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Assessing the value of roadless areas in a conservation reserve strategy: biodiversity and landscape connectivity in the northern Rockies

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Summary

1. Roadless areas on United States Department of Agriculture (USDA) Forest Service lands hold significant potential for the conservation of native biodiversity and ecosystem processes, primarily because of their size and location. We examined the potential increase in land-cover types, elevation representation and landscape connectivity that inventoried roadless areas would provide in a northern Rockies (USA) conservation reserve strategy, if these roadless areas received full protection.

2. For the northern Rocky Mountain states of Montana, Wyoming and Idaho, USA, we obtained GIS data on land-cover types and a digital elevation model. We calculated the percentage of land-cover types and elevation ranges of current protected areas (wilderness, national parks and national wildlife refuges) and compared these with the percentages calculated for roadless and protected areas combined. Using five landscape metrics and corresponding statistics, we quantified how roadless areas, when assessed with current protected areas, affect three elements of landscape connectivity: area, isolation and aggregation.

3. Roadless areas, when added to existing federal-protected areas in the northern Rockies, increase the representation of virtually all land-cover types, some by more than 100%, and increase the protection of relatively undisturbed lower elevation lands, which are exceedingly rare in the northern Rockies. In fact, roadless areas protect more rare and declining land-cover types, such as aspen, whitebark pine, sagebrush and grassland communities, than existing protected areas.

4. *Synthesis and applications*. Landscape metric results for the three elements of landscape connectivity (area, isolation and aggregation) demonstrate how roadless areas adjacent to protected areas increase connectivity by creating larger and more cohesive protected area 'patches.' Roadless areas enhance overall landscape connectivity by reducing isolation among protected areas and creating a more dispersed conservation reserve network, important for maintaining wide-ranging species movements. We advocate that the USDA Forest Service should retain the Roadless Area Conservation Rule and manage roadless areas as an integral part of the conservation reserve network for the northern Rockies.

Key-words: conservation, elevation zones, land-cover types, landscape metrics, national forests, reserve design

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Introduction

A growing body of scientific evidence indicates that the current USA system of federal protected areas (designated wilderness areas, national parks and national wildlife refuges) may be too small and disconnected to protect against the decline and loss of native species diversity or to accommodate large natural ecosystem processes (Wright, Dixon & Thompson 1933; MacArthur & Wilson 1967; White 1987; Wilcove 1989; Baker 1992; Turner *et al*. 1993; Noss & Cooperrider 1994; Reice 1994; Newmark 1995; Sinclair *et al*. 1995; Soule & Terborgh 1999). Expanding road networks, human settlements, resource extraction and other encroachments on the landscape have increased the fragmentation and loss of natural areas. Such disturbances have isolated many protected areas, causing them to function as terrestrial 'islands' surrounded by a matrix of lower quality altered lands (Harris 1984; Pickett & White 1985; Wiens, Crawford & Gosz 1985; Turner 1989; Saunders, Hobbs & Margules 1991). The long-term persistence of many species within protected areas is dependent on the degree of human activities and land-use practices on lands adjacent to and near protected areas. There is a need to identify relatively undisturbed lands located outside protected areas that may increase the potential of protected areas in maintaining native biodiversity and certain ecological processes, and to include these lands within the conservation reserve system before they are lost or altered.

Inventoried roadless areas, large tracts of relatively undisturbed land on USA Forest Service lands, are often left out of landscape assessments for identifying functional conservation reserves. Only two studies (DeVelice & Martin 2001; Strittholt & DellaSala 2001) have analysed the contribution that roadless areas make to the current protected areas reserve network. However, more than one-third of inventoried roadless areas on national forests are adjacent to protected areas (DeVelice & Martin 2001). They hold the potential to increase the size and connectivity of designated wilderness areas, national parks and national wildlife refuges, thus increasing the ability of protected areas to maintain natural landscape dynamics and native species population viability over the long term. Smaller, isolated roadless areas are also important because they may contain rare species, capture more habitat variation, including underrepresented habitat types, and may function as 'stepping stones' that connect current protected areas across a landscape (Shafer 1995; Strittholt & DellaSala 2001).

