Introduction

Extinction is irreversible. The restoration of habitats, ecological processes, and ecosystem services is complex but possible (Dobson et al. 1997a). We cannot, however, restore the building blocks of those higher levels of biological organization once species go extinct. For this reason, above all, we must consider minimization of the species extinction rate our most urgent target and the measure of conservation success. Molnar et al., Higgins et al., Cowling et al., and Pressey (2004, this issue) contribute a variety of insights on this matter, and for clarity of response, we synthesize their insights into five topics. We start by addressing the proposals of these authors for considering data and targets for three other scales of ecological organization: habitats or other spatial classifications (hereafter land types, following Pressey), ecological processes, and ecosystem services. We then tackle the issue of surrogacy between data types. Finally, we address some of the problems with species-based approaches.

We were invited to write our initial essay (Brooks et al. 2004a) to build on discussions of setting targets for biodiversity conservation planning and “argue that, despite a range of shortcomings, species data provide the best basis for setting these targets.” We were not charged to report on the World Parks Congress in general (i.e., the role of the Durban Accord, [http://www.iucn.org/themes/wcpa/wpc2003/pdfs/outputs/wpc/durbanaccord.pdf]) or to report on Workshop Stream 7 (Building Comprehensive Protected Area Systems), which we do elsewhere (Brooks et al. 2004b) in collaboration with a number of the authors who respond here to our Conservation Biology article. We emphasize that our use of the word “armchair” was not intended as derogatory. Indeed, the respondents to our essay include some of the world’s leading natural historians.

Species Data, Environmental Data, or Both

There is considerable agreement between our views and those of Higgins et al., Cowling et al., and Pressey that conservation planning should make the best use of both species and environmental data. What are the disagreements? There is a difference in our respective concerns. We called for species data to remain central to conservation planning. In contrast, the respondents fear the exclusion of the use of environmental data or of land types determined from such data. In our view, there is no danger of the latter, but there is a risk that in this technological age conservation planners may be tempted to rely on remote-sensing data and computer models without incorporation of the available species data (e.g., Faith et al. 2001).

The main disagreement, however, concerns the reasons why environmental data are important. From our perspective, this information is essential because it can help us correct biases and fill gaps in species knowledge. A different view, explicit in Molnar et al., at least, is that land types are biodiversity entities, and therefore conservation targets, in their own right.

We presented some arguments as to why we disagree with this perspective, but we expand on these here. We view land types as components of classification systems, somewhat arbitrary mind constructs that help us organize ideas in a complex and biodiverse world. We agree with Pressey that ideally, if we had perfect species data (on the distributions and on the ecological interactions), we would no longer need environmental data for conservation planning. Although we currently need such data, we must keep in mind their subjective nature and the need to interpret the results of conservation planning based on environmental data in the context of the particular classification system chosen to create them.

Take, for example, the broadest land-type system, biomes. A major announcement at the Fifth World Parks Congress was that the 10% target has been surpassed for 9 out of 14 major terrestrial biomes (Fig. 1), based on the Udvardy (1975) biome classification system (Chape et al. 2003). If the more recent biome classification of Olson et
Figure 1. Percentage of protected area in each biome according to the 2003 World Database on Protected Areas (WDPA; World Database on Protected Areas Consortium 2003). Results according to the Olson et al. (2001) and Udvardy (1975) classifications (Chape et al. 2003). The results according to the Olson et al. (2001) classification were obtained through an overlap of their corresponding biome layer with that of the WDPA. Arrows indicate broad correspondence between biomes in the different classification systems.

al. (2001) had been used instead, it would have revealed that the 10% target is surpassed for only 8 of 16 biomes. Additionally, different conclusions would have been extracted about the coverage of particular biomes: for example, 12.8% protection of Tropical Dry Forests/Woodlands would have been achieved under Udvardy’s classification (1975), but Olson et al.’s classification (2001) would have yielded only 7.9% protection of Tropical and Subtropical Dry Broadleaf Forests. It would therefore be unwise to get too attached to the components of a particular classification system and to take these representation figures too literally in assessing progress toward global conservation efforts, as Molnar et al. propose. These systems will be redefined as better species data become available, in the same way the system proposed by Olson et al. (2001) refined Udvardy (1975).

