Effectiveness of Environmental Surrogates for the Selection of Conservation Area Networks

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Abstract: *Rapid biodiversity assessment and conservation planning require the use of easily quantified and estimated surrogates for biodiversity. Using data sets from Québec and Queensland, we applied four methods to assess the extent to which environmental surrogates can represent biodiversity components: (1) surrogacy graphs; (2) marginal representation plots; (3) Hamming distance function; and (4) Syrjala statistical test for spatial congruence. For Québec we used 719 faunal and floral species as biodiversity components, and for Queensland we used 2348 plant species. We used four climatic parameter types (annual mean temperature, minimum temperature during the coldest quarter, maximum temperature during the hottest quarter, and annual precipitation), along with slope, elevation, aspect, and soil types, as environmental surrogates. To study the effect of scale, we analyzed the data at seven spatial scales ranging from 0.01° to 0.10° longitude and latitude. At targeted representations of 10% for environmental surrogates and biodiversity components, all four methods indicated that using a full set of environmental surrogates systematically provided better results than selecting areas at random, usually ensuring that ≥90% of the biodiversity components achieved the 10% targets at scales coarser than 0.02°. The performance of surrogates improved with coarser spatial resolutions. Thus, environmental surrogate sets are useful tools for biodiversity conservation planning. A recommended protocol for the use of such surrogates consists of randomly selecting a set of areas for which distributional data are available, identifying an optimal surrogate set based on these areas, and subsequently prioritizing places for conservation based on the optimal surrogate set.*

Key Words: area selection, biodiversity, conservation planning, place prioritization, reserve network selection, surrogate species

Efectividad de Sustitutos Ambientales para la Selección de Redes de Áreas de Conservación

Resumen: *La evaluación rápida y la planificación de la conservación de biodiversidad requiere del uso de sustitutos de la biodiversidad fácilmente estimados y cuantificados. Utilizando datos de Québec y Queensland, aplicamos cuatro métodos para evaluar el grado en que los sustitutos ambientales pueden representar a los componentes de la biodiversidad: (i) gráficos de subrogación; (ii) parcelas de representación marginal; (iii) función de distancia Hamming; y (iv) prueba estadística de Svrjala para congruencia espacial. Para Québec, utilizamos como componentes de biodiversidad a 719 especies de fauna y flora, y para Queensland utilizamos 2348 especies de plantas. Consideramos como sustitutos ambientales a cuatro tipos de parámetros climáticos (temperatura media anual, temperatura mínima durante el trimestre más frío, temperatura máxima durante el trimestre más cálido y precipitación anual), la pendiente, la altitud, el aspecto y los tipos de suelo. Para estudiar el efecto de la escala, analizamos los datos en siete escalas espaciales que variaron de 0.01° a 0.10° de longitud y de latitud. En representaciones dirigidas a 10% de los sustitutos ambientales y los componentes de la biodiversidad, los cuatro métodos indicaron que un conjunto completo de sustitutos ambientales sistemáticamente proporcionó mejores resultados que la selección de áreas al azar, asegurando generalmente que*

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≥ 90% de los componentes de biodiversidad alcanzaron los objetivos de 10% en escalas más gruesas que 0.02°. El rendimiento de los sustitutos mejoró con resoluciones espaciales más gruesas. Por lo tanto, los conjuntos de sustitutos ambientales son herramientas útiles para la planificación de conservación de la biodiversidad. Un protocolo recomendado para el uso de tales sustitutos consiste en la selección aleatoria de un conjunto de áreas de las que se dispone de datos de distribución, la identificación de un conjunto óptimo de sustitutos con base en esas áreas y la subsiguiente definición de prioridades de sitios para la conservación con base en el conjunto óptimo de sustitutos.

Palabras Clave: biodiversidad, especies sustitutas, planificación de la conservación, priorización de sitios, selección de áreas, selección de red de reservas

Introduction

Systematic conservation planning requires the use of surrogates to represent biodiversity in planning protocols because the standard components of biodiversity (e.g., all species, entire ecosystems) cannot usually be surveyed adequately within the temporal and budgetary constraints of a planning process (Austin & Margules 1986; Reyers et al. 2000). Surrogacy is a relationship between an "indicator" parameter and an "objective" parameter (sometimes called a "target" parameter, what we ultimately hope to conserve). An indicator parameter represents or replaces the objective parameter in planning protocols (Sullivan & Chesson 1993). In theory the objective parameter for biodiversity conservation is general biodiversity (Sarkar & Margules 2002). By definitional convention, the objective parameter is usually taken to be the diversity of genes, species, and ecosystems (Meffe & Carroll 1994). In practice this parameter is usually reduced to subsets of species or other taxa, for instance, species at risk (Sarakinos et al. 2001). Following Sarkar and Margules (2002), we call this objective parameter the "true surrogate" because it is intended to represent general (or true) biodiversity in conservation planning.

Indicator parameters, hereafter called estimator surrogates, are intended to represent true surrogates. Estimator surrogates must be (1) quantifiable (i.e., capable of quantitative assessment) and (2) capable of being estimated (i.e., their distributions must be realistically obtainable, for instance, from limited field surveys, remotely sensed data, or theoretical models). Given a set of true surrogates, whether a set of estimator surrogates adequately represents it is an empirical question (Landres et al. 1988). The use of estimator surrogates rests on an implicit assumption that there is a biological model linking the estimator surrogate set and the components of biodiversity that form the true surrogate set.

