
Operationalizing biodiversity for conservation planning

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Biodiversity has acquired such a general meaning that people now find it difficult to pin down a precise sense for planning and policy-making aimed at biodiversity conservation. Because biodiversity is rooted in place, the task of conserving biodiversity should target places for conservation action; and because all places contain biodiversity, but not all places can be targeted for action, places have to be prioritized. What is needed for this is a measure of the extent to which biodiversity varies from place to place. We do not need a precise measure of biodiversity to prioritize places. Relative estimates of similarity or difference can be derived using partial measures, or what have come to be called biodiversity surrogates. Biodiversity surrogates are supposed to stand in for general biodiversity in planning applications. We distinguish between true surrogates, those that might truly stand in for general biodiversity, and estimator surrogates, which have true surrogates as their target variable. For example, species richness has traditionally been the estimator surrogate for the true surrogate, species diversity. But species richness does not capture the differences in composition between places; the essence of biodiversity. Another measure, called complementarity, explicitly captures the differences between places as we iterate the process of place prioritization, starting with an initial place. The relative concept of biodiversity built into the definition of complementarity has the level of precision needed to undertake conservation planning.

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1. Introduction

Biodiversity is the variety of life. The concept of biodiversity includes the entire biological hierarchy from molecules to ecosystems, or the entire taxonomic hierarchy from alleles to kingdoms, all the logical classes in between (individuals, genotypes, populations, species, etc.), and all of the different members of all those classes. It also includes the diversity of living interactions and processes at all these levels of organization. This is such a wide-ranging description that it has kept the definition of the term “biodiversity” vague and ensured that its measurement remains capricious. Both problems are widely acknowledged among conservation biologists though precious little is done about them. The upshot is that it is still difficult to apply the term for practical

purposes such as influencing public policy, or integrating the protection of biodiversity into land use planning and management strategies. For those purposes we need a much more precise definition. Planners and policy-makers need to know what they are aiming for.

In this paper we review some recent developments in conceptualizing biodiversity, use these developments to try to add some precision to the concept of biodiversity, and thereby make its quantitative assessment for policy and planning applications more feasible. This is done initially by returning the discussion of what biodiversity means from the abstract space in which it has lately occurred to the definite historically contingent context in which it originated. This context is the one in which short-term human needs and desires led to broad scale destruction of the biological inheritance of the planet,

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and in turn gave rise to a movement aimed at protecting that inheritance. This movement has the implicit goal of protecting the variety of life, which is a different goal from the equally legitimate one of preserving particular species though, of course, the two are not mutually exclusive.

Placing biodiversity in this context leads to two interesting conclusions, as will be shown below. First, contrary to the type of theorizing that deifies generality and de-contextualization, assessments of biodiversity and strategies for its conservation cannot ignore that fact that biodiversity is rooted in *place* – precise points on Earth at definite times. Second, while social (including economic) constraints often prevent fully satisfying biodiversity conservation goals, it turns out that social constraints can often be incorporated into policy decisions with little adverse effect on biodiversity conservation.

2. What is “biodiversity”?

The term “biodiversity” was coined by Walter G Rosen at some point during the organization of the 21–24 September 1986 “National Forum on BioDiversity” held in Washington DC, under the auspices of the US National Academy of Sciences and the Smithsonian Institution (Takacs 1996). This forum met only shortly after the founding of the US Society for Conservation Biology in 1985, followed by the publication of Michael E Soule’s (1985) manifesto, “What Is Conservation Biology?”, also in 1985. An obviously synergistic interaction between the use of “biodiversity” and the growth of conservation biology as a discipline led to the re-configuration of environmental studies that we see today in which biodiversity conservation has emerged as a central focus of environmental concern.

The term “biodiversity” found wide use immediately following its coining. As Takacs (1996) has pointed out: “In 1988, *biodiversity* did not appear as a keyword in *Biological Abstracts*, and *biological diversity* appeared once. In 1993, *biodiversity* appeared seventy-two times, and *biological diversity* nineteen times” (p. 39 italics in the original). The first journal with “biodiversity” in its title, *Canadian Biodiversity*, appeared in 1991; a second, *Tropical Biodiversity*, surfaced in 1992; *Biodiversity Letters* and *Global Biodiversity* followed in 1993. Meanwhile conservation biology as *the* science with the explicit goal of conserving biodiversity emerged as a highly visible enterprise with considerable political appeal in Europe and neo-Europe. Richard B Primack (1993) published the first textbook on conservation biology in 1993; Gary K Meffe and C Ronald Carroll (1994) followed with their own comprehensive text in 1994.

