

# Mapping Spatial Pattern in Biodiversity for Regional Conservation Planning: Where to from Here?

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**Abstract.**—Vast gaps in available information on the spatial distribution of biodiversity pose a major challenge for regional conservation planning in many parts of the world. This problem is often addressed by basing such planning on various biodiversity surrogates. In some situations, distributional data for selected taxa may be used as surrogates for biodiversity as a whole. However, this approach is less effective in data-poor regions, where there may be little choice but to base conservation planning on some form of remote environmental mapping, derived, for example, from interpretation of satellite imagery or from numerical classification of abiotic environmental layers. Although this alternative approach confers obvious benefits in terms of cost-effectiveness and rapidity of application, problems may arise if congruence is poor between mapped land-classes and actual biological distributions. I propose three strategies for making more effective use of available biological data and knowledge to alleviate such problems by (1) more closely integrating biological and environmental data through predictive modeling, with increased emphasis on modeling collective properties of biodiversity rather than individual entities; (2) making more rigorous use of remotely mapped surrogates in conservation planning by incorporating knowledge of heterogeneity within land-classes, and of varying levels of distinctiveness between classes, into measures of conservation priority and achievement; and (3) using relatively data-rich regions as test-beds for evaluating the performance of surrogates that can be readily applied across data-poor regions. [Biodiversity; regional conservation planning; surrogates.]

The term biodiversity has been greatly used and abused since it first entered the scientific vocabulary less than 20 years ago (Harper and Hawksworth, 1994), inspiring some to regard it as a “buzzword” (Goldstein, 1999) or “little more than a brilliant piece of wordsmithing” (Bowman, 1993). The simplicity of the word certainly belies the enormous complexity of the patterns and processes to which it refers and the paucity of our understanding of this complexity, even after many decades of evolutionary and ecological research. Nevertheless, the term is now inextricably linked to a widening of focus in conservation effort beyond preserving particular species of ecological or social significance (“biospecifics”; Faith, 1997), and maintaining essential ecosystem functions and services, to embrace the challenge of conserving the global variety of all species, the genes they contain, and the ecosystems in which they occur.

Establishment of protected areas is a vital component of most global and regional strategies to mitigate the ongoing loss of biodiversity (e.g., World Resources Institute, 1992). However, recognition is growing that conservation objectives can rarely be achieved by dedication of strict reserves alone (Reid, 1996). Such reserves are of-

ten viewed now as forming the core of a broader network of areas protected by a range of measures, including multiple-use management zones and conservation incentives and controls on private land. In this paper I refer generically to all such areas as conservation areas (after Pressey, 1997). The appropriateness of different types of protective management will vary according to regional circumstances. A more fundamental problem confronting all efforts to retain biodiversity by establishing conservation areas is how to decide which areas are most worthy of protection. Where should scarce conservation resources be most productively directed, given constraints imposed by social and economic considerations?

This problem can be addressed at many different spatial scales. Assessments at a global scale can provide an indication of the relative conservation priority of broad regions of the world (e.g., Bibby et al., 1992; Olson and Dinerstein, 1998; Myers et al., 2000). However, most decisions about the actual location of new conservation areas are made at finer spatial scales (Cooper and du Plessis, 1998; da Fonseca et al., 2000; Mace et al., 2000; Soberón et al., 2000). Global assessments help to focus attention on regions of particular conservation concern,

but a more detailed assessment is required within each of these regions to prioritize areas for protective management (Margules and Redhead, 1995; Dinerstein et al., 2000; Groves et al., 2000)—a process referred to here as regional conservation planning. The region of interest can be variously defined as a natural region or ecoregion, or as an administrative region such as a province, state, or country. In this paper I focus on issues relating primarily to terrestrial regions, although some of the ideas discussed may also be of relevance to aquatic or marine environments.

In the past, conservation areas have often been selected in an ad hoc or opportunistic manner or based on considerations other than biodiversity conservation. However, during the past two decades substantial effort has been devoted to developing more explicit or systematic techniques for prioritizing and selecting protected areas to conserve biodiversity. Some of these techniques rely primarily on the intuition of experts familiar with the biota of a region (e.g., Dinerstein et al., 1995, 2000). Such expert-driven approaches are increasingly being supplemented by data-driven approaches in which spatial data on biodiversity and other environmental and socioeconomic factors are used to guide decision-making (Pressey et al., 1993; Pressey, 1999a; Margules and Pressey, 2000). These approaches are inherently quantitative, and often use computer-based decision-support tools to assist in prioritizing and selecting conservation areas. Despite the recent proliferation of data-driven approaches, algorithms, and software packages for use in systematic conservation planning, most of these techniques share a common purpose. Because in any given region the total amount of land that can be managed for conservation is limited by various social and economic factors, the basic purpose of systematic conservation planning is to establish a system of conservation areas that maximizes long-term conservation of biodiversity, subject to socioeconomic constraints.

To achieve this purpose, systematic planning must address considerations of both pattern and process (Smith et al., 1993; Cowling et al., 1999; Margules and Pressey, 2000). Conservation areas not only should be selected to include or represent as many elements of biodiversity as possible, but also should be sufficiently large, well-connected,

and well-replicated to promote long-term persistence of this diversity. Much of the early literature on systematic conservation planning focused on techniques for maximizing representation of biodiversity in conservation areas (reviewed by Pressey et al., 1993; Williams, 1998a; Margules and Pressey, 2000). The more recent literature points to an increasing interest in extending these earlier techniques to better address the problem of persistence (e.g., Balmford et al., 1998; Nicholls, 1998; Cowling, 1999; Cowling et al., 1999; Araújo and Williams, 2000; Margules and Pressey, 2000; Williams and Araújo, 2000; Cabeza and Moilanen, 2001; Faith et al., 2001). This requires consideration of a daunting array of factors, including vulnerability to threatening processes, the effects of reserve size and connectedness on population viability, and the role played by ecological and evolutionary processes in maintaining existing levels of diversity and ongoing diversification. Despite the vital importance of this work, it would be wrong to interpret the recent shift in focus towards process-related issues as somehow implying that the challenge of designing conservation areas to achieve representation of existing patterns of biodiversity has already been conquered.

Admittedly a wide choice of algorithms and software packages now exist to help design representative systems of conservation areas (e.g., Bedward et al., 1992a; Church et al., 1996; Csuti et al., 1997; Pressey, 1999b; Ferrier et al., 2000a; Possingham et al., 2000), thanks to nearly two decades of research and development work in this field. However, all of these techniques require information on the spatial distribution of biodiversity throughout a region of interest. Such data are an essential prerequisite to any quantitative assessment of the effectiveness of alternative configurations of conservation areas. In an ideal world, regional conservation planning would be based on a complete and detailed knowledge of the distribution of all entities of biodiversity (genes, populations, species, communities, ecosystems) occurring within the region of interest. In reality, our knowledge of the distribution of individual biodiversity entities is far from complete. Even in relatively data-rich regions, most entities—particularly at the species and genetic levels—are yet to be discovered, let alone have their distributions surveyed and mapped. A common

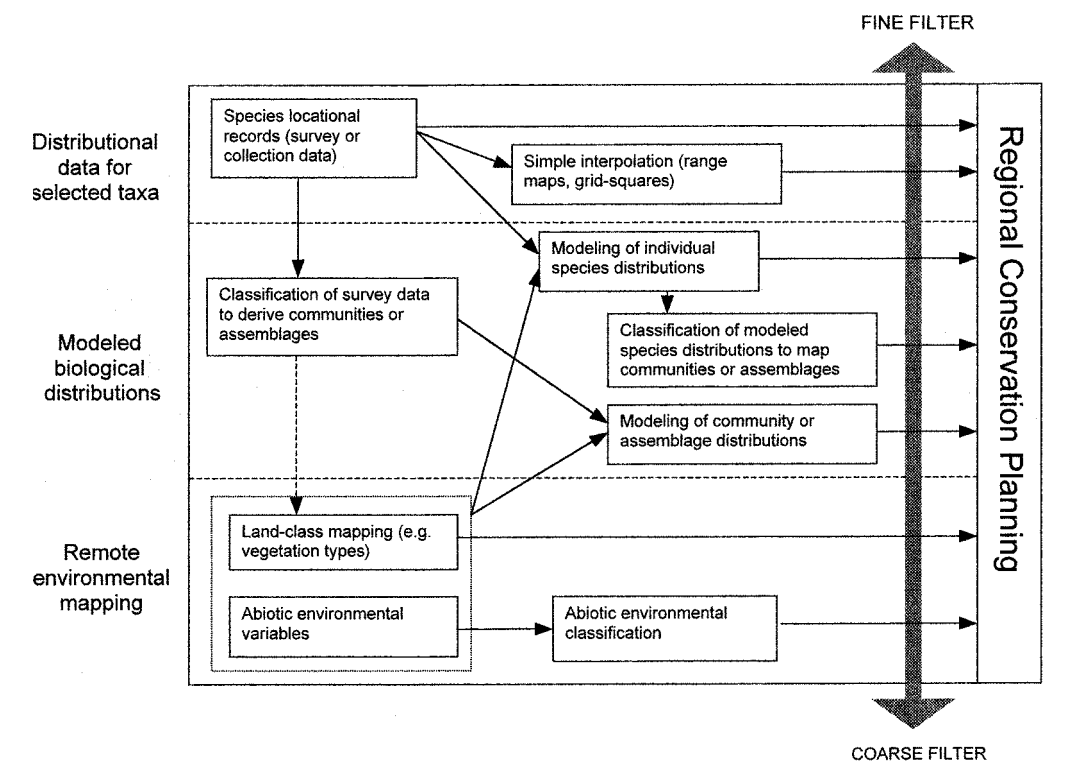


FIGURE 1. Surrogates commonly used in regional conservation planning to achieve representation of spatial pattern in biodiversity.

solution to this problem is to use those entities for which we do have distributional information as surrogates for spatial pattern in biodiversity as a whole (Fig. 1) (Noss, 1990; Humphries et al., 1995; Vane-Wright, 1996; Ferrier, 1997; Margules and Pressey, 2000).

BIODIVERSITY SURROGATES: THE STATUS QUO

Distributional data for selected species, or higher taxa (e.g., genera, families), are often used as surrogates in conservation planning. Such surrogates can include individual species of particular ecological or social significance (e.g., threatened, focal, or flagship species [Lambeck, 1997; Simberloff, 1998; Caro and O'Doherty, 1999; Chase et al., 2000]) or all species within one or more indicator groups (e.g., beetles [Anderson and Ashe, 2000] or butterflies [Kremen, 1994]). However, the use of selected species as surrogates for the rest of biodiversity presents two potential problems. The first problem concerns the level of congruence

between distributional patterns exhibited by surrogate species and the patterns exhibited by biodiversity as a whole. Despite considerable work on this question (e.g., Prendergast et al., 1993; Balmford, 1998; Howard et al., 1998; Reid, 1998; van Jaarsveld et al., 1998a; Moritz et al., 2001), no definitive answers have yet emerged. Apparently, cross-taxon congruence can vary greatly depending on the particular taxa being investigated, the biogeographic history of the region concerned, and the spatial scale of analysis.