We developed and extended methods for assessing the empirical adequacy of estimator surrogate sets. The most stringent test requires that the spatial distribution of the estimator surrogates correctly predicts the spatial distribution of the true surrogate set. This problem is equivalent to determining the adequacy of spatially explicit niche models based on estimator surrogate sets as inputs. Significant progress has been made in niche modeling during the last decade (summarized in Scott et al. 2002). Nevertheless, these methods, which generally predict the occurrence of one species at a time, are still too cumbersome for use in "rapid biodiversity assessment" (Nix et al. 2000; Guisan et al. 2002). Moreover, success in predicting spatial distributions is too strong a requirement in a planning context. In that context, the only requirement is the adequate representation of the diversity of true surrogates in a set of places selected to represent estimator surrogates (a network of conservation areas), not the representation of any particular true surrogate in a specified area.

Consequently, attempts to assess the adequacy of estimator surrogate sets should focus on whether (1) the use of the estimator surrogates to prioritize places for inclusion in a conservation area network achieves a targeted representation of the true surrogates, (2) the diversity of estimator surrogates in a region is spatially correlated with the diversity of true surrogates in a set of selected areas, and (3) the set of areas selected using the estimator surrogate set is spatially congruent with the set of areas that would have been selected using the true surrogate set. These tests can be carried out even when the biological model presumed to connect true and estimator surrogates has not been explicitly specified. But what an adequate surrogate set must ultimately ensure is only the full representation of the true surrogates; therefore, spatial correlation and congruence are not as important as adequate representation.

We present four methods of analysis. Surrogacy graphs, which are a generalization of the species accumulation curves used by Ferrier and Watson (1997) and Ferrier (2002), answer question 1. Marginal representation analysis answers question 2. A distance measure, based on the Hamming distance between binary strings, answers question 3, as does a version of the Syrjala test (Syrjala 1996). We developed the method of surrogacy graphs in earlier work (Sarkar et al. 2000; Garson et al. 2002*a*). To the best of our knowledge, marginal representation analysis is new. The Hamming distance measure is common in ecology and evolutionary biology (e.g., Christensen et al.

2002; Iwasa et al. 2004). The Syrjala test was previously used by Lawler et al. (2003).

We also used distributional data from two widely differing regions, Québec and Queensland, to study the performance of environmental parameter estimator surrogates. A general motivation for this analysis came from several reports indicating that using surrogates to represent biodiversity performs no better than selecting conservation areas at random (Andelman & Fagan 2000; Lund & Rahbeck 2002). (Such pessimistic results generally have been obtained when taxa have been used as estimator surrogates, however, and even then most authors have expressed guarded optimism about the use of surrogates [Pharo et al. 2000; Fleishman et al. 2001].)

The particular interest in environmental parameter estimator surrogates is that they can be easily obtained through a combination of remotely sensed data, field data, and climate models. Faith and Walker (1996) advocated using a specific measure of environmental diversity (ED) as an estimator surrogate. The ED value of an area is the decrease in the summed distance from all points in the ordination space to the nearest point already selected for conservation. Maximizing the ED value is supposed to maximize true surrogate diversity. Using all available species in Europe as true surrogates, although only at a very coarse spatial resolution of 50×50 km^2, Araújo et al. (2001) criticized the use of ED, arguing that it does little better than select cells randomly. However, Araújo et al. used a measure of ED that differed from that of Faith and Walker (1996) (see Faith [2003] for a response and Araújo et al. [2003] for a rejoinder). The ED, though, represents only one measure of environmental diversity. We used simple partitions of environmental parameter classes as estimator surrogate sets (Ferrier & Watson 1997; Armstrong & van Hensbergen 1999). We also studied the performance of several subsets of these sets in an attempt to find an optimal surrogate subset. Kirkpatrick and Brown (1994) used a different hierarchical partitioning of environmental parameter classes as estimator surrogate sets.

Additionally, we studied the effect of spatial scale on the performance of estimator surrogate sets. We analyzed the data at seven spatial scales ranging from 0.01° longitude $\times$ 0.01° latitude to 0.10° longitude $\times$ 0.10° latitude. For surrogacy graphs, it was intuitively clear that both the use of estimator surrogates and the random selection of areas should perform better at coarser spatial resolutions than at finer ones because larger cells will contain more true surrogates. We analyzed whether the relative performance of the estimator surrogates compared with random selection improved at coarser scales and, if so, whether there was a limiting scale beyond which there was no further gain (in which case, that should be the preferred scale for the use of estimator surrogates in conservation planning). A previous study of the effects of spatial scale, using birds as estimator surrogates for species at risk (the true surrogates) in southern Québec, yielded positive answers to both questions (Garson et al. 2002*a*).

Spatial scale analysis, in the sense of a comparative study of the performance of estimator surrogate sets at different spatial resolutions, is relatively new in surrogacy analysis. Ferrier and Watson (1997) analyzed two Australian data sets at two spatial resolutions of 0.04 and 25.0 km^2. Andelman and Fagan (2000) considered data at different spatial resolutions but did not perform any comparative analyses. Their data at different resolutions came from different regions. M. Tognelli (unpublished data) used all mammal species of Latin America as true surrogates, and several estimator surrogate sets, including World Conservation Union (IUCN)-listed (vulnerable, endangered, or critically endangered) species, geographically rare species, flagship species, and large mammal species. He analyzed data at the continental scale for Latin America and the national scale for Brazil, but the spatial resolution of the data (land-unit size) remained the same.