Biodiversity is what must be conserved if we do not want to lose the biological inheritance bequeathed to us. In practice this means that we have to choose targets to aim for and it is evident that this choice is not trivial. The biological realm – patterns and processes – is marked by variability and complexity at every level of organization. It is useful at this stage to distinguish between biological diversity and what has come to be called biological integrity. Integrity refers to the persistence of ecosystem processes such as the generation of biomass or the flow of nutrients and energy within specific bounds. The conservation of biodiversity is presumably related in some way to the maintenance of biological integrity. At one time it was widely believed that complexity of process pathways led to the stability of ecosystems (MacArthur 1955; Elton 1958). Since increased diversity at almost any level of biological organization leads to increased complexity, and stability presumably implies integrity, such a complexity-stability relationship implies a biodiversity-integrity relationship (see McCann 2000, for a recent review). However, there remains little uncontroversial theoretical rationale (May 1973) or empirical results (Pimm 1984, 1991; Shrader-Frechette and McCoy 1993) supporting the diversity-stability relationship. Nevertheless, it is at least likely that the maintenance of ecosystem processes will contribute to the conservation of biodiversity since it may ensure that all important biological processes persist (Karr 1991; Angermeier and Karr 1994; Margules and Pressey 2000).

In the present context, we will restrict our attention to patterns, including entities and dynamic patterns such as migrations and other behaviours. Two different hierarchical schemes are usually used for the classification of biological entities: (i) a spatial or (generalized) ecological hierarchy starting from biological molecules and macromolecules, through cell organelles, cells, individuals, populations and meta-populations, communities, ecosystems (communities and their physical habitats) ultimately to the biosphere; and (ii) a taxonomic hierarchy from alleles through loci, linkage groups, genotypes, subspecies, species, genera, families, orders, classes, phyla and kingdoms. (Many intermediate levels are ignored in this description.) Both hierarchies reflect evolutionary history and are constrained by evolutionary mechanisms. Since conservation practice should take full cognizance of operative evolutionary processes, understanding the relationships between phylogeny and these two hierarchies is, in principle, critical to the design of conservation strategies. In practice we almost never know these relationships fully but must proceed anyway. We will therefore ignore this fundamental detail.

Two points should be noted about both hierarchies. First, they are not clean in the sense that biological entities fall neatly into well-defined classes without

exception. Second, there is heterogeneity at every level leading to biological diversity. The second point is almost trivial and a few examples will suffice to delineate its scope. Almost any two populations, even of the same subspecies, differ in their genetic profiles. Except for some clonal organisms, almost any two individuals of the same species have different genotypes; there are virtually no two identical ecological communities anywhere, and so on. The first point is equally important: while some entities such as organelles and cells are reasonably well-defined, cases such as fungi, symbionts, and clonal organisms show that even “individual” is not always precisely defined. Asexual species are notoriously hard to define and even sexual species, usually defined by the ability to interbreed and produce fertile offspring (Mayr 1957), present problems. A striking example is the existence of “ring species”. In Britain, the herring gull (*Larus argentatus*) is easily distinguished – on morphological as well as reproductive grounds – as a separate species from the lesser black-backed gull (*Larus fuscus*). However, as we go east beginning with the Scandinavian countries, and continuing around the North Pole, different subspecies of the herring gull are found which can each interbreed with the one (geographically) preceding it. Ten such subspecies are found as we traverse Siberia, cross the Bering Straits and continue through Alaska and Canada. The terminal subspecies in Britain is *Larus fuscus*, which does not breed with *Larus argentatus* (Maynard Smith 1975). Thus, the usual definition of species turns out to be non-transitive!

Biodiversity, then, refers to all biological entities, which is an intimidating idea because it seems impossible to operationalize it. The standard move at this stage is to suggest that three entities capture what is important about biodiversity: genes (alleles), species, and ecosystems. As a simplifying proposal in the face of apparently intractable complexity, this convention has some merit. If we conserve allelic heterogeneity completely, we take care of much of the diversity below the genotypic and individual levels of the two hierarchies. If we conserve all species, we do conserve all entities at higher levels of the taxonomic hierarchy though we may not conserve interspecific hybrids which, because of the leakage in our classificatory scheme, may not qualify for conservation. If we conserve all ecosystems we may conserve many communities, though this is hard to gauge. Although its use is common, the term “ecosystem” is about the worst-defined in the biological literature.

