

Complementarity as a biodiversity indicator strategy

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Richness, rarity, endemism and complementarity of indicator taxon species are often used to select conservation areas, which are then assumed to represent most regional biodiversity. Assessments of the degree to which these indicator conservation areas coincide across different taxa have been conducted on a variety of vertebrate, invertebrate and plant groups at a national scale in Britain, Canada, USA and South Africa and at a regional scale in Cameroon, Uganda and the USA. A low degree of spatial overlap among and within these selected indicator conservation areas has been demonstrated. These results tend to suggest that indicator conservation areas display little congruence across different taxa. However, some of these studies demonstrate that many conservation areas for indicator taxa capture a high proportion of non-target species. Thus it appears that indicator conservation areas might sample overall biodiversity efficiently. These indicator conservation areas may, however, exclude species essential for effective conservation, e.g. rare, endemic or endangered species. The present study investigated the value of indicator taxa as biodiversity surrogates using spatial congruence and representativeness of different indicator priority conservation areas. The conservation status of species excluded by the indicator approaches is also assessed. Indicator priority conservation areas demonstrate high land area requirements in order to fully represent non-target species. These results suggest that efficient priority area selection techniques must reach a compromise between maximizing non-target species gains and minimizing land-use requirements. Reserve selection procedures using indicator-based complementarity appear to be approaches which best satisfy this trade-off.

Keywords: biodiversity; indicator; surrogacy; conservation; reserves; hot spots

1. INTRODUCTION

Concern over the rapid degradation of the world's biological resources and the implications for global biosphere integrity and human welfare is mounting. There is a widely recognized need to design appropriate policy and management strategies to conserve remaining biodiversity resources. The establishment of protected areas for *in situ* biodiversity conservation is one such management strategy. However, the effectiveness of *in situ* conservation strategies depends on the existence of adequate databases about the distribution of species and other natural features. In addition, the need to minimize the costs associated with land acquisition and foregone opportunities for other land uses when reaching a conservation goal requires efficient procedures for selecting minimum or near minimum sets of sites that represent these species or features (Kirkpatrick 1983; Bedward *et al.* 1992; Nicholls & Margules 1993; Pressey *et al.* 1993; Freitag & Van Jaarsveld 1997).

Balmford & Gaston (1999) argue that without high-quality biodiversity inventories, representative conservation areas will be larger than necessary, thus increasing demands on already limited conservation resources. However, as a rule neither the time nor the resources required to survey all regional biodiversity are available. Thus the selection of representative minimum-set conservation areas often depends on substitute or surrogate biodiversity data which can be surveyed in a more cost- and time-efficient manner (Noss 1990; Vane-Wright *et al.*

1991; Ryti 1992; Belbin 1993; Gaston & Williams 1993; Pressey 1994; Williams & Gaston 1994; Margules & Redhead 1995; Pressey & Logan 1994; Faith & Walker 1996; Gaston 1996*b*; Williams 1998). Species-based surrogacy approaches include using measures of species richness, rarity, endemism or complementarity of one or more groups of indicator taxa that have been well surveyed (Prendergast *et al.* 1993; Lombard 1995; Williams *et al.* 1996; Flather *et al.* 1997; Howard *et al.* 1998; Van Jaarsveld *et al.* 1998). These approaches assume that a species-rich area, areas rich in endemics or complementary areas for indicator groups will be indicative of similar trends in unsurveyed taxa. Consequently, priority conservation areas identified from survey data of one or two indicator groups are capable of conserving most regional biodiversity.

These assumptions of surrogacy require rigorous testing before their implementation. One route to assessing the value of potential indicator taxa is to quantify the degree to which spatial patterns of species richness, endemism, rarity and complementarity coincide across different taxa (Prendergast *et al.* 1993; Lombard 1995; Gaston 1996*a*; Flather *et al.* 1997). Although it seems that the distribution of well-studied taxa can act as indicators for the distribution of poorly studied taxa at global and continental scales (Scott *et al.* 1987, 1993; Pearson & Cassola 1992), at finer scales (e.g. national and regional) this assumption appears questionable. Prendergast *et al.* (1993), and Prendergast & Eversham (1997) did not find general support for the use of indicator taxa in their British studies, as species richness hot spots (10 km² grid cell sets) for various vertebrate and invertebrate taxa did

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not coincide. Similarly in South Africa, Lombard (1995) demonstrated a lack of congruence of species richness, endemism and rarity hot spots (sets of 25 km × 25 km grid cells) within and among six vertebrate taxa. Williams *et al.* (1996) found that bird richness hot spots were not efficient at representing all British birds, while Williams & Gaston (1998) using 10 km² grid cell richness data on British fauna agree that the value of indicator taxa for biodiversity conservation planning is far from established. Van Jaarsveld *et al.* (1998) discovered limited overlap between 25 km × 25 km grid cells selected in South Africa using species richness, rarity and complementarity measures between various vertebrate, invertebrate and plant taxa. In a qualitative assessment of richness hot spots for the USA and Canada for a variety of vertebrate, invertebrate and plant taxa, Flather *et al.* (1997) found a general lack of overlap between cross-taxon hot spots. Lawton *et al.* (1998) found that no single vertebrate or invertebrate taxon served as a good indicator for changes in species richness of other taxa with changing disturbance levels in Cameroon.

