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Abstract: *In the face of limited funding, knowledge, and time for action, conservation efforts often rely on shortcuts for the maintenance of biodiversity. The umbrella species concept—proposed as a way to use species requirements as a basis for conservation planning—has recently received growing attention. We reviewed the literature to evaluate the concept's general usefulness. An umbrella species is defined as a species whose conservation is expected to confer protection to a large number of naturally co-occurring species. This concept has been proposed as a tool for determining the minimum size for conservation areas, selecting sites to be included in reserve networks, and setting minimum standards for the composition, structure, and processes of ecosystems. Among the species suggested as potential umbrellas, most are large mammals and birds, but invertebrates are increasingly being considered. Eighteen research papers, most of which were based on hypothetical reserves or conservation networks, have provided evaluations of umbrella species schemes. These show that single-species umbrellas cannot ensure the conservation of all co-occurring species because some species are inevitably limited by ecological factors that are not relevant to the umbrella species. Moreover, they provide evidence that umbrella species from a given higher taxon may not necessarily confer protection to assemblages from other taxa. On the other hand, multi-species strategies based on systematic selection procedures (e.g., the focal species approach) offer more compelling evidence of the usefulness of the concept. Evaluations of umbrella species schemes could be improved by including measures of population viability and data from many years, as well as by comparing the efficiency of the proposed scheme with alternative management strategies.*

Utilidad del Concepto de Especie Paraguas como Herramienta de Conservación

Resumen: *Ante la escasez de financiamiento, de conocimiento y tiempo para actuar, los esfuerzos de conservación a menudo confían en métodos rápidos para el mantenimiento de la biodiversidad. El concepto de especie paraguas - propuesto como una manera de utilizar los requerimientos de las especies como base para la planeación de conservación – ha recibido mayor atención recientemente. Revisamos la literatura para evaluar la utilidad general del concepto. Una especie paraguas se define como una especie cuya conservación conferiría protección a un gran número de especies que coexisten naturalmente. Este concepto se ha propuesto como una herramienta para determinar el tamaño mínimo de áreas de conservación, seleccionar sitios a incluir en redes de reservas y para fijar las normas mínimas para la composición, estructura y procesos de los ecosistemas. La mayoría de las especies que se sugieren como paraguas potenciales son mamíferos y aves mayores, pero se están considerando a los invertebrados cada vez más. Dieciocho artículos científicos, la mayoría basados en reservas o redes de conservación hipotéticas, han proporcionado evaluaciones de proyectos con especies paraguas. Estos muestran que una sola especie paraguas no puede asegurar la conservación de todas las especies coexistentes porque algunas especies inevitablemente están limitadas por factores ecológicos que no son relevantes para la especie paraguas. Más aun, proporcionan pruebas de que especies paraguas de un taxón alto determinado necesariamente no confiere protección a los conjuntos de otros taxones. Por otro lado, estrategias multiespecíficas basadas en procedimientos de selección sistemáticos (por ejemplo, el método de la especie focal) ofrecen evidencia más convincente de la utilidad del concepto. Se debe mejorar la evaluación*

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de los proyectos de especies paraguas incluyendo medidas de viabilidad poblacional, datos de muchos años, así como comparando la eficiencia del proyecto propuesto con estrategias de manejo alternativas.

Introduction

Following the emergence of the concept of biological diversity, conservation biologists showed growing interest in developing shortcuts to the conservation of whole biota. The umbrella species concept has been proposed as a way to use species requirements to guide ecosystem management. Its main premise is that the requirements of demanding species encapsulate those of many co-occurring, less demanding species (Lambeck 1997). By directing management efforts toward the requirements of the most exigent species, one is likely to address the requirements of many cohabitants that use the same habitat. The umbrella species concept is intuitively appealing and offers a simple, ecologically based shortcut for the management of communities. Yet the assumption that providing for the requirements of a few species results in the protection of most species present in the same area rarely has been addressed rigorously. Indeed, many authors have recently made a plea for the empirical validation of this concept (Caro & O'Doherty 1999; Simberloff 1999; Angelstam et al. 2001; Fleishman et al. 2001).