Nevertheless, any such proposal falls afoul of the diversity of biological phenomena and does so in a rather spectacular manner. Consider the case of the monarch butterfly (*Danaus plexippus*), which has two migratory populations in North America. Beginning in late August, the eastern population migrates to Mexico for five months.

Individuals aggregate in millions in the high-altitude fir forests of the Sierra Transvolcanica, some 80 km west of Mexico City. There are nine such overwintering sites all within an area of 800 sq km on isolated mountain ranges between 2900 and 3400 m. The butterflies remain reproductively inactive throughout the winter. Survivors migrate north, starting in late March, and lay eggs on milkweed (*Asclepias* sp.) along the Gulf Coast. These eight-month-old remigrants die but their offspring continue migrating north towards Canada. Two or three more generations are produced over the summer. By the end of summer, the last summer generation enters reproductive diapause and instinctively begins a southerly migration towards Mexico. The western population shows similar behaviour, migrating to about forty known overwintering sites in California. What is striking about this behaviour in both populations is that the migratory instinct is hereditary and, yet, the precise geographical migration pattern is so specific.

In California some measures have been taken to protect overwintering sites but the cost of real estate may result in only a few of the sites getting the necessary protection. The future of the Mexican sites appears to be even more bleak. Until recently, the high-altitude fir forests of Mexico had been relatively free from human interference, but they now face at least six threats (Brower and Malcolm 1991): (i) large-scale legal and illegal logging for timber and firewood; (ii) village expansion up the mountains; (iii) increased use of fire to clear land; (iv) invasion of the forests by lepidopteran pests; (v) spraying of *Bacillus thuringiensis*, an organic pesticide, the effect of which on monarch butterflies is unknown; and (vi) increased tourism. If the overwintering sites in Mexico disappear, it will mean the end of the eastern migratory population; if the sites also disappear in California, the western migratory population will come to an end.

The disappearance of overwintering sites will not necessarily mean the extinction of monarch butterflies as a species: there are numerous non-migratory tropical populations. However, what will disappear is the remarkable migratory behaviour of the two populations discussed above, which has come to be seen as an example of “endangered biological phenomena” (Brower in Meffe and Carroll 1994, p. 104–106). Other examples include the seasonal migrations of African wildebeest and the synchronous flowering of bamboo in India. While the former certainly is spectacular and in danger of disappearing because of the construction of fences along migratory paths, the latter is even more peculiar (Bahadur 1986). One bamboo species, *Thyrsostachys oliveri*, flowered in Burma in 1891 and seeds were sent to Kolkata and Dehra Dun, about 1500 km apart. Clumps raised at both of these places flowered simultaneously in 1940. In 1961

there was simultaneous flowering of Muli bamboo (*Melocanna baccifera*) in Assam and Dehra Dun, about 1500 km apart. In 1970–71, there was simultaneous flowering of spiny bamboo (*Bambusa arundinacea*) throughout India after a lapse of 45 years. Clearly, a very precise biological clock exists in these species. In these cases, extinction of the species would also lead to the extinction of the phenomenon of synchronous flowering. More interesting, in this context, is that in extended habitats consisting of forests of a single bamboo species, flowering occurs in waves, starting at one end and propagating to the other. This unique phenomenon would disappear if these habitats do, even if the species persist elsewhere (for instance, as isolated stands in botanical gardens).

Saving the holy trinity of genes, species and ecosystems will not save these phenomena; targets of conservation action must, therefore, be expanded beyond these canonical entities. But there is no reason for despair. The holy trinity as well as endangered biological phenomena – in fact, everything except those (generally small) populations being cultivated in captivity – can be accommodated if we acknowledge that the appropriate target of conservation action must always be a *place*, or a network of *places*. This takes us into intuitively trivial but, strangely, philosophically uncharted territory. A place is geographically rooted and loses its sense of place as soon as it is generalized about. But a place – a precise biogeographic location – is what matters for conservation: it alone meaningfully retains the heterogeneity that is responsible for biological diversity. A preference for place is not merely a preference for an ecosystem or even a habitat, both of which are supposed to admit abstract characterization: the same habitat at different places may hold a different complement of genes, species, or communities. Places are what matter for conservation. We will not be able to conserve all places that contribute to biodiversity because that would be every place on Earth. Given limited resources and other demands on places, we will need to prioritize them. The prioritization procedure will operationalize and implicitly define what “biodiversity” should be taken to be in the context of its conservation. But, to prioritize places in this fashion – and this is a critical point – an absolute concept or measure of biodiversity is not needed. We merely need to be able to decide the extent to which the biodiversity of place *A* is similar or different to the biodiversity of place *B* and then use that knowledge to measure, then implement, complementarity, as described below.

