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# Beta Diversity and Nature Reserve System Design in the Yukon, Canada

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**Abstract:** *Design of protected areas has focused on setting targets for representation of biodiversity, but often these targets do not include prescriptions as to how large protected areas should be or where they should be located. Principles of island biogeography theory have been applied with some success, but they have limitations. The so-called SLOSS (single large or several small reserves) debate hinged on applications of island biogeography theory to protected areas but was resolved only to the point that parties agreed there might be different approaches in different situations. Although proponents on both sides of the SLOSS debate generally agree that replicating protected areas is desirable, it is difficult to determine how to replicate reserves in terms of number and spatial arrangement. More important, many targets for representation often do not address issues of species persistence. Here, we used a geographic information system in a study of disturbance-sensitive mammals of the Yukon Territory, Canada, to design a protected-areas network that maintains a historical assemblage of species goals for component ecoregions. We simultaneously determined patterns of diversity as Whittaker's beta and compositional turnover and examined how these two measures can give further insights into reserve location and spatial arrangement. Both regional heterogeneity and compositional turnover between nonadjacent sites were significant predictors of the number of protected areas necessary to represent mammals within each ecoregion. Thus, protected-area planners can use diversity measures to identify number and spacing of protected areas within ecologically bounded regions.*

**Key Words:** biodiversity representation, Bray-Curtis index, protected areas, reserve-selection algorithms, SLOSS, spatial turnover

Diversidad Beta y Diseño del Sistema de Reservas Naturales en el Yukon, Canadá

**Resumen:** *El diseño de áreas protegidas se ha enfocado a definir blancos para la representación de biodiversidad, pero a menudo estos blancos no incluyen recomendaciones en cuanto al tamaño que deben tener de las áreas protegidas o donde deberán situarse. Los principios de la teoría de biogeografía de islas se han aplicado con cierto éxito, pero tienen limitaciones. El debate denominado SLOSS (una reserva grande o varias pequeñas) articulaba aplicaciones de la teoría de biogeografía de islas pero solo fue resuelto hasta el punto en que las diferentes opiniones acordaron que puede haber enfoques diferentes en situaciones diferentes. Aunque los proponentes de ambos puntos de vista del debate SLOSS generalmente están de acuerdo en que es deseable la replicación de áreas protegidas, es difícil determinar como replicar reservas en términos de número y arreglo espacial. Más notablemente, muchos blancos para representación a menudo no abordan aspectos de la persistencia de especies. Aquí, utilizamos un sistema de información geográfica (SIG) en un estudio de mamíferos sensibles a la perturbación en el Territorio Yukon, Canadá, para diseñar una red de áreas protegidas que mantenga un ensamble histórico de especies en las ecoregiones que lo componen. Simultáneamente determinamos los patrones de biodiversidad beta de Whittaker y de recambio de composición y examinamos como estas dos medidas pueden proporcionar mayor entendimiento sobre la localización de reservas y su arreglo espacial. Tanto la heterogeneidad regional como el recambio en la composición entre sitios no adyacentes*

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fueron predictores significativos del número de áreas protegidas necesario para representar a los mamíferos en cada ecoregión. Por lo tanto, los planificadores de áreas protegidas pueden utilizar medidas de diversidad para identificar el número y espaciamiento de áreas protegidas en regiones limitadas ecológicamente.

**Palabras Clave:** algoritmos para la selección de reservas, áreas protegidas, índice de Bray-Curtis, representación de la biodiversidad, recambio espacial, SLOSS

## Introduction

Agencies responsible for delineating and managing protected areas are often faced with the challenges of limited funds and finite space to set aside for conservation. To optimize both ecological and socioeconomic goals, protected-areas networks must be designed to maintain ecological systems and processes as efficiently and effectively as possible. This often means that protected areas are selected to maximize representation of natural systems such as ecoregions and minimize costs. For the purposes of this study, the term *protected area* refers to an area designated to maximize biodiversity protection.

### The Yukon Study: Ecosystem Representation

As part of a regional protected areas strategy, the government of the Yukon Territory, Canada, initially sought to establish one protected area to represent the biodiversity of each of the territory's ecoregions (Department of Renewable Resources 1998), which have been delineated based on vegetation and topography (Oswald & Senyk 1977; Fig. 1). Since the initiation of the Yukon protected-areas strategy, a new government put a halt to the protected-areas planning process. Nonetheless, our analysis presents a useful case study for determining minimum requirements in general for protected areas within ecoregions because many jurisdictions have adopted similar representation goals (e.g., IUCN 1993; Hummel 1996).

Representation goals are an important component in designing reserve networks because they ensure that areas of significant biogeographical importance are protected (Naveh & Lieberman 1990). In addition, protecting a suite of ecological elements increases the chance that local and regional processes (e.g., dispersal, adaptation to habitats) that give rise to and maintain local biodiversity will remain intact (Noss 1992). Any ecologically defined region will never be completely homogeneous; thus, to capture the diversity of organisms within the region, protected areas will most likely have to be replicated across the landscape (Noss 1996; Nekola & White 1999; Fairbanks et al. 2001). Additionally, such redundancy of protected areas acts as insurance against stochastic events that may jeopardize species' persistence and possibly captures greater genetic diversity for those species that occur in more than one protected area (Lucas 1984).

