Getting the most connectivity per conservation dollar

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The importance of connectivity for species conservation has resulted in myriad attempts to identify corridors linking habitat patches and conservation areas. However, making smart decisions for restoring connectivity requires information beyond simple maps of corridors. Here, we combine land-parcel cost estimates with a new analytical approach that pinpoints where barrier removal can best improve connectivity to develop a return-on-investment framework for connectivity restoration. An iterative series of barrier analyses followed by simulated restorations allowed us to incorporate cumulative effects of previous restoration decisions, which can alter the potential value of future restorations. To demonstrate our approach, we identify specific sites that, if restored, would most increase habitat connectivity for the Washington ground squirrel (*Urocitellus washingtoni*). The analysis was performed in two ways: first without consideration of economic costs and then again, explicitly incorporating the costs of land purchase and restoration. We found that accounting for land costs could reduce overall restoration costs by 55% and increase the area of land restored by 30%. These methods can be tailored to meet different connectivity objectives and can complement reserve design selection methods that prioritize conservation of contiguous natural areas.

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Habitat loss and fragmentation are key drivers of population declines and species endangerment (Wilcove *et al.* 1998). The response to these threats has largely involved land-protection efforts that prioritize large, intact patches of habitat for conservation (eg Thomson *et al.* 2009). However, even when such patches are protected, conserving functional connectivity among them is necessary to maintain gene flow, population viability, and species diversity (Crooks and Sanjayan 2006). Moreover, connectivity will be increasingly critical for maintaining adaptive capacity and facilitating species range shifts under climate change (Heller and Zavaleta 2009; Sexton *et al.* 2011).

Plans for improving connectivity are proliferating at scales varying from local to national (Beier *et al.* 2011). Such plans rely on analyses that identify potential movement corridors between habitat patches or natural areas and can therefore guide conservation investments. However, these analyses do not provide sufficient guidance to determine which parcels of land should be protected or restored for maximum conservation benefit, complicating efforts to allocate limited funds as effectively as possible.

Many movement pathways highlighted in connectivity analyses pass through human-dominated landscapes, where agriculture and other types of human land use impede movement. Restoration of these altered landscapes is an important tool for enhancing connectivity (Baldwin *et al.* 2012), and there are many opportunities for its implementation; in the US, for instance, public and private entities are funding multi-million-dollar programs that support restoration projects for species conservation as well as objectives such as reduced soil erosion. Identifying where restoration may have the greatest potential to increase movement will improve practitioners' ability to strategically target areas for conservation investment.

All else being equal, the most effective areas in which to invest funds aimed at restoring connectivity are those where restoration will most enhance movement between important habitat areas by reducing the distance a species must travel and/or decreasing the resistance encountered en route. However, the efficacy of restoration investments will also depend heavily on land and restoration costs. Prioritizing conservation actions without taking costs into account can lead to unsuccessful outcomes (Ando *et al.* 1998; Murdoch *et al.* 2007; Withey *et al.* 2012).

Here, we describe a new method for prioritizing land parcels for restoration, based on their potential to enhance connectivity within complex habitat networks. We illustrate the approach using data for the Washington ground squirrel (*Urocitellus washingtoni*), a candidate for listing under the US Endangered Species Act. We applied this approach using a recently developed tool for selecting lands that offer the best restoration opportunities for connectivity. Unlike previous techniques, this software quantifies the degree to which these areas, if restored, would enhance connectivity between distant habitat patches. We used the outputs from the tool to prioritize areas for restoration for the ground squirrel. We