3. Complementarity

Two points emerge from the discussion of the last section: (i) the scope of “biodiversity” is broad; and (ii) it is unlikely that any single precise definition will capture

all of its intended referents. However, we will now show that such precision is not necessary for efforts to target places for protection, accepting that these efforts are always going to fall short of complete success. At this stage, traditional accounts of biodiversity and its conservation, usually without warning that any conceptual transition is taking place, shift attention from diversity to “richness”: how many of the units of concern (for instance, species) there are in a given place. Places are then usually prioritized according to richness. Those places with the most species, tropical forests and heaths, for example, receive top priority (e.g. Huston 1993) while desert and tundra places are given little attention.

This move is a mistake for two related reasons. First, it is well-established that prioritizing places by richness is usually not an effective or efficient way of targeting diversity (Pressey and Nicholls 1989; Williams *et al* 1994; Margules and Pressey 2000). For instance, the top two (or more) places may be rich in the targeted features (e.g. species) but may have very similar features. Conserving both may replicate protection of these features which, of course, is desirable for their security, especially if it is affordable. However, conserving both may well add nothing or very little to what would be obtained by conserving just one of them and then using scarce conservation resources to add some other place with a very different set of features, thus increasing the total number of features conserved (Margules and Gaston 1994). The second reason why selecting places on the basis of richness is ineffective is that, even intuitively, richness is not the same as diversity. Diversity, including biodiversity, connotes “difference” and “unlikeness” – the amount of variety. Richness does not capture this connotation.

If we accept this connotation of diverseness or variety to capture the intuition of biodiversity that is relevant for our purposes, and we acknowledge that our purpose is to prioritize places, it becomes straightforward to give an operationally precise definition of biodiversity as a relative concept. This definition is relative in two ways: (i) the definition will only try to say if place *A* has higher (or the same or lower) biodiversity than *B*; (ii) and it will do so only against a background set of places Π . We will assume that, for each place and for the background set, a list of features that are supposed to provide a representation of biodiversity is available. These features may be anything ranging from species or genera to habitat types or environmental variables. The problem of which features to use as biodiversity surrogates is the problem of providing a sufficient measure of biodiversity for place prioritization. We return to that problem in the next section; suffice it here to note that it is a problem that is only partly soluble but, nevertheless, whatever solution is obtained will have to be used in practice.

It is now possible to define “biodiversity”: place A contributes more (same/less) biodiversity than B relative to Π if and only if, its list of features has more (less/the same number of) entries not in the list of Π than the feature list of B . This definition is iterative and can be used in a straightforward way to generate additions to a system of reserves. The principle of adding places by maximizing the number of new features is called “complementarity” in the literature. This principle appears to have been discovered independently at least four times (Kirkpatrick 1983; Ackery and Vane-Wright 1984; Margules *et al* 1988; Rebelo and Siegfried 1990), though the term “complementarity” was introduced by Vane-Wright (Vane-Wright *et al* 1991).

However, to initiate the iteration invoked in our definition, we need to specify a base-line: how Π is to be constructed from the null set. In practice this is rarely a problem. Existing networks of protected areas provide the reference set though, because these places have traditionally been selected using criteria other than biodiversity (sublime landscapes, wildernesses, etc.), though such reference sets may not be repositories of high biodiversity (Pressey 1994). In any case, leaving aside this practical aspect, for the sake of definitional completeness, we must be able to solve the problem of defining the reference set *ab initio*.

If we wish to maintain formal consistency, then the initial place to be selected should be identified on the basis of richness (Kirkpatrick 1983). The place that has the most number of features *ipso facto* is the one with the highest number of features that are not included in the list of places so far selected (the null set). However, to be consistent with the principal intuition that has guided the definition of biodiversity we proposed above, that is, trying to capture an intuition of variety or diversity, it makes more sense to select the first place(s) on the basis of rarity (Margules *et al* 1988). If there are places with features that occur nowhere else, these enter Π at the beginning. If not, we choose the place(s) with the largest number of rarest features that are present in the data set. The two starting points deliver different solutions, but usually not dramatically so. There is also an empirical reason to prefer the latter starting point. In the one comparative study of a wide variety of place prioritization algorithms, using the distributions of terrestrial vertebrate species of Oregon, algorithms based on complementarity that were initialized by rarity were found to outperform those initialized by richness, that is, they achieved the target of representation in the reserve network with fewer selected places (Csuti *et al* 1997).