These results seem to suggest that at a scale relevant to practical conservation planning, the use of indicator taxa for biodiversity conservation has limited potential. However, although hot spots display little congruence among taxa and are less efficient at representing the full complement of species than complementarity approaches (Kirkpatrick 1983; Margules *et al.* 1988, 1994; Pressey & Nicholls 1989; Bedward *et al.* 1992; Nicholls & Margules 1993; Freitag *et al.* 1997; Pressey *et al.* 1997; Van Jaarsveld *et al.* 1998), conservation planning in the real world is only able to protect a limited number of sites (Reid 1998). The question then is what proportion of overall diversity can be captured in these conservation areas identified by hot-spot approaches.

The previously mentioned studies appear to undermine the use of indicator hot spots; however, when viewed from an alternative perspective, hot spots for an indicator taxon appear to sample overall biodiversity quite efficiently. Both Prendergast *et al.* (1993) and Lombard (1995) showed that a high proportion of species was captured within hot spots of other taxa, ranging from 48 to 100% ($\xi=80.4\%$) and 66 to 92%, respectively. In Oregon, USA, complementary areas representing one taxon were good at representing the diversity of other terrestrial taxa (unpublished data in Csuti *et al.* (1997)). Similarly, Howard *et al.* (1998) using the approach developed by Williams *et al.* (2000), found that despite little spatial congruence in species richness of a variety of taxa in Uganda, complementary areas chosen using information on one taxon effectively captured overall diversity. Thus spatial congruence in cross-taxon species richness may be an inadequate assessment of the value of across-taxon biodiversity indicator value (Balmford 1998; Howard *et al.* 1998). Possibly measures of degrees of representativeness (how completely the reserve system includes the species pool of a region (Margules & Usher 1981)) of various taxa within indicator areas is a more appropriate method of assessment. Areas containing high levels of diversity for one indicator taxon selected by richness, rarity or complementarity approaches are likely to include a diversity of habitats and therefore a large amount of diversity for other taxa (Reid 1998).

One shortcoming of this approach towards assessing the value of indicator taxa is that although indicator-derived conservation areas may capture a large amount of regional diversity they may be missing species essential for effective conservation, e.g. rare or endangered species. Consequently, richness hot spots may capture a high percentage of overall species diversity, but many rare species do not occur in these hot spots (Prendergast *et al.* 1993). Red data book listed species and endemic species in South Africa were not well represented within hot spots (Lombard 1995). The distributions of rare species were found to be not strongly nested within the distributions of more widespread species in a study on British birds (Williams *et al.* 1996). Endangered species hot spots in the USA rarely captured endangered species of other taxa and at least half of the rare species do not occur in hot spots in Australia and Britain (Curnutt *et al.* 1994; Dobson *et al.* 1997).

The present study investigated the across-taxon value of indicator taxa using spatial congruence and representativeness of richness hot spots, rarity hot spots as well as areas selected by complementarity-based richness and rarity algorithms. In addition, a critical evaluation of the conservation status of species overlooked by indicator conservation areas was conducted.

2. METHODS

(a) *Study area and databases*

The study area comprises the Northern Province of South Africa (figure 1), which represents approximately 10% (122 305 km²) of one of the most biologically rich nations in the world (WCMC 1992). Information on species presence within 25 km × 25 km grid cells (*ca.* 670 km²; $n=215$) was collated for birds (Aves), butterflies (Lepidoptera: superfamilies Hesperioidea, Papilionoidea), mammals (Mammalia) and vascular plants (Plantae) (table 1).

These taxa are all well surveyed within the study area and reflect little survey bias (Harrison 1992; Freitag & Van Jaarsveld 1995; Freitag *et al.* 1998) with the possible exception of the butterfly data set, which contains the lowest number of records surveyed in the fewest grid cells (table 1). The butterfly data set is the best available invertebrate data set for the study region and has the additional advantage of being a taxonomically well-known group (Muller 1999). Only endemic plant species (species that were not recorded outside of the former Transvaal Province) were included in the analyses, since the representation of all plant species sets unattainable formal conservation goals, requiring over 50% of the study area to represent all species once (B. Reyers, unpublished data). All grid cells have been surveyed for plant species; however, only 88.4% of the grid cells contain endemic plant species (table 1).

(b) *Priority conservation area identification*

Richness and rarity hot spots were identified within the study area for all four taxa separately, as well as for all taxa combined. Richness hot spots were defined as the 5% richest grid cells containing records for that particular taxon or group of taxa. Rarity hot spots were identified as grid cells containing rare species defined by Gaston (1994) as the 25% species with the lowest abundances or number of distribution records (Williams *et al.* 1996).

