Remote Areas as Potential Restoration Sites in Conservation Landscapes

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ABSTRACT

The effects of roads and trails on species composition and diversity at landscape scales are uncertain. This leads to uncertainty about the best way to select sites for restoration. Three datasets were used in this analysis: a model that estimates the remoteness of a landscape by calculating the energetic cost required to walk through it, a set of 246 0.1 ha plant species abundance samples, and a remotely sensed plant community map. These data were used to ask three questions about the selection of restoration sites in Great Smoky Mountains National Park (Tennessee and North Carolina, US). First, does compositional similarity within a plant community change as a function of remoteness? Second, does plant species diversity, particularly of rare species, change with remoteness? Finally, how does the patch area of plant communities change as a function of remoteness? Compositional distance among pairs of sites increased as difference in energetic cost to reach the sites increased. Regression of Shannon-Wiener diversity against the multiplicative effects of energetic cost and community type revealed no significant effect of accessibility on diversity. Energetic cost also showed no significant effect on the proportion of species which occur only once in the dataset. Analysis of the landscape distribution of vegetation communities revealed that the average area of community patch does not vary by remoteness. These results suggest that accessible restoration sites are equivalent to remote sites for conserving diversity and landscape structure. Species composition of remote sites does help inform the acceptable variance in composition of restored communities.

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INTRODUCTION

The selection of restoration sites for plant communities and individual species depends on the spatial and temporal arrangement of landscape elements (White and Walker 1997). In addition to environmental suitability (e.g. soil type, water availability, and temperature), landscape patch characteristics like patch area and shape affect suitability of a site for restoration (Bell *et al.* 1997). Further, spatial patterns of human disturbance, be they through fragmentation, economic harvesting, or the spread of exotic invasive species also affect restoration priorities on a landscape. It is these human effects on the selection of potential restoration sites that are the focus of this manuscript; in particular, the effects on vegetation structure of disturbance facilitated by roads and trails.

Areas distant from roads could be good targets for restoration both of communities and individuals species. Remote areas are less likely to harbor invasive species. (Rentch *et al.* 2005; Flory and Clay 2006). They are also less likely to be disturbed by hikers (Giles-Corti *et al.* 2005). Finally, there is some evidence that native species tend to increase in abundance as distance from a road increases (Rentch *et al.* 2005). There is converse evidence though, that roadsides are better restoration targets than remote areas, because they facilitate habitat connectivity (Crossman and Bryan 2006). Further, while roads do have a negative impact on species diversity, those effects may decrease rapidly with distance from the road (on the order of tens of meters; Watkins *et al.* 2003).

So, there remains a great deal of uncertainty surrounding the effects of roads on species diversity and consequently, their role in prioritizing areas for restoration. Further, the previous studies on the relative importance of roads in restoration have treated the effects in a somewhat simplistic way. It is not merely linear distance from roads that may impact the suitability of a site for restoration. Roads are conduits for human movement, humans are conduits for dispersal of invasive species (King *et al.* 2009), collectors of economically important species (Godoy and Bawa 1993), and vectors of general disturbance (Frid and Dill 2002). In previous work, Jobe and White (2009) developed a model of landscape remoteness that estimates the energetic cost required to walk to any point in a landscape from the nearest road. This model can provide precise estimates of how human effects are likely to disperse through the landscape and by extension, the disturbance they create. In this manuscript, the model of Jobe and White (2009) is used to assess the relationships between human accessibility and plant species diversity, plant species composition, and the distribution of vegetation communities in Great Smoky Mountains National Park (North Carolina and Tennessee, US; GRSM). These relationships are assessed with particular emphasis on the potential for remote areas to serve as restoration sites; sites removed from the consequences of landscape dissection by roads and trails.