Note that because more than one place may have the same biodiversity (relative to some Π) any prioritization algorithm must incorporate other rules in order to be deterministic. However, this characteristic should be

viewed as a resource rather than as a constraint: it allows the incorporation of other desirable features, other than maximizing biodiversity, into place prioritization. For instance, it permits the incorporation of distance considerations. We may want to select those places closest to ones already in Π , an option implemented by Nicholls and Margules (1993) in a prioritization of coastal Eucalyptus forests of south-eastern New South Wales. This would favour the size augmentation of existing reserves which is one, perhaps controversial, way of going beyond mere diversity and paying attention to the long-term viability of populations in a reserve system.

Alternatively, or in addition, we may incorporate considerations of social costs in terms of demand or use values, or opportunities lost, and so on (e.g. Faith and Walker 1996a). A need to minimize forgone opportunity costs is often a major factor in place prioritization for real-world applications when implemented by governments. In a recent country-wide planning study in Papua New Guinea (Nix *et al* 2000), place prioritization was guided by four different kinds of spatial constraints: opportunity costs represented by timber volume and agricultural suitability; commitments represented by existing protected areas; masks, represented by small map units and areas of high land use intensity; and preferences, represented by human population density and a previous study of conservation priority areas based on expert opinion. In the last case, all else being equal, areas with low human population density or areas coinciding with others chosen by experts were preferred. Stakeholder preferences can also be used to guide prioritization. In a case reported by Pressey (1998), forestry and conservation interests were traded off against one another by running solutions weighted by the different stakeholders in real time around the negotiating table, examining the resultant maps, and reaching compromise solutions. These are examples that demonstrate how socio-economic considerations can be directly incorporated into policy-making which takes the conservation of biodiversity as an explicit important aim.

Two points about this procedure should be noted: (i) the use of other rules along with complementarity makes the relative biodiversity status of a place history-dependent. It depends on what has already entered the reference set Π . However, this history-dependence is mild insofar as this status does not depend on the order in which other places entered Π ; and (ii) these procedures operate on complete lists of features (such as species) at each place. Data are usually gathered in this form in the field but, unfortunately, often recorded and reported by summary statistics such as richness. If biodiversity conservation through place prioritization is a goal, then such treatment of data at the time of recording and reporting is inimical to that purpose and should not be practiced.

These algorithms implicitly define the concept of biodiversity developed here; it is what a complementarity-based place prioritization algorithm maximally selects for. With some rhetorical flourish we may just as well say that what really matters is complementarity: the concept of biodiversity rides on that of complementarity.

4. Measurement and surrogacy

If the definition of “biodiversity” given above is to have any practical application, two problems must be solved. The first, a relatively theoretical one: what is to be measured? The second, a practical one: are the data that we want realistically obtainable (Williams *et al* 1994)? The former is the problem of *quantification*; the latter is the problem of *estimation*. To solve both problems requires choices of “surrogates”.

The discussion in §2 should have made it clear that, because of the breadth and accompanying imprecision in the meaning of “biodiversity”, no single parameter, whether or not it can be realistically estimated, is capable of capturing all the biological features that we may find of interest. To solve the quantification problem, we will have to use “surrogates” that serve as “indicators” of general biodiversity. Surrogacy is a relation between a surrogate or indicator variable and a target variable. The surrogate variable represents the target variable in the sense that it stands in for the target variable in subsequent analyses (that is, it replaces the target variable completely in those analyses). The term “surrogate” (or alternatives like “proxy” or “partial measure”) has come to be used rather indiscriminately. In the section below, we make a distinction that might bring some order to the often confusing discussion of finding and measuring surrogates.

This distinction is one between “true surrogates” and “estimator-surrogates”. True surrogates are supposed to represent general biodiversity, that is, the target variable is supposed to capture general biodiversity. The only constraint on a true surrogate is that, in principle, it should be amenable to sufficient quantification to enable the preferential ordering of places required by our definition of “biodiversity”. Thus, once a true surrogate is chosen, the problem of quantification is solved to the required extent. The trouble, of course, is that because we do not know what general biodiversity is, we will never be able to assert beyond controversy that we have found the true surrogate. Worse, empirical considerations alone will not allow a complete solution of this problem because of the indeterminacy of “biodiversity”. Empirical arguments can only settle questions about relations between empirically well-specified entities. Conventions must enter into any determination of true surrogacy and these con-

ventions have to be justified. The justification is based on both practical and apparently theoretical considerations.

4.1 True surrogates

Turning to the theoretical considerations, we are faced with the doubly unfortunate situation that there are several candidates for true surrogacy and that justifications for any of them are theoretical only insofar as they are guided by deeply-held “theoretical” intuitions. Consider three common – and plausible – candidates:

(i) *Character or trait diversity* (Vane-Wright *et al* 1991; Faith 1992; Williams *et al* 1994): The intuition behind this candidate is that evolutionary mechanisms *usually* impinge directly on traits of individuals in populations. The trouble is that “trait” is not a technical term within biology (Sarkar 1998): what we choose to call traits of organisms (or other entities) is largely determined by purely pragmatic considerations, for instance, what can be easily studied in a given research context. Trait diversity is, therefore, not precise enough to solve the quantification problem adequately.

(ii) *Species diversity*: This can be made sufficiently precise and, in practice, it is the true surrogate that is usually invoked, often implicitly. Moreover, species diversity is the measure most commonly used in almost all practical discussions of biodiversity. This may well be because it is regarded as an adequate estimator-surrogate (see below) rather than as a true surrogate. Nevertheless, it is important to note that species are the most well-defined category above the genotype in the taxonomic hierarchy and, because of that, the intuition that species diversity is a good true surrogate has some theoretical merit. The trouble is that we know very well that there is much more to biodiversity than the variety of species.

(iii) *Species assemblage, or landscape pattern, or life zone diversity*: These terms are used in different parts of the world by different people to mean similar things, though the spatial scale may vary. They reflect the intuitions that (a) what is important is the variety of biotic communities with their associated patterns of interactions; and (b) focusing on communities will *ipso facto* take care of species since communities are composed of species. The chief disadvantage is that, at least on the surface, the quantification problem seems intractable: any classification of communities seems to involve arbitrary conventions. Life zone classification provides a partial way out: it involves coupling the characteristics of some communities in a place, in particular, vegetation, with environmental parameters such as elevation, precipitation and temperature (and, sometimes, soil types). For many areas of the world, fairly precise classifications exist, for instance, the life-zone classifications of Holdridge (1967)

for central America and Ohsawa (1987) for the Bhutan Himalaya, the land system classifications and bioregions of Australia (Christian and Stewart 1968; Laut *et al* 1977; Thackway and Cresswell 1995), and similar classifications of eco-regions in Canada (e.g. Bastedo 1986). Because of this, for many regions, the quantification problem has a reasonably satisfactory solution. Nevertheless, there remains the nagging worry that life zone diversity does not fully take into account species, or even community, diversity simply because only a few communities are used to define life zones.

There is no non-conventional solution to the true surrogacy problem. To choose any of these three candidates – or any other – will require the use of pragmatic criteria, in other words, the adoption of some convention. Moreover, because of the reasons mentioned in each case, no single convention (that is, one that selects only one of our candidates) is obviously preferable to the others and it makes sense to use several when possible, for instance, the second and third of our list, simultaneously.

4.2 Estimator surrogates

The decisive practical consideration is that there has to be a tractable estimator-surrogate for the true surrogate we choose. In contrast to true surrogates, estimator-surrogates have a true surrogate as the target variable. Since whichever true surrogate we choose will have to be reasonably precisely demarcated though, perhaps, only by convention (even if we choose a true surrogate as problematic as trait diversity) the estimator-true surrogacy relationship is quantitatively precise. Moreover – and this is a point that cannot be over-emphasized – it is an empirical relation that must be investigated through field work (Landres *et al* 1988).

Traditionally, species richness (the number of species at a place) has been the most popular estimator-surrogate for the true surrogate, species diversity, and Gaston (1996) lists five lines of evidence that point to its efficacy: (i) species richness can be correlated to many measures of ecological diversity and it functions better than most estimator-surrogates including the α -diversity of species as measured by indices such as the Shannon-Weaver index (Whittaker 1975; see also Magurran 1988); (ii) species richness is sometimes positively correlated with the number of higher taxa such as genera; (iii) when species richness is relatively high, it is correlated with trait richness; (iv) though this remains controversial, some parameters that are supposed to measure the complexity of community webs (including the number of edges and the length of directed paths along trophic levels) seem to be correlated with species richness; (v) relatively

high species richness is also correlated with increasing topographic diversity. Of these five points, the second and third are irrelevant to the search for estimator surrogates for species diversity since they refer to richness at the level of higher taxa or traits rather than species; the third assumes that complexity of trophic webs is related to species diversity, which is unproven in the field; and the first and fifth are relevant only if we accept environmental diversity as a true surrogate, not species diversity. Using environmental diversity in such a way is counter-intuitive because it is not a direct representation of biological variety as we expect in a true surrogate. Other problems with environmental diversity will be mentioned below when we discuss environmental parameter composition as a potential estimator-surrogate.

There are, moreover, the two strong arguments already mentioned above against using species richness or, for that matter, richness of any estimator-surrogates, to prioritize places: (i) places should be prioritized using complementarity; and (ii) richness is not the same as diversity. Diversity, including biodiversity, connotes “difference” and “unlikeness” – the amount of variety.

There are at least five other plausible candidates for estimator-surrogates. Each of these reflects the surrogate composition or diversity of a place, compiled as a list, which can be used by the algorithms of the previous section:

(i) *Environmental parameter composition*: The most theoretically-justified intuition behind this idea is that each point of the space spanned by environmental parameters is a putative niche to be occupied by some species (Nix 1982; Faith and Walker 1996b). Moreover, thinking in terms of environmental parameters brings us closer to actual places than the other candidates that will be discussed below. Diversity of environmental parameters is also defined well enough to solve the quantification problem adequately. Note that since the environmental space is sampled uniformly, the problem that niches are not defined independently of organisms is avoided (Hutchinson 1957). However, not all putative niches will be occupied, and the correlation between biodiversity – in the sense of diversity somehow associated with living organisms – and environmental parameters may not be very good. Again, since we cannot measure biodiversity directly, we also cannot estimate quantitatively how good this correlation is. Because of this there is the potential problem of an inefficient use of resources if places are chosen on the basis of environmental parameters. Finally, when selecting places, if this is done using environmental parameters on large enough spatial scales, there is also the danger of losing convergent but different species and other biological units. As an extreme example, this would happen if Australian places with marsupial analogues

of placentals are not included because similar environmental parameter sets were selected only west of the Wallace line.

(ii) *Vegetation class or type*: Vegetation types represent various combinations of species and the interactions between them and thus incorporate certain ecological processes, another component of biodiversity, as well as lists of species. Conspicuous organisms such as plants interact with, and are linked spatially to, smaller organisms such as nematodes, arthropods, fungi, protozoa and bacteria, which have enormous radiations in comparison (McKenzie *et al* 1989). Protecting vegetation types might protect many of the more inconspicuous species.

Often, (i) and (ii) are used simultaneously (e.g. Nix *et al* 2000). They have the obvious advantage of being relatively easily assessed. For instance, temperature and precipitation data are widely recorded or can be inferred from reliable models. Vegetation type can be inferred through remote sensing, and so on. These data can then be combined, either explicitly in a numerical clustering or ordination algorithms, or intuitively as in the traditional life zone classifications, to derive ecological classes. Thus the estimation problem has a good solution. However, the empirical question of the relation of these data to species diversity (let alone other potential true surrogates) remains unresolved. This question is being systematically investigated in New South Wales (Ferrier 1997) and Texas (Sarkar *et al* 2000) (and, very possibly, other places).

(iii) *Species composition*: Recall that species composition or diversity, expressed as the set or list of species per place, needs to be distinguished from species richness and, to the extent that species can be used to address the problem of true surrogacy, it is the former that matters. This is the principal point that emerges from our definition of "biodiversity" based on complementarity. Because of this, one would expect species diversity to be at least a plausible candidate for estimator-surrogacy. If it were one, we also have a relatively robust measure, the list of species at each place.

(iv) *Genus or other higher taxon composition*: Higher taxa such as genera and families may represent lower level classes such as species. Williams *et al* (1994) have shown that species richness can be predicted from higher taxon richness for some taxa in particular places. In order to use higher taxa as estimator surrogates for the true surrogate, species diversity, a correlation between the spatial distribution patterns of the higher taxa and the spatial distribution patterns of species would have to be established and described.