The use of estimator surrogate sets leads to testable predictions and we describe an explicit protocol for such tests. To the best of our knowledge, such a protocol has not been explicitly suggested.

Methods

For both regions, we used a geographic information system (GIS) model that consisted of a set of cells, $\Sigma(\sigma_j \in \Sigma, j = 1, 2, \ldots, n)$, with each cell representing an area for potential inclusion in a conservation area network. Associated with this set were sets of surrogates, $\Lambda(\lambda_i \in \Lambda, i = 1, 2, \ldots, m)$. These could be sets of both estimator and true surrogates. The basic data consisted of the matrix $\mathbf{P} = (p_{ij})$ $(i = 1, 2, \ldots, n; j = 1, 2, \ldots, m)$, where p_{ij} is the expectation of finding λ_j (the jth surrogate) at σ_i (the ith cell). Because the data were presence and absence, the p_{ij} were 1 or 0, but our methods could be used with probabilistic data (Sarkar et al. 2004).

Surrogate Sets

We analyzed Québec and Queensland because reliable presence-absence point data from records and surveys were available. These were the cells used in this analysis. For Québec the true surrogate set consisted of 719 floral and faunal species, over 50% of which were species at risk. Floral data covered all available families, whereas faunal data were restricted to vertebrates (additional details in Sarakinos et al. 2001). Because species at risk are usually regarded as important components of biodiversity, they have often been used as true surrogates (Dobson et al. 1997; Sarakinos et al. 2001; Garson et al. 2002*a*). Moreover, results of at least one study show that if species at risk are among the estimator surrogates and all species with available distributions are used as true surrogates, species at risk perform better than other groups (Lawler et al. 2003).

For Queensland the true surrogate set consisted of 2348 plant species (195 families; additional details in Moritz et al. 2001). The motivation behind this choice of a true surrogate set was that, in practice, extensive varied representation of any kingdom (and, preferably, all kingdoms) comes as close as possible to the ideal of using all species. Results of some studies show that if endangered plant species are used as estimator surrogates and other endangered species are used as true surrogates, the former maximize the protection of the latter (Dobson et al. 1997).

We chose estimator surrogate sets consisting of those environmental parameters for which global coverages can be freely downloaded and computed. Thus, any conservation planner has access to these data. The sets included four climatic parameters (annual mean temperature, minimum temperature during the coldest quarter, maximum temperature during the hottest quarter, and annual precipitation), along with slope, elevation, aspect, and soil types. The climate layers were created from the GTOPO30 DEM, which is a 30 arc-second digital elevation map (DEM) available from the U.S. Geological Survey (USGS; 1998), and the worldwide agroclimatic database of the Food and Agricultural Organization (FAOCLIM; FAO 2000). We used ANUSPLIN 4.1 (Hutchinson 2000) and ANUCLIM 5.1 (Houlder et al. 2000) software packages to compute these climate parameters. Procedures used for running ANUSPLIN and ANUCLIM were identical to those used in the Australian BioRap analyses (Hutchinson 1991; Hutchinson et al. 1996). In ANUSPLIN, the SELNOT and SplineB programs were used with the same default values as in the BioRap analyses.

We obtained elevation data from the GTOPO30 DEM. We created slope and aspect layers with the Spatial Analyst extension in ArcGIS 8.1 (ESRI 2002) from the DEM as specified in the Hydro 1K elevation derivative database methodology also available from the USGS (1998). Soil classifications were obtained from the world soil resources map (FAO 1993).

We divided annual mean temperature, annual precipitation, and elevation parameters into 10 equal interval classes. In general, finer divisions of environmental surrogate parameters are expected to give better representation of true surrogates. Computational complexity increases, however, with the number of classes. We chose 10 classes because preliminary results indicated that using more classes did not affect results. The minimum temperature of the coldest period of the year and the maximum temperature of the warmest period of the year were divided into four equal interval classes to ensure that each class had the same range as each annual mean temperature class. The use of equal intervals assumed that protecting sets of cells that contain all four classes will ensure that biotic features found in rare temperature regimes are adequately represented in a conservation plan. Slope was divided into five classes based on standard deviations. The use of standard deviations assumed that mid-range slopes are more important for biodiversity than extremes. In these regions this pattern was found for the richness of true surrogate distributions. Soil data were divided into four classes for Québec and two classes for Queensland, corresponding to the soil association types in the world soil map (FAO 1993). These are the coarsest measures in our study. Aspect data were divided into the standard nine classes of 40° each. Preliminary results indicated that a finer division did not affect results.

For each region we analyzed four different estimator surrogate sets. The climatic parameter classes and soil type classes were common to all sets. In the others, slope, aspect, and elevation were sequentially removed because these were also used to model the climatic parameters. For Québec the initial set (1) had 56 surrogates. Subsequent removal of parameter types led to 51, 42, and 32 surrogates in each set 2, 3, and 4, respectively. For Queensland we started with 54 surrogates in set 1 that were then reduced to 49, 40, and 30 surrogates in sets 2, 3, and 4. Because the environmental surrogate sets consist of modeled data, these were known for every cell in a region. But because our data for the true surrogates were point data from records and surveys, these were available for only a fraction of the cells. We used only those cells in which at least one true surrogate was present in our analyses.

