Ecological Applications, 22(1), 2012, pp. 87–103

Use of land facets to design linkages for climate change

Brian M. Brost[1] and Paul Beier

School of Forestry and Merriam-Powell Center for Environmental Research, Northern Arizona University, Flagstaff, Arizona 86011-5018 USA

Abstract. Least-cost modeling for focal species is the most widely used method for designing conservation corridors and linkages. However, these linkages have been based on current species' distributions and land cover, both of which will change with large-scale climate change. One method to develop corridors that facilitate species' shifting distributions is to incorporate climate models into their design. But this approach is enormously complex and prone to error propagation. It also produces outputs at a grain size (km^2) coarser than the grain at which conservation decisions are made. One way to avoid these problems is to design linkages for the continuity and interspersion of land facets, or recurring landscape units of relatively uniform topography and soils. This coarse-filter approach aims to conserve the arenas of biological activity rather than the temporary occupants of those arenas. In this paper, we demonstrate how land facets can be defined in a rule-based and adaptable way, and how they can be used for linkage design in the face of climate change. We used fuzzy *c*-means cluster analysis to define land facets with respect to four topographic variables (elevation, slope angle, solar insolation, and topographic position), and least-cost analysis to design linkages that include one corridor per land facet. To demonstrate the flexibility of our procedures, we designed linkages using land facets in three topographically diverse landscapes in Arizona, USA. Our procedures can use other variables, including soil variables, to define land facets. We advocate using land facets to complement, rather than replace, existing focal species approaches to linkage design. This approach can be used even in regions lacking land cover maps and is not affected by the bias and patchiness common in species occurrence data.

Key words: adaptation; climate change; coarse-filter approach; connectivity; conservation planning; corridor; ecological process; land facets; topography.

Introduction

Shifts in species' geographical distributions have been the most important mechanism through which plants and animals coped with previous large-scale climate changes (Graham and Grimm 1990, Huntley 2005), and have already begun in response to the current episode of climate change (Grabherr et al. 1994, Parmesan 1996, Thomas and Lennon 1999). Though some species may be capable of adapting to future climatic conditions (Millar et al. 2007, Skelly et al. 2007), it is likely that many species will only persist if they are capable of colonizing newly suitable habitat (Williams et al. 2005). However, habitat fragmentation can interfere with the ability of species to track shifting climatic conditions. Consequently, many advocate the need for conservation corridors and linkages between existing natural areas as a means to support movements necessary for species' range shifts (summarized by Mawdsley et al. 2009).

Least-cost modeling for focal species is the most widely used method for designing corridors to connect wildland blocks (e.g., Walker and Craighead 1997, Singleton et al. 2002, Beier et al. 2006, 2007). The objective of least-cost modeling is to identify the swath of land that minimizes the ecological cost of movement through a landscape for a species (Adriaensen et al. 2003, Beier et al. 2008). Each swath of land represents a corridor, and corridors for multiple focal species are combined into a linkage design. Like most other conservation plans, these designs have been based on current species' distributions and land cover. However, as climate changes, it is likely that some species currently occupying a given area may no longer do so, while other species may be new arrivals.

One approach to develop corridors that accommodate species' shifting distributions is to incorporate climate models into their design. We are aware of two efforts that use this approach, both for the Cape Proteaceae of South Africa. Williams et al. (2005) identified dispersal chains for individual species through 2050, each chain consisting of temporally and spatially contiguous habitat intended to allow a species to shift its range in response to climate change. Phillips et al. (2008) used network flow models to optimize the identification of dispersal chains. Both efforts relied on several linked components—emissions scenarios, general circulation models, regional circulation models, and models of climate envelopes—each of which, unfortunately, con-

Manuscript received 8 February 2011; revised 8 June 2011; accepted 20 June 2011; final version received 27 July 2011. Corresponding Editor: T. G. O'Brien.

[1] Present address: Great Lakes Indian Fish and Wildlife Commission, P.O. Box 9, Odanah, Wisconsin 54861 USA. E-mail: bmbrost@gmail.com

tains some uncertainty. For example, emissions scenarios differ sixfold in predicted annual CO_2 emissions by the year 2100 and climate projections differ vastly among the seven commonly used general circulation models (Intergovernmental Panel on Climate Change 2001, Raper and Giorgi 2005). Divergence increases further among regional circulation models which project outputs from a general circulation model onto a scale more useful for modeling habitat change. Climate envelope models require additional assumptions and necessarily exclude some important components (e.g., species interactions and altered disturbance regimes) that influence species' distributions (Williams et al. 2005). Furthermore, species–climate associations determined from climate envelope modeling performed no better than chance for predicting the current distributions of 68 of 100 European bird species (Beale et al. 2008). Because these models are linked, errors propagate from each model to the next. Additionally, errors and uncertainties are compounded as models project further into the future. Finally, these models produce mapped corridors with a grain size (km^2) that is coarser than the scale at which conservation corridors are implemented.

To avoid these problems, Hunter et al. (1988), Anderson and Ferree (2010), and Beier and Brost (2010) suggested a coarse-filter strategy to conserve biodiversity in the face of climate change. Conventional coarse-filter conservation strategies target biotic communities as the unit of conservation (Noss 1987), but these communities will not respond predictably to climate change. In fact, many communities in existence today are <8000 years old, each component species having responded individualistically to past environmental changes (Webb 1987, Hunter et al. 1988). Thus "basing the coarse-filter approach on physical environments as 'arenas' of biological activity, rather than on communities, the temporary occupants of those arenas," may be a better way to maintain a high level of biodiversity for long-term persistence (Hunter et al. 1988:380).

The central concept underlying this approach is that diverse physical environments support diverse species today (Kirkpatrick and Brown 1994, Faith and Walker 1996, Burnett et al. 1998, Nichols et al. 1998, Cowling et al. 1999, Reyers et al. 2002, Anderson and Ferree 2010) and will interact with future climates to support new assemblages of species in the future (see Plate 1). Protecting diverse physical environments may also ensure the persistence of the ecological and evolutionary processes that maintain and generate biodiversity (Cowling et al. 1999, Noss 2001, Moritz 2002, Cowling et al. 2003, Rouget et al. 2006, Pressey et al. 2007, Klein et al. 2009). Thus, a linkage designed to provide continuity for all physical environments should not only provide connectivity for the full diversity of plants and animals, but also help sustain key processes.

Two efforts have considered physical environments in linkage design, but without a clear, objective landscape classification scheme. Beier et al. (2006, 2007) evaluated the topographic composition of preliminary linkages designed to serve multiple focal species, and expanded some of them in an ad-hoc manner to better represent elevation, slope angle, aspect, and landform classes. Rouget et al. (2006) designed conservation corridors to capture large-scale processes, including biotic response to climate change, by aligning corridors with upland-lowland and macroclimatic gradients.

This paper demonstrates how physical units can be defined in a rule-based and flexible way, and how they can be used for linkage design in the face of climate change. Wessels et al. (1999) defined *land facets* as recurring areas of relatively homogenous topography and soils, such as flat plains with deep alluvial soils, or steep shaded slopes on calcareous bedrock. Because soil maps in our planning areas were incomplete and contained unmapped heterogeneity, in this illustration we define land facets based only on topographic variables. However, our approach uses both categorical and continuous variables and can readily accommodate categorical soil variables (e.g., soil type) and continuous soil variables (e.g., soil depth or moisture).

To illustrate our approach, we developed linkage designs based on land facets for three topographically diverse landscapes in Arizona, USA. As with connectivity planning for focal species, we distinguish between *corridor* (a continuous swath that optimizes connectivity for a single land facet or feature) and *linkage* (the union of corridors, typically with several strands). Each land facet corridor is intended to support movement by species associated with that facet, today and in the future. To better accommodate rapid, short-distance range shifts, interactions between species, and ecological and evolutionary processes that require interspersion, we also included a corridor to optimize high interspersion of land facets (Cowling et al. 1999, Fairbanks et al. 2001, Rouget et al. 2006). We also included a riverine corridor because rivers and drainages promote the movement of animals, sediment, water, and nutrients (Forman 1995). Streams also provide routes to higher elevation without any reversals in elevation along their courses.

Methods

We used a combination of ArcGIS 9.3 (ESRI, Redlands, California, USA) and R statistical software (R Development Core Team 2009) to define land facets (Fig. 4), and developed procedures to delineate corridors entirely within ArcGIS 9.3 (Fig. 8). We packaged these procedures into R functions and an ArcGIS extension that allow users to modify each critical value, such as what fraction of cells to exclude as outliers (*available online*).[2] In this section, we state the values

[2] www.corridordesign.org

PLATE 1. Different combinations of elevation, slope, and topographic position support different land cover types in the linkage planning area between the Tumacacori Mountains and the Santa Rita Mountains (on the horizon). Photo credit: P. Beier.

that produced reasonable results in the three landscapes we analyzed.

Linkage planning areas

We designed linkages based on land facets for three landscapes in Arizona, USA (Table 1; Figs. 1–3). Detailed information regarding each area's ecological significance, existing conservation investments, threats to connectivity, and patterns of land ownership and land cover are available in Beier et al. (2007).

Beier et al. (2007) delineated two protected wildland blocks to be connected in each landscape (Figs. 1–3). Each wildland block is a large area without highways or major paved roads and owned by agencies with a mandate to retain the land in natural condition. We refer to the land between and around the wildland blocks as *matrix*. We defined the analysis areas to include both wildland blocks plus enough topographically diverse matrix to allow our procedures to identify highly nonlinear corridors (Beier et al. 2008).

Defining land facets

We defined land facets using three continuous variables, namely elevation, slope angle, and annual solar insolation, and one categorical variable, topographic position (Fig. 4). These variables were derived from the 1 arc-second (i.e., 30-m resolution) United States Geological Survey National Elevation Dataset, which typically has a vertical root-mean-square error $\leq$ 7 m (United States Geological Survey 2000). Slope angle and solar insolation were computed using the Spatial Analyst extension in ArcGIS 9.3 (solar insolation model developed by Fu and Rich [2002]). We computed annual solar insolation by summing instantaneous radiation at half-hour intervals for one day per month over a calendar year. Insolation integrates the effect of latitude, aspect, slope angle, elevation, daily and seasonal changes in sun angle, and topographic shading on incoming solar radiation for a location. Using the CorridorDesigner toolbox to ArcGIS 9.3 (Majka et al. 2007), we assigned each 30×30-m grid cell to one of three topographic positions, namely canyon bottom, ridge, or slope, by subtracting the elevation of a focal cell from the mean elevation of cells within a 200-m radius. We defined cells with differences ≤ -8 m as canyon bottoms, cells with differences ≥ 8 m as ridges, and cells with differences between -8 and $+8$ m as slopes. Prior to calculating solar insolation, we buffered

TABLE 1. Characteristics of planning areas and wildland blocks used in our analyses.

Planning area	Area (km^2)	# of 30-m cells in planning area	Minimum distance between wildland blocks (km)	Western-most wildland block		
				Area (km^2)	Elev. (m)	Major geographic features
Santa Rita-Tumacacori (111.0° W, 31.6° N)	2475.9	2 706 667	13.0	480.6	1050–1950	Tumacacori, Atascosa, and Pajarito Mountains
Black Hills-Munds Mountain (111.9° W, 34.7° N)	3817.4	4 241 503	16.8	372.8	1080–2385	Black Hills
Wickenburg-Hassayampa (112.8° W, 33.9° N)	9786.6	10 874 001	26.4	1606.3	360–1735	Harquahala and Big Horn Mountains; Hassayampa Plain

Note: Elev. stands for elevation range.

the analysis area by 5 km to account for shading by distant topography; a 200-m buffer was used to mitigate edge effects on calculations for slope angle and topographic position.

Each of these variables represents an indirect (elevation, slope angle, and topographic position) or direct (solar insolation) ecological gradient that is biologically important in mountainous landscapes (Franklin 1995). Elevation is associated with gradients in temperature and precipitation (Franklin 1995). Slope angle influences the velocity of water runoff and is related to soil moisture content and soil development (Franklin 1995). Insolation is related to heat load, photosynthetic potential, evaporation, transpiration, and soil moisture near the surface (Lookingbill and Urban 2004). Topographic position captures the major components of land curvature, namely canyon bottoms and ridges, and is easily interpreted. It also represents differences in substrate development (canyon bottoms are depositional environments whereas ridges and steep slopes are erosional) and is related to sun and wind exposure (Valverde et al. 1996).