However, from a conservation perspective it is the overall regional biodiversity that is of interest, not just the extremes of

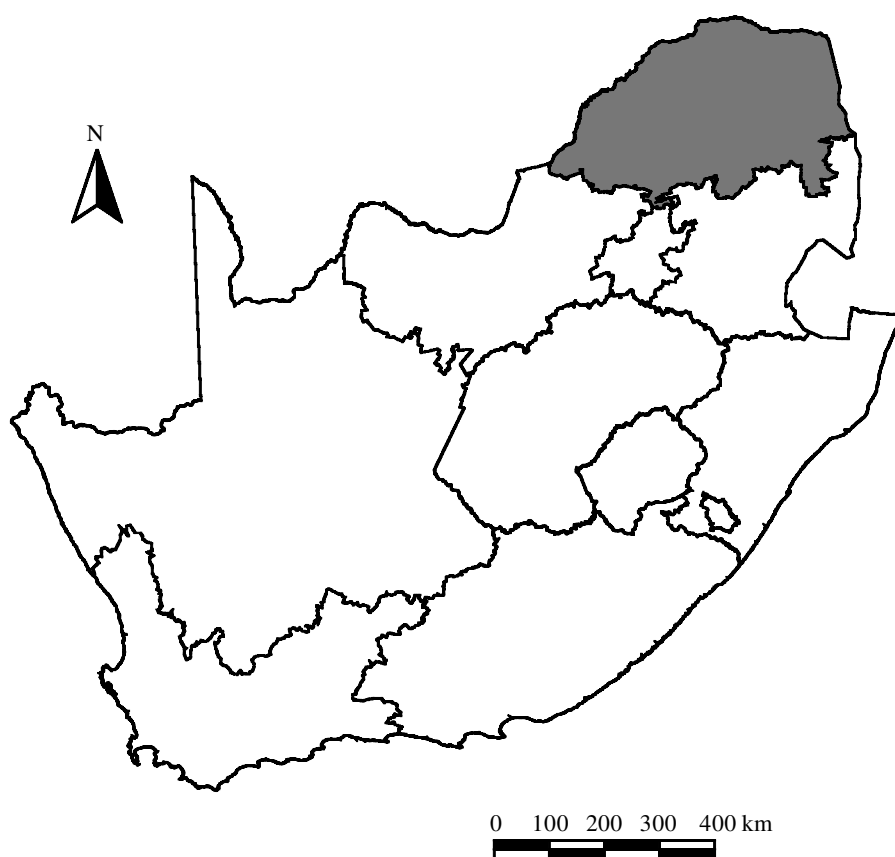


Figure 1. Map of South Africa showing location of Northern Province study area.

Table 1. *Species distribution data*

taxon	unique records	unique species	rare species	endemic species	grids surveyed
birds	49 089	574	141	63	214 (99%)
butterflies	2062	328	79	4	84 (39.1%)
mammals	5218	214	56	1	183 (85.1%)
plants	2694	472	125	472	190 (88.4%)
combined	59 063	1588	353	540	215 (100%)

the diversity continuum represented within hot spots (Gaston 1996a). For this reason the principle of complementarity, which recognizes the identity of units or species within grid cells, is included in this study. Complementary sets of grid cells representing all species at least once were identified using a rarity-based complementarity algorithm based on Nicholls & Margules (1993) as well as a richness-based complementarity algorithm. These reserve selection procedures are based on simple heuristic algorithms which proceed in a stepwise fashion, adding grid cells on at each step that contain features most complementary to those in the grid cells already reserved. The algorithms are essentially similar, varying in their point of departure. The former starts with grid cells containing unique features and adds sites progressively according to which contains the rarest unrepresented feature (Nicholls & Margules 1993). The richness-based algorithm begins with the most species-rich grid cell and sequentially includes grid cells that add the most unrepresented species (Kirkpatrick 1983; Howard *et al.* 1998). These algorithms were run on all four taxa separately and then on all taxa combined.

(c) *Spatial congruence in species diversity*

The degree of spatial overlap among conservation networks varies substantially, but consistently, when using different measures (B. Reyers, unpublished data). A measure of proportional overlap used by Prendergast *et al.* (1993) and Lombard (1995) provides the most appropriate assessment: proportional overlap = N_c / N_s , where N_c is the number of common grid cells in a pair of priority areas and N_s is the number of grid cells in the smallest priority set of areas containing data for both groups, i.e. the maximum number of overlapping grid cells possible.