Three questions are answered in this paper. First, does compositional similarity within a plant community change as a function of accessibility? If two sites with different accessibility have similar composition, then restoration of individual species could proceed equivalently for both regardless of their accessibility. Second, does plant species diversity, particularly of rare species, change with accessibility? If remote sites harbor more rare species than accessible sites, this suggests that human disturbance as a result of accessibility may be playing a role in reducing diversity. It also suggests that the accessible sites, not remote ones, are in need of restoration at a community level and that
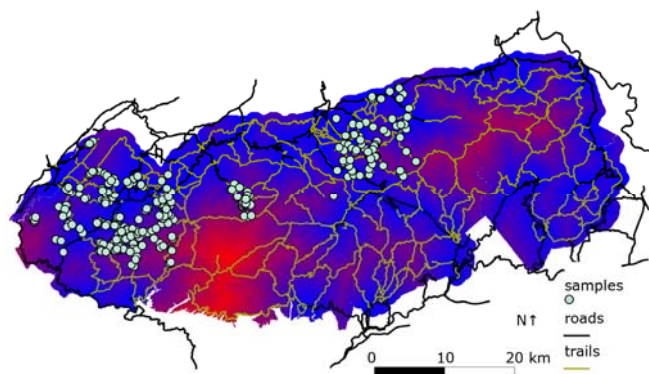
Fig. 1 Energetic cost of travel map for GRSM. Low energetic costs are blue. High energetic costs are red. Values vary from 0 Jkg^{-1} to 1.6E5 Jkg^{-1}. Also shown are the vegetation samples used in this analysis.

individual species restoration will proceed best in the remote sites. Finally, how does the patch area of vegetation community change as a function of accessibility? If remote sites are to be restoration targets, their spatial characteristics, such as average patch area, should be amenable to this.

MATERIALS AND METHODS

Data

1. Modelling remoteness

The accessibility model of Jobe and White (2009) provides estimates of the energetic cost required to walk round-trip along the least-cost path from the nearest trailhead to any part of the Park. The output is a raster covering GRSM where the value of each cell is the sum of individual cell costs along the least-cost path both from and returning to the trailhead (**Fig. 1**). The units for these costs are Jkg^{-1} and the cells have a resolution of 100 m^2. The Path-distance function in ArcGIS9.2 (ESRI 2006) was used to calculate the costs using the least cost paths.

The traversal cost (C) for a single cell along the least cost path is a combination of surface distance (S), isotropic (I, direction-independent) costs and anisotropic (E, direction-dependent) costs:

$$C = S \times I \times A \times E \qquad (1)$$

where E is a constant that converts surface distance in meters to energetic cost in Jkg^{-1}.

The isotropic costs are associated with walking on trails, walking through vegetation and crossing streams. These costs of traversal are the same no matter the direction from which the cell is approached. The isotropic cost coefficients were taken from the empirical estimates of Soule and Goldman (1972) who recorded oxygen consumption for soldiers walking on and off trails, through light and heavy brush, and through swamps. The stream traversal coefficients vary proportionally to stream discharge as described by Manning's equation (Gore 1996).

Energetic costs due to walking on slopes are anisotropic. For a slope of fixed aspect it is usually easier to walk down the slope than up it. So, approaching a slope from the uphill side should have lower energetic costs than approaching it from the downhill side, and traversal perpendicular to the slope should have intermediate costs. There has been a great deal of physiological research on the energetic costs of humans walking on slopes from treadmill studies (see Rose and Gamble 2006, for a review). The model uses two quadratic functions whose coefficients are fitted from Minetti *et al.* (2002). The maximum traversable slope is 60 degrees. Slopes greater than this are considered impossible to cross. Details on the coefficient values and formulation of the energetic cost model can be found in Jobe and White (2009).

2. Vegetation data

The species abundance data were taken from the Carolina Vegetation Survey (CVS, Peet *et al.* 1998). These data record species

abundance for all vascular plants within a 20 m × 50 m plot (0.1 ha). A total of 236 samples were used. Species taxonomy follows Weakley (2008).

Each sample was assigned a vegetation association following the U.S. National Vegetation Classification System (NatureServe 2006). This was done by expert opinion and each sample classification was assigned a confidence on the degree of fit from 1-5 as described in Gopal and Woodcock (1994). These communities are described by the dominant species and are given a 4-digit code (CEGL code). The 236 samples occur in 27 different vegetation communities (**Table 1**).

The geolocation is recorded for each sample. An energetic cost from the accessibility model is retrieved from that location and associated with sample. The remotely sensed vegetation classification (described in the next section) is also assigned to each sample.

3. Remotely-sensed communities

An alternative way to assign communities to a location is through the interpretation of aerial photos. Madden *et al.* (2004) did this for the entire Park. The result is a raster for the Park where each cell is assigned a CEGL code. The classification was verified by Jenkins (2007). A total of 38 communities were classified with a minimum of 80% accuracy. The analysis is limited to only the 27 communities expertly assigned to the species abundance data.