The second problem in using species as surrogates in conservation planning relates to the geographical coverage of available data. Most distributional data are ultimately derived from locational records; that is, a species is observed or collected at a particular geographical location (Kress et al., 1998; Funk et al., 1999; Soberón et al., 2000). Although access to locational data held by museums throughout the world is improving at a rapid rate, thanks to initiatives such as the Internet-based Species Analyst (Vieglais, 1998; Krishtalka and Humphrey, 2000), the geographical coverage of such information

is extremely sparse for most regions. Survey or collection sites are often separated by extensive areas of unsurveyed land, and the location of such sites is usually biased towards population centers and access routes (Margules and Austin, 1994; Cooper and du Plessis, 1998; Lawes and Piper, 1998; Maddock and du Plessis, 1999; Soberón et al., 2000). A species may incorrectly appear to be absent from a particular location simply because that location has never been surveyed. The problem posed by false-absences is less severe for global- or continental-scaled conservation assessments, where the spatial units of analysis (e.g., coarse grid-cells or whole ecoregions) are sufficiently large for each unit to have a high probability of containing survey or collection data. However, the situation changes dramatically when moving to the finer spatial scale at which most regional conservation planning must be performed (i.e., prioritizing conservation action *within* rather than *between* regions). The spatial framework for conservation decisions at this scale usually consists of relatively small planning units (e.g., individual watersheds or cadastral parcels), of which a region may contain many thousands (Davis et al., 1999; Heijnis et al., 1999; Richardson and Funk, 1999; Ferrier et al., 2000a; Nix et al., 2000). In most cases only a very small proportion of such units will have been subjected to any kind of direct biological survey (Ferrier, 1991, 1997; Freitag and van Jaarsveld, 1995; Freitag et al., 1996).

Simple forms of spatial interpolation are often used to fill gaps in the geographical coverage of locational information. Range maps, such as those depicted in biological field-guides and handbooks, provide a broad interpolation of species distributions. These may be useful for coarse-scaled conservation assessments but are generally unsuitable for finer-scaled regional planning (Freitag and van Jaarsveld, 1995; Pressey and Ferrier, 1995; Freitag et al., 1996; Fjeldsø and Rahbek, 1997; Lawes and Piper, 1998; van Jaarsveld et al., 1998b; Fjeldsø et al., 1999). This is because, in alleviating the problem of false-absences, use of range maps at fine spatial scales introduces a new type of problem involving false-presences. A given species is assumed to be present in all planning units within the mapped range of that species, whereas in reality, the species probably occurs in only a proportion of these units,

being absent from the remainder due to a lack of suitable habitat or because of other fine-scale factors. Another popular technique for interpolating locational records is to assign these records to larger grid-cells within a matrix of cells superimposed over the region of interest (Williams, P., et al., 1996; Williams, P. H., et al., 1996; Kress et al., 1998; Lombard et al., 1999; Maddock and du Plessis, 1999; Richardson and Funk, 1999; Soberón et al., 2000). If planning units are substantially smaller than the grid-cells to which locational records have been assigned, then this procedure may again result in a high rate of false-presences when the data are used in conservation planning. Reducing the size of the grid-cells used to represent locational information may reduce the frequency of false-presences but can also simultaneously increase the frequency of false-absences, particularly if the density and coverage of underlying locational records are poor. Where conservation planning decisions need to be made at a relatively fine spatial scale in regions with sparse biological data, it may be impossible to find a cell size for representing biological distributions that keeps both false-absence and false-presence rates acceptably low.

An alternative strategy for overcoming problems caused by sparse biological data is to base regional conservation planning on data derived from remote environmental mapping. Rather than attempting to map distributions of individual species, the region of interest can instead be divided into a discrete set of land-classes (e.g., ecosystems, vegetation types) that are believed to concord with patterns in the distribution of biodiversity as a whole and can therefore be used as surrogates in regional conservation planning (Austin and Margules, 1986; Bourgeron, 1988; Hunter et al., 1988; Hunter, 1991; Franklin, 1993; Klijn and Udo de Haes, 1994; Lapin and Barnes, 1995; Naveh, 1995; Noss, 1996; Bowker, 2000). By mapping land-classes and then designing a system of conservation areas to include examples of each class, planners assume that most species associated with these classes will also be conserved. The principal advantage of land-classes is that, unlike individual species, they can often be mapped remotely, thereby providing information covering all planning units within a region relatively cheaply and rapidly.

Major ecosystems and vegetation types can be mapped by manual or automated interpretation of images generated by various forms of remote sensing (e.g., aerial photography, satellite imagery) supplemented, where possible, by ground-truthing. The entire land surface of the planet is now covered by medium-scale (1-km<sup>2</sup> grid resolution) digital mapping of broad ecosystem types derived from satellite imagery (Loveland et al., 2000). More detailed ecosystem or vegetation mapping is also available for many regions. In some cases these detailed vegetation maps are derived through a combination of remote sensing and direct field observation by experts, or just field observation alone. Vegetation maps based at least partly on field observation are likely to be more accurate, and therefore more useful for conservation planning, than are maps based exclusively on remote sensing.

Alternatively, environmental classes, or domains, can be derived from abiotic environmental (climate, terrain, substratum) layers stored within a geographical information system (GIS) by using simple overlay techniques (Ferrier and Watson, 1997; Armstrong and van Hensbergen, 1999; Pressey et al., 2000) or more sophisticated numerical classification procedures (Mackey et al., 1989; Bernert et al., 1997; Fairbanks and Benn, 2000; Nix et al., 2000). Again, the entire planet is covered by data of potential use in deriving such environmental classifications. For example, complete coverage of digital elevation data is now available at 1-km<sup>2</sup> grid resolution (US Geological Survey, 2000). These data can be used to derive a wide range of abiotic indices by applying powerful new techniques for terrain- and climate-surface modeling (Moore et al., 1993; Hutchinson et al., 1997).

For land-classes to work effectively as a basis for regional conservation planning, there must be strong congruence between these mapped classes and the actual distributions of the myriad of species that make up biodiversity. Desirably, each species should occur in a high proportion of locations (planning units) mapped as belonging to a particular subset of land-classes and in a low proportion of locations within the remaining classes. Although the assumption of congruence between mapped land-classes and actual biological distributions has rarely been tested (Pressey, 1994; Ferrier and Watson, 1997), in

many situations this congruence is likely to be poor. Species may be distributed patchily within a land-class if they are responding to environmental variation at a spatial scale finer than that of the land-class mapping or to environmental variables other than those considered in deriving the classes. Patchiness in the distribution of species within land-classes can also result from a wide range of biological and historical factors (e.g., competition, predation, local extinction, presence of dispersal barriers).

### THE CHALLENGE AHEAD

Most of the regions identified by global assessments as being of high priority for conservation action are data-poor. Lack of adequate spatial data in such regions is often cited as a major impediment to implementing systematic planning approaches and is sometimes used as an argument against the general utility of these methods (Prendergast et al., 1999; Cabeza and Moilanen, 2001). Deficiencies in coverage and quality of biological data limit the wider applicability of many of the techniques currently used to map biodiversity patterns in relatively data-rich regions. In such situations, remotely-derived land mapping is often seen as the only practical basis for regional conservation planning (Franklin, 1993; Noss, 1996; Maddock and du Plessis, 1999; Nix et al., 2000; Pressey et al., 2000). By using various forms of remote mapping—for example, interpretation of satellite imagery or abiotic environmental classification—systematic planning techniques potentially can be applied to regions with very poor availability of biological data. This approach offers obvious benefits in terms of cost-effectiveness and rapidity of application. However, real risks are associated with relying too heavily on remote mapping as a basis for regional conservation planning. A system of conservation areas designed to maximize representation of land-classes may not maximize representation of biodiversity as a whole, particularly if congruence is poor between these classes and actual biological distributions.

In the rest of this paper I describe and discuss three strategies that may help alleviate some of the problems associated with using remotely mapped surrogates in conservation planning. My purpose is not to argue against the use of such surrogates but rather to

suggest some more effective ways in which limited biological data and knowledge might be used to guide and refine the application of these surrogates. I examine three strategies: (1) deriving better surrogates in data-poor regions by more closely integrating biological and environmental data through predictive modeling, with an emphasis on modeling collective properties of biodiversity rather than individual entities; (2) making better use of remotely mapped surrogates in conservation planning by incorporating knowledge of biological heterogeneity within land-classes, and of varying levels of biological distinctiveness between classes, into measures of conservation priority and achievement; and (3) using relatively data-rich regions as test-beds for evaluating the performance of surrogates that are readily applicable across data-poor regions.

#### DERIVING BETTER SURROGATES IN DATA-POOR REGIONS: USING MODELING TO INTEGRATE BIOLOGICAL AND ENVIRONMENTAL DATA

Both major types of data traditionally used in regional conservation planning—distributional data for selected species, and remote environmental mapping—have strengths and weaknesses. Biological survey or collection data provide direct information on the distribution of selected entities of biodiversity but usually have insufficient spatial coverage. Mapped land-classes readily provide complete spatial coverage, but their level of congruence with the actual distributions of species may be poor or, more often, simply unknown. Because the strengths of these two data types are complementary, it often makes good sense to use both approaches in parallel in regional conservation planning (Ferrier, 1997; Noss et al., 1999). An early, and widely applied, example of such integration is the so-called coarse-filter/fine-filter strategy (Noss, 1987). Conservation areas are selected to include examples of each member of a set of mapped land-classes (e.g., ecosystems or vegetation types), thereby sampling the broad biophysical variation encompassed by a region (the coarse filter), while at the same time including known locations of species of particular conservation concern (the fine filter).

Using biological and environmental data in parallel, as in the coarse-filter/fine-filter

strategy, may not take full advantage of the information contained within these datasets. Some of this information can be extracted only by examining relationships between patterns exhibited by the two types of data. For example, records for a given species (or group of species) may be concentrated within a particular set of land-classes or a particular combination of environmental conditions, thereby providing a basis for extrapolating biological distributions across areas that have not yet been surveyed. Numerous analytical techniques have been developed during the past 20 years for modeling biological distributions in relation to remotely mapped variables.

#### *Current Modeling Approaches*

The best known, and most widely used, modeling approach involves modeling distributions of individual species in relation to mapped land-classes (e.g., vegetation types) or environmental variables (e.g., climate, terrain, substratum variables). At its most basic level this may simply entail using expert knowledge to define the habitat requirements of a species in terms of a combination of mapped variables, (e.g., “species *x* occurs in areas of tall eucalypt forest, with a mean annual rainfall between 1500 and 2000 mm, and a soil fertility index >3”). The mapped distribution of areas satisfying such requirements can be readily derived with basic GIS techniques (Scott and Jennings, 1998). Alternatively, biological survey or collection data can be used in conjunction with statistical or heuristic model-fitting techniques, to induce a model describing the relationship between known locations of a species and a suite of environmental variables (see reviews by Franklin, 1995; Ferrier and Watson, 1997; Austin, 1998; Guisan and Zimmermann, 2000). Again, GIS can be used to extrapolate and map distributions predicted by such statistical models. Modeling distributions of individual species can be viewed as a way of reducing the frequency of false-absences inherent in raw locational datasets, while at the same time avoiding the increased frequency of false-presences incurred by using coarse-scaled range mapping.

By linking statistical modeling with numerical classification techniques, we can also model distributions of species assemblages

or communities, rather than individual species (Franklin, 1995; Margules and Redhead, 1995; Guisan and Zimmermann, 2000; Ferrier et al., 2002). This is usually achieved using one of two strategies: (1) classification-then-modeling, in which the available biological survey data are first subjected to numerical classification, thereby deriving either groups of sites with similar species (i.e., communities) or groups of species that occur at similar sites (i.e., species assemblages), and then the distributions of these groups are modeled in relation to mapped environmental variables (e.g., Moore et al., 1991; Keith and Bedward, 1999); or (2) modeling-then-classification, in which the distributions of individual species are first modeled and extrapolated, and these predicted distributions are then subjected to numerical classification, thereby again deriving mapped communities or species assemblages (e.g., Lenihan, 1993; Austin, 1998).

#### *Shifting the Focus from Entities to Collective Properties*

Modeling of individual species, or higher-level entities of biodiversity (species assemblages or communities), works well in regions with good coverage and density of biological survey or collection data (Ferrier and Watson, 1997; Austin, 1998; Guisan and Zimmermann, 2000). However, these approaches are likely to be less effective in regions with very sparse or biased coverage of biological data. An individual species can be modeled successfully only if sufficient locational data (or expert knowledge of habitat requirements) are available for that species. Modeling of individual species is also a relatively time-consuming and expensive process. For these reasons, use of modeled distributions in regional conservation planning is often restricted to a relatively small number of priority species, such as selected vertebrate or vascular plant species of special conservation concern. At the species level, and even at the community and assemblage levels, many of the biodiversity entities warranting consideration in conservation planning may not have been surveyed at all, let alone surveyed to the extent needed to facilitate distributional modeling. The additional survey effort required to bring these data to a suitable standard will often be unachievable, given the tight financial

and temporal constraints usually imposed on real-world planning projects.

This problem is most severe in poorly surveyed regions rich in biological diversity, particularly those in the tropics. Even for relatively well known groups such as vascular plants, any approach to mapping biodiversity based on modeling of individual entities is likely to be rendered impracticable by the sheer number of taxa involved and the paucity of data for most of these taxa, many of which will be range-restricted. This situation only gets worse if we consider the more diverse and less well-known groups, such as invertebrates. If we are serious about confronting the challenge of mapping spatial pattern of biodiversity as a whole in highly diverse yet data-poor regions, then we probably need to look beyond approaches based on modeling individual biodiversity entities.

A promising alternative in such situations is to shift the focus of modeling from individual entities to collective properties (Austin, 1999) of biodiversity. To date, the most widespread manifestation of this alternative strategy has involved modeling of species richness. A now sizeable literature describes regional-scaled regression models that relate species richness, recorded at a sample of locations within a region, to a range of remotely mapped environmental variables (e.g., Birks, 1996; Heikkinen and Neuvonen, 1997; Nøhr and Jørgensen, 1997; Leathwick et al., 1998; Lwanga et al., 1998; Wohlgemuth, 1998). Although such models enable patterns of species richness to be extrapolated across entire regions at a reasonably fine spatial scale, they have rarely been used in regional conservation planning because species richness, in itself, does not provide an adequate basis for designing a representative system of conservation areas. To understand why, consider an example in which 10 planning units must be selected for conservation from a total set of 100 units. Assuming that species richness has been estimated for each unit, a simple selection strategy might be to select those 10 units with the greatest richness values. However, such a strategy is unlikely to maximize the total number of species conserved. The selected units may all occur in similar environments and therefore share a large proportion of species. If so, the resulting system of conservation areas will probably fail to include

species that occur only within planning units of lesser species richness. To maximize the number of species represented by a selected set of units requires additional information describing patterns of dissimilarity in species composition, or complementarity (Pressey et al., 1993), between units.

Complementarity has traditionally been viewed as a property of the relationship between pairs (or sets) of planning units that can be estimated only after appropriate surrogate data (e.g., vegetation types or species occurrences) have been assembled for these units (Pressey et al., 1993; Howard et al., 1998; Reyers et al., 2000; Virolainen et al., 2000; Williams et al., 2000). Here I adopt an alternative view in which complementarity is considered explicitly in the initial derivation of surrogates, thereby opening up new possibilities for modeling spatial patterns of biodiversity in data-poor regions. Before the term biodiversity was even invented, Whittaker (1972, 1977) introduced a conceptual framework for partitioning species diversity into seven components. Four of these components describe levels of inventory diversity—the total numbers of species occurring *within* areas of various sizes (e.g., an individual sampling point, a homogeneous patch of habitat, a landscape, or a large region). The other three components describe levels of differentiation diversity—the change in composition of species *between* different sampling points, habitats, or geographical locations. Despite considerable inconsistency in definition and terminology in the subsequent literature, three components of diversity—one of inventory diversity and two of differentiation diversity—have emerged as being of particular relevance to regional conservation planning: (1) alpha ( $\alpha$ ) diversity, the number of species (i.e., species richness) in a homogeneous patch of a given type of habitat or environment; (2) beta ( $\beta$ ) diversity, the difference in composition of species between different habitats or environments located close together in the same landscape; and (3) gamma ( $\gamma$ ) diversity, the difference in composition of species between geographically isolated occurrences of the same habitat or environment (Cody, 1975, 1993; Cowling, 1990; Pimm and Gittleman, 1992; Tuomisto et al., 1995; Simmons and Cowling, 1996; Ferrier et al., 1999; Scott et al., 1999; Purvis and Hector, 2000). Note that some authors re-

fer to  $\gamma$  as delta ( $\delta$ ) diversity (Whittaker, 1977; Stoms and Estes, 1993; McNaughton, 1994; Scott and Jennings, 1998; Vanclay, 1998).

If we could estimate both the species richness ( $\alpha$  diversity) of individual planning units within a region, and the level of compositional dissimilarity ( $\beta$  and  $\gamma$  diversity) between these units, we would be in a good position to predict the total level of diversity sampled (represented) by alternative sets of planning units. Such predictions could in turn provide a basis for selecting a set of units that maximizes representation of regional diversity. This raises an interesting question: Can patterns of differentiation diversity be modeled across a region in a similar fashion as existing modeling of species richness? One might argue that any use of remote environmental mapping as a surrogate for biodiversity is based on an implicit model of differentiation diversity. Consider, for example, the increasingly popular approach of using remotely derived abiotic variables to divide a region into environmental classes, by either numerical classification or simple GIS overlay. This approach is underpinned by a key assumption—that the measure of environmental dissimilarity used to derive classes is a good predictor of biological dissimilarity (i.e., differentiation diversity). However, to estimate environmental dissimilarity based on a set of environmental variables, one must make decisions as to the weighting and scaling of these variables. By transforming variables in different ways (e.g., applying a log transformation to mean annual rainfall) and applying different weighting schemes to these variables when estimating environmental dissimilarity, markedly different classifications can be obtained for the same region from the same input data. The effectiveness with which these alternative classifications function as biodiversity surrogates is likely to vary, depending on how closely the weighting and scaling of variables in each classification matches biological reality. Yet, in most applications of abiotic environmental classification, variables are weighted and scaled in a largely arbitrary manner.

One way of making the weighting and scaling of environmental variables less arbitrary is to use available biological data to fit a statistical model that explicitly predicts differentiation diversity as a function of environmental diversity. In other words, available biological data can be used to constrain



the way in which environmental variables are combined to measure environmental dissimilarity, such that the correlation between environmental dissimilarity and biological dissimilarity is maximized.

### *A New Approach to Modeling Differentiation Diversity*

Consider a set of biological survey sites scattered across a region of interest. At each site, species in a given biological group (e.g., plants, reptiles, beetles) have been recorded as either present or absent. The compositional dissimilarity (Faith et al., 1987; Colwell and Coddington, 1994; Williams, 1996) between all pairs of sites can be calculated using, for example, the Bray–Curtis measure (Bray and Curtis, 1957) to generate a sites-by-sites dissimilarity matrix. The values in this matrix will vary between 0 (for two sites that have exactly the same species) and 1 (for two sites that have no species in common).

One possible approach to modeling such a dataset is to use permutational matrix regression (Manly, 1986; Smouse et al., 1986; Legendre et al., 1994) to model the level of compositional dissimilarity between pairs of sites as a function of the environmental and geographical separation of these sites. Matrix regression is an extension of the popular matrix correlation approach to testing correlations between distance matrices (Burgman, 1987; Legendre, 1993). In its original form, the technique is simply a multiple linear regression performed by using data from two or more symmetric matrices, with significance testing based on Monte Carlo permutation to overcome the problem of lack of independence between site pairs. In the application of interest here, the response variable consists of values from the sites-by-sites compositional dissimilarity matrix (Poulin and Morand, 1999; Ferrier et al., 1999). Each explanatory variable is also prepared as a sites-by-sites matrix. For example, to relate compositional dissimilarity to mean annual rainfall, a matrix is prepared in which each value is the difference in rainfall between a pair of sites. Ferrier et al. (1999) used matrix regression to analyze regional patterns of differentiation diversity in ground-dwelling arthropods, vertebrates, and vascular plants in northeast New South Wales.

A potential problem in using matrix regression to model patterns of differentiation

diversity is that the assumption of linearity underpinning the technique is unlikely to be satisfied in most real-world datasets. As is well-established, the relationship between ecological separation of sites and observed compositional dissimilarity is not linear but instead curvilinear (Gauch, 1973; Faith et al., 1987). Most measures of dissimilarity (including the Bray–Curtis measure) are constrained between 0 and 1. As ecological separation increases, sites share progressively fewer species until, once no species are shared, the dissimilarity measure takes on a constant value of 1 regardless of how much further the ecological separation is increased. The relationship between ecological separation and compositional dissimilarity is therefore asymptotic, approximately linear when ecological separation is small but approaching an asymptote of 1 as separation increases. The matrix regression approach described above assumes a linear relationship between ecological separation and compositional dissimilarity. This approach is therefore unlikely to perform well when applied to datasets collected in regions exhibiting high differentiation diversity and therefore containing compositional dissimilarities close to, or equal to, 1.

A further assumption inherent in the above approach is that the rate of compositional change, or turnover, remains constant across the range of a given environmental variable. For example, a 300-mm difference in mean annual rainfall between two sites with rainfalls of 600 and 900 mm, respectively, is assumed to result in the same level of compositional change as between two sites with rainfalls of 2,500 and 2,800 mm. Violations of this assumption may be common in real-world datasets (Whittaker, 1977; Wilson and Mohler, 1983; McNaughton, 1994; Oksanen and Tonteri, 1995; Simmons and Cowling, 1996), partly because environmental variables are measured on essentially arbitrary scales. The measurement scale used for a given environmental gradient may not necessarily concord well with patterns of compositional change in the biota occurring along that gradient (e.g., log-transformed rainfall may provide better concordance than untransformed rainfall).

My research group has recently extended and refined the technique of matrix regression to address both of these problems (Fig. 2). In the resulting approach, referred

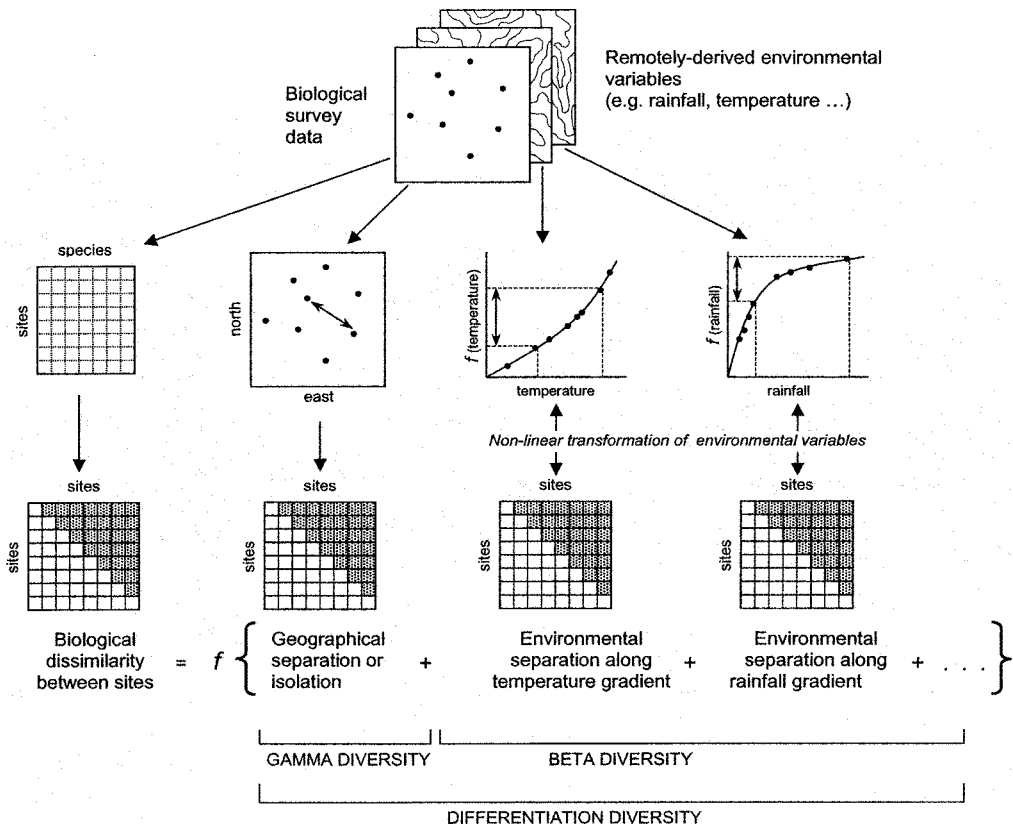


FIGURE 2. Diagrammatic illustration of the generalized dissimilarity modeling (GDM) approach to modeling differentiation diversity.

to as generalized dissimilarity modeling (GDM) (Ferrier et al., 2002; Ferrier et al., unpubl. manuscript), models are fitted by using generalized linear modeling (McCullagh and Nelder, 1989) instead of ordinary linear regression. The curvilinear relationship between ecological separation and compositional dissimilarity is accommodated through specification of appropriate link and variance functions. Variation in the rate of compositional turnover along environmental gradients is accommodated through automated nonlinear transformation of environmental variables, which we achieve using monotonic I-splines, based on the method described by Winsberg and De Soete (1997). The GDM approach is also being adapted to better handle biological data collected by ad hoc surveys (i.e., presence-only data rather than presence/absence data) and to accommodate interactions between environmental predictors (e.g., allowing the rate of compositional turnover relating to soil fertility to vary

with mean annual rainfall). A more detailed description of the approach is provided in Ferrier et al. (2002). Matrix regression approaches, including GDM, provide a natural means of incorporating geographical separation as an additional predictor in modeling of compositional dissimilarity. To date, most abiotic environmental classifications used in conservation planning have ignored the important role that geographical separation or isolation can play in shaping spatial pattern in biodiversity. Such classifications usually focus exclusively on  $\beta$  diversity, that is, the change in composition of species between different habitat types or environments. Two areas of exactly the same abiotic environment or habitat type are assumed to contain the same set of species, regardless of where these areas are located within the region of interest. In reality, compositional dissimilarity between two areas of the same habitat type is likely to be greater if these areas are well-separated

geographically than if they are located close together. This is the phenomenon of  $\gamma$  diversity. The importance of  $\gamma$  diversity relative to  $\beta$  diversity is likely to vary depending on the extent and biogeographic history of the region involved and on the vagility of the taxa of interest (Ferrier et al., 1999; Nekola and White, 1999). Geographical turnover in species composition within a given environment or habitat type is expected to be high in regions in which historical barriers to dispersal have promoted vicariant evolution, particularly within taxa of low vagility. At the most basic level,  $\gamma$  diversity can be considered in matrix regression modeling by using the straight-line (i.e., Euclidean) distance between pairs of sites as a simple measure of geographical separation (Ferrier et al., 1999). Alternatively, more sophisticated measures of isolation potentially may be derived by using remotely mapped environmental data—linked, where possible, to palaeoclimatic modeling—to estimate the level of impedance to dispersal between sites.

Matrix regression (including GDM) is only one of several multivariate techniques that could be used to model patterns of differentiation diversity in relation to environmental and geographical gradients. Constrained ordination techniques such as canonical correspondence analysis (CCA) and redundancy analysis (RDA) (ter Braak, 1986; Jongman et al., 1995) have been applied widely in ecology to analyze relationships between biological and environmental datasets. These techniques generate ordination axes constrained to be linear combinations of environmental variables. Although such analyses provide a potential basis for extrapolating patterns of differentiation diversity, they rarely have been used in regional conservation planning (although see Kremen, 1992, 1994; Sætersdal and Birks, 1993; Taggart, 1994; Faith et al., 2001). For conservation planning applications, GDM offers several advantages relative to existing constrained ordination techniques (Ferrier et al., 2002), and these advantages will, one hopes, engender increased interest in modeling differentiation diversity.

#### *Benefits of Modeling Differentiation Diversity*

The modeling approach just described offers a relatively simple and cost-effective

means of modeling, and thereby mapping, spatial patterns of differentiation diversity in data-poor regions. The approach can take direct advantage of the ever-improving spatial coverage and resolution of remotely derived data, including abiotic environmental layers (e.g., the global 1-km digital elevation model and derived topographic and climatic variables) and land-cover data extracted from satellite imagery (either raw spectral data or derived land-classes). Using available biological survey data to model differentiation diversity as a function of variation in these remote data layers confers two important advantages over traditional forms of environmental classification. First, such modeling can provide a more objective (i.e., less arbitrary) basis for weighting and scaling environmental variables, thereby improving the accuracy with which patterns of  $\beta$  diversity can be predicted. Second, by allowing geographical separation or isolation to be incorporated as an additional predictor of compositional turnover, the approach provides a means of integrating considerations of both  $\beta$  diversity (environmental turnover) and  $\gamma$  diversity (geographical turnover).

By modeling collective properties of biodiversity (inventory or differentiation diversity) rather than modeling individual entities (species, communities, or assemblages), we can make more effective use of biological datasets with sparse or biased spatial coverage. To understand why this is so, imagine an extensive region encompassing high levels of  $\beta$  and  $\gamma$  diversity. Biological survey effort in the region has been both sparse and localized; that is, large areas of the region are devoid of any biological data. Deriving distributional models for entities of biodiversity (e.g., species) recorded in the available survey data may reveal little about patterns of biodiversity in these unsurveyed areas. Because rates of environmental and geographical turnover in species composition are high, species occurring in the surveyed areas are likely to be replaced by other species in unsurveyed areas. Modeling individual species, or other entities such as communities or assemblages, has limited capacity to make predictions about spatial pattern in biodiversity beyond the environmental and geographical limits of the particular entities involved. This limitation is much less severe when making predictions based on modeling of collective properties

such as differentiation diversity. To extrapolate patterns of differentiation diversity from surveyed to unsurveyed areas, we need only assume that rates of environmental and geographical turnover in species composition observed in the surveyed areas will be similar in the unsurveyed areas. We can therefore make predictions about spatial pattern in biodiversity across areas for which we have no knowledge of the exact identity of taxa occurring in these areas. Where appropriate, modeling of differentiation diversity within one region (e.g., an ecoregion) might even be used to extrapolate patterns across other regions with similar environments and biogeographic histories.

Another advantage of modeling differentiation diversity, rather than individual entities of biodiversity, is an improved capacity to analyze datasets containing high levels of taxonomic diversity (i.e., large numbers of taxa). Such datasets are likely to become more common as a result of increasing research interest in the biodiversity of less conspicuous, yet extremely diverse, taxa (e.g., arthropods) and increasing application of techniques for rapid biodiversity assessment, including parataxonomic approaches (Oliver and Beattie, 1993, 1996; Basset et al., 2000). Modeling the distributions of individual taxa included in such datasets would be a daunting task, particularly given that a large proportion of these taxa are likely to have been recorded at only a very small number of sites. On the other hand, modeling differentiation diversity not only copes readily with high levels of taxonomic diversity but also is likely to attain greater power in detecting patterns of compositional turnover as the total number of taxa and the frequency of rarer (narrow-range) taxa are increased.

The discussion so far has assumed that differentiation diversity is measured simply in terms of dissimilarity in species composition; that is, how little overlap there is between species lists obtained at different sites. A final, yet vitally important, advantage of matrix regression modeling is the flexibility with which this technique can be applied to other measures of differentiation diversity. Potentially, any measure of biological dissimilarity or divergence between sites can be used as a response in place of compositional dissimilarity. Possibilities include measures of phylogenetic distance derived from information

on phylogenetic relationships within a set of taxa, or measures of genetic differentiation within a single taxon (Moritz, 1995; Moritz and Faith, 1998; Smith et al., 2000).

### *Potential Applications in Regional Conservation Planning*

There are two main ways in which modeling of differentiation diversity might be used in regional conservation planning (Fig. 3). The first alternative involves using predictions from such models to constrain, or guide, the derivation of environmental classifications. Consider, by way of illustration, a region covered by gridded (e.g., 1-km<sup>2</sup>) GIS data for several remotely mapped abiotic environmental and land-cover variables. Numerical classification techniques can be used to divide such a region into environmental classes or domains. This is ordinarily achieved by using the available environmental data to estimate levels of environmental similarity or dissimilarity between all grid-cells within the region, thereby providing a basis for numerically clustering similar grid-cells into groups. However, by using predicted biological dissimilarities between grid-cells (e.g., from a model fitted using GDM) instead of environmental dissimilarities, a classification can be derived that is likely to better reflect regional patterns of  $\beta$  and  $\gamma$  diversity. Classes produced this way can then be used in conservation planning exactly the same way as any other remotely mapped land classification.

The second alternative involves a more direct use of predicted biological dissimilarities in prioritizing and selecting conservation areas. Faith and Walker (1996a, 1996b) pioneered the development of new techniques for selecting conservation areas through use of continuous environmental data instead of discrete land classifications. In their approach, the representativeness of alternative sets of conserved sites (or planning units) is measured in terms of how well these sites cover the multidimensional environmental space encompassed by a region. The environmental diversity (ED) measure is calculated directly from environmental distances between pairs of sites in this multidimensional space. By replacing environmental dissimilarities with predicted biological dissimilarities based on GDM, derived estimates of ED are once again likely

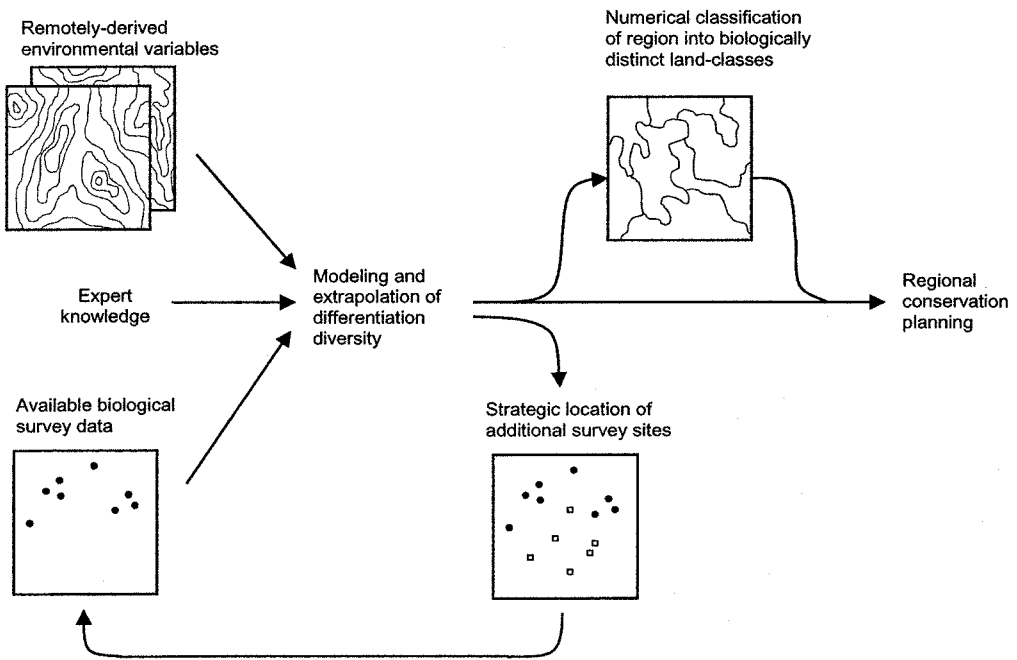


FIGURE 3. Integrated strategy for applying modeling of differentiation diversity in regional conservation planning.

to better reflect real patterns of  $\beta$  and  $\gamma$  diversity. The general idea of viewing spatial pattern in biodiversity as a continuum deserves more attention in conservation planning (an issue to which I return in the next section; see also DeVelice et al., 1988; Sætersdal and Birks, 1993; Debinski and Brussard, 1994; Taggart, 1994; Belbin, 1995; Araújo et al., 2001). Combining predictions of differentiation diversity between planning units (e.g., by using GDM) with predictions of  $\alpha$  diversity within planning units (based on modeling of species richness) also provides the scope to develop more explicit measures of representativeness to guide the prioritization and selection of conservation areas—estimates, for example, of the proportion of total species diversity of a region represented by a given conservation scenario. Recent advances in the theory of predicting regional diversity from local estimates of richness and turnover offer some hope in this regard (e.g., Lande, 1996; Mawdsley, 1996; Hubbell, 1997; Harte et al., 1999; Plotkin et al., 2000; Wagner et al., 2000).

Approaches such as ED, which can measure representativeness in terms of an environmental continuum, also have particular application in the design of biological

surveys. Given likely constraints on available time and resources for conducting further survey work in data-poor regions, it is crucial that any such surveys are cost-effective—that they be designed to return a maximum amount of information per unit survey effort (Austin and Heyligers, 1989; Ferrier and Smith, 1990; Raven and Wilson, 1992; Haila and Margules, 1996; Debinski and Humphrey, 1997; Wessels et al., 1998; Vanclay, 1998; Balmford and Gaston, 1999; Fisher, 1999). Locating survey sites to maximize sampling of environmental or biological diversity within a region is a problem very similar to that of locating conservation areas to maximize representation of biodiversity. My research group has recently linked modeling of differentiation diversity (using GDM) with a GIS-based tool for locating biological survey sites to maximize the proportion of diversity sampled within a region (using ED). The tool can also incorporate constraints imposed by accessibility. This type of integration provides an objective basis for cost-effectively refining information on the spatial pattern in biodiversity within data-poor regions.

An iterative strategy for achieving such refinement is illustrated in Figure 3. In this

strategy, existing biological data are used to derive an initial model of differentiation diversity, which serves as a basis for strategically locating additional survey sites to maximize improvement in the environmental and geographical coverage of sampling. Data from these additional surveys are then used to evaluate and refine the initial model, thereby providing an improved basis for selecting any further survey sites. By repeating this process iteratively, information on the spatial pattern in biodiversity can be refined progressively over time, subject to the availability of resources to conduct survey work. In many regions, the existing data may be insufficient to derive an initial model of differentiation diversity. In such situations expert knowledge of biological patterns can be used to specify initial parameters for the model, thereby providing a basis for locating an initial set of survey sites. The iterative strategy depicted in Figure 3 is currently being trialed in regions in Australia and Guyana (the latter using data described in this issue by Funk and Richardson, pp. 303–316).

#### MAKING BETTER USE OF SURROGATES IN CONSERVATION PLANNING: ADDRESSING HETEROGENEITY AND DISTINCTIVENESS

It makes good sense to devote effort to ensuring that remote environmental mapping reflects real patterns of biodiversity as accurately as possible. However, regardless of the mapping approach used, concordance between remotely mapped land-classes and actual distributions of individual entities of biodiversity (e.g., species) will never be perfect. Any given species may occur in more than one land-class and may often be distributed patchily within each of these classes. Each land-class will therefore exhibit internal biological heterogeneity, and different pairs of land-classes will vary in the extent to which they share species (i.e., distinctiveness). Yet regional conservation planning usually treats land-classes as if they were homogeneous units, equally distinctive from one another. Better incorporation into conservation planning of knowledge of heterogeneity within, and distinctiveness between, land-classes may greatly enhance the effectiveness of remote environmental mapping as a surrogate for spatial pattern in biodiversity.

#### *Problems Relating to Heterogeneity and Distinctiveness*

Consider a hypothetical region divided into discrete planning units (e.g., watersheds) that will serve as candidate areas, or building blocks, for designing a representative system of conservation areas (Fig. 4). The region is also covered by some form of remotely mapped land classification. The exact nature of this classification is of no great importance; it could be a map of ecosystems or vegetation types derived from interpretation of satellite imagery or aerial photography, a purely abiotic environmental classification, or a classification derived through integrated analysis of environmental and biological data (e.g., by using the GDM approach discussed in the previous section). For the sake of simplicity, assume that, although each land-class can occur in multiple planning units, each planning unit is covered by a single class; that is, planning units are nested within land-classes. An objective of systematic conservation planning in such a region might be to design a system of conservation areas that would include a specified proportion (e.g., 10%) of the total extent of each land-class. These conservation areas could be chosen manually or through some form of computer-based analysis. Numerous algorithmic approaches to solving this type of problem have been developed during the past 20 years. Most of these techniques attempt to identify a set of planning units that meets all conservation targets (in this case, a proportion of each land-class) while minimizing the cost of implementation. Cost may be measured either indirectly, in terms of total conserved area, or directly, in terms of estimated cost of acquisition or forgone opportunity for other land-uses.

By conserving a specified proportion of each land-class in a region such as this, are we necessarily achieving good representation of biodiversity as a whole? That probably depends not only on the quality and resolution of the mapping used but also on the exact approach used to locate conservation areas within each mapped class. All land-classes will contain at least some biological heterogeneity (Scott et al., 1989; Pressey and Logan, 1994). Many of the species occurring within a particular class (e.g., a mapped ecosystem or vegetation type) will be distributed patchily within

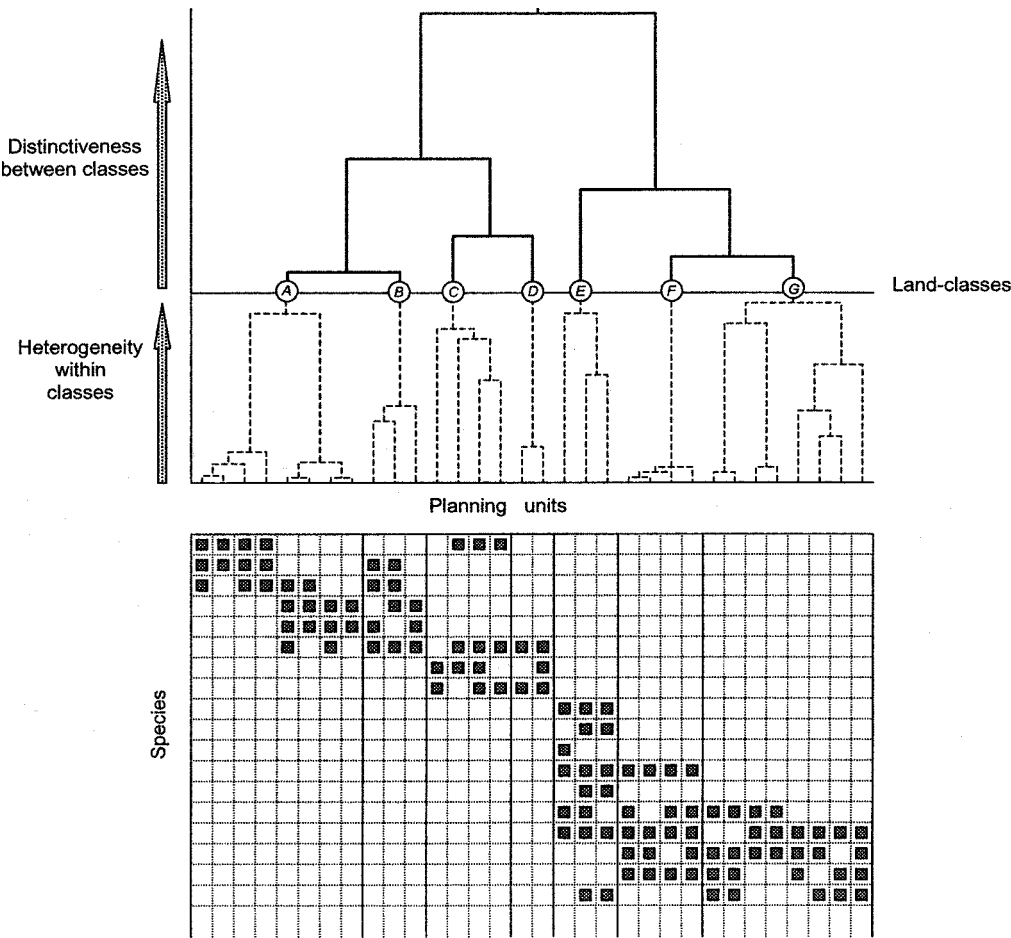


FIGURE 4. Illustration of patterns of heterogeneity within, and varying levels of distinctiveness between, seven hypothetical land-classes (e.g., environmental domains or vegetation types). The matrix at the bottom indicates the species actually occurring within each planning unit (e.g., watershed) covered by these land-classes. The dendrogram at the top depicts relative levels of dissimilarity between planning units, based on remotely mapped information, and is not derived from the biological data in the matrix below.

that class as the result of a wide range of factors, including fine-scaled environmental variation and stochastic processes of colonization and extinction within metapopulations. If the spatial grain of this patchiness is such that many species occur in only a subset of planning units within a given land-class, then these species will not necessarily be represented by simply conserving a specified proportion of the class. The theory of species–area relationships is often suggested as a means of predicting what proportion of species will be represented, or will persist, as a result of conserving a given proportion of a land-class or region (e.g., Soulé and Sanjayan, 1998; Rosenzweig, 1999; Kinzig and Harte, 2000; Pimm and Raven, 2000). However, a

major problem with such predictions is the assumption that the sampled (conserved) area within a land-class or region is distributed randomly relative to the distributions of individual species. In the real world, conservation areas are rarely chosen at random.

Within our hypothetical region, consider a land-class consisting of a mosaic of two community types that contain very different suites of species, with only a small proportion of species occurring in both types (e.g., land-class A in Fig. 4). One of the types occurs in the more productive areas of the class (e.g., flat topography with deep, fertile soil), and the other occurs in less productive areas (e.g., steep topography with shallow soil).

Imagine that 200 planning units are mapped as belonging to this land-class (only 8 of these units are depicted in Fig. 4) and that these are evenly divided between the two community types—100 planning units contain the first community, whereas the other 100 units contain the second community. Assuming that all of the planning units are of similar size, then to conserve 10% of the land-class, we need to conserve 20 planning units. If these 20 units were selected at random, then we would expect them to contain a reasonable mix of the two community types and thereby represent a high proportion of all species occurring within the land-class. However, a more likely scenario in the real world would be for the selection of units to be biased towards those that are least expensive to acquire or would cause least socioeconomic impact. In the above example this might well result in locating all 20 conserved planning units within less productive areas, thereby providing good representation of species occurring within one of the community types but failing to provide any representation of those species that occur only within the other community.

Selecting contiguous clusters of planning units to achieve good reserve design (e.g., large reserves with low perimeter-to-area ratio) is another factor that can result in biased sampling of internal heterogeneity within land-classes. The severity of this problem is likely to depend on the number of separate reserves established within a given land-class (i.e., degree of spatial replication), and the average size and spacing of these reserves relative to the spatial grain of biological heterogeneity within the class. Say, for example, the two community types in land-class A (Fig. 4) exhibit little spatial clumping at the planning unit scale; that is, planning units containing the two communities are well interspersed throughout the land-class rather than being clumped into groups of planning units of the same type. Conserving one contiguous block of 20 units within land-class A would then probably sample almost as much heterogeneity as would conserving 20 separate units scattered throughout the class. However, if the community types do exhibit a marked pattern of clumping, i.e., if planning units of a given type are clumped into large homogeneous patches, then conserving one contiguous block of 20 units would probably sample less heterogeneity

than would conserving 20 widely scattered units.

In general, the problem posed by heterogeneity within land-classes diminishes with increasing refinement in the spatial scale and classification resolution of mapping (Pressey and Bedward, 1991; Pressey and Logan, 1994, 1995). This problem is therefore often addressed by subdividing classes perceived to encompass unacceptably high heterogeneity, in an attempt to derive finer-scaled classes exhibiting greater homogeneity. With the advent of GIS technology, deriving very large numbers of classes for any region through environmental or geographical subdivision is now a relatively simple task. Although they may be easy to generate, dealing with large numbers of land-classes in conservation planning presents special challenges. Too often, conservation planning treats land-classes as a simple set of discrete entities; that is, as if they are equally distinct from one another in terms of biological composition. In reality, however, the distinctiveness of classes within a given land classification will usually vary dramatically. Some pairs of classes will exhibit considerable overlap (or similarity) in biological composition—that is, a large proportion of the species occurring in the first class also occur in the second class—whereas other pairs of classes will exhibit little or no overlap in composition (Fig. 4).

Failure to consider patterns of distinctiveness between land-classes can cause problems when assessing the relative conservation priority of different areas (planning units) within a region. Consider a simple example based on the data in Figure 4. Assume that land-classes A, C, and D are the only land-classes currently represented within conservation areas. Two planning units are being evaluated as candidates for addition to the existing conservation network. The first unit is covered by land-class B, while the second unit occurs in land-class F. If the information on distinctiveness is ignored then these two areas might be evaluated as being of equal conservation priority; that is, protection of either planning unit would achieve representation of a previously unrepresented land-class. However, by considering the distinctiveness of the classes involved, clearly the planning unit in land-class F should be assigned greater priority, because this land-class is less similar to the classes already protected and is therefore likely to contribute a



greater number of previously unrepresented species.

As in the case of heterogeneity within land-classes, the potential problems caused by failing to consider distinctiveness between classes may be aggravated by efforts to minimize the cost, or socioeconomic impact, of conservation action (Armesto et al., 1998). This is of particular concern, given the increasingly widespread promotion of automated multi-criteria analysis techniques as a means of identifying regional planning solutions that balance, or trade-off, biodiversity conservation against alternative land-uses (e.g. Faith et al., 1996; Faith and Walker, 1996c; Ando et al., 1998; Rothley, 1999; Snyder et al., 1999; van Langevelde et al., 2000; Drechsler and Wätzold, 2001). Most such approaches purposely seek solutions that either minimize the socioeconomic impact associated with achieving a fixed level of biodiversity conservation, or maximize the level of biodiversity conservation achieved within fixed constraints imposed by socioeconomic considerations. Caution needs to be exercised in applying these approaches to overly-simplistic measures of biodiversity conservation. For example, optimizing the number of land-class targets achieved for a given socioeconomic impact may not be a good strategy for maximizing representation of biodiversity per se. Such an analysis may simply direct conservation towards a biased subset of land-classes (e.g., those in environments of least value for other land-uses) and toward a biased subset of the environmental and biological heterogeneity within each of these classes.

#### *Potential Approaches to Addressing Heterogeneity and Distinctiveness*

The problems of heterogeneity and distinctiveness are intimately, albeit inversely, related. As the classification resolution of a region is refined—that is, the region is divided into more classes—the problem posed by heterogeneity within classes is likely to decrease in importance, whereas the need to consider patterns of distinctiveness between classes increases. There is an urgent need to further develop and apply measures of representation of biodiversity that better address patterns of both biological heterogeneity within land-classes and variation in biological distinctiveness between classes.

Several recently developed analytical techniques offer considerable potential in this regard, using information on the relationships between all members of a set of entities to measure how effectively any given subset samples the total diversity of the set. The techniques are of two main types: those that assume that the relationships between entities are structured hierarchically (as a tree), and those that treat the entities as residing within a continuous multivariate space.

The hierarchical approach is of particular relevance to dealing with distinctiveness between land-classes, because relationships between such classes are often depicted as a hierarchical dendrogram (Fig. 4). If viewed in this way, the problem of considering distinctiveness when prioritizing conservation of land-classes is clearly directly analogous to the more widely studied problem of considering phylogenetic relationships when prioritizing conservation of species. A sizeable literature describes analytical techniques for addressing the latter problem (e.g., Weitzman, 1993; Faith, 1994, 1996; Krajewski, 1994; Humphries et al., 1995; Witting and Loeschcke, 1995; Crozier, 1997; Clarke and Warwick, 1998). These techniques are designed to prioritize species (or other taxa) for conservation attention in a way that maximizes representation of phylogenetic diversity, which in turn is assumed to maximize representation of genetic and phenotypic diversity. By considering phylogenetic relationships, these workers argue that species can be used more effectively as surrogates for finer levels of diversity. The same logic can be applied to land-classes: By considering distinctiveness in terms of likely overlap in species composition, land-classes can be used more effectively as surrogates for species-level diversity (Faith and Walker, 1996a).

Many of the analytical techniques developed to assess phylogenetic diversity are directly applicable to assessments based on land-classes but, to date, have rarely been applied in this context (although see Woinarski et al., 1996; Faith and Walker, 1996a; Ferrier et al., 2000a). This general approach is worthy of much wider attention. Wherever land-classes are derived by numerical classification of remotely mapped environmental variables (including the GDM-based approach described in the previous section), quantitative information describing the hierarchical

relationship between classes should be readily available. Such information should also be available for vegetation maps in which classes have been derived by subjecting vegetation survey data to some form of numerical classification. Even in the absence of direct information on distinctiveness between land-classes, expert opinion may be used to construct an approximate dendrogram for use in conservation planning.

If information is available on the hierarchical structure of heterogeneity within land-classes, then this heterogeneity could also be addressed by using techniques derived from analyses of phylogenetic diversity. However, in most cases, heterogeneity within classes might be more appropriately addressed by a technique such as ED, which can treat individual locations (planning units) within a class as residing in a continuous environmental or biological space. The required estimates of dissimilarity between planning units may be predicted as a weighted combination of geographical separation and differences in one or more environmental variables, with the weighting and scaling of variables being based either on expert opinion or statistical modeling of available biological data (e.g., using GDM).

The two analytical approaches just described might be combined in many different ways, depending on the exact nature of the land classification used. At one extreme, an entire region could be regarded as belonging to a single land-class, and all heterogeneity within this class could be addressed in conservation planning by applying continuous approaches such as ED. If a region is divided into multiple land-classes, then a mix of the two analytical approaches may need to be used; for example, assessing distinctiveness between classes by using a hierarchical approach and assessing heterogeneity within classes by a continuous approach. At the other extreme, by taking the refinement of classification resolution to its ultimate limit, one can define every location (planning unit) within a region as a separate class. In this case either a hierarchical or a continuous approach could be used, depending on the way in which relationships between planning units are defined. Interestingly, the two extremes described here are effectively equivalent, again highlighting the intimate linkage between distinctiveness and heterogeneity.

Although the analytical techniques described above provide a good starting point for incorporating considerations of distinctiveness and heterogeneity into conservation planning, further research and development work is urgently needed. This work should focus most urgently on developing more robust and informative summary measures (indices) of the effectiveness with which a given set of conservation areas represents the biodiversity of a region. Such measures are badly needed to replace the overly-simplistic indices currently used to assess the conservation status of regions and to compare the effectiveness of alternative conservation scenarios, such as indices of the proportion of each land-class conserved or the number of land-classes in a region for which conservation targets have been achieved (Scott et al., 1989; Pressey and Logan, 1994). The new generation of measures should aim to estimate overall representation of biodiversity by integrating considerations of both differentiation diversity (heterogeneity within land-classes and distinctiveness between classes) and  $\alpha$  diversity (relative species richness of classes). As discussed in the previous section, current advances in spatial modeling of both differentiation and  $\alpha$  diversity may help facilitate the development of more explicit measures of representation for use in future conservation planning.

#### USING DATA-RICH REGIONS AS TEST-BEDS FOR EVALUATING SURROGATES

The increasingly widespread use of biodiversity surrogates in regional conservation planning raises an important question: How well do these surrogates perform as a basis for selecting representative conservation areas? Or, in other words, by selecting conservation areas to maximize representation of the diversity exhibited by a surrogate (or a set of surrogates), to what extent are we in turn maximizing representation of biodiversity as a whole? This is a question not only of academic interest but also of considerable practical relevance to real-world planning. Although there is usually no alternative but to base planning on best-available surrogate data, such planning will be more effective if it can incorporate some knowledge of the error, or uncertainty, with which representation of diversity within a surrogate correlates

with representation of biodiversity per se (Conroy and Noon, 1996; Flather et al., 1997). Information on the relative performance of different types of surrogates can also provide an objective basis for focusing and directing future efforts in data collection and analysis.

Empirical evaluation of the performance of surrogates presents many challenges. Extensive data are required, not only for the surrogates to be evaluated (surrogate data) but also for independent elements of biodiversity against which these surrogates can be assessed (evaluation data). This type of work is therefore best suited to regions with an abundance of field-survey data for a wide range of biodiversity elements. Unfortunately, only a small proportion of the world's regions fall into this category. These data-rich regions can nevertheless play a valuable role as test-beds for evaluating the performance of surrogates. In other words, biological survey data from such a region can be used to evaluate the performance of surrogates that are more readily available in data-poor regions.

### *Defining Objectives and Data Requirements*

Given the extensive reliance of regional conservation planning on surrogates, surprisingly little research effort has so far been devoted to evaluating their performance. Many studies have dealt with various issues of indirect relevance to surrogate performance, but very few have directly addressed the key question of interest here: How well do surrogates perform as a basis for selecting conservation areas that are representative of biodiversity as a whole?

At this point, we must clearly distinguish this particular question from related questions pertaining to the spatial accuracy of mapped data. A sizeable literature describes and applies analytical techniques for using field-survey data to measure the accuracy of mapped land classifications (e.g., Congalton, 1991; Edwards et al., 1998; Stehman and Czaplewski, 1998) or the accuracy of modeled species distributions (e.g., Flather and King, 1992; Edwards et al., 1996; Elith, 2000; Pearce and Ferrier, 2000). Without denying the importance of such analyses for other purposes, these techniques do not, in themselves, address the question of how well a given land classification, or a set

of modeled species distributions, performs as a surrogate for biodiversity as a whole. Techniques for assessing the accuracy of mapping usually analyze the concordance between two measures of the same attribute, for example, remotely mapped vegetation type versus field-surveyed vegetation type, or modeled species occurrence versus field-surveyed species occurrence. Although this provides information on the accuracy with which entities (e.g., vegetation types or selected species) are mapped within a region, it says little about how well these entities will perform as surrogates for unmapped elements of biodiversity. The performance of a surrogate depends not only on how accurately the entities that make up the surrogate are mapped but also on how well these entities concord with (predict or explain) patterns of biodiversity as a whole. Assessing the accuracy of mapping, therefore, addresses only part of the problem.

Of those studies that have directly addressed the performance of biodiversity surrogates, many are of questionable relevance to regional conservation planning because of problems of spatial scale and the appropriateness of surrogate and evaluation data used. For example, studies of cross-taxon congruence often use data for two or more taxa (e.g., plants and beetles) collected at a common set of field-survey sites (e.g., Oliver et al., 1998; Pharo et al., 1999). The results of this work are of direct relevance to conservation activities that involve on-site assessment of relatively small areas (e.g., environmental impact appraisal) but are of less relevance to regional conservation planning, because such planning rarely uses raw biological field-data as a primary surrogate. Gaps in the geographical coverage of field-data must usually be addressed by some form of interpolation, modeling, or environmental classification. Evaluation of the performance of surrogates in regional conservation planning should therefore ideally focus on these remotely mapped data types.

Other studies have assessed congruence between taxa by using coarse-scaled distributional data (e.g., Pearson and Cassola, 1992; Prendergast et al., 1993; Flather et al., 1997; Kerr, 1997; van Jaarsveld et al., 1998a; Gaston, 2000). These data are generally derived by using collection records or range maps to denote species as being present or absent in a set of grid-cells covering the area

of interest. These assessments may provide useful information on the performance of different taxa as surrogates for conservation prioritization at a global or continental scale, but again the results are of limited applicability to finer-scaled regional conservation planning because the grid-cells used in such assessments are usually very large relative to the scale at which most regional planning work must be conducted. Patterns of congruence exhibited by taxa at a coarse spatial scale do not necessarily hold at finer spatial scales (Pearson and Carroll, 1999). Reducing the size of grid-cells used in such studies will not, in most cases, resolve this problem. As discussed earlier, a reduction in cell size is usually accompanied by an increase in false-absence errors or false-presence errors, or both, depending on the exact approach used to interpolate the occurrence of species. Such errors will confound any evaluation of the performance of one taxon as a surrogate for other taxa because the evaluation data themselves are now interpolated surrogates—that is, the presence or absence of a given species in a given grid-cell has not been determined by direct field survey but rather by some form of indirect interpolation or prediction. One set of predictions is therefore being used to evaluate another set of predictions. Similar problems will arise whenever one surrogate is used to evaluate another, for example, when using a vegetation map to evaluate the performance of an abiotic environmental classification (Kirkpatrick and Brown, 1994).

Such problems can be avoided by observing three general rules when selecting and preparing data to evaluate the performance of surrogates in regional conservation planning:

1. The spatial scale of the analysis should match the scale at which regional planning is likely to be conducted. In other words, the analysis should use spatial units approximately the same size as the parcels of land for which real planning decisions are made.
2. The surrogate data used should be potentially applicable to regional conservation planning; that is, the surrogates can be readily mapped across an entire region of interest.
3. The evaluation data used need to be available for only a sample of spatial units,

but they must be recorded very accurately. In general, evaluation data should be collected by direct field survey of selected elements of biodiversity, within each spatial unit used in the analysis.

### *Identifying Appropriate Analytical Techniques*

Assuming that suitable data are available, the next challenge in evaluating surrogates is selecting an appropriate analytical approach. Several different approaches have been used in previous studies. In studies of cross-taxon congruence, simple correlations between species richness values recorded for two or more taxa across a common set of sites or grid-cells have been widely reported (e.g., Pearson and Cassola, 1992; Balmford and Long, 1995; Beccaloni and Gaston, 1995; Kerr, 1997; Prendergast, 1997; Lawton et al., 1998; Williams, 1998b). However, such analyses fail to address an important principle of real-world conservation planning, that of complementarity (Flather and King, 1992; Ryti, 1992; Howard et al., 1998). For one taxon to perform well as a surrogate for other taxa, what really matters is not the level of correlation between species richness values for different taxa at individual sites, but rather the correlation between numbers of species in different taxa accumulated within sets of multiple sites. One cannot predict the latter from the former without also knowing something about patterns of complementarity, or dissimilarity, in species composition between sites.

Congruence in patterns of complementarity exhibited by different taxa can be assessed by matrix correlation analysis (Ferrier and Watson, 1997; Howard et al., 1998; Oliver et al., 1998). This involves deriving two sites-by-sites matrices, one containing dissimilarities in species composition (e.g., Bray–Curtis dissimilarities; Bray and Curtis, 1957) between all pairs of sites based on the surrogate taxon, and the other containing dissimilarities based on an evaluation taxon. The statistical significance of the correlation between these two sets of dissimilarities must be tested by using Monte Carlo permutation to avoid problems arising from the nonindependence of such data. Matrix correlation analysis can also be used to evaluate surrogates derived from remote environmental mapping (Ferrier and Watson, 1997). In this

case, instead of the two matrices containing dissimilarities based on two different taxa, the matrix for the surrogate taxon is replaced with a matrix of environmental dissimilarities or distances. If the environmental surrogate consists of discrete classes (e.g., mapped vegetation types), then all distances in this matrix will be either 0 (if two sites occur in the same class) or 1 (if two sites occur in different classes), in which case the analysis is equivalent to an ANOSIM analysis (Clarke, 1993; Wessels et al., 1999). The congruence between mapped land-classes and directly observed patterns of biological variation has also been evaluated with a range of other univariate and multivariate statistical techniques, including analysis of variance (Rykken et al., 1997), G-tests (King et al., 2000), and homogeneity analysis (Bedward et al., 1992b).

Matrix correlation analysis and related techniques evaluate congruence between the pattern of complementarity exhibited by a surrogate and the pattern exhibited by biodiversity as a whole (or, at least, selected elements of biodiversity). Although valuable, this information still does not provide a direct answer to the fundamental question of interest here: By selecting conservation areas to maximize representation of diversity within a surrogate, to what extent will we in turn maximize representation of biodiversity *per se*? The most direct way of addressing this question is by simulation, in which sites with both surrogate and evaluation data are treated as candidate areas for conservation (Kiestner et al., 1996; Ferrier and Watson, 1997; Andelman and Fagan, 2000; Williams et al., 2000; Araújo et al., 2001). The surrogate data are used to guide the selection of a hypothetical set of conservation areas that maximizes representation of diversity within the surrogate. This set of areas is then assessed in terms of how well it also represents diversity within the evaluation data. This analytical strategy should not be confused with related approaches in which two sets of conservation areas are derived—one based on the surrogate data and the other on the evaluation data—and surrogate performance is then measured in terms of the spatial overlap of the two sets of areas (Prendergast et al., 1993; Lombard, 1995; van Jaarsveld et al., 1998a; Reyers et al., 2000) or of the rank correlation of the order in which areas are selected (Reyers and van Jaarsveld,

2000; Reyers et al., 2000). Such approaches are likely to underestimate surrogate performance, because they fail to consider the important role that flexibility plays in selecting conservation areas (Balmford, 1998; Reyers and van Jaarsveld, 2000).

Simulations designed to assess surrogate performance generally select sites in a step-wise fashion, using some form of iterative heuristic algorithm (Ferrier and Watson, 1997; Andelman and Fagan, 2000; Williams et al., 2000). The site selected at each step is the one providing the greatest improvement in representation of diversity within the surrogate. For example, if the surrogate is a vegetation map, then sites might be selected in the order that maximizes the number of types, or the mean proportion of each type, represented at each step. The evaluation data are then used to assess the number of species actually represented after each selection. This process generates a species accumulation curve depicting the relationship between the cumulative number of sites selected (*x*-axis) and the cumulative number of species represented (*y*-axis). A simple measure of surrogate performance is the height reached by this curve for some predefined threshold of representation for the surrogate; for example, at least one instance, or some minimum proportion, of each surrogate entity represented. Alternatively, the area under the curve can be used as an overall measure of how rapidly species in the evaluation dataset are accumulated within sites selected by using the surrogate.

Ferrier and Watson (1997) introduced several refinements to the species accumulation approach that substantially improved the utility of this technique as a basis for surrogate evaluation (Fig. 5). They derived a species accumulation index by scaling the area under the accumulation curve (obtained by using the surrogate) in relation to areas under two other accumulation curves: (1) a mean random curve, which is the mean of a large number of individual random curves, each derived by selecting sites in random order without reference to the surrogate data; and (2) an optimum curve, derived by selecting sites on the basis of the evaluation data instead of the surrogate data (i.e., at each step, the site is selected that most improves the number of evaluation species represented). The species accumulation index (SAI) is then calculated

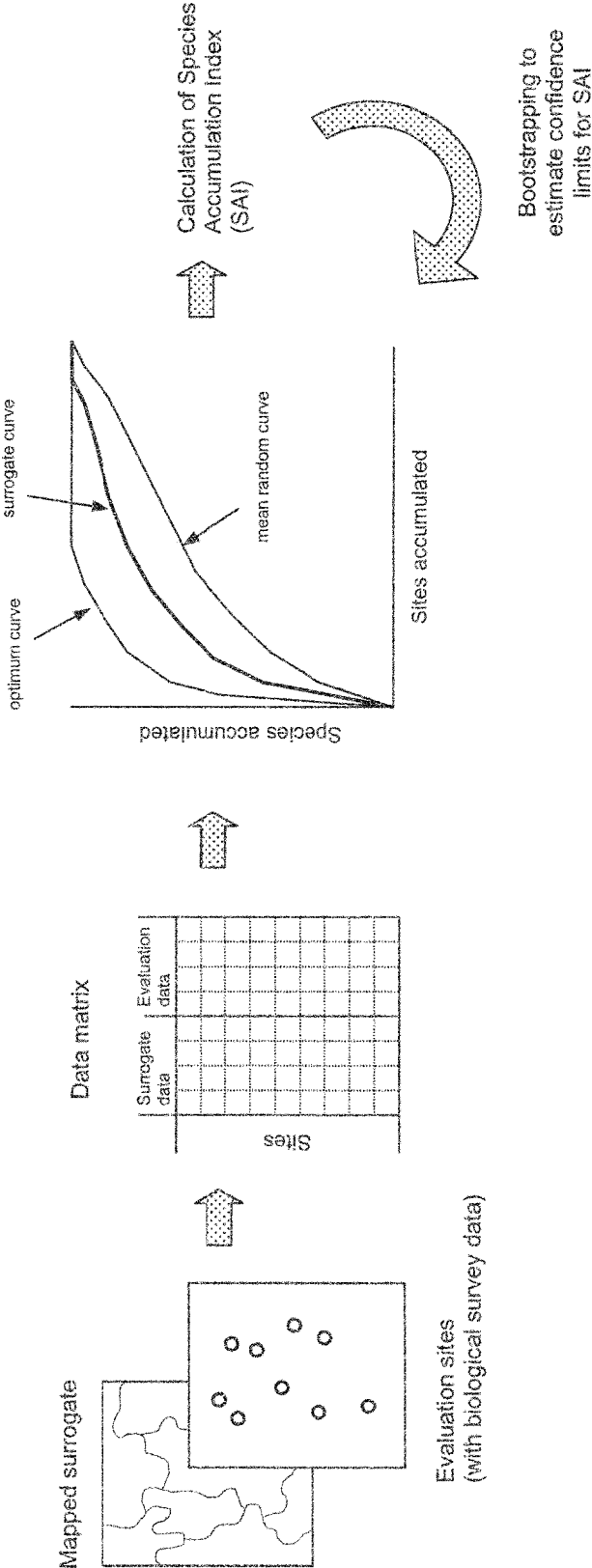


FIGURE 5. Steps involved in evaluating the performance of biodiversity surrogates by the species accumulation approach.

as follows:

$$\text{SAI} = (s - r)/(o - r)$$

where  $s$  = area under the surrogate curve,  $r$  = area under the mean random curve, and  $o$  = area under the optimum curve. The index can range from 1 for a perfect surrogate to 0 or less for a surrogate that performs no better than a random selection of sites. Ferrier and Watson (1997) also described an approach to estimating confidence limits for the SAI, based on bootstrapping (Efron and Tibshirani, 1993). The SAI is calculated repeatedly for a series of bootstrap samples. Each sample is generated by randomly selecting sites, with replacement, until the number of sites in the sample equals the number of sites used in the original analysis. Each bootstrap sample is used to derive a surrogate curve, an optimum curve, and a mean random curve. The SAI values calculated from these curves are then used to estimate a standard error and confidence limits for the observed index. These refinements enable more rigorous statistical evaluation and significance testing of differences in performance of multiple surrogates across multiple evaluation taxa.