As pointed out by Pressey *et al.* (1993), Margules *et al.* (1994) and Williams *et al.* (1996), flexibility is an inherent characteristic of most complementary sets of areas. Thus perhaps measures of proportional overlap are not sufficient in comparing overlap between complementary sets. Few studies have been conducted on the similarities of sets of complementary areas based on different taxa, providing limited evidence of similarities (Ryti 1992; Saetersdal *et al.* 1993; Vane-Wright *et al.* 1994; Gaston *et al.* 1995). A method similar to that of Williams *et al.* (1994) and

Table 2. *Results on efficiency, representativeness and rare and endemic species representation within the priority conservation areas selected*

priority conservation area	grid cells selected (%)	total species represented (%)	additional grid cells to represent all species (%)	total grids to represent all species (%)	excluded species that are rare and endemic (%)	excluded species that are common (%)	rare and endemic species represented (%)	rare and endemic species excluded (%)
richness hot spots								
all taxa	5.12	82.93	35.81	40.93	90.04	9.96	64.48	35.52
birds	5.12	77.90	35.81	40.93	91.45	8.55	53.28	46.72
butterflies	1.86	59.19	39.07	40.93	62.96	37.04	40.61	59.39
mammals	4.19	82.93	38.60	42.79	75.04	24.96	26.93	73.07
plants	4.65	73.24	36.28	40.93	68.47	31.53	57.64	42.36
average	4.19	75.24	37.12	41.30	77.59	22.41	48.59	51.41
rarity hot spots								
all taxa	54.88	99.94	0.47	55.35	0.00	100.00	100.00	0.00
birds	81.86	99.69	1.86	83.72	100.00	0.00	99.27	0.73
butterflies	16.74	92.07	25.12	41.86	93.65	6.35	82.82	17.18
mammals	24.65	93.83	21.86	46.51	96.94	3.06	86.17	13.83
plants	24.65	96.03	16.28	40.93	92.06	7.94	91.56	8.44
average	40.56	96.31	13.12	53.67	76.53	23.47	91.97	8.03
richness algorithm								
all taxa	40.93	100.00	0.00	40.93	0.00	0.00	100.00	0.00
birds	11.16	85.14	31.16	42.33	93.65	6.35	65.65	34.35
butterflies	14.42	89.99	26.98	41.40	92.21	7.79	79.33	20.67
mammals	12.09	87.59	29.30	41.40	92.79	7.21	71.91	28.09
plants	30.23	97.67	12.09	42.33	89.66	10.34	96.22	3.78
average	21.77	92.08	19.91	41.67	92.08	7.92	82.62	21.72
rarity algorithm								
all taxa	40.93	100.00	0.00	40.93	0.00	0.00	100.00	0.00
birds	11.16	85.08	30.70	41.86	93.31	6.69	65.50	34.50
butterflies	14.42	90.11	26.98	41.40	92.76	7.24	79.48	20.52
mammals	12.09	84.38	30.23	42.33	88.77	11.23	64.34	35.66
plants	29.77	97.42	12.56	42.33	87.88	12.12	95.78	4.22
average	21.67	91.40	20.09	41.77	90.68	9.32	81.02	23.73

Gaston *et al.* (1995), using the selection order of grid cells for complementary sets as an indication of the grid cell's diversity value (in terms of richness or rarity; and complementarity) is applied. The grid cells selected first would thus be assumed to have the highest diversity value. A comparison of the sequences of grid cell selection within different complementary networks allows for a comparison of patterns of between-taxon diversity. The selection orders of the richness- and rarity-based complementary algorithms were analysed by Pearson's product moment correlations.

(d) *Species representation*

The number of species falling into priority conservation areas was calculated for each of the four taxa as well as for all taxa combined. The number of additional grid cells required to represent all taxa once was calculated.

The performance of priority sets in representing overall diversity was evaluated following the approach developed by Williams and colleagues (Williams *et al.* 2000), and subsequently employed by Howard *et al.* (1998). The manner in which cumulative percentage species increased as a function of cumulative percentage grid cells selected was determined. This was done for all indicator groups, richness and rarity hot spots, as well as their complementary areas selected using richness- and rarity-based algorithms.

(e) *Rare and endemic species representation*

The ability of the various indicator-based priority conservation areas to represent rare and endemic species was investigated. Endemic butterfly, mammal and plant species were defined as species occurring only within the former Transvaal Province and rare species as in Gaston (1994). There are no birds restricted to the former Transvaal Province, thus endemic birds were defined as birds occurring only in South Africa (table 1). The percentage of rare and endemic species represented within the priority conservation areas was calculated.

The relationship between cumulative representation of rare and endemic species and the number of grid cells selected within each priority conservation area was examined using an approach similar to that of Williams *et al.* (2000). The rate at which species and especially rare and endemic species are represented within priority conservation areas could then be ascertained.