Although the umbrella species concept has been discussed in the biological conservation literature, no comprehensive review has been made that allows assessment of its general utility as a conservation tool. Some authors have discussed this concept more thoroughly than others (e.g., Simberloff 1998; Caro & O'Doherty 1999; Zacharias & Roff 2001; Caro 2003), but their accounts—although rich in insight—do not cover all its variants or extensively examine the empirical evidence for its utility. We sought to (1) review the history of the umbrella species concept and distinguish its different uses, (2) evaluate the extent to which the concept has been validated empirically, and (3) suggest directions for using umbrella species in conservation planning.

History and Uses of the Umbrella Species Concept

The exact origin of the umbrella species concept is nebulous. To our knowledge, Frankel and Soulé (1981) were the first to use the term *umbrella* to suggest that conservation measures directed at the largest species could confer protection to what they called "denser species." A few years later Wilcox (1984) proposed that management focus on those species whose habitat requirements are "at least as comprehensive as that of the rest of the community," thus providing a "protective umbrella" for other species. Other authors had put forward the same basic idea before that, although without using the term *umbrella* (Eisenberg 1980; East 1981; Mealy & Horn 1981). Therefore, this concept was probably used implicitly before it was defined (Caro 2003). The biological conservation literature from the 1980s includes a number of references to the umbrella species concept (e.g., Ehrlich & Murphy 1987; Murphy 1988; Peterson 1988), but most of these papers only state the theoretical appeal of that concept without evaluating its validity. Since the beginning of the 1990s, attention to the umbrella species approach has grown. Instead of merely discussing the appeal of this idea, many researchers have critically examined the potential usefulness of proposed umbrella taxa for management (e.g., Ryti 1992; Beier 1993; Launer & Murphy 1994; Berger 1997; New 1997; Fleury et al. 1998), and others have suggested ecologically based methods or criteria for the selection of umbrella species (e.g., Lambeck 1997, 1999; Caro & O'Doherty 1999; Fleishman et al. 2000, 2001).

Definitions

A large number of definitions have been proposed for *umbrella species* that emphasize different uses and properties (Zacharias & Roff 2001). This has resulted in some confusion about the meaning of the term. Fleishman et al. (2000) recently suggested a broadly applicable definition for an umbrella species: a "species whose conservation confers a protective umbrella to numerous co-occurring species." This definition is somewhat tautological, however, because it includes the term *umbrella*. A potentially consensual alternative could be a species whose conservation confers protection to a large number of naturally co-occurring species. We use this general definition as a basis throughout this review and define narrower variants of the concept in context-specific applications. We use the phrase *umbrella scheme* to describe any proposed conservation plan based on one or several umbrella species. The co-occurring species that are likely to be protected by conservation activities directed at the umbrella species are hereafter referred to as *beneficiary species*. Several more or less overlapping subconcepts of umbrella species can be distinguished, all of which conform to our general definition.

Umbrella Species with Large Area Requirements

In its classic form and at the local scale, the umbrella species concept refers to the minimum area requirements of a population of a wide-ranging species (Wilcox 1984).

It hinges on the assumption that providing enough space for species with large area requirements will also shelter a whole suite of species with more modest spatial needs. Because organisms with a large body size also tend to have large home ranges (McNab 1963), maintaining viable populations of those species requires the conservation of large tracts of habitat. For that reason, large-bodied organisms have been favored as prospective umbrellas. Species in this category are usually vertebrates, typically large mammalian carnivores (Eisenberg 1980; East 1981; Peterson 1988; Shafer 1990; Noss et al. 1996; Carroll et al. 2001), herbivores (Mealy & Horn 1981; Wallis de Vries 1995; Berger 1997), or birds (Martikainen et al. 1998; Suter et al. 2002).

Umbrella Species Used to Select Sites

In addition to its use in determining minimum area for protection, the umbrella species concept has been proposed as a tool for defining reserve networks at larger geographic scales. In the site-selection umbrella concept, the occurrence of single- or multi-species umbrellas, or, alternatively, the species richness of an umbrella taxon, is used as a basis for the selection of sites—habitat patches, ecosystems, planning units, or even large grid squares—to be preserved in a conservation network. The general methodology consists of setting aside for protection the totality or a given proportion of the sites where the umbrella(s) occur(s) or where species diversity for the umbrella taxon is high (Kerr 1997). It is presumed that populations of a number of beneficiary species should be protected in the network (Ryti 1992; Launer & Murphy 1994; Kerr 1997; Fleishman et al. 2000, 2001).