There is a precedent for the protection of national forest roadless areas. The USA Congress has designated as wilderness more than half, 6 million ha, of roadless areas that the Forest Service inventoried in national forests in the 1970s. In 1998, the Forest Service began to devise regulations aimed at protection of roadless area characteristics in national forests. In May 2000, the agency released its proposed rule, familiarly known as the Roadless Rule, and draft environmental impact statement. Eight months later, the Forest Service adopted the rule. In July 2004, the Forest Service proposed to repeal the Roadless Rule and replace it with a state petition and rule-making process, which would offer less protection by presumably opening national roadless areas to all forest service activities and requiring state governors to 'opt in' Roadless Rule protections affirmatively for any roadless area.

Included in the Roadless Rule environmental impact statement was an evaluation of the potential contribution that protection of roadless areas could make to the conservation of biodiversity at a national scale (USDA Forest Service 2000b). In that evaluation, DeVelice & Martin (2001) found that the inclusion of roadless areas in the network of federal protected areas would expand representation of ecoregions in protected areas, increase the acreage of reserved areas at lower elevations, and increase the number of areas large enough to provide refuge for wide-ranging species.

Strittholt & DellaSala (2001) focused on similar questions at a regional scale for the Klamath-Sikiyou area in southern Oregon and northern California, USA. They found that roadless areas protect a wide range of ecological attributes, especially at mid- to lower elevations, important in this region. They also concluded that roadless areas increase the connectivity among ecoregions.

The northern Rocky Mountain states of Montana, Wyoming and Idaho comprise a region particularly rich in roadless areas, roughly 2·6 million ha, providing a unique opportunity to create a relatively intact reserve design that captures important elements of conservation for the northern Rockies. Using two key concepts in conservation biology, biodiversity representation and landscape connectivity, we investigated the potential contributions of national forest roadless areas to the protected areas reserve network across the northern Rocky Mountain region.

DIVERSITY REPRESENTATION

An important goal in the design and establishment of conservation reserves is to represent a full range of native biodiversity (Shelford 1926; Margules, Nicholls & Pressey 1988; Church, Stoms & Davis 1996; Possingham, Ball & Andelman 2000). Even though this goal has been articulated for some time, most protected areas are demarcated around areas with high scenic and recreational attributes (Davis *et al*. 1996). As a result, existing protected areas in the northern Rockies are, for the most part, concentrated at higher elevations, where other important elements of biodiversity are most likely to be poorly represented (Scott *et al*. 2001).

Representation of a full range of biodiversity in reserves requires an understanding of all species and ecosystem processes operating within a given landscape. However, many researchers have used ecological communities and elevation ranges as coarse-scale surrogates for native biodiversity in the design of conservation reserves (Scott *et al*. 1993; Host *et al*. 1996). This concept is based on the idea that if a full range of ecological communities and elevation ranges is protected, it is more likely that many ecological communities, wide-ranging species and ecosystem processes will be maintained in the reserves. In the northern Rockies, ecological communities are often associated with elevation gradients (Hansen & Rotella 1999). Hence, roadless areas situated at middle and lower elevations may make valuable contributions in protecting many elements of biodiversity that are currently not well represented in protected areas (DeVelice & Martin 2001).

LANDSCAPE CONNECTIVITY

Connectivity refers to the degree to which the structure of a landscape helps or hinders the movement of wildlife species or natural processes such as fire (Wiens, Crawford & Gosz 1985; Turner *et al*. 1993; Noss & Cooperrider 1994; Bascompte & Solé 1996; With 1999). A 'well-connected' area can sustain important elements of ecosystem integrity, namely the ability of species to move and natural processes to function, and is more likely to maintain its overall integrity compared with a highly fragmented area.

Roads are highlighted in the scientific literature as major causes of landscape fragmentation, and function as barriers to organism movements, resulting in a reduction of overall landscape connectivity for many native species. The effects of roads are broad and include mortality from collisions, modification of animal behaviour, disruption of the physical environment, alteration of chemical environments, spread of exotic and invasive species, habitat loss, increase in edge effects, interference with wildlife life-history functions and degradation of aquatic habitats through alteration of stream banks and increased sediment loads (Franklin & Forman 1987; Andrews 1990; Noss & Cooperrider 1994; Reice 1994; Reed, Johnson-Barnard & Baker 1996; Trombulak & Frissell 2000; McGarigal *et al*. 2001). Thus, the addition of roadless areas to existing protected areas reserve is likely to maintain or increase landscape connectivity, as well as increase the integrity of protected areas.