3. RESULTS

(a) *Priority conservation areas*

Table 2 shows the percentage of grid cells required for priority conservation areas based on all four indicator groups, as well as for all groups combined. The grid cell requirements for these conservation areas vary from 1.9% for the butterfly richness hot spots to 81.9% for the bird

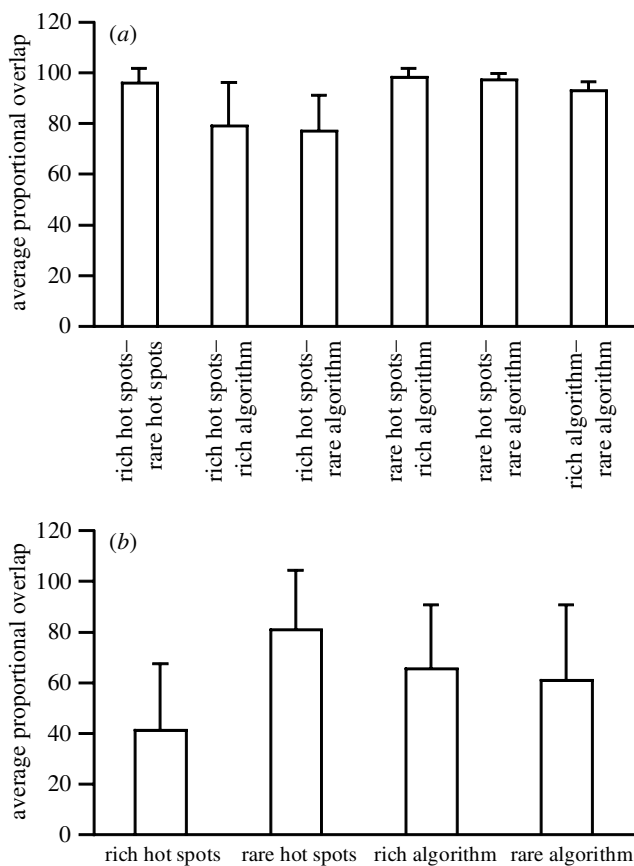


Figure 2. The degree of proportional overlap (mean \pm s.d.): (a) between pairs of conservation areas generated by means of different prioritization criteria (richness and rarity hot spots, richness- and rarity-based complementarity algorithms), and (b) within conservation areas based on different indicator taxa (rich, richness; rare, rarity).

rarity hot spots. In general, rarity hot spots required many grid cells while richness hot spots required fewer grid cells. The richness- and rarity-based complementarity networks contained almost identical numbers of grid cells. The birds and combined taxa required the most grid cells within the richness and rarity hot spots while the combined taxa and endemic plants required the most grid cells within the richness- and rarity-based complementarity networks.

(b) Spatial congruence in species diversity

The measure of proportional spatial congruence suggests a high degree of spatial overlap between pairs of priority conservation areas (figure 2a), and a moderate degree of overlap among priority conservation areas based on indicator taxa (figure 2b). Overlap between rarity-based complementarity networks and rarity hot spots was highest, with overlap between rarity-based complementarity networks and richness hot spots being lowest (figure 2a). Rarity hot spots and richness hot spots demonstrate the highest and lowest overlap between indicator groups, respectively (figure 2b).

The selection order of the complementary sets of grid cells showed no significant correlations between taxa. The richness- and rarity-based complementarity networks based on the same taxa were significantly positively correlated ($r > 0.8$; $p < 0.05$).

(c) Species representation

The percentage of species captured in priority conservation areas was high (table 2); ranging from 59.2% for butterfly richness hot spots to 99.9% for the richness hot spots based on all taxa combined. This excludes the 100% representation achieved by the richness- and rarity-based algorithms run on all taxa combined, as these algorithms run until the target representation of 100% of species is achieved (table 2). Richness hot spots display the lowest degree of species representativeness ($\xi = 75.2\%$) with rarity-based complementarity networks, richness-based complementarity networks and rarity hot spots displaying higher average species representation percentages across all indicator taxa ($\xi = 91.4, 92.1$ and 96.3% , respectively).

The additional grid cells required to represent all species once at least range from 0.5% for rarity hot spots based on all taxa combined to 39.1% for butterfly richness hot spots (table 2). The total percentage grid cells required (i.e. grid cells selected as part of priority conservation areas and additional grid cells required to represent all species once) are similar for the various priority conservation areas (ca. 41%), with the exception of the rarity hot spots for all taxa combined and for birds (55.3 and 83.7%, respectively) (table 2).

Although it would appear that the percentage of species excluded by the priority conservation areas is low (table 2), upon closer examination these species are primarily rare and endemic species. Out of the species from non-target groups excluded by the indicator priority conservation areas, on average 77.6, 76.5, 92.1 and 90.7% are rare and endemic species missed by richness hot spots, rarity hot spots, richness-based complementarity networks and rarity-based complementarity networks, respectively (table 2). From a different perspective, the richness hot spots, richness-based complementarity networks, rarity-based complementarity networks and rarity hot spots for indicator groups exclude on average 51.4, 21.7, 23.7 and 8.0% of the rare and endemic species from non-target groups, respectively (table 2).

Figure 3 illustrates the rate at which species are represented within the priority conservation areas. The initial rate of representation is rapid, with an average of 70, 87.9, 88% and 86.2% of all species represented within less than 10% of the study area for indicator richness hot spots, rarity hot spots, richness-based complementarity networks and rarity-based complementarity networks, respectively. The rate then slows dramatically as all priority conservation areas target the representation of all species.

The rate of representation of rare and endemic species is lower than the rate of representation for all species illustrated in figure 3. This slower rate, with richness hot spots, rarity hot spots, richness-based complementarity networks and rarity-based complementarity networks respectively capturing 48.6, 71.6, 74.7 and 75.3% of the rare species within 10% of the study area, is demonstrated in figure 4. The rate also slows further as full representation of all rare and endemic species is targeted.

4. DISCUSSION

The results from the present study provide qualified support for the use of indicator taxa in the selection of

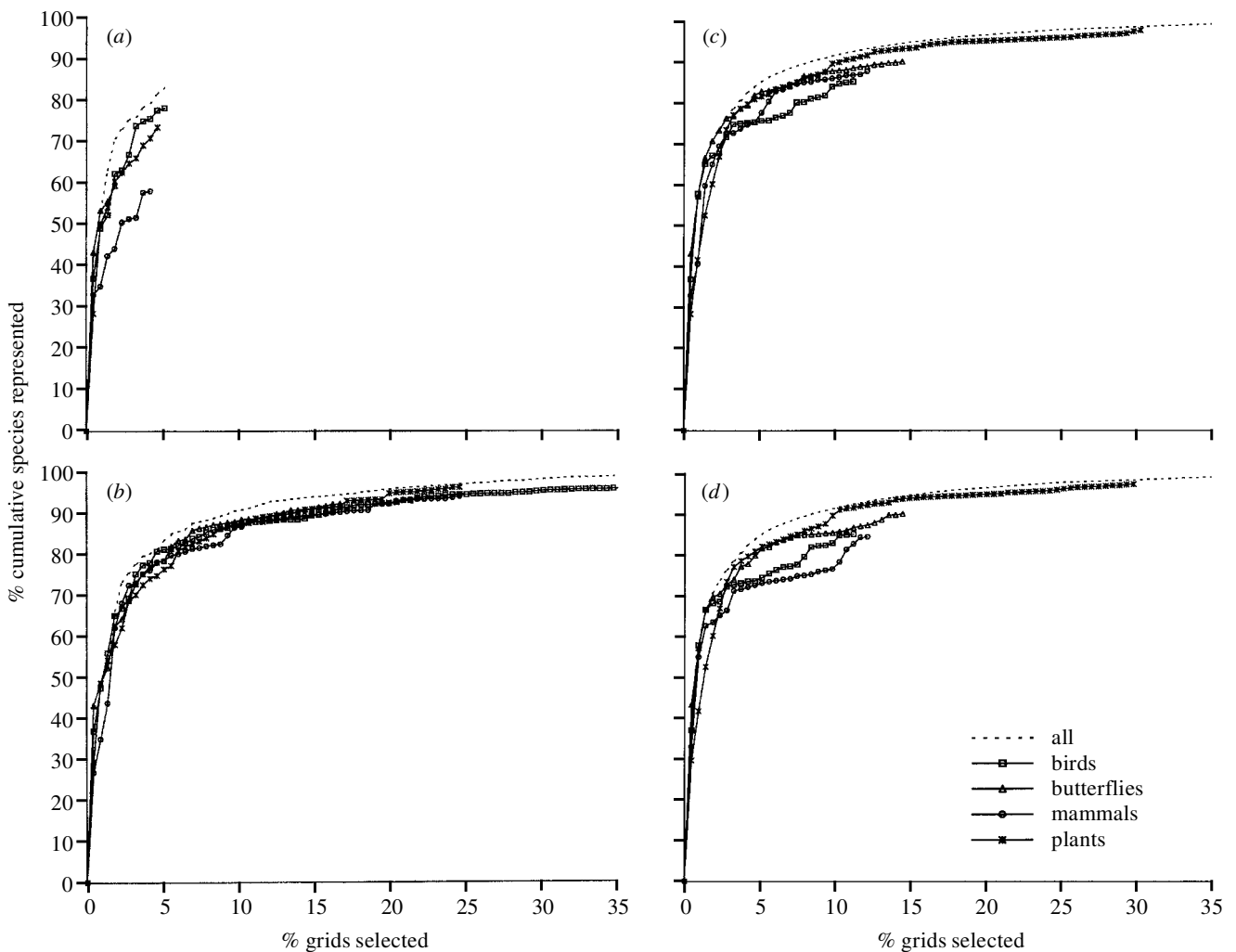


Figure 3. Cumulative percentage representation of all four taxa (birds, butterflies, mammals and plants) and all taxa combined as a function of cumulative percentage grid cells selected by (a) richness hot spots, (b) rarity hot spots, (c) the richness-based complementarity algorithm, and (d) the rarity-based complementarity algorithm.

representative conservation areas. The high levels of spatial congruence are encouraging, but due to the lack of general support from previous studies (Prendergast *et al.* 1993; Lombard 1995; Van Jaarsveld *et al.* 1998), this result should be interpreted with caution. The high levels of species representation within the indicator priority conservation areas would appear to support Prendergast *et al.* (1993), Balmford (1998), Howard *et al.* (1998) and Reid (1998) in their suggestion that conservation areas species rich for one indicator taxon may represent considerable diversity in other non-target taxa. However, within the species representation analyses as well as within the spatial congruence assessments, the effect of conservation area size is often overlooked. An extensive indicator conservation area has a much higher probability of coinciding with another indicator conservation area, and also stands a greater chance of capturing higher levels of regional biodiversity than restricted conservation areas. This is obvious from the results where complementary networks and rarity hot spots (all large areas) coincide more with one another than with the smaller richness hot spots and also have higher species representation values, capturing more regional species diversity than smaller richness hot spots.