Another problem with taking land types too literally as conservation targets is the assumption that they represent natural spatial subdivisions of biological organization. We may forget that discontinuities that are very clear to the human eye are not necessarily important for species, and we may fail to detect what species perceive as major habitat changes. Consider, for example, the North Central Rockies Forest and Northern Short Grassland ecoregions in North America (Fig. 2). To our eyes, they are very distinct, being dominated by quite different biomes: Temperate Coniferous Forests and Temperate Grasslands, Savannas, and Shrublands, respectively (Olson et al. 2001). In contrast, the Northwestern Andean Montane Forests ecoregion is represented as a single ecological unit. We find higher levels of faunal similarity, however, in comparing the Rockies with the Temperate Grasslands than in comparing the northern and southern portions of the Andean Montane Forests ecoregion. In other words, from the perspectives of amphibian and bird (although not mammal) species, the northern and southern parts of the Northwestern Andean Montane Forests are more distinct than are two different ecoregions within two different biomes in North America. Pressey argues that planners “use land types as generalizations about environmental variation assumed to be relevant for at least a proportion of the species lacking descriptions, adequate point records, or reliable models,” but it is difficult to trust in the relevance of these classes for unknown species when they are not obviously adjusted to the distribution patterns of the species we do know.

When land types are used as biodiversity units for conservation planning, targets are typically set such that a given percentage of each should be protected (e.g., Stritholt & Boerner 1995; Powell et al. 2000; Pressey et al. 2000). This approach would ensure that we at least represent the Rockies forests and the Northern Short Grasslands, but nothing would guarantee that both the northern and southern part of the Andes Montane Forests and
Figure 2. Faunal similarity of land types (Olson et al. 2001). Tables (on the maps) present information comparing the similarity between the fauna composition of (a) the North Central Rockies Forests in relation to the Northern Short Grasslands ecoregions and (b) the northern section of the Northwestern Andean Montane Forests in relation to the southern section. We assessed similarity with the Jaccard coefficient (J). For two regions A and B, $J = a/(a + b + c)$, where $a$ is the number of species common to both regions, $b$ is the number of species present in (a) but not (b), and $c$ is the number of species present in (b) but not (a). The $J$ varies between 0 (minimum) and 1 (maximum similarity). See Brooks et al. (2004a) for data sources.

Another point of debate concerns the ordering of information and analysis: which should take precedence, species data or environmental data? Higgins et al. and Cowling et al. enthuse about the coarse- and fine-filter approach of Noss (1987), which would incorporate environmental data first. In contrast, we argue that species data should take precedence, with environmental information being used to expand the value of the species data. Put another way, conservation planning should have solid roots in what we already know about species and build from that information, rather than starting with untested assumptions, interpretations, or classifications about the way species perceive environmental variation. For example, the methods mentioned by Cowling et al. of “combining environmental and available species data to produce land classes that reflect biological heterogeneity associated with compositional turnover” include two quite distinct approaches. One is the environmental diversity (ED) method (Faith & Walker 1996; Faith 2003) applied to select areas that are complementary in a multidimensional environmental space. The other is the approach in which the observed spatial patterns of species turnover are modeled using environmental data (Ferrier 2002; Ferrier et al. 2002). The former is based on a set of assumptions on how species are distributed in the environmental space, and the latter is based on the observed patterns of species distribution in such space. We would avoid the former, but see the latter as a promising approach (as we noted in our essay).

Ecological Process

We fully agree with Pressey that conservation planning requires not only representation of ecological pattern but also of process, on which biodiversity depends for long-term persistence. Our statement (Brooks et al. 2004a) that techniques for mapping and measuring ecological processes are still in their infancy was not intended to suggest that the aim of representing process should be abandoned because it is too difficult. The extraordinary, pioneering work in this field by Pressey, Cowling, and others (e.g., Cowling et al. 2003) has contributed much to tackling this problem. Rather, we intended simply to highlight the huge task still ahead. The first challenge is to explicitly define the full set of processes we want or need to conserve. At any given site the list of candidate processes could be endless; for example, the interactions between every pair of species (e.g., predation), biogeochemical processes (e.g., nitrogen cycle), population dynamics (e.g., migration), and disturbance dynamics (e.g., fire). Although in some cases some processes are clearly vital, such as fire dynamics in Mediterranean systems (Keeley & Fotheringham 2001), we cannot list all the critical processes in a particular region, let alone
understand how to best address them through conservation planning.