With the advent of landscape metrics, it is now possible to quantify connectivity for landscapes, land-cover types, species' habitats, species' movements and ecosystem processes across a given region (O'Neill *et al*. 1988; McGarigal & Marks 1995; Gustafson 1998; With 1999). Many different metrics that quantify spatial characteristics of patches or entire landscape mosaics have been described (Turner & Gardner 1991; McGarigal & Marks 1995; Ritters *et al*. 1995; Hargis, Bisonette & David 1998; Dale 2000; Jaeger 2000; McGarigal & Holmes 2002). We chose metrics that measure three elements of landscape connectivity: area, isolation and aggregation.

Area

It is known that larger areas (patches) generally contain more species, more individuals, more species with large home ranges and/or sensitive to human activity, and more intact ecosystem processes than smaller areas (Robbins, Dawson & Dowell 1989; Turner *et al*. 1993; Newmark 1995; Shafer 1995). Higher numbers of patches will usually contribute to greater resilience of populations and may also increase the utility of patches that act as 'stepping stones' or connectors across a landscape (Buechner 1989; Lamberson *et al*. 1992).

Isolation

The distance between patches plays an important role in many ecological processes. Studies have shown that patch isolation is the reason that fragmented habitats often contain fewer bird and mammal species than contiguous habitats (Murphy & Noon 1992; Reed, Johnson-Barnard & Baker 1996; Beauvais 2000; Hansen & Rotella 2000). As habitat is lost or fragmented, residual habitat patches become smaller and more isolated from each other, species movement is disrupted, and individual species and local populations become isolated (Shinneman & Baker 2000).

Aggregation

The spatial arrangement of patches may help to explain how certain species are found in patches located close together and are not found in patches that are more isolated, or vice versa (Ritters *et al*. 1995; He, DeZonia, & Mladenoff 2000). This concept generally follows the ideas developed in island biogeography theory (MacArthur & Wilson 1967) and metapopulation theory (Levins 1969, 1970).

For some species or natural processes, the isolation or aggregation of patches across the landscape may be more important, for others, area may be the key element. Together, these three elements offer a comprehensive assessment of the importance of roadless areas to the maintenance of overall landscape connectivity and ecosystem integrity of current protected areas in the northern Rockies.

In this study, we aimed to assess the extent to which roadless areas increase biodiversity representation and landscape connectivity when they are included in the protected areas reserve network for the northern Rockies.

Methods

STUDY AREA

Of the 84 million ha of land that stretch across Montana, Wyoming and Idaho in the USA, roadless areas cover 2·6 million ha and existing federal protected areas (wilderness areas, national parks, special management areas and national wildlife refuges) protect almost 8·7 million ha. Within this region, three large, relatively

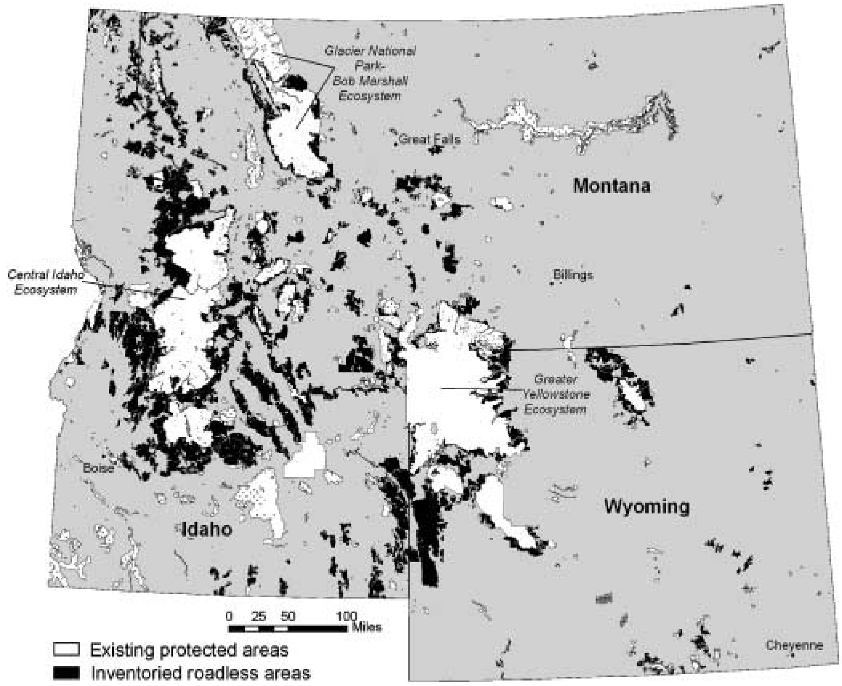

Fig. 1. Roadless areas and protected areas across the states of Idaho, Montana and Wyoming, USA.

undisturbed, mountain ecosystems are delineated around national parks and/or wilderness complexes. These are the Greater Yellowstone Ecosystem, Glacier National Park–Bob Marshall Ecosystem, and the Central Idaho Ecosystem (Fig. 1).