In accordance with findings by Lombard (1995) and Williams *et al.* (1996) richness hot spots contain the highest number of species records per grid cell and thus would appear to be the most effective at representing large numbers of species within fewer grid cells. Taking the present limited state of financial and land resources for conservation into account, this is perhaps an important result. However, this result is misleading and should be interpreted with caution. Although richness hot spots may appear to be the most efficient at representing near-maximum regional biodiversity in a minimum number of areas, these richness hot spots exclude up to one-quarter of the species in non-target groups and perhaps more importantly they exclude half of the rare and endemic species in non-target groups (table 2; figure 5). Rarity hot spots represent species, as well as rare and endemic species, of non-target taxa very well, but this comes at a high land cost, requiring over 40% of the land available (table 2; figure 5). Thus it would appear that, as Pressey *et al.* (1993) and Williams (1998) argue, indicator complementary sets of grid cells are perhaps the most efficient conservation solution. These areas protect high levels of non-target biodiversity (92%), missing only 20% of the rare and endemic species (a result similar to the very

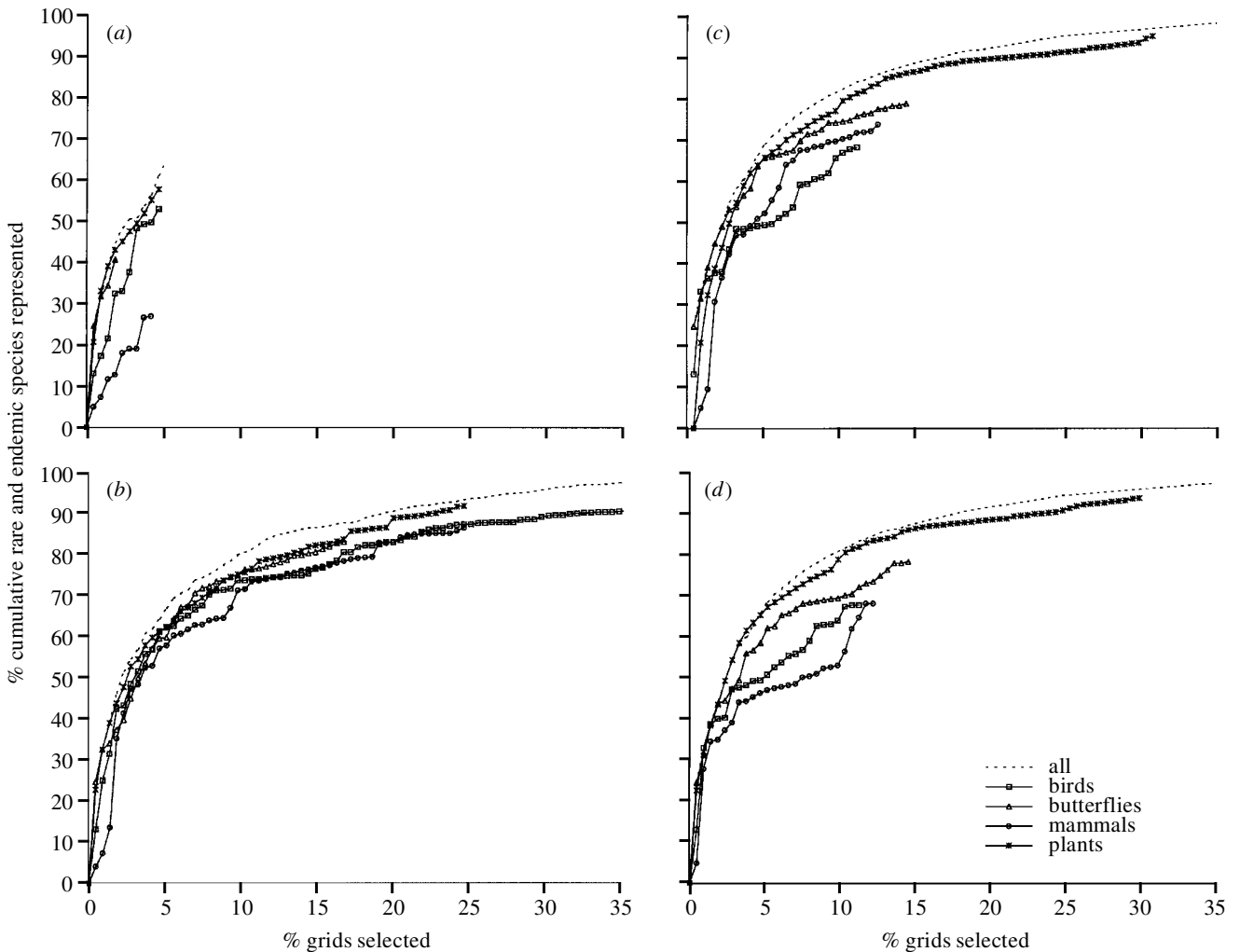


Figure 4. Cumulative percentage representation of rare and endemic species of birds, butterflies, mammals, plants and all taxa combined as a function of cumulative percentage grid cells selected by (a) richness hot spots, (b) rarity hot spots, (c) the richness-based complementarity algorithm, and (d) the rarity-based complementarity algorithm.