The Extended Umbrella Concept

The umbrella species concept builds on the assumption that the requirements of demanding species should encompass those of many other species (Lambeck 1997). This assumption is stated explicitly for area needs in the subconcept of area-demanding umbrella species. But why should this tool be restricted to area requirements? In a variant that we would like to call the extended-umbrella species concept, the basic idea is broadened to include other attributes of landscapes such as habitat connectivity, the occurrence of various ecosystem processes, or the distribution of scarce resources. For example, Fleury et al. (1998) and van Langevelde et al. (2000) used, respectively, the California Gnatcatcher (*Polioptila californica*) and the European Nuthatch (*Sitta europaea*) as umbrella bird species for reserve network planning. Instead of using only the occurrences or area requirements of these birds for reserve site selection, they also considered their need for connectivity. Fleury et al. (1998) did so by simulating movement corridors to link subpopulations, whereas van Langevelde et al. (2000) used threshold between-patch distances for allowing dispersal in the umbrella species. The underlying assumption here is that landscapes that are sufficiently connected for the umbrella species should also be functional for many other species.

Lambeck (1997) gave new life to the umbrella species idea by extending it to a large range of factors that threaten species persistence in managed landscapes. He proposed to identify a suite of "focal species" that would be used to define the spatial, compositional, and functional attributes that must be present in a landscape. Lambeck's process involves identifying the main threats and selecting focal species among the species that are most sensitive to each threat. The requirements of those species would then be used to guide conservation or restoration. Thus, the focal species approach is consistent with the general definition of umbrella species. It simply goes beyond earlier approaches by addressing habitat quality and by proposing systematic criteria for the selection of a suite of umbrella ("focal") species. Lambeck (1997) suggests four threat categories for focal species: area-limited, resource-limited, dispersal-limited, or process-limited. Each of these categories should be represented by one or a few focal species.

By reviewing the conservation biological literature on the umbrella species concept, we assessed the relative prevalence of (1) the main variants of the concept and (2) the different taxa proposed as umbrellas. We examined biological database information and reference lists from relevant papers. We only considered papers published in English. In this review we included 110 peer-reviewed articles, book chapters, and papers from conference proceedings that discussed the umbrella species concept. Papers dealing with this concept without using the term *umbrella* were included if they complied with one of the three variants of the concept described above. Because we addressed an applied science issue, we also considered published governmental research papers and technical reports. We evaluated papers that dealt with one or more of the three main umbrella categories (Table 1). Not surprisingly, mammals, birds, and to a lesser extent—insects dominate as suggested or evaluated umbrella species. Although mammals have often been proposed as area-demanding umbrellas, birds and insects seem to have been preferred for the site-selection and extended-umbrella concepts.

Evaluating the Umbrella Species Concept

If the umbrella species concept is to be promoted from an interesting management hypothesis or social hook (Lindenmayer & Fischer 2003) to an actual conservation tool,

Table 1. The main variants of the umbrella species concept in the biological conservation literature.*

Umbrella species category	*Field of application*	*Total no. of papers discussing concept*	*Number of papers suggesting or evaluating different taxa*						
			mammals	*birds*	*herptiles*	*fish*	*invertebrates*	*plants*	*no suggestion or evaluation*
Area-demanding umbrella	setting the minimum size for a nature reserve	56	23	6	1	0	0	1	29
Site-selection umbrella	prioritizing of patches to be included in a reserve network	15	4	7	1	1	6	3	2
Extended umbrella concept, including the focal-species approach	setting minimum values for landscape composition, configuration, resources, or processes	48	8	16	3	1	12	1	24
All categories		110	31	26	5	2	18	4	51

**Based on 110 reviewed papers. Rows and columns are not additive because one paper may discuss several umbrella categories and suggest or evaluate species from several taxa.*

it is crucial that the approach be validated empirically. A common remark is that the umbrella species concept has rarely if ever been tested (Simberloff 1999). Contrary to classic scientific hypotheses, the umbrella species concept is not subject to falsification (Lindenmayer et al. 2002). Obviously, lack of support for the validity of the concept in certain conditions does not constitute a proof of the general invalidity of the tool. Moreover, the results of such "tests" usually cannot be classified simply as successes or failures in a binary manner, but must rather be evaluated according to some quantitative measure.