Methods for Assessing Surrogates

SURROGACY GRAPHS AND PLACE PRIORITIZATION ALGORITHMS

Surrogacy graphs are an extension and generalization of species accumulation curves developed by Sarkar et al. (2000) and Garson et al. (2002*a*). Typically, a species accumulation curve has the number of cells selected in a potential network as the independent variable and the number of species represented as the dependent variable. Surrogacy graphs are of two types. Both have the fraction of true surrogates that have met their target as the dependent variable. In the first type, the independent variable is the fraction of estimator surrogates that have met their specified targets. In the second, it is the fraction of the total area so far selected. Each estimator and true surrogate may have a different specified target of representation depending on the biological and other requirements for its conservation. For instance, an endangered species may have a target close to 100%, whereas a common alien species may have a target of 0% (Sarakinos et al. 2001). The level of representation for true surrogates reached in a surrogacy graph measures the performance of an estimator surrogate set. If all true surrogate targets are set to one representation, the second type of surrogacy graph reduces to a species accumulation curve. Here, we used a common target of 10% for both true and estimator surrogate sets.

We used the ResNet software package to carry out place prioritization for cell selection (Garson et al. 2002*b*). This

package implements a rarity-complementarity algorithm belonging to the family of algorithms introduced by Margules et al. (1988). Initialization was by rarity, following the protocol of Sarkar et al. (2002). We used the Surrogacy software package to compute surrogacy graphs (Garson & Sarkar 2002). Each curve in a surrogacy graph that corresponded to an estimator surrogate set represented an average of 100 different solutions generated by randomization of the order of entries in the data set. Randomizations led to new solutions because the place prioritization algorithm selected cells based on lexical position if there was no unique best cell determined by rarity and complementarity (Sarkar et al. 2002). The "random" graph shows the result of randomly selecting the same number of cells as was picked by the estimator surrogate sets when they achieved either the level of representation or the area specified by the x-axis. The random graphs show the average of 100 such random selections (Figs. 1–4).

We used standard deviation to represent the range of variation in our graphs because the standard errors were too small to depict. We describe results as significantly different if there was no overlap of error bars of 2 SDs. Assuming normality and independence of two sets of results, this corresponds to a p value of <0.003. This method of computing significance results, however, does not take into account the possibility of sampling error. Given the large number of cells in our data set (Table 1), sampling error is likely to be significant for Queensland only at the coarsest scales.

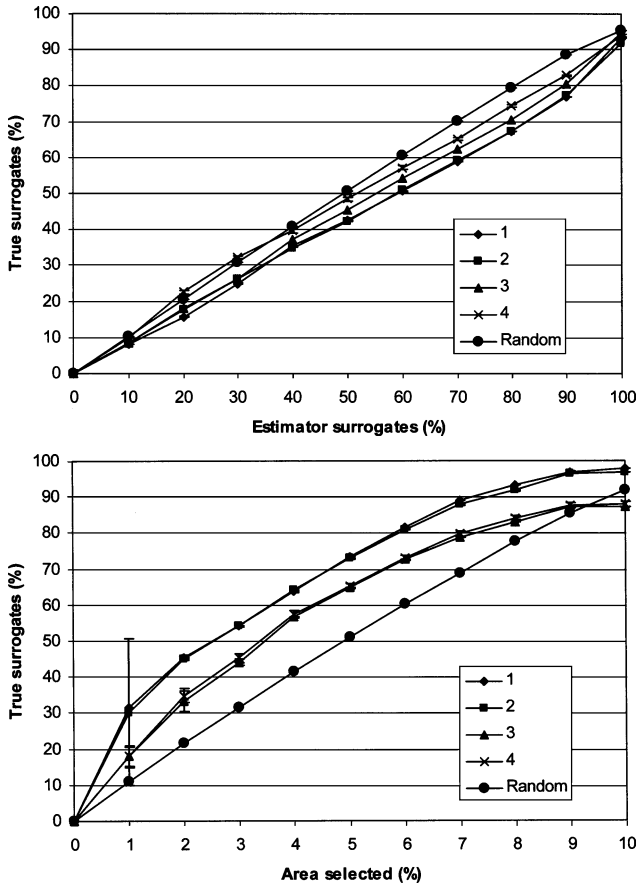

Figure 1. Surrogacy graphs for Québec: (top) Québec at the 0.01° × 0.01° longitude × latitude scale. Type I surrogacy graph: x-axis, percentage of estimator surrogates that have achieved their targets, and y-axis, percentage of true surrogates that have achieved their targets. Error bars show standard deviations from 100 different runs rather than standard errors because the latter were too small to be depicted. (bottom) Québec at the 0.10° × 0.10° longitude × latitude scale. Type II surrogacy graph: x-axis, percentage of area that has been selected and y-axis, percentage of true surrogates that have achieved their targets.

MARGINAL REPRESENTATION CONTRIBUTION

Surrogacy graphs can be used only when surrogates have a specified target of representation. The use of targets in conservation planning (including cell selection), however, has been criticized recently because most targets that have been used in practice do not have a firm biological basis (Soulé & Sanjayan 1998). Consequently, it is of some interest to develop a measure—one that is independent of target specification—of the correlation between the contributions an individual cell makes in representing true and estimator surrogates. For either type of surrogate, with the notation introduced above, the marginal representation (ρ_j), of cell σ_j is

$$\rho_j = \frac{\sum_{k\in\Lambda} p_{kj}}{\left(\sum_{l\in\Sigma}\sum_{k\in\Lambda} p_{kl} - \sum_{k\in\Lambda} p_{kj}\right)},$$

provided that the denominator is not equal to 0. The numerator consists of the expected number of surrogate occurrences in the cell σ_j (Sarkar et al. 2004). The denominator is the expected number in all other cells. Thus, ρ_j provides a relative measure of the surrogate representation that σ_j adds to the other cells.