We used numerical clustering procedures to define land facets based on the attributes of cells inside of the wildland blocks only, thereby ensuring that our classification reflected the topographic composition of the wildland blocks. This step is necessary to later identify portions of the matrix most similar to the wildland blocks for inclusion in the linkage design. Although the user can define facets based on cells in the entire analysis area, such a procedure might identify some land facets that occur only in the matrix and not in the wildland blocks.

We defined land facets by first sorting on topographic position, and then clustering on combinations of values for the continuous variables within each topographic position. Although some cluster analyses can be performed on continuous and categorical variables simultaneously, we felt that a land facet with homogeneous topographic position would be more interpretable than a land facet that included a mixture of canyon bottoms, ridges, and slopes.

We divided slopes into land facets based on all three continuous variables (elevation, slope angle, and insolation), but used only slope angle and elevation to divide ridges and canyon bottoms into land facets. Insolation was not used to identify subclasses of ridges or canyon bottoms because these topographic positions are often symmetrical features. For example, a classification that used insolation to define land facets within the "ridge" topographic position would identify different facets for their opposing sides, such as north-facing and south-facing ridges, despite their otherwise similarity. This unnecessarily complicates corridor design because the opposing sides of canyon bottoms and ridges are close to each other and can be treated as a unit for conservation purposes.

We used kernel density estimation to identify outliers, i.e., cells with combinations of values for continuous variables that often occur in small, isolated patches, or may only occur in one wildland block. Outliers produce less compact clusters (i.e., cells within a cluster span a larger range in attribute space) with a diluted ecological significance. Outliers also shift the position of the cluster centroids toward a sparser region of attribute space.

Kernel density estimation is a nonparametric procedure that estimates the probability density function of a random variable (Silverman 1986). We used package *ks* (Duong 2009) in R for multivariate kernel density estimation. Because our data sets were large, we were forced to group individual cells according to their attribute values into bins of equal interval across the range of each variable (details in Appendix A). Individual cells were then assigned the kernel density estimate of the bins into which they were grouped.

Cells were identified as outliers if they occurred in the 10th percentile "tail" of the multivariate distribution generated from the kernel density estimation (Fig. 5). Thus, outliers were identified based not only on their distance from the data's centroid, but also on the data's multivariate shape. Because outliers were defined relative to cells inside of the wildland blocks, the proportion of cells in the matrix classified as outliers was higher or lower than 10% (e.g., higher than 10% in

TABLE 1. Extended.

Eastern-most wildland block			Matrix between and around wildland blocks	
Area (km^2)	Elev. (m)	Major geographic features	Elev. (m)	Major geographic features
429.4	1100–2885	Santa Rita Mountains	665–2200	Patagonia and San Cayetano Mountains; Santa Cruz River bisects planning area
374.0	1050–2090	Mogollon Rim, Munds Mountain, Schnebly Hill, Horse Mesa, and House Mountain	915–2385	Mogollon Rim and the Antelope Hills; Verde River bisects planning area
1682.9	430–2429	Wickenburg, Weaver, Hieroglyphic, Bradshaw, Buckhorn, and Sheep Mountains	275–2325	Harcuvar and Vulture Mountains; Hassayampa Plain, Aguila Valley, Butler Valley, and the Hassayampa and Agua Fria Rivers

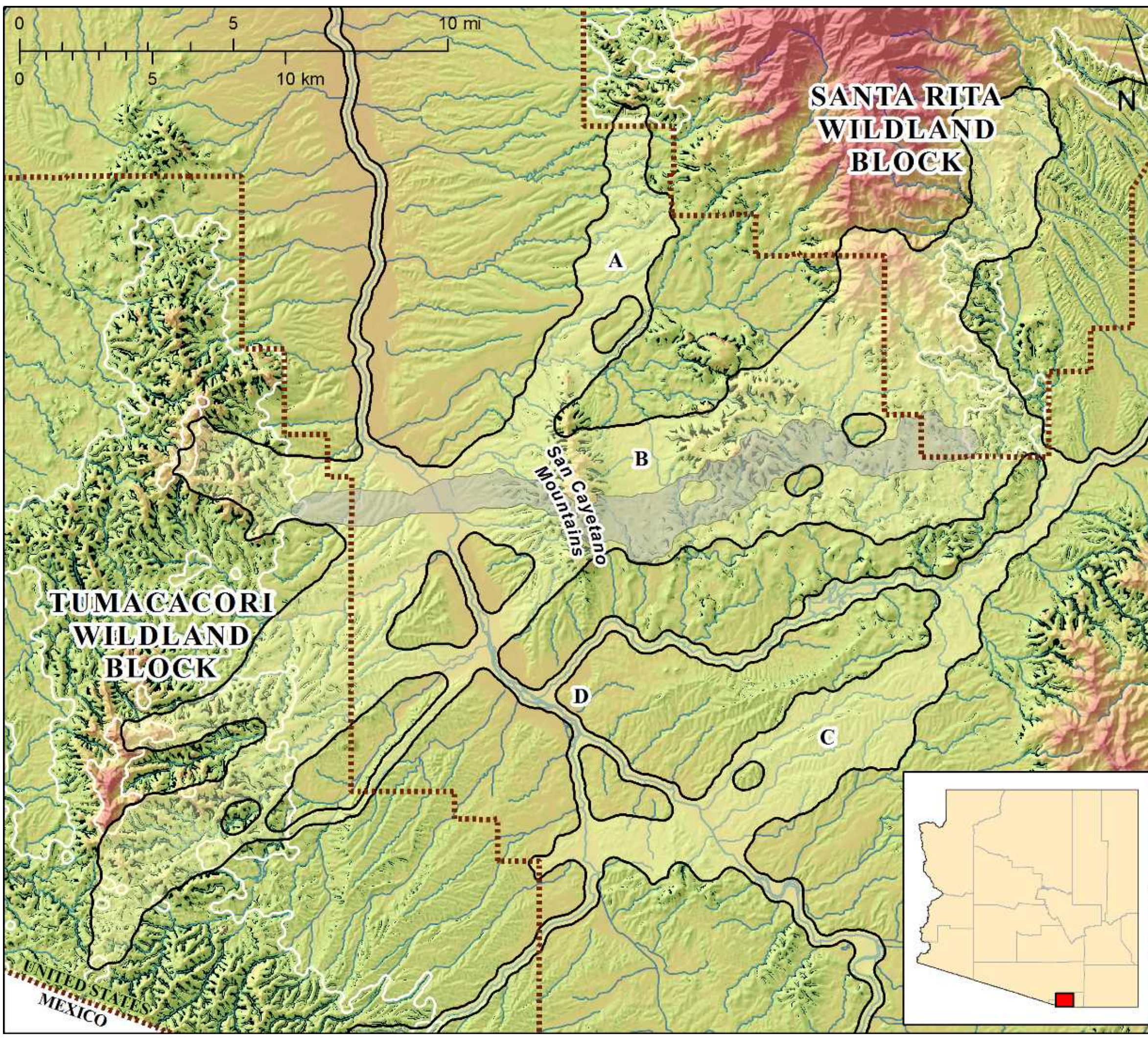


FIG. 1. Map of the land facets linkage design (outlined in black) for the Santa Rita-Tumacacori planning area. Linkage strands consisted of corridors for (A) high-elevation, steep canyon bottoms; (B) low-elevation, gentle canyon bottoms and ridges; mid-elevation, gentle canyon bottoms and ridges; mid-elevation, steep canyon bottoms and ridges; high-elevation, steep ridges; mid-elevation, steep, cool slopes; mid-elevation, steep, hot slopes; high-elevation, gentle, hot slopes; and high diversity of land facets; (C) low-elevation, gentle, warm slopes; and (D) riparian habitat. Instances of the mid-elevation, steep canyon bottom land facet are shown in black. The corresponding least-cost corridor (gray) minimizes the resistance (green–red color ramp; green = low resistance, red = high resistance) between corridor termini (outlined in white). The inset shows location within Arizona, USA.

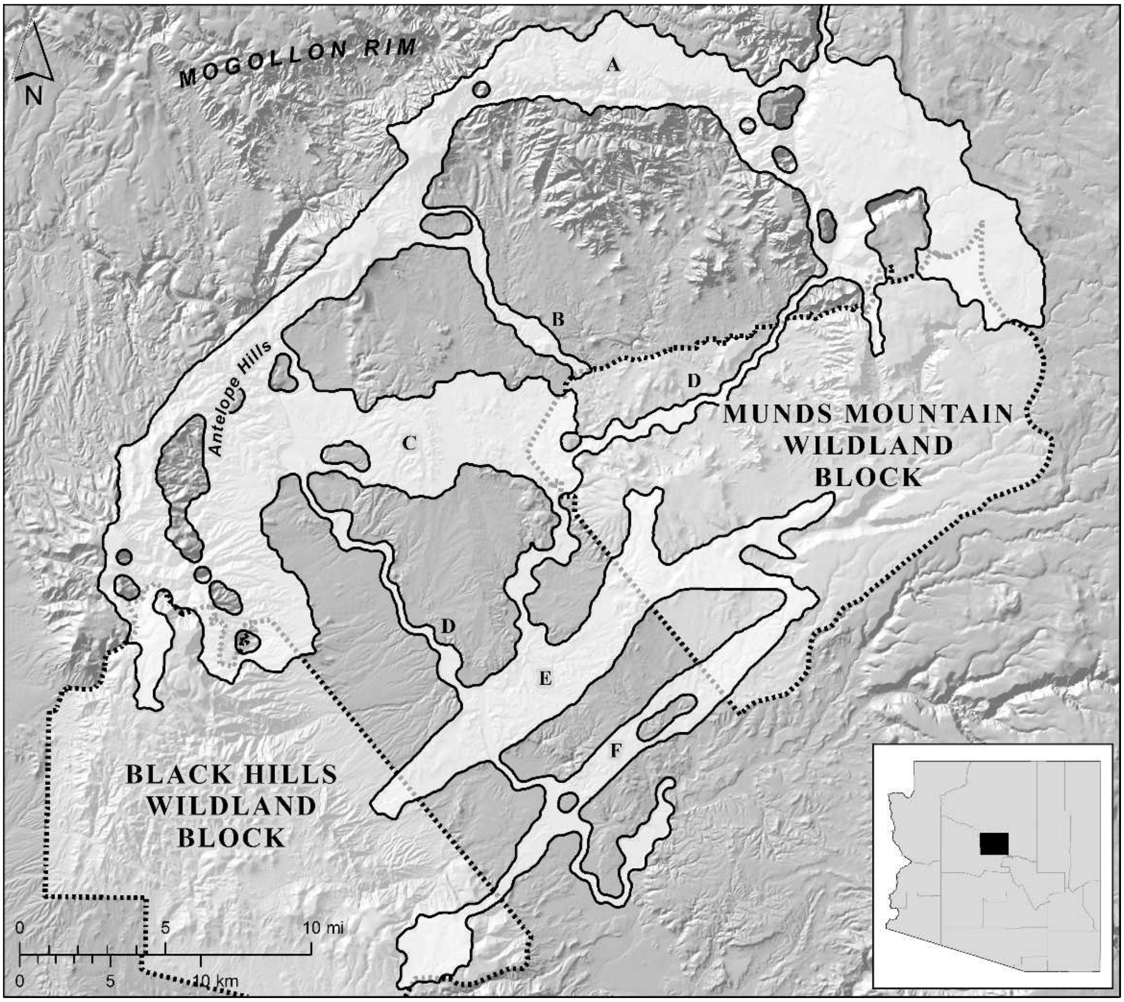


FIG. 2. Map of the land facets linkage design (outlined in black) for the Black Hills-Munds Mountain planning area. Linkage strands consisted of corridors for (A) high-elevation, gentle canyon bottoms and ridges; and high-elevation, gentle, hot slopes; (B) high diversity of land facets; (C) low-elevation, gentle, canyon bottoms and ridges; and low-elevation, gentle, warm slopes; (D) riparian habitat; (E) mid-elevation, steep canyon bottoms and ridges; low-elevation, steep, cool slopes; and mid-elevation, steep, warm slopes; and (F) mid-elevation, gentle, warm slopes. The inset shows location within Arizona, USA.

Fig. 5) when the matrix topography differed from that of the wildland blocks.