Analysis

1. Similarity analysis

If remote sites are to be suggested as candidates for restoration, then there is a need to know whether species composition varies from near to remote locations. This was tested by comparing the compositional similarity among samples as a function of similarity in energetic cost for samples within the same community and for samples from different communities. This was done using multivariate mantel regression using the ecodist package (Goslee and Urban 2007) of the R software (R Development Core Team 2009). The response variable was compositional similarity as measured by Bray-Curtis distance. The predictor variables were the difference in energetic cost between sample pairs and a binary variable describing whether the sample pair came from the same community or from different community.

2. Diversity analysis

The next task was to determine how diversity was distributed as a function of remoteness. If rare species within a given community occurred more frequently near trailheads than remote locations, it would suggest that remote locations are good targets for restoration. Conversely, more rare species in remote areas lends credence to the hypothesis that areas near trailheads are more likely to be disturbed habitats.

Diversity was analyzed as a function of accessibility in two ways. First, the Shannon-Wiener diversity index (Gurevitch *et al.* 2002) was regressed against energetic cost and community classification. Second, a generalized linear model was created that evaluated the relationship between rare species and accessibility. The predictor variables were the same as in the previous regression. The response variable was the number of species in each sample that occurred only once in the entire dataset. Because the response was species counts, a Poisson family glm with a log link function was used.

Landscape plant community distributions

The patch distribution of communities may vary as a function of accessibility. If remote sites are thought to be good candidates for restoration, then average area of a remote vegetation community patch should be the same as the patches near the road. The area of each unique vegetation patch was recorded along with its community type and mean accessibility in the GIS software GRASS (GRASS Development Team 2008). Then, the log of area was regressed against energetic cost and community type using a gene-

Table 1 Scientific name and CEGL codes for vegetation communities used in this analysis.

| Code	Community
CEGL004973	*Aesculus flava - Betula alleghaniensis - Acer saccharum / Acer spicatum / Caulophyllum thalictroides - Laportea canadensis* Forest
CEGL007695	*Aesculus flava - Acer saccharum - (Fraxinus americana, Tilia americana* var. *heterophylla) / Hydrophyllum canadense - Solidago flexicaulis* Forest
CEGL006271	*Quercus (prinus, coccinea) / Kalmia latifolia / (Galax urceolata, Gaultheria procumbens)* Forest
CEGL007710	*Liriodendron tulipifera - Aesculus flava - (Fraxinus americana, Tilia americana* var. *heterophylla) / Actaea racemosa - Laportea canadensis* Forest
CEGL006192	*Quercus rubra - Acer rubrum / Calycanthus floridus - Pyrularia pubera / Thelypteris noveboracensis* Forest
CEGL007267	*Quercus prinus - (Quercus rubra) - Carya spp. / Oxydendrum arboreum - Cornus florida* Forest
CEGL007230	*Quercus alba - Quercus (rubra, prinus) / Rhododendron calendulaceum - Kalmia latifolia - (Gaylussacia ursina)* Forest
CEGL007097	*Pinus pungens - Pinus rigida - (Quercus prinus) / Kalmia latifolia - Vaccinium pallidum* Woodland
CEGL007543	*Liriodendron tulipifera - Betula lenta - Tsuga canadensis / Rhododendron maximum* Forest
CEGL007285	*Betula alleghaniensis - Fagus grandifolia - Aesculus flava / Viburnum lantanoides / Eurybia chlorolepis - Dryopteris intermedia* Forest
CEGL007300	*Quercus rubra / (Vaccinium simulatum, Rhododendron calendulaceum) / (Dennstaedtia punctilobula, Thelypteris noveboracensis)* Forest
CEGL007878	*Quercus rubra - Tilia americana* var. *heterophylla - Halesia tetraptera* var. *monticola / Collinsonia canadensis - Tradescantia subaspera* Forest
CEGL006256	*Picea rubens - (Betula alleghaniensis, Aesculus flava) / Viburnum lantanoides / Oxalis montana - Solidago glomerata* Forest
CEGL007517	*Pinus strobus - Quercus alba - (Carya alba) / Gaylussacia ursina* Forest
CEGL007519	*Pinus strobus - Quercus (coccinea, prinus) / (Gaylussacia ursina, Vaccinium stamineum)* Forest
CEGL006286	*Quercus prinus - Quercus rubra / Rhododendron maximum / Galax urceolata* Forest
CEGL007130	*Picea rubens - (Abies fraseri) / (Rhododendron catawbiense, Rhododendron maximum)* Forest
CEGL007131	*Picea rubens - (Abies fraseri) / Vaccinium erythrocarpum / Oxalis montana - Dryopteris campyloptera / Hylocomium splendens* Forest
CEGL007219	*Liriodendron tulipifera - Acer rubrum - Robinia pseudoacacia* Forest
CEGL007861	*Betula alleghaniensis - (Tsuga canadensis) / Rhododendron maximum / Leucothoe fontanesiana* Forest
CEGL004242	*Danthonia compressa - (Sibbaldiopsis tridentata)* Herbaceous Vegetation
CEGL007102	*Pinus strobus - Tsuga canadensis / Rhododendron maximum - (Leucothoe fontanesiana)* Forest
CEGL007136	*Tsuga canadensis / Rhododendron maximum - (Clethra acuminata, Leucothoe fontanesiana)* Forest
CEGL007692	*Quercus alba - Quercus rubra - Quercus prinus / Collinsonia canadensis - Podophyllum peltatum - Amphicarpaea bracteata* Forest
CEGL003890	*Vitis aestivalis* Vine-Shrubland
CEGL006130	*Fagus grandifolia / Carex pensylvanica - Carex brunnescens* Forest
CEGL007298	*Quercus rubra / Carex pensylvanica - Ageratina altissima* var. *roanensis* Forest

