by splitting them at highways (Spencer et al. 2010). In the northern Appalachians, Baldwin et al. (2010) defined natural landscape blocks on the basis of protection status, ecological integrity, and habitat cores for pine marten (*Martes americana*). We describe the advantages and disadvantages of each option.

#### EXPERT OPINION

Experts can use their knowledge of natural history, including unpublished information, to rapidly draw natural landscape blocks across large extents at low cost, but this approach is not transparent, quantitative, or repeatable. Beazley et al. (2010) provide procedures to increase transparency by documenting the discussions and decision-making processes of experts.

#### AREAS OF HIGH ECOLOGICAL INTEGRITY

Ecological integrity (Spencer et al. 2010) equivalent to naturalness (Theobald 2010) or the inverse of the human footprint (Woolmer et al. 2008) – is an index of the degree to which an area retains natural land covers, has low road density, and lacks intensive land uses and edge effects from adjacent human activities. In this approach for defining natural landscape blocks, ecological integrity is calculated as a weighted function of these variables, and contiguous clusters of grid cells that are above a certain threshold integrity score and above a minimum area threshold are identified as natural landscape blocks. An elongated strip of land (spur), such as a power line right of way in an urban area, may be too narrow to contribute to ecological integrity; conversely, small gaps within a natural area may not disrupt integrity. Shape algorithms (Girvetz & Greco 2007; Spencer et al. 2010) can help define blocks that ignore these spurs and gaps.

Integrity-based maps are more difficult to parameterize with field data than species-specific habitat maps. Integrity-based maps are also difficult to validate because they do not focus on specific, measurable flows such as animal movement. Nonetheless, integrity-based approaches to identifying large natural areas are transparent, repeatable, and relatively simple. They can also be complemented with analyses that focus on individual species. Hoctor et al. (2000), Carr et al. (2002), Marulli and Mallarach (2005), and Spencer et al. (2010) all used integrity to identify natural landscape blocks, whereas the Washington Habitat Connectivity Workgroup (2010) mapped blocks on the basis of both integrity and habitat for focal species.

To maximize transparency, we recommend use of a small number of easy-to-understand attributes (e.g., natural land cover and a road variable) to define ecological integrity (e.g., Theobald 2010). In all efforts in which we participated, analysts developed alternative maps of natural landscape blocks that reflected different rules for combining and weighting attributes and different minimum size thresholds, and end users chose the rules and thresholds that produced a useful, readable map.

#### PROTECTED AREAS

In a protected-areas approach to defining natural landscape blocks (illustrated by Nordhaugen et al. 2006 and Wildlife Conservation Division 2010), one selects all parcels that meet a certain level of protection, such as all lands in certain gap analysis programs or International Union for Conservation of Nature protection classes. Contiguous protected parcels above a minimum size are designated as natural landscape blocks. The approach is straightforward and unambiguous, and precludes mapping connectivity areas to lands that could be converted to other cover types or uses in the future. The approach excludes areas of high ecological integrity that are not currently protected. Some such areas may be relatively unlikely to be developed, and others could be protected in the future. Because using protection status as the sole determinant of a natural landscape block fails to include some high-integrity areas, we recommend use of protection status in conjunction with ecological integrity. For example, Spencer et al. (2010) and Baldwin et al. (2010) identified areas with either the highest protection status or the highest naturalness scores as natural landscape blocks.

#### SITE-OPTIMIZATION ALGORITHMS

Site-optimization algorithms (e.g., simulated annealing; Ball & Possingham 2000) maximize representation of conservation targets (e.g., species, populations, or communities) while minimizing cost. Two aspects of cost are typically considered: total land required (expressed in area or dollars) and amount of edge (because conservation becomes more difficult and costly as amount of edge increases).

High-priority areas identified by such algorithms can be treated as an existing conservation map (see "Existing Maps of Conservation Priorities") or can be used in combination with other approaches to define natural landscape blocks. Additionally, implementing agencies can use these algorithms to help prioritize their linkage conservation efforts (step 7). However, use of optimization algorithms as the sole approach to define natural landscape blocks may result in selection of only the smallest landscape areas needed to meet representation goals. This may be appropriate when one is allocating scarce dollars for acquisition or easements, but in our experience stakeholders typically want to identify potential connections for all natural landscape blocks in the region.