To be considered for empirical evaluation of the umbrella species concept (Table 2), a study had to fulfill two criteria. First, it had to present an evaluation of a hypothetical or actual conservation scheme (e.g., spatially delimited reserve or network) based on an umbrella species. Merely describing general patterns of co-occurrence over an entire region provides information on the indicator value of the different species but is not sufficient for constituting an evaluation of the umbrella function. Second, the study had to provide a quantitative measure of the level of protection conferred to beneficiary species, such as the number of species represented in the conservation network or the probability of beneficiary species maintaining viable populations. Among the 110 research papers we included in this review, only 18 evaluated the performance of an umbrella species scheme according to these criteria.

Evaluations of Area-Demanding Umbrella Species

Most empirical evaluations of the umbrella species concept based on area requirements suggest that it has a limited effectiveness (Table 2). Noss et al. (1996) investigated the umbrella value of proposed grizzly bear (*Ursus arctos*) recovery zones by looking at how many species of different taxa would have more than 10% of their statewide distribution captured by the conservation plan (i.e., a surrogate for population viability). Although birds, mammals, and amphibians would be well covered, other taxa such as reptiles would be underrepresented. A recent study by Carroll et al. (2001) based on modeling habitat suitability for the grizzly bear, fisher (*Martes pennanti*), lynx (*Lynx canadensis*), and wolverine (*Gulo gulo*) illustrated the need for a multi-species approach if those carnivores are to be used as umbrella species. Unfortunately, these authors only assessed the overlap in priority areas among those four carnivores and did not evaluate the umbrella function for other species. In an evaluation of the black rhinoceros (*Diceros bicornis*) as an umbrella species, Berger (1997) used a different approach. He examined the umbrella value of the rhinoceros for six large herbivore species by calculating the frequency with which the mean population size for each species would be maintained at a given level within the area needed by the rhinoceros population. Annual differences in rainfall

Table 2. Evaluations of the usefulness of different types of umbrella species for conservation planning.

Umbrella species category and citation	*Ecosystem type*	*Investigated umbrella taxon/taxa*[a]	*Targeted beneficiary taxa*	*Protection conferred*[b]
Area-demanding umbrella				
Noss et al. 1996	Rocky Mountains, northern U.S.	grizzly bear, *Ursus arctos* (S)	amphibians, reptiles, birds, mammals, and plant communities	limited
Berger 1997	African desert	black rhinoceros, *Diceros bicornis* (S)	six large herbivore species	limited
Martikainen et al. 1998	boreal forest, Fennoscandia	White-backed Woodpecker, *Dendrocopos leucotos* (S)	threatened saproxylic beetles	limited
Andelman & Fagan 2000	diverse regions of the continental U.S.	large carnivores of concern (S,M)	species "of concern" from various taxa	limited to ineffective, depending on databases and on surrogate scheme
Andelman & Fagan 2000	diverse regions of the continental U.S.	most widespread species of concern, from diverse taxa (M)	species "of concern" from various taxa	limited to ineffective, depending on databases and on surrogate scheme
Caro 2001	East African deciduous forests, floodplains, and fields	large mammals (M)	small, nonvolant mammals	ineffective
Suter et al. 2002	alpine coniferous forests, Switzerland	Capercaillie, *Tetrao urogallus* (S)	birds	effective for red-listed mountain birds; ineffective for bird diversity in general
Caro 2003	East African deciduous forest	large mammals (M)	large and middle-sized mammals, small carnivores, small native rodents and insectivores	effective for large and middle-sized mammals as well as small carnivores; ineffective for rodents and insectivores
Site-selection umbrella				
Murphy & Wilcox 1986	high-elevation boreal habitats separated by arid scrub; canyon riparian habitats, western North America	birds and mammals (M)	butterflies	limited to effective, depending on spatial scale
Ryti 1992	islands and canyons of southwestern U.S.	plants and birds (M)	plants, birds, mammals, and reptiles	limited (birds) to effective (plants)
Launer & Murphy 1994	serpentine soil-based grasslands, southwestern U.S.	bay checkerspot butterfly, *Euphydryas editha bayensis* (S)	plants	limited
Kerr 1997	North America north of Mexico	mammalian carnivores (M)	invertebrates	ineffective
Andelman & Fagan 2000	diverse regions of the continental U.S.	habitat specialists of concern, from diverse taxa (M)	species "of concern" from various taxa	limited to ineffective, depending on databases and on surrogate scheme
Fleishman et al. 2000	mountain canyons in the Great Basin, western U.S.	butterflies (M)	butterflies	effective
Fleishman et al. 2001	coastal chaparral shrubland; eastern broadleaf forest; xeric shrub steppe, North America	butterflies and birds (M)	butterflies and birds	effective within taxa; limited across taxa
Poiani et al. 2001	mixture of grassland and forest, northern U.S.	Greater Prairie Chicken, *Tympanuchus cupido* (S)	rare plants and animals, natural communities	limited
Rubinoff 2001	coastal sage scrub, southwestern U.S.	California Gnatcatcher, *Polioptila californica* (S)	three specialized insect species (Lepidoptera)	ineffective
Bonn et al. 2002	southern Africa	threatened and/or endemic birds (M)	birds	limited
Extended umbrella species concept				
Fleury et al. 1998	coastal sage scrub, southwestern U.S.	California Gnatcatcher (S)	plant and animal species of concern	limited
Watson et al. 2001	temperate woodland remnants, southeastern Australia	Hooded Robin, *Melanodryas cucullata*, and Yellow Robin, *Eopsaltria australis* (M)	woodland birds	effective with ideal guidelines; limited with less stringent guidelines adapted to the social context

[a] *Abbreviations: S, single-species umbrella; M, multispecies umbrella.*
[b] *Interpretation (by the authors of this review) of the original authors' conclusions. The protection conferred by the umbrella scheme was summarized in three classes: effective, limited, and ineffective.*

caused fluctuations in population size and movements for the six species, but the rhinoceros populations did not vary accordingly. Berger (1997) concluded that the population of 28 rhinoceroses was unlikely to assure the populations of the other species in excess of 250 individuals.

In East Africa, Caro (2001, 2003) observed that populations of edible ungulates and small carnivores were lower outside than inside a national park designed for large mammals. On the other hand, average species diversity and abundance of small mammals were greater outside than inside the reserve. Based on these observations he concluded that delineating a reserve using umbrella species may benefit populations of some background taxa but by no means all. As discussed by Caro (2001), in such studies it is crucial to consider the identity of the potential beneficiary species in addition to their richness and abundance. Attention should be given to the species of concern that are sensitive to human disturbances (e.g., Fleury et al. 1998; Lambeck 1999; Andelman & Fagan 2000). In an assessment of the potential of the Capercaillie (*Tetrao urogallus*) as an umbrella species, Suter et al. (2002) examined separately the umbrella effect for all bird species and for mountain species of concern included in the Swiss Red List. The distribution of the capercaillie was related to high species richness in mountain birds of concern, but this was not the case when ubiquitous bird species were included in the analyses.

Suter et al.'s (2002) study provided one of the few examples of substantial support for the concept of area-demanding umbrella species. This is explained by the fact that they considered variations in vegetation structure in their study area and addressed the question of whether the potential beneficiary species had, as a group, specialized habitat requirements similar to those of the umbrella species. Similarly, Martikainen et al. (1998) provided evidence for the potential umbrella value of the White-backed Woodpecker (*Dendrocopos leucotos*) for threatened beetles dependent on the same resources—that is, decaying deciduous wood within successional deciduous forest. Contrary to the approaches of Suter et al. (2002) and Martikainen et al. (1998), however, most other approaches to the concept of area-demanding umbrella species have been based coarsely on the area requirements of the purported umbrella species without attention to the habitat needs of the potential beneficiary species.

Evaluations of Site-Selection Umbrella Species

The different evaluations of the site-selection umbrella concept have yielded varied results (Table 2). Murphy and Wilcox (1986) demonstrated that the validity of vertebrate-based management for maintaining butterfly diversity is scale dependent. They concluded that regional management of vertebrates would probably provide for the requirements of invertebrates, but that intensive fragmentation on a local scale may cause declines in invertebrates without affecting vertebrates. Kerr (1997), however, provided evidence that a hypothetical system of large-scale reserves designed to include all carnivore species in a minimum of sites would not provide good protection for invertebrates. For gulf islands and canyons in California, Ryti (1992) found that a reserve network containing at least one occurrence of all plant species found in the regional pool covered vertebrates well, whereas such a network for birds did not provide equivalent protection for other taxa. However, the plant network required setting aside an area much larger than the area needed for the bird network. Thus, the relative performance of these two taxa as umbrellas surely would have been different had issues of efficiency been considered.

Using occurrence data for species of concern from a variety of taxa, Andelman and Fagan (2000) evaluated a variety of site-selection umbrella schemes and compared their efficiency to that of random sets of species. Only a few umbrella schemes proved more efficient than random schemes made up of similar numbers of species. On this basis, they concluded that there is little evidence supporting the utility of umbrella species. One limitation of their study is that they automatically included in a given surrogate scheme all species in the databases that fulfilled the selection criteria for that scheme. For example, their "habitat specialist" scheme was based on the occurrences of all habitat specialist species found in the databases, resulting in the need to set aside a very large proportion of the sites. Many such schemes performed well in terms of species protection but were excessively costly (and thereby less efficient) because they required too many conservation areas. Hence, these authors showed that multi-species schemes might fail to provide an efficient management alternative if the suite of umbrella species were selected without addressing issues of parsimony or complementarity. In Southern Africa, Bonn et al. (2002) simulated complementary networks representing threatened and endemic birds with the minimum possible number of conservation areas and assessed whether many other bird species would be conserved in these areas. These networks performed better than random schemes, although they did not guarantee the representation of overall species diversity.

Fleishman et al. (2001) evaluated different site-selection umbrella strategies of butterflies and birds and compared their efficiency to that of random schemes. They ranked species according to their value as umbrellas based on three criteria: medium rarity, sensitivity to human disturbance, and percentage of co-occurring species (Fleishman et al. 2000). Their multispecies umbrella schemes proved to be efficient conservation tools that allowed the area to be set aside for achieving a given level of species protection to be minimized. Launer and Murphy (1994), Poiani et al. (2001), and Rubinoff (2001) assessed the validity of a butterfly, a tetraonid bird, and a passerine bird as single-species umbrellas for plants, rare animals and plants, and invertebrate species, respectively (Table 2). They came to a common conclusion: single species are unlikely to function as effective site-selection umbrellas for the protection of other taxonomic groups.

Most of those researchers used the occurrences of the umbrella species as a basis for reserve site selection and assumed complete data sets. It is possible that some of the recorded absences of the umbrella species were due to imperfections of the inventory technique. In such cases, the planner would fail to include some of the sites that should actually be set aside for protection. On the other hand, incomplete data sets on the occurrences of the potential beneficiary species would result in an underestimation of the efficiency of the umbrella scheme.

Evaluations of the Extended Umbrella Concept

The extended umbrella concept has rarely been evaluated (Table 2). Fleury et al. (1998) designed a hypothetical reserve for the California Gnatcatcher, including corridors to connect subpopulations and buffer zones. It afforded only limited protection to red-listed animal and plant species because some species required localized habitat types or had area needs larger than those of the gnatcatcher. Thus, this species alone cannot provide the basis from which to derive minimum standards for landscape attributes in this coastal sage scrub ecosystem (see also Rubinoff 2001). Similarly, proposed reserves for the Northern Spotted Owl (*Strix occidentalis*) in the Pacific Northwest were insufficient to conserve Marbled Murrelets (*Brachyramphus marmoratus*) and some aquatic ecosystems (summarized in Franklin 1994; Wilcove 1994), which is not surprising given that the owl lives on land. Bonn and Schröder (2001) and Ranius (2002) partially evaluated the potential of carabid beetles as umbrella species. Although these researchers provided evidence for the indicator value of their target beetle species, they did not (contrary to the studies included in Table 2) evaluate any hypothetical conservation scheme based on their prospective umbrella species.

The focal species approach has been only partially validated. The focal species selection process has been applied in a few case studies in Australia (Lambeck 1999; Brooker 2002), Italy (Bani et al. 2002), and the United States (Hess & King 2002), but these investigations did not include evaluation of the umbrella function of the selected species. In eastern Australia, Watson et al. (2001) proposed concrete guidelines for conservation planning based on the needs of sensitive birds and modeled the probability of occurrence of different species in remnants of various size and habitat complexity. They concluded that their revegetation guidelines would provide habitat for about 95% of the resident woodland birds in the region.

Synthesis

Evaluations of the subconcept of area-demanding umbrella species provide little support for its utility for the conservation of biodiversity as a whole. Conservation schemes based uniquely on area requirements will inevitably be flawed unless they also incorporate the needs of sensitive species requiring specialized habitat types. The site-selection umbrella species concept, on the other hand, appears more useful. The umbrella value of single species is generally low because some species are limited by ecological factors that are not relevant to the umbrella species. However, rigorous assessments using multiple species and systematic selection criteria show that umbrella species can be an effective tool for prioritizing remnants to be included in conservation networks (e.g., Fleishman et al. 2000, 2001). The extended-umbrella species concept has rarely been evaluated. Lambeck's (1997) focal species approach has been assessed only partially, and it remains to be seen whether landscapes designed for the most sensitive suite of species can retain nearly all co-occurring species.

What would constitute a robust, empirical evaluation of the umbrella species concept? The examples provided above stress the need to measure the efficiency of the umbrella scheme—that is, to present the results in the form of a ratio of the benefits (e.g., number of species or habitat types protected) to the costs (e.g., total area or number of sites required). This allows for comparison of the efficiency of the umbrella scheme with that of alternative strategies. A number of researchers have looked at whether the umbrella schemes performed significantly better than random schemes or null models (Andelman & Fagan 2000; Fleishman et al. 2001; Poiani et al. 2001). Although this makes sense from a statistical point of view, one may wonder whether more ecologically relevant criteria could be used instead. For instance, comparing the effectiveness of an umbrella scheme with that of measures based on general ecological principles would be much more informative from a management perspective (Poiani et al. 2001). Examples of such measures could be restoration of a nominated proportion of a landscape to create a variety of patches of the main native land types, planning for corridors between isolated patches, and restoration of watercourses and associated riparian vegetation (Hunter 1999; Lindenmayer et al. 2002).

Another limitation of many evaluations of the umbrella species concept is that they often rely on presence and absence "snapshot" data without distinguishing between viable or extinction-prone populations (Ryti 1992; Andelman & Fagan 2000; Fleishman et al. 2001; but see Berger 1997; Fleury et al. 1998; Bonn et al. 2002). In landscapes where fragmentation is a relatively recent phenomenon, some populations in remnants may be sinks or transients (Watson et al. 2001). Moreover, metapopulation theory predicts that a number of suitable patches are unoccupied at any point in time (Hanski 1999). Therefore, data covering many years is preferable for assessing the viability of the (sub)populations and increasing the likelihood of including all suitable habitat in the conservation network. Moreover, because many species vary in their habitat requirements at different times of the year, surveys should ideally cover more than one season.

Finally and most important, none of the studies listed in Table 2 (except Caro 2001, 2003) provides a direct evaluation of the basic assumption of the umbrella species concept, to show that the conservation measures directed at the umbrella species actually protect many other species. Their conclusions are based on hypothetical reserves or conservation networks derived from current species distributions, which in turn are dependent on the current structures of landscapes. Hence, they do not demonstrate that the implementation of the conservation schemes in the real world would give the same results. This remains the greatest challenge in evaluating the umbrella species concept. In that respect, investigations such as Caro's (2001, 2003) based on data from existing protected areas and their surroundings are of great interest.

Directions for Using Umbrella Species in Conservation Planning

A frequent criticism of the umbrella species concept is that it is improbable that the requirements of one species would encapsulate those of all other species (Noss et al. 1997; Basset et al. 2001; Hess & King 2002). Evaluations of the utility of single-species umbrellas have shown convincingly that they do not offer total coverage for whole communities (Table 2). Hence, there is a need for multi-species strategies as a means to broaden the width of the protective umbrella (e.g., Miller et al. 1998; Fleishman et al. 2000, 2001; Carroll et al. 2001). Among the different multi-species approaches, Lambeck's (1997) focal species approach seems the most promising because it provides a systematic procedure for selection of umbrella species (Lambeck 1999; Watson et al. 2001; Bani et al. 2002; Brooker 2002; Hess & King 2002).