Articulating conservation targets in terms of the need to replicate reserves evokes the SLOSS (single large or several small) debate (Diamond 1975; Simberloff & Abele 1976; Soulé & Simberloff 1986). Although this debate was never fully resolved (in part because applications of island biogeography theory to reserve design were replaced with theory from the emerging fields of landscape ecology and metapopulation theory), recent models of representative reserve networks (Nekola & White 1999; Rodrigues & Gaston 2001; Cabeza 2003; Wiersma & Nudds 2005) give the opportunity for us to reexamine the debate. Those on both sides of the SLOSS debate acknowledge that several reserves would generally capture more diversity. However, minimum thresholds below which "small" reserves would be considered "too small" have not been articulated.

### Representation and Persistence

Previous targets for representation have been concerned mainly with capturing the full suite of species richness within a region. In only a few cases has the question of whether the protected areas will maintain their biodiversity over time been addressed (e.g., Rodrigues et al. 2000; Reyers et al. 2002; Solomon et al. 2003). Wiersma and Nudds (2005) advocate setting a minimum reserve area (MRA) for long-term species persistence before determining how many replicates of reserves of such a size would be necessary to capture the full suite of diversity within an ecological region. They refer to an MRA estimate empirically derived by Gurd et al. (2001) for disturbance-sensitive mammals in southeastern Canada. Gurd et al. (2001) estimated the minimum size of a reserve should be 5,037 km<sup>2</sup> with lower and upper confidence limits of 2,700 and 13,000 km<sup>2</sup>, respectively. Thus, they hypothesized that a reserve of less than 2,700 km<sup>2</sup> would no longer contain its historical complement of mammals sensitive to human disturbances. Because Gurd et al. (2001) examined species extinctions prior to widespread European settlement, this MRA serves as a reasonable estimate of the minimum area threshold that ensures species persistence. How many reserves of minimum reserve size are needed to fully represent diversity and how far apart they should be within a target ecological region is unknown; thus, aspects of the SLOSS debate remain unresolved. Whether a representative protected-areas network can be most efficiently delineated with several MRA-sized reserves or a