The topography of the northern Rocky Mountain states spans steep physical gradients in elevation, slope, aspect, temperature and precipitation that give rise to diverse vegetation types. Elevations range from 150 m to 4200 m. Average precipitation ranges from 28 cm to 51 cm (Franklin 1983). The northern Rockies comprise a variety of non-forested and coniferous forest types. Low-lying valleys are characterized by grasslands, sagebrush (*Artemisia* spp.) and desert shrublands, interspersed with juniper (*Juniperus* spp.) and riparian woodlands. Ponderosa pine *Pinus ponderosa* dominates lower elevation montane forests, while xeric coniferous forests of mainly Douglas fir *Psuedotsuga mensiezia*, ponderosa pine, grand fir *Abies grandis*, lodgepole pine *Pinus contorta* and aspen *Populus tremuloides* occur at mid-elevations. Mesic forests in the north and west largely contain western larch *Larix occidentalis*, grand fir, western red cedar *Thuja plicata* and mountain hemlock *Tsuga mertensiana*. Higher elevations are composed of Engelmann spruce *Picea engelmannii*, subalpine fir *Abies lasiocarpa*, alpine larch *Larix lyalli* and white-bark pine *Pinus albicaulis* intermixed with subalpine meadows. Herb lands, rock, alder *Alnus sinuata* shrub-fields and snowfields/ice occur at the highest elevations.

DATA COLLECTION

We used a land management status GIS coverage and classification system developed by the USA Geological Survey's Biological Resources Division in its nation-wide GAP Analysis Programme (Scott, Tear & Davis 1996) to delineate 'protected areas'. This programme devised a ranking scheme to represent various levels of protection, ranging from the least protected lands (category 4, e.g. private lands) to those with the highest level of protection (category 1, e.g. wilderness areas) for all public lands in the GIS spatial database. For this study, we assumed that categories 1 and 2 represent adequate protection as their primary management objective is conservation (Scott, Tear & Davis 1996), and selected these categories as our protected areas on all forest service lands located in the three states.

We used the federal inventoried roadless areas GIS database (USDA Forest Service 2000a). This includes areas that are greater than 2000 ha in size, where road building is prohibited under current National Forest Plan decisions and where road building is presently allowed. We recognize that our decision leaves out smaller roadless areas that were not considered during the inventory of federal roadless areas and that these areas serve important conservation goals (Strittholt & DellaSala 2001). For this study, the term 'roadless areas' refers to inventoried roadless areas.

We used three independently derived land cover maps for Montana, Wyoming and Idaho from the GAP Analysis Programme (Scott, Tear & Davis 1996). The Montana and Idaho GAP products were produced based on classification techniques by Redmond *et al.* (1998) for raw Landsat Thematic Mapper (TM) satellite imagery. Spatial resolution of the grid was 90 m for Montana and 30 m for Idaho. The Wyoming GAP Analysis Programme digitized land cover data in a vector format from Landsat TM satellite imagery at a scale of 1 : 100 000 (Gap Analysis Wyoming 1996). We converted Wyoming's vector map into a grid format and resampled the three data sets to 90-m resolution. Then we merged the three land cover maps into a single image and a common land cover classification scheme (Appendix 1).

Similar to most GIS databases, errors are associated with the land management status, inventoried roadless areas and land-cover grids. These grids represent a composite of data from many sources and include variations in mapping procedures and possible misclassifications that could potentially cause inconsistencies that are difficult to detect. However, we believe, based on professional judgement, that the error rate is not large enough to affect conclusions drawn from this large regional-scale analysis.

To investigate the representation of roadless areas at various elevation classes, we downloaded a digital elevation model from the 30-m National Elevation Dataset produced by the USA Geological Survey's EROS Data Center (Sioux Falls, SD). We reclassified the elevation range into 21 equal-interval classes ranging in 200-m increments from approximately 150 m to 4200 m.

DATA ANALYSIS

All data analyses were conducted in ARC/INFO and ArcView GIS software from Environmental Systems Research Institute (Redlands, CA).