#### EXISTING MAPS OF CONSERVATION PRIORITIES

Many agencies have developed spatially extensive maps of areas they wish to conserve. Examples include The Nature Conservancy's ecoregional portfolios (The Nature Conservancy 2011), areas of conservation emphasis identified in U.S. State Wildlife Action Plans and critical habitat for species listed under the U.S. Endangered Species Act. Such maps may be used to designate natural landscape blocks. However, these data layers may fail to recognize large, functioning ecosystems with low species diversity or few special-status species (Kareiva & Marvier 2003). Moreover, some designated critical habitat and some rare species occur in landscapes with little natural land cover, and some rare species occur in small, naturally isolated populations.

Other potentially useful maps include maps of wetlands, rarity-weighted locations of high species diversity, and locations of species of concern. We caution against using a map layer that covers only part of the region. For example, the U.S. Bureau of Land Management designates "areas of critical environmental concern," but only on federal land, so use of this map to help define blocks would be biased against nonfederal lands.

Maps of critical habitat designated under the U.S. Endangered Species Act are problematic because critical habitat is designated to minimize economic impact and avoid private lands. Instead of or in addition to critical habitat maps, we recommend using maps of areas that include features essential to survival and recovery of a species, as determined prior to consideration of economic impacts and land ownership.

Because of these biases, the mapping efforts we participated in gave a minor role to existing conservation maps in defining natural landscape blocks.

#### HABITAT CORES FOR A SPECIES OR SUITE OF SPECIES

Areas of known or modeled habitat can be used to define natural landscape blocks. For example, in a 2500 $km^2$ region of northern Italy, Bani et al. (2002) defined core areas for a suite of forest birds and carnivores as areas above a minimum size and minimum number of detections of those species in over 1000 point counts and transects of the area. Similarly, Menon et al. (2005) mapped the distribution of known elephant populations as core areas. Because species distributions are expensive to determine empirically for most species across large areas, most researchers used modeled or expert-based species distributions. For example, the Southern Rockies Ecosystem Project (2005) convened experts to hand draw habitat core areas for 27 focal species and 176 linkage areas among these core areas in Colorado. In 2008–2010, the Washington Habitat Connectivity Workgroup selected 16 focal species to represent 5 major vegetation types and modeled core habitats and least-cost corridors for each species. They then combined maps of core habitat and corridors for each of the 16 species into 3 maps representing habitat cores and linkages for 3 species guilds.

On the one hand, most end users are comfortable with species conservation as a goal, and many government agencies have regulatory authority to protect and manage species. Furthermore, linkages are usually intended to promote species movement; a linkage based on ecological integrity could fail to provide connectivity for some species. On the other hand, it is difficult to select focal species that represent the entire biota of a region and to reliably model each species' core habitat. It is especially difficult to overlay the maps for individual species to produce a coherent set of natural landscape blocks. This extra effort may be worthwhile if the resulting areas more accurately represent natural landscapes or are more widely accepted than maps drawn on the basis of ecological integrity.

#### LINEAR BARRIERS AS BLOCK BOUNDARIES

Unless mitigated by crossing structures, a single highway, railroad, or canal can block gene flow for mammals, reptiles, amphibians, or sedentary birds (Delaney et al. 2010 and citations therein). Therefore, it is reasonable to split preliminary natural landscape blocks into smaller blocks on the basis of such barriers.

### Step 5: Determine which Pairs of Blocks Would Benefit from Connectivity

We refer to the process of identifying pairs of natural landscape blocks to connect as "drawing sticks" because the process produces a map of blocks with centroids connected by straight lines (sticks) (e.g., Fig. 3). The stick is a placeholder that can be replaced by a connectivity polygon (step 6) and eventually by a polygon representing a linkage design. If there are 100 natural landscape blocks, there are 4950 potential linkages between pairs of blocks. But each block does not necessarily need to connect to every other block. Simple procedure scan identify blocks that are adjacent to or near a given block, but more complex rules are required to identify pairs that are important and feasible to connect. For example, block pairs that are adjacent or close may be separated by urbanized lands that do not facilitate connectivity.

To draw sticks among the 850 natural landscape blocks in California, Spencer et al. (2010) applied a set of 6 rules: (1) connect every block to at least one neighbor; (2) create more than one connection from a large ($> 500$ $km^2$) block or cluster to a larger cluster of blocks; (3) do not draw a stick that represents a linkage across areas with land cover so dissimilar to the natural landscape blocks that connectivity is implausible; (4) minimize unnecessary redundancy, preferentially deleting sticks that represent linkages across land covers and land uses most dissimilar to the landscape blocks; (5) do not delete a connection with land cover similar to land cover of the blocks, even if connectivity can be achieved by an alternative chain of sticks; and (6) draw a stick between any 2 blocks that are separated only by a linear barrier where crossing structures could restore connectivity. Manual implementation of these rules (e.g., Spencer et al. 2010) can be tedious and subjective. WHCWG (2010) developed an automated geographic information system procedure that increased speed, transparency, and repeatability.