We used marginal representation plots, which are two-dimensional plots of the true surrogate and estimator surrogate ρ_j value for each cell in a region, to analyze correlations between the marginal representations of the estimator and true surrogates. Preliminary analysis showed a nonlinear relationship between the marginal representations of the estimator and true surrogates. Low values were obtained for the Pearson product-moment correlation coefficient even when the marginal representation plots visually indicated a clear association between the data. For this reason, we used the nonparametric Spearman's rank correlation test for nonlinear correlations.

SPATIAL CONGRUENCE ANALYSIS

The spatial congruence between cells selected based on the true surrogate set and those selected based on the

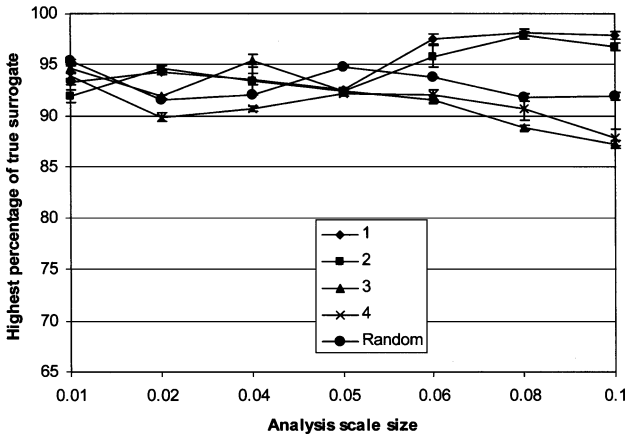

Figure 2. Québec surrogacy scale analysis: x-axis, cell boundary size in longitude/latitude, and y-axis, representation level of true surrogates when 100% representation of estimator surrogates has been achieved. The error bars show SDs from 100 different runs rather than SEs because the latter were too small to be depicted.

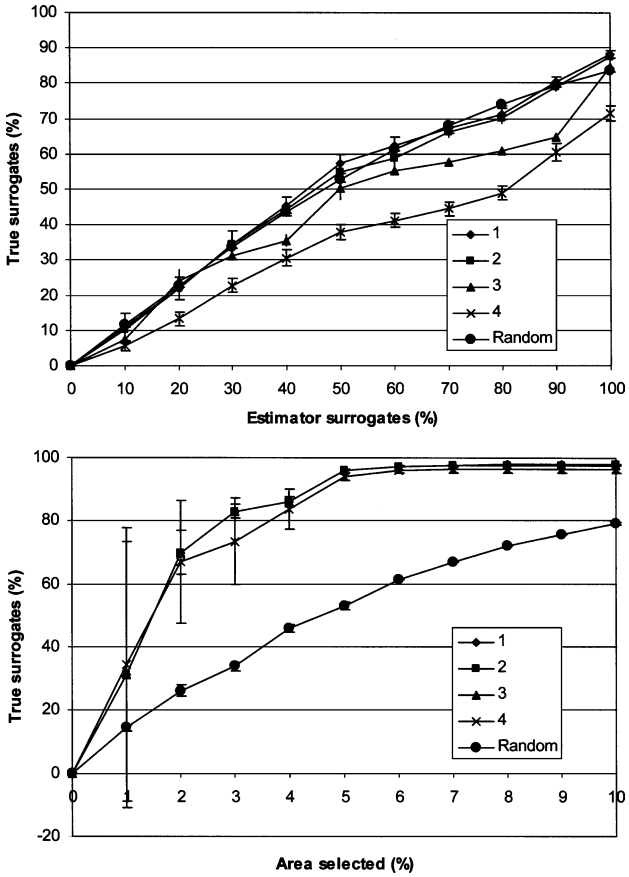

Figure 3. Surrogacy graphs for Queensland: (top) Queensland at the 0.01° × 0.01° longitude × latitude scale; (bottom) Queensland at the 0.10° × 0.10° longitude × latitude scale. For further detail, see the legend for Fig. 1.

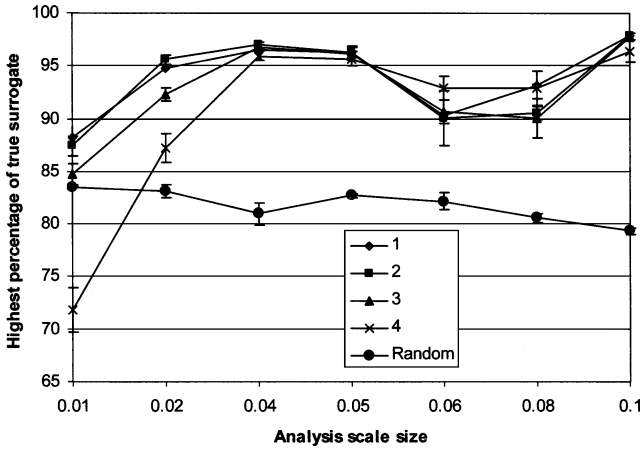

Figure 4. Queensland scale analysis: x-axis, cell boundary size in longitude/latitude, and y-axis, representation level of true surrogates when 100% representation of estimator surrogates has been achieved. The error bars show standard deviations from 100 different runs rather than standard errors because the latter were too small to be depicted.