Next, we used fuzzy c-means cluster analysis to classify the non-outliers (Fig. 6a). Fuzzy c-means cluster analysis is an iterative procedure of finding the c partitions in a data set that minimizes the within-cluster variances of the classified objects (Bezdek 1981). The number of clusters, c, is defined by the user. Unlike other classification methods that assign each object to one and only one class, fuzzy c-means cluster analysis assigns each observation membership to all c clusters. Membership ranges between 0 and 1, with larger values indicating higher similarity between an object and a cluster centroid. We used package *e1071* (Dimitriadou et al. 2009) in R statistical software for fuzzy c-means cluster analysis.

Membership of cell i to cluster j is calculated as

$$\mu_{ij} = \frac{\left[(d_{ij})^2\right]^{-1/(\varphi-1)}}{\sum_{j'=1}^{c}\left[(d_{ij'})^2\right]^{-1/(\varphi-1)}} \tag{1}$$

where d_{ij} is the Euclidean distance (in attribute space) between cell i and cluster centroid j, φ is the "fuzziness" parameter used in the cluster analysis, and j' is an index over all c clusters (Bezdek 1981). We used $\varphi = 1.5$ because it represents a compromise between a crisp classification with non-overlapping clusters ($\varphi = 1$) and larger values giving a fuzzier classification (Burrough et al. 2001). The denominator in Eq. 1 standardizes the membership values; thus $\sum_{j=1}^{c} \mu_{ij} = 1$ for all i.

Prior to clustering, we standardized variables with respect to the mean and standard deviation of the cells

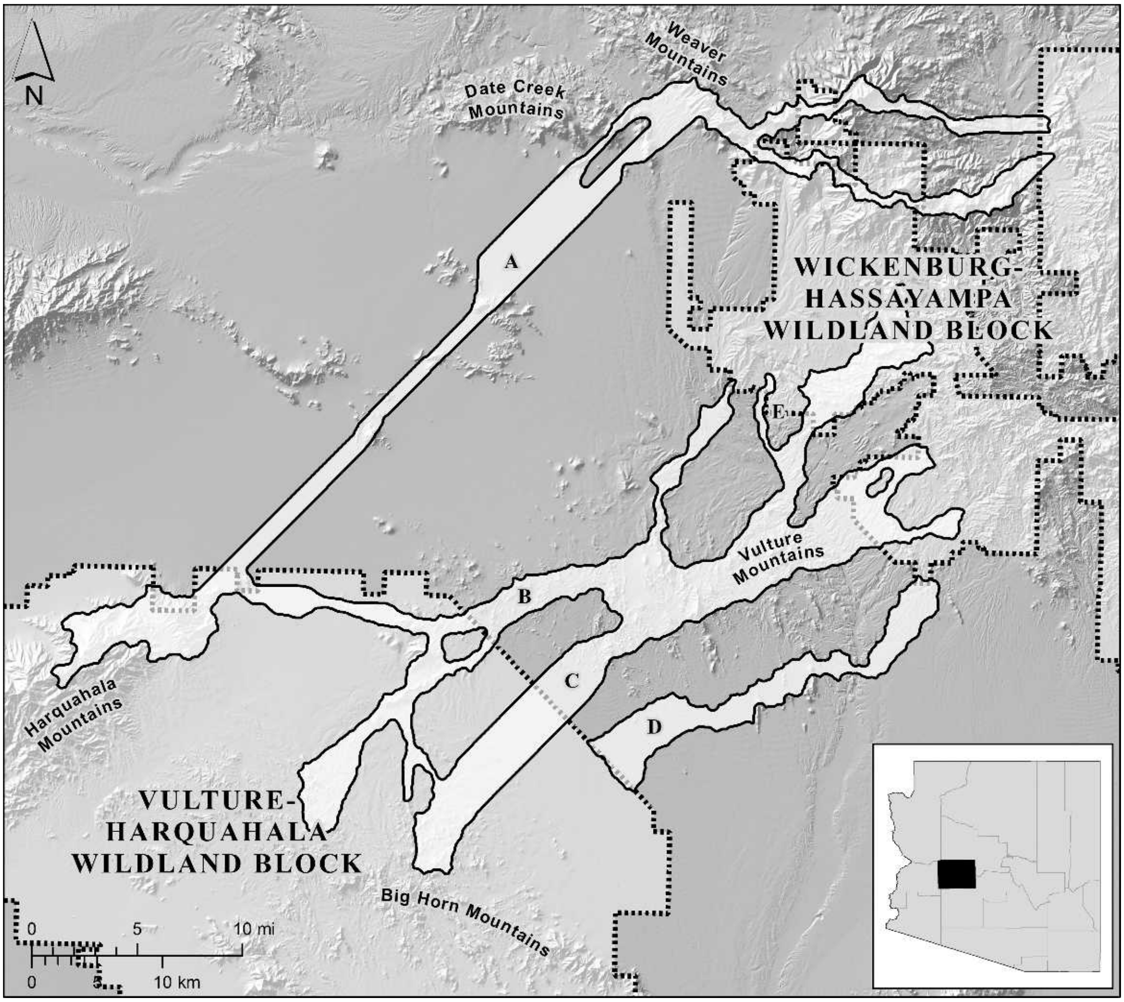


FIG. 3. Map of the land facets linkage design (outlined in black) for the Wickenburg-Hassayampa planning area. Linkage strands consisted of corridors for (A) high-elevation, steep canyon bottoms and ridges; (B, C) low-elevation, gentle canyon bottoms and ridges; low-elevation, steep canyon bottoms and ridges; mid-elevation, steep, cool slopes; high-elevation, steep, warm slopes; and high diversity of land facets; (D) low-elevation, gentle, warm slopes; and (E) riparian habitat. Inset shows location within Arizona, USA.

included in the analysis (i.e., cells within a topographic position inside of the wildland blocks that were not outliers). Next, we identified the optimal number of clusters, k, as the classification that best corresponded to the natural multivariate structure in the continuous variables. To determine k, we varied c in the range of $2 \leq c \leq 10$ and computed eight cluster validity indices for each value of c (three indices are illustrated in Fig. 7). Each of the indices is based on the compactness within and/or separation between clusters. We identified k as the number of clusters c that produced the largest marginal improvements in all or most of the eight indices. No evidence suggested an optimal solution exceeding five clusters for any of our data sets. Situations in which the indices did not clearly indicate a single optimal number of clusters are addressed in Appendix C.

We performed 100 iterations of the fuzzy c-means cluster analysis for each c (i.e., $2 \leq c \leq 10$) to detect cases in which more than one partition for a given c minimized the within-cluster variance (e.g., $c = 7$ in the Davies-Bouldin plot in Fig. 7). If this occurred for the optimal number of clusters, the fuzzy-c partition with the best validity index values was selected.

Using Eq. 1, fuzzy membership values to the k optimal clusters were computed for all non-outlier cells in the planning area within the respective topographic position. To gauge how well each cell was classified, we computed a confusion index as the ratio of its second largest membership value to its largest membership value (Burrough et al. 2000). If the confusion index is near 0, then the cell is highly associated with the cluster centroid to which it has greatest membership; if the cell's confusion index is near 1, then the difference between its

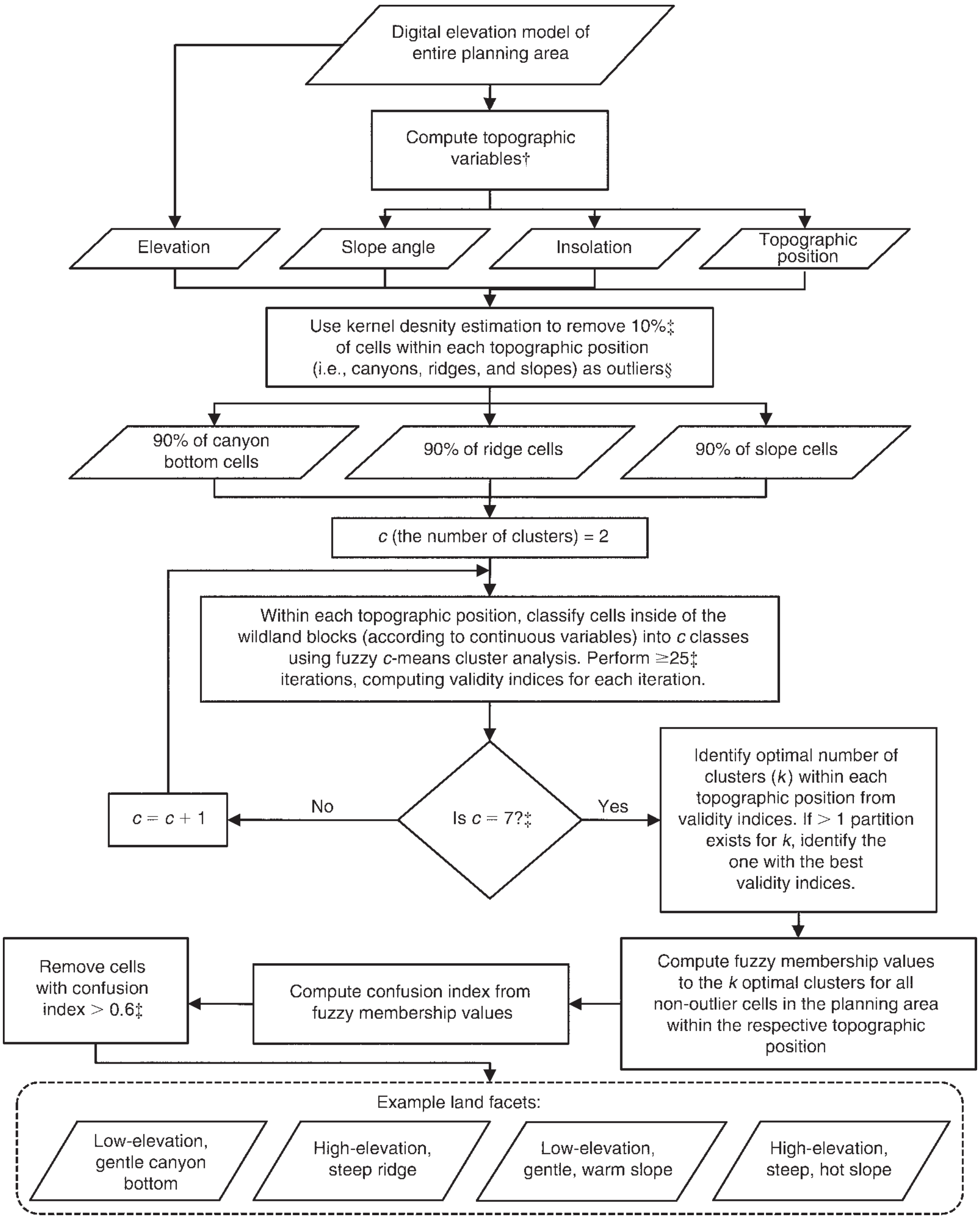


FIG. 4. Sequence of operations (rectangles) and products (parallelograms) used to define land facets. The first operation occurs in ArcGIS; the remaining operations occur in R statistical software.

† The analyst can use other topographic variables or include soil variables.

‡ These parameters can be changed.

§ We identified outliers and clusters with respect to elevation and slope angle for cells within the canyon bottom and ridge topographic positions, and with respect to elevation, slope angle, and solar insolation for cells within the slope topographic position. Outliers and clusters were defined with respect to cells inside of the wildland blocks only.

two largest membership values is small, and there is confusion about the most closely associated centroid (Fig. 6b). Following Burrough et al. (2000), we considered cells with a confusion index > 0.6 as poorly classified. Cells with a confusion index ≤ 0.6 were allocated to the cluster for which they had highest membership, and thus represented the land facets upon which corridors were designed (Fig. 6c). Cells with a confusion index > 0.6 (and those identified as outliers) were not allocated to a land facet.