ralized linear model (Gaussian family, log link function). Finally, the squared residuals were regressed against energetic cost to test whether the variance in patch area differed between remote and accessible locations.

RESULTS

The 236 vegetation samples are biased toward accessible locations (**Fig. 2**). Previous vegetation datasets analyzed in GRSM show similar patterns (Jobe and White 2009). Unlike previous work, however, the peak energetic costs are around 4.5E4 Jkg^{-1}; not the most accessible areas in the Park. This pattern matches with the site selection algorithm for the CVS, where experts try to locate samples in the middle of a contiguous patch of a particular community (Peet *et al.* 1998). The remotely sensed communities are distributed with a few very common vegetation types (>100 km^2) and many rare types, a pattern similar to the rank abundance of species (**Fig. 3**). The remotely sensed community types corresponded to the expert community classification in 25% of the samples. This lack of correspondence is partially due to the fact that the set of communities used by the remotely sensed data is smaller than that of the expertly classified communities.

Similarity

Compositional distance among pairs of sites increased as difference in energetic cost to reach the sites increased (**Fig. 4**). This increase in dissimilarity was greater for samples from the same vegetation community than for samples from different communities. A multivariate mantel regression showed significant effects of differences in energetic cost of sample pairs, and whether samples came from the same community or different ones (**Table 2**). This model explained about 18% of the total variance in compositional similarity ($R^2 = 0.179$).
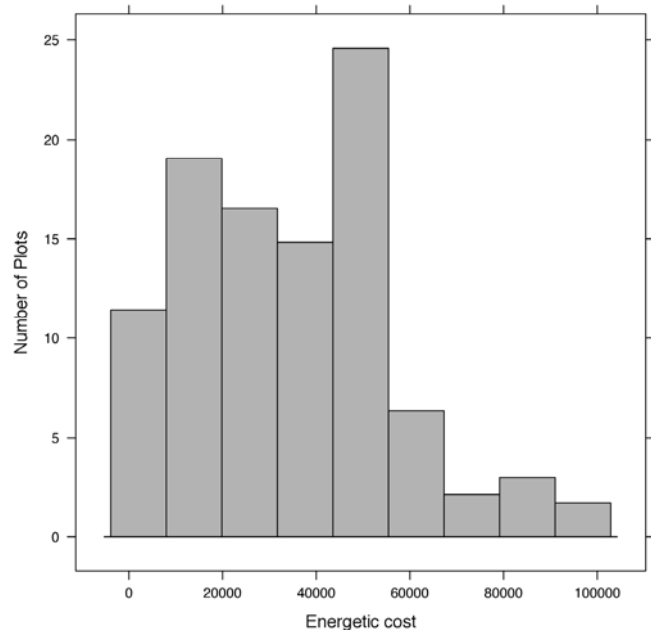
Fig. 2 Histogram of energetic costs for the plant species abundance samples in GRSM. Energetic costs are in units of Jkg^{-1}.