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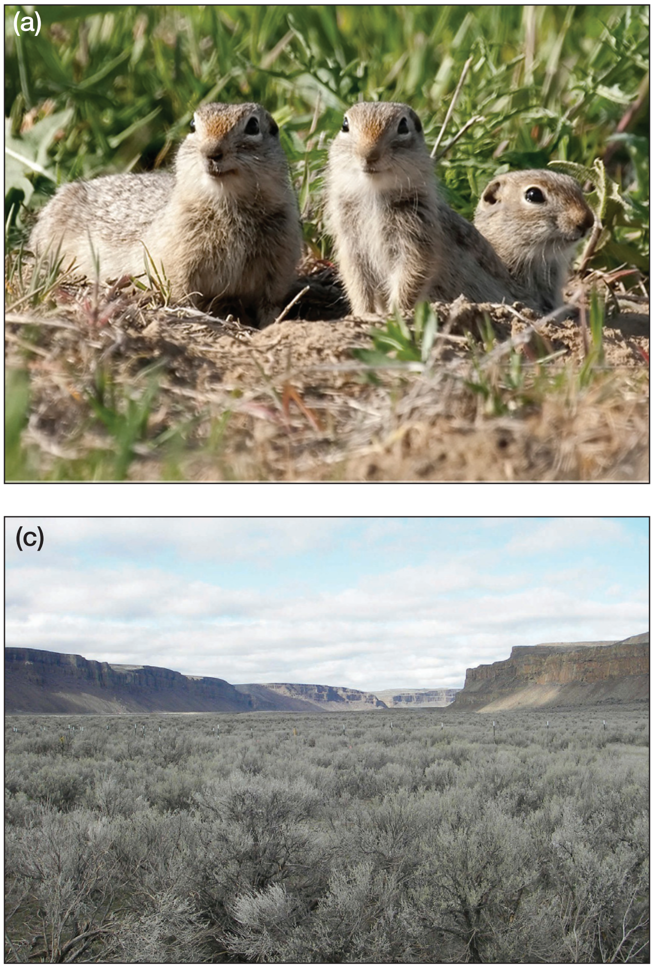

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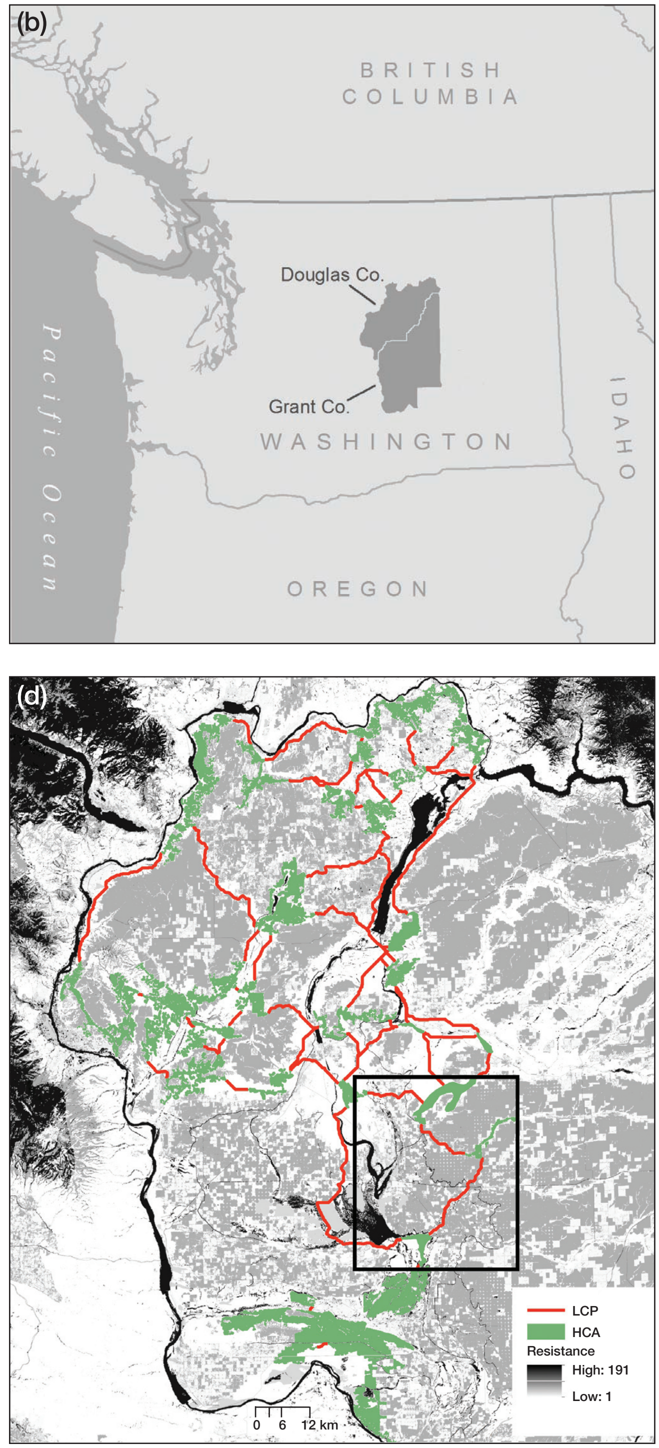

