Beta diversity and nature reserve system design: a case study from the Yukon, Canada

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Abstract

Protected areas design 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 also with limitations. The so-called "SLOSS" (single large or several small reserves) debate hinged on applications of island biogeography theory to protected areas, but was only resolved to the point of agreeing that there might be different approaches in different situations. While proponents on both sides of the SLOSS debate generally agreed that replication of protected areas was desirable, it proved difficult to determine how to replicate reserves in terms of number and spatial arrangement. More importantly, many targets for representation often do not address issues of species persistence. Here, we use a case study for disturbance-sensitive mammals of the Yukon Territory, Canada, to design a protected areas network using Geographic Information Systems (GIS) that achieves representation goals for component ecoregions with reserves that are predicted to be large enough to maintain their historical assemblage of species. We simultaneously measure patterns of diversity, and show how measures of beta diversity (or species turnover) can given further insights to questions about reserve location and spatial arrangement. Two commonly used methods of measuring beta diversity, regional heterogeneity and compositional turnover between non-adjacent sites, were significant predictors of the number of protected areas necessary to represent mammals within each ecoregion.

Introduction

Agencies responsible for delineating and managing protected areas (nature reserves) are often faced with challenges of limited funds and finite space to set aside for conservation. As well, planners may face political limitations and socio-economic conflicts with stakeholder groups and other landowners. To optimize both ecological and socio-economic 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, while minimizing costs. Protected areas can take on many different forms and accommodate a range of uses, however, for the purposes of this study, we use the term "protected area" generally, to refer to an area that is designated so as to maximize biodiversity protection.

The Yukon case study: ecosystem representation

As part of a regional protected areas strategy, the government of the Yukon Territory, Canada initially set out a policy goal to establish one protected area to represent the biodiversity of each of the territory's ecoregions (Yukon Protected Areas Strategy 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 has been elected which has put a halt to the protected areas planning process. Nonetheless, the analysis carried out here presents a useful case study for determining minimum requirements generally for

protected areas within ecosystems, as 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 (such as dispersal, adaptation to habitats, etc.) that gave rise to and maintain local biodiversity will remain intact (Noss 1992). Any ecologically defined region will never be completely homogeneous, and thus, to capture the diversity of organisms within the region, protected areas will likely have to be replicated across the landscape (Noss 1996; Nekola & White 1999; Fairbanks et al. 2001). Such redundancy of protected areas has the additional benefit of acting as an insurance against stochastic events that may jeopardize species' persistence, while also possibly capturing greater genetic diversity for those species that occur in more than protected area (Lucas 1984). In addition, redundancy can potentially buffer against uncertainty due to data limitations.

Articulating conservation targets in terms of the need to replicate reserves to ensure representation evokes the SLOSS ("single large or several small") debate about reserve design (Diamond 1975; Simberloff & Abele 1976; Soulé & Simberloff 1986). While 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 in press) allow us to re-examine the debate. Both

sides of the SLOSS debate acknowledged that several reserves would generally capture more diversity. However, the debate did not articulate minimum thresholds below which "small" reserves would be considered "too small".

Representation and persistence

Previous targets for representation have been mainly concerned 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 (see for examples Rodrigues et al. 2000; Reyers et al. 2002; Cabeza & Moilanen 2003; Solomon et al. 2003; Wiersma & Nudds in press). In another Canadian case study, Wiersma & Nudds (in press) advocated setting a minimum reserve area for long-term species persistence a priori, 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 used an estimate of minimum reserve area (MRA) empirically derived by Gurd et al. (2001) for disturbance-sensitive mammals in southeastern Canada. Gurd et al. (2001) estimated a minimum size of 5037 km^2, with lower and upper confidence limits of 2700 and 13,000 km^2, respectively. Thus, Gurd et al. (2001) hypothesized that a reserve between 2700-13,000 km^2 was the minimum area below which parks would no longer contain their historical complement of mammals sensitive to human disturbances (but not necessarily viable populations), and this MRA is believed to be a reasonable threshold for estimating a minimum size to ensure species persistence. Wiersma & Nudds (in press) subsequently used sample plots of the MRA size (5037 km^2) and plots that met the