(v) *Subsets of species composition*: Species sub-sets such as birds, plants, butterflies, etc. and combinations of these, are the most easily recognized and widely accepted

representation of diversity. The data can be compiled from museums and herbaria, and/or the many other collections held by natural resource management agencies. Collections from these sources usually suffer severe problems of spatial bias, with collecting sites mapping road networks (Margules and Austin 1994), although data treatments are available for partially reducing such biases (see, e.g. Margules *et al* 1995; Hutchinson *et al* 1996; Austin and Meyers 1996; Hilbert and van den Muyzenberg 1999). A recent empirical study also suggests that so-called flagship (charismatic) species and umbrella (wide-ranging) species may not perform much better as surrogates than species selected randomly from the same data sets (Andelman and Fagan 2000).

There has been very little empirical work establishing the adequacy of any of these estimator-surrogates as predictors of true surrogates. If species diversity is taken to be the (only) true surrogate, the adequacy of species composition as an estimator-surrogate is obviously trivially guaranteed; for other true surrogates the problem of determining empirical surrogacy remains. Moreover, trying to use total species composition as an estimator-surrogate is unjustified for the simple reason that it cannot be assessed rapidly and easily, as is required for such surrogates.

There is no reason to believe that the same estimator-surrogates will be the best ones for all regions. But such universality is not necessary so long as the estimator-surrogates that are chosen are shown to be adequate for the region in which they are to be used. Therefore, a first step in conservation planning within a region or biome should be to establish the relationship between an estimator surrogate and the set of entities that has been chosen as the true surrogate. This process will require detailed surveys of the true surrogates in at least some suitably randomized places within that region or biome.

5. Conclusions

Biodiversity is rooted in place, and is similar or different from place to place. The task of conserving biodiversity requires that places be prioritized for conservation action. Place prioritization cannot be effectively accomplished using richness as the only biodiversity index because richness does not capture the variety and differences in composition between places, which is crucial to the concept of biodiversity. In contrast, complementarity explicitly captures and measures the differences between places as we iterate the process of place selection, starting with an initial place.

Once we contextualize biodiversity to the problem of place prioritization, and acknowledge that the problem of

true surrogacy in unsolvable without invoking pragmatic considerations, two conclusions emerge: (i) there is no non-conventional absolute measure of biodiversity because there is no entirely non-conventional solution to the problem of true surrogacy; and (ii) nevertheless, the absence of such a measure presents no serious problem for the task of biodiversity conservation since the relative concept of biodiversity is all that is required to prioritize places for conservation action. Even this relative concept has a conventional element built into it because it relies on estimator surrogates for true surrogates and, whereas the former are subject to empirical justification, the latter are still dependent on convention.

This (partial) reliance on conventional elements in our argument may seem unsatisfying. A philosophical point, widely appreciated by philosophers of science, but often not explicitly acknowledged by scientists, deserves to be noted in relation to this: conventional elements almost always enter into theoretical reasoning in science (Nagel 1961; Sarkar 1998). But “conventional” does not mean “arbitrary”: it means that there were choices to be made, no single option was dictated by the facts at hand, and a choice was justified instrumentally by its ability to achieve the purpose for which it was intended.

When we choose to describe a natural system, especially if it is even slightly complex, we make choices about what to include as the state variables. Once we choose these, and presume a structure or dynamics in our model of the system, all that we require is that we can predict, with some specified standard of precision, other aspects of the system, for instance, other parts of its structure or its state in the future. When we choose our state variables we routinely simplify our picture of the system, leave out certain aspects, approximate others, and so on. It is, as a practice, possible to model the same system in a variety of ways. The route we follow is indicated by the purpose for which a model is intended.

The case of biodiversity is only special because the most general purpose, that of protecting the variety of the patterns and processes of life, is not as clearly demarcated as the purposes that have to be achieved in most modelling situations. Ultimately, whether or not we have chosen the appropriate true surrogates will be indicated by whether, at the end of each stage of our conservation efforts, we feel that we are achieving the type of protection we set out to achieve. This will not be a quantitative judgement. However, once we accept this as an unavoidable part of biodiversity conservation efforts, the framework for place prioritization using the relative concept of biodiversity that we defined earlier is free of convention. Because of this, and because that definition is fully operational, it has a level of precision sufficient to proceed with prioritizing places during conservation planning.

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