Figure 1. *(a) Populations of the Washington ground squirrel (*Urocitellus washingtoni*) are in decline in Washington State, US. (b) Our analyses focused on Douglas and Grant counties. (c) Shrub–steppe and dry grasslands, which serve as habitat for the squirrel, have largely been fragmented by agriculture and development, leaving relatively isolated patches of habitat. (d) Green areas represent core areas (Habitat Concentration Areas [HCA]), gray shading represents landscape resistance to squirrel movement (with darker areas posing higher resistance), and red lines represent least-cost paths (LCP) connecting patches. Patches, resistances, and LCP were identified by the Washington Wildlife Habitat Connectivity Working Group (WWHCWG 2012). The black box in (d) shows an area for which results are illustrated in Figure 2.*

made two sets of prioritizations, one based solely on the potential to increase connectivity and one that incorporated land and restoration costs and hence estimated the potential increase in connectivity per dollar spent.

Methods

Study species

We piloted our approach using previously developed connectivity models for the Washington ground squirrel (Figure 1a), a species endemic to the Columbia Plateau Ecoregion of the northwestern US. The species historically occupied native shrub–steppe and grasslands throughout much of eastern Washington and north-central Oregon (Finger *et al.* 2004). Populations have declined over the past 150 years, mostly because of conversion of habitat to agriculture (Betts 1990). Remnant populations of *U washingtoni* have become disconnected (Finger *et al.* 2004) because movement between colonies is impeded by roads, urban land use, and intensive agriculture (WWHCWG 2012). These barriers limit genetic exchange between populations, increase the risk of extirpation by catastrophic events (such as disease or fire), and limit opportunities for movement to new areas should current habitat become unsuitable due to land-use or climatic changes.

Study area

We conducted our analyses within the Columbia Plateau Ecoregion in Washington State, US (Figure 1b). The Plateau was once covered by sagebrush-dominated shrub–steppe and grasslands (Figure 1c), but today much of the region has been converted to cropland. We focused our analysis on Douglas and Grant counties (Figure 1b), which contain important blocks of occupied Washington ground squirrel habitat and where the Arid Lands Initiative (a consortium of non-governmental organizations, state and federal agencies, and private entities) is working to coordinate efforts to conserve and restore native shrub-steppe and grassland ecosystems.

Existing corridor maps

We sought sufficient data to develop, evaluate, and illustrate a method for combining connectivity, restoration, and return-on-investment analyses in a way that could readily be used to enhance connectivity analyses commonly implemented by conservation planners. We started with previously developed models of habitat patches, landscape resistance (the degree to which different elements of the landscape restrict or impede movement), and corridors connecting habitat patches, all of which are being used to make conservation decisions in Washington State. This information was collected by the Washington Wildlife Habitat Connectivity Working Group (WWHCWG), based on expert opinion and occurrence data (WWHCWG 2012). Although expert-based models of habitat quality and resistance have their shortcomings, in many cases they constitute the only models available for studying species of conservation concern (Zeller *et al.* 2012). These data provided a sufficient starting point to demonstrate our approach. WWHCWG first mapped contiguous habitat patches (hereafter "core areas"; Figure 1d). They then modeled (at 90-m resolution) the resistance to Washington ground squirrel movement posed by different landscape features, using spatial data on roads, railroads, housing, transmission lines, wind turbines, land cover, land use, and irrigation canals. This resolution was judged to be fine enough to capture Washington ground squirrel dispersal movements, which have been estimated to be 991 m on average (median of 880 m; Klein 2005). Areas consisting of high-quality squirrel habitat were assigned a resistance of 1, where resistance values represent the cost of movement, with higher resistance values assigned to areas containing land-cover types such as roads, developed areas, and agricultural lands through which it is more difficult for squirrels to move (see WWHCWG [2012] for details). WWHCWG decided to delineate important connections between adjacent core areas using least-cost corridor modeling (Adriaensen *et al.* 2003), a commonly used approach. For each corridor, the least-cost distance (LCD, a measure of the total movement cost or weighting incurred when an animal moves from one patch to another along the least-cost path) was also calculated (WWHCWG 2012).