### Step 6: Depict Connectivity Areas

If those conducting a regional effort have sufficient time and money, or if there are only a few sticks in the region, we recommend developing a detailed linkage design (Beier et al. 2008) for each stick. More commonly, however, limited resources lead to use of placeholders to depict connectivity areas, with the intent that linkage designs will be developed over time. The 3 types of placeholders, listed in order of increasing scientific rigor and utility to users, are sticks, hand-drawn arrows or polygons, and modeled polygons. A stick is a reasonable placeholder to represent potential connectivity between 2 landscape blocks separated by only a road or other linear barrier, but does not adequately represent connectivity between more widely separated blocks. Because a stick has no area, analysts cannot describe the size, naturalness, and other biological attributes of the connectivity area it represents. More importantly, a project proponent or regulatory agency cannot use a map in which connectivity is represented by sticks to assess whether a proposed project might affect connectivity.

Participants in the 2001 California Missing Linkages effort (Penrod et al. 2001) hand drew arrows, and participants in the Arizona Wildlife Linkage Assessment (Nordhaugen et al. 2006) hand drew polygons to represent connectivity areas. Although hand drawing can depict many connectivity areas quickly at low cost, the approach may not be repeatable or transparent. If hand-drawn placeholders must be used due to time or budget constraints, a polygon will convey more spatially explicit information than an arrow.

Modeled polygons are produced by transparent and repeatable procedures. If this option is used, we recommend generating these polygons by least-cost modeling (Adriaensen et al. 2003; Beier et al. 2008). The primary input to a least-cost model is a resistance surface, which represents the difficulty of movement (for species or ecological flows) associated with each grid cell. Resistance surfaces can be conceptualized in 1 of 2 ways. The first is landscape resistance for each of several focal species. Least-cost corridors (Adriaensen et al. 2003) for each species can be modeled and joined into a preliminary linkage design (Beier et al. 2008). We recommend this option only if the union of corridors for that group of focal species is likely to support movement for almost all species. Corridors for only a few focal species, especially if those species are generalists, probably will not support movement by species with specialized resource requirements. An advantage of estimating species-specific resistance is that empirical estimates are possible (e.g., by making inferences from observed movements [Sutcliffe et al. 2003] or patterns of genetic relatedness [e.g., Perez-Espona et al. 2008]). However, resistance is usually estimated by expert opinion (Beier et al. 2008).

The second way to conceptualize resistance surfaces is by departure from naturalness. The key assumption is that as naturalness increases, resistance to the ecological movements of interest decreases. Spencer et al. (2010) calculated resistance on the basis of naturalness, reflecting contemporary resistance to movement (80% of the resistance score), and protection status, reflecting human commitment not to decrease naturalness (and thus increase resistance) in the future (20%). Similarly, Baldwin et al. (2010) calculated resistance on the basis of the human footprint (Woolmer et al. 2008). These procedures are simple, repeatable, and easy to understand. A drawback is that linkages derived from naturalness may not contain enough diversity and continuity of land covers to provide connectivity for specialists. Another drawback is that resistance scores are assigned subjectively. On the basis of our experience with focal species models, we recommend allowing resistances to vary by a factor of at least 100 and assigning extreme values to the most highly-altered types of land cover.

Whether least-cost modeling is based on focal species or naturalness, it will produce connectivity polygons to replace the placeholder sticks (step 5). The WHCWG (2010) developed algorithms that automatically calculate least-cost corridors among many natural landscape blocks, given sticks and a map of resistances.

Selecting the size threshold for connectivity areas is a key issue in least-cost modeling. Spencer et al. (2010) used the most permeable 5% of the analysis area to map connectivity areas. They selected this threshold because the resulting polygons were similar in shape and size to 11 linkage polygons delineated for focal species (Fig. 4). Similarly, WHCWG (2010) mapped corridors by widening all least-cost paths by a species-specific cost-weighted distance. We suggest each regional analysis experiment with a range of parameter values in several highly divergent linkage areas and select those likely to encompass the movements of local species.

If the map will be used as a decision-support tool (step 7), we recommend that it depict relatively large connectivity areas. Regional maps are necessarily derived from coarse-grained data and often consider only a few species and will thus be imprecise and uncertain. Larger areas will more likely include areas that would be identified for conservation intervention by subsequent fine-grained linkage designs (Fig. 4). If a connectivity area is relatively small, decision makers might not be aware that a project might reduce connectivity for some focal species. Connectivity areas that capture larger swaths are also more likely to overlap future linkage designs intended to accommodate range shifts driven by climate change.