Rare species analysis

Regression of Shannon-Wiener diversity against the multiplicative effects of energetic cost and community type revealed no significant effect of accessibility on diversity (coefficient = -5E-06, p-value = 0.61128). Individually, two communities had significantly lower diversity than average: *Fagus grandifolia / Carex pensylvanica - Carex brunnescens* Forest (CEGL 6130) and *Picea rubens - (Abies fraseri) / Vaccinium erythrocarpum / Oxalis montana – Dryopteris campyloptera / Hylocomium splendens* Forest (CEGL 7131). None of the interactions between energetic
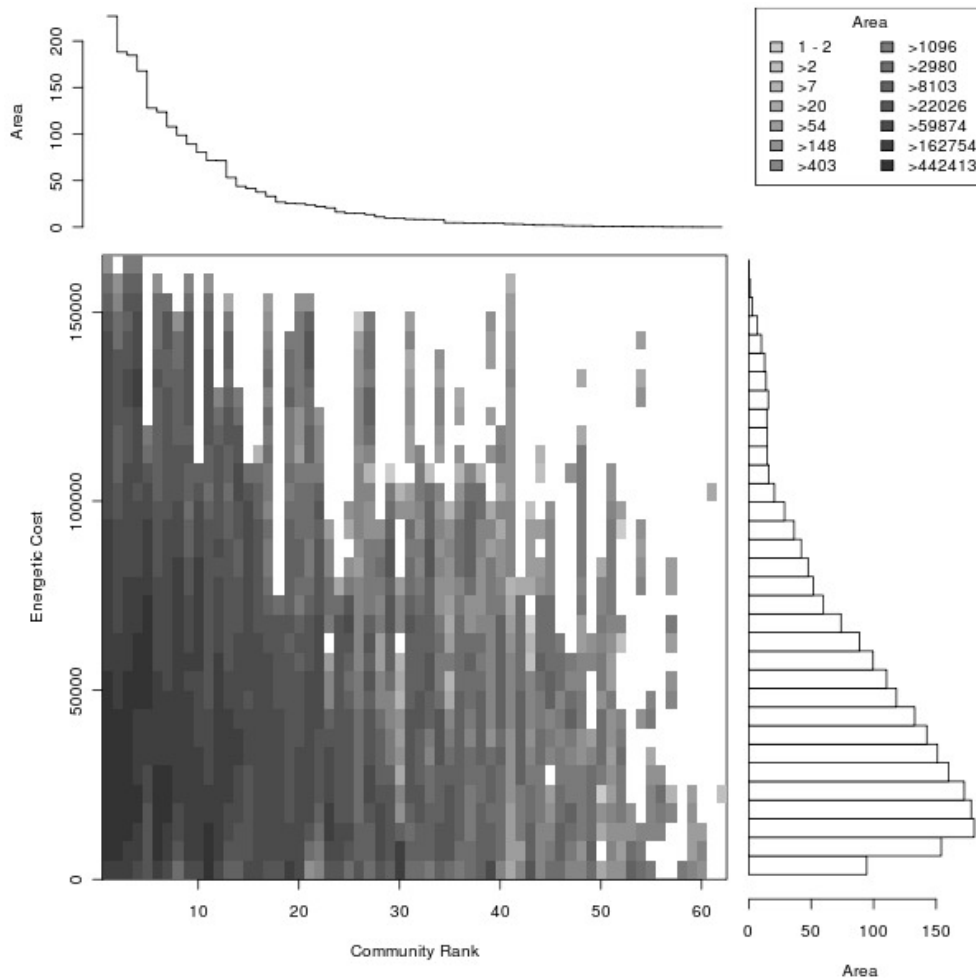
Fig. 3 Joint distributions of accessibility and remotely sensed vegetation associations sorted by rank abundance in the Park. Frequencies are the number of 10m x 10m cells. Marginal distributions of both variables are also plotted. Areas are in km^2.
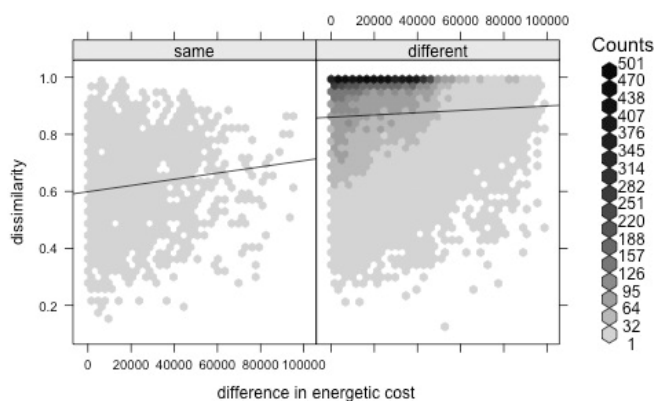