Identifying the most important barriers to connectivity

We used Barrier Mapper software (McRae 2012) to identify potential barriers to movement. A barrier is defined as a landscape feature that impedes movement between ecologically important areas, the removal of which would increase the potential for movement between those areas (McRae *et al.* 2012). The software identifies where restoration would create "shortcuts" that would most reduce LCD between patches. It searches a circular neighborhood of user-specified size (eg a circle with a radius of 450 m) around each pixel (the smallest unit in a digital raster image) in the landscape. For each pixel location, it determines the LCD between patches if the entire circle were restored to a cover type that is permeable to movement (ie with a low resistance value). The result is a continuous surface that, for each pixel, shows the LCD of the best corridor that would pass through the search neighborhood around the pixel if the neighborhood area were restored.

A simple metric of connectivity improvement that would result from restoring the search neighborhood is:

$$\text{Improvement score} = \text{LCD} - \text{LCD}_r \qquad \text{(Eq 1)}$$

where LCD is the cumulative resistance of the optimal path connecting patches before restoration, and LCD_r is the cumulative resistance of the best path crossing the restored area. If LCD_r is less than LCD, then restoration would decrease isolation and increase connectivity between the two patches. Improved corridors may follow the same route (if a barrier lies on the original least-cost path), or may be completely re-routed following barrier removal (if a barrier was forcing a corridor to detour around it).

We first identified barriers using a search window radius of 450 m, a scale consistent with agricultural field restoration projects in the study area. For each pair of core areas, Barrier Mapper assigned each pixel in the landscape an improvement score, reflecting the reduction in LCD if all barriers within 450 m of the pixel were completely removed, reducing their resistance to 1.

We then took several additional steps to prioritize barriers for restoration. Because a primary restoration strategy of the Arid Lands Initiative focuses on agricultural lands, we limited our analysis to sites with at least 75%

agricultural land cover and that lacked other potential barriers such as roads, water bodies, and housing. From these sites, we selected the barrier with the largest improvement score.

Because the restoration of a given site can change the degree to which restoration of other areas can improve connectivity (McRae *et al.* 2012), we developed an iterative algorithm to sequentially prioritize restoration sites. First, the algorithm identified the site with the highest improvement score and then simulated restoration of the site by converting the resistance values of all pixels in the 450-m radius circle to 1, making the circle completely permeable to movement. Next, it repeated the entire modeling process: running the corridor analysis, identifying barriers, selecting the barrier with the largest improvement score, and restoring it. The algorithm repeated this process until 2000 acres (809 ha, or 13 sites) were restored, consistent with annual restoration goals in this area.

Incorporating land and restoration costs

We conducted a second prioritization that incorporated acquisition and restoration costs into the site-selection process. We estimated the per-hectare purchase cost using the 2011 tax-assessed parcel value, applying the cost only to the area we intended to restore. To this we added the cost of restoring the site, calculated at $1131.74 per hectare using 2011 seed prices for native shrubs and grasses. We repeated the iterative analysis described above, but instead of selecting the barrier with the largest improvement score alone, we selected the barrier with the largest improvement score per dollar of combined purchase and restoration cost. This produced a second, comparable set of 13 restoration sites.

Evaluating sensitivity to different scenarios

The analyses above incorporated a number of simplifying assumptions about restoration scale, costs, and conservation benefit. The size of individual restoration projects may differ, and converting sites to non-optimal habitat types that still improve their connectivity value may be more cost effective in some cases. We also assumed that connectivity benefit was directly related to the reduction in LCD, regardless of corridor length, but managers may wish to prioritize shorter or longer corridors depending on the dispersal abilities of target species as well as management goals (eg promoting movement for foraging, recolonization of vacant habitats, or long-distance gene flow).