Land cover representation

Using ARC/INFO, we combined the protected areas database with the land cover map. To calculate the percentage representation of each land-cover type, we divided the protected portion of each land-cover type by the total area of each land-cover type across the study area. Next, we appended the national forest inventoried roadless areas to the existing protected areas and repeated the same calculation described above to measure the additional representation of each land-cover type because of the inclusion of roadless areas. In addition, we calculated the percentage increase between each land cover percentage representation for protected areas alone and protected areas and roadless areas combined. This measure quantified the 'relative' ecological contribution from roadless areas for each land-cover type. We then ranked these land-cover types according to the level of representation within the existing protected areas.

Elevation representation

Using ARC/INFO, we combined the protected areas database with the 30-m digital elevation model. Similar to the procedure for land-cover types described above, we added the roadless areas to the existing protected areas, intersected this image with the elevation data, and calculated the change in representation for each elevation class provided by protection of roadless areas.

To examine the potential increase of landscape connectivity caused by roadless areas, we used ARC/INFO and FRAGSTATS (McGarigal & Marks 1995; McGarigal & Holmes 2002), a computer program developed to quantify heterogeneity of the landscape. We identified five landscape metrics available in FRAGSTATS to assess our three elements of landscape connectivity (McGarigal & Holmes 2002). To assess area, we used the metrics percentage land (PLAND), number of patches (NP) and patch size (AREA). We included the metrics NP and AREA to help explain the context of an increase in PLAND. For example, an increase in PLAND and AREA and a decrease in NP would indicate that the added roadless patches were located next to existing conservation patches, resulting in an increase in the size of patches and a decrease in the number of patches across the landscape. Conversely, a decrease in AREA and an increase in NP would indicate that the added patches were generally smaller and did not combine with existing patches.

To assess isolation we used nearest neighbour distance (ENN). A decrease or increase in ENN would indicate that patches are either located closer together or farther apart, respectively, across the landscape.

To assess aggregation, we used contagion (CONTAG). An increase in CONTAG would indicate that patches are, to a certain extent, aggregated together across the landscape.

Using FRAGSTATS, we selected and ran our five landscape metrics on the two grids described above (current protected areas only, and roadless areas and current protected areas combined). Each grid was a binary map where all grid cells that comprised the 'protected' and 'roadless' patches were classified as 1 and all other 'non-protected' grid cells were masked out as background (–99). For each landscape metric, we computed the mean, area-weighted mean and coefficient of variation where applicable. We then compared the differences in metrics between the two grids. In addition, differences in the mean, area-weighted mean and coefficient of variation helped to explain how the range of values for each metric were distributed when existing protected areas were compared with the conservation system including roadless areas.

Results

LAND COVER REPRESENTATION

In existing protected areas, burned forest and snowfields/ice had the highest land cover representation, 88% and 86%, respectively. Representation of other land-cover types, such as alpine meadows, whitebark pine, exposed rock/soil, subalpine meadows, wetlands, mixed subalpine forest and lodgepole pine, ranged from 31% to 71%.

The inclusion of roadless areas increased the representation of all land-cover types except for one, sand dunes (Table 1). Relative percentage increases ranged

Table 1. Additional representation and percentage increase in representation of each land-cover type across the northern Rockies when national forest roadless areas are added to existing protected areas

Land-cover type	Existing level of representation (%)	Potential level of representation including roadless areas (%)	Percentage increase including roadless areas
Burned forest	88·12	93·09	5·65
Snowfields/ice	86·12	97·48	13·19
Alpine meadow	71·51	94·18	31·70
Mixed whitebark pine	59·62	84·94	42·46
Exposed rock/soil	44·67	59·92	34·12
Subalpine meadow	40·49	68·85	70·05
Wetlands	37·34	38·68	3·61
Mixed subalpine forest	32·20	68·63	113·11
Lodgepole pine	31·35	59·42	89·54
Mixed barren lands	21·66	22·61	4·37
Sand dunes	18·44	18·44	0·00
Mixed conifer	16·97	37·24	119·44
Mesic upland shrub	10·74	26·14	143·44
Shrub-dominated riparian	7·98	12·77	59·91
Forest-dominated riparian	7·18	12·14	69·11
Sagebrush	6·33	9·91	56·55
Juniper	5·87	6·80	15·95
Xeric upland shrub	5·85	7·97	36·33
Vegetated sand dunes	5·69	6·03	5·89
Western red cedar	5·57	22·00	295·08
Mud flats	5·33	7·39	38·79
Ponderosa pine	4·94	9·88	99·97
Aspen	4·48	25·99	479·80
Shrub–grassland associations	4·25	5·89	38·46
Western hemlock	3·36	23·62	602·54
Grasslands	2·49	3·64	46·31
Grass-dominated riparian	2·15	3·07	43·01
Salt-desert shrub flats	1·58	1·71	8·63
Bur oak woodland	0·00	2·40	NA