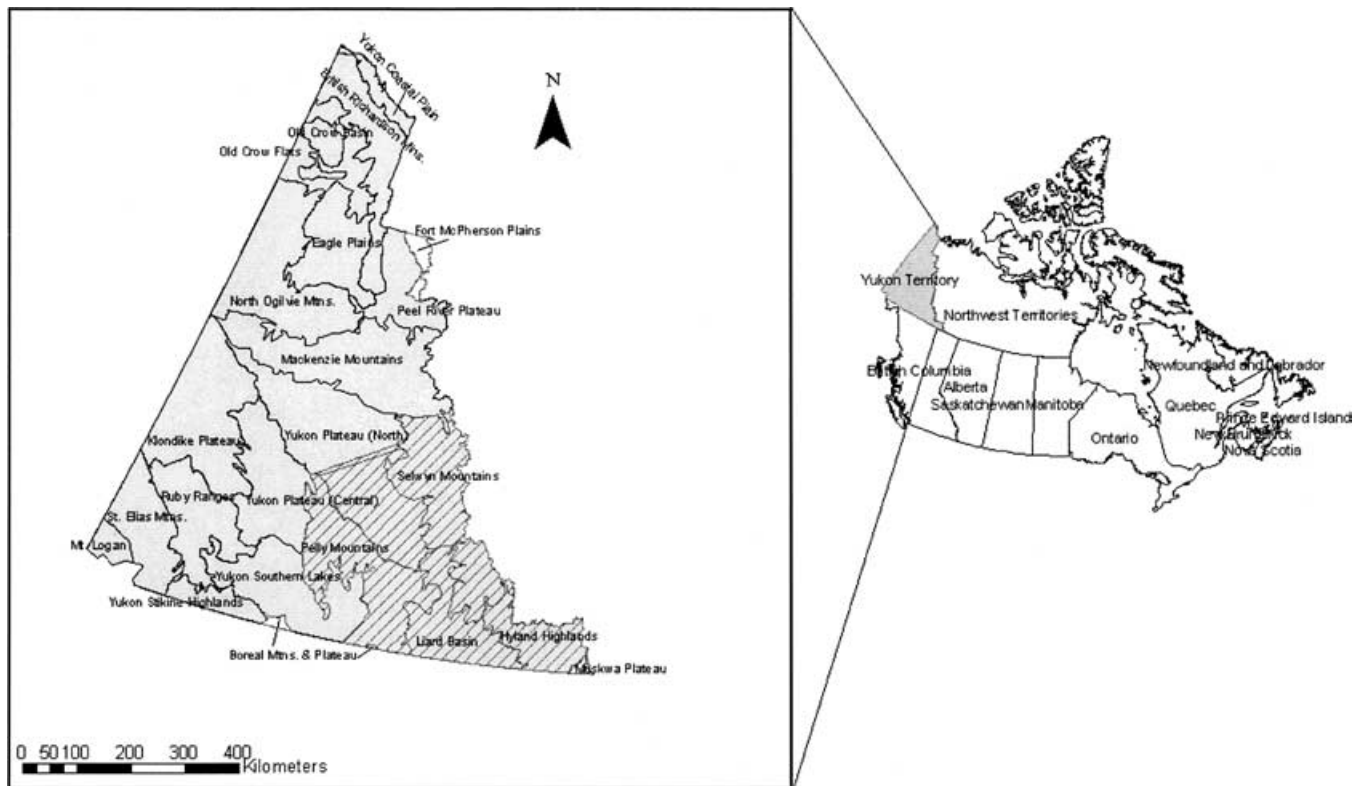


Figure 1. The 23 ecoregions of the Yukon Territory. Four ecoregions were excluded from this study—Mt. Logan, Fort McPherson Plains, Boreal Mountains and Plateau, and Muskwa Plateau—because the majority of their areas lie outside the political boundaries of the territory. The southeast supercoregion is shown with hatched lines.

single reserve larger than the MRA depends on spatial patterns in species turnover.

### Reserve Selection

It is intuitive that the minimum number of replicate sites required to represent all species within a given area depends on the degree of heterogeneity (beta diversity) among sites (Noss 1996; Nekola & White 1999; Condit et al. 2002). Beta diversity may be as important as within-site diversity (alpha diversity) for conservation, but it is argued that diversity patterns are scale dependent and/or site specific (Loreau 2000; Condit et al. 2002; Reyers et al. 2002). We contend that the most common empirical estimate of beta diversity, regional heterogeneity, actually ignores the issue of species turnover central to the original definition of the term. Although some researchers (Noss 1996; Nekola & White 1999; Fairbanks et al. 2001) acknowledge the importance of measuring species turnover along a species gradient in order to address the question of how many reserves are necessary to represent all species, only Fairbanks et al. (2001) measured turnover explicitly and incorporated it into reserve selection algorithms. We predict that the spatial patterns of species distributions

are likely to affect how reserves are replicated and where they should be located more than overall heterogeneity.

We estimated minimum targets for protected-areas networks that would simultaneously achieve representation of all disturbance-sensitive mammal species (Table 1) and increase probability of species persistence within each of the ecoregions of the Yukon Territory. We hypothesized that the number of protected areas needed per ecoregion and the distance between them depend on the degree of turnover in species composition across the ecoregions. We used two measures of beta diversity to compare the utility of the more commonly used metric of regional heterogeneity (Whittaker's beta) with a measure of beta diversity based on between-sample compositional dissimilarity ( $d_{ij}$ ). We predicted that ecoregions with high beta diversity (i.e., Whittaker's beta) across the region would require more reserves than ecoregions with low beta diversity.

The advantage of using compositional dissimilarity (species turnover) is that it explicitly compares two samples or sites; thus, this index can be georeferenced, which may identify whether dissimilarity patterns vary with latitude, elevation, or other biophysical gradients. In particular, we were interested in whether  $d_{ij}$  shows local spatial structure (i.e., autocorrelation) and whether it shows

**Table 1.** Disturbance-sensitive mammals included in the representation analysis for protected-areas networks in the Yukon Territory.\*

Scientific name	Common name
<i>Sorex cinereus</i>	masked shrew
<i>Sorex obscurus</i>	dusky shrew
<i>Sorex palustris</i>	American water shrew
<i>Sorex arcticus</i>	Arctic shrew
<i>Microsorex boylii</i>	pigmy shrew
<i>Ochotona princeps</i>	American pika
<i>Lepus americanus</i>	snowshoe hare
<i>Eutamias minimus</i>	least chipmunk
<i>Marmota caligata</i>	hoary marmot
<i>Spermophilus parryii</i>	Arctic ground squirrel
<i>Tamiasciurus hudsonicus</i>	American red squirrel
<i>Glaucomys sabrinus</i>	northern flying squirrel
<i>Castor canadensis</i>	American beaver
<i>Neotoma cinerea</i>	bushy-tailed wood rat
<i>Clethrionomys rutilus</i>	northern red-backed vole
<i>Lemmus sibiricus</i>	brown lemming
<i>Synaptomys borealis</i>	northern bog lemming
<i>Phenacomys intermedius</i>	heather vole
<i>Ondatra zibethicus</i>	muskrat
<i>Microtus longicaudus</i>	long-tailed vole
<i>Microtus chrotorrhinus</i>	rock vole
<i>Zapus princeps</i>	western jumping mouse
<i>Canis lupus</i>	wolf
<i>Ursus arctos</i>	grizzly bear
<i>Ursus maritimus</i>	polar bear
<i>Martes americana</i>	American marten
<i>Mustela nivalis</i>	least weasel
<i>Gulo gulo</i>	wolverine
<i>Lontra canadensis</i>	river otter
<i>Felis concolor</i>	mountain lion
<i>Lynx lynx</i>	lynx
<i>Rangifer tarandus</i>	caribou
<i>Odocoileus bhemionus</i>	mule deer
<i>Alces alces</i>	moose
<i>Oreamnos americanus</i>	mountain goat
<i>Ovis dalli</i>	Dall's sheep

\*Nomenclature follows that of Banfield (1974).

any spatial trends over the region (i.e., patterns with respect to distance or direction or is correlated with biophysical gradients). We hypothesized that the strength of large-scale trends in compositional dissimilarity dictates the arrangement and spacing of sites in a protected-areas network. We predicted that ecoregions with very low or constant turnover rate, as measured by the Bray-Curtis index ( $d_{ij}$ ), may be able to have all the species in the ecoregion captured within a single protected area. Ecoregions that have a high turnover rate over short distances may be best represented with a single, larger reserve (i.e., several minimum-reserve-sized areas next to each other).