We therefore evaluated how our results would change under different parameterizations that characterize restoration scales (search window radii), connectivity objectives (using improvement in LCD versus percent improvement), and target cover types (restoring to pasture versus shrub–steppe). We describe these analyses in detail in the Supplementary Material.

Results

Many areas with potential to improve connectivity overlapped the original least-cost paths identified by the WWHCWG, whereas others highlighted new, alternate routes (Figure 2a). These restoration opportunities occurred across land parcels that varied substantially in purchase cost (Figure 2b), ranging from $94 569 to $2.1 million.

Accounting for land and restoration costs altered the locations of selected sites (Figure 2c) and produced more cost-effective outcomes (Figure 2d). For example, by accounting for the cost of purchasing and restoring the land, one can improve connectivity for Washington ground squirrels by 147 resistance-weighted kilometers (the units used to measure LCD) for approximately $2 million. By contrast, prioritizing parcels of land solely on their improvement score would require over $4.4 million to achieve the same benefit, with 23% less habitat restored. Similarly, spending a fixed amount of $1.3 million on restoration that is prioritized with land and restoration costs in mind would yield 36% more connectivity benefit and, because of lower parcel costs, would result in more than twice as much area restored.

Our sensitivity analyses (Figure 3; WebPanel 1) showed that savings, and to a large extent locations of restoration sites, were consistent across a range of restoration-project scales (Figure 3b; WebFigure 1). Smaller restoration projects (identified using smaller search radii) tended to overlap sites selected using larger search radii (Figure 3a) but also tended to fall close to the least-cost path and not to necessitate re-routing corridors. Savings were also consistent for restorations favoring shorter corridors, selected on the basis of percent improvement instead of on absolute improvement scores (WebFigure 2, a and b). Identifying restoration sites that were within a certain LCD of a core area produced solutions targeting potential stepping-stone habitat patches; that is, restored patches would provide stopover habitat reachable from either core area (WebFigure 3, a–d). Using such thresholds could decrease the risk of restoring habitat in long, potentially nonviable corridors, but also reduces the number of restorable corridors and areas (WebFigure 3, e and f). Converting sites to pasture instead of native shrub–steppe produced results contingent on cost assumptions. Conversion to pasture produced modestly more efficient connectivity gains than restoration to native habitat if all conversion costs could be recovered by future revenue from managing pasture lands, but similar gains if only half the conversion costs could be recovered (Figure 3, c and d).

Discussion

Although useful, current connectivity modeling and spatial optimization methods do not provide conservation practitioners with the level of detail needed to allocate connectivity restoration funds most effectively. The approach demonstrated here does just that, by targeting sites where restoration would lead to the greatest improvement in connectivity per dollar spent. Our results demonstrate how costs can be incorporated into analyses that pinpoint restoration projects at fine scales, achieving the same degree of improvement in connectivity and restoration of more primary habitat for 45% of the cost. These savings were robust to modeling choices such as restoration scale and prioritization of shorter versus longer corridors.

Although recognition of the importance of including costs in conservation planning is not new (eg Ando *et al.* 1998; Murdoch *et al.* 2007), a lack of computationally efficient tools has to date prohibited the inclusion of costs in connectivity restoration analyses. Our algorithm overcomes these limitations (see WebPanel 1). This means that aside from assembling cost data, the additional effort required to implement this approach is modest, particularly as compared with resistance modeling and other tasks required by connectivity analysis. Moreover, these methods are particularly suited to situations that involve choosing among actions that differ greatly in scope and nature. Although we focused on cropland restoration, such strategies could be analyzed alongside others (eg mitigating the impact of roads).