Despite the current popularity of the species accumulation approach, it is only one of several potential approaches to using simulation to assess surrogate performance. My research group is currently testing a new approach in which a large number of alternative conservation scenarios are generated by randomly selecting a fixed number of sites from the total set of evaluation sites (e.g., 50 sites selected from a total set of 500 sites). Two measures of representation are calculated for each scenario, one measuring representation in terms of the surrogate dataset (e.g., proportion of vegetation types conserved), and the other measuring representation in terms of the evaluation dataset (e.g., proportion of species conserved). The correlation between these two measures (across all scenarios) provides a direct indication of the extent to which representation of diversity within a surrogate can serve as a predictor of representation of diversity within one or more evaluation taxa. As in the case of matrix correlation analysis, the statistical significance of this correlation must be tested by using Monte Carlo permutation to overcome problems of nonindependence. Other

workers (D. P. Faith, pers. comm.) have developed a related approach based on randomly selected sets of sites. In their approach, however, the interest is not in the level of representation achieved by each set of sites per se but rather what improvement in representation would be afforded by conserving an additional randomly selected site. The improvement in representation, or complementarity of the additional site relative to the existing set of sites, is calculated for both the surrogate and the evaluation datasets. The correlation between these two measures provides an indication of the extent to which complementarity based on a surrogate can serve as a predictor of complementarity based on evaluation taxa. Further work is required to assess the respective strengths and weaknesses of these new approaches.

### *An Australian Case Study*

The species accumulation approach described above has been used to evaluate surrogates in several Australian environments, including temperate and subtropical northeast and arid northwest, New South Wales (Ferrier and Watson, 1997), and moist-tropical north Queensland (Moritz et al., 2001). The most comprehensive of these studies was that for northeast New South Wales, a region covering ~80,000 km<sup>2</sup>. In the late 1980s the New South Wales National Parks and Wildlife Service initiated the establishment of a comprehensive environmental GIS database for this region, including a wide range of environmental variables, describing long-term mean climate (rainfall, temperature, solar radiation), terrain (topographic position, ruggedness), substratum (lithology, soil depth, soil fertility, soil moisture), vegetation type (from satellite imagery and aerial photography), and degree of recent disturbance. These variables were used to design extensive flora and fauna surveys to collect data that would supplement existing biological datasets. Survey sites were purposely located to representatively sample major environmental and geographical gradients within the region (Ferrier et al., 2000b). By the early 1990s >277,000 locational records had been assembled for 4,207 species of vascular plants, vertebrates, and ground-dwelling arthropods. These data were collected primarily to support a series of government-led planning processes, which

culminated in extensive additions to the region's reserve system (Ferrier, 1997, 2000; Ferrier et al., 2000a). In parallel with this work, however, the data were also used to evaluate the performance of a wide range of biodiversity surrogates (Ferrier and Watson, 1997).

The surrogates evaluated included (1) various types and scales of vegetation mapping derived from interpretation of satellite imagery and aerial photography; (2) environmental classes (domains) derived from numerical classification of abiotic environmental variables, at two spatial scales (grid resolutions of 200 m  $\times$  200 m and 5 km  $\times$  5 km); (3) environmental units derived by simple overlay of abiotic variables (at two spatial scales); (4) environmental ordination (at two spatial scales); (5) raw environmental distances; (6) canonical correspondence analysis (ter Braak, 1986) of abiotic environmental and biological data; and (7) modeling of species distributions in relation to abiotic environmental variables (by using generalized additive modeling; Hastie and Tibshirani, 1990). A later study further evaluated approaches based on distributional modeling of communities and species assemblages, derived by using both the classification-then-modeling and modeling-then-classification strategies (Ferrier et al., unpubl. manuscript). All of the surrogates were evaluated by using survey data for 11 biological groups: ants, beetles, spiders, reptiles, birds, bats, rainforest canopy trees, rainforest understory plants, open-forest canopy trees, and open-forest understory plants. Independence between the biological data used to derive some of the surrogates (e.g., species models) and the data used to evaluate those surrogates was enforced by randomly splitting the biological survey sites into two sets of equal size: a model-development set and an evaluation set.

The evaluation revealed clear differences in performance of surrogates for this region, both between different types of surrogates and between different biological groups. All surrogates performed poorly for ground-dwelling arthropods. However, reasonably consistent differences in performance between broad types of surrogates were apparent across all vertebrate and vascular plant groups. The most poorly performing surrogates were those derived purely from abiotic environmental data (i.e., environmental

classifications and ordinations). Vegetation mapping generally outperformed all types of environmental classification and ordination, for both vertebrate fauna and vascular flora. The best overall performance of any surrogate was achieved by modeling species distributions, especially when modeling was applied to species within the biological group under evaluation. Using models for one biological group as a surrogate for other biological groups also appeared to have potential. In particular, modeling of canopy tree species generally performed better than vegetation mapping as a surrogate for both canopy and understory flora and for vertebrates. Modeling communities and species assemblages also generally outperformed traditional vegetation mapping and abiotic environmental classification.

### *Future Needs*

Extrapolating surrogate evaluation results obtained in any one region, such as northeast New South Wales, to other regions should be done cautiously. The performance of some surrogates may vary between different environments, or between regions with different biogeographic histories. Performance may also vary across different spatial scales. The best way of improving our understanding of these relationships is to extend research into surrogate performance to cover a wider variety of regions throughout the world. The number of regions with sufficient biological data to serve as test-beds for such research is increasing. Even in the tropics suitable data are now available for several regions: for example, parts of Uganda (Howard et al., 1998), Guyana (Funk et al., 1999; Richardson and Funk, 1999; Funk and Richardson, 2002), and north Queensland, Australia (Moritz et al., 2001; Moritz, 2002). This research must also be extended to evaluate a wider range of surrogates. To date, most studies of surrogate performance have focused on cross-taxon congruence. Very few studies have evaluated the performance of remote environmental mapping, and modeling of biological distributions, as surrogates for biodiversity, yet these are the very types of data on which conservation planning in data-poor regions is likely to rely.

Further effort also needs to be devoted to refining the analytical techniques used to evaluate surrogates. A major weakness of



all current techniques (including the species accumulation approach described above) is the assumption that, in the absence of surrogate information, sites should be selected at random. In other words, the null hypothesis in most statistical tests of surrogate performance is that a surrogate performs no better than a random selection of sites. This implies that random selection of conservation areas is the worst-case scenario for a region. Yet, in the real world, conservation areas are rarely chosen at random. In the absence of systematic conservation planning, reservation is usually biased towards areas of lowest cost, either in terms of direct cost of acquisition or indirect costs associated with forgone opportunity for other land uses (Pressey et al., 1996; Armesto et al., 1998). A system of conservation areas selected in this manner will probably contain a biased (i.e., nonrepresentative) sample of the total environmental and biological diversity of a region. In contrast, a truly random selection of sites might be expected to provide a relatively good representation of a region's diversity. However, the exact level of representation achieved by random selection is not easy to predict, because that depends on what components of biodiversity are being targeted and on how these components are distributed across the region of interest.

Future studies of surrogate performance need to consider better the potentially crucial effect that biased (i.e., nonrandom) selection of sites has on conservation planning in the real world. Preliminary trials conducted by my research group indicate that incorporating probable sources of real-world bias into conservation simulations can greatly affect the resulting estimates of surrogate performance. In the species accumulation approach, this effect is manifested in changes not only to the shape of the random curve (now called a null curve because sites are no longer selected in completely random order) but also to the shape of surrogate curves. In particular, differences in performance between coarse-scaled and fine-scaled surrogates are accentuated. To understand why this happens, consider two land classifications for a region, one containing 10 classes mapped at a coarse spatial scale, the other containing 100 classes mapped at a fine spatial scale. If analyzed by the original species accumulation approach, the fine classification may perform only slightly

better than the coarse classification. Even though the classes in the coarse classification probably contain greater internal biological heterogeneity than do those for the fine classification, this heterogeneity is nevertheless represented reasonably well because the sites conserved within each coarse class are selected at random from all sites within that class. By more realistically biasing the selection of sites to, for example, the least productive sites in each class, the performance of the coarse classification is now reduced relative to that of the fine classification because the sites selected in each coarse class are no longer representative of the variation encompassed by that class. Furthermore, because these selected sites are probably less threatened than those occurring in the more productive portion of the class, the difference in performance between coarse and fine classifications would probably be even more marked if long-term persistence were factored into the evaluation.

Clearly, greater realism needs to be injected into future simulations that are designed to evaluate the performance of surrogates. Failure to do so runs the risk of underestimating true differences in performance between different types of surrogates, or between different scales of mapping within the same type (e.g., various scales of vegetation mapping), with potentially dire consequences for future conservation planning.

## CONCLUSION

Many of the world's regions identified as being of high priority for conservation action are likely to contain high levels of  $\alpha$ ,  $\beta$ , and  $\gamma$  diversity, particularly those in the tropics. Yet most of these regions are relatively data-poor. If systematic conservation planning approaches are to make a worthwhile contribution in such regions, they cannot do so based on biological survey or collection data alone. At the relatively fine spatial scale at which most regional conservation planning must be performed, these data usually provide poor spatial coverage. In such situations, regional planning may need to be based heavily on various forms of remote environmental mapping. This approach confers significant benefits in terms of cost-effectiveness and rapidity of application, particularly in light of recent improvements in the global coverage of relatively fine-scaled abiotic and

land-cover data. However, in our rush to take advantage of these new data sources, we should not be blinded to the risks involved with relying too heavily on remotely mapped surrogates for biodiversity.

This paper suggests three broad ways in which available biological data and knowledge might be used to alleviate such risks, by adding value to the information contained within remote environmental mapping. Predictive modeling offers considerable potential as a means of more closely integrating biological and environmental data. However, effective realization of this potential in highly diverse yet data-poor regions probably requires a shift in emphasis from modeling individual entities (e.g., species) to modeling collective properties of biodiversity (e.g., patterns of differentiation diversity). Incorporating consideration of heterogeneity within, and distinctiveness between, land-classes into measures of conservation priority and achievement may further enhance the rigor with which such surrogates can be used as a basis for regional conservation planning. Increased use of data-rich regions to evaluate the performance of surrogates may help not only to provide direction to data acquisition and analysis efforts in data-poor regions but also to give planners a better idea of the level of uncertainty associated with particular surrogates and thus place these individuals in a better position to exercise appropriate precaution in decision-making.

In this paper I have focused specifically on surrogates that can be used to achieve one particular goal of regional conservation planning; that is, representation of existing patterns of biodiversity. However, as acknowledged in the introduction, conservation areas not only should be designed to include as many elements of biodiversity as possible, but also should be sufficiently large, well-connected, and well-replicated to promote long-term persistence of this diversity. Decisions about how to configure and manage conservation areas to promote persistence will often need to be based on surrogates quite different from those used to guide achievement of representation. Maps of fine-scaled environmental variation, or distributional data for narrow-range taxa, may perform well as surrogates for achieving representation of spatial pattern in biodiversity but will provide little guidance as to the

required size and connectedness of conservation areas. Conversely, the requirements of wide-ranging vertebrate species (e.g., top carnivores) can help guide decisions about reserve size and connectedness but may perform poorly as surrogates for spatial pattern in biodiversity as a whole (Andelman and Fagan, 2000; Linnell et al., 2000; Williams et al., 2000). The only sensible answer to this dilemma, at least in the near future, is to use both types of surrogates in parallel in regional conservation planning. There is no point in designing a system of conservation areas to include a high proportion of a region's biodiversity if the individual areas are so small and isolated that much of the diversity they contain is unlikely to persist in the longer term. Similarly, there is little point in designing large, well-connected reserves for wide-ranging vertebrates if these areas exclude a sizeable proportion of the total diversity of a region. One of the biggest challenges facing the science of regional conservation planning in coming years will be to find better ways of balancing and integrating the achievement of both representation and persistence of biodiversity.

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