We were interested in examining how patterns of beta diversity relate to the number of protected areas needed. If clear patterns emerge, then knowledge about diversity patterns may help planners in other jurisdictions iden-

tify targets for the minimum number of protected areas needed to capture the full range of diversity.

## Methods

### Study Area and Data Set

We used 19 of the 23 ecoregions (Oswald & Senyk 1977) in the Yukon Territory, Canada (Fig. 1), as replicates to test whether diversity patterns influence the number of protected areas required. The majority of the area of the remaining four ecoregions in the territory is in adjacent jurisdictions (British Columbia, Alaska, Northwest Territories); thus, we did not include them in the study. We chose ecoregions as the smallest target regions for delineating representative protected areas because they align with the territorial government's planning units. An area in the southeast part of the territory is of interest to environmental groups (Canadian Parks and Wilderness Society 2001). Thus, we repeated the analysis for this region by combining the parts of the ecoregions that overlap this area into one "superecoregion" (Fig. 1). Finally, we considered the territory as a whole (Table 2).

We used digital range maps (Banfield 1974) of 36 disturbance-sensitive mammals (defined below) resident in the Yukon (Table 1) as the data source. These range maps represent historical distributions ("extent of occurrence" sensu van Jaarsveld et al. 1998) of mammals before widespread European settlement in North America (Banfield 1974). Because the landscape in the Yukon remains relatively unaltered, however, we believe these maps to be a good approximation of present-day ranges. Glenn and Nudds (1989) originally defined the list of disturbance-sensitive mammals (sensu Humphreys & Kitchener 1982) for Canada based on species' sensitivity to human disturbance. Disturbance-sensitive mammals were chosen because (1) they may act as an "umbrella" for other taxa owing to their wide-ranging habitats and sensitivity to habitat insularization (Schmiegelow & Nudds 1987; Hager & Nudds 2001) and (2) MRA has been estimated for disturbance-sensitive mammals, at least in southern Canada (Gurd et al. 2001). In the absence of any similar empirical estimates for an MRA for northern regions, we assumed this reserve size was appropriate for mammals in the Yukon as well. We did not consider disturbance-tolerant species (defined by Glenn & Nudds 1989) because these are widespread and common and can persist without the benefit of protected areas. We assumed that mammals are a useful umbrella group for overall biodiversity. Thus, delineating a protected-areas network that represents all mammals will capture the full biodiversity of plants and birds. This assumption, however, has not been tested. It may also be possible to use a smaller subset of mammals as an umbrella group for all mammals

**Table 2.** Spatial extent (km<sup>2</sup>), gamma ( $\gamma$ ) diversity (total number of species in the ecoregion), Whittaker's beta ( $\beta = \gamma/\alpha_{\text{mean}}$ ), and the minimum number of representative protected areas to capture all species in at least one protected area for each target ecoregion in the Yukon.

Target ecoregion	Area (km <sup>2</sup> )	$\gamma$ diversity	$\beta$	No. of protected areas
British Richardson Mountains	22,989	26	1.24	2
Eagle Plains	20,394	26	0.81	1
Hyland Highlands <sup>a</sup>	14,660	32	1.10	2
Klondike Plateau	38,206	28	0.88	2
Liard Basin <sup>a</sup>	21,121	33	1.07	2
Mackenzie Mountains	190,238	26	0.77	1
North Olgilvie Mountains	39,203	26	0.82	1
Old Crow Basin	14,589	25	1.11	2
Old Crow Flats	5,964	25	1.08	1
Peel River Plateau	14,812	26	0.83	1
Pelly Mountains <sup>a</sup>	34,194	33	1.08	2
Ruby Ranges	22,720	28	0.89	1
Selwyn Mountains <sup>a</sup>	35,541	32	0.96	2
St. Elias Mountains	17,603	26	0.75	1
Yukon Coastal Plain	4,402	15	1.17	1
Yukon Plateau (central)	26,803	30	0.93	2
Yukon Plateau (north) <sup>a</sup>	57,037	31	0.93	2
Yukon Southern Lakes	29,899	32	1.03	2
Yukon Stikine Highlands	6,972	30	0.93	1
Southeast superecoregion <sup>b</sup>	162,554	35	1.11	3
Yukon Territory <sup>b</sup>	476,560	36	1.20	4

<sup>a</sup>The southeast superecoregion included parts of these ecoregions (see Fig. 1).

<sup>b</sup>The southeast superecoregion and Yukon Territory were not included in the logistic regression analysis.

in the territory (Y. F. Wiersma, unpublished report to the Canadian Parks and Wilderness Society–Yukon Chapter).