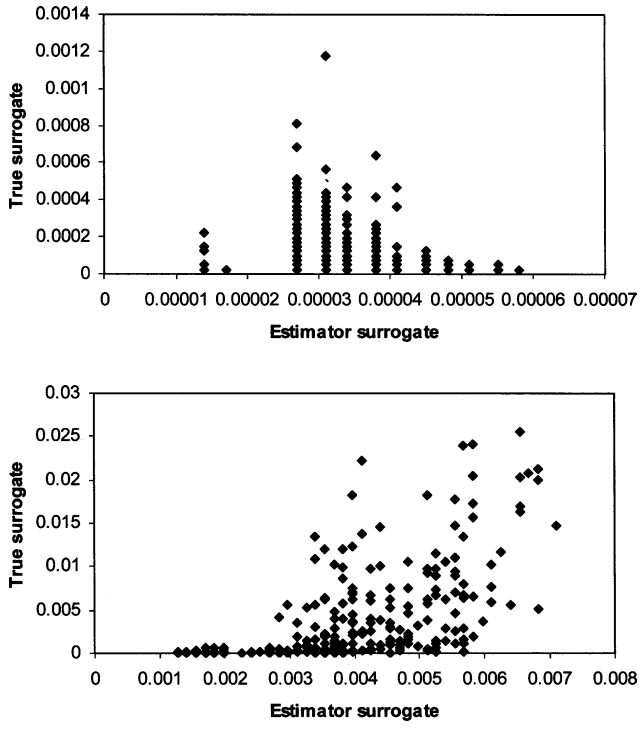

Figure 5. Marginal species representation plots: (top) Québec, environmental surrogate set 1 at the 0.01° × 0.01° longitude × latitude scale (each point represents the marginal representation of the estimator surrogates [x-axis] and true surrogates [y-axis] of an individual cell) and (bottom) Queensland, environmental surrogate set 1 at the 0.10° × 0.10° longitude × latitude scale.

Table 1. Landscape properties of the areas examined for Québec and Queensland at the seven spatial scales of our analysis.

	Québec		*Queensland*	
Scale (degrees)	*number of cells*	*average area km² (SD)*	*number of cells*	*average area km² (SD)*
0.01	33,967	0.850 (0.0190)	3,828	1.18 (0.00519)
0.02	23,474	3.38 (0.0788)	2,227	4.72 (0.0223)
0.04	12,940	13.4 (0.322)	931	18.9 (0.0978)
0.05	10,125	21.0 (0.506)	693	29.5 (0.158)
0.06	8,156	30.1 (0.733)	518	42.4 (0.229)
0.08	5,589	53.4 (1.31)	350	75.4 (0.446)
0.10	3,890	83.3 (2.10)	251	118 (0.676)

estimator surrogate set is another measure of the performance of estimator surrogate sets. We used the Hamming distance between strings of 0s (absence) and 1s (presence) as a quantitative measure of the spatial congruence between the set of cells selected by true surrogates and that selected by estimator surrogates. Our distance function consisted of the number of unshared cells between the two sets divided by the total number of cells in both the sets taken independently (that is, shared cells were counted twice). Let A be one set of cells and B be the other. Then the Hamming distance between A and B is given by $(|A \cup B| - |A \cap B|)/(|A| + |B|)$, where the function "$|\cdot|$" indicates the cardinality of the set inside it. This measure varies between 0 and 1. If the two sets are identical, the distance is 0. If they are disjoint, the distance is 1. There were 100 distance calculations between sets selected by true and estimator surrogate sets for each surrogate set (1–4) at each scale and for each data set.

We used the statistical Syrjala test, a generalization of the two-sample Cramér-von Mises test, to determine whether the spatial distribution of cells selected by the true surrogates was identical to that selected by the estimator surrogates (Syrjala 1996). Again, there were 100 pair-wise comparisons between sets selected by true and estimator surrogate sets for each surrogate set (1–4), at each scale, and for each data set. We used a uniform density function over the selected cells and 100 permutations to determine the level of significance of the test results.

Spatial Resolution/Scale

Québec and Queensland were both analyzed at seven spatial resolutions: 0.01° of longitude × 0.01° of latitude, 0.02° × 0.02°, 0.04° × 0.04°, 0.05° × 0.05°, 0.06° × 0.06°, 0.08° × 0.08°, and 0.10° × 0.10°. The number of cells with data decreased at coarser scales for both regions (Table 1). At coarser scales, cells were assumed to contain each of the surrogates represented at finer scales.

Results

For the Québec data set at the spatial resolution of 0.01°, surrogacy graphs were approximately linear for both types of surrogacy graph (Fig. 1). When the spatial resolution was 0.10°, performance was enhanced but this linearity was lost for the second type of surrogacy graph (Fig. 1), whereas the first type remained linear. Intermediate spatial scales produced intermediate results in performance (data not shown). At the finest spatial scale, the use of environmental surrogates performed no better than selecting cells at random with respect to representing true surrogates. At coarser scales, however, the use of the surrogates led to significantly better performance. The full estimator surrogate set 1 performed better than any of the subsets. The smallest subsets (3 and 4) performed no better than random even at coarser spatial scales. The full estimator surrogate set 1 achieved a representation of 97.90% at the 0.10° scale. There was little change, though, in the performance of the full estimator surrogate set 1 with spatial scale (it varied between 92.57% and 98.16%; Fig. 2).