lower (2700 km^2) and upper (13,000 km^2) 95% confidence limits of the MRA requirements, together with heuristic reserve selection algorithms and found that the number of reserves needed to capture the full suite of mammalian diversity in southeastern Canada did not differ significantly between the size of the sample plot. Thus, they concluded that replicates of smaller reserves, which nevertheless met minimum size requirements, more efficiently captured the representative diversity of mammals than a single, larger reserve. However, even with the caveat added that these several reserves can be no smaller than an MRA in order to maximize the chance of species persistence, how many such reserves are needed to fully represent diversity and how far apart they should be within a target ecological region is unknown, and thus aspects of the SLOSS debate remain unresolved.

Reserve selection

It is intuitive that the minimum number of replicate sites required to represent all species within a given area should depend on the degree of heterogeneity (beta diversity) between sites (Noss 1996; Nekola & White 1999; Condit et al. 2002). Recent studies have examined beta diversity, and suggested that it may be as important as within-site diversity (alpha diversity) for conservation (Loreau 2000; Condit et al. 2002; Reyers et al. 2002). However, these studies have argued that diversity patterns are scale-dependent and/or site-specific. In addition, there is lingering confusion that stems in part from the definitions of diversity (e.g., Whittaker et al. 2001). 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. While some studies (Noss 1996; Nekola & White 1999; Fairbanks et al. 2001) have acknowledged 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 one of these (Fairbanks et al. 2001) measured turnover explicitly and incorporated it into reserve selection algorithms. We predict that the spatial patterns of species distributions will likely affect how reserves are replicated and where they should be located, more so than overall heterogeneity.

Here, 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 persistence with reserves, 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, depended on the degree of turnover in species composition across the ecoregions. We used two measures of beta diversity, which allowed us to compare the utility of the more commonly used metric of regional heterogeneity to a measure of beta diversity based on between-sample compositional dissimilarity.

Diversity measures

Species diversity is generally quantified as alpha (α), beta (β), or gamma (γ) diversity. Alpha diversity is defined as species richness in a specific sampling area (Whittaker 1970), while beta diversity is "the degree of change in species composition of communities along a gradient" (Whittaker 1970:39). Gamma diversity

is generally accepted to be the 'landscape-level' or 'regional' diversity. Some authors define landscape and regional diversity separately based on geographic extent (see Whittaker et al. 2001 for a complete discussion). Here, by gamma diversity we mean the total species richness of the target ecoregion for identifying representative protected areas.

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:

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

where γ is the regional diversity and α_{mean} is the average alpha diversity in sample sites. High values of β indicate regions with a high degree of heterogeneity, and sampling theory would predict that these would require a higher number of sites to achieve full representation in a protected areas network.

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 indices of similarity (or its complement, dissimilarity) have been devised (see 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 & Curtis (1957) defined compositional dissimilarity for presence/absence data as:

$$d_{ij} = 1 - 2W/(A + B) \qquad \qquad \text{(Eq. 2)}$$

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.

Clearly, the average between-site dissimilarity must be related to the ratio of gamma to alpha diversity. In particular, if species-area relationships hold, then as sample (site) size decreases, alpha-diversity decreases, beta diversity increases, and between-sample compositional dissimilarity increases. Thus, we should be able to express relationships between regional and local (gamma and alpha) diversity, on average, equivalently in terms of β or compositional dissimilarity.

The advantage of using dissimilarity (compositional turnover) as a basis for this discussion is that it explicitly compares two samples or sites; thus this index can be georeferenced, which may identify whether dissimilarity patterns vary with latitude, altitude, or other biophysical gradients. In particular, we were interested in whether d_{ij} shows local spatial structure (i.e., autocorrelation), and whether it shows any spatial trends over the region (i.e., patterns with respect to distance, direction or correlated with biophysical gradients). We hypothesized:

1. The intensity and scale of spatial autocorrelation in compositional dissimilarity should dictate the number of replicates of MRA-sized reserves needed per ecoregion to capture the full diversity of mammal species in the Yukon. We predicted that ecoregions with high beta diversity (i.e., Whittaker's beta) across the region would require more reserves than an ecoregion with low beta diversity.