Corridor design for individual land facets

For each focal land facet type (e.g., mid-elevation, steep canyon bottom), we defined corridor termini

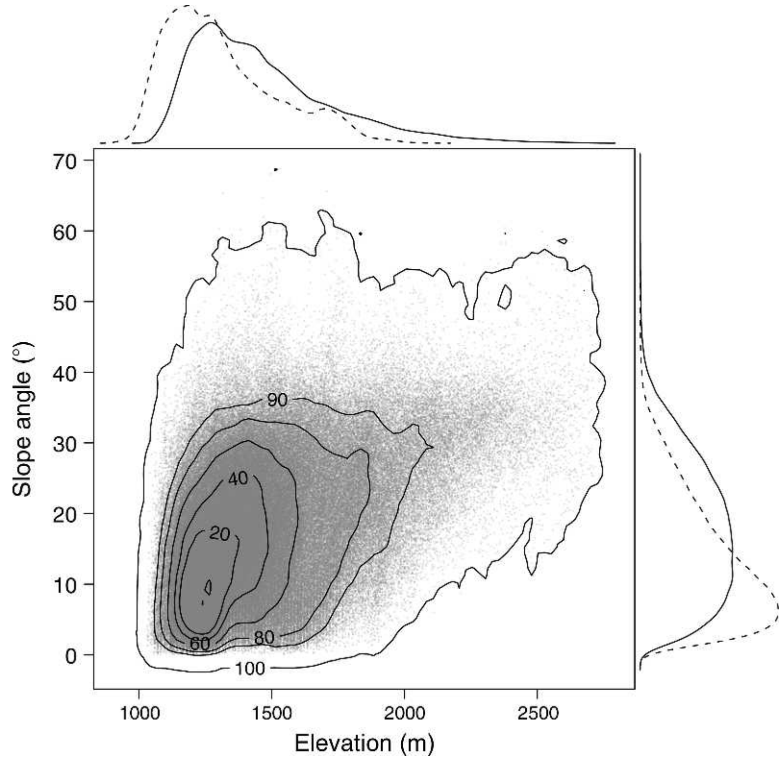


FIG. 5. Example kernel density estimation for the canyon bottom topographic position in the Santa Rita-Tumacacori planning area. Contour lines in the main plot contain the densest proportion of cells as indicated by the labels. We defined outliers as those cells occurring outside of the 90% contour (i.e., the least dense 10% of cells). The marginal plots show how the distribution of cells in the canyon bottom topographic position inside the wildland blocks (solid line) differed from those in the matrix (dashed line). Because kernel density estimation was based on cells inside the wildland blocks only, the proportion of cells in the entire planning area classified as outliers deviated from 10% depending on the extent and location of overlap in the marginal distributions.

(starting/ending locations for a corridor) as polygons within the wildland blocks that contained the most occurrences of the focal land facet (Fig. 1). We aggregated all cells with at least one occurrence of the focal facet type within a three-cell radius into polygons, and defined termini as those polygons that were greater than or equal to one-half the size of the largest polygon in each respective wildland block. Although we used a low density threshold (one cell within a three-cell radius), we found that the largest polygons always contained a high density of the focal facet type. In situations where the largest polygons do not contain a high density of the focal facet type, our thresholds would select larger polygons more sparsely populated by the focal land facet over smaller but more densely populated polygons.

We designed one corridor per land facet using least-cost corridor analysis (Fig. 8). Underlying this approach is a resistance surface wherein the value of a cell represents the difficulty of moving through it (Adriaensen et al. 2003). In least-cost modeling for a focal species, resistance is usually estimated as departure from optimal habitat suitability (Beier et al. 2008; alternatively, it can be estimated from data on movement or gene flow). In the land facet approach to corridor design, we similarly defined resistance as the departure of a cell's attributes from the ideal attributes of the focal land facet (Fig. 1). To create resistance values, we used Mahalanobis distance, a multivariate distance measure standardized by the variance–covariance matrix of the independent variables (Clark et al. 1993, Gotelli and Ellison 2004).

Mahalanobis distance is calculated as

$$D^2 = (\mathbf{x} - \boldsymbol{\mu})'\boldsymbol{\Sigma}^{-1}(\mathbf{x} - \boldsymbol{\mu}) \quad (2)$$

where $\mathbf{x}$ is a vector of attributes associated with each cell in the analysis area, $\boldsymbol{\mu}$ is a vector representing the attributes of the ideal cell of the focal land facet, and $\boldsymbol{\Sigma}$ is the variance–covariance matrix of the independent variables. Using the Mahalanobis Distances extension to ArcGIS 9.3 (Jenness Enterprises 2010), we computed Mahalanobis distance on the same variables used to define land facets, and an additional variable, namely the relative density (scaled 0 to 1) of the focal land facet within a three-cell radius. Values in μ for elevation, slope angle, and solar insolation (slope topographic position only) were calculated as the mean of the respective attributes of the cells inside of the wildland blocks allocated to the focal land facet; the value for density was set to 1 because an ideal cell of the focal facet type would be surrounded by other cells of the focal facet type. The variance–covariance matrix ($\boldsymbol{\Sigma}$) was also calculated on the cells inside of the wildland blocks allocated to the focal land facet.

To prevent a corridor from passing through urban or developed areas such as mines, these areas were digitized from aerial photographs (National Agricultural Imagery Program; *available online*)[3] and assigned "no data" values in the resistance surfaces.

In least-cost modeling, each cell in the planning area is assigned a cost-distance equal to the lowest possible sum of resistance values in a chain of cells to termini in each wildland block (Adriaensen et al. 2003). The two cost-distance maps (one for each wildland block) are summed to produce the cumulative cost surface. A given proportion of cells with the lowest cumulative cost values is a least-cost corridor connecting the edges of termini in both wildland blocks (Fig. 1). For each land facet, we examined multiple least-cost corridors containing different proportions of cells (e.g., 0.5–5.0% in 0.5% increments) and selected the one with an approximate minimum width of 1 km over its length. We used this minimum width because it represents a compromise between narrower corridors that would not serve many species and wider corridors that would be too costly to conserve. Most focal species corridors in these landscapes were also approximately this width (Beier et al. 2007). After the multiple, partly overlapping corridors are joined to create a linkage design, each strand typically averages 2–4 km in width (e.g., Figs. 1–3). We used the "Cost distance" tool in the Spatial Analyst extension of ArcGIS 9.3 and the "Create corridor slices" tool in the CorridorDesigner ArcGIS toolbox (Majka et al. 2007) for these procedures.

Corridor design for high diversity of facets

A single corridor was also designed to optimize connectivity for high diversity (i.e., high interspersion) of land facets. We used Shannon's index (Magurran 1988) to measure diversity of land facets in a circular neighborhood with a five-cell radius. Shannon's index is calculated as

$$H' = -\sum p_i \ln(p_i) \tag{3}$$

where p_i is the proportion of cells classified as land facet i relative to cells in the neighborhood classified as any land facet, and the summation is over all land facets present in the landscape. Shannon's index increases with both richness and evenness.

We calculated resistance of a cell as $(H' + 0.1)^{-1}$; adding 0.1 precludes undefined values which could occur if no cells in the neighborhood were classified as a land facet. Thus cells with a high diversity index have low resistance. As in designing corridors for individual land facets, areas unsuitable for providing connectivity were also removed from this surface. We defined the corridor termini by first aggregating into polygons all cells inside the wildland blocks in the upper 50th percentile of Shannon's index values. Of these polygons, we retained those that were greater than or equal to one-half the size of the largest polygon as termini. We selected these thresholds because the resulting termini were the largest areas of high land facet diversity inside the wildland blocks. Both thresholds were defined with respect to cells in each wildland block separately. As before, least-cost corridor analysis was used to identify the corridor with an approximate minimum width of 1 km over its length.

Linkage design

We created the final linkage design by taking the union of all least-cost corridors (one for each facet type and one for the diversity of facets) and the best riverine or riparian habitat in the analysis area as identified by Beier et al. (2007), who asked local experts to identify the reaches of major streams and rivers with the best perennial flow or (if no stream had such flows) the best riparian habitat. To mitigate edge effects, we buffered the linkage design by 150 m and each riverine corridor by 200 m (Beier et al. 2007).

Results

Nine to 12 land facets were defined per landscape; three to five were defined per topographic position in each landscape (details in Appendix B). Each land facet could be described by a simple phrase, such as "low-elevation, steep canyon bottom" or "high-elevation, gentle, hot slope."

Each linkage design consisted of multiple strands and each strand consisted of one to 11 corridors (Figs. 1–3). In each of the three landscapes, corridors overlapped extensively (Table 2). On average, the area encompassed by a single corridor increased with distance between wildland blocks (Table 2). However, the Black Hills-Munds Mountain planning area contained the smallest and largest corridors; its linkage design was also the largest of the three.

The proportion of cells identified as outliers in each landscape deviated from the a priori 10% threshold described in *Methods* (Table 2; Fig. 5). In the Black Hills-Munds Mountain and Santa Rita-Tumacacori planning areas, the wildland blocks (mountainous) differed sharply from the matrix (dominated by a broad flat valley). Thus, more than 10% of matrix cells (those of the lowest elevation and slope angle) were identified as outliers. Conversely, fewer than 10% of cells were defined as outliers in the Wickenburg-Hassayampa planning area because the southern wildland block was topographically similar to the matrix. On average, 4.9% of cells were identified as poorly classified (confusion index > 0.6; Table 2); this proportion did not vary systematically among topographic positions.

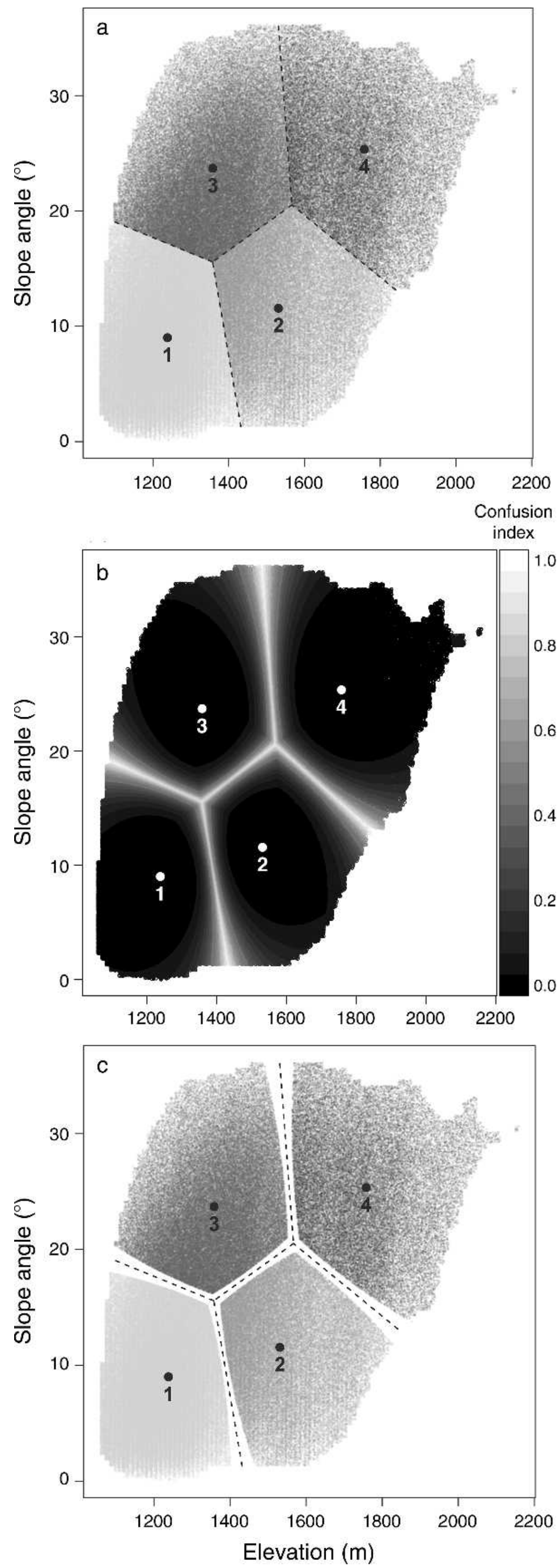
In all three planning areas, the wildland blocks were relatively rugged compared to the matrix. Accordingly,

[3] http://www.fsa.usda.gov/FSA/apfoapp?area=home&subject=prog&topic=landing

the proportion of cells allocated to more rugged land facets (e.g., canyon bottoms and ridges) was higher in the wildland blocks than in the matrix. In the Wickenburg-Hassayampa planning area, the northern wildland block was more mountainous than the southern wildland block (Fig. 3). Consequently, with exception to the low-elevation, gentle, warm slope land facet, all termini in the southern wildland block occurred in areas most similar to the northern wildland block, namely the Big Horn and Harquahala Mountains.