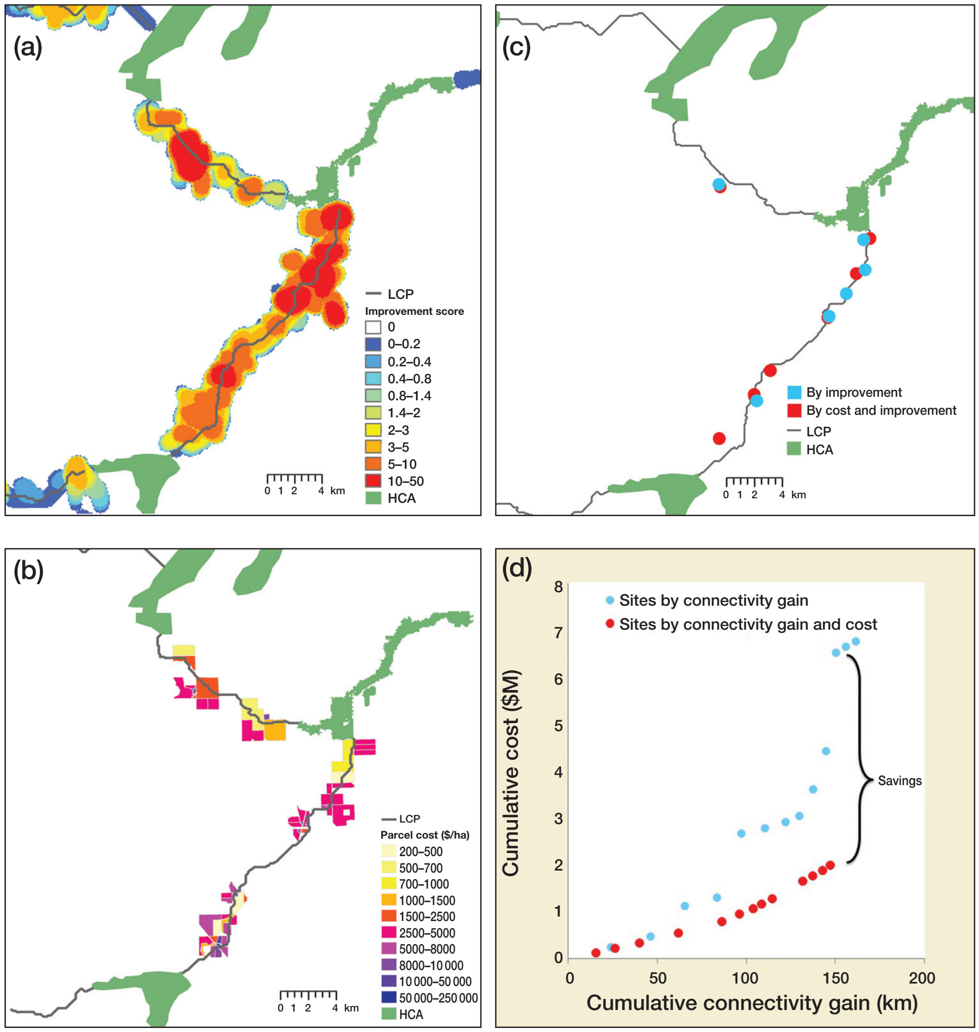

Figure 2. *(a) Barriers to connectivity identified in a portion of our study area; warmer colors represent larger potential connectivity improvements (in resistance-weighted kilometers). (b) Costs of parcels (US dollars) in which we identified potential restoration sites. (c) Locations of restoration sites prioritized on the basis of improvement score alone (blue circles) and improvement score per dollar of purchase and restoration cost (red circles); HCA = Habitat Concentration Areas (WWHCWG 2012), which we refer to here as core areas. LCP = least-cost path connecting core areas. (d) Cumulative costs and improvement scores for restoration sites prioritized based solely on improvement score (blue circles) and based on improvement scores and costs (red circles). Considering costs when selecting restoration sites reduced resistance across the habitat network by 147 resistance-weighted kilometers while saving $2.4 million and restoring 30% more area to native shrub–steppe.*

Our algorithms could also be modified to identify restoration sites using multiple search window and restoration sizes, or to calculate benefits in a way that incorporates complex relationships between dispersal distance and connectivity benefit. Modeling frameworks other than least-cost corridors could be used; for example, barriers can be detected using circuit theory (McRae *et al.* 2012) or other new approaches currently being developed, such as random low-cost paths (K McGarigal, BW Compton, and SD Jackson, pers comm). Different restoration costs for different land-cover types could also be accommodated.

Incorporating costs led to solutions that targeted areas with high conservation value and low land prices, whether raw improvement scores or the percent improvement were considered or not. For instance, 11 of 13 sites were shared between solutions based on raw improvement and percent improvement when costs were considered (Figure 2a; WebFigure 2a); only seven were shared when costs were ignored. Similar effects were observed between restoration scales. Thus, the uncertainty that results from considering multiple representations of model outputs (raw values or percentages) or restoration scales is less apparent and proves less of a barrier to decision making when costs are incorporated.