The Queensland data produced similar surrogacy graphs (Fig. 3; intermediate scales yielded intermediate results [data not shown]). With coarser spatial scales, the full estimator surrogate set 1 performed better at representing true surrogates than cells selected at random (Fig. 3). At finer spatial scales, however, the smaller estimator surrogate sets (for instance, 4) performed worse. The performance of the full estimator surrogate set 1 was appreciably better at the 0.10° scale (97.93%) than at the 0.01° scale (88.17%; Fig. 4). Even though there was no strict monotonic increase through the intermediate scales

(for any estimator surrogate set), there was a clear trend. A significant improvement over random selection began at the 0.02° scale, at least for the full estimator surrogate set 1 (Fig. 4).

The Spearman rank test indicated a significant correlation ($p < 0.01$) between marginal representations of the estimator and true surrogates for both data sets and all surrogate sets at all scales except for estimator surrogate sets 3 and 4 for Québec at the finest scale (Fig. 5). For Queensland the correlation was weakest for estimator surrogate set 3 at all scales. The correlations showed a nonmonotonic increase with coarser scales. The highest correlations were $r_S = 0.58$ for estimator surrogate set 2 for Québec and 0.71 for Queensland for estimator surrogate set 4, both at the 0.10° scale.

The average Hamming distances between solutions based on estimator and true surrogates decreased with spatial scale for both Québec and Queensland (Table 2). This increase in congruence was expected. At coarser spatial scales, on average, each cell contained a larger number of different surrogates, but there were fewer cells, allowing less flexibility in selecting cells to achieve surrogate representation targets. In each case the set of cells selected using an estimator surrogate set was being compared with the set selected using the true surrogate set; both sets had a target of 10% for the representation of surrogates. For both data sets, results were similar for all estimator surrogate sets. Lower figures were obtained for Queensland, which produced results with greater variability. For both Québec and Queensland, the distance between solutions based on the estimator surrogates and solutions based on the true surrogates depended on scale (one-way analysis of variance, for all four surrogate sets). Although the distance between the solutions did not decrease monotonically with increasing scale (data not shown), a simple linear model approximately fit the pattern. For Québec surrogate set 1 had the best fit with the linear model ($r = 0.881$), whereas for Queensland surrogate set 4 had the best fit ($r = 0.720$). The variance in the distance at a given scale did not decrease with increasing scale (data not shown).

With a significance level of $\alpha = 0.05$ the Syrjala test did not reject the null hypothesis that the two maps (generated using true and estimator surrogate sets) were identical for most of the scales and estimator surrogate sets. For both Québec and Queensland, no p value differed from 1 at the 0.01° and 0.02° scales for all four estimator surrogate sets. For Queensland the Syrjala test did not reject the null hypothesis at any scale for any estimator surrogate set. For Québec the test did not reject the null hypothesis for all estimator surrogate sets at the 0.04°, 0.05°, and 0.06° scales. At the 0.08° scale, the null hypothesis was rejected for 7% of the solutions for estimator surrogate set 4. For all other estimator surrogate sets, the null hypothesis was never rejected. At the 0.10° scale, the null hypothesis was never rejected for estimator surrogate set 1. For estimator surrogate sets 2 and 3, it was rejected for 7% and 4% of the solutions. For estimator surrogate set 4, however, it was rejected 64% of the time. As was the case in the rest of our analysis, the smallest estimator surrogate set (4) performed worse than all the others.

Discussion

The surrogacy graphs present our most important results. They directly address the critical question of whether the use of environmental estimator surrogate sets results in

Table 2. Means (SD) of the Hamming distances for 100 different solutions at each scale for each estimator surrogate set for Québec (top pair of numbers) and Queensland (bottom pair of numbers).*

Estimator surrogate set	*0.01°*	*0.02°*	*0.04°*	*0.05°*	*0.06°*	*0.08°*	*0.10°*
	0.918	0.895	0.877	0.896	0.855	0.861	0.862
1	(0.00366)	(0.00219)	(0.00583)	(0.00517)	(0.00697)	(0.00542)	(0.00652)
	0.947	0.915	0.910	0.895	0.925	0.883	0.702
	(0.00595)	(0.0105)	(0.0128)	(0.0218)	(0.0140)	(0.0575)	(0.0282)
	0.918	0.898	0.901	0.890	0.871	0.876	0.919
2	(0.00350)	(0.00218)	(0.00526)	(0.00563)	(0.00575)	(0.00626)	(0.00377)
	0.958	0.904	0.907	0.892	0.919	0.883	0.692
	(0.00551)	(0.0110)	(0.0126)	(0.0234)	(0.0115)	(0.0575)	(0.0273)
	0.904	0.912	0.901	0.872	0.882	0.863	0.919
3	(0.00225)	(0.00479)	(0.00585)	(0.00670)	(0.00533)	(0.00620)	(0.00406)
	0.962	0.932	0.906	0.889	0.915	0.890	0.684
	(0.00617)	(0.0129)	(0.0109)	(0.0232)	(0.0119)	(0.0549)	(0.0281)
	0.919	0.907	0.889	0.901	0.894	0.877	0.872
	(0.00406)	(0.00207)	(0.01362)	(0.00636)	(0.00622)	(0.00645)	(0.00637)
4	0.962	0.939	0.898	0.883	0.902	0.864	762
	(0.00464)	(0.0115)	(0.00847)	(0.0201)	(0.0164)	(0.0499)	(0.0257)