### Sampling Candidate Minimum Reserve Areas

We used MRA-sized sample plots to sample the mammal diversity of the territory. We selected a subset of plots with a rarity-based reserve selection algorithm to identify a minimum reserve network that captured all species at least once. Because Wiersma and Nudds (2005) found that the number of plots needed to meet representation requirements did not differ significantly with the variation in MRA size, we restricted our analysis to the lower 95% confidence limit of the best-available estimate for the MRA that would still contain a historical complement of species—even when partly surrounded by human development (Gurd et al. 2001). The lower limit of the MRA estimate (2700 km<sup>2</sup>) allowed us to maximize the number of sample plots within each ecoregion and thus better discriminate potential trends between diversity patterns and minimum number of sites required. Final reserve boundaries may have to encompass an area larger than 2,700 km<sup>2</sup>, however, to ensure the persistence of certain key species (e.g., minimum requirements for viable populations of grizzly bears [scientific names are provided in Table 1] have been estimated to be as high as 13,500 km<sup>2</sup> [Shaffer & Samson 1985]).

We delineated sample plots of 2700 km<sup>2</sup> with the ArcView (v.3.2, Environmental Systems Research Institute, Redlands, California) Samples extension (v 3.03,

Quantitative Decisions, Merion Station, Pennsylvania) and used these plots to sample the range maps for all disturbance-sensitive mammals (Table 1). We sampled the three largest replicate areas (Table 2) with these plots: the Yukon Territory, the southeast superecoregion, and the Yukon Plateau (north) ecoregion. We used square plots to be consistent with Gurd et al.'s (2001) sampling method. We overlaid these sample plots on the mammal range maps in ArcInfo (v. 8.1, Environmental Systems Research Institute, Redlands, California) to identify the mammal composition in these plots. The remaining ecoregions were dealt with in a slightly different manner, as discussed below.

### Reserve Selection

A useful tool in achieving maximum representation with a minimum set of protected areas is complementarity-based algorithms (e.g., Margules et al. 1988; Bedward et al. 1992; Freemark et al. 1999). We used a simple heuristic algorithm based on maximizing presence of rare species to select the minimum set of complementary reserves that represented all species at least once.

To determine minimum requirements for a representative protected-areas network, we selected protected areas from each set of sample MRA plots in the Yukon Territory, the southeast superecoregion, and the Yukon Plateau (north) ecoregion with a rarity-based algorithm (Margules et al. 1988; Pressey et al. 1993). Because the sample plots met MRA requirements (Gurd et al. 2001), the networks obtained were predicted to simultaneously

address representation and persistence goals, the latter of which are not addressed in most representation analyses.

Within the remaining 18 individual ecoregions, we did not use the square MRA-sized plots for sampling because the shape of the ecoregions did not allow for adequate sampling of square plots, even though their areas were sufficient to contain at least one MRA (Table 2). Rather, we identified the location of the most rare species in each ecoregion and mapped a 2700-km<sup>2</sup> plot over it (and allowed it to spill into adjacent ecoregions). Then we examined whether all species in the ecoregion were captured within this plot and, if not, we identified the location of the next most rare species not already captured in a sample plot and repeated the process. This analysis was also applied to the Yukon Territory, the southeast superecoregion, and the Yukon Plateau (north) ecoregion to allow for a comparison of results with those obtained through the use of the sample MRA plots.

### Diversity Measures

Species diversity is generally quantified as alpha, beta, or gamma diversity. A conventional measure of beta diversity (Whittaker 1972) based on sample observations (sites) is computed as the ratio of regional (gamma) diversity and average sample (alpha) diversity,

$$\beta = \gamma / \alpha_{\text{mean}}. \quad (1)$$

An alternative definition of beta diversity is based on the notion of compositional similarity along a gradient, familiar to community ecologists as the basis for indirect ordination and classification. Myriad indexes of similarity (or its complement, dissimilarity) have been devised (summary in Legendre & Legendre 1998). Here, we frame the discussion in terms of the Bray-Curtis (1957) index, recognizing that the appropriate index might depend on the data set. Bray and Curtis (1957) define compositional dissimilarity for presence and absence data as

$$d_{ij} = 1 - 2W / (A + B), \quad (2)$$

where  $W$  is the number of species held in common between two sites  $i$  and  $j$  and  $A$  and  $B$  are the total number of species on each of the two sites, respectively.

To measure diversity, we exported the species range maps as raster grids in ArcInfo. We applied a cell size of 2500 km<sup>2</sup> to all grids to approximate the MRA sample plots. We used the total species richness for each 2500-km<sup>2</sup> cell as the alpha diversity for that location. For each ecoregion we calculated the average alpha diversity by summing all full and partial cells in the region and dividing by the number of cells. We calculated gamma diversity as the total number of species in the ecoregion (Table 2) and calculated beta for each target region as Whittaker's beta (Eq. 1). We also calculated average east-west, south-north, and total Bray-Curtis values within each ecoregion for each of the iterations (adjacent cells, and cells one to three cell widths apart) of the Bray-Curtis analysis.