2. The strength of large-scale trends in compositional dissimilarity due to latitudinal, longitudinal, and/or other gradients should dictate the arrangement and spacing of sites in a protected areas network. Thus, we hoped to relate, specifically, how protected areas of a specified MRA are

to be spatially allocated for a given amount of species turnover across an ecoregion. A map of Bray-Curtis values will illustrate the degree of dissimilarity (turnover) within ecoregions. Thus, ecoregions with very low, or constant turnover rate, as measured by the Bray-Curtis index, may be able to have all the species in the ecoregion captured with a single protected area. Ecoregions that have a high turnover rate, but over short distances, may be best represented with a single, larger reserve (i.e., several MRA-sized areas next to each other). Conversely, if there is a high turnover rate over longer distances, then replication of MRA-sized reserves spaced an appropriate distance apart within an ecoregion might most efficiently capture the full diversity of mammals.

In this study, we are ultimately interested in examining how beta-diversity patterns relate to the number of protected areas needed. If clear patterns emerge, then knowledge about diversity patterns may help planners in other jurisdictions identify targets for the minimum number of protected areas needed to capture the full range of diversity. However, reserve selection algorithms may still be necessary to determine the location of protected areas on the landscape. In the face of conflicts with other land uses, more complex tools such as SITES (Andelman et al. 1999) or C-Plan (Pressey et al. 1995) may be useful to optimize goals among various stakeholders in the delineation of protected areas boundaries.

Methods

Study area and data set

Nineteen of the 23 ecoregions (Oswald & Senyk 1977) in the Yukon

Territory, Canada (Fig.1) were used as replicates to test whether diversity patterns

influenced the number of protected areas required. The majorities of the areas of the

remaining four ecoregions in the territory are in adjacent jurisdictions (British

Columbia, Alaska, Northwest Territories) and were not considered further.

Ecoregions were chosen 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), and thus the analysis was repeated

for this region by combining the five ecoregions that overlap this area into one 'super-

ecoregion' (Fig. 1). Finally, the territory was considered as a whole (Table 2).

Terrestrial mammals were chosen as the target group to test the hypothesis

that the number of protected areas needed to achieve representation is related to

patterns of diversity. Digital range maps (Banfield 1974) of 36 disturbance-sensitive

mammals (defined below) resident in the Yukon (Table 1) were used as the data

source. These range maps represent historical distributions ("extent of occurrence"

sensu van Jaarsveld et al. 1998) of mammals prior to widespread European settlement

in North America (Banfield 1974); however, since the landscape in the Yukon

remains relatively unaltered, we believe these maps are a good approximation of

present-day ranges. Glenn & Nudds (1989) originally defined the list of disturbance-

sensitive mammals (sensu Humphreys & Kitchner 1982) for Canada based on

species' sensitivity to human disturbance. Disturbance-sensitive mammals were

chosen since: (1) they may act as an 'umbrella' for other taxa due to their wide-

ranging habitats and sensitivity to habitat insularization (Schmiegelow & Nudds 1987; Hager & Nudds 2001) and (2) minimum reserve area (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 a MRA for mammals, we assumed this reserve size was appropriate for mammals in the Yukon as well. We used mammal ranges from the Yukon mammal province (Hagmeier 1966) – which extends beyond the political boundaries of the territory – to enable the measurement of spatial turnover at the political boundaries of the territory. We did not consider 'disturbance-tolerant' species (defined by Glenn & Nudds 1998), since these are widespread, common, and often so-called 'tramp' species that can persist without the benefit of protected areas. We assume that mammals are a useful 'umbrella' group for overall biodiversity, and thus delineating a protected areas network that represents all mammals will capture the full biodiversity of plants and birds. However, this has not been tested. It may also be possible to use a smaller subset of mammals as an 'umbrella group' for all mammals in the territory (Y. Wiersma, unpublished report to the Canadian Parks and Wilderness Society – Yukon Chapter).