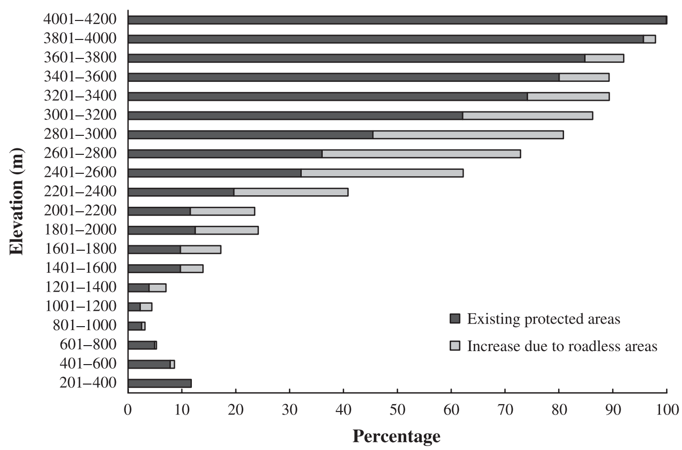

Fig. 2. Additional representation of elevation ranges resulting from the inclusion of roadless areas with protected areas for the northern Rockies. The *x*-axis represents elevation in 200-m increments and the *y*-axis shows absolute increase in percentage representation when roadless areas are added to protected areas. Black bars represent protected areas and grey bars represent roadless areas.

from 5% to 600%. Fifteen land-cover types increased by more than 40%, among them important ecological communities, western hemlock, aspen, ponderosa pine, western red cedar and sagebrush, each of which has less than 10% representation in current protected areas. Moreover, the addition of roadless areas represented one land-cover type, bur oak *Quercus macrocarpa* woodland, not present in protected areas.

ELEVATION REPRESENTATION

Our elevation analyses showed that elevations in the range of 2200–4200 m were well represented in protected areas (Fig. 2). The addition of roadless areas resulted in a large increase in representation of lands at elevations ranging from 1000 m to approximately 3400 m. For elevation ranges below 1000 m and above 3400 m, the

Table 2. Landscape metrics comparing the spatial pattern of protected areas alone with a scenario that includes protected areas and national forest roadless areas combined for the northern Rockies. + and – indicate an increase or decrease, respectively, in the metric value caused by the addition of roadless areas

Landscape Metrics	Protected areas	Protected and roadless areas	+/ –
Area			
Class area (ha)	8 814 900	15 673 600	+
Percentage land	9	16	+
Number of patches	770	722	–
Patch size (mean, ha)	11 447·92	21 708·59	+
Patch size (area-weighted mean)	1 105 055·78	2 505 909·11	+
Patch size (coefficient of variation)	977·39	1 069·74	+
Isolation			
Nearest neighbour (m)	7 013·72	5 353·11	–
Nearest neighbour (area-weighted mean)	3 153·73	2 518·75	–
Nearest neighbour (coefficient of variation)	122·47	134·16	+
Aggregation			
Contagion index	72·56	58·64	–

contribution of roadless areas was small. However, the proportion of area represented at lower elevations increased when we included roadless areas with protected areas.

CONNECTIVITY

Results from the landscape metrics showed that the addition of roadless areas increased regional connectivity for all three connectivity elements (Table 2). Area metrics demonstrated that the addition of roadless areas almost doubled the amount of area protected, rising from 9% to 16%, and the mean patch size in protected areas changed from 11448 ha to 21709 ha. The number of patches decreased from 770 to 722. Area-weighted mean patch size increases and the patch size coefficient of variation increased from 977 to 1070. Isolation metrics showed a decrease in the mean and area-weighted mean nearest-neighbour metrics when roadless areas were added. The mean distance between nearest protected patches decreased from 7014 m to 5353 m. The decrease in the area-weighted mean was less than the overall mean when patches of all sizes were considered. The coefficient of variation also increased for this metric. The aggregation metric (contagion) decreased from 72·56 to 58·64 when roadless areas were included, signifying more dispersion of patches across the landscape.