With this said, we argue that one of the main advantages of species data is precisely to inform the spatial requirements for biodiversity persistence. Setting targets for the processes mentioned in Pressey’s Table 1 can only be based on information on species’ ecological requirements. Hence, the importance of soil interfaces (e.g., Rouget et al. 2003) and of areas of climatic stability (e.g., Fjeldså et al. 1999) as speciation centers is obvious only because of observed patterns in species endemism. Migration areas and dispersal barriers are revealed by data on species distribution and movements (e.g., Powell & Bjork 1995); connectivity is dependent on the dispersal ability of species (e.g., D’Eon et al. 2002); and habitat suitability and effective population sizes are clearly relative to particular species (e.g., Allen et al. 2001). This is not to say that ensuring the persistence of the species that we know would be a sufficient umbrella or adequate surrogate for the persistence of all biodiversity. But it is not clear how the persistence of a land type could be assessed at all without looking at the persistence of its component species.

**Ecosystem Services**

We consider species an important biodiversity conservation target in their own right, but we fully agree with Molnar et al. on the need to address the maintenance of the ecosystem services that biodiversity provides to humankind. What we fail to understand are the claims that a species-based approach is intrinsically contrary to an approach that values ecosystem services. It is even less clear to us why an approach based on land-type representation is better in addressing ecosystem services than an approach based on species, as Molnar et al. claim. In the same way that not all land types are equally valuable for species representation, presumably not all land types are equally important for providing ecosystem services. Their argument that “a major advantage of conservation goals that are based on habitats is that every place on the planet remains a candidate for conservation protection” is bizarre—every place on the planet has species as well as habitats.

We were unconvinced by the examples given by Molnar et al. as proof that there is an incongruity in an approach focused on retaining global species diversity and one based on retaining ecosystem services. Salt marshes and other highly productive wetlands are not neglected by a species-based conservation approach because the same productivity that makes them valuable to us makes them valuable to a set of other species. For example, 69% of the important bird areas (a species-based approach) identified in Europe are wetlands because wetlands are crucial breeding, nonbreeding, and stopover habitat for many bird species (Heath & Evans 2000). In contrast to Molnar et al., our proposal does not suggest that conservation priorities should be defined based on the length of species lists, but rather that species information, especially information about irreplaceability and threat, should underlie decisions on conservation priorities.

We were unable to confirm the origin of Molnar et al.’s statement that Canada “is in the top 10% in the value of its ecosystem services per unit area.” The table published by Sutton and Costanza (2002; http://www.du.edu/~psutton/esiindexisee/Table2complete.xls) ranks Canada fiftieth in a list of countries sorted by decreasing value of land ecosystem services product (ESP) per square kilometer (the first country is the Maldives, and the second is Monaco; it is not clear that ESP/km² is a particularly useful measure). Interestingly, in terms of absolute land ESP, 12 of the top 20 nations are megadiversity countries (Mittermeier et al. 1997). Although both species endemism and absolute ESP are related to land area (explaining why countries such as Brazil and Australia score high on both lists), land area alone does not explain why a country such as Papua New Guinea ranks twentieth in absolute ESP, whereas it ranks fifty-fifth in total area. A reasonable hypothesis might be that this wealth of ecosystem services is at least in part driven by its megadiversity.