Sampling candidate MRAs

We sampled the mammal diversity of the territory using MRA-sized sample plots, from which we selected a subset of plots using a rarity-based reserve selection algorithm to identify a minimum reserve network that captured all species at least once. Because Wiersma & Nudds (in press) 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 minimum reserve area (MRA) that would still contain a historic complement of species − even when partly surrounded by human development (Gurd et al. 2001). The lower limit of the MRA estimate (2700 km^2) 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. However, we acknowledge that final reserve boundaries may have to encompass an area larger than 2700 km^2 to ensure the persistence of certain key species (for example, minimum requirements for viable populations of grizzly bears (Ursus arctos) have been estimated to be as high as 13,500 km^2 (Shaffer & Samson 1985)).

Sample plots of 2700 km^2 were delineated in ArcView^{TM} (v.3.2, ESRI, Redlands, CA) using the Samples extension (v 3.03, Quantitative Decisions, Merion Station, PA) and used to sample the range maps for all disturbance-sensitive mammals (Table 1). The three largest replicate areas (Table 2) were sampled with these plots: the Yukon Territory, the southeast super-ecoregion, and the Yukon Plateau (North) ecoregion. Square plots were used to be consistent with Gurd et al.'s (2001) sampling method. These sample plots were overlaid on the mammal range maps in ArcInfo^{TM} (v. 8.1, Environmental Systems Research Institute, Redlands, CA.) to identify the mammal composition in these plots.

Reserve selection

A useful tool in achieving maximum representation with a minimum set of protected areas is the use of complementarity-based algorithms (e.g., Margules et al. 1988; Pressey & Nicholls 1989; Bedward et al. 1992; Pressey et al. 1996; Freemark et al. 1999). Several software programs exist to automate reserve selection, these include C-Plan (Pressey et al. 1995), SITES (Andelman et al. 1999), and PORTFOLIO (Urban 2001). However, for this analysis, we have chosen to use a simple heuristic algorithm based on maximizing presence of rare species.

We selected protected areas from each set of sample MRA plots in the Yukon territory, the southeast 'super-ecoregion' and the Yukon Plateau (North) ecoregion to determine minimum requirements for a representative protected areas network using 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 are predicted to simultaneously address representation and persistence goals, the latter of which is 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 (non-square) MRA (Table 2). Rather, we identified the location of the most rare species in each ecoregion, and mapped a 2700 km^2 plot over it (and allowed for 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 and repeated the process. This analysis was also applied to the Yukon Territory, the southeast super-ecoregion, and the Yukon Plateau (North)

ecoregion to compare results with those obtained through the use of the sample MRA plots.

Diversity measures

To measure diversity, the species range maps were exported as raster grids in ArcInfo. A cell size of 2500 km^2 was applied to all grids to approximate the MRA sample plots. The total species richness for each 2500 km^2 cell was taken 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. Gamma diversity was calculated as the total number of species in the ecoregion (Table 2), and beta was calculated for each target region as Whittaker's beta (equation 1). As well, we calculated average east west, south north, and total Bray-Curtis values within each ecoregion for each of the iterations (adjacent cells, and cells 1-3 cell widths apart) of the Bray-Curtis analysis, which is described in more detail below.

We measured compositional turnover using the Bray-Curtis index (equation 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 along an east to west gradient. That is, for each cell, the AML calculated the dissimilarity in species composition compared to that cell's neighbour 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. Finally, the two output raster maps (south to north, and east to west) were combined to create a layer representing overall turnover across both latitudinal and longitudinal gradients. The AML was then modified and re-run to perform an identical analysis, but this time with pairs of cells separated by a distance of 50-150 km (1-3 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^2 reserve) would effectively capture the full diversity of mammals. If non-adjacent 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 comprised of three (or more) adjacent cells.

Results

Reserve selection

The results for protected areas selection using the heuristic algorithms for the Yukon Territory, the southeast super-ecoregion, and Yukon Plateau (North) ecoregion suggest that between 2-4 protected areas were needed using a rarity-based greedy algorithm (Fig. 2).