We measured compositional turnover with the Bray-Curtis index (Eq. 2). A program written in Arc Macro Language (AML) iterated through each grid on a species-by-species basis and calculated dissimilarity between pairs of adjacent cells along a south to north and an east to west gradient. That is, for each cell, the AML calculated the dissimilarity in species composition compared with that cell's neighbor to the north and to the west. Thus, a pair of cells could have identical alpha diversity in terms of species richness, but if the species composition of the cells differed, the AML would report a Bray-Curtis value  $> 0$ . Thus, a higher Bray-Curtis value indicates a higher dissimilarity in species compositions between pairs of cells. To avoid artificial inflation of Bray-Curtis values at the political boundaries of the territory due to spatial edges in the data set, we extended the grid analysis beyond the territorial boundaries to cover the entire Yukon mammal province (Hagmeier 1966) and then only examined Bray-Curtis values within the territory itself.

Finally, we combined the two output raster maps (south to north and east to west) to create a layer representing overall turnover across both latitudinal and longitudinal gradients. The AML was then modified and rerun to perform an identical analysis, but this time with pairs of cells separated by 50–150 km (one to three cell widths). This allowed us to investigate the effect of distance on dissimilarity within ecoregions. Thus, if adjacent cells had high dissimilarity, a single reserve overlapping the two cells (i.e., a 5000-km<sup>2</sup> reserve) would effectively capture the full diversity of mammals. If nonadjacent cells within an ecoregion had high dissimilarity, two separate protected areas would more efficiently capture the full range of mammal diversity than a single large one comprising three (or more) adjacent cells.

## Results

### Reserve Selection

The results for protected areas selection based on the heuristic algorithms for the Yukon Territory, the southeast superecoregion, and Yukon Plateau (north) ecoregion showed that between two and four protected areas were needed in a rarity-based greedy algorithm. The heuristic algorithms in the 18 smaller ecoregions showed that individual ecoregions required either one or two protected areas to capture the full suite of diversity (Table 2). In the Yukon Territory, the southeast superecoregion, and the Yukon Plateau (north), this method yielded the same number of protected areas (and in the same general locations) to meet representation requirements as when the sampling and heuristic algorithms were applied. Because the number of protected areas in each individual ecoregion was not normally distributed, we converted the results for the individual ecoregions to a binary output (0, only one protected area; 1, two protected areas required

**Table 3.** Correlation coefficients for different measures of beta diversity based on measurements across 19 ecoregions in the Yukon Territory.<sup>a</sup>

Distance (km) <sup>b</sup>	$\beta^c$	East-west				North-south				Overall		
		0	50	100	150	0	50	100	150	0	50	100
East-west												
0	0.620**	1										
50	0.496*	0.189	1									
100	0.484*	0.149	0.964***	1								
150	0.045	-0.245	0.404	0.383	1							
North-south												
0	0.768***	0.858***	0.344	0.295	0.096	1						
50	0.806***	0.909***	0.287	0.267	-0.103	0.944***	1					
100	0.775**	0.907***	0.203	0.197	-0.196	0.903***	0.988***	1				
150	0.666**	0.849***	0.103	0.098	-0.321	0.849***	0.907***	0.918***	1			
Overall												
0	0.679**	0.938***	0.266	0.210	-0.074	0.933***	0.930***	0.903***	0.828***	1		
50	0.608**	0.114	0.923***	0.906***	0.493*	0.366	0.330	0.261	0.102	0.252	1	
100	0.588**	0.079	0.872***	0.893***	0.482*	0.375	0.332	0.273	0.141	0.243	0.979***	1
150	0.419	-0.051	0.690**	0.698***	0.604**	0.296	0.234	0.198	0.045	0.115	0.859***	0.899***

<sup>a</sup> $p < 0.05$ ; <sup>\*\*</sup> $p < 0.01$ ; <sup>\*\*\*</sup> $p < 0.001$ .

<sup>b</sup>Average Bray-Curtis turnover values within each ecoregion are reported along an east-west and a south-north gradient for cells adjacent (0 km) and 50, 100, and 150 km apart. Overall Bray-Curtis values are calculated as the overall east-west and north-south turnover combined.

<sup>c</sup>Whittaker's beta ( $\beta$ ) is measured as the ratio of regional ( $\gamma$ ) to average alpha ( $\alpha$ ) diversity within each ecoregion.

to capture the full diversity of mammals in the ecoregion) in order to apply logistic regression analysis. The log-transformed area of the ecoregion was not a significant explanatory variable (chi-square analysis of deviance,  $p = 0.256$ ) for the number of protected areas needed to achieve representation, so the number of reserves is not simply a function of ecoregion area.

### Diversity Measures

The two measures of beta diversity, Whittaker's beta and turnover along geographic gradients, were significantly correlated among ecoregions (Table 3). A map of overall turnover shows "ecotones" of high Bray-Curtis values generally running along a southeast to northwest gradient (Fig. 2).