Discussion

BIODIVERSITY REPRESENTATION

A review of the literature suggests that a given vegetation community is adequately represented when 12–25% of it is included in a conservation area (World Commission on Environment & Development 1987; Noss & Cooperrider 1994), although it is not certain that these thresholds are truly adequate to protect vegetation communities. Based on this range, we define land-cover types above 25% as adequately protected, land-cover types within the range of 12–25% as minimally protected, and those below 12% as underrepresented, similar to DeVelice & Martin (2001).

Our results show that roadless areas make a substantial contribution in maintaining regional biodiversity. One of our most important findings is that roadless areas would protect a wider range of land-cover types and elevation ranges than protected areas alone, especially those characteristic of mid- to low elevations that are underrepresented in protected areas. These lands are among the last remnants of biologically productive lands that have not been significantly altered through human settlements, resource extraction and road construction (Scott *et al*. 2001; Strittholt & DellaSala 2001). We also found that protected areas adequately represent land-cover types that are characteristic of higher elevations. This finding supports the generally accepted notion that wilderness areas and national parks mainly protect higher elevation ecological communities (Davis *et al*. 1996; Possingham, Ball & Andelman 2000). Contrary to DeVelice & Martin (2001), whose study found that roadless areas mainly occurred at mid- to lower elevations, but similar to Strittholt & DellaSala (2001), we found that roadless areas considerably increase the protection of higher elevations and corresponding cover types as well. The different results are probably because of the scale at which the studies were implemented. DeVelice & Martin's (2001) study included all roadless areas across the nation, incorporating a wide range of elevations from sea level to the highest peaks. Our study, and that of Strittholt & DellaSala (2001), focused on smaller regions at higher elevations.

Across the northern Rockies region (Montana, Wyoming and Idaho), protected areas adequately represent nine land-cover types, whereas five biologically important land-cover types, western hemlock, aspen, ponderosa pine, western red cedar and mesic upland shrub, are underrepresented in protected areas. However, the addition of roadless areas increases representation of two cover types (western hemlock and western red cedar) to the minimally protected threshold and two cover types (aspen and mesic upland shrub) to the adequately represented threshold (greater than 25%). Ponderosa pine, even though it increases by nearly 100%, remains underrepresented. Overall, the magnitude of the increased representation, from 100% to 600%, indicates that roadless areas can make substantial contributions to the protection of land-cover types that are not well represented in protected areas.

Increased representation of certain rare ecological communities is particularly important in a northern Rockies conservation strategy. Aspen, for example, is thought to be declining in the northern Rockies (Gallent *et al*. 1998). When roadless areas are added to protected areas, aspen moves up two full categories: from underrepresented to adequately represented, a 480% increase in representation for this forest type, on which many avian species depend upon (Hansen & Rotella 2000). Representation of whitebark pine changes from 60% to 85% when roadless areas are added. Whitebark pine is declining throughout North America due to blister rust *Cronartium ribicola*, an introduced disease, and is a 'keystone species' important for many higher elevation species (Keane, Morgan & Menakis 1994).

Elevation representation results demonstrate that protected areas are mainly located at higher elevations. We also found that roadless areas are generally concentrated at mid- to high elevations and represent a wider range of elevations, especially low- to mid elevations, than protected areas. However, our results show that protected areas encompass more lower elevation lands than roadless areas. This situation is somewhat deceiving. Representation of lower elevations in protected areas is largely a result of two well-placed low-elevation conservation areas: Hell's Canyon National Recreation Area and Missouri Breaks National Monument. In fact, low-elevation lands below 1000 m are not well represented in either protected areas or roadless areas. As a majority of lower elevation lands in the northern Rockies have been converted to other uses, it is of utmost importance to increase representation of lower elevation sites in protected areas (Strittholt & DellaSala 2001). Protection of these lower elevation roadless areas would contribute greatly to the conservation of lower elevation species and ecological communities that are poorly represented in protected areas.

LANDSCAPE CONNECTIVITY

Our analyses of three elements of connectivity show that roadless areas increase connectivity across the northern Rockies, and increase both the area and size of protected area patches. In addition, the number of protected area patches decreases with the addition of roadless areas because they combine with protected areas to form one larger patch. Larger patches will protect more species and more individuals, species with large home ranges, species sensitive to human activity, and more intact ecosystem processes than smaller areas (Askins, Philbrick & Sugeno 1987; Robbins, Dawson & Dowell 1989; Turner *et al*. 1993; Newmark 1995; Shafer 1995). Roadless areas also reduce the distance between protected areas and create a more evenly dispersed reserve system, critical for maintaining many species' movements and a large distribution of local populations (MacArthur & Wilson 1967; Murphy & Noon 1992; Reed, Johnson-Barnard & Baker 1996; Ritters *et al*. 1996; Beauvais 2000; Hansen & Rotella 2000; He, DeZonia, & Mladenoff 2000; Shinneman & Baker 2000).