The analysis in the 18 smaller ecoregions showed that individual ecoregions required either 1 or 2 protected areas to capture the full suite of diversity (Table 2). In the Yukon Territory, the southeast super-ecoregion, 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. Since the number of protected areas in each individual

ecoregion was not normally distributed, the results for the individual ecoregions were

converted to a binary output (0 = only one protected area; 1 = two protected areas

required 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, confirming that the

number of reserves is not simply a function of ecoregion area.

Diversity measures

The two measures of beta diversity, Whittaker's beta (β) 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. 3a).

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), while using 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 non-adjacent cells was a significant predictor for 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). Patterns

of dissimilarity within ecoregions and the effect on the number of protected areas

needed is illustrated in Fig. 3b, which shows that ecoregions requiring more than one representative MRA overlap with areas where there is a wide range in dissimilarity (high turnover) values.

Overall, it appears that the government target of establishing one protected area per ecoregion in the Yukon will only be sufficient to protect the full range of mammal species diversity in 47% of the ecoregions (Table 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. Given the real policy constraint of one protected area in each ecoregion, the most efficient alignment of protected areas across the territory might be to space reserves 150 km apart on south-north gradient. Such a hypothetical reserve network (Fig. 4) could capture all the mammals in the Yukon at least once, although not in all the ecoregions in which they are present.

Discussion

It is not known specifically what environmental and/or habitat gradients may be underlying the observed pattern of Bray-Curtis turnover values along the southeast to northwest gradient (Fig. 3a); however, the pattern mimics well-known climatic and vegetation patterns for this part of the country (such as the tree line).

The results of this case study 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 non-adjacent 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 (equation 1) may be a sufficient metric for estimating the number of protected areas needed to achieve representation within an ecologically bounded region. Further analyses of the type presented here might yield an equation that explicitly relates Whittaker's beta to the number of protected areas needed. If such a relationship were robust, then planners would only need to know average alpha and regional gamma diversity to estimate the number of protected areas needed to capture the full range of species diversity within the region. However, 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 about tropical (Pitman et al. 2001; Condit et al. 2002) and savannah (Reyers et al. 2002) biodiversity.

While the Yukon government has articulated protected areas 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 suggest some new insights 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. 3a). In the southeast, there are areas of high turnover spaced close together, and thus in this part of the territory it may be more efficient to create one very large reserve (i.e.,

larger than 2500 km^2) that captures all of 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 MRA-sized) reserves to capture the full diversity. Finally, in the north, where there are large areas with little or no change in composition, might only require a single MRA-sized reserve to capture the full diversity of species.

An examination of the composition of the protected areas selected here, shows that the majority of the species are captured more than once between ecoregions. Thus, for mammals at least, defining protected areas targets in the context of ecoregions (that are themselves defined based on vegetation and topography) appears to be inappropriate. A better policy for mammal conservation might be to plan protected areas in the wider territorial context. Better yet might be a protected areas strategy targeted at the extent of the entire Yukon mammal province (Hagmeier 1966), thus avoiding truncating ecological regions at political boundaries. However, diversity patterns may only provide guidelines for target numbers of protected areas within ecologically defined regions. In real world planning, reserve selection algorithms, such as the one used here, or more complex tools such as C-Plan (Pressey et al. 1995) or SITES (Andelman et al. 1999) will be useful tools to identify specific locations for protected areas, and may allow for the incorporation of data on other taxa and features of interest.

The use of dissimilarity measures can help 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 is 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

to be made. We only tested dissimilarity in species composition 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 global climate change

scenarios (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 ~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. 4).

Moreover, constraining the inter-reserve distance along a north south axis means that

a large part of the territory (the east central region in Fig. 4) 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. However, it may be more appropriate to re-examine the policy constraint and articulate conservation targets within larger spatial extents, as discussed above.