Size of the linkage design depended more on the topography of the planning area than on the distance between wildland blocks or the number of land facets in a landscape. In the Santa Rita-Tumacacori planning area, 12 of 13 corridors contained some part of the topographically diverse San Cayetano Mountains (Fig. 1, strands A and B). These mountains lay between the wildland blocks and thus contributed to a relatively compact linkage design. Four of 11 corridors in the Black Hills-Munds Mountain planning area captured the Antelope Hills or Mogollon Rim, even though this indirect route was up to four times the distance between wildland blocks (Fig. 2, strands A and B). In the Wickenburg-Hassayampa planning area, all but the corridor for low-elevation, gentle, warm slopes (strand D) captured the Vulture, Date Creek, or Weaver Mountains (Fig. 3). No cells allocated to the high-elevation, steep canyon bottom and ridge land facets occurred in the matrix directly between the wildland blocks in this landscape; therefore, these corridors (strand A) resulted in straight paths between the Harquahala and Date Creek Mountains. These straight paths were poor corridors for the focal facet types

On average, approximately 148 hours were required to run all analyses for a single linkage planning area on a Microsoft Windows XP platform with 3.0 GHz Intel Core 2 Duo processor (Microsoft, Redmond, Washington, USA). The most time-consuming step was iterating the fuzzy c-means cluster analysis for each c ($\sim$134 hours). Time invested in this step could be reduced $> 80\%$ by performing fewer iterations (we performed 100), and only testing values of $c < 7$ (we tested values as high as 10) as the time required for the cluster analysis increases exponentially with c. As few as 25 iterations are adequate because in instances where more than one partition was present, the less common partition comprised 32.2% of the



→

Fig. 6. Example output of fuzzy c-means cluster analysis for the canyon bottom topographic position in the Santa Rita-Tumacacori planning area. (a) Plot of non-outlier cells assigned to the cluster centroid for which they have highest membership (ignoring fuzziness of the classification). (b) Confusion index indicating how well each cell is classified. Values near 1 indicate high confusion, whereas values near 0 indicate perfect classification. (c) Plot showing composition of land facets, i.e., cells with confusion index ≤ 0.6. Despite the "fuzziness" in the classification, the joint distributions of attributes for the resulting land facets are mutually exclusive.

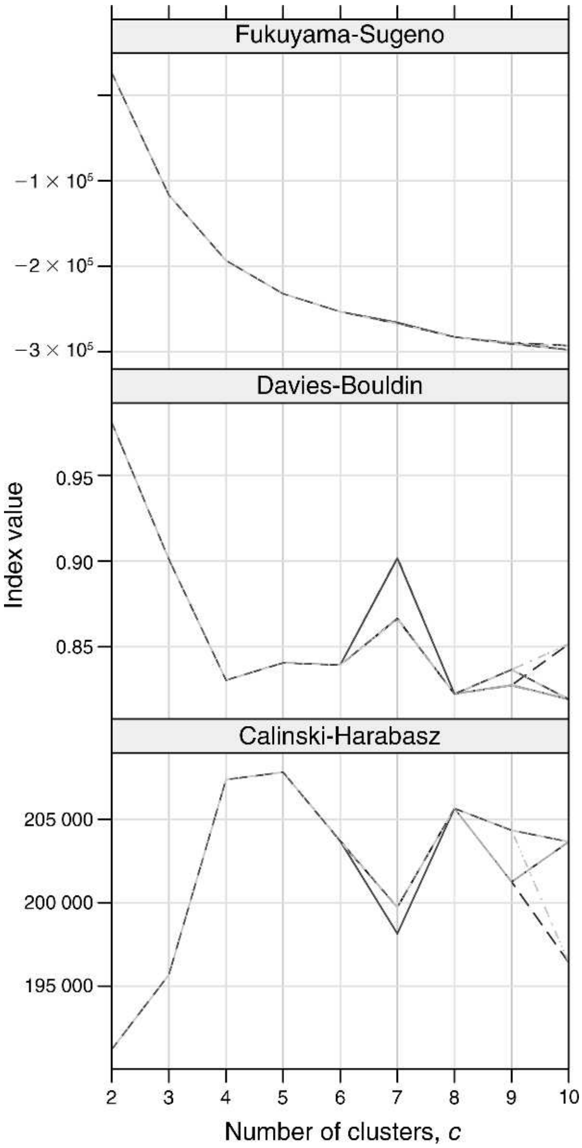


FIG. 7. Example cluster validity indices for the classification of cells in the canyon bottom topographic position of the Santa Rita-Tumacacori planning area. One hundred iterations of the cluster analysis were performed for each number of clusters (i.e., $2 \leq c \leq 10$), and indices were computed for each iteration. The Fukuyama-Sugeno index decreases monotonically as a function of c; an "elbow" in the plot indicates a good partition (Zhang et al. 2008). The best partition corresponds to the lowest value of the Davies-Bouldin index and the highest value of the Calinski-Harabasz index (Maulik and Bandyopadhyay 2002). In addition to the indices illustrated here, we also used the Average Within-Cluster Distance, Xie-Beni, Xie-Beni*, PBMF (Pakhira-Bandyopadhyay-Maulik), and Fuzzy Silhouette indices to help determine the optimal number of clusters (Campello and Hruschka 2006, Celikyilmaz and Turksen 2008). Iterations for a single index diverge where multiple fuzzy-c partitions minimize the within-cluster variance for a given number of clusters (e.g., for c = 7, 9, and 10 for the Davies-Bouldin and Calinski-Harabasz indices). In this case, we identified the optimal number of clusters as four.

iterations on average (range: 6.7–46.7%). Thus, performing 25 iterations yields a 99.99% probability of detecting multiple partitions on average, and an 82% probability for the least-common partition that we observed. Although most steps were relatively mechanical (including an automated script for iterating the cluster analysis), others like choosing the optimal number of clusters, selecting a corridor of the appropriate width, and modifying the resistance surface or potential termini required user involvement and judgment (see Appendix C).

DISCUSSION

In this paper, we describe and illustrate a new approach to designing linkages to provide connectivity in the context of climate change. Our approach optimizes connectivity of land facets, or landscape units defined by topographic and soil variables. Each linkage includes about a dozen corridors for individual land facets, a corridor with high interspersion of facets, and a riverine corridor. Each corridor for an individual land facet is intended to support movement by plants and animals associated with that land facet during periods of climatic quasi-equilibrium. The corridor with highly interspersed land facets is intended to provide less mobile species quick access to favorable land facets during periods of rapid climate change. Interspersion can also support interspecific interactions and expose species to non-core habitat, thereby providing opportunities for speciation (Cowling et al. 1999, Fairbanks et al. 2001, Rouget et al. 2006). Areas of high topographic diversity (high climate heterogeneity) served as refugia during past periods of climate change (Hewitt 2000) and are likely to do so in the future. However, these latter benefits of interspersion are best provided in wildland blocks because they can support larger populations of species and a broader array of facets of various sizes, juxtaposed in more complex ways.

We illustrated our approach in terms of connecting protected wildland blocks of a size (~500–2000 km^2) and spacing (~10–30 km between blocks) common in many regions, such as the western United States, boreal Canada, far northeastern United States and adjacent Canada, and large parts of East Africa, South Africa, and South America. In landscapes like these, a network of land facet linkages between adjacent wildland blocks can be an effective and practical strategy to support range shifts that may need to be much longer than any individual linkage. In this scenario, a species would shift its range 10–30 km during a couple decades (via one or more single-facet corridors and the high-diversity corridor), could shift to another land facet with more suitable habitat (partly in these corridors but mostly in the recipient wildland block), and would then move through the next 10–30 km linkage in the next couple decades. The wildland blocks are probably essential to long-distance range shifts because they provide opportunities for growth to large population

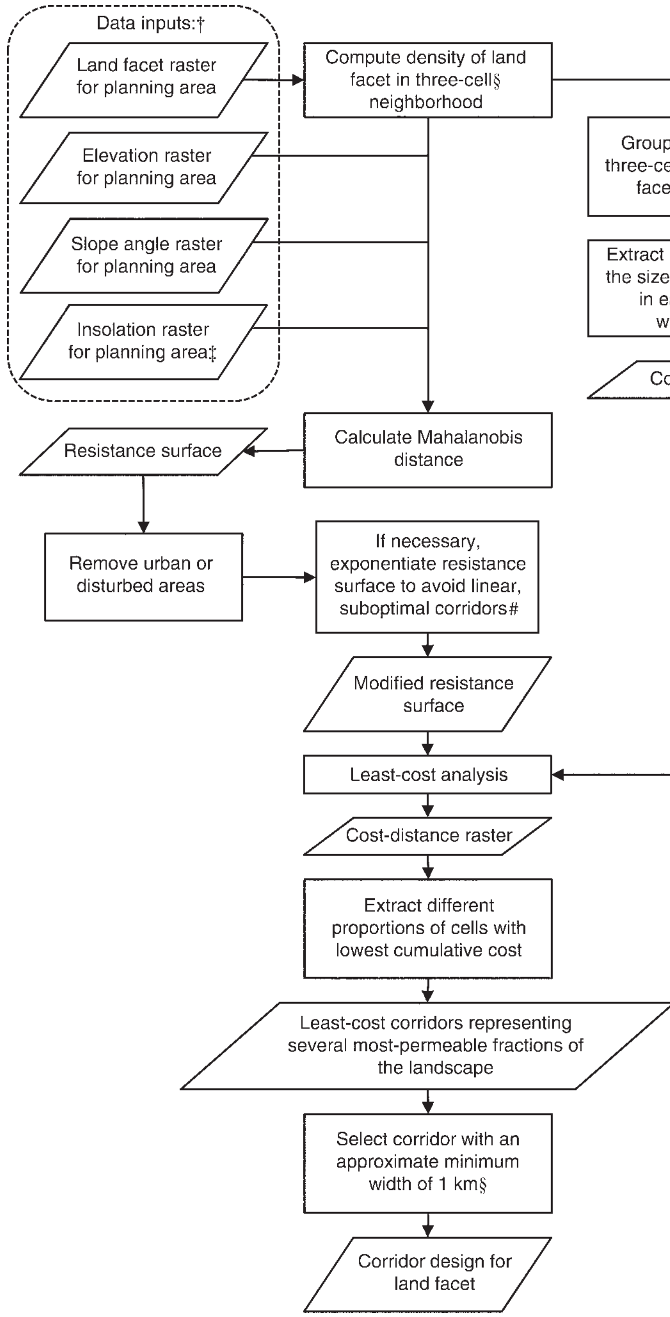


FIG. 8. Sequence of operations (rectangles) and products (parallelograms) used to design a corridor for one land facet. All operations occur in ArcGIS, and the process is repeated for each land facet. The resulting corridors, plus a corridor for high diversity of land facets and riparian habitat, are then joined to create the linkage design.

† The analyst can use other topographic variables or include soil variables.

‡ We included solar insolation for land facets in the slope topographic position only.

§ These parameters can be changed.

¶ The area threshold for defining termini can be adjusted to avoid highly linear corridors.

See Appendix A.

TABLE 2. Characteristics of linkage designs based on land facets.

Planning area	Cells classified as outliers (%)	Cells poorly classified (%)	Number of corridors	Number of corridors for which procedures were modified†	
				Resistance surface	Corridor termini
Santa Rita-Tumacacori	19	5	13	1	2
Black Hills-Munds Mountain	26	6	12	1	0
Wickenburg-Hassayampa	8	4	10	1	1

Notes: Percentage of overlap between corridors represents the percentage of cells in the linkage design overlapped by two or more corridors. Area of linkage design represents the linkage design after inclusion of riparian habitat and buffering to address edge effects.

† See Appendix A for details on how resistance surfaces and corridor termini were modified in these six cases.

‡ Excluding area inside of the wildland blocks.

size, evolutionary adaptation, and diversification. In contrast, a long corridor from suitable habitat in 2010 to future habitat in 2110 (assuming we could design it reliably) is unlikely to succeed without such "staging areas." Large protected natural areas will also provide the most opportunities for future occupancy for all species. This approach is practical because it takes advantage of society's existing investments in conservation and minimizes the need for expensive corridors outside those areas.