Although smaller restorations were less expensive (Figure 3b), direct comparison across scales is inappropriate because differing amounts of primary habitat would be restored and because fixed transaction costs likely mean that per-hectare costs are higher for smaller projects. Moreover, restoring an intelligently placed strip of fixed width (eg 100 m) across selected sites instead of restoring an entire circle (so that restoration area would increase linearly with the search radius instead of with its square) would result in cost savings at larger search radii relative to smaller ones. This efficiency derives from the identification of corridor re-routes that are undetectable at smaller radii and points to an obvious next step for improving these algorithms – that is, giving them the ability to identify which parts of the search windows would need to be restored to allow passage through them.

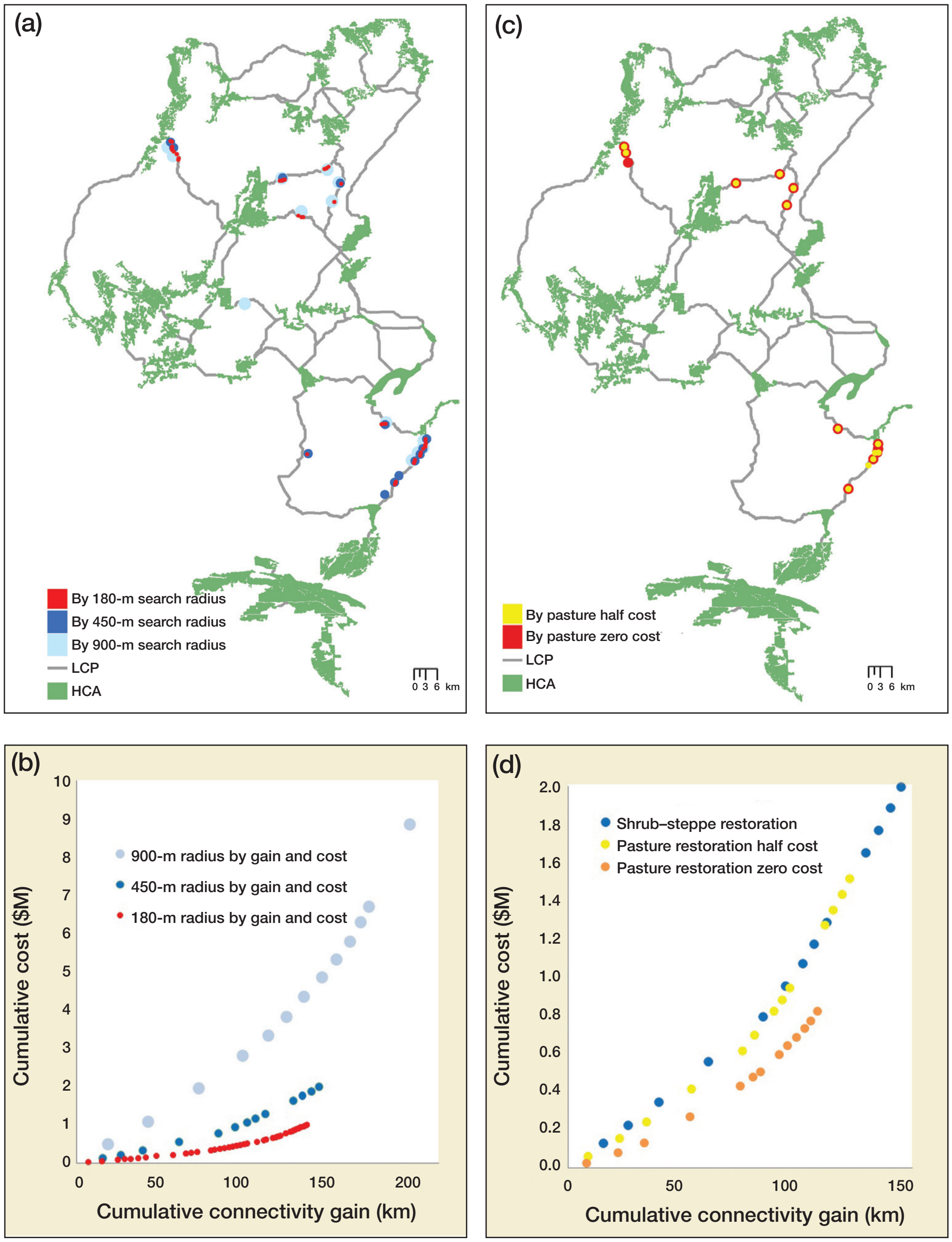

Figure 3. *(a) Map showing 13 restorations at 450 m and 900 m, and 40 restorations at 180 m, with sites chosen on the basis of improvement and cost. (b) Cumulative costs and improvement scores for sites shown in panel (a). (c) Map of pasture restoration sites chosen under two cost assumptions: all restoration costs could be recovered by future revenue from managing pasture lands, or only half the restoration costs could be recovered; all half-cost-recovered pasture sites and all but two all-cost-recovered pasture sites coincided with shrub–steppe sites. (d) Cumulative costs and improvement scores for two pasture restoration scenarios with 450-m shrub–steppe scenario for comparison. HCA = Habitat Concentration Areas (WWHCWG 2012), which in this study we refer to as core areas; LCP = least-cost path.*

Potential savings from conversion to pasture instead of shrub–steppe restoration were promising. Some species use certain agricultural plant types much more readily than others (eg carnivore use of orchards versus row crops in California; Nogeire *et al.* 2013), and could benefit from changes in crop types. If such conversions promote movement and are truly economically feasible, they may be useful when working with landowners who prefer (or are mandated, in the case of agencies) to keep land in some form of economic production. Conversely, restoration to shrub–steppe within a certain LCD of a core area could provide stepping-stone habitat patches, which may be crucial both for dispersal and for range shifts (Saura *et al.* 2014). In addition, both in the Columbia Plateau Ecoregion and elsewhere, there are likely to be multiple opportunities for conserving and enhancing connectivity with different associated costs. One alternative for agricultural lands in the US is the Conservation Reserve Program (CRP), in which farmers are paid to remove land from production. Similarly, some states and counties in the US provide tax incentives for managing timberlands or wildlife habitat.