When logistic regression was applied to the number of protected areas needed to fully represent mammals in each ecoregion, Whittaker's beta was a reasonable predictor (chi-square analysis of deviance,  $p = 0.022$ ). The average Bray-Curtis values for adjacent cells yielded results that were not significantly different from random (east-west,  $p = 0.55$ ; south-north,  $p = 0.79$ ; overall,  $p = 0.76$ ). The average Bray-Curtis values for nonadjacent cells were a significant predictor of the number of protected areas when overall dissimilarity was measured for cells separated by 50 km ( $p = 0.052$ ), 100 km ( $p = 0.035$ ), and 150 km ( $p = 0.031$ ). Ecoregions requiring more than one representative MRA overlapped with areas where there were relatively high dissimilarity (high turnover) values (Fig. 2). On average, one protected area captured approximately 90% of the total richness of disturbance-sensitive mammals in the regions in which reserve selection was applied.

### Discussion

It is not known specifically what environmental or habitat gradients may underlie the observed pattern of



**Figure 2.** Overall species composition turnover for adjacent cells in 2500-km<sup>2</sup> cells in and around the Yukon Territory. Dark areas indicate areas with high Bray-Curtis values (high dissimilarity). For comparison between dissimilarity values and the number of protected areas needed to achieve full representation of all species in each ecoregion, the ecoregions that require more than one protected area to achieve full representation of species have a diagonal-line fill.

Bray-Curtis turnover values along the southeast to north-west gradient (Fig. 2); the pattern, however, mimics well-known climatic and vegetation patterns for this part of the country (such as the tree line).

Our results for the Yukon suggest that beta diversity is an important driver for determining the number of protected areas required to achieve biodiversity representation. Both Whittaker's beta and the Bray-Curtis values for nonadjacent pairs of cells were significant predictors of the number of protected areas needed within individual ecoregions. The high correlation between Whittaker's beta and the Bray-Curtis values (Table 3) and the similar magnitude of the  $p$  values suggests that the more straightforward Whittaker's beta (Eq. 1) may be a sufficient metric for estimating the number of protected areas needed to achieve representation within an ecologically bounded region, at least for a single-taxon study conducted at a coarse scale. A disadvantage of using Whittaker's beta is that important inferences about reserve location and spacing cannot be made (see discussion on estimating inter-reserve distance below). Nonetheless, the importance of beta diversity for determining conservation requirements shown for the Yukon is consistent with predictions from the literature on tropical (Pitman et al. 2001; Condit et al. 2002) and savannah (Reyers et al. 2002) biodiversity.

Although the Yukon government has articulated protected-area planning for individual ecoregions, an examination of the patterns of turnover independent of ecoregion boundaries may assist in determining how to best replicate protected areas between ecoregions and add to the SLOSS debate. If the assumption is that areas with high turnover should be the priority areas for efficient biodiversity representation, then several patterns for the Yukon emerge (Fig. 2a). In the southeast are areas of high turnover spaced close together. Thus, in this part of the territory it may be more efficient to create one very large reserve (i.e., larger than 2500 km<sup>2</sup>) that captures all these high turnover areas. Conversely, the southwestern part of the territory has areas of high turnover that are spaced farther apart. Here it may be more appropriate to replicate several smaller (but still the size of the MRA) reserves to capture the full diversity.

Finally, the north, where there are large areas with little or no change in composition, might require only a single minimum-reserve-sized reserve to capture the full diversity of species. The extreme far north of the territory has high turnover values, much of which is due to the presence of marine mammals that spend part of their time on land, such as polar bears. Turnover in species composition due to an interface between dramatically different ecosystem types (land and water) might require different conservation strategies such as the inclusion of marine protected areas or protection of key coastal areas.

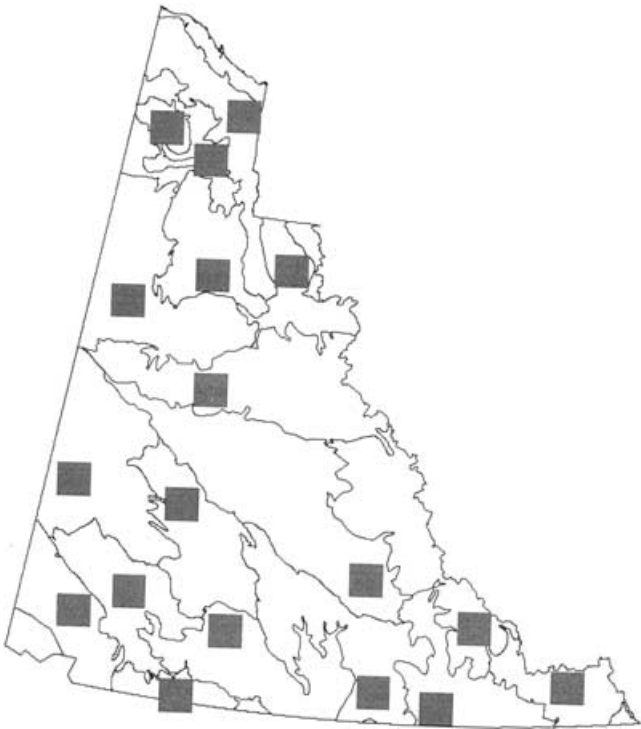
An examination of the composition of the protected areas selected here showed that the majority of the species were captured more than once between ecore-

gions. Thus, for mammals at least, defining protected-area targets in the context of ecoregions (that are themselves defined based on vegetation and topography) appears to lead to redundancy, which has obvious conservation benefits. Using mammals to delineate protected areas, however, may not be an efficient way to delineate an optimum protected-areas network for other taxa. In real-world planning, more complex tools such as C-Plan (Pressey et al. 1995) or SITES (Andelman et al. 1999) will be useful to identify specific locations for protected areas and may allow for the incorporation of data on other taxa and features of interest.