Fig. 4 Scatter plots of compositional similarity among pairs of vegetation samples against the difference in energetic costs. The left pane uses pairs of samples, which have the same vegetation associations. The right pane uses pairs of samples that come from different associations.

Table 2 Multiple mantel regression results for community similarity as a function of the difference in community type and accessibility.

	Bray-Curtis dist	p-value
Intercept	8.601E-01	<0.001
community	-2.614E-01	<0.001
energetic cost	3.937E-07	<0.001
comm*energy	6.963E-07	<0.001

cost and community were significant.

The pure effect of energetic cost also showed no significant effect on the number of species which occur only once in the dataset (coefficient = -2E-9, p-value = 0.990).

One community had an estimate of unique species significantly greater than 0: *Danthonia compressa* - (*Sibbaldiopsis tridentata*) Herbaceous Vegetation (CEGL 4242). The regression estimate of the number of singleton species per sample within this community was approximately 2 (p-value < 0.001). The interaction between energetic cost and this community was also significant. So, sites of this community with greater energetic cost had a lower number of unique species (coefficient = -4E-5, p-value < 0.001). This effect is likely spurious, however, since there were only 2 samples in the dataset with this vegetation type.

Landscape vegetation distributions

Analysis of the landscape distribution of vegetation communities revealed that community patches do not vary significantly in their average area from near to remote sites. Two communities have significantly larger average patch size: *Liriodendron tulipifera - Betula lenta - Tsuga canadensis / Rhododendron maximum* Forest (CEGL 7543) and *Aesculus flava - Acer saccharum - (Fraxinus americana, Tilia americana var. heterophylla) / Hydrophyllum canadense - Solidago flexicaulis* (CEGL 7695). One significant interaction between energetic cost and community was shown. *Pinus strobus - Tsuga canadensis / Rhododendron maximum - (Leucothoe fontanesiana)* Forest (CEGL 7102) tends to have larger patches in more remote areas.

DISCUSSION

Does compositional similarity within a plant community change as a function of accessibility?

The results suggest that, at least for GRSM, sites with dif-

ferent accessibilities tend to have greater compositional dissimilarity than sites with similar energetic cost (**Fig. 4**). And, this trend is more pronounced within communities than between communities. The implications for selection of restoration sites are twofold. First, the reference condition to which sites are restored will be skewed if the data on which they are based come only from samples located near the road. The vegetation samples used here show a strong bias for accessible sites (**Fig. 2**). The maximum energetic cost in the dataset is 9.9E4 Jkg^{-1} and the maximum energetic cost in the Park is 50% larger than that (1.6E5 Jkg^{-1}). If the trend of increasing compositional dissimilarity with energetic cost continued to the most remote areas of the Park, then the average Bray-Curtis distance between a site near the road and an extremely remote site of the same community would be around 0.8. Sites within the same community of similar accessibility have a Bray-Curtis distance of 0.6. This suggests that when choosing reference sites for community descriptions, both near and far sites should be included to maximize variability among samples within the community. It also suggests that remote patches of a community have a unique composition; one that might be more amenable to particular species than near sites. By studying the full breadth of this variability restoration sites for individual species could be selected that match the remoteness of sites where it already occurs. This could increase the likelihood of restoration success.