Our results show an increase in the coefficient of variation for patch size and isolation metrics, which may be an important consideration in delineating conservation reserve systems capable of maintaining movements of various species and ecological processes (Wiens & Milne 1989; Wilcove & Murphy 1991; Noss 1992; Noss *et al*. 1996; O'Neill *et al*. 1996). Smaller patches may supplement larger reserves by protecting rare species that occur only in certain areas (Franklin & Forman 1987; Hansen *et al*. 1991; Shafer 1995). The dispersion of roadless areas may also contribute to greater resilience or survival of island populations by allowing a greater chance for species exchange, essentially maintaining a metapopulation or source–sink population structure (Wiens, Crawford & Gosz 1985; Pullium 1988; Gilpin & Hanski 1991; Murphy & Noon 1992). Many studies are investigating how species move through landscapes and their use of stepping-stone habitats, especially in fragmented landscapes (Freemark *et al*. 1993; With 1999; Beauvais 2000; Hansen & Rotella 2000; Holloway, Griffiths & Richardson 2003; Johnson, Seip & Boyce 2004). Being relatively undisturbed and well-distributed among protected areas, roadless areas are top candidates for the delineation of high-quality 'habitat connections' across the northern Rockies, particularly those that target rare or declining species. The loss or alteration of roadless areas may further reduce the movement of species among interdependent island populations located in protected areas and roadless areas, resulting in greater isolation.

Moreover, the addition of roadless areas increases the effective size of the three largest wilderness and national park complexes in the northern Rockies: the Greater Yellowstone Ecosystem, the Glacier National Park–Bob Marshall Ecosystem and the Central Idaho Ecosystem, where management challenges include maintaining large-scale ecological processes such as species' movements and natural fire across jurisdictional boundaries (Pickett & White 1985; Turner *et al*. 1993). Roadless areas not immediately adjacent to these complexes are dispersed in the surrounding landscape, which helps to decrease the degree of isolation between the complexes and possibly allows for species movement among these ecosystems.

MANAGEMENT IMPLICATIONS

Using research to guide reserve design and develop land protection policies is the strongest approach in conservation. The importance of intact, functioning natural ecosystems to the maintenance of native biodiversity and ecological processes is unquestioned (Wright, Dixon & Thompson 1933; MacArthur & Wilson 1967; Usher 1987; White 1987; Shafer 1995; Noss, O'Connell & Murphy 1997). The negative impacts of roads in natural areas are well known (Andrews 1990; Foreman & Wolke 1992; Reed, Johnson-Barnard & Baker 1996; Spellerberg 1998; Trombulak & Frissell 2000; McGarigal *et al*. 2001). Our landscape assessment demonstrates how roadless areas, the remaining relatively undisturbed forested lands in the northern Rockies, are essential for maintaining biodiversity and landscape connectivity in a conservation reserve strategy for this area. This has direct bearing on management decisions regarding the protection of roadless areas in this region. Our results, along with the findings of DeVelice & Martin (2001) and Strittholt & DellaSala (2001), highlight the important role of roadless areas in USA conservation efforts and contribute to the larger policy dialogue surrounding roadless areas.

The methods used in this study can help land managers determine appropriate guidelines to identify and assess roadless areas that are critical in maintaining regional biodiversity, ecosystem processes, landscape connectivity and overall intact ecosystem integrity. Land managers should avoid activities such as road building, logging, spread of exotic species, off-road vehicle use and exurban development in roadless areas that would result in their degradation or loss. If roadless areas are not protected from these activities as a matter of priority, it is possible that their potential contribution to conservation effort in the future will be diminished and existing protected areas surrounded by or in close proximity to roadless areas will be negatively affected as well. We recommend that roadless areas receive full protection and are managed responsibly, so that they can function as an important part of the current conservation reserve system in the USA.

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Supplementary material

The following material is available from http://www.blackwellpublishing.com/products/journals/suppmat/JPE/JPE996/JPE996sm.htm.

Appendix 1. Land-cover types across the northern Rocky Mountain region reclassified from USA Geological Survey's Biological GAP Analysis Programme (Scott, Tear & Davis 1996).

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