An effective protected areas network will simultaneously meet goals for both ecological representation and persistence (Rodrigues et al. 2000; Reyers et al. 2002; Cabeza & Moilanen 2003; Solomon 2003; Wiersma & Nudds in press). This study has used a minimum reserve area (MRA) estimate from southeastern Canada (Gurd et al. 2001) as a surrogate for meeting persistence criteria. However, Gurd et al. (2001) stressed that their MRA estimates were no guarantee of long-term species persistence. Their estimate of the MRA found the threshold below which parks no longer contained their historical complement of disturbance-sensitive mammals. Thus, their analysis 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, Rangifer tarandus). Inter-reserve distances that contribute to species persistence will have to be taken into account in the process of delineating boundaries of protected areas.

These 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 sites-based planning process (Poiani 1998).

The literature on reserve selection and the design of protected areas networks is voluminous (e.g., Possingham 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, replication of 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 appears 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, this study combines principles from island biogeography and landscape ecology to suggest new combinations of existing techniques for reserve design. Since this study yields an optimal protected areas network for the Yukon (at least for mammals), the guidelines and techniques used here may assist landscape planners at other locations to design protected areas networks that efficiently meet ecological criteria.

Acknowledgements

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Table 1. List of disturbance-sensitive mammals included in the analysis.

Nomenclature follows that found in Banfield (1974).

Scientific name	Common Name
Sorex cinereus	Masked shrew
Sorex obscurus	Dusky shrew
Sorex palustris	American water shrew
Sorex arcticus	Arctic shrew
Microsorex hoyi	Pigmy shrew
Ochotona princeps	American pika
Lepus americanus	Snowshoe hare
Eutamias minimus	Least chipmunk
Marmota caligata	Hoary marmot
Spermophilus parryii	Arctic ground squirrel
Tamiasciurus hudsonicus	American red squirrel
Glaucomys sabrinus	Northern flying squirrel
Castor canadensis	American beaver
Neotoma cinerea	Bushy-tailed wood rat
Clethrionomys rutilus	Northern red-backed vole
Lemmus sibiricus	Brown lemming
Synaptomys borealis	Northern bog lemming
Phenacomys intermedius	Heather vole
Ondatra zibethicus	Muskrat

Microtus longicaudus	Long-tailed vole
Microtus chrotorrhinus	Rock vole
Zapus princeps	Western jumping mouse
Canis lupus	Wolf
Ursus arctos	Grizzly bear
Ursus maritimus	Polar bear
Martes americana	American marten
Mustela nivalis	Least weasel
Gulo gulo	Wolverine
Lontra canadensis	River Otter
Felis concolor	Mountain lion
Lynx lynx	Lynx
Rangifer tarandus	Caribou
Odocoileus hemionus	Mule deer
Alces alces	Moose
Oreamnos americanus	Mountain goat
Ovis dalli	Dall's sheep

Table 2. Spatial extent (km^2), gamma (γ) diversity (total number of species in the ecoregion), Whittaker's beta ($\beta = \gamma/\alpha_{mean}$) 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. Ecoregions listed in italics were combined to create the southeast super-ecoregion. The Yukon Territory included all ecoregions as well as four smaller ones which were not analyzed separately (see Fig. 1). The southeast super-ecoregion and Yukon Territory were not included in the logistic regression analysis.

Target ecoregion	Area (km^2)	γ diversity	β	Number of protected areas
British Richardson Mountains	22,989	26	1.24	2
Eagle Plains	20,394	26	0.81	1
Hyland Highlands	14,660	32	1.10	2
Klondike Plateau	38,206	28	0.88	2
Liard Basin	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	34,194	33	1.08	2
Ruby Ranges	22,720	28	0.89	1

Selwyn Mountains	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)	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 super-ecoregion	162,554	35	1.11	3
Yukon Territory	476,560	36	1.20	4

Table 3. Correlation coefficients for different measures of beta diversity based on measurements across nineteen ecoregions in the Yukon Territory. Whittaker's beta (β) is measured as the ratio of regional (γ) to average alpha (α) diversity within each ecoregion. The average Bray-Curtis turnover values within each ecoregion are reported along an east-west, and a north-south 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. Italics: $p < 0.05$; underlined: $p < 0.01$; underlined italics: $p < 0.001$, bold: $p < 0.0001$.