What qualities should a "dream team" of focal species possess to be a dependable tool of biodiversity assessment and conservation planning? First, it should cover the main ecosystem or landscape types of concern in a region (Angelstam 1998*a*, 1998*b*; Hess & King 2002). Here it might be argued that simply conserving all landscape types would constitute a more straightforward alternative. However, given the need to establish concrete and quantitative landscape design criteria, it is essential to refer to the requirements of the species to know how much is enough (Hansen et al. 1993; Lambeck 1997, 1999; Angelstam et al. 2003). For each landscape type, the most sensitive group of species in terms of resources, area requirements, connectivity, and natural processes (e.g., fire and flooding regimes) should be selected (Lambeck 1997). Depending on the context of application, the suite of focal species may need to represent a range of spatial scales from bioregions and landscapes (Lambeck 1999) to localized habitats and microhabitats (Mühlenberg et al. 1991). In forested landscapes, for example, birds and mammals may include species that are among the most sensitive to threatening factors operating at landscape and bioregional scales (Lambeck 1999), whereas species of invertebrates and nonvascular plants could be among the most sensitive to threats operating at finer spatial scales (Angelstam 1998*a*; Ranius 2002).

One shortcoming of the focal species approach lies in the difficulty of identifying the most sensitive species for each threat, given that many taxa are still poorly known (e.g., invertebrates) (Lindenmayer et al. 2002; Lindenmayer & Fischer 2003). Moreover, there is an obvious lack of data about requirements that are difficult to study quantitatively, such as dispersal (Koenig et al. 1996). New knowledge on habitat thresholds for the persistence of sensitive species (Fahrig 2001) will contribute to filling those gaps. In the face of incomplete data, one can use expert judgment obtained through workshops or surveys (Lambeck 1999; Hess & King 2002).

Lindenmayer et al. (2002) assert that a ridiculously large number of species may be needed and that this would render the focal species approach inefficient. Although this certainly may be true in ecologically complex landscapes such as those found in Australia (Clark 1990), development of umbrella strategies based on a suite of species may be attempted in simpler systems, such as boreal regions. Yet it remains that multi-species umbrella strategies require more data than do classic applications of single area-demanding umbrellas. In situations where time is limited, a philosophy of adaptive management should be advocated (Walters 1986) whereby strategies based on such multi-species umbrellas are implemented in some case studies and are later improved or rejected as more knowledge becomes available. In any case, such an approach would represent a significant conservation shortcut compared with species-by-species management or planning for habitat re-creation after further destruction.

Conclusions

Species are going extinct at unprecedented rates, even if we ignore the possibility of a considerable extinction debt (Pimm et al. 1995; Hanski & Ovaskainen 2002). The urgency of the situation leaves no room for "paralysis by overanalysis" (sensu Carroll & Meffe 1994). It is no longer legitimate to assert that the umbrella species concept has not been tested and therefore should not be applied. Although there is little evidence for the usefulness of single-species umbrellas selected only on the basis of their large area requirements, some multi-species schemes considering the occurrence of a range of habitat types and landscape attributes offer promising conservation avenues. Using the umbrella species concept could therefore provide an appealing and sound approach for rapid action.

The umbrella species concept is not a panacea. Even the most sophisticated umbrella schemes probably cannot guarantee the protection of absolutely all species. The real issue, however, is whether the umbrella species concept constitutes an effective conservation tool compared with alternative methods. If used alone, general guidelines based on the conservation of the main native land types would be difficult to implement because they do not provide clear estimates of how much is needed of different ecological attributes. On the other hand, the extended umbrella species concept provides explicit and quantitative guidelines that could be useful for the assessment of status and trends as well as for conservation planning. In the face of incomplete knowledge about species requirements and ecosystem processes, the precautionary principle advises us to employ a combination of methods. The umbrella species concept deserves consideration as one of these.

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