Defining land facets for conservation linkages

Two broad approaches have been used to define physical landscape types (variously termed land facets, geophysical settings, bioenvironments, or landtypes) in conservation planning. One approach is to define a landscape type for each cross-classification of several categorical variables, such as geologic substrates, landforms, and elevation classes. The only computational steps are transforming continuous variables (e.g., elevation) into categories, followed by cross-tabulation. This approach has some advantages, namely computational simplicity and readily interpretable land facets (e.g., high elevation valleys on calcareous rock). However, cross-classification of a handful of categorical variables can yield hundreds of land facets (e.g., 676 types [Reyers et al. 2002] or 126 types [Carlson et al. 2004]). It would be cumbersome to integrate corridors for so many land facets into a coherent linkage design, and the rarity of some land facets may make it impossible to design an effective corridor; this discouraged us during our early attempts to use this approach.

Therefore, we defined land facets using a second family of approaches, broadly termed numerical classification, that reduce complex multivariate data into relatively few land facets. These procedures identify natural modes and breakpoints in multivariate space, and avoid creating "empty" or rare cross-classifications. Fuzzy c-means clustering is capable of classifying large data sets in a repeatable manner, which is its advantage over many other numerical classifications (Beier and Brost 2010). Although numerical classification helped us avoid a design that included hundreds of corridors, we caution against identifying too few land facets. Compared to a few coarse classes, a set of many finely divided classes almost certainly supports more species. One drawback of numerical classification is that it could fail to recognize small, rare, physical settings known to have high conservation value (e.g., rare limestone sinkholes and associated pools). If connectivity for such a setting is ecologically important and feasible, analysts can take a hybrid approach of recognizing that setting in addition to the numerical classes.

Both approaches to defining land facets are rule-based, and are thus structured in a way that allows for uncertainty analysis, an important next step in the land facets approach to linkage design. For example, a strategy similar to Beier et al. (2009) could be adopted to determine how sensitive modeled corridors are to the parameters (e.g., φ in fuzzy c-means cluster analysis, size of neighborhoods used to define corridor termini, range of resistance values) and decision rules in our approach (e.g., thresholds for defining outliers, poorly classified cells, or corridor termini), as well as to errors in digital elevation models.

Coarse-filter and fine-filter approaches to linkage design for climate change

Despite widespread prescriptions for conservation corridors and linkages to aid species' range shifts in response to climate change (Hannah and Hansen 2005, Heller and Zavaleta 2009, Mawdsley et al. 2009), prior to this study only Williams et al. (2005) and Phillips et al. (2008) provided an approach that designed corridors specifically to accommodate climate change. They used a fine-filter approach, that is, an approach to allow range shift of particular species at risk. Fine-filter approaches rely on models of emissions, climate response to emissions, and mapping the expected future spatial locations of climate envelopes of the focal species.

We provide a very different coarse-filter approach. Our approach exploits the fact that topography and soils are major drivers of biodiversity, and thus relies only on factors that are more stable with respect to climate. Our approach avoids the enormous complexity and the high level of uncertainty associated with modeling climate and climate envelopes. It also avoids the assumption

TABLE 2. Extended.

Average area of corridor termini (km^2) (range)	Average area of corridors‡ (km^2) (range)	Area of union of least-cost corridors‡ (km^2)	Overlap between corridors (%)	Area of linkage design‡ (km^2)
40 (2, 185)	32 (22, 44)	187	45	316
29 (1, 133)	43 (16, 116)	370	72	431
86 (5, 1331)	53 (36, 78)	360	68	412

that climate envelopes are constant, i.e., that species can't evolve to tolerate new climate regimes.

Ironically, a coarse filter approach based on land facets has a much finer grain size than current fine-filter approaches. Even after downscaling, global circulation models produce predictions with grain sizes measured in km^2. Conservation interventions to support connectivity (e.g., conserving particular parcels of land) are typically made at resolutions closer to the 30×30-m cells used in land facet designs. In the future, higher-resolution global circulation models, or downscaled regional circulation models, may allow development of fine-filter approaches that are also fine-grained.

Coarse filter approaches based on land facets are not afflicted by the patchiness common in species occurrence data and are not biased toward data-rich areas. Land facet linkages can be designed anywhere because digital elevation models are available for all continents (*available online*).[4] Although we advocate using soil data to help define land facets if good soil maps are available, we believe land facet linkages derived solely from digital elevation models provide meaningful depictions of connectivity for species.

Other coarse-filter approaches to linkage design are feasible. For instance, identifying rivers as linkages is a coarse-filter approach that has been proposed without reference to any formal procedure for identifying geophysical land units (e.g., Rouget et al. 2006). Rouget et al. (2006) also suggest another coarse-filter approach, grounded in the idea that species will shift their ranges by sequentially colonizing areas that lie along monotonic elevation and temperature gradients. Assuming these gradients are conserved in a changing climate, it may be possible to identify corridors along current environmental gradients, without the need for uncertain models of future climate.

Integrating coarse-filter and fine-filter approaches to linkage design

A coarse filter linkage design could fail to provide connectivity for some focal species, even in the absence of climate change (Reyers et al. 2002); including corridors for a large number of land facets reduces but does not eliminate this risk. Conversely, species-based approaches may not represent habitat for some non-modeled species and inherently cannot be used for species with unknown distributions. Therefore, a linkage design that integrates coarse-filter approaches for a changing climate (land facets, rivers, temperature gradients) with fine-filter approaches for focal species under current conditions may best address the shortcomings of species data and the limitations of land facets.

There are also practical reasons to integrate the two approaches. Many nations have laws (e.g., the U.S. Endangered Species Act) mandating species conservation and there is a culture of species conservation in wildlife agencies, land management agencies, and even transportation agencies. Such laws and culture to conserve land facets is lacking. Furthermore, land facets are not charismatic to civil society. On the other hand, a growing number of managers and citizens are aware that species will need to move during climate change, and some will be unwilling to invest in strategies based solely on utility for focal species in today's landscape. Bundling the two approaches into an integrated linkage design makes good political sense.

We believe that the use of land facets is a simple and effective strategy to design linkages for climate change. In conjunction with focal species approaches to linkage design, they can provide connectivity for most species and help conserve the ecological and evolutionary processes that sustain and generate biodiversity. Brost (2010) found that land facet linkage designs served most focal species well in these three landscapes. If this pattern is generally true, the land facets approach could also be used in lieu of focal species in areas where species models cannot be developed.

ACKNOWLEDGMENTS

J. Jenness (Jenness Enterprises) packaged our procedures for delineating corridors based on land facets into an ArcGIS extension. We thank Brett Dickson, Margaret Moore, and two anonymous reviewers for helpful comments on earlier drafts of this paper. Our work was supported by the Arizona Board of Forestry and the U.S. Forest Service Rocky Mountain Research Station.

LITERATURE CITED

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.

Anderson, M. G., and C. E. Ferree. 2010. Conserving the stage: climate change and the geophysical underpinnings of species diversity. PLoS ONE 5(7):e11554.

[4] http://www.gdem.aster.ersdac.or.jp/

Beale, C. M., J. J. Lennon, and A. Gimona. 2008. Opening the climate envelope reveals no macroscale associations with climate in European birds. Proceedings of the National Academy of Sciences USA 105:14908–14912.

Beier, P., and B. Brost. 2010. Use of land facets to plan for climate change: conserving the arenas, not the actors. Conservation Biology 24:701–710.

Beier, P., D. Majka, and T. Bayless. 2007. Linkage designs for Arizona's missing linkages. Arizona Game and Fish Department, Phoenix, Arizona, USA.

Beier, P., D. R. Majka, and S. L. Newell. 2009. Uncertainty analysis of least-cost modeling for designing wildlife linkages. Ecological Applications 19:2067–2077.

Beier, P., D. R. Majka, and W. D. Spencer. 2008. Forks in the road: choices in procedures for designing wildland linkages. Conservation Biology 22:836–851.

Beier, P., K. Penrod, C. Luke, W. Spencer, and C. Cabanero. 2006. South Coast missing linkages: restoring connectivity to wildlands in the largest metropolitan area in the USA. Pages 555–586 *in* K. R. Crooks and M. A. Sanjayan, editors. Connectivity conservation. Cambridge University Press, Cambridge, UK.

Bezdek, C. J. 1981. Pattern recognition with fuzzy objective function algorithms. Plenum Press, New York, New York, USA.

Brost, B. 2010. Use of land facets to design conservation corridors: conserving the arenas, not the actors. Thesis. Northern Arizona University, Flagstaff, Arizona, USA.

Burnett, M. R., P. V. August, J. H. Brown, Jr., and K. T. Killingbeck. 1998. The influence of geomorphological heterogeneity on biodiversity: I. A patch-scale perspective. Conservation Biology 12:363–370.

Burrough, P. A., P. F. M. van Gaans, and R. A. MacMillan. 2000. High-resolution landform classification using fuzzy *k*-means. Fuzzy Sets and Systems 113:37–52.

Burrough, P. A., J. P. Wilson, P. F. M. van Gaans, and A. J. Hansen. 2001. Fuzzy *k*-means classification of topo-climatic data as an aid to forest mapping in the Greater Yellowstone Area, USA. Landscape Ecology 16:523–546.

Campello, R. J. G. B., and E. R. Hruschka. 2006. A fuzzy extension of the silhouette width criterion for cluster analysis. Fuzzy Sets and Systems 157:2858–2875.

Carlson, B. D., D. Wang, D. Capen, and E. Thompson. 2004. An evaluation of GIS-derived landscape diversity units to guide landscape-level mapping of natural communities. Journal for Nature Conservation 12:15–23.

Celikyilmaz, A., and I. B. Turksen. 2008. Validation criteria for enhanced fuzzy clustering. Pattern Recognition Letters 29:97–108.

Clark, J. D., J. E. Dunn, and K. G. Smith. 1993. A multivariate model of female black bear habitat use for a geographic information system. Journal of Wildlife Management 57:519–526.

Cowling, R. M., R. L. Pressey, A. T. Lombard, P. G. Desmet, and A. G. Ellis. 1999. From representation to persistence: requirements for a sustainable system of conservation areas in the species-rich Mediterranean-climate desert of southern Africa. Diversity and Distributions 5:51–71.

Cowling, R. M., R. L. Pressey, M. Rouget, and A. T. Lombard. 2003. A conservation plan for a global biodiversity hotspot—the Cape Floristic Region, South Africa. Biological Conservation 112:191–216.

Dimitriadou, E., K. Hornik, F. Leisch, D. Meyer, and A. Weingessel. 2009. *e1071*: misc functions of the Department of Statistics (e1071), TU Wien. R package version 1.5-19. http://CRAN.R-project.org/package=e1071

Duong, T. 2009. *ks*: kernel smoothing. R package version 1.6.5. http://CRAN.R-project.org/package=ks

Fairbanks, D. H. K., B. Reyers, and A. S. van Jaarsveld. 2001. Species and environment representation: selecting reserves for the retention of avian diversity in KwaZulu-Natal, South Africa. Biological Conservation 98:365–379.

Faith, D. P., and P. A. Walker. 1996. Environmental diversity: on the best-possible use of surrogate data for assessing the relative biodiversity of sets of areas. Biodiversity and Conservation 5:399–415.

Forman, R. T. T. 1995. Land mosaics: the ecology of landscapes and regions. Cambridge University Press, Cambridge, UK.

Franklin, J. 1995. Predictive vegetation mapping: geographic modelling of biospatial patterns in relation to environmental gradients. Progress in Physical Geography 19:474–499.

Fu, P., and P. M. Rich. 2002. A geometric solar radiation model with applications in agriculture and forestry. Computers and Electronics in Agriculture 37:25–35.

Gotelli, N. J., and A. M. Ellison. 2004. A primer of ecological statistics. Sinauer Associates, Sunderland, Massachusetts, USA.

Grabherr, G., M. Gottfried, and H. Pauli. 1994. Climate effects on mountain plants. Nature 369:448.

Graham, R. W., and E. C. Grimm. 1990. Effects of global climate change on the patterns of terrestrial biological communities. Trends in Ecology and Evolution 5:289–292.

Hannah, L., and L. Hansen. 2005. Designing landscapes and seascapes for change. Pages 329–341 *in* T. E. Lovejoy and L. Hanna, editors. Climate change and biodiversity. Yale University Press, New Haven, Connecticut, USA.

Heller, N. E., and E. S. Zavaleta. 2009. Biodiversity management in the face of climate change: a review of 22 years of recommendations. Biological Conservation 142:14–32.

Hewitt, G. 2000. The genetic legacy of the Quaternary ice ages. Nature 405:464–475.