		β	East-west				North-south				Overall		
			0	50	100	150	0	50	100	150	0	50	100
East west	0	.620	1										
	50	.496	.189	1									
	100	.484	.149	.964	1								
	150	.045	-.245	.404	.383	1							
North-south	0	.768	.858	.344	.295	.096	1						
	50	.806	.909	.287	.267	-.103	.944	1					
	100	.775	.907	.203	.197	-.196	.903	.988	1				
	150	.666	.849	.103	.098	-.321	.849	.907	.918	1			
Overall	0	.679	.938	.266	.210	-.074	.933	.930	.903	.828	1		
	50	.608	.114	.923	.906	.493	.366	.330	.261	.102	.252	1	
	100	.588	.079	.872	.893	.482	.375	.332	.273	.141	.243	.979	1
	150	.419	-.051	.690	.698	.604	.296	.234	.198	.045	.115	.859	.899

List of Figures

Figure 1. The 23 ecoregions of the Yukon Territory. The following four ecoregions were excluded from this study: Mt. Logan, Fort McPherson Plains, Boreal Mountains and Plateau, and Muskwa Plateau, as the majority of their area lies outside of the political boundaries of the territory.

Figure 2. Species-accumulation curves for reserve selection at three spatial extents, the Yukon Territory (476,560 km^2, circles), the southeast super-ecoregion (162,554 km^2, squares) and the Yukon Plateau North ecoregion (57,037 km^2, triangles). Protected areas were selected using a rarity-based heuristic algorithm. Selection was from candidate reserves that meet the lowest estimate of minimum reserve area (MRA) requirements (2700 km^2) from Gurd et al. (2001).

Figure 3a. Overall turnover for adjacent cells in 2500 km^2 cells in and around the Yukon Territory. Dark areas indicate areas with high Bray-Curtis values (high dissimilarity). b. For comparison between dissimilarity values and the number of protected areas needed to achieve full representation of all species in each ecoregion, the ecoregions are overlaid on the map in (a). Those ecoregions that require more than one protected areas to achieve full representation of species have a diagonal line fill.