**Surrogacy**

A key issue mentioned in all four responses is surrogacy. The surrogacy value of land types or ED in representing species diversity is frequently assumed (e.g., Powell et al. 2000; Pressey et al. 2000; Faith et al. 2001) but rarely tested. An adequate test of surrogacy of land types or ED in representing species diversity must address the following question: If one selects a set of protected areas based on land types or ED, how well does such a network perform in representing species diversity? Measuring performance requires comparing the levels of species representation obtained using the surrogate with what would be obtained if the same area had been selected at random and if the same area had been selected using the species information directly (Ferrier 2002). Without this information, the effectiveness of the surrogate being tested cannot be assessed. For example, Araújo et al. (2001) found that the selection of the set of 52 cells that maximized ED represented 83% of all bird species. This appears to be evidence of high surrogacy, but they reported that randomly selected sets of 52 cells would likely perform even better (5% upper tail equals 86%) and that it would have been possible to represent 100% of all bird species twice in the same area. These results underpin Araújo et al.’s (2001) conclusion that maximizing ED is not an adequate surrogate strategy for maximizing species diversity.
Naturally, as Pressey points out, their test is valid only for a given region (Europe); a given set of species (plants, birds, mammals, and amphibians); a given scale (50 × 50 km grid cells); and a given method, ED (Faith & Walker 1996). Nevertheless, this remains the only study of which we are aware that meets the criteria for an adequate test of environmental surrogacy.

The analyses of Kiest er et al. (1996), Ward et al. (1999), and Lombard et al. (2005), among others, present inconclusive results on the issue. The first study, for example, found that five cells maximizing diversity of vegetation classes (defined by dominant cover species) represented 76% of 357 vertebrate species analyzed. Although Kiest er et al. indicate that a maximum of 93% of the species could have been represented in the same number of cells, they provide no information on how many species would have been represented by an average, randomly selected, set of five cells.

Pressey and Higgins et al. refer to several studies as providing “more encouraging” evidence for the surrogacy of land types (Wessels et al. 1999; Pharo & Beat tie 2001; Cushman & McGarigal 2002; Mac Nally et al. 2002; Oliver et al. 2004; Su et al. 2004). In fact, all these are analyses of the association between land type and species assemblages, not surrogacy tests. For example, Mac Nally et al. (2002) found positive associations between “biodiversity management units” (based on biotic, climatic, and physical characteristics) and assemblages of tree species, birds, and mammals. This analysis indicates that species distributions and abundances respond to the same variables used to define the land types, which is valuable ecological information but does not prove or disprove that these classes are adequate surrogates for species in reserve planning. Indeed, there are a number of ways in which land types may be distinct, with quite different meanings for conservation planning. For example, a land type with an impoverished or degraded species composition would be considered quite distinct (Table 1), but does not automatically become a biodiversity element that ought to be represented in its own right, and it adds nothing in terms of species representation to a reserve network that already represents the more intact species assemblage. A land type with a different species composition, on the other hand, adds new species (maybe even endemic species) and deserves a different level of attention altogether from the perspective based on complementarity (Faith et al. 2001).

We therefore retain our statement that there is currently no evidence supporting the use of land types as surrogates for species representation, and recommend this as a priority line of research. Equally important is to further investigate the extent to which subsets of species are, or are not, good surrogates for the representation of other species. Previous studies have yielded mixed results in this regard: Dobson et al. (1997b) present evidence of surrogacy, whereas Virolainen et al. (2000) found surrogacy value for some taxa but not for others. We are in full agreement with the cautionary comment by Higgins et al. that “including all known taxa [in defining conservation priorities] will not guarantee coverage of all biodiversity.” At least, however, it would guarantee coverage of all known taxa as conservation targets in their own right. It remains to be seen whether using land types as surrogates would ensure even that.

### Difficulties Facing Species-Based Approaches

The responses to our essay highlight two serious difficulties facing species-based approaches: the limitations of existing sampling and the cost of extending sampling. All the respondents concentrate on the former. We agree that these are limitations but see them as incentives for further sampling efforts rather than reasons for neglecting to use the existing species data. The variability of abundance across species ranges might mean that even low sampling (if well distributed spatially) can provide useful information in identifying those areas most important for species persistence (Gaston & Rodrigues 2003).

Pressey is right that false negatives plague species distribution data sets, but we contend that these are far less serious than the false positives introduced by environmental data would be (Loisel le et al. 2003). Accepting false negatives is precautionary in assuming that conservation efforts should be aimed at places where we know that species are present (even if more appropriate places are subsequently found), whereas accepting false positives could allow a species’ extinction because we assume that we are conserving it where it does not actually

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### Table 1. Hypothetical values of abundance for nine species (S₁ to S₉) across five land types (L₁ to L₅).

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*Each of the classes L₂ to L₅ was compared with L₁ with the Bray-Curtis dissimilarity index (also used in Wessels et al. [1999], Mac Nally et al. [2002], and Su et al. [2004] to distinguish between land types; this index varies between 0 [minimum dissimilarity] and 1 [maximum dissimilarity]). The L₂ is a degraded version of L₁ (same species but in lower abundances, Bray-Curtis index = 0.43); L₃ is an impoverished version of L₁ (fewer species but ones remaining occur in the same abundances, Bray-Curtis index = 0.50); L₄ is a degraded and impoverished version of L₁ (Bray-Curtis index = 0.76); and L₅ includes four of the species in L₁ (in the same abundances) but adds three more (Bray-Curtis index = 0.38). Despite the fact that L₁ has species that do not occur in L₁, it is considered by the Bray-Curtis index as less dissimilar from L₁ than the degraded or impoverished land types.*
occur. Biased taxonomic coverage is a bigger concern, but exciting current initiatives have revealed developments in this area that would have seemed unattainable a few years ago. Examples include the emergence of comprehensive and conservation-relevant species data for plant groups such as conifers (Farjon & Page 1999) and cycads (Donaldson 2003), terrestrial invertebrates as diverse as tiger beetles (Cassola & Pearson 2000) and ants (Wilson 2003), and a range of coral reef taxa (Roberts et al. 2002). In our opinion, the gap most urgently requiring attention is for freshwater: global assessments of taxa such as fish and dragonflies are an extremely high priority.

Molnar et al. and Cowling et al. are also concerned about the cost of increasing sampling coverage. These costs are certainly high, but it is essential to see them in terms of both their immediate value and of current expenditure in other sectors. Investment in collection and compilation of species data yields great value for the money in conservation planning (e.g., Balmford & Gaston 1999). More generally, although we suspect that the estimate of $5 billion for describing all species is an underestimate, it is still cheap at the price. The human genome project, a task of comparable biological discovery, cost approximately $5 billion (Wilson 2000) and has generated invaluable information across topics as diverse as human evolution, physiology, and health. Similarly, we see improved data for conservation planning as just one of the many benefits to humanity that would be delivered by the massive increase in the sampling of biodiverse regions and taxa. For example, such a project would achieve tremendous human welfare benefits in its delivery of education, training, and job opportunities for developing countries, where the majority of the species to be described and mapped are found. Finally, it has been pointed out that field research is often an effective conservation tool in itself (e.g., Oates 1999), so in many cases the direct consequence of producing data on species becomes saving them.

Several of the respondents believe that we claimed that species data on their own are equivalent to conservation results. We do not claim this: they are not. But these data are a precondition of conservation because we cannot understand the relationships between the components of biodiversity without knowing what those components are. Collar (1997) summed up the issue succinctly: “Taxonomy precedes conservation. This is as basic as to say that language precedes education. Without the formal structure of names and an agreed system of usage, there can be no understanding of what exists to be conserved.”

Conclusion

We wholeheartedly agree with Cowling et al. that the main challenges to biodiversity conservation are in the implementation of conservation plans (e.g., Pressey 1998). But even though we recognize the need to act as opportunities arise, we are also wary of the options lost when conservation planning is driven by opportunity (Pressey 1994). Before systematic conservation planning, decision makers were most likely acting with the best possible intentions when they created the current protected-area network that is so biased toward the rocky and icy parts of the planet (Scott et al. 2001). We worry that there may be similar risks in creating networks that are representative of land types that may prove not to be good biodiversity surrogates. Efforts to compile more and better species data are indeed needed, not to replace the implementation process but to support it. Above all, we cannot afford to ignore the species data that already exist.

Literature Cited