The polygons produced by the preceding procedures might not include the major rivers and streams connecting landscape blocks. Because many species travel along rivers and streams, we recommend including them in regional connectivity maps, as has been done in Florida (Hoctor et al. 2000), South Africa (Rouget et al. 2006), and California (Fig. 1) (Spencer et al. 2010).

### Step 7: Provide Guidance to End Users

The connectivity map is not complete without supporting documentation, descriptive statistics for each natural landscape block and connectivity area, and recommendations for how to use the map. Most regional connectivity maps are intended to be used as decision-support tools by agencies whose primary mission is not conservation, such as a transportation agency or the land-planning office of a U.S. county. To determine whether a proposed project (e.g., highway or urban development) in a connectivity area is incompatible with connectivity, Spencer et al. (2010) recommended that the responsible agency should develop a fine-grained linkage design that would replace the coarse-grained connectivity area, provide site-specific recommendations to mitigate negative effects, and guide conservation and management of the connectivity area.

Stakeholders often want guidance on which linkages are most important. Because ranking or prioritizing linkages may provoke discord among potential partners (and depends on stakeholder values), analysts may prefer to simply provide descriptive statistics that each implementing agency can use to set their own priorities (e.g., Spencer et al. 2010; WHCWG 2010). If one wishes to identify priorities for all users, we suggest identification of an ensemble of connectivity areas the conservation or restoration of which would do the most to create a network of natural landscape blocks in the region (e.g., Hoctor 2004; Menon et al. 2005), rather than a ranked list of areas.

If the map is based on connectivity for focal species, we think the accompanying documentation should discuss the extent to which the network is expected to support gene flow and dispersal of each species. Documentation for maps that are based on ecological integrity should also address connectivity for focal species. For instance, Spencer et al. (2010) described the extent to which the integrity-based map overlapped previously mapped corridors for desert bighorn sheep (*Ovis canadensis*) and other species. Spatially explicit population models (Carroll et al. 2003) also can estimate extinction risk and population sizes for each focal species in a given configuration of natural areas.

When a map is released, a communication strategy can help users and civil society understand the importance of corridors and the value of the map. For example, Washington state planners identified several key audiences including planners, regulators, and elected officials and conducted interviews and surveys to target materials for each audience. Two Countries, One Forest created a well-documented online conservation atlas.

## Emerging Approaches for Connectivity Analysis

Individual-based movement models (Grimm & Railsback 2005) are an alternative to least-cost models for generating connectivity polygons for focal species in both coarse-grained connectivity maps and fine-grained linkage designs. The models simulate animal movement, consider the effect of mortality on movement, and produce connectivity areas that often have multiple strands and wide areas suitable for foraging or resting (e.g., Hargrove et al. 2004; Tracey 2006). These models have not yet been used to produce regional connectivity maps, in large part because few data exist with which to estimate model parameters, such as behaviors (e.g., turning angles, travel speeds) and mortality probabilities in different land-cover and edge types.

Least-cost modeling is an extension of graph theory. Other extensions of graph theory, particularly circuit theory (McRae et al. 2008) and centrality analyses (Estrada & Bodin 2008), can be used to identify portions of connective areas where movement is constricted and to quantify the extent to which particular landscape blocks and linkages contribute to connectivity of the entire network. We believe these approaches could be applied immediately to prioritization analyses in step 7.

New applications of least-cost modeling (Compton et al. 2007), centrality analysis (Carroll 2010), and circuit theory (M. Anderson, unpublished data) may produce maps of areas important for connectivity without the need to identify a priori landscape blocks. Future development of such approaches may lead to the integration of our steps 4–6 into a single step.

## Mapping Areas That May Provide Connectivity as Climate Changes

In all the regional maps described above, connectivity was based on current landscape conditions. However, climate change will reassemble plant communities (Hunter et al. 1988) and influence the distribution of one of the most crucial current conditions, namely land covers. Three approaches can produce maps of areas that may provide connectivity during and after periods of rapid climate changes: temporal corridors, ecological land units or land facets, and naturalness. Temporal corridor modeling tracks how the locations of areas with suitable climate for a species may shift as climate changes. The approach links models projecting future emissions of greenhouse gasses, atmospheric and oceanic responses to these gasses, and bioclimatic envelopes for each species. Then a dispersal chain model (Williams et al. 2005) or a network flow model (Phillips et al. 2008) identifies cells with suitable temperature and moisture regimes that will be contiguous for long enough that the species could establish populations in cells that become newly suitable as currently occupied cells become unsuitable. Although dispersal-chain and network-flow models are conceptually sound, the utility of the models is limited by uncertainties in emission and climate models (Beier & Brost 2010). Ensemble modeling for corridors (building dozens of corridors on the basis of various combinations of emission scenarios, circulation models, and climate envelope models) may help identify corridors that are relatively robust to these uncertainties. We recommend using temporal corridor models in conservation plans only if the corridors are based on ensemble modeling.