Second, the fact that remote patches of a community tend to have different species composition than the same communities near the road might lead managers to conclude that one of these locations needs to be restored to look like the other. On the one hand, a manager could reason that human disturbance is more frequent near the road and that the accessible patches need to be restored to look like the remote ones. On the other hand, the manager could have more field data near the road and incorrectly conclude the remote sites should be restored to look like the accessible sites. As the answer to the next question points out though, both interpretations may be incorrect. Changes in compositional similarity do not necessarily correlate with changes in diversity, nor are they indicative of disturbance. More likely they represent the effects of distance-decay of compositional similarity (Nekola and White 1999). Samples are biased toward accessible locations and so do not capture the full variability of vegetation communities (**Fig. 2**). The correct interpretation is to recognize that the variation within a community is not random with respect to accessibility and assessment of a community for restoration must include both near and remote sites.

Does plant species diversity, particularly of rare species, change with accessibility?

The initial hypothesis was that if remote sites harbor more rare species than accessible sites, then human disturbance may be playing a role in reducing diversity. There was no support for this hypothesis in the data. Further, it is the accessible sites not remote ones that are in need of restoration at a community level. Individual species restoration will proceed best in the remote sites. There is no relationship between the Shannon-Wiener diversity index of a vegetation sample and the energetic cost to reach that site. Further, the number of species occurring only once in the data is not correlated with accessibility, except for a single community, and this correlation is likely due to low sampling effort within the community. These results support previous work suggesting that the affect of roads on diversity disappears after a few tens of meters (Watkins *et al.* 2003). Virtually, all of the CVS sample locations are greater than 50 meters from a trailhead.

So, what are the implications for restoration site selection given that diversity does not change with accessibility? Before answering that question, we must remember that GRSM has been in conservation for 75 years, and some human disturbances are mitigated within the Park. It is,

however, the most visited national park in the United States. So, its conservation status cannot wholly assuage direct human impacts. It seems more likely that the lack of correlation between diversity and accessibility is a general result beyond the context of GRSM. Human disturbances associated with accessibility, while they could still affect compositional similarity, do not affect gross diversity (i.e. species richness and evenness). Disturbances such as human dispersal of exotic invasive species are likely more intense along trails, but these effects are not seen in gross measures of diversity.

How does the patch area of vegetation communities change as a function of accessibility?

Even if there is little difference in the diversity of remote patches and patches near a road, remote sites could be less fragmented and have greater core area. Large core areas are vital for restoration (Saunders *et al.* 1991). Again, the hypothesis that remote sites have large patch area is not supported by the data. Nor does the variance in patch area change with accessibility. Unlike the lack of correlation between diversity and accessibility, however, it is likely that the lack of correlation between patch sizes and accessibility is a result of the long conservation history of GRSM. There are few direct landscape-scale alterations apart from the harvesting of economically important species like ginseng (*Panax quinquefolius*; Rock *et al.* 1999) that might be concentrated in accessible areas.

Remote areas in GRSM offer few or no advantages as restoration sites in terms of increased diversity or landscape patch characteristics. Diversity will be roughly equal whether restoration sites are chosen close to roads and trails or whether they are in the most remote parts of the Park. Average patch area will also be the same for remote and near sites. The implications of these conclusions are actually comforting for how restoration site selection is typically done. Having to restore remote areas would likely be more costly in terms of man-hours. The results confirm that the common practice of choosing sites for restoration that are easily accessible should not have negative impacts on broader patterns of diversity. Accessibility cannot be the main driver of selecting which sites should be restored within a community.

Accessibility can help determine what the reference community for a restoration site should look like. Compositional similarity does vary with accessibility. This suggests that while the number of dominant species and the number of rare species remains the same for near and remote sites, the identities of common and rare species change with accessibility. Accessible areas tend to conform to particular environmental gradients (Jobe and White 2009), and it is well known that species within communities change along these gradients (Whittaker 1956). Making sure that community descriptions for restoration sites includes the full range of variability in that community requires sampling in remote areas. Such analysis of community breadth will also play a key role in designing restoration sites that are resilient to climate change (Harris *et al.* 2006).

CONCLUSIONS

A model of landscape remoteness that estimates the energetic cost of walking on landscapes was applied to questions pertinent in the restoration of communities and species. The results suggest that choosing restoration sites that are easily accessible will not be detrimental in conserving diversity or landscape structure. The different species composition of remote locations provide valuable insight into what restoration targets at a community level should look like, whether those sites be accessible or remote.

ACKNOWLEDGEMENTS

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