**In each case what is being compared are the set of cells selected using an estimator surrogate set and the set selected using the true surrogate set, both with a target of 10% for the representation of surrogates.*

an adequate representation of the true surrogates in a set of selected conservation areas. At least for Québec and Queensland, the use of environmental surrogates was a significant improvement over random selection of conservation areas at larger spatial scales (more specifically, at and above the 0.02° scale). Moreover, the routine achievement of a representation level of more than 90% of the true surrogates should be regarded as more than adequate when such coarse-grained environmental surrogate sets (only 56 classes for Québec and 54 for Queensland) are all that can be used for conservation planning. Although our results show that estimator surrogate set performance improved as spatial scale increased, the results were not as striking as those obtained by Garson et al. (2002*a*). For all these results, though, our tests of significance did not take the possibility of sampling error into account. Such error is likely to increase at coarser scales as the number of cells with data decreases.

The marginal representation analysis showed significant nonlinear correlations between the marginal contributions of estimator and true surrogates to the surrogate representation within individual cells. Our distance analysis, however, showed that the set of cells selected by the estimator and true surrogate sets were typically very different. Nevertheless, the representation targets were achieved to a high degree. This result supports the claim made in the Introduction that requiring success at predicting spatial distributions is an unnecessarily stringent requirement for the use of estimator surrogates. The Hamming distance, however, merely measures whether or not a cell is present in two sets without taking spatial distances between the selected cells in the two sets into account. The Hamming distance remains appropriate as a measure of the difference between two sets of selected cells for conservation area networks, when what matters is whether an individual cell is included or not. But it is not an adequate measure of the extent to which two sets of selected cells are spatially dissimilar. The results of the Syrjala test suggest that the cells selected by the estimator and true surrogate sets remained spatially correlated, at least to the extent that the null hypothesis that the maps are identical could not be rejected. (The smallest estimator surrogate set, set 4, was an exception for the Québec data set.)

These optimistic results contrast with those reported by Araújo et al. (2001), who used a measure of ED (although a different one than Faith and Walker [1996]). We used a direct partitioning of environmental parameter types to generate our estimator surrogate sets. Our optimistic conclusions should be treated with caution. We analyzed only two different data sets and, even though they are from different biogeographic realms and latitudes, these analyses must be repeated for a representative variety of other regions before any definitive recommendation can be made about using environmental surrogate sets. Moreover, any assessment of the performance of an estimator surrogate set depends on the choice of that set, the choice of a true surrogate set, and the nature and quality of the available data. We pointed out in the Introduction that the choice of species at risk (for Québec) and as many varied species in a kingdom as possible (for Queensland) are reasonable choices for true surrogates. Other plausible true surrogate sets should also be tested.

We used point data from records and surveys that were interpreted as presence and absence data. Even if these data are misinterpreted as presence-only data, however, it would not detract from the reliability of our conclusions. A cell evaluated as containing a true surrogate using presence-only data would also be evaluated as such using presence and absence data. If the data were presence only, the procedure we used was conservative. It would lead to a higher representation than targeted for the true surrogates because some cells would contain true surrogates that were not recorded in the presence-only data.

Should the adequacy of the use of environmental surrogate sets survive further scrutiny (or some other adequate estimator surrogate sets be found), we suggest the following protocol for their use and testing: (1) select a true surrogate set and a group of candidate estimator surrogate sets; (2) divide the planning region into cells of the appropriate size and project the region into an environmental space; (3) randomly select a set of locations (the calibration set) from the environmental ordination space (the larger this set, the better); (4) survey the cells in (geographical) space for the true and all the estimator surrogate sets; (5) construct surrogacy graphs for the sampled cells to determine the best or "optimal" estimator surrogate set; and (6) use the optimal estimator surrogate set for conservation planning for the entire region. In principle, this protocol can be carried out for any potential estimator surrogate set without prior knowledge of its adequacy. However, such prior knowledge—for instance, knowing that a particular type of environmental surrogate set is likely to be adequate—will help determine what group of candidate estimator surrogate sets should be analyzed. In practical planning contexts, in the presence of temporal and budgetary constraints, this type of prior knowledge is critical for rational planning. Caro and O'Doherty (1999) also argue, without providing a protocol, that pilot studies should be carried out before any species sets are adopted as surrogates.

This protocol can also be easily extended to make testable predictions. Stages 1–5 can be viewed as a process of calibration of estimator surrogate sets. Stage 6 can then be replaced with, randomly select a second disjoint set of cells (the test set) in geographical space. In stage 7 use surrogacy graphs to predict the expected number of true surrogates that would satisfy their targets in cells that are selected using the optimal estimator surrogate set. Finally in stage 8 survey these cells to determine if the predictions are correct. If resources permit, such predictive tests are obviously recommended before one uses an

estimator surrogate set to select a conservation area network. Such a test can be carried out for any candidate estimator surrogate set, although there is little motivation for performing it on nonoptimal sets. In the general context of determining whether there are any adequate estimator surrogate sets, successful predictive tests would increase confidence in our results, which support the claim that such surrogate sets are useful tools for biodiversity conservation planning.

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