To develop conservation maps that might be robust to climate changes without relying on projected emissions of greenhouse gases, air-ocean circulation models, and climate-envelope models, Hunter et al. (1988), Beier and

Brost (2010), and Anderson and Ferree (2010) advocate setting conservation targets in terms of areas with relatively homogeneous topography, insolation, and soils. The key assumption is that conservation areas with sufficient diversity, interspersion, and continuity of such land facets will support populations of and movements by most species, regardless of future climate. Brost and Beier (2012) describe use of such areas in the design of corridors to support movements of species as climate changes.

In regions where much of the land has been modified by humans, we think large connectivity polygons defined on the basis of naturalness provide a simple and efficient coarse-filter regional connectivity map. Any future linkage design—whether one bases it on contemporary focal species, future climate envelopes, or land facets—is likely to fall within areas that have not been converted to urban or industrial uses. In an ongoing effort, Washington is using data on naturalness, current climate, and topography to identify potential connectivity areas that follow current climatic gradients. This process does not require detailed modeling of climate and species' habitats. Such linkages are assumed to capture pathways that species are likely to follow as climate changes.

## Financial Cost

Although the large amount of staff time donated by stakeholders and partners makes it impossible to accurately tally costs, the expense of developing a connectivity map is small compared with that of land acquisition or restoration. Two efforts in which experts drew polygons at workshops (Penrod et al. 2001; Nordhaugen et al. 2006) cost less than $100,000 each. The Two Countries, One Forest and California Essential Habitat Connectivity reports (Spencer et al. 2010) were produced for about $500,000 each. The Washington Connected Landscapes Project may eventually cost twice this much because it will include development of new geographic information system tools, modeling for 16 focal species, and analyses of climate change.

## Effect of Regional Connectivity Maps

Of the regional connectivity efforts we have been involved with, only 2 have existed long enough for their conservation impact to be considered, California Missing Linkages (Penrod et al. 2001) and Arizona Wildlife Linkage Assessment (Nordhaugen et al. 2006). We believe that these projects profoundly changed the way connectivity is treated in these states. When these 2 reports were released, state and local transportation agencies immediately began to consider the effect of new highway projects early in their planning process, and collaborations between state transportation and wildlife agencies increased dramatically. Arizona, for example, has tested experimentally the effectiveness of different underpass designs and roadside fences for facilitating animal movements and is using the information in new projects. Moreover, in 2011 Arizona built 2 overpasses for wild animals and has committed to build 3 more. The statewide maps in California and Arizona stimulated county and ecoregional connectivity maps, 11 linkage designs in California (Beier et al. 2006; South Coast Wildlands 2008), and 16 linkage designs in Arizona (Beier et al. 2007). All 27 linkage designs are being implemented. Over 100,000 ha of natural lands have been conserved in the 11 linkage designs in southern California. Although conserving connectivity was not the sole reason for most of these acquisitions, the linkage designs significantly influenced these decisions. These statewide and regional connectivity maps, like the earlier maps for Yellowstone to Yukon and Spine of the Continent, have captured the imagination of citizens, leading to increased consideration of connectivity in local planning efforts.

Connectivity analyses have also helped build lasting collaborations. Early connectivity efforts in Washington (e.g., Singleton et al. 2002) spurred land exchanges and commitments to build overpasses for wild animals on an interstate highway, eventually expanding into the Washington Connected Landscapes Project. In Washington, California, and Arizona, transportation and wildlife agencies and nongovernmental organizations have increasingly developed trust and commitment to connectivity.

We think a regional connectivity map is a highly cost-effective conservation tool because it provides an inspiring vision and alerts regulators and decision makers to proposed land development projects that may adversely affect connectivity. The recent upsurge in statewide efforts and federal efforts that cross state boundaries supports voluntary and regulatory activities to promote connectivity. Although these maps are not implementable linkage designs, they may spur the development of such plans. The 7 steps we outlined provide a scientific basis for developing a connectivity map; the last 3 steps require extensive analysis. We hope this paper will stimulate increasingly rigorous statewide and regional connectivity-mapping projects to help conserve and restore connectivity.

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