Hunter, M. L., Jr., G. L. Jacobson, Jr., and T. Webb III. 1988. Paleoecology and the coarse-filter approach to maintaining biological diversity. Conservation Biology 2:375–385.

Huntley, B. 2005. North temperate responses. Pages 109–124 *in* T. E. Lovejoy and L. Hannah, editors. Climate change and biodiversity. Yale University Press, New Haven, Connecticut, USA.

Intergovernmental Panel on Climate Change. 2001. Climate change 2001: the scientific basis. IPCC, Geneva, Switzerland.

Jenness Enterprises. 2010. Mahalanobis Distances extension for ArcGIS. http://www.jennessent.com

Kirkpatrick, J. B., and M. J. Brown. 1994. A comparison of direct and environmental domain approaches to planning reservation of forest higher plant communities and species in Tasmania. Conservation Biology 8:217–224.

Klein, C., K. Wilson, M. Watts, J. Stein, S. Berry, J. Carwardine, M. S. Smith, B. Mackey, and H. Possingham. 2009. Incorporating ecological and evolutionary processes into continental-scale conservation planning. Ecological Applications 19:206–217.

Lookingbill, T., and D. Urban. 2004. An empirical approach towards improved spatial estimates of soil moisture for vegetation analysis. Landscape Ecology 19:417–433.

Magurran, A. E. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton, New Jersey, USA.

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

Maulik, U., and S. Bandyopadhyay. 2002. Performance evaluation of some clustering algorithms and validity indices. IEEE Transactions on Pattern Analysis and Machine Intelligence 24:1650–1654.

Mawdsley, J. R., R. O'Malley, and D. S. Ojima. 2009. A review of climate-change adaptation strategies for wildlife management and biodiversity conservation. Conservation Biology 23:1080–1089.

Millar, C. I., N. L. Stephenson, and S. L. Stephens. 2007. Climate change and forests of the future: managing in the face of uncertainty. Ecological Applications 17:2145–2151.

Moritz, C. 2002. Strategies to protect biological diversity and the evolutionary processes that sustain it. Systematic Biology 51:238–254.

Nichols, W. F., K. T. Killingbeck, and P. V. August. 1998. The influence of geomorphological heterogeneity on biodiversity: II. A landscape perspective. Conservation Biology 12:371–379.

Noss, R. F. 1987. From plant communities to landscapes in conservation inventories: a look at the Nature Conservancy (USA). Biological Conservation 41:11–37.

Noss, R. F. 2001. Beyond Kyoto: forest management in a time of rapid climate change. Conservation Biology 15:578–590.

Parmesan, C. 1996. Climate and species' range. Nature 382:765–766.

Phillips, S. J., P. Williams, G. Midgley, and A. Archer. 2008. Optimizing dispersal corridors for the Cape Proteaceae using network flow. Ecological Applications 18:1200–1211.

Pressey, R. L., M. Cabeza, M. E. Watts, R. M. Cowling, and K. A. Wilson. 2007. Conservation planning in a changing world. Trends in Ecology and Evolution 22:583–592.

R Development Core Team. 2009. R version 2.10.1. R Project for Statistical Computing, Vienna, Austria. www.r-project.com

Raper, S. C. B., and F. Giorgi. 2005. Climate change projections and models. Pages 199–210 *in* T. E. Lovejoy and L. Hanna, editors. Climate change and biodiversity. Yale University Press, New Haven, Connecticut, USA.

Reyers, B., K. J. Wessels, and A. S. van Jaarsveld. 2002. An assessment of biodiversity surrogacy options in the Limpopo Province of South Africa. African Zoology 37:185–195.

Rouget, M., R. M. Cowling, A. T. Lombard, A. T. Knight, and G. I. H. Kerley. 2006. Designing large-scale conservation corridors for pattern and process. Conservation Biology 20:549–561.

Silverman, B. W. 1986. Density estimation for statistics and data analysis. CRC Press, Boca Raton, Florida, USA.

Singleton, P. H., W. Gaines, and J. F. Lehmkuhl. 2002. Landscape permeability for large carnivores in Washington: a geographic information system weighted-distance and least-cost corridor assessment. USDA Forest Service Research Paper, PNW-RP 549. Pacific Northwest Field Station, Portland, Oregon, USA.

Skelly, D. K., L. N. Joseph, H. P. Possingham, L. K. Freidenburg, T. J. Farrugia, M. T. Kinnison, and A. P. Hendry. 2007. Evolutionary responses to climate change. Conservation Biology 21:1353–1355.

Thomas, C. D., and J. J. Lennon. 1999. Birds extend their ranges northwards. Nature 399:213.

United States Geological Survey. 2000. US GeoData Digital Elevation Models factsheet. United States Geological Survey, Reston, Virginia, USA

Valverde, P. L., J. A. Zavala-Hurtado, C. Montana, and E. Ezcurra. 1996. Numerical analyses of vegetation based on environmental relationships in the southern Chihuahuan Desert. Southwestern Naturalist 41:424–433.

Walker, R., and L. Craighead. 1997. Analyzing wildlife movement corridors in Montana using GIS. Pages 1–18 *in* Proceedings of the ESRI International User Conference, San Diego, California. ESRI, Redlands, California, USA.

Webb, III, T. 1987. The appearance and disappearance of major vegetational assemblages: long-term vegetational dynamics in eastern North America. Vegetatio 69:177–187.

Wessels, K. J., S. Freitag, and A. S. van Jaarsveld. 1999. The use of land facets as biodiversity surrogates during reserve selection at a local scale. Biological Conservation 89:21–38.

Williams, P., L. Hannah, S. Andelman, G. Midgley, M. Araujo, G. Hughes, L. Manne, E. Martinez-Meyer, and R. Pearson. 2005. Planning for climate change: identifying minimum-dispersal corridors for the Cape Proteaceae. Conservation Biology 19:1063–1074.

Zhang, Y., W. Wang, X. Zhange, and Y. Li. 2008. A cluster validity index for fuzzy clustering. Information Sciences 178:1205–1218.

Supplemental Material

Appendix A

Details about binning data for outlier identification, sample size for fuzzy *c*-means cluster analysis, and modifying resistance surfaces or corridor termini to better capture focal land facets (*Ecological Archives* A022-005-A1).

Appendix B

Topographic attributes of land facets, as well as location and number of land facets relative to topographic complexity of the three landscapes (*Ecological Archives* A022-005-A2).

Appendix C

Further discussion about least-cost modeling, cluster validity indices, subjective decisions, and potential timesaving shortcuts in using land facets to design linkages (*Ecological Archives* A022-005-A3).

Appendix. Supplementary Methods, Results, and Discussion to
B. Brost and P. Beier, Use of Land Facets to Design Linkages for Climate Change

METHODS

Defining land facets

To estimate kernel density in R package *ks*, we used the iterative "plug-in" option with diagonal bandwidth matrix because it works well with binned data. We grouped cells in the canyon bottom and ridge topographic positions into a 2-dimensional array of 151^2 bins; we grouped cells in the slope topographic position into a 3-dimensional array of 91^3 bins. We selected these array sizes because they provide high resolution and reasonable computational efficiency.

Due to memory limitations, R cannot run fuzzy *c*-means cluster analysis for datasets consisting of more than 1.25 million cells. For the one landscape that had > 1.25 million cells in a topographic position (namely the slope topographic position in the Wickenburg-Hassayampa planning area), we based each iteration on a random sample of 1.25 million cells, and a new sample was taken for each of the 100 iterations at each value of *c*. We found that fuzzy *c*-means cluster analysis is robust to sample size, even for samples as small as 10% of the original population.

Modifying resistance surfaces or corridor termini to produce corridors that better capture the focal land facet

For six of 35 corridors (Table 2), our procedures produced a highly linear corridor when a longer, less-linear corridor would better optimize continuity for the focal land facet (or diversity of facets). This happened when the relatively few matrix cells resembling the focal facet occurred far outside the straight paths between potential termini in opposing wildland blocks. In effect, resistances of cells of the focal land facet or cells resembling the focal facet were not low enough relative to the cost of travel through dissimilar cells to "pull" the corridor toward the low-cost cells. We developed two strategies to address this. Our first strategy was to exaggerate the cost of travel through cells dissimilar to the non-focal land facet by exponentiating the resistance surface by a power of 1.05, and increasing the exponent incrementally, stopping when the corridor shifted to incorporate clusters of low-cost cells. This strategy worked in three of the six cases; the largest exponent was 4. Before this stopping point was reached in the other three cases, the corridor developed wide "balloons" in regions of low resistance with narrow pinchpoints elsewhere. In these three cases, we used an alternative strategy, namely to relax the area threshold (or Shannon's index threshold for high diversity of land facets) used to define corridor termini. For example, retaining polygons that were ≥ 25% of the size of the largest polygon often produced termini located in additional sections of the wildland blocks, such that low-cost matrix cells occurred more directly between termini in opposing wildland blocks.

Results

TABLE A1. Mean and range of topographic attributes of each land facet in each planning area. Although land facets overlapped in range of elevation, slope angle, and solar insolation, their joint distributions did not (Fig. 6). "Hot," warm," and "cool" refer to relative amounts of insolation.

Planning area	Land facet description	Mean elevation (m) (range)	Mean slope (°) (range)	Mean insolation (kWh^{-1}) (range)
Santa Rita-Tumacacori	Canyon bottom: low elevation, gentle	1216.7 (1059.6, 1401.1)	8.5 (0.0, 18.0)	--
	Canyon bottom: mid elevation, gentle	1540.4 (1375.4, 1828.4)	11.4 (1.3, 19.7)	--
	Canyon bottom: mid elevation, steep	1354.6 (1096.6, 1551.2)	23.6 (16.2, 36.1)	--
	Canyon bottom: high elevation, steep	1753.0 (1563.0, 2158.5)	25.4 (13.8, 36.1)	--
	Ridge: low elevation, gentle	1257.5 (1104.1, 1449.0)	9.8 (0.1, 20.1)	--
	Ridge: mid elevation, gentle	1597.2 (1425.2, 1946.7)	12.5 (0.7, 21.2)	--
	Ridge: mid elevation, steep	1424.8 (1156.1, 1635.7)	26.2 (18.2, 39.5)	--
	Ridge: high elevation, steep	1859.6 (1662.7, 2248.2)	26.4 (14.3, 37.4)	--
	Slope: low elevation, gentle, warm	1180.9 (1031.7, 1449.3)	6.2 (0.0, 20.8)	1638.5 (1435.9, 1777.6)
	Slope: mid elevation, steep, cool	1370.8 (1072.7, 1953.5)	22.5 (12.7, 36.9)	1384.9 (1015.7, 1556.5)
	Slope: mid elevation, steep, hot	1449.7 (1131.5, 1933.0)	22.0 (13.3, 36.0)	1708.2 (1527.7, 1875.1)
	Slope: high elevation, gentle, hot	1583.9 (1390.9, 1954.2)	7.7 (0.0, 19.4)	1726.9 (1501.9, 1893.4)
Black Hills-Munds Mountain	Canyon bottom: low elevation, gentle	1314.3 (1049.9, 1603.6)	9.8 (0.0, 21.1)	--
	Canyon bottom: mid elevation, steep	1540.6 (1168.0, 1938.0)	27.8 (17.9, 43.6)	--
	Canyon bottom: high, elevation, gentle	1829.2 (1544.7, 2090.9)	14.6 (2.3, 28.5)	--
	Ridge: low elevation, gentle	1366.3 (1103.4, 1646.8)	10.6 (0.0, 23.4)	--
	Ridge: mid elevation, steep	1635.6 (1199.1, 2044.8)	29.9 (19.0, 49.2)	--
	Ridge: high elevation, gentle	1922.4 (1625.4, 2326.3)	13.1 (1.0, 27.3)	--
	Slope: low elevation, gentle, warm	1188.5 (1047.1, 1529.4)	4.8 (0.0, 16.5)	1561.5 (1411.7, 1671.4)
	Slope: low elevation, steep, cool	1387.2 (1067.2, 2056.3)	18.2 (10.2, 35.9)	1381.4 (987.6, 1552.0)

	Slope: mid elevation, gentle, warm	1518.2 (1300.1, 1822.9)	4.8 (0.0, 11.7)	1642.3 (1494.1, 1750.5)
	Slope: mid elevation, steep, warm	1586.0 (1111.3, 2103.9)	18.1 (11.1, 35.6)	1678.7 (1492.1, 1867.0)
	Slope: high elevation, gentle, hot	1986.5 (1690.3, 2384.3)	4.7 (0.0, 15.9)	1729.7 (1546.2, 1886.8)
Wickenburg-Hassayampa	Canyon bottom: low elevation, gentle	785.9 (452.0, 1284.0)	8.5 (0.0, 16.5)	--
	Canyon bottom: low elevation, steep	909.1 (493.0, 1244.0)	22.7 (14.9, 35.5)	--
	Canyon bottom: high elevation, steep	1435.2 (1137.0, 1865.0)	18.3 (4.4, 32.6)	--
	Ridge: low elevation, gentle	827.8 (497.0, 1337.0)	10.4 (0.8, 18.3)	--
	Ridge: low elevation, steep	932.7 (511.0, 1362.0)	25.4 (17.7, 36.7)	--
	Ridge: high elevation, steep	1514.7 (1170.0, 2019.0)	19.1 (5.4, 33.1)	--
	Slope: low elevation, gentle, warm	588.5 (353.0, 974.0)	1.7 (0.0, 16.2)	1500.9 (1381.8, 1581.5)
	Slope: mid elevation, steep, cool	800.8 (419.0, 1713.0)	15.9 (6.9, 31.9)	1363.5 (1020.7, 1517.8)
	Slope: high elevation, steep, warm	1028.4 (488.0, 1995.0)	10.9 (0.0, 33.3)	1587.4 (1445.2, 1856.3)

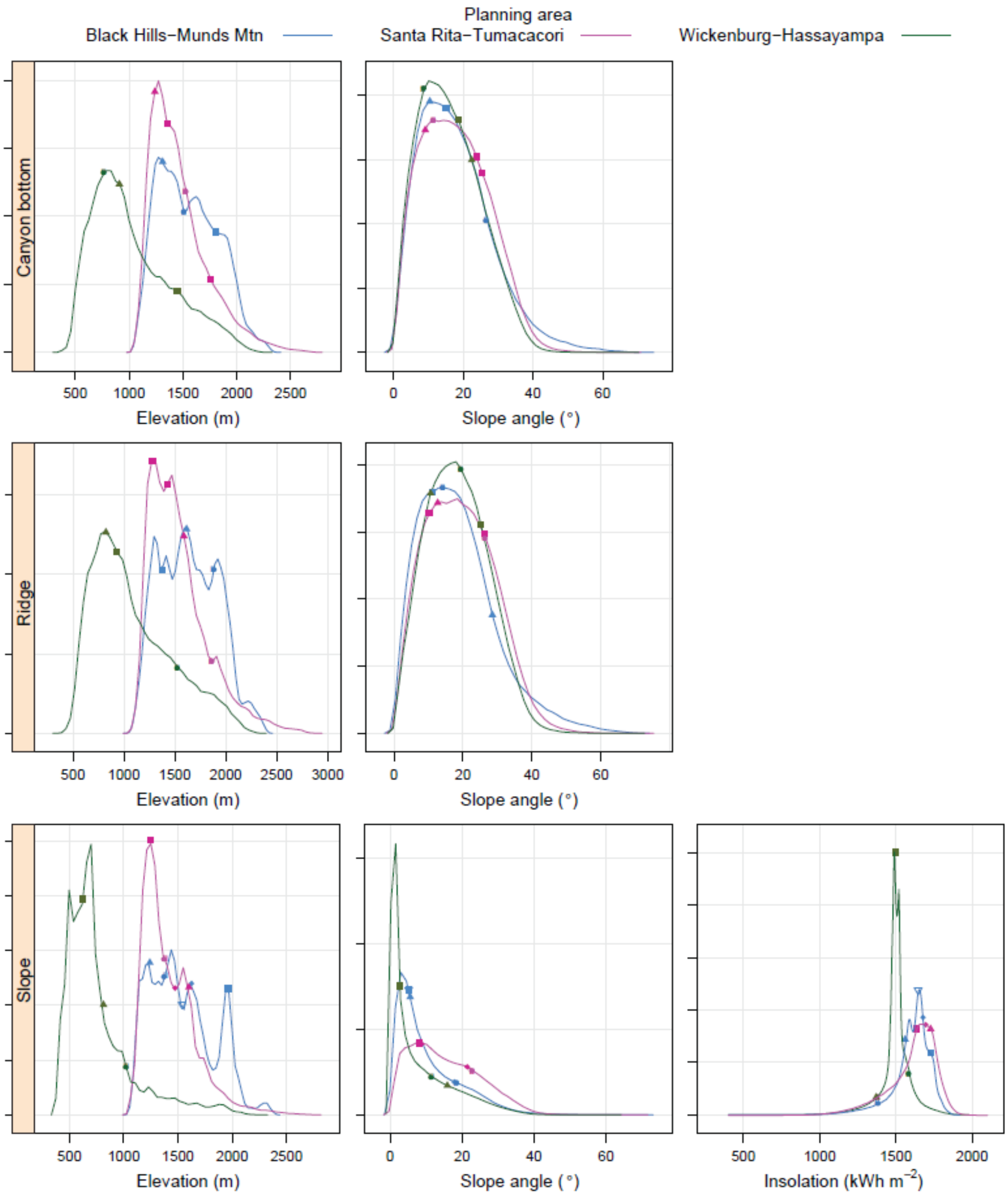


FIG. A1. Univariate distributions demonstrating the topographic complexity of cells in each topographic position for the three landscapes. Points indicate location of cluster centroids, and symbols differentiate between clusters within the same topographic position and landscape. The main pattern is that there were more land facets within a topographic position in more complex landscapes. For example, cells in the slope topographic position of the Wickenburg-Hassayampa planning area, which were only classified into three land facets, were narrowly distributed with respect to elevation, slope angle, and insolation (bottom row). Conversely, cells in the slope topographic position of the Black Hills-Munds Mountain planning area, which were classified into five land facets, had a multi-modal distribution with respect to elevation and a wider distribution with respect to slope angle and insolation.

DISCUSSION

In least-cost modeling, resistance values interact with distance. The lower the range of values from low resistance to high resistance, the more likely cost distance will minimize distance versus selecting cells with lower resistance. Thus the difference between high and low resistance values can significantly affect results. This affects all least-cost models, not just those for land facets. To understand the impact of the range in resistance values, analysts should experiment with diverse ranges of resistance values (Hoctor 2003, Beier et al. 2009).

Our clustering procedures cannot test $c = 1$ (i.e., no partitioning of a data set) because the validity indices either cannot indicate an optimal partition for $c = 1$ (the Fukuyama-Sugeno and Average Within-Cluster Distance criteria, which are equivalent for $c = 1$; Fig. 7) or are undefined for $c = 1$ (all other indices are based on distances between clusters or an object's two highest membership values). In situations where our procedures indicate a two cluster solution where one is truly optimal, the resulting land facets should be similar and the corresponding corridors would overlap extensively as if only one land facet was present.

Subjective decisions

We comment on several subjective decisions in our approach:

Which variables to use to define land facets: Our flexible procedures can accommodate a variety of topographic variables. Topographic variables suitable for defining land facets, such as those derived from a digital elevation model, must be mapped continuously over the extent of the analysis area. For a discussion of topographic variables that can be derived from a digital elevation model, see Moore et al. (1991) and Franklin (1995). Where soil maps are complete and do not contain unmapped heterogeneity, we believe soil attributes should help define land facets. Categorical variables (relating to soil or topography) can be integrated into these procedures in the same way we treated topographic position, or they could be "converted" to continuous variables that reflect the density of the categories within a neighborhood. Where soil maps are inadequate, land facets defined solely by topographic variables can represent a useful diversity of habitats (Franklin 1995, Hoersch et al. 2002).

To maintain easily interpretable and biologically meaningful land facets, it is best to limit the number of variables (Beier and Brost 2010). Each variable should be viewed in a functional perspective and judged for its influence on the availability and distribution of heat, light, water, or nutrients (Mackey et al. 1988). For example, elevation contributes meaningfully to the definition of land facets in mountainous landscapes, but in flatter landscapes elevation may not be relevant. In flatter landscapes, soils information may be important for defining land facets, or higher resolution digital elevation models, such as those derived from LIDAR, might be necessary to detect subtle differences in slope angle, solar insolation, or other topographic characteristics.

How many land facets to recognize: If two or three values of c seemed equally apt for the optimal number of clusters, we usually selected the smaller number of clusters within the canyon bottom and ridge topographic positions and a larger number within the slope topographic position. We did this because cells classified as canyon bottoms and ridges were relatively rare, and recognizing a higher number of clusters would have produced facets that were extremely rare. We also evaluated interpretability of classes and draped maps of facets over a topographic hillshade to assess whether the c clusters corresponded to natural units.

How to define outliers: The 10% threshold we used to define outliers separated regions in attribute space densely populated by cells from those more sparsely populated (Fig. 5). In other landscapes, examination of 2- or 3-dimensional plots of the cells in attribute space may indicate a more appropriate threshold.

How to modify the resistance map or termini to produce corridors that better capture the focal *land facet*: When transforming a resistance surface, we recommend starting with a small exponent, such as 1.05, and exploring sequentially larger values (i.e., 1.1, 1.5, 2, . . .) if necessary. While larger exponents may produce longer, less-linear corridors when desired, they are also more likely to cause ballooning and pinchpoints in the resulting corridor. Similarly, thresholds used in defining termini should be relaxed only enough to yield additional termini, such that low-cost matrix cells occur between potential termini in opposing wildland blocks. However, it is important to keep in mind that relaxing these thresholds recognizes smaller termini (or termini with lower diversity) that are less able to support area-sensitive species or ecological processes.

Applying minimum width to corridors: Identifying the least-cost corridor with an approximate minimum width of 1 km over its length was often challenging because corridors do not have a constant width, being wider in areas of low resistance and narrower in areas of high resistance. When selecting a corridor, we aimed to have no more than 10-20% of its length below 1 km in width; however, in some instances this target was not attainable because doing so caused severe ballooning in other sections of the corridor. In these cases, we attempted to identify the corridor that represented the best compromise between sections that were too narrow and too wide.

Potential shortcuts

In the Discussion section of the main paper, we recommend two ways to shorten the most time-consuming step (fuzzy cluster analysis). Because these recommendations are based on our trial-and-error experiments and calculations, there is little risk that these shortcuts would result in poor classifications that could lead to unreliable corridors and linkage designs.

Here we list several other shortcuts that would reduce computation time. Before applying these shortcuts to conservation plans, we recommend running the procedures with and without these shortcuts to verify that the shortcut has negligible effect on corridors and linkage designs (e.g., Hoctor 2003, Beier et al. 2009). We discuss shortcuts in order of the sequence of procedures:

Use only continuous variables to define land facets: Because many procedures are repeated for each value of a categorical variable (e.g., land form, soil type), not using any categorical variables would reduce computation time and simplify the process substantially. We caution that categorical variables are ecologically important in most landscapes, and this shortcut would be inappropriate in such cases.

Skip the procedure to remove outliers from the analysis: In our experiments, retaining outliers affected cluster centroids (because extreme values have strong effects on group means); this in turn would affect the Mahalanobis distances used as resistance values. However, retaining outliers might have only trivial impact on the location of the linkage design. If so, this step could be eliminated.

Skip the procedure to iterate fuzzy clustering to detect cases in which more than one partition minimizes within-cluster variance for a given value of c: The location of the linkage may not depend much on which cluster solution is used when > 1 optimal solution exists. If so, iterating the cluster analysis could be dropped, saving many hours of computing time.

Literature Cited

Hoctor. T. S. 2003. Regional landscape analysis and reserve design to conserve Florida's biodiversity. Ph.D. dissertation. University of Florida, Gainesville.

Hoersch, B., G. Braun, and U. Schmidt. 2002. Relation between landform and vegetation in alpine regions of Wallis, Switzerland: a multiscale remote sensing and GIS approach. Computers, Environment and Urban Systems 26:113-139.

Mackey, B. G., H. A. Nix, M. F. Hutchinson, J. P. MacMahon, and P. M. Flemming. 1988. Assessing representativeness of places for conservation reservation and heritage listing. Environmental Management 12:501-514.

Moore, I. D., R. B. Grayson, and A. R. Ladson. 1991. Digital terrain modelling: a review of hydrological, geomorphological, and biological applications. Hydrological Processes 5:3-30.