Using dissimilarity measures helps illustrate spatial gradients along which reserves could be aligned to maximize representation of species diversity. In the Yukon there appears to be more turnover along a south-north gradient than along an east-west gradient. Thus, it may be more important to align reserves south to north to meet representation goals efficiently.

A further advantage to measuring beta diversity as spatial turnover is that it allows for inferences about inter-reserve distance. We tested dissimilarity in species composition only at separation distances of up to 150 km. At this distance, average dissimilarity was 9.8% along the south-north gradient (min: 2.8%, max: 33.6%), 7.2% along the east-west gradient (min: 2.7%, max: 14.7%), and 14.9% overall (min: 8.7%, max: 28.8%). These dissimilarity values may help guide decision makers about spacing of protected areas along south-north gradients, particularly in the face of global climate change. If vegetation patterns expand northward, as is predicted under scenarios of global climate change (Scott et al. 2002), then protected areas should be spaced so as to provide refuges for species as their ranges shift (Halpin 1997; Hannah et al. 2002). Although it is not known exactly how vegetation patterns will change in response to climate change (Scott et al. 2002), some similarity in species composition may accommodate any lags in species' responses to changing vegetation patterns.

Along the north-south axis, the average length of the ecoregions in the Yukon is approximately 165 km (min: 40 km; max: 280 km). Thus, with a real policy constraint of one protected area per ecoregion, it is theoretically possible to develop a protected-areas network following a strategy of spacing protected areas in each ecoregion 150 km apart in a north-south direction. Such a hypothetical protected-areas network could capture all the mammals in the territory at least once but not in every ecoregion in which they are present (Fig. 3). Moreover, constraining the inter-reserve distance along a north-south axis means a large part of the territory (the east-central region in Fig. 3) may not be adequately represented under future climate-change scenarios and may currently contain non-mammalian features that are not captured in protected areas elsewhere. It may be more appropriate to reexamine the policy constraint, however, and articulate conservation targets within larger spatial extents.



*Figure 3. A hypothetical protected-areas network (gray squares) for the Yukon Territory constructed under the political constraint of allowing only one protected area per ecoregion. Protected areas are further constrained to meet the lower 95% CI for minimum reserve area requirement (2700 km<sup>2</sup>; Gurd et al. 2001) and are spaced no more than 150 km (edge-to-edge) apart in a north-south direction (predicted to have an average 9.8% dissimilarity [min: 2.8%; max: 33.6%] in species composition). This network captures all the mammals in the territory at least once, although not necessarily in each ecoregion in which they are present. A large area in the east-central part of the territory is without a protected area under these constraints.*

An effective protected-areas network will simultaneously meet goals for both ecological representation and persistence (Rodrigues et al. 2000; Reyers et al. 2002; Solomon et al. 2003). Gurd et al.'s (2001) MRA estimate, however, did not take into account long-term population dynamics; it is implied that above the MRA, dynamics internal to the reserve are sufficient to maintain species even in the face of habitat isolation. Spatial population dynamics will also influence inter-reserve distance requirements for species persistence (Shafer 2001). In terms of metapopulation dynamics, the inter-reserve distances we used in our analysis of spatial turnover may be far too large for some species (e.g., rodents) and too small for others (e.g., caribou). Inter-reserve distances that contribute to species persistence have to be taken into account in the process of delineating boundaries of protected areas.

Overall, it appears that the government target of establishing one protected area per ecoregion in the Yukon will be sufficient to protect the full range of mammal species diversity in only 47% of the ecoregions (Table 2). Our results suggest generally where protected areas in the Yukon should be located to maximize representation of disturbance-sensitive mammals. When implementing protected-areas design, the actual boundaries of protected areas should follow ecological boundaries such as watersheds (Noss et al. 1999) or use approaches such as The Nature Conservancy's site-based planning process (Poiani et al. 1998).

The literature on reserve selection and the design of protected-areas networks is voluminous (e.g., Possingham et al. 2000; Pressey & Cowling 2001), yet general prescriptions for how to meet conservation targets do not exist. We designed a protected-areas network to maximize representation and probability of persistence of species and ecosystems simultaneously. This coarse-filter analysis for mammals in the Yukon suggests two basic guidelines. First, replicating protected areas often appears to be necessary, even when the focus is on a single taxonomic group within an ecologically bounded target area. Second, how many replicates of protected areas are necessary within the target ecological region and how they should be arranged on the landscape appear to be related to the degree of heterogeneity in species richness (turnover/beta diversity) across it. This last finding is particularly interesting given the low overall (gamma) diversity at northern latitudes. Thus, our study combines principles from island biogeography (minimum reserve size calculations) and landscape ecology (spatial patterns in species diversity) to suggest new combinations of existing techniques for reserve design. Because our results yielded a representative protected-areas network for the Yukon (at least for mammals), the guidelines and techniques we used may assist landscape planners at other locations in designing protected-areas networks that efficiently meet ecological criteria.

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