Such strategies require evaluating trade-offs between the benefits of restoring primary habitat and those associated with connecting existing habitats. Unfortunately, much more research is needed to better understand these trade-offs, which will undoubtedly be species-specific. Even if trade-offs remain poorly understood for some species, however, an advantage of using a return-on-investment framework is that it forces practitioners to explicitly articulate assumptions about the relative values of different actions and explore their effects (Murdoch *et al.* 2007).

Our framework can readily enhance increasingly common connectivity planning exercises, but we caution that several things must be carefully considered prior to its implementation. First, the barrier analyses described here are sensitive to errors in habitat and resistance models in exactly the same way as are standard, least-cost corridor models (McRae *et al.* 2012). Approaches to evaluating such sensitivities have been reviewed elsewhere (eg Beier *et al.* 2009; Rayfield *et al.* 2010) and are equally applicable to our methods (and should be applied in the primary connectivity analysis before restoration analyses are conducted). Second, the conservation status of core habitat areas should be evaluated before connectivity investments are made. If core areas are threatened, then ensuring their protection may be more important than connectivity restoration. Finally, we urge practitioners to carefully approach each step of analytical processes like these, and not to rely solely on analytic results. Examining potential restoration sites to verify underlying base data, assessing willingness of landowners to engage in restoration, and/or identifying incidental benefits for other species would strengthen the applicability of such results.

The framework presented here is the first to prioritize restoration actions in a way that maximizes connectivity of habitat networks per dollar spent. It provides a flexible way of including both costs and ecological effects of previous restoration choices in selecting future restoration sites, leading to a substantial reduction in costs and/or an increase in the total area of land that can be restored with a fixed budget. The framework thus complements previous approaches that maximize compactness and contiguity of protected areas while minimizing costs (Thomson *et al.* [2009] and references therein). We hope it will help to bridge the gap between spatial optimization methods and those developed to analyze connectivity among geographically distinct habitat patches.

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