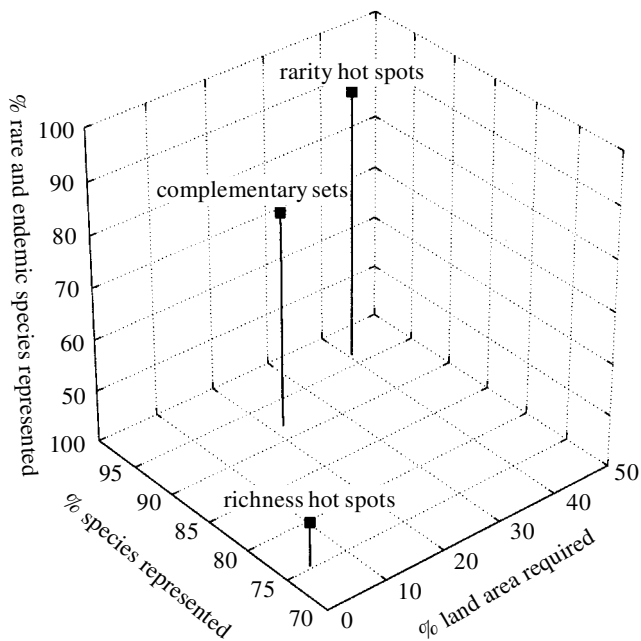


Figure 5. Three-dimensional scatter plot of the land-use efficiency and non-target species representation (including rare and endemic species) of richness hot spots, rarity hot spots and complementarity-based reserve selection algorithms.

high levels attained by the rarity hot spots), in only half of the area required by the rarity hot spots (figure 5).

Although these priority indicator areas appear to efficiently represent a large percentage of regional biodiversity and thus perhaps support the notion of indicator taxa as valuable biodiversity surrogates, two important issues emanating from the present study remain problematic. First, attempts to achieve full representation of all known regional biodiversity will be expensive in terms of land requirements irrespective of which indicator approach is used. This is emphasized by the high number of grid cells (40% of the study region) required to achieve 100% representation of all taxa within all the generated conservation areas. Also, representative networks can be very fragmented and scattered, as is the case with most of the current conservation areas and these highly fragmented or diffuse networks require intensive management and therefore demand high management costs (Bedward *et al.* 1992).

Second, although species missed by the indicator conservation areas represent a small fraction of the species known to occur within the region, this small component is important in conservation terms. More than half of these excluded species are rare and endemic, and add to the fact that a significant portion of all the

rare and endemic species within the region are missed by the various indicator priority conservation networks. Thus, existing methods used to identify indicator priority conservation areas do not seem to be efficient at representing rare and endemic species across taxa and represent them at a very slow rate. This obviously has significant implications for regional conservation planning, as it suggests that the rare and endemic taxa from different groups may be found in different areas (Dobson *et al.* 1997). It also highlights the need to clarify conservation goals and to decide whether the goal of total species representation, or rare and endemic species representation is the most appropriate.

5. CONCLUSION

This study supports the use and importance of indicator taxa as surrogates for regional biodiversity. The occasional lack of cross-taxon congruence between indicator conservation areas (overlap values generally being higher than 90% with values of 76 and 78% between richness-based complementary areas and rarity and richness hot spots, respectively (figure 2)), is not sufficient to invalidate the use of indicators as surrogates. High levels of cross-taxon species representativeness within the indicator conservation areas (75–96%) seem to lend support to the assumption that areas of conservation importance to one taxon will capture high levels of diversity for non-target taxa. Although encouraging, this result does not extend to regionally rare and endemic taxa (indicator areas excluding between 8 and 50% of rare and endemic species) and should therefore be implemented with caution. The lack of unqualified support for the indicator taxon strategy, the absence of complete biodiversity inventories and the lack of standard assessment techniques for indicator taxa as surrogates (Flather *et al.* 1997) all raise important questions about the validity of the surrogate indicator approach.

High levels of species representation, especially of rare and endemic species, appear to come at a cost, requiring large areas of land ranging from 40 to 50% of the land available. This trade-off between land-use efficiency and the representation of species, especially rare and endemic species, suggests that an indicator strategy that manages to reach a compromise between land-use requirements and species representation may be appropriate. It would seem from these assessments that the complementarity indicator approach is still the most efficient approach for maximizing non-target species gains in the minimum area possible.

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