Figure 4. A hypothetical protected areas network 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% confidence interval for minimum reserve area requirement (2700 km^2; 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). The network pictured here would capture all the mammals in the territory at least once, although not necessarily in each ecoregion in which they are present. Note that a large area in the east-central part of the territory is without a protected area under these constraints.
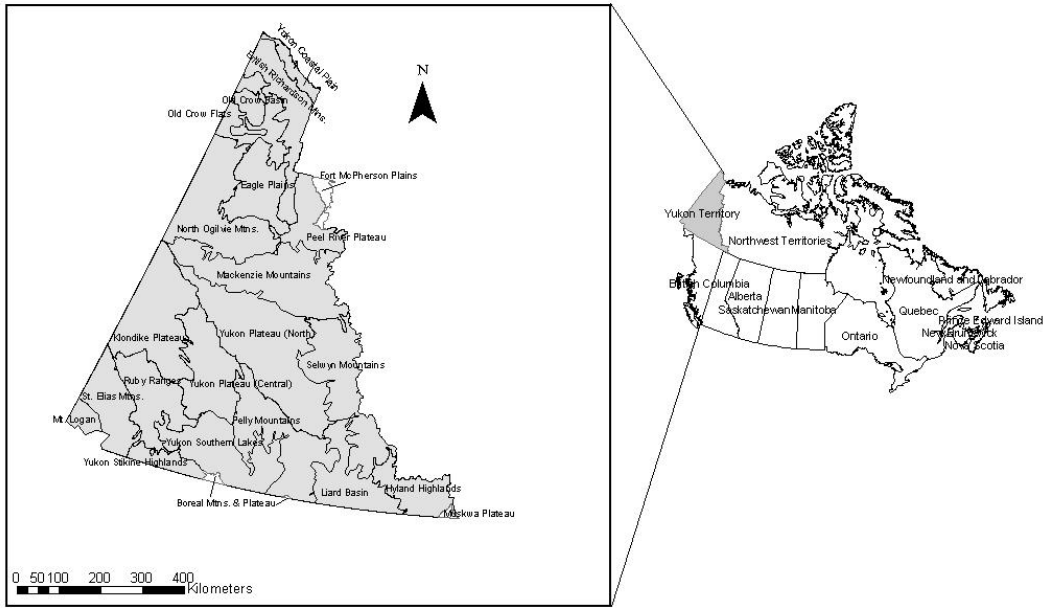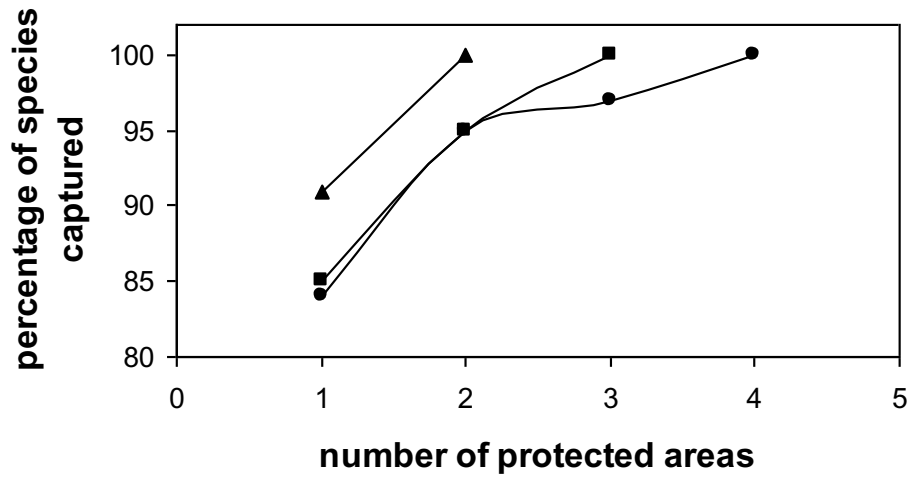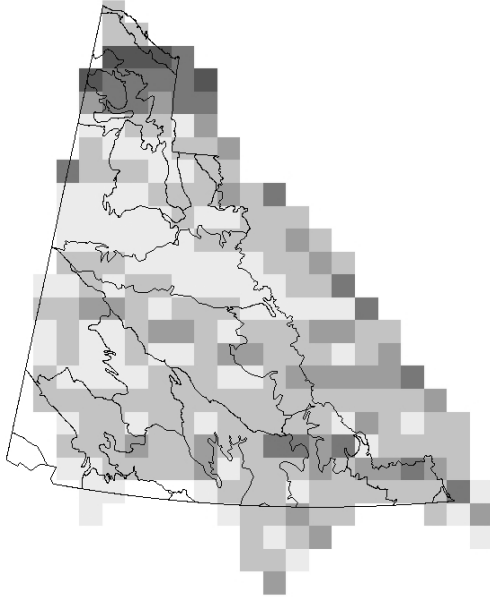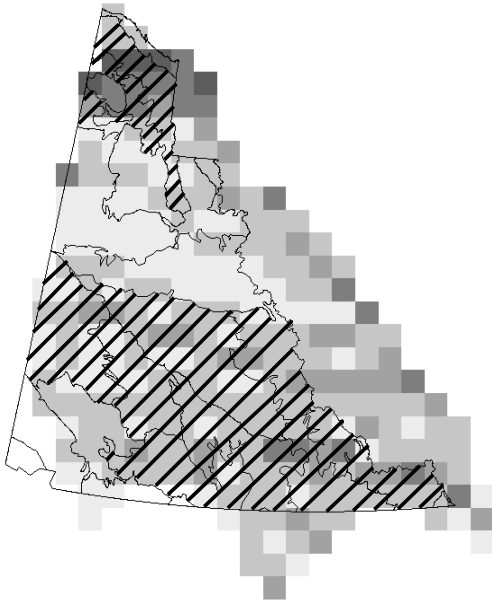
Figure 1.

Figure 2.

a.

b.

Figure 3.

Figure 4.