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THE DISTRIBUTION OF SELECTED *SCARABAEOID (COLEOPTERA)* TAXA IN SOUTH AFRICA AND NAMIBIA: PROSPECTS FOR THEIR CONSERVATION

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The distribution of selected Scarabaeoid (Coleoptera) taxa in South Africa and Namibia: Prospects for their conservation

by

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ABSTRACT

Despite being the focus of an international research effort spanning decades, the spatial distribution of southern African scarab beetles remains poorly documented. Besides reinforcing the magnitude of the challenge facing biodiversity scientists, this raises real concerns about best practice conservation strategies in the absence of detailed distribution information. However, dung beetles appear to be well represented in established conservation areas. This apparent contradiction could be ascribed to anthropogenic transformation, successful conservation efforts, the presence of dung generalists and reserve-biased or mesic-biased dung beetle collection efforts. It is suggested that all of the above contribute to the observed pattern to varying degrees. The implications of selecting areas that are either rich in species, contain rare species or contain taxonomically distinct species from a group whose taxonomy is well known but for which inadequate distribution data exist are explored. Best practice, in the face of inadequate data, appears to revolve around a subtle interplay between advantages and disadvantages associated with data interpolation techniques, reserve selection algorithms that use criteria more robust than database rarity (such as taxonomic distinctiveness) and the long-term economic costs of proceeding with the data at hand versus investing in biological surveys.

The use of biodiversity indicator taxa as distribution surrogates for poorly known taxa has been widely investigated. The degree to which two groups of selected mammal taxa found in four of South Africa's provinces are representative of dung beetle species found in this area is examined. Two iterative, complementarity-based reserve selection algorithms are employed to determine 1) the proportion of dung beetle species represented in reserves (= inclusiveness) selected for mammals only and 2) the proportion of dung beetle species represented in the areas of overlap between reserves selected for mammals and for dung beetles, respectively. The performances of these two methods and of the two potential mammal indicator groups are assessed and evaluated. The interpretation of these results is found to depend on whether absolute or relative dung beetle inclusiveness values are considered. Although the representation of absolute rather than relative numbers of dung beetle species is more appropriate for practical conservation planning, relative figures remove the effect of sample size and are thus useful indicators of how well a particular biodiversity indicator or a given analytical method performs. In addition, dung beetle inclusiveness within the reserve networks generated by the algorithms is contrasted with that obtained from randomly picked reserve networks. The resulting observation, that the two do not differ substantially, implies that the mammals perform poorly as biodiversity indicators for the dung beetles. However, the nature of the particular databases that were used in these analyses may have biased the results towards such an outcome. Despite the fact that dung beetle inclusiveness in the reserves generated by the algorithms is similar to that in reserves generated by the random draw method, the former is more useful since, unlike the latter, this method ensures the selection of sites that are complementary to one another and hence networks that are less fragmented.

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DISCLAIMER

This M.Sc. dissertation comprises chapters and appendices that have been prepared for submission to or publication in a range of journals. Consequently, chapter and appendix formats contain some inconsistencies and overlap to secure publishable entities.

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CHAPTER 1

Introduction

> "The most wonderful mystery of life may well be the means by which it created so much diversity from so little physical matter. The biosphere, all organisms combined, makes up only about one part in ten billion of the earth's mass. It is sparsely distributed through a kilometer-thick layer of soil, water, and air stretched over a half billion square kilometers of surface. If the world were the size of an ordinary desktop globe and its surface were viewed edgewise an arm's length away, no trace of the biosphere could be seen with the naked eye. Yet life has divided into millions of species, the fundamental units, each playing a unique role in relation to the whole."
>
> E.O. Wilson, 1993

Exactly how unique are the roles played by each species, i.e. should time and money be invested in the conservation of as much biodiversity as possible, or does it suffice to concentrate on a few selected species only? This question must be addressed, considering the fact that the astronomical population growth of humans across the globe and the consequent increase in consumption rates is resulting in species extinction levels unprecedented for the past 65 million years (Fry and Lonsdale, 1991; New, 1993; Richardson and Cowling, 1993; Wilson, 1993; Meffe *et al.*, 1997; Raven and McNeely, 1998). It has been argued that the demise of each species should be of grave concern to all humans for reasons that can be classed into four main categories: economic, ecological, ethical and aesthetic (McNeely, 1992; Pressey *et al.*, 1993; Margules *et al.*, 1994; Kunin and Lawton, 1996; Raven and McNeely, 1998). A closer examination of the arguments put forward in each of the four categories (see Kunin and Lawton, 1996 and Raven and McNeely, 1998) reveals that, in order to ensure sustainable use of natural resources and thus human welfare, conservationists and policy makers need to be concerned with the protection of all biodiversity (McNeely, 1992; Pressey *et al.*, 1993; Margules *et al.*, 1994; Kunin and Lawton, 1996; Lugo, 1998), not just selected components thereof. A quote from Kunin and Lawton (1996) portrays this position well: "Each species lost from a community represents dozens of lost interactions, leaving a potentially gaping hole in the ecological web." Despite these facts, it is alarming that past and, to some extent, present animal conservation efforts have been in favour of certain groups such as mammals and birds, while groups like the invertebrates have received comparatively little attention, except when they have been of importance to humans (New, 1993; Heywood, 1994; Hunter and Hutchinson, 1994; Samways, 1994; Vane-Wright *et al.,* 1994).

Insects are amongst the invertebrate taxa that have largely been neglected by the conservation community, despite the fact that they form the greatest single part of the world fauna, outnumbering all other groups in terms of numbers and species (Fry and Lonsdale, 1991; Samways, 1993, 1994; Scholtz and Chown, 1993, 1995). More importantly, insects perform critical functions as pollinators, seed dispersors and drivers of nutrient cycling (Fry and Lonsdale, 1991; Ehrlich, 1992; Samways, 1994; New and Yen, 1995), they act as natural controls for some invertebrate pest species, and they provide a food source for many vertebrates (Lonsdale, 1991b; New and Yen, 1995), all of which make them an essential component of biological and ecological processes. Furthermore, because insects respond to landscape disturbances, they have proved to be useful as environmental monitors (Pearson and Cassola, 1992; Kremen *et al.,* 1993; New, 1993; Samways, 1993, 1994; Oliver and Beattie, 1995; Scholtz and Chown, 1995). Given these facts, Samways (1994) emphasises that insect conservation is vital for the maintenance of sustainable agriculture as well as a sustainable biosphere.

In view of limited resources and the competition from other forms of land use, it is essential that conservation be conducted in a manner that maximises biodiversity gains derived from each conservation action (Pressey *et al.*, 1993; Beissinger *et al.*, 1996; Freitag *et al.,* 1996; Flather *et al.,* 1997). To this end, numerous iterative conservation area selection algorithms, based on the principle of complementarity, have been developed to identify systems of protected areas that, through step-wise procedures, capture all species in an efficient, flexible near-minimum set of sites (Vane-Wright *et al.*, 1991; Bedward *et al.,* 1992; Nicholls and Margules, 1993; Pressey *et al.*, 1993; Pressey *et al.,* 1994; Freitag and van Jaarsveld, 1995; Lombard, 1995a,b; Pressey *et al.,* 1997). These algorithms have proved to be invaluable tools for conservation planners, and different algorithms that suit the particular needs of the user exist. However, the results obtained from such algorithms are dependent on the quality of the datasets on which they are run (Freitag *et al.,* 1998a). To a greater or lesser degree, distribution data invariably suffer from spatial bias. Collection efforts are often biased towards conveniently accessible areas such as around major towns or cities as well as reserves (Davis *et al.,* 1990; Stork, 1994; Freitag *et al.,* 1998b), whereas more remote areas tend to be under-sampled (e.g. Drinkrow and Cherry, 1995; Gelderblom *et al.,* 1995; Lombard, 1995b). This results in the selection of conservation networks by the algorithms that exclude sites in which species are found but which have not been surveyed. Similarly, when presence-only data are used, the results obtained from complementarity procedures are not optimal because species that are not recorded in a particular site are assumed to be absent from that area. For these reasons, the assumption that sites selected by algorithms are more valuable to conservation planning than unselected sites is a general shortcoming of heuristic algorithms. This problem is discussed by Pressey *et al.* (1997). It is, therefore, imperative that the limitations of databases used in conservation area selection exercises, and conservation planning in general, are known and taken into consideration when results are interpreted. In addition, inaccuracies and uncertainties within a database that stem from errors made during the compilation stage can be minimised by following a few simple guidelines such as those provided by Richardson (1994).

Consequently, conservation area selection procedures are most effective if up-to-date, detailed distribution databases are used. However, because such databases often do not exist or are incomplete and outdated, especially where smaller, less "charismatic" species are concerned, and because the gathering of such data is often not feasible from both a time and a monetary point of view, the use of indicator taxa has been promoted (Pearson and Cassola, 1992; Vane-Wright *et al.,* 1994; Williams and Gaston, 1994; Oliver and Beattie, 1995; Flather *et al.,* 1997; Howard *et al.,* 1998). The most appropriate indicator taxon to be used as a biodiversity indicator (*sensu* McGeoch, 1998) depends on the particular situation at hand. Usually, a group of taxa whose distributions are better known or easier to acquire than those of the target taxon and whose taxonomy is sound would be employed (McGeoch, 1998). The biodiversity indicator, whose use relies on a predictive relationship between it and the more poorly studied target group (McGeoch, 1998; Pimm and Lawton, 1998), is indicative of distribution patterns of the target group in a specified area (McGeoch, 1998).

The conservation of dung beetles (Coleoptera, Scarabaeidae) in South Africa and Namibia (Fig. 1) forms the topic of this dissertation. Although these insects have been relatively well studied in southern Africa, compared to many other insect groups,

Figure 1. Map of Africa showing the study areas: South Africa and Namibia.

they have not featured in conservation plans. This is despite the fact that these beetles play a crucial environmental role by breaking down dung and recycling plant nutrients and organic matter found in dung (Lonsdale, 1991a; Scholtz and Holm, 1996). The rapid and efficient disposal of dung, produced by domestic as well as wild herbivores, plays an important nutrient cycling role in ecosystem function. In the absence of this nutrient recycling, layers of dung would quickly accumulate on grasslands, resulting in a progressive decline of their productivity and increases in dung-breeding insect pests (Waterhouse, 1977; Lonsdale, 1991a). In this dissertation, the distributions of 509 dung beetle species were obtained from various sources and employed in conservation planning analyses. The current conservation status of dung beetles within Namibia's and South Africa's existing reserves was assessed, and additional potential conservation areas for the beetles in these two countries were identified with the use of two complementarity-based algorithms as well as species richness hotspots; the use of the complementarity-based methods versus the hotspot approach for the conservation of these beetles was evaluated. A quality assessment of the dung beetle dataset was taken into consideration during the interpretation of these results. In addition, the use of mammals, an intensely researched taxon, as a possible indicator taxon for dung beetles in four of South Africa's provinces was assessed. Two selected mammal datasets were used, and two complementarity-based methods employed to determine the degree to which mammal distributions represent dung beetle distribution patterns. The performances of the two mammal datasets were compared, and the two analytical approaches were contrasted and evaluated.

Attached at the end of this dissertation are two manuscripts that emanated during the course of this study and which made use of the dung beetle data collected for it.

References

Bedward, M., Pressey, R.L. and Keith, D.A. (1992) A new approach for selecting fully representative reserve networks: addressing efficiency, reserve design and land suitability with an iterative analysis. *Biol. Cons.* **61**, 115-125.

Beissinger, S.R., Steadman, E.C., Wohlgenant, T., Blate, G. and Zack, S. (1996) Null models for assessing ecosystem conservation priorities: threatened birds as titers of threatened ecosystems in South America. *Conserv. Biol.* **10**, 1343-1352.

Davis, F.W., Stoms, D.M., Estes, J.E., Scepan, J. and Scott, J.M. (1990) An information systems approach to the preservation of biological diversity. *Int. J. GIS* **4**, 55-78.

Drinkrow, D.R. and Cherry, M.I. (1995) Anuran distribution, diversity and conservation in South Africa, Lesotho and Swaziland. *S. Afr. J. Zool.* **30**, 82-90.

Ehrlich, P.R. (1992) Population biology of checkerspot butterflies and the preservation of global biodiversity. *Oikos* **63**, 6-12.

Flather, C.H., Wilson, K.R., Dean, D.J. and McComb, W.C. (1997) Identifying gaps in conservation networks: of indicators and uncertainty in geographic-based analyses. *Ecol. Appl.* **7**, 531-542.

Freitag, S., Nicholls, A.O. and van Jaarsveld, A.S. (1996) Nature reserve selection in the Transvaal, South Africa: what data should we be using? *Biodiv. Conserv.* **5**, 685-698.

Freitag, S., Nicholls, A.O. and van Jaarsveld, A.S. (1998a) Dealing with established reserve networks and incomplete distribution data sets in conservation planning. *S. Afr. J. Sci.* **94**, 79-86.

Freitag, S., Hobson, C., Biggs, H.C. and van Jaarsveld, A.S. (1998b) Testing for potential survey bias: the effect of roads, urban areas and nature reserves on a southern African mammal data set. *Anim. Conserv.* **1**, 119-127.

Freitag, S. and van Jaarsveld, A.S. (1995) Towards conserving regional mammalian species diversity: a case study and data critique. *S. Afr. J. Zool.* **30**, 136-144.

Fry, R. and Lonsdale, D. (1991) Introduction. *In Habitat Conservation for Insects – a Neglected Green Issue* (R. Fry and D. Lonsdale, eds), pp. 1-14 . England: The Amateur Entomologist's Society.

Gelderblom, C.M., Bronner, G.N., Lombard, A.T. and Taylor, P.J. (1995) Patterns of distribution and current protection status of the Carnivora, Chiroptera and Insectivora in South Africa. *S. Afr. J. Zool.* **30**, 103-114.

Heywood, V.H. (1994) The measurement of biodiversity and the politics of implementation. *In Systematics and Conservation Evaluation* (P.l. Forey, C.J. Humphries and R.I. Vane-Wright, eds), pp. 15-22. Oxford: Clarendon Press.

Howard, P.C., Viskanic, P., Davenport, T.R.B., Kigenyi, F.W., Baltzer, M., Dickinson, C.J., Lwanga, J.S., Matthews, R.A. and Balmford, A. (1998) Complementarity and the use of indicator groups for reserve selection in Uganda. *Nature* **394**, 472-475.

Hunter, M.L. and Hutchinson, A. (1994) The virtues and shortcomings of parochialism: conserving species that are locally rare, but globally common. *Conserv. Biol.* **8**, 1163-1165.

Kremen, C., Colwell, R.K., Erwin, T.L., Murphy, D.D., Noss, R.F. and Sanjayan, M.A. (1993) Terrestrial arthropod assemblages: their use in conservation planning. *Conserv. Biol.* **7**, 796-808.

Kunin, W.E. and Lawton, J.H. (1996) Does biodiversity matter? Evaluating the case for conserving species. *In Biodiversity* (K.J. Gaston, ed.), pp. 283-308. Oxford: Blackwell Science.

Lombard, A.T. (1995a) Introduction to an evaluation of the protection status of South Africa's vertebrates. *S. Afr. J. Zool.* **30**, 63-70.

Lombard, A.T. (1995b) The problems with multi-species conservation: do hotspots, ideal reserves and existing reserves coincide? *S. Afr. J. Zool.* **30**, 145-163.

Lonsdale, D. (1991a) Grassland habitats: the dung of livestock. *In Habitat Conservation for Insects - a Neglected Green Issue* (R. Fry and D. Lonsdale, eds), pp. 93-115. England: The Amateur Entomologist's Society.

Lonsdale, D. (1991b) Preface. *In Habitat Conservation for Insects - a Neglected Green Issue* (R. Fry and D. Lonsdale, eds), pp. xi-xii. England: The Amateur Entomologist's Society.

Lugo, A.E. (1998) Biodiversity and public policy: the middle of the road. *In Protection of Global Biodiversity* (L.D. Guruswamy And J.A. McNeely, eds), pp. 33-45. London: Duke University Press.

Margules, C.R., Cresswell, I.D. and Nicholls, A.O. (1994) A scientific basis for establishing networks of protected areas. *In Systematics and Conservation Evaluation* (P.L. Forey, C.J. Humphries and R.I. Vane-Wright, eds), pp. 327-350. Oxford: Clarendon Press.

McGeoch, M.A. (1998) The selection, testing and application of terrestrial insects as bioindicators. *Biol. Rev.* **73**, 181-201.

McNeely, J.A. (1992) The sinking ark: pollution and the worldwide loss of biodiversity. *Biodiv. Conserv.* **1**, 2-18.

Meffe, G.K., Carroll, C.R. and Contributors (1997) *Principles of Conservation Biology*. Massachusetts: Sinauer Associates.

New, T.R. (1993) Angels on a pin: dimensions of the crisis in invertebrate conservation. *Am. Zool.* **33**, 623-630.

New, T.R. and Yen, A.L. (1995) Ecological importance and invertebrate conservation. *Oryx* **29**, 187-191.

Nicholls, A.O. and Margules, C.R. (1993) An upgraded reserve selection algorithm. *Biol. Conserv.* **50**, 51-75.

Oliver, I. and Beattie, A.J. (1995) Invertebrate morphospecies as surrogates for species: a case study. *Conserv. Biol.* **10**, 99-109.

Pearson, D.L. and Cassola, F. (1992) World-wide species richness patterns of tiger beetles (Coleoptera: Cicindelidae): indicator taxon for biodiversity and conservation studies. *Conserv. Biol.* **6**, 376-391.

Pimm, S.L. and Lawton, J.H. (1998) Planning for biodiversity. *Science* **279**, 2068-2069.

Pressey, R.L., Humphries, C.J., Margules, C.R., Vane-Wright, R.I. and Williams, P.H. (1993) Beyond opportunism: key principles for systematic reserve selection. *TREE* **8**, 124-128.

Pressey, R.L., Bedward, M. and Keith, D.A. (1994) New procedures for reserve selection in New South Wales: maximising the chances of achieving a representative network. *In Systematics and Conservation Evaluation* (P.L. Forey, C.J. Humphries and R.I. Vane-Wright, eds), pp. 351-373. Oxford: Clarendon Press.

Pressey, R.L., Possingham, H.P. and Day, J.R. (1997) Effectiveness of alternative heuristic algorithms for identifying indicative minimum requirements for conservation reserves. *Biol. Conserv.* **80**, 207-219.

Raven, P.H. and McNeely, J.A. (1998) Biological extinction: its scope and meaning for us. *In Protection of Global Biodiversity* (L.D. Guruswamy and J.A. McNeely, eds), pp. 13-32. London: Duke University Press.

Richardson, B.J. (1994) The industrialisation of scientific information. *In Systematics and Conservation Evaluation* (P.L. Forey, C.J. Humphries and R.I. Vane-Wright, eds), pp. 123-131. Oxford: Clarendon Press.

Richardson, D. and Cowling, R. (1993) Biodiversity of ecosystem processes: opportunities in Mediterranean-type ecosystems. *TREE* **8**, 79-80.

Samways, M.J. (1993) Dragonflies (Odonata) in taxic overlays and biodiversity conservation. *In Perspectives on Insect Conservation* (K.J. Gaston, T.R. New and M.J. Samways, eds), pp. 111-123. Andover: Intercept.

Samways, M.J. (1994) *Insect Conservation Biology*. London: Chapman & Hall.

Scholtz, C.H. and Chown, S.L. (1993) Insect conservation and extensive agriculture: the savanna of southern Africa. *In Perspectives on Insect Conservation* (K.J. Gaston, T.R. New and M.J. Samways, eds), pp. 75-95. Andover: Intercept.

Scholtz, C.H. and Chown, S.L. (1995) Insects in southern Africa: how many species are there? *S. Afr. J. Sci.* **91**, 124-126.

Scholtz, C.H. and Holm, E. (1996) Order Coleoptera. *In Insects of Southern Africa* (C.H. Scholtz and E. Holm, eds), pp. 188-280. Pretoria: University of Pretoria.

Stork, N.E. (1994) Inventories of biodiversity: more than a question of numbers. *In Systematics and Conservation Evaluation* (P.L. Forey, C.J. Humphries and R.I. Vane-Wright, eds), pp. 81-100. Oxford: Clarendon Press.

Vane-Wright, R.I., Humphries, C.J. and Williams, P.H. (1991) What to protect? - Systematics and the agony of choice. *Biol. Conserv.* **55**, 235-254.

Vane-Wright, R.I., Smith, C.R. and Kitching, I.J. (1994) Systematic assessment of taxic diversity by summation. *In Systematics and Conservation Evaluation* (P.L. Forey, C.J. Humphries and R.I. Vane-Wright, eds), pp. 309-326. Oxford: Clarendon Press.

Waterhouse, D.F. (1977) The biological control of dung. *In The Insects* (T. Eisner and E.O. Wilson, eds), pp. 314-322. San Francisco. W.H. Freeman and Company.

Williams, P.H. and Gaston, K.J. (1994) Measuring more of biodiversity: can higher-taxon richness predict wholesale species richness? *Biol. Conserv.* **7**, 211-217.

Wilson, E.O. (1993) *The Diversity Of Life.* England: Penguin Books.

CHAPTER 2

Conservation strategies for poorly surveyed taxa: a dung beetle (Coleoptera, Scarabaeidae) case study from southern Africa *

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Introduction

Increasing human impact on natural ecosystems has resulted in the degradation of many habitats to simpler systems (Vane-Wright *et al.,* 1991; Ehrlich, 1992). This reduction of intact habitats and increasing competition with alternative land uses is decreasing the options for biodiversity conservation (Peters and Darling, 1985; McNeely, 1992; Pressey *et al.,* 1993; Richardson and Cowling, 1993). In response, a global effort is underway to maximise the conservation of biodiversity in representative area networks (Davis *et al.,* 1990; Pressey *et al.,* 1993; Margules *et al.,* 1994; Lombard *et al.,* 1995). Part of the rationale underlying this current effort is the realisation that past species-specific efforts have not been sufficient for conservation of a broad array of taxa (Heywood, 1994; Hunter and Hutchinson, 1994; Drinkrow and Cherry, 1995). Nonetheless, in many cases, conservation prioritisation continues to be biased towards vertebrates (Hunter and Hutchinson, 1994), despite the importance of other taxa in terrestrial systems, such as insects (e.g. Janzen, 1987; Fry and Lonsdale, 1991; Gaston, 1991; Ehrlich, 1992; New, 1993; Samways, 1993, 1994; Scholtz and Chown, 1993, 1995; McGeoch, 1998). In consequence, reserves and national parks have generally not been designed for the conservation of invertebrate taxa, and this trend seems to be continuing. However, formal conservation areas do contribute towards the conservation of invertebrates (Samways, 1994), but the extent to which these animals are represented within such areas is not well known. As a result, the efficacy of protected areas for invertebrate conservation remains poorly assessed.

In the present study, we investigated the representativeness of existing protected areas in South Africa and Namibia for the conservation of dung beetles (Coleoptera, Scarabaeidae), a diverse insect taxon (see Scholtz and Holm, 1996). We did this in three ways. First, we evaluated the spatial congruence between the existing reserve system and conservation area networks selected for dung beetles using our database and iterative, complementarity-based reserve selection algorithms. Second, we calculated the proportion of overall dung beetle species richness (obtained from a compilation of collection records from taxonomic reviews and museum specimens), captured by quarter degree grid cells with 25% to 100% of their surface areas represented in reserves. Third, we determined the number of grids required to represent all dung beetle species using the selection algorithms but with pre-selection of grids whose area is partly or completely under formal protection.

Dung beetles were chosen for this study for three reasons. First, southern African dung beetles have been intensively researched, and a large, comprehensive reference collection for these species has been compiled, predominantly by the Dung Beetle Research Unit (DBRU) and the Transvaal Museum. The DBRU, whose establishment in Pretoria (South Africa) in 1971 was funded by the CSIRO (Australia) and the Australian Meat Research Commission, conducted an intensive, wide-ranging dung beetle collection program until its closure in 1986 (Bornemissza, 1976; Waterhouse, 1977). Hence, distribution data for these beetles is routinely assumed to be relatively complete and up-to-date compared to many other southern African insect groups (an assumption we also test). Second, because many dung beetle species are specialised to feed on particular dung types (Davis, 1994), especially those of large herbivores, we assume that they should be well represented in current reserve networks that were primarily established for the conservation of large herbivorous mammals (Infield, 1988; Siegfried, 1991). Finally, these beetles, which are found in a variety of southern African habitats ranging from dry, arid to moist tropical areas, are important contributors to ecosystem functioning, especially in summer (Waterhouse, 1977; Davis, 1996; Scholtz and Holm, 1996).

Methods

Presence-only, species-level distribution data (from 1900 onwards) for the majority of the Scarabaeidae from South Africa and Namibia (excluding Lesotho and Swaziland) were obtained from published records (Paschalidis, 1974; Ferreira, 1978; Holm and Scholtz, 1979; Mostert and Holm, 1982; Davis, 1986; Howden and Scholtz, 1987; Scholtz and Evans, 1987; Scholtz and Howden, 1987a,b) and from museum specimens held at the Transvaal Museum (Pretoria, South Africa) and the National Collection of Insects (NCI) (Pretoria, South Africa). Five hundred and nine species belonging to 59 genera were examined (total of 7819 distribution records). Since the precise latitude and longitude of the point localities were not always given, these co-ordinates were identified with the aid of gazetteers and 1:500 000 maps of the two countries. Furthermore, each distribution data point was assigned to a quarter by quarter degree (15' x 15' = 25km x 25km) grid cell, and analyses were carried out at this level of generalisation. A few ‘undated records’ present in the data set (1.3%; n = 106 records) were retained for the final analyses.

A preliminary temporal evaluation of these data was performed to assess the number of unique records per species (i.e. abundance of species was not taken into account) recorded during each decade from 1900 – 1992. This revealed that the bulk of the records in the database came from more recent collections made after 1969. Based on this assessment, as well as our understanding of collection effort (see discussion), pre-1970 data were considered ‘old data’ (including undated records), whereas data from 1970 on were considered ‘new data’. Comparative analyses were carried out on the complete data set and on ‘new data’ only to determine the influence of collector bias on conservation assessments.

Record density maps for the complete data set as well as the ‘new data’ were generated by summing the number of unique localities per species in each grid cell. These maps were used to assess the degree of spatial bias contained in the database as well as the spatial coverage of the dung beetles.

Scarabaeid species richness in South Africa and Namibia was determined by summing the number of species found within each grid cell, and richness hotspots were identified as the top 5% of grids ranked by species richness. The relationship between record density and species richness was established to test for collector bias in the database.

Two complementarity-based, iterative reserve selection algorithms were used in the present study to generate potential conservation area networks for the dung beetles. These algorithms identify a system of areas that capture all species within the database at least once in the minimum possible number of grid squares. The first algorithm follows the rules of Nicholls and Margules (1993) and is based on database rarity, i.e. sites initially selected by the algorithm are those that contain the ‘rarest’ species with the fewest records in the database. This algorithm was run on the complete data set as well as ‘new data’ (post - 1969) only. Outputs were compared spatially to evaluate the potential for bias emanating from old data. The second algorithm employed is a variation of the composite rarity-based iterative reserve selection (CRIRS) algorithm formulated by Freitag *et al.* (1997). It uses the relative taxonomic distinctiveness (RTD) of species to prioritise the order of species representation, targeting sites containing species with the highest RTD scores first.

These scores were calculated for each species using the following formula (Freitag and van Jaarsveld, 1997):

$$\mathrm{RTD} = \frac{1}{\sqrt{(f \times g \times s)}} \qquad \text{(Eq. 1)}$$

where f is the number of regionally (South Africa and Namibia here) represented families in the order to which the taxon belongs, g is the number of regionally represented genera in the family and s is the number of regionally represented species in the genus to which a certain species belongs. The higher the RTD score of a species, the more taxonomically distinct it is. The rarity and taxonomic distinctiveness algorithms were compared in terms of their land use efficiencies, which were calculated as follows (Pressey and Nicholls, 1989):

$$\text{Efficiency} = 1 - \frac{X}{T} \qquad \text{(Eq. 2)}$$

where X is the number of grids needed to represent all species a required number of times and T is the total number of grids in the area under consideration. Efficiency increases as X decreases.

Percentage overlap of the grids selected by the two algorithms, with existing protected areas was determined using the Jaccard coefficient (Gotelli and Graves, 1996), which is calculated as follows:

$$\text{Jaccard coefficient} = \frac{N_c}{(N_1 + N_2 - N_c)} \text{ x } 100 \qquad \text{(Eq. 3)}$$

where N_1 and N_2 are the number of grids selected in two analyses and N_c is the number of grids common to N_1 and N_2. In addition, the spatial coincidence of the grids selected by (1) the rarity algorithm, (2) the taxonomic distinctiveness algorithm, and (3) species richness hotspots was assessed using the Jaccard coefficient.

To determine the extent to which formal conservation areas protect dung beetle richness, the percentage of all dung beetle species (in the database) included in grid cells with ≥ 25%, ≥ 50%, ≥ 75% and 100% of their area included in formal conservation areas was calculated. As a second means of assessing the adequacy of existing South African and Namibian reserves for the protection of dung beetle species, the rarity and taxonomic distinctiveness algorithms were run using four pre-selection constraints (grids containing distribution data and are ≥ 25%, ≥ 50%, ≥ 75% or 100% protected are initially selected). Taking into account the species contained in pre-selected grids, additional grids (with no protection) are then systematically added to achieve full beetle representation. The efficiencies of the two algorithms were compared in terms of the number of additional grids required to achieve full species representation.

Results

From 1900 to 1969, the number of unique records per species per decade remained low, reaching a maximum of 133 records collected between 1960 and 1969. A large increase in the number of records (8448) was observed during the 1970's, followed by a substantial decline in subsequent years (Fig. 1). The dramatic increase in survey effort in the 1970's was primarily due to the unparalleled beetle collection efforts of the CSIRO Dung Beetle Research Unit (collection presently housed in the National Collection of Insects - Pretoria, South Africa) and the Transvaal Museum. Prior to this intensive effort, distribution data were collected on an *ad hoc* basis by a number of different people. Hence, these early records can be expected to suffer more from variations in sampling intensity and spatial bias than later ones. Consequently, survey bias most likely occurred before 1970, and therefore we evaluated the impact of pre-1970 data on beetle conservation area assessments.

Applying the routinely employed, rarity-based conservation area selection algorithm to the 'new data set' (post-1969) and the 'complete data set', resulted in a marginal decrease in land-use efficiency from 86 to 92 grid cells. A spatial overlap of 82% (Jaccard coefficient) was achieved between the two generated conservation area networks. Furthermore, a comparison of the record density maps of the two datasets revealed that there were only slight differences between the two, and only nine species (1.8% of 509 species) were excluded from the 'new data set' and. Thus, pre-1970 data had limited influence on the outcome of conservation area assessments, which is why the complete data set was employed during all subsequent assessments.

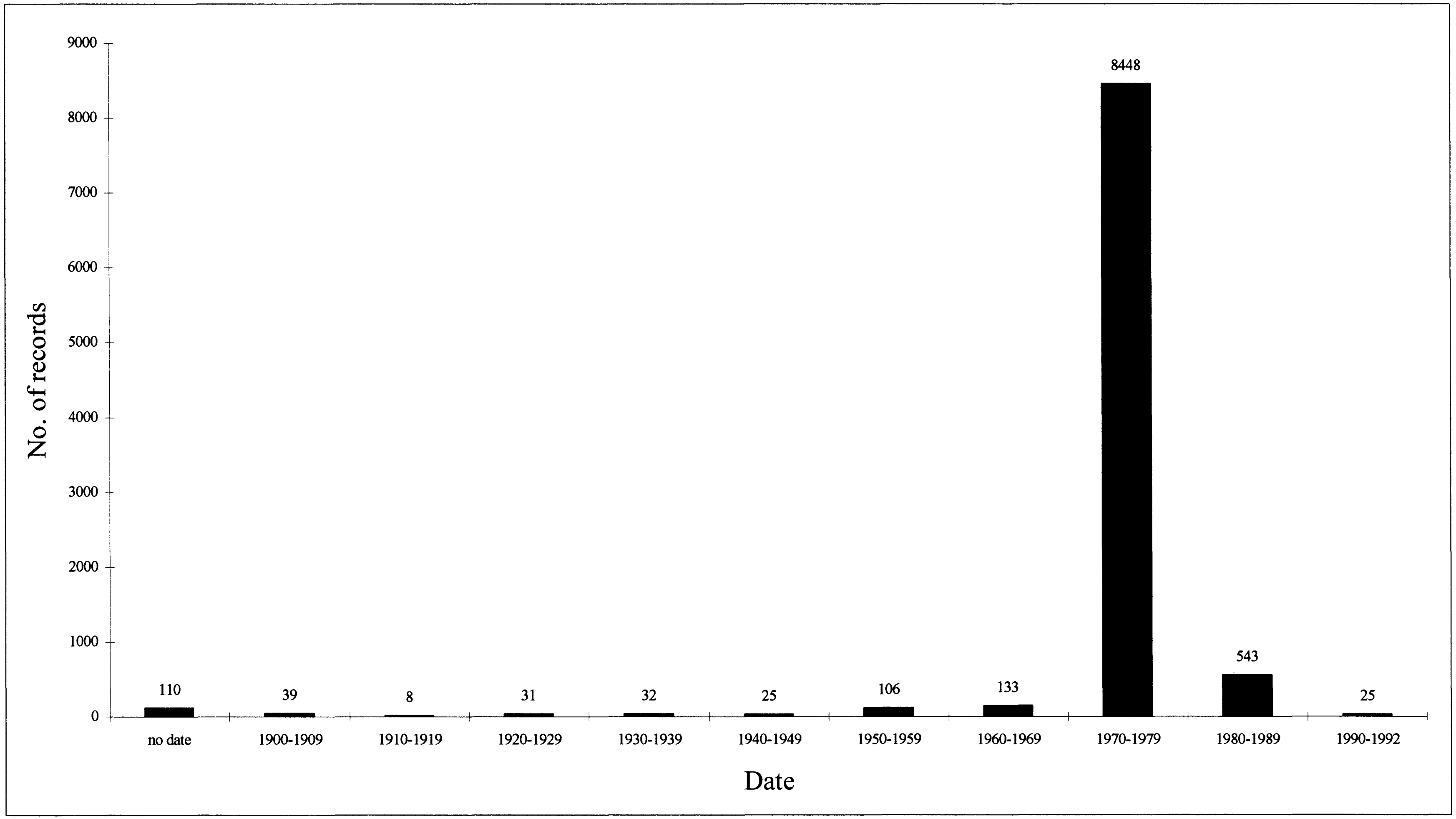

Figure 1. Number of unique dung beetle distribution records per species per decade (1900-1992).

The 92 grid cells selected by the rarity algorithm to achieve total species representation (Table 1) are evenly spread throughout Namibia, while in South Africa there is evidence of clustering of grid cells in Gauteng and the Northern Province as well as in the north of Kwazulu Natal (Fig. 2a). In the Karoo region of South Africa, the beetles are clearly under-represented.

Table 1. Spatial implications of employing different conservation area identification procedures on South African and Namibian dung beetle data (figures in parentheses indicate total number of grid cells selected).

	Rarity algorithm	Richness hotspots	Taxonomic distinct. algorithm
1) No. of grid cells selected	92	49	95
2) Efficiency of algorithm	0.972	-	0.971
3) No. of species represented	509	379	509
4) Proportion (%) of species represented	100	74	100
5) No. of additional grid cell required to represent all species after pre-selection of grid cells that are			
≥ 25% protected	64 (208)	-	65 (209)
≥ 50% protected	76 (169)	-	77 (170)
≥ 75% protected	79 (145)	-	81 (147)
100% protected	81 (125)	-	85 (129)

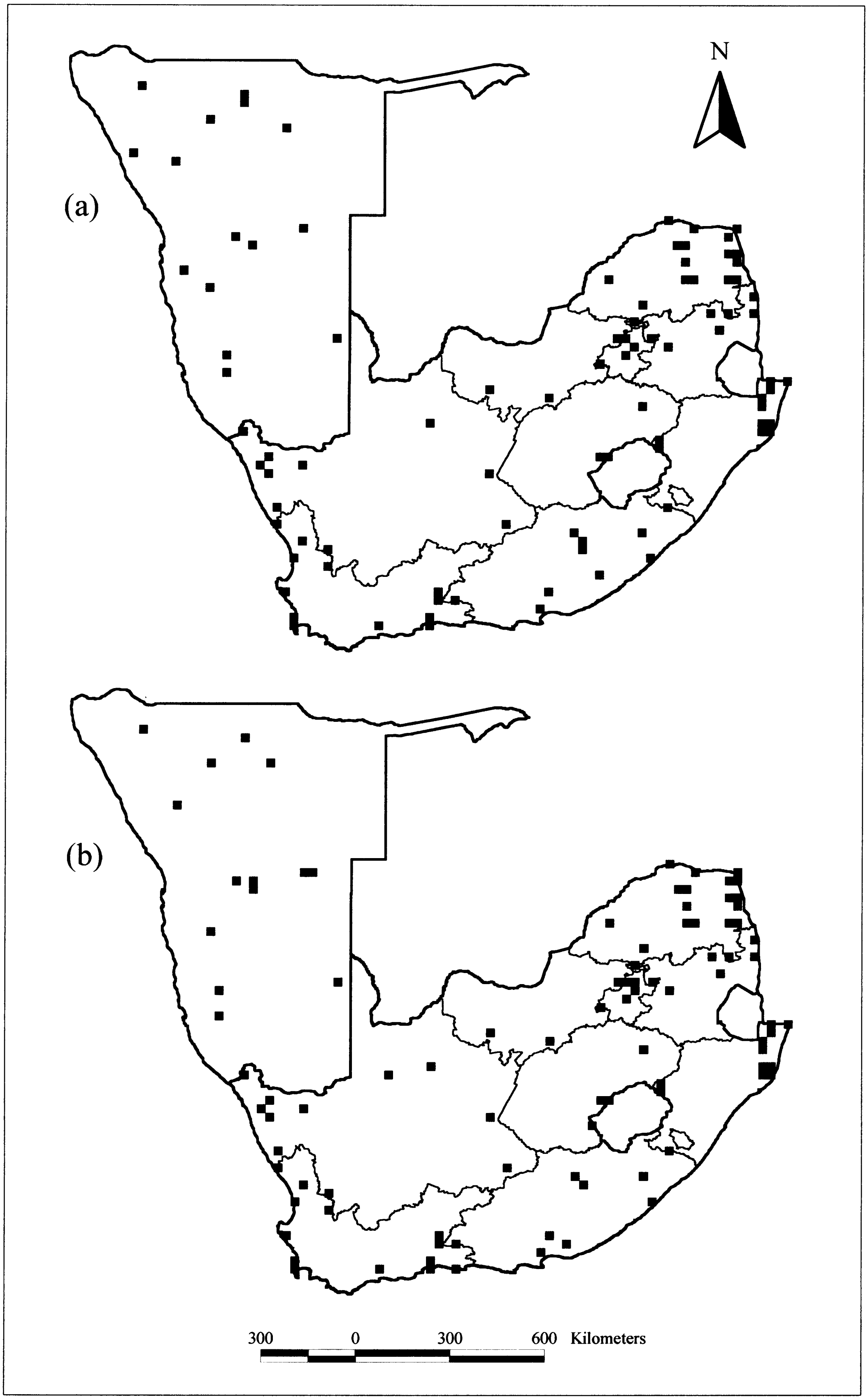

Figure 2. Priority conservation areas generated for the dung beetles in South Africa and Namibia using a) the rarity algorithm and b) the taxonomic distinctiveness algorithm.

To represent all the scarabaeids examined here, the taxonomic distinctiveness algorithm required three more grid cells than the rarity algorithm (Table 1), the conservation area networks selected by these two algorithms (Fig.'s 2a,b) being similar, with a spatial overlap of 81.5% (Table 2). However, the sequence with which grid cells were added to these respective networks differed considerably (see Table 1, Appendix 1).

Table 2. Coincidence of conservation areas identified using different conservation area identification procedures for South African and Namibian dung beetle data.

	Percentage overlap (Jaccard coefficient)		
	Rarity algorithm	Richness hotspots	Taxonomic distinct. algorithm
Conservation area identification procedure (complete data set)			
- Rarity algorithm	-	23%	81.5%
- Richness hotspots		-	18.3%
- Taxonomic distinctiveness algorithm			-

Of the 92 grids selected by the rarity algorithm, 50 (54%) were found to coincide with grids that have some form of formal protection. Likewise, of the 95 grids selected by the taxonomic distinctiveness algorithm, 53 grids (56%) overlapped with grids that are, to some degree, formally protected. Grids with their total surface area protected captured some 166 dung beetle species (36% of the total species richness in the database), whereas those with 75%, 50% and 25% protection captured 208 (41%), 253 (50%), and 366 (72%) species, respectively.

The number of additional sites required to represent all species in South Africa and Namibia after pre-selection of grid cells containing different degrees of protection is presented in Table 1. For both the rarity and taxonomic distinctiveness algorithms, these values increased as grids containing increasing conservation coverage were pre-selected. Overall, however, fewer grids were needed to protect all species as conservation coverage increased (see values in parentheses, Table 1).

Of the 509 species examined in this study, 379 (74%, Table 1) are encompassed by the identified species richness hotspots. The 49 grids representing these hotspots contain between 27 and 139 species (Fig. 3b), and of these 49 grids, 35 (71%) coincide with protected grids. The hotspots are located predominantly in and around the Kwazulu-Natal game parks, in the Kruger National Park in Northern and Mpumalanga Provinces and around the Pretoria region in Gauteng, which is most likely an artefact of collector bias (see Freitag *et al.*, 1998 for similar results using mammals).

The comparative performances of the three different approaches used for identifying potential conservation areas (species richness hotspots and taxonomic distinctiveness- and rarity-based algorithms) are summarised in Table 1. The species richness hotspot approach was most land-use efficient. However, assuming that species representation is a conservation goal, the richness hotspots performed poorly (encompassed only 74% of all species, Table 1). Moreover, the rarity-based algorithm consistently performed better than the taxonomic distinctiveness algorithm, irrespective of the criterion used to evaluate this performance (Table 1). Such an outcome suggests that rarity-based algorithms are preferable for conservation area assessments. However, this assumes that the beetles are adequately sampled.

Dung beetle record densities and species richness patterns are shown in Fig. 3. Of the 3240 grid cells constituting the two countries, 918 grids were occupied by between 1 and 139 species (Fig. 3b), while the majority of the grid cells contained between one and three records (Fig. 3a).

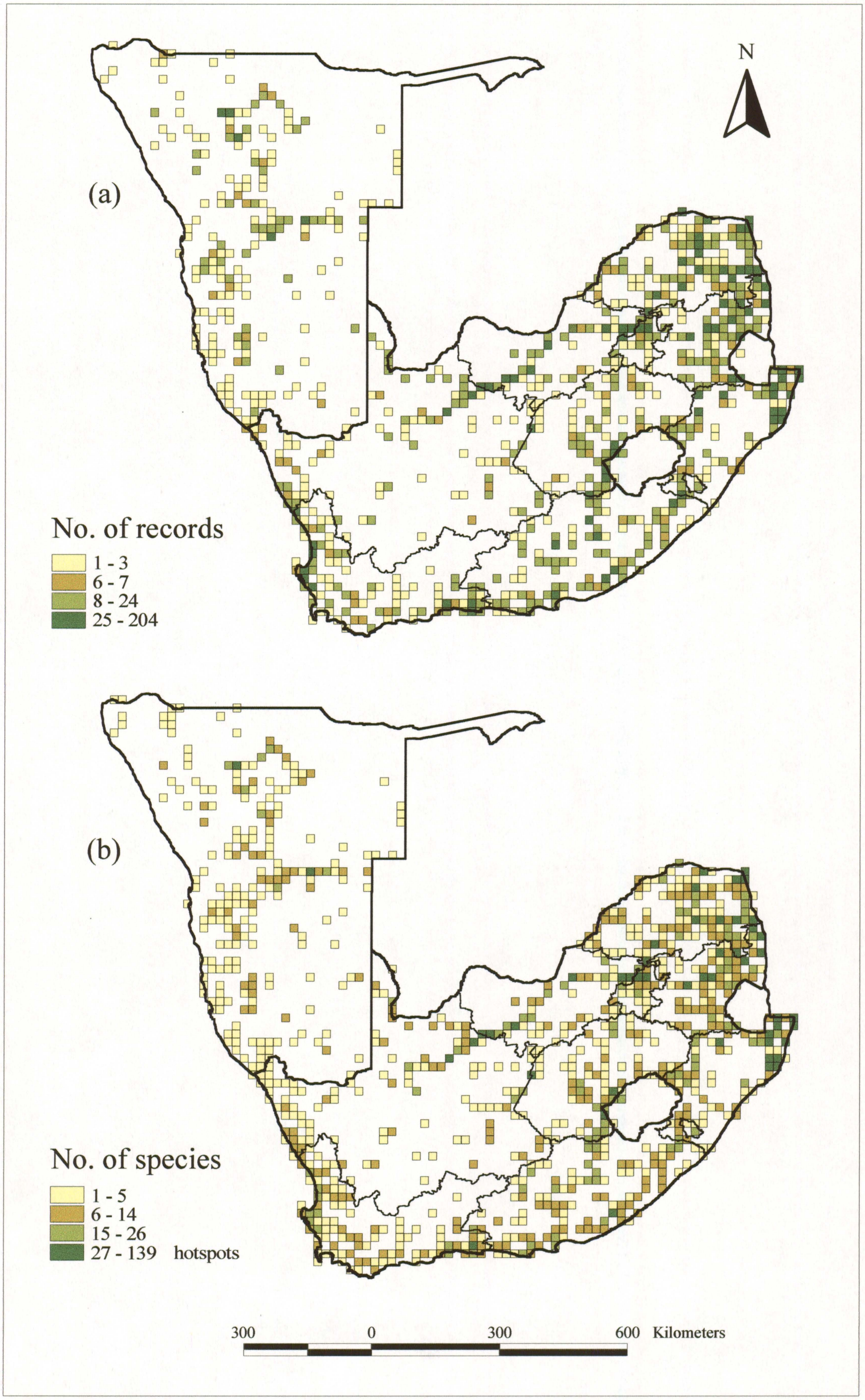

Figure 3. Dung beetle distribution record density (complete dataset) (a) and species richness (b) in South Africa and Namibia.

The relationship between record density and species richness is shown in Fig. 4 and, together with the large number of 'vacant' grid cells, illustrates that the scarabaeids are poorly documented in southern Africa, with richness being highly dependent on sampling effort.

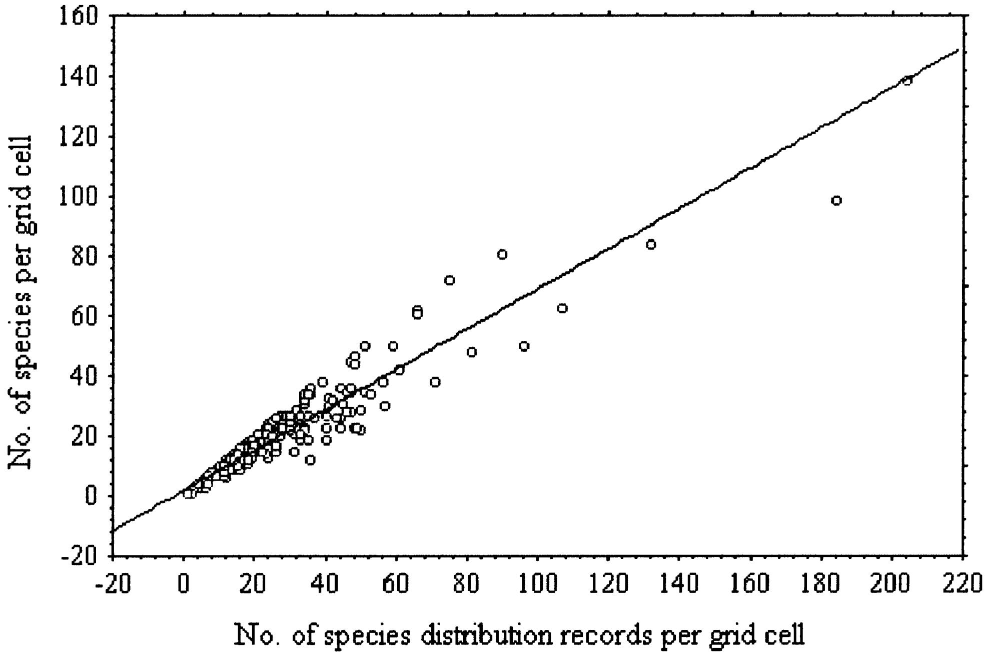

Figure 4. Relationship of dung beetle species richness with record density; $y = 0.673\ x + 1.740$, $r^2 = 0.933$, $F(1, 704) = 9772.9$, $p < 0.00001$.

Discussion

The temporal data evaluation was aimed at determining the extent to which conservation networks based on 'new data' differ from those incorporating 'old data'. Record density maps for the two data sets revealed that sampling intensity per grid is almost identical. In addition, the two reserve networks generated by the rarity algorithm differed by only six grid squares, and overlap of the two conservation networks was relatively high (82%). Thus, there is little evidence that 'old data' significantly bias dung beetle conservation area assessments. Of graver concern, however, is the fact that nine species in this database are represented only amongst the older records. This suggests that any conservation areas designated for the protection of these species, based on the area selections undertaken here, would be ineffectual. It is more than likely that the areas in which these species were originally collected have been transformed to the extent that the species have become extinct. For example, *Aphengoecus clypeatus* Péringuey was last collected in 1892 at Stellenbosch and has not been recorded since, despite considerable collection efforts in the area (Fig. 3a). Likewise, although all records of *Gyronotus glabrosus* Scholtz and Howden (including the types) are restricted to a localised region of the eastern escarpment between Tzaneen and Duiwelskloof in Northern Province, a recent search of the area, which has been transformed considerably by commercial afforestation, has failed to locate a single specimen of this species (Davis *et al.*, submitted ms).

The picture for the species collected more recently appears, at least on first inspection, to be much less gloomy. The most conservative estimate (i.e. based on grids whose entire area is under formal protection) suggests that 166 of the 509 species investigated here (33%) are protected by existing reserve networks, while the most generous estimate (based on grids with 25% conservation status) puts this figure at 72% (366 species). Thus, despite being proclaimed largely for the conservation of mammals (Infield, 1988; Siegfried, 1991), the southern African reserve network seems to be reasonably effective in capturing, and hence conserving, dung beetles. Nonetheless, this has been achieved in a rather inefficient way, as total representation of the dung beetle fauna will require many additional, and geographically widely separated sites (grid cells). Such widely dispersed reserves are not ideal from both the management and long-term population viability points of view (Nicholls and Margules, 1993; Pimm and Lawton, 1998). However, the outcomes of reserve selection algorithms, which are valuable tools for conservation planners, are indicative rather than prescriptive (Pressey *et al.,* 1997), providing a platform on which to base further conservation actions.

Be that as it may, there are at least five mechanisms that could have led to the relatively high representation of dung beetle species in existing formal conservation areas.

1. Artefact of human activity I. A considerable number of southern African dung beetle species are coarse dung specialists, which feed predominantly on the dung of non-ruminant herbivores such as elephant, rhinoceros and zebra (Edwards, 1991; Davis, 1994, 1997; A.L.V. Davis, pers. obs.). The disappearance of these large mammal species in most areas, but their continued survival in reserves, has meant that the beetles specialised to feed on their dung have disappeared in all but those areas where the mammals have had a continued historical presence. This is readily illustrated by the fact that in Kwazulu-Natal (South Africa), reserves such as Mkuze and Hluhluwe, which have had rhino for many years, have retained a coarse dung specialist fauna (Davis, 1997), whereas the relatively newly proclaimed Itala game reserve seems to be missing such a fauna (A.L.V. Davis, S.L. Chown, and C.H. Scholtz, unpublished data). In consequence, the relatively high representation of dung beetle species in conservation areas is, to some extent, an artefact of human activity.

2. Artefact of human activity II. The continued presence of a variety of game species, especially browsers, in reserves, compared to their absence (and a preponderance of grazers, e.g. cattle) outside reserves (Siegfried and Brown, 1992; Scholtz and Chown, 1993) may have led to the survival of certain specialist feeders within the protected areas (Davis, 1997). Although this mechanism should strictly also be considered an artefact of human activity, it does indicate that reserves are fulfilling the purpose now ascribed to them, that is the conservation of biodiversity (Siegfried, 1991).

3. Generalist feeding behaviour. Despite the fact that some species are primarily attracted to a single dung type, many others are attracted to a variety of dung types (Edwards, 1991; Davis, 1994). Consequently, they are likely to occur over a broad range of habitats within their area of occupancy (*sensu* Gaston, 1994) and are thus likely to be sampled by reserves, irrespective of reserve placement.

4. Collection artefact I. Much of the intensive collection efforts made by the DBRU focussed on conservation areas (usually larger reserves), where researchers knew that a suite of dung beetle species was likely to be present. The aim of this program was to seek out and identify dung beetle species that could be translocated to Australia (Waterhouse, 1977), and hence high diversity areas were targeted. In consequence, our database may be biased towards records in conservation areas, thus inflating congruence between species richness hotspots and conservation areas to an extent larger than that caused by mechanisms 1 and 2. Indeed, the hotspot analyses provide considerable support for this assumption. Areas in Kwazulu-Natal, Gauteng and the Northern Province of South Africa, that were all favoured collection and study areas of the DBRU (Doube, 1991; Davis, 1996), emerge as hotspots (Fig. 3b).

5. Collection artefact II. This mechanism is closely linked to the previous one. If much collection has been done in reserve areas in the mesic parts of southern Africa (especially South Africa), but very little in the more arid regions, such as the Karoo (South Africa), then it is inevitable that overlap between reserves and beetle richness will be high. There are few conservation areas in the Karoo (Siegfried, 1991; Siegfried and Brown, 1992; Low and Rebelo, 1996), and little in the way of beetle sampling has been undertaken there (Fig. 3a). The converse is true in the more mesic regions of South Africa, and hence the chances of overlap are likely to be higher in these regions. The under-representation of taxa in the drier areas of South Africa, as a consequence of sampling bias, has been identified in a variety of groups (e.g. Drinkrow and Cherry, 1995; Gelderblom *et al.,* 1995; Lombard, 1995), but the effect of this on estimates of conservation efficacy has not previously been evaluated. Similarly, dung beetle sampling in Namibia appears to be spatially biased (Fig. 3a).

Of these five mechanisms, it appears likely that all have contributed to the observed pattern, at least to some extent. However, of most concern is the fact that we currently have no way of correcting for the influence of mechanisms 4 and 5, which are likely to pose the most significant impediment to conservation decisions regarding dung beetles. Indeed, the significant relationship between collection effort (number of individuals collected) and species richness in the database (Fig. 4) suggests that the effects of collection artefacts are large. Thus, despite initial perceptions that, at least amongst the southern African Coleoptera, dung beetles are well surveyed (e.g. van Jaarsveld *et al*., 1998a), this is clearly not the case. This finding has important implications.

Foremost among these is the fact that conservation networks, selected on the basis of current beetle datasets, are unlikely to adequately represent the species constituting these Coleoptera. One solution is to use existing data and to interpolate distributions using environmental surrogates (Faith and Walker, 1996; Margules and Redhead, 1995; Robinson *et al.,* 1997a,b; Leathwick *et al.,* 1998). However, this approach is not always reliable (see Davis *et al.,* 1998), requires the existence of appropriate environmental data, and requires testing to determine its suitability for the taxa concerned (Wessels, 1998; Hull *et al*., submitted ms). A further implication of survey inadequacy is that area selection algorithms based on rarity are likely to be less useful than those based on taxonomic distinctiveness (even though they may be more efficient – Table 1) because rarity, in this instance, is an artefact of collection efforts, whereas the taxonomy is more likely to be reliable (e.g. Mostert and Scholtz, 1986).

In the face of database inadequacy, one argument is that conservation planning should proceed with the data at hand (van Jaarsveld *et al*., 1998b), particularly because conservation is ultimately a crisis discipline and land use planning will continue, whether data are available or not. Although this argument is in a certain sense correct, proceeding this way has long-term costs. Balmford and Gaston (1999) have demonstrated that, in many instances, biodiversity surveys may have a lower economic cost than the selection of reserves in the absence of suitable data.

This finding, together with the findings of a variety of authors, that well-surveyed taxa are unlikely to prove to be useful surrogates for poorly surveyed ones (Prendergast *et al.*, 1993; McGeoch, 1998; van Jaarsveld *et al.*, 1998a), suggests that the only way we are likely to improve the prospects for the conservation of non-vertebrate taxa is through additional surveys (see e.g. Margules and Redhead, 1995; Wessels, 1998).

References

Balmford, A. and Gaston, K.J.C. (1999) Why biodiversity surveys are good value. *Nature* **398**, 204-205.

Bornemissza, G.F. (1976) The Australian dung beetle project 1965-1975. *Aust. Meat Res. Comm. Rev.* **30**, 1-30.

Davis, A.L.V. (1986) Three new Afrotropical dung beetles (Coleoptera: Scarabaeinae) in the genera *Kheper* Janssens, *Gymnopleurus* Illiger and *Onitis* Fabricius, with notes on related species. *J. ent. Soc. sth. Afr.* **49**, 373-387.

Davis, A.L.V. (1994) Associations of Afrotropical Coleoptera (Scarabaeidae: Aphodiidae: Staphylinidae: Hydrophilidae: Histeridae) with dung and decaying matter: implications for selection of fly-control agents for Australia. *J. Nat. Hist.* **28**, 383-399.

Davis, A.L.V. (1996) Seasonal dung beetle activity and dung dispersal in selected South African habitats: implications for pasture improvement in Australia. *Agric., Ecosyst. Environm.* **58**, 157-169.

Davis, A.L. (1997) Climatic and biogeographical associations of southern African dung beetles (Coleoptera: Scarabaeidae s. str.). *Afr. J. Ecol.* **35**, 10-38.

Davis, A.J., Jenkinson, L.S., Lawton, J.H., Shorrocks, B. and Wood, S. (1998) Making mistakes when predicting shifts in species range in response to global warming. *Nature* **391**, 783-786.

Davis, F.W., Stoms, D.M., Estes, J.E., Scepan, J. and Scott, J.M. (1990) An information systems approach to the preservation of biological diversity. *Int. J. GIS* **4**, 55-78.

Doube, B.M. (1991) Dung beetles of southern Africa. *In Dung Beetle Ecology* (I. Hanski and Y. Cambefort, eds), pp. 133-155. Princeton: Princeton University Press.

Drinkrow, D.R. and Cherry, M.I. (1995) Anuran distribution, diversity and conservation in South Africa, Lesotho and Swaziland. *S. Afr. J. Zool.* **30**, 82-90.

Edwards, P.B. (1991) Seasonal variation in the dung of African grazing mammals, and its consequences for coprophagous insects. *Funct. Ecol.* **5**, 617-628.

Ehrlich, P.R. (1992) Population biology of checkerspot butterflies and the preservation of global biodiversity. *Oikos* **63**, 6-12.

Faith, D.P. and Walker, P.A. (1996) Environmental diversity: on the best-possible use of surrogate data for assessing the relative biodiversity of sets of areas. *Biodiv. Conserv.* **5**, 399-415.

Ferreira, M.C. (1978) The genus *Onitis* F. of Africa south of the Sahara (Scarabaeidae, Coleoptera). *Mem. Natl Mus.* **10**, 1-410.

Freitag, S., Hobson, C., Biggs, H.C. and van Jaarsveld, A.S. (1998) Testing for potential survey bias: the effect of roads, urban areas and nature reserves on a southern African mammal data set. *Anim. Conserv.* **1**, 119-127.

Freitag, S. and van Jaarsveld, A.S. (1997) Relative occupancy, endemism, taxonomic distinctiveness and vulnerability: prioritising regional conservation actions. *Biodiv. Conserv.* **6**, 211-232.

Freitag, S., van Jaarsveld, A.S. and Biggs, H.C. (1997) Ranking priority biodiversity areas: and iterative conservation value-based approach. *Biol. Cons.* **82**, 263-272.

Fry, R. and Lonsdale, D. (1991) Introduction. *In Habitat Conservation for Insects – a Neglected Green Issue* (R. Fry and D. Lonsdale, eds), pp. 1-14 . England: The Amateur Entomologist's Society.

Gaston, K.J. (1991) The magnitude of global insect species richness. *Conserv. Biol.* **5**, 283-296.

Gaston, K.J. (1994) *Rarity.* London: Chapman & Hall.

Gelderblom, C.M., Bronner, G.N., Lombard, A.T. and Taylor, P.J. (1995) Patterns of distribution and current protection status of the Carnivora, Chiroptera and Insectivora in South Africa. *S. Afr. J. Zool.* **30**, 103-114.

Gotelli, N.J. and Graves, G.R. (1996) *Null Models In Ecology.* Washington: Smithsonian Institution Press.

Heywood, V.H. (1994) The measurement of biodiversity and the politics of implementation. *In Systematics and Conservation Evaluation* (P.l. Forey, C.J. Humphries and R.I. Vane-Wright, eds), pp. 15-22. Oxford: Clarendon Press.

Holm, E. and Scholtz, C.H. (1979) A revision of the genus *Pachysoma* M'Leay with an evaluation of the subtribe Pachysomina Ferreira and its genera (Coleoptera: Scarabaeidae). *J. ent. Soc. sth. Afr.* **42**, 225-244.

Howden, H.F. and Scholtz, C.H. (1987) A revision of the African genus *Odontoloma* Boheman (Coleoptera: Scarabaeidae: Scarabaeinae). *J. ent. Soc. sth. Afr.* **50**, 155-192.

Hunter, M.L. and Hutchinson, A. (1994) The virtues and shortcomings of parochialism: conserving species that are locally rare, but globally common. *Conserv. Biol.* **8**, 1163-1165.

Infield, M. (1988) Attitudes of a rural community towards conservation and a local conservation area in Natal, South Africa. *Biol. Cons.* **45**, 21-46.

Janzen, D.H. (1987) Insect diversity of a Costa Rican dry forest: why keep it, and how? *Biol. J. Linn. Soc.* **30**, 343-356.

Leathwick, J.R., Burns, B.R. and Clarkson, B.D. (1998) Environmental correlates of tree alpha-diversity in New Zealand primary forests. *Ecography* **21**, 235-246.

Lombard, A.T. (1995) The problems with multi-species conservation: do hotspots, ideal reserves and existing reserves coincide? *S. Afr. J. Zool.* **30**, 145-163.

Lombard, A.T., Nicholls, A.O. and August, P.V. (1995) Where should nature reserves be located in South Africa? A snake's perspective. *Conserv. Biol.* **9**, 363-372.

Low, A.B. and Rebelo, A.G. (1996) Vegetation of South Africa, Lesotho, and Swaziland. Department of Environmental Affairs and Tourism, Pretoria.

Margules, C.R., Cresswell, I.D. and Nicholls, A.O. (1994) A scientific basis for establishing networks of protected areas. *In Systematics and Conservation Evaluation* (P.L. Forey, C.J. Humphries and R.I. Vane-Wright, eds), pp. 327-350. Oxford: Clarendon Press.

Margules, C.R. and Redhead, T.D. (1995) *BioRap: Guidelines forUusing the BioRap Methodology and Tools*. Australia: CSIRO.

McGeoch, M.A. (1998) The selection, testing and application of terrestrial insects as bioindicators. *Biol. Rev.* **73**, 181-201.

McNeely, J.A. (1992) The sinking ark: pollution and the worldwide loss of biodiversity. *Biodiv. Conserv.* **1**, 2-18.

Mostert, L.E. and Holm, E. (1982) Notes on the flightless Scarabaeina (Coleoptera: Scarabaeidae) with a description of a new species. *Cimbebasia (A)* **5**, 273-284.

Mostert, L.E. and Scholtz, C.H. (1986) Systematics of the subtribe Scarabaeina (Coleoptera: Scarabaeidae). *Entomol. Mem.* **65**, 1-25.

New, T.R. (1993) Angels on a pin: dimensions of the crisis in invertebrate conservation. *Am. Zool.* **33**, 623-630.

Nicholls, A.O. and Margules, C.R. (1993) An upgraded reserve selection algorithm. *Biol. Conserv.* **50**, 51-75.

Paschalidis, K.M. (1974) The genus *Sisyphus* Latr. (Coleoptera: Scarabaeidae) in southern Africa. MSc, University of Rhodes, Grahamstown.

Peters, R.L. and Darling, D.S. (1985) The greenhouse effect and nature reserves. *BioScience* **35**, 707-717.

Pimm, S.L. and Lawton, J.H. (1998) Planning for biodiversity. *Science* **279**, 2068-2069.

Prendergast, J.R., Quinn, R.M., Lawton, J.H., Eversham, B.C. and Gibbons, D.W. (1993) Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature* **365**, 335-337.

Pressey, R.L., Humphries, C.J., Margules, C.R., Vane-Wright, R.I. and Williams, P.H. (1993) Beyond opportunism: key principles for systematic reserve selection. *TREE* **8**, 124-128.

Pressey, R.L. and Nicholls, A.O. (1989) Efficiency in conservation evaluation: scoring versus iterative processes. *Biol. Conserv.* **50**, 199-218.

Pressey, R.L., Possingham, H.P. and Day, J.R. (1997) Effectiveness of alternative heuristic algorithms for identifying indicative minimum requirements for conservation reserves. *Biol. Conserv.* **80**, 207-219.

Richardson, D. and Cowling, R. (1993) Biodiversity of ecosystem processes: opportunities in Mediterranean-type ecosystems. *TREE* **8**, 79-80.

Robinson, T., Rogers, D. and Williams, B. (1997a) Univariate analysis of tsetse habitat in the common fly belt of southern Africa using climate and remotely sensed vegetation data. *Med. Vet. Entomol.* **11**, 223-234.

Robinson, T., Rogers, D. and Williams, B. (1997b) Mapping tsetse habitat suitability in the common fly belt of southern Africa using multivariate analysis of climate and remotely sensed vegetation data. *Med. Vet. Entomol.* **11**, 235-245.

Samways, M.J. (1993) Dragonflies (Odonata) in taxic overlays and biodiversity conservation. *In Perspectives on Insect Conservation* (K.J. Gaston, T.R. New and M.J. Samways, eds), pp. 111-123. Andover: Intercept.

Samways, M.J. (1994) *Insect Conservation Biology*. Chapman & Hall. London.

Scholtz, C.H. and Chown, S.L. (1993) Insect conservation and extensive agriculture: the savanna of southern Africa. *In Perspectives on Insect Conservation* (K.J. Gaston, T.R. New and M.J. Samways, eds), pp. 75-95. Andover: Intercept.

Scholtz, C.H. and Chown, S.L. (1995) Insects in southern Africa: how many species are there? *S. Afr. J. Sci.* **91**, 124-126.

Scholtz, C.H. and Evans, A.V. (1987) A revision of the African Ochodaeidae (Coleoptera: Scarabaeoidea). *J. ent. Soc. sth. Afr.* **50**, 399-426.

Scholtz, C.H. and Holm, E. (1996) Order Coleoptera. *In Insects of Southern Africa* (C.H. Scholtz and E. Holm, eds), pp. 188-280. Pretoria: University of Pretoria.

Scholtz, C.H. and Howden, H.F. (1987a) A revision of the southern African genus *Epirinus* Reiche (Coleoptera: Scarabaeidae: Scarabaeinae). *J. ent. Soc. sth. Afr.* **50**, 121-154.

Scholtz, C.H. and Howden, H.F. (1987b) A revision of the African Canthonina (Coleoptera: Scarabaeidae: Scarabaeinae). *J. ent. Soc. sth. Afr.* **50**, 75-119.

Siegfried, W.R. (1991) Conservation status of terrestrial ecosystems and their biota. *In Biotic Diversity in Southern Africa: Concepts and Conservation* (B.J. Huntley, ed.), pp. 186-201. Cape Town: Oxford University Press.

Siegfried, W.R. and Brown, C.A. (1992) The distribution and protection of mammals endemic to southern Africa. *S. Afr. J. Wildl. Res.* **22**, 11-16.

van Jaarsveld, A.S., Freitag, S., Chown, S.L., Muller, C., Koch, S.O., Hull, H., Bellamy, C., Krüger, M., Endrödy-Younga, S., Mansell, M.W. and Scholtz, C.H. (1998a) Biodiversity assessment and conservation strategies. *Science* **279**, 2106-2108.

van Jaarsveld, A.S., Gaston, K.J., Chown, S.L. and Freitag, S. (1998b) Throwing biodiversity out with the binary data? *S. Afr. J. Sci.* **94**, 1-5.

Vane-Wright, R.I., Humphries, C.J. and Williams, P.H. (1991) What to protect? - Systematics and the agony of choice. *Biol. Conserv.* **55**, 235-254.

Waterhouse, D.F. (1977) The biological control of dung. *In The Insects* (T. Eisner and E.O. Wilson, eds), pp. 314-322. San Francisco. W.H. Freeman and Company.

Wessels, K.J., van Jaarsveld, A.S., Grimbeek, J.D. and van der Linde, M.J. (1998) An evaluation of the gradsect biological survey method. *Biodiv. Conserv.* **7**, 1093-1121.

Appendix 1.

Table 1. Grid cells generated by the relative taxonomic distinctiveness (RTD) and rarity algorithms and the orders in which the grid cells were selected. The number of dung beetle genera as well as species occurring within the selected grid cells is indicated. Locality names for the grid cells in South Africa were obtained from the Government Printers in Pretoria, South Africa. For Namibia, the name of a town or farm falling within a given one degree grid cell (finer resolution was not possible) was used to label the grid cells; * denotes Namibian grid cells.

Selection order	RTD	Locality	No. of genera	No. of species	Rarity	Locality	No. of genera	No. of species
1	2732CA	Ubombo	37	139	2732CA	Ubombo	37	139
2	3218AB	Lambert's Bay	9	22	2430DC	Ohrigstad	20	48
3	2821AC	Upington	12	21	2822AB	Lilyvale	20	38
4	3423AA	Knysna	15	21	2431DD	Tshokwana	29	81
5	2829CC	Cathedral Peak	5	14	2832AC	Mtubatuba	32	99
6	2527DB	Brits	22	34	3318AA	Saldanha	12	26
7	2516CC	Helmeringhausen*	4	11	1915BB	Etosha Reserve*	20	33
8	3128BC	Mjika	6	8	2832AD	St. Lucia Estuary	20	63
9	2217CA	Windhoek*	9	13	2829CC	Cathedral Peak	5	14
10	3322CD	George	16	22	2528DB	Sokhulumi	4	11
11	2832AC	Mtubatuba	32	99	3323AC	Barandas	11	16
12	1915BB	Etosha Reserve*	20	33	2528AB	Pienaarsrivier	25	61
13	2231CB	Machayipan	18	35	2927AB	Ladybrand	14	32
14	1816BD	Etosha Reserve*	5	6	2431BD	Satara	24	62
15	2816BD	Khubus	3	4	3322CD	George	16	22
16	3418AB	Cape Peninsula	3	3	2229DD	Wyllie's Poort	19	31
17	3017DB	Garies	1	1	3117BB	Ruitersvlei	5	12
18	2430DC	Ohrigstad	20	48	2217CC	Windhoek*	10	22
19	2832AD	St. Lucia Estuary	20	63	2528CD	Rietvleidam	2	12
20	3318AA	Saldanha	12	26	2329BD	Ramokgopa	14	26
21	2832AA	Ntondweni	31	72	3126BC	Brosterlea	7	15
22	3029CB	Kokstad	10	19	2231AD	Pafuri	14	27
23	3228BB	The Haven	5	8	2832AB	Hluhluwe	30	84
24	2330CC	Tzaneen	11	19	2724AA	Lykso	13	23

25	2431BD	Satara	24	62	3124BA	Dwaal	5	9
26	3323AC	Barandas	11	16	3318CD	Cape Town	4	9
27	2628AA	Johannesburg	10	20	2331CC	Phalaborwa	15	36
28	2229AB	Mapungubwe	13	20	2331AB	Shingwedzi	11	23
29	2331AB	Shingwedzi	11	23	2632CD	Ndumu	18	45
30	2832AB	Hluhluwe	30	84	2014BD	Khorixas*	7	11
31	2917DA	Spektakel	4	5	3029CB	Kokstad	10	19
32	3420BB	Heidelberg (Cape)	6	9	2229AB	Mapungubwe	13	20
33	3119CD	Botterkloof	1	1	2329DD	Haenertsburg	18	33
34	2822AB	Lilyvale	20	38	2331AA	Shigomane	7	11
35	2528DB	Sokhulumi	4	11	2725BD	Makwassie	2	5
36	2528CA	Pretoria	11	35	2917DA	Spektakel	4	5
37	2231AD	Pafuri	14	27	2732AC	Jozini	21	42
38	2632CD	Ndumu	18	45	2832AA	Ntondweni	31	72
39	2331AD	Dzombo	10	15	3322BA	Seekoegat	3	9
40	2528AB	Pienaarsrivier	25	61	3322BC	De Rust	4	8
41	2331CD	Masorini	12	24	2529CD	Middelburg	7	13
42	2927CC	Vanstadensrus	13	29	2728DA	Tweeling	2	3
43	2616CA	Aus*	5	7	3128BC	Mjika	6	8
44	2724AA	Lykso	13	23	2527DB	Brits	22	34
45	2530BD	Nelspruit	15	24	2229DC	Waterpoort	9	14
46	2217CC	Windhoek*	10	22	2230AC	Messina	15	27
47	2014BD	Khorixas*	7	11	2327DC	Afguns	7	10
48	2415BB	Sesriem*	7	11	3325BB	Kommadagga	4	5
49	2428DA	Naboomspruit	13	32	2530BD	Nelspruit	15	24
50	3117BB	Ruitersvlei	5	12	2431CC	Bosbokrand	16	31
51	3219AD	Grootberg	3	6	2331AD	Dzombo	10	15
52	3325BB	Kommadagga	4	5	3017DB	Garies	1	1
53	3322BA	Seekoegat	3	9	2816BD	Khubus	3	4
54	3322BC	De Rust	4	8	1816BD	Etosha Reserve*	5	6
55	2431DD	Tshokwana	29	81	3418AB	Cape Peninsula	3	3
56	3326AD	Salem	6	14	2216DA	Otjimbingwe*	8	13
57	3325DA	Addo	12	22	3119CD	Botterkloof	1	1
58	2529CD	Middelburg	7	13	2924CA	Hopetown	5	6
59	1917BA	Tsumeb*	3	3	2732AB	Sihangwane	20	44
60	3126DB	Vaalbank	6	15	3422AB	Pacaltsdorp	7	15

61	3124BA	Dwaal	5	9
62	2329BD	Ramokgopa	14	26
63	3126BC	Brosterlea	7	15
64	2924CA	Hopetown	5	6
65	1813BB	Opuwo*	1	1
66	2229DC	Waterpoort	9	14
67	2917BA	Kosies	1	1
68	3318CD	Cape Town	4	9
69	2917AD	Harras	2	2
70	2918BC	Hunites	2	7
71	3118DA	Van Rhynsdorp	6	13
72	2218BD	Witvlei*	2	3
73	2327DC	Afguns	7	10
74	2216DA	Otjimbingwe*	8	13
75	2519DA	Koes*	7	14
76	2528CD	Rietvleidam	2	12
77	2927AB	Ladybrand	14	32
78	2528CB	Silverton	19	36
79	2331AA	Shigomane	7	11
80	2331CC	Phalaborwa	15	36
81	2732AC	Jozini	21	42
82	2829CA	Oliviershoek	8	18
83	2728DA	Tweeling	2	3
84	2229DD	Wyllie's Poort	19	31
85	2230AC	Messina	15	27
86	2329DD	Haenertsburg	18	33
87	2927BA	Kilmarnock	3	5
88	2218BC	Witvlei*	8	15
89	2627AD	Carletonville	6	12
90	2725BD	Makwassie	2	5
91	2431CC	Bosbokrand	16	31
92	2231CA	Punda Maria	23	50
93	2732AB	Sihangwane	20	44
94	3422AB	Pacaltsdorp	7	15
95	2632DD	Kosi Bay	22	47

1813BB	Opuwo*	1	1
2315CA	Gobabeb*	3	9
2528CA	Pretoria	11	35
2428DA	Naboomspruit	13	32
3228BB	The Haven	5	8
1918AC	Grootfontein*	6	10
2918BC	Hunites	2	7
2628AA	Johannesburg	10	20
3118DA	Van Rhynsdorp	6	13
2330CC	Tzaneen	11	19
2927BA	Kilmarnock	3	5
2917AD	Harras	2	2
3126DB	Vaalbank	6	15
1816DB	Etosha Reserve*	9	15
2231CA	Punda Maria	23	50
2632DD	Kosi Bay	22	47
2616AB	Aus*	3	10
3325DA	Addo	12	22
2627AD	Carletonville	6	12
2415BB	Sesriem*	7	11
3420BB	Heidelberg (Cape)	6	9
2218BC	Witvlei*	8	15
3219AD	Grootberg	3	6
2616CB	Aus*	3	6
2331CD	Masorini	12	24
3218AB	Lambert's Bay	9	22
2013BA	S of Sesfontein*	2	3
3126DD	Queenstown	12	17
3227CB	Stutterheim	2	2
2519DA	Koes*	7	14
2829CA	Oliviershoek	8	18
2917BA	Kosies	1	1

CHAPTER 3

An investigation into the use of mammals as conservation surrogates for dung beetle species*

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Introduction

Concern regarding the rapid decline in biodiversity world-wide has precipitated a need for species distribution inventories that can be generated rapidly and at low cost (Williams and Gaston, 1994, 1998; Andersen, 1995; Oliver and Beattie, 1996). Because it is not feasible or often even possible to survey the biodiversity of a region, the use of surrogates for this diversity has been widely advocated (Prendergast *et al.*, 1993; Williams and Gaston, 1994; Williams and Humphries, 1994; Faith and Walker, 1996b; Williams *et al.,* 1997). Surrogates are defined by Gaston and Blackburn (1995) as "quantities which are more easily determined and which correlate strongly with those measures of biodiversity which ultimately are desired", and take three main forms, *viz.* indicator groups, environmental variables and higher taxon richness (Williams and Gaston, 1994; Beccaloni and Gaston, 1995; Gaston and Blackburn, 1995; Williams *et al.,* 1997). The use of surrogates for biodiversity assessments has been keenly investigated at a variety of spatial scales (e.g. Landres *et al.,* 1988; Pearson and Cassola, 1992; Williams and Gaston, 1994; Andersen, 1995; Beccaloni and Gaston, 1995; Faith and Walker, 1996b,c; Gaston and Blackburn, 1995; Balmford *et al.,* 1996a,b; Oliver and Beattie, 1996; Dobson *et al.,* 1997; Williams *et al.,* 1997; Howard *et al.,* 1998; McGeoch, 1998; van Jaarsveld *et al.,* 1998). These studies have shown that the spatial scale at which surrogacy studies are performed affects the way in which the diversity of the target taxon is reflected by the indicator taxon (see also Prendergast *et al.,* 1993; Curnutt *et al.,* 1994; McGeoch, 1998; Reid, 1998). Consequently, there is consensus that biodiversity indicators often work at large spatial scales (i.e. continental or global), whereas the indicator/target taxon relationship generally breaks down at small spatial scales (see Prendergast *et al.,* 1993; Gaston and David, 1994; Dobson *et al.,* 1997; Reid, 1998; van Jaarsveld *et al.,* 1998).

Here we test the utility of the biodiversity indicator (*sensu* McGeoch, 1998) surrogacy approach at a regional (subcontinental) scale (South Africa's four northern provinces) using mammals and dung beetles, two comparatively well-surveyed taxa that are thought to have a close association because mammal dung forms the food source of these beetles (Edwards, 1991; Davis, 1994) and because dung beetles are thought to have radiated in synchrony with the ungulate radiations in Africa (Scholtz and Chown, 1995). The approach we use in the present study makes use of one or more groups of "indicator" taxa whose geographic distributions in the region are known (in this case mammals). Areas or sets of areas in which these groups are species-rich are assumed to be rich in general, and hence a network of protected areas selected for the indicators is taken to be representative of a particular target taxon (in this case dung beetles) or of the biodiversity in the region as a whole (Beccaloni and Gaston, 1995; Faith and Walker, 1996a; Flather *et al.,* 1997). Specifically, we employ two methods that are currently used in conservation planning using biodiversity indicators. In the first approach, the extent to which priority conservation areas selected for the indicator group capture species richness in other taxa is examined (see Balmford, 1998; Howard *et al.,* 1998). In the second approach we combine the first method with one that examines the extent to which priority conservation areas generated for the potential indicator taxon are congruent with those generated for other taxa (Prendergast *et al.,* 1993; Beccaloni and Gaston, 1995; Lombard ,1995; Faith and Walker, 1996b; Flather *et al.,* 1997; Reid, 1998; van Jaarsveld *et al.,* 1998). We specifically selected taxa that are comparatively well surveyed and that have a close association, so as to provide a reasonably rigorous test of the biodiversity indicator approach. If mammals do not perform well as biodiversity indicators for dung beetles in southern Africa, then biodiversity indicators are unlikely to be useful at this scale.

Material and methods

Distribution data at the quarter degree grid cell scale (15' x 15') for 314 dung beetle species (Scarabaeidae) and selected mammal orders found in the Mpumalanga, Gauteng, Northern and Northwest Provinces of South Africa (Fig. 1) were used in this study. Two mammal datasets comprising species from selected orders were compiled, based on the type of dung produced by the mammals, viz. Mammals 1 (M1), which includes all orders excluding the Rodentia, Chiroptera, Insectivora, Lagomorpha and Macroscelidea (n = 120 spp.), and Mammals 2 (M2), which includes only the ungulate orders Artiodactyla, Perissodactyla and Proboscidea (n = 35 spp.) because African dung beetles are thought to have radiated with the ungulates (Scholtz and Chown, 1995).

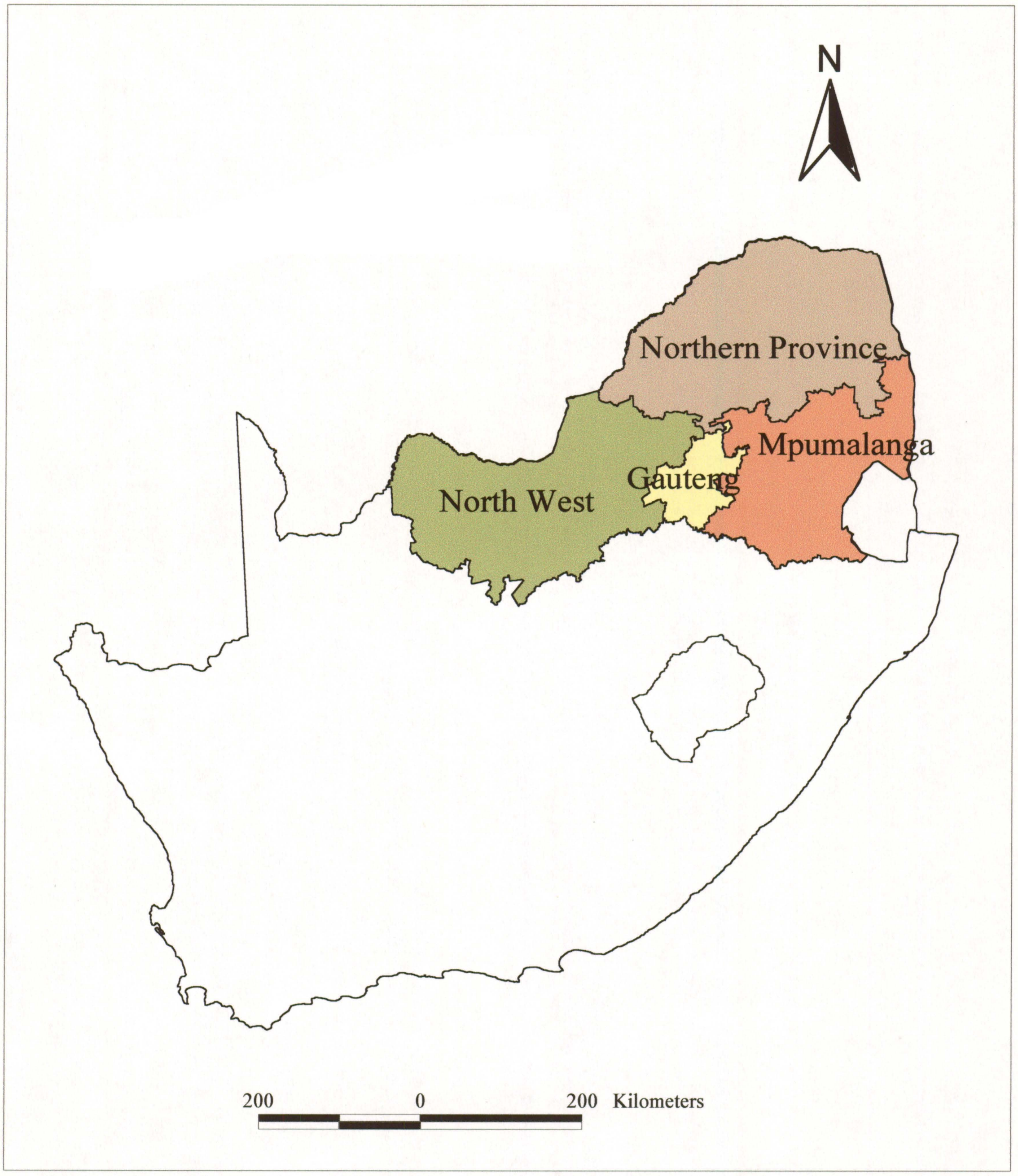

Figure 1. Map of South Africa and the four provinces under investigation.

Two iterative, complementarity-based priority area selection algorithms were used in this study. The first, a modified version of the Nicholls and Margules (1993) algorithm (hereafter referred to as the random area selection algorithm (RASA); see Appendix 1 for algorithm rules), was applied to each of the two mammal databases for the identification of reserve networks that capture all species at least once. Commencing with a randomly selected grid cell, the algorithm was run through 20 iterations, yielding 20 conservation area networks for each of the two mammal datasets. Mean (± S.D.) dung beetle species richness in each of the 20 networks was determined; this degree to which dung beetle species (that is, database species richness for dung beetles) are represented within selected mammal grid cells is termed "inclusiveness".

The second priority area selection algorithm (hereafter referred to as the rarity algorithm), followed the rules of the Nicholls and Margules (1993) algorithm and was applied to both the mammal and the dung beetle data. Only one iteration of the algorithm, which starts off by selecting the grid containing the most database-rare species, was run on each of the three datasets (M1, M2 and dung beetles), and dung beetle inclusiveness in the grid cells common to the selected dung beetle network and either the M1 network or the M2 network, was ascertained.

Dung beetle inclusiveness results obtained from the preceding analyses were also standardised to a "per grid cell" value by dividing the number of dung beetle species represented in a given mammal network by the total number of grid cells in that network.

Finally, the degree to which randomly drawn (RD) networks, as opposed to those systematically generated by algorithms, represent dung beetle species was also assessed. This was achieved by randomly drawing 1000 times from the grid cells in the study area the same number of grid cells selected by the two algorithms for the M2 and M1 groups, respectively. Therefore, in the case of the RASA analyses, 22 and 13 grid cells for the M1 and M2 mammal groups (see Table 1), respectively, were randomly selected from all grid cells in the study area containing mammal distribution data only. In the case of the rarity algorithm analyses, five grid cells (i.e. the number of overlapping mammal and dung beetle grid cells) for both the M1 and M2 mammal sets (see Table 2) were randomly selected from all grid cells in the study area having both mammal and dung beetle distribution data. Subsequently, the number of dung beetle species present in each of the 1000 networks was determined, and the probability of randomly obtaining the same numbers of dung beetle species that are represented in the mammal networks generated with the algorithms was calculated.

Results

The degree to which the dung beetles in this study are represented in the mammal priority conservation areas generated by the RASA is shown in Table 1. Every one of the 20 iterations using the M2 dataset produced an identical network of 13 grids, an artefact of this database that comprises only 13 grid cells, each of which has to be selected by the algorithm for complete mammal representation. These each included 32.8% of the species in the dung beetle database (Table 1).

Table 1. Degree of inclusiveness of dung beetles within the mammal priority conservation areas generated by the RASA.

	M1 priority area network	M2 priority area network
- Mean no. of grid cells selected ± S.D.	22.4 ± 0.7	13.0 ± 0
- Mean % (no.) of dung beetle spp represented ± S.D.	43.8 ± 2.8 (137.7 ± 9.0)	32.8 ± 0 (103.0 ± 0)
- Mean % of dung beetle spp represented per grid cell ± S.D.	2.0 ± 0.1	2.5 ± 0

The same analysis performed on the M1 dataset resulted in a mean of 22.4 grids selected, which represent a mean of 43.8% of all beetle species. Thus, the inclusiveness of the M1 network is about 11% higher than that of the M2 network. This is to be expected since there are 120 mammal species in the M1 group and only 35 species in the M2 group. Consequently, more grid cells are required for complete representation of all mammals in the M1 group (nine more grid cells in this case, Table 1) and, hence, more dung beetle species are present in the M1 network.

The standardised inclusiveness values portray a different scenario; there is a marginally higher representation of dung beetle species per selected mammal grid cell in the M2 network than in the M1 network (Table 1). Standard deviations are low in all cases.

Of the 21 and 13 grid cells selected by the rarity algorithm for the M1 and M2 mammal groups, respectively, five grid cells in both groups overlapped with the 55 grid cells selected for the dung beetles by the same algorithm (Table 2). Absolute dung beetle inclusiveness in these overlapping grid cells is lower than that found in the previous analysis (Table 1). However, inclusiveness in this analysis was based on only five grids in each case, whereas in the previous analysis inclusiveness was based on 21 and 13 grid cells, respectively. Thus, relative (per grid cell) representation of dung beetle species richness in this analysis (Table 2) was more than double that found in the previous analysis (Table 1).

Table 2. Summary data for overlap of priority area networks identified for the mammals and dung beetles using the rarity algorithm.

	M1 priority area network	M2 priority area network	Dung beetle priority area network
- No. of grid cells selected	21	13	55
Dung beetle priority area network:			
- no. of grid cells overlapping with mammal grid cells	5	5	-
- % (no.) of dung beetle spp represented in five overlapping grid cells	28.7 (90)	30.9 (97)	-
- % of dung beetle spp represented per overlapping grid cell	5.7	6.2	-

With the exception of the M2 RASA analysis (see above), dung beetle inclusiveness values obtained using the randomly drawn networks were lower than those obtained using either the M1 mammal database for selecting conservation networks or those using the grid cells that overlapped following selection of priority area networks (PAN) based on the mammal and dung beetle databases (Table 3). In most cases, these values were either significant (overlap between M2 and dung beetle PAN's) or closely approached significance (all others with the exception of the M2 RASA analysis).

Table 3. Random draw (RD) results. The number of grid cells selected in each RD relates to the category for which the RD's were performed. The four categories presented as table headings represent the following: 1) M1 priority area network (PAN) generated by the RASA; 2) M2 PAN generated by the RASA; 3) overlapping M1 and dung beetle (DB) PAN's generated by the rarity algorithm; 4) overlapping M2 and DB PAN's generated by the rarity algorithm.

	1 M1 RASA	2 M2 RASA	3 M1 + DB rarity	4 M2 + DB rarity
- No. of grid cells that were randomly selected per draw	22	13	5	5
- Range of dung beetle spp numbers within 1000 networks	24 - 172	103	10 - 141	43 - 97
- Mean % (no.) of dung beetle spp represented in random networks ± S.D.	31.8 ± 8.0 (99.9 ± 25.3)	32.8 ± 0 (103.0 ± 0)	16.3 ± 6.7 (51.1 ± 21.0)	25.5 ± 3.5 (80.1 ± 10.9)
- % probability of obtaining the same mean no. of dung beetle spp as that in a network generated by one of the two algorithms	6.8	100.0	5.3	2.5

Discussion

Based on the absolute inclusiveness values obtained here, it appears that mammals may be a useful surrogate for dung beetle species richness. On average, the area network selected by the RASA on the basis of all mammal species captured 44% of the dung beetle species in the database. Curiously, despite the purported association between dung beetles and herbivorous mammals (Waterhouse, 1977; Scholtz and Chown, 1995; Davis, 1997), the M2 priority network had a lower inclusiveness than the M1 network. However, it should be noted that the number of mammal species included in the M1 group was over three-fold higher than that in the M2 group, which is why more grid cells were required to protect the M1 mammals than to protect the

M2 mammals. In consequence, it is to be expected that fewer dung beetle species would be captured by the M2 network. On the other hand, a comparison of the more indicative relative inclusiveness values, i.e. per grid cell, suggests that using the ungulates alone may indeed capture a greater species richness of dung beetles, as would be expected on the basis of the biology of these beetles (see Edwards, 1991; Scholtz and Chown, 1995; Davis, 1997).

The considerable increase in relative inclusiveness values in the networks based on both the mammal and dung beetle data suggests that it cannot be automatically assumed that a large proportion of dung beetle species will be represented in priority conservation area networks generated for mammals simply because dung beetles rely on mammals for food and brood material. Thus, conservation planning for dung beetles may be far more effective if the dung beetle data are used in conjunction with the mammal data set than if data from mammals only are used. In addition, it is important to note that the grid cells selected on the basis of both dung beetle and mammal distribution data generally had a significantly greater inclusiveness than did those cells selected by the random draw method based on the same criteria. In contrast, dung beetle inclusiveness based on the mammal area networks alone was no higher than that obtained by randomly drawing similar numbers of grid cells from the pool of grid cells that contained the appropriate mammal data. This suggests that, despite the apparent potential for mammals to act as useful surrogates for dung beetle species richness, they really perform no better than a random draw of the grid cells containing only mammal data. Similar pessimistic conclusions regarding the use of surrogates at small scales have been reached by (Prendergast *et al.,* 1993; Gaston and David, 1994; Dobson *et al.,* 1997; Lawton *et al.,* 1998; Reid, 1998; van Jaarsveld *et al.,* 1998). If species that are thought to show close relationships, such as dung beetles and mammals, have poor surrogacy value, this does not bode well for other taxa that have no functional relationship (see Prendergast *et al.,* 1993). This paints a particularly gloomy picture for surrogates in general, and this case in particular. However, in this instance, three additional issues are pertinent.

First, the ungulate data set was constrained by the small number of grid cells, and hence equivalence of the RD and RASA results is to be expected. Second, even though the RD and RASA results only verged on significance in the case where solely mammals were used, the numbers of dung beetle species represented are not the only concern; the configuration of the selected networks should also be taken into consideration. The fragmentary networks resulting from random draws would be expensive in their establishment as well as prone to species loss as a result of edge effects and isolation (Howard *et al.,* 1998), whereas the sites within the networks selected on the basis of priority area selection algorithms are complementary to one another and are likely to show reduced fragmentation. Thus, even if a similar number of species is captured, the use of systematic tools for the selection of conservation networks, such as the algorithms employed in this study, is preferable to the random placement of reserves (see also Howard *et al.,* 1998). Finally, the rather poor performance of the mammal surrogate as opposed to the random draws may be a consequence of the quality of the dung beetle data set. Although this group has been well-surveyed compared with many other southern African insect taxa (e.g. antlions, Freitag and Mansell, 1997; buprestid beetles, Hull *et al.,* 1998), there are many areas that have not been sampled (Koch *et al.,* submitted ms.). In consequence, a large number of grid cells is required to represent all of the species because it is not known whether the species in question may coexist elsewhere, which would reduce the number of cells required. Thus, a random draw may provide as much coverage of the dung beetle species richness as the mammal data set simply because the dung beetle species are essentially randomly distributed amongst the grid cells that have been surveyed. This is unlikely to be a reflection of the true situation because longitudinal and latitudinal gradients in species richness in southern Africa have been detected in many other taxa (O'Brien, 1993; Drinkrow and Cherry, 1995; Gelderblom *et al.,* 1995). Thus, although it appears that mammals are not serving as effective biodiversity indicators (see McGeoch, 1998 for further discussion) or surrogates for dung beetle species richness at this scale, this conclusion may be a false outcome of the poor quality of the dung beetle data which have been used to test the hypothesis. The most interesting consequence of this conclusion is that, not only are surveys cost-effective in the long term because of a reduction in the number of conservation areas required (Balmford and Gaston, 1999), but having well-surveyed taxa with which to test hypotheses may also fundamentally alter perceptions of the utility of surrogates.

References

Andersen, A.N. (1995) Measuring more of biodiversity: genus richness as a surrogate for species richness in Australian ant faunas. *Biol. Cons.* **73**, 39-43.

Balmford, A. (1998) On hotspots and the use of indicators for reserve selection. *TREE* **13**, 409.

Balmford, A. and Gaston, K.J. (1999) Why biodiversity surveys are good value. *Nature* **398**, 204-205.

Balmford, A., Green, M.J.B. and Murray, M.G. (1996a) Using higher-taxon richness as a surrogate for species richness: I. Regional tests. *Proc. R. Soc. Lond. B* **263**, 1267-1274.

Balmford, A., Jayasuriya, A.H.M. and Green, M.J.B. (1996b) Using higher-taxon richness as a surrogate for species richness: II. Local applications. *Proc. R. Soc. Lond. B* **263**, 1571-1575.

Beccaloni, G.W. and Gaston, K.J. (1995) Predicting the species richness of neotropical forest butterflies: Ithomiinae (Lepidoptera: Nymphalidae) as indicators. *Biol. Cons.* **71**, 77-86.

Curnutt, J., Lockwood, J., Luh, H.-K., Nott, P. and Russell, G. (1994) Hotspots and species diversity. *Nature* **367**, 326-327.

Davis, A.L.V. (1994) Associations of Afrotropical Coleoptera (Scarabaeidae: Aphodiidae: Staphylinidae: Hydrophilidae: Histeridae) with dung and decaying matter: implications for selection of fly-control agents for Australia. *J. Nat. Hist.* **28**, 383-399.

Davis, A.L. (1997) Climatic and biogeographical associations of southern African dung beetles (Coleoptera: Scarabaeidae s. str.). *Afr. J. Ecol.* **35**, 10-38.

Dobson, A.P., Rodriguez, J.P., Roberts, W.M. and Wilcove, D.S. (1997) Geographic distribution of endangered species in the United States. *Science* **275**, 550-553.

Drinkrow, D.R. and Cherry, M.I. (1995) Anuran distribution, diversity and conservation in South Africa, Lesotho and Swaziland. *S. Afr. J. Zool.* **30**, 82-90.

Edwards, P.B. (1991) Seasonal variation in the dung of African grazing mammals, and its consequences for coprophagous insects. *Funct. Ecol.* **5**, 617-628.

Faith, D.P. and Walker, P.A. (1996a) Integrating conservation and development: incorporating vulnerability into biodiversity-assessment of areas. *Biodiv. Conserv.* **5**, 417-429.

Faith, D.P. and Walker, P.A. (1996b) Environmental diversity: on the best-possible use of surrogate data for assessing the relative biodiversity of sets of areas. *Biodiv. Conserv.* **5**, 399-415.

Faith, D.P. and Walker, P.A. (1996c) How do indicator groups provide information about the relative biodiversity of different sets of areas?: on hotspots, complementarity and pattern-based approaches. *Biodiv. Letters* **3**, 18-25.

Flather, C.H., Wilson, K.R., Dean, D.J. and McComb, W.C. (1997) Identifying gaps in conservation networks: of indicators and uncertainty in geographic-based analyses. *Ecol. Appl* **7**, 531-542.

Freitag, S. and Mansell, M.W. (1997) The distribution and protection status of selected antlion species (Neuroptera: Myrmeleontidae) in South Africa. *Afr. Entomol.* **5**, 205-216.

Gaston, K.J. and Blackburn, T.M. (1995) Mapping biodiversity using surrogates for species richness: macro-scales and New World birds. *Proc. R. Soc. Lond. B.* **262**, 335-341.

Gaston, K.J. and David, R. (1994) Hotspots across Europe. *Biodiv. Letters* **2**, 108-116.

Gelderblom, C.M., Bronner, G.N., Lombard, A.T. and Taylor, P.J. (1995) Patterns of distribution and current protection status of the Carnivora, Chiroptera and Insectivora in South Africa. *S. Afr. J. Zool.* **30**, 103-114.

Howard, P.C., Viskanic, P., Davenport, T.R.B., Kigenyi, F.W., Baltzer, M., Dickinson, C.J., Lwanga, J.S., Matthews, R.A. and Balmford, A. (1998) Complementarity and the use of indicator groups for reserve selection in Uganda. *Nature* **394**, 472-475.

Hull, H.E., Freitag, S., Chown, S.L. and Bellamy, C.L. (1998) Identification and evaluation of priority conservation areas for Buprestidae (Coleoptera) in South Africa, Lesotho, Swaziland and Namibia. *Afr. Entomol.* **6**, 265-274.

Landres, P.B.J., Verner, J. and Thomas, J.W. (1988) Ecological uses of vertebrate indicator species: a critique. *Conserv. Biol.* **2**, 316-328.

Lawton, J.H., Bignell, D.E., Bolton, B., Bloemers, G.F., Eggleton, P., Hammond, P.M., Hodda, M., Holt, R.D., Larsen, T.B., Mawdsley, N.A., Stork, N.E., Srivastava, D.S. and Watt, A.D. (1998) Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. *Nature* **391**, 72-76.

Lombard, A.T. (1995) The problems with multi-species conservation: do hotspots, ideal reserves and existing reserves coincide? *S. Afr. J. Zool.* **30**, 145-163.

McGeoch, M.A. (1998) The selection, testing and application of terrestrial insects as bioindicators. *Biol. Rev.* **73**, 181-201.

Nicholls, A.O. and Margules, C.R. (1993) An upgraded reserve selection algorithm. *Biol. Conserv.* **50**, 51-75.

O'Brien, E.M. (1993) Climatic gradients in woody plant species richness: towards an explanation based on an analysis of southern Africa's woody flora. *J. Biogeog.* **20**, 181-198.

Oliver, I. and Beattie, A.J. (1995) Invertebrate morphospecies as surrogates for species: a case study. *Conserv. Biol.* **10**, 99-109.

Pearson, D.L. and Cassola, F. (1992) World-wide species richness patterns of tiger beetles (Coleoptera: Cicindelidae): indicator taxon for biodiversity and conservation studies. *Conserv. Biol.* **6**, 376-391.

Prendergast, J.R., Quinn, R.M., Lawton, J.H., Eversham, B.C. and Gibbons, D.W. (1993) Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature* **365**, 335-337.

Reid, W.V. (1998) Biodiversity hotspots. *TREE* **13**, 275-280.

Scholtz, C.H. and Chown, S.L. (1995) The evolution of habitat use and diet in the Scarabaeoidea: a phylogenetic approach. *In Biology, Phylogeny, and Classification of Coleoptera* (J. Pakaluk and S.A. Slipinski, eds), pp. 355-374. Warszawa: Muzeum i Instytut Zoologii PAN.

van Jaarsveld, A.S., Freitag, S., Chown, S.L., Muller, C., Koch, S.O., Hull, H., Bellamy, C., Krüger, M., Endrödy-Younga, S., Mansell, M.W. and Scholtz, C.H. (1998) Biodiversity assessment and conservation strategies. *Science* **279**, 2106-2108.

Waterhouse, D.F. (1977) The biological control of dung. *In The Insects* (T. Eisner and E.O. Wilson, eds), pp. 314-322. San Francisco: W.H. Freeman and Company.

Williams, P.H. and Gaston, K.J. (1994) Measuring more of biodiversity: can higher-taxon richness predict wholesale species richness? *Biol. Conserv.* **67**, 211-217.

Williams, P.H. and Gaston, K.J. (1998) Biodiversity indicators: graphical techniques, smoothing and searching for what makes relationships work. *Ecography* **21**, 551-560.

Williams, P.H., Gaston, K.J. and Humphries, C.J. (1997) Mapping biodiversity value worldwide: combining higher-taxon richness from different groups. *Proc. R. Soc. Lond. B* **264**, 141-148.

Williams, P.H. and Humphries, C.J. (1994) Biodiversity, taxonomic relatedness, and endemism in conservation. *In Systematics and Conservation Evaluation* (P.L. Forey, C.J. Humphries and R.I. Vane-Wright, eds), pp. 269-287. Oxford: Clarendon Press.

Appendix 1

Random area selection algorithm (RASA)

This algorithm was modified from the Nicholls and Margules (1993) algorithm by S.O. Koch and H.E. Hull (1999).

Selection rules are as follows:

For each iteration of the algorithm, a different species reference file containing all species in random order is used.

Step 1. Randomly select one of the grid cells within the study area, and delete all species occurring in that grid cell from the species reference file.

Step 2. Select the grid cell in which the first species at the top of the species reference file occurs and delete all species occurring in that grid cell from the species reference file.

Step 3. If there is a choice, select the grid cell which contributes the largest number of as yet unrepresented species.

Step 4. If there is still a choice, select the grid cell which is nearest to one already selected.

Step 5. If there is still a choice, select the grid cell which contributes the rarest as yet unrepresented species.

Step 6. If there is still a choice, select the grid cell which contributes the next rarest as yet unrepresented species.

Step 7. If there is still a choice, select the grid cell with the highest species richness.

Step 8. If there is still a choice, select the first grid cell in the list.

CHAPTER 4

Conclusion

The following constitute the main findings and conclusions drawn from this dissertation:

- Despite an extensive history of research on this taxon, the quality of the dung beetle distribution data used in this dissertation proved to be surprisingly, and alarmingly, poor (Chapter 2). The sampling bias contained within this database is a general problem encountered when dealing with species distribution data, especially of invertebrates. Despite the need to make the best use of existing, albeit incomplete, data for conservation planning purposes (Flather *et al.,* 1997; van Jaarsveld *et al.,* 1998), there is also an urgent requirement to improve the quality of these data (Scholtz and Chown, 1993, 1995). Since conservation actions are only as good as the quality of the data on which they are based, it is imperative that biodiversity surveys be invested in. Although the compilation of biodiversity inventories is very costly in terms of time and money, Balmford and Gaston (1999) have shown that the use of well-sampled data obtained from detailed surveys results in the requirement of smaller representative reserve networks than when incomplete data are used. Hence, it may be more costly to use poor distribution data in reserve planning than it is to invest in obtaining good quality data from biodiversity surveys.

- The choice of a particular conservation area selection algorithm depends on the quality of the database to which it is going to be applied. This means that, not only should efficiency be taken into consideration when selecting an algorithm, but that the algorithm characteristics should also be taken into account. Thus, although the taxonomic distinctiveness algorithm used in Chapter 2 was less land-use efficient than the rarity algorithm, it was considered more appropriate, as the taxonomy of the dung beetles used in this dissertation was more reliable than the data on their distributions.

- The priority conservation areas selected by the rarity and taxonomic algorithms in Chapter 2 were unevenly scattered throughout the landscape due to the uneven distribution records of species. Such a network, consisting of widely dispersed reserves, is not ideal. Furthermore, it goes without saying that the reservation of each of the selected grid cells is an unrealistic target, which is why it has been proposed that the minimum set of sites selected by an algorithm should act as a core around which to build conservation actions, rather than the final reserve network (Nicholls and Margules, 1993). In addition, because the sites selected by an algorithm may frequently not be suitable or available for conservation purposes, Pimm and Lawton (1998) suggested that these algorithms should rather select sites adjoining existing reserves. In all probability, it is more viable to add land for conservation to existing protected areas than to establish new reserves. In South Africa, though, this ignores the fact that in some biomes few reserves have been proclaimed (Low and Rebelo, 1996; Freitag and Mansell, 1997). Ultimately, however, it is important to realise that, although the actual establishment of reserves might take the goals derived from reserve selection algorithms into consideration, political and socio-economical factors, among others, probably influence the final decision-making process the most (Pressey *et al.,* 1994; Lombard, 1995; Saberwal and Kothari, 1996).

- The protection of species richness hotspots identified in Chapter 2 would require far less grid cells than that of the networks generated by either of the two algorithms, which means that the hotspot approach is more land-use efficient. However, although hotspots, which represent areas of immense biological abundance, are valuable tools for and should be included in conservation planning actions, their conservation does not ensure the protection of all species because they are arbitrarily defined and usually encompass only a proportion of all the species under consideration (Lombard, 1995; Mugo *et al.,* 1995). Furthermore, species-rich sites do not necessarily contain those species which require special attention in conservation actions, such as those that are rare or threatened. Therefore, to secure the protection of all species under consideration and at the same time protect sites rich in species, it is useful to combine hotspot and algorithm-based analyses in conservation planning. Ideally, hotspots and the sites selected by an algorithm should coincide, and the areas in which they do should be afforded special attention and be given conservation priority because of their high conservation value.

- Existing formal reserves in South Africa and Namibia perform relatively well at representing the dung beetle species under investigation (Chapter 2). Although this is an encouraging finding, it should be viewed with caution because of the spatial bias contained within the dung beetle database. As a large part of the beetle sampling was biased towards reserves, the overall proportion of species represented within these protected areas will, of necessity, be high. However, a different picture may well emerge if evenly sampled, unbiased distribution data were employed.

- Despite the mentioned shortcomings of conservation area selection algorithms, the analyses in Chapter 3 have demonstrated that they are superior to random area selection methods. The former are generally more land-use efficient than the latter, and the selected sites are complementary to one another, which reduces fragmentation of the selected sites and is of utmost importance in conservation area selection procedures.

- The surrogacy analyses performed in Chapter 3 have shown how the use of relative versus absolute values influences the interpretation of a given set of results. In surrogacy analyses performed for the purpose of practical conservation planning, the absolute number of target taxa represented by the surrogate taxon is of importance, since the objective is to protect the largest number of species overall, not per unit area. However, relative values provide a useful means for comparing the performances of potential surrogates constituting differing numbers of taxa.

In conclusion, it remains to be said that the most realistic strategy for conservation planning in general is to use the various conservation methods presented in this dissertation to '...establish the extent of reserves with an eye on the home ranges and resource needs of the charismatic megavertebrates, the areal requirements of "big things that run the world" (Terborgh, 1988), but to locate the reserves with attention to habitat diversity required by the "little things that run the world" (Wilson, 1987)' (in Ehrlich, 1992).

References

Balmford, A. and Gaston, K.J.C. (1999) Why biodiversity surveys are good value. *Nature* 398, 204-205.

Ehrlich, P.R. (1992) Population biology of checkerspot butterflies and the preservation of global biodiversity. *Oikos* 63, 6-12.

Flather, C.H., Wilson, K.R., Dean, D.J. and McComb, W.C. (1997) Identifying gaps in conservation networks: of indicators and uncertainty in geographic-based analyses. *Ecol. Appl.* 7, 531-542.

Freitag, S. and Mansell, M.W. (1997) The distribution and protection status of selected antlion species (Neuroptera: Myrmeleontidae) in South Africa. *Afr. Entomol.* 5, 205-216.

Lombard, A.T. (1995) Introduction to an evaluation of the protection status of South Africa's vertebrates. *S. Afr. J. Zool.* 30, 63-70.

Low, A.B. and Rebelo, A.G. (1996) Vegetation of South Africa, Lesotho, and Swaziland. Department of Environmental Affairs and Tourism, Pretoria.

Mugo, D.N., Lombard, A.T., Bronner, G.N., Gelderblom, C.M. and Benn, G.A. (1995) Distribution and protection of endemic or threatened rodents, lagomorphs and macrosceledids in South Africa. *S. Afr. J. Zool.* 30, 115-126.

Nicholls, A.O. and Margules, C.R. (1993) An upgraded reserve selection algorithm. *Biol. Conserv.* 50, 51-75.

Pimm, S.L. and Lawton, J.H. (1998) Planning for biodiversity. *Science* 279, 2068-2069.

Pressey, R.L., Bedward, M. and Keith, D.A. (1994) New procedures for reserve selection in New South Wales: maximising the chances of achieving a representative network. *In Systematics and Conservation Evaluation* (P.L. Forey, C.J. Humphries and R.I. Vane-Wright, eds), pp. 351-373. Oxford: Clarendon Press.

Saberwal, V.K. and Kothari, A. (1996) The human dimension in conservation biology curricula in developing countries. *Conserv. Biol.* 10, 1328-1331.

Scholtz, C.H. and Chown, S.L. (1993) Insect conservation and extensive agriculture: the savanna of southern Africa. *In Perspectives on Insect Conservation* (K.J. Gaston, T.R. New and M.J. Samways, eds), pp. 75-95. Andover: Intercept.

Scholtz, C.H. and Chown, S.L. (1995) Insects in southern Africa: how many species are there? *S. Afr. J. Sci.* 91, 124-126.

Terborgh, J. (1988) The big things that run the world – a sequel to E.O. Wilson. *Conserv. Biol.* 2, 402-403.

van Jaarsveld, A.S., Gaston, K.J., Chown, S.L. and Freitag, S. (1998) Throwing biodiversity out with the binary data? *S. Afr. J. Sci.* 94, 1-5.

Wilson, E.O. (1987) The little things that run the world (the importance and conservation of invertebrates). *Conserv. Biol.* 1, 344-346.

APPENDIX 1

Biodiversity assessment and conservation strategies

Biodiversity Assessment and Conservation Strategies

Albert S. van Jaarsveld,* Stefanie Freitag, Steven L. Chown, Caron Muller, Stephanie Koch, Heath Hull, Chuck Bellamy, Martin Krüger, Sebastian Endrödy-Younga, Mervyn W. Mansell, Clarke H. Scholtz

The efficient representation of all species in conservation planning is problematic. Often, species distribution is assessed by dividing the land into a grid; complementary sets of grids, in which each taxon is represented at least once, are then sought. To determine if this approach provides useful surrogate information, species and higher taxon data for South African plants and animals were analyzed. Complementary species sets did not coincide and overlapped little with higher taxon sets. Survey extent and taxonomic knowledge did not affect this overlap. Thus, the assumptions of surrogacy, on which so much conservation planning is based, are not supported.

Practical conservation uses surrogate information, such as richness of indicator taxa, endemism (taxa restricted to a given area), or higher taxon richness (that is, genus or family richness) to identify possible conservation areas (*1–8*). Although not universally accepted (9), there is broad agreement that conservation areas should strive to sample regional features, a goal that is most efficiently accomplished with complementary sets (*10, 11*). These are sets of grids that contain all species in a taxon at least once (*10, 12*); the complementarity principle ensures that conservation areas represent all species efficiently and that rare species are included (*10*). Although the outcome of such a complementarity analysis provides a sound basis for the efficient conservation of the focal taxon, it is commonly assumed that the outcome is more widely applicable to other taxa (*13*).

The value of species richness, species rarity, and higher taxon richness as biodiversity surrogate measures ("traditional" surrogates) has been explored, and the consensus is that richness "hotspots" (highly species-rich areas) and "coldspots" (areas poor in species) rarely coincide; nor do hotspots and rare (restricted range) taxa generally coincide (*6, 14–17*). However, the surrogacy value of complementary sets has not been assessed. Here, the relation between traditional surrogate measures and complementary sets, as well as the degree of overlap among complementary sets across taxa, is investigated.

The study incorporated 9119 species, including well-studied taxa that are frequently used as biodiversity indicators (4), such as vascular plants (Plantae), mammals (Mammalia), birds (Aves), and butterflies (Hesperioidea and Papilionoidea), and less well-known taxa, such as termites (Isoptera), antlions (Myrmeleontidae), buprestid beetles (Buprestidae), and scarabaeoid beetles (Scarabaeoidea) (*18*). These taxa vary considerably with regard to survey extent and taxonomic knowledge. For example, birds are surveyed in all grid cells and all species are included, whereas ~20% of antlion species are included and these are surveyed in 8% of the grid cells in the study area. Species that were chosen for inclusion in the poorly surveyed taxa represent either the known fauna for the region (for example, buprestids and scarabs) or, where the majority of the fauna has not been adequately cataloged, a well-known monophyletic unit (antlions). In one instance (termites), only an incomplete set of published data from a systematic survey was available, resulting in poor species coverage (*19*). In none of these cases was there reason to presume that the species chosen are a nonrandom subset of the taxon as a whole with regard to geographic distribution.

Data from the Transvaal region (now including Gauteng, Mpumalanga, Northern, and part of North-West provinces; South Africa) were mapped on a 25 km by 25 km grid ($n = 474$), and complementary sets for each of the taxa were identified by means of a rarity-based algorithm (*12*). The study area is about the size of the United Kingdom and comprises 20% of the surface area of one of the most species-rich countries in the world. Richness hotspots and coldspots reflect the top 5% of species-rich and species-poor 25-km squares, respectively (*14*). Rare species are defined as those occurring in less than 24 squares (5% of 474 squares), and this rarity may be the consequence of a restricted range or inadequate sampling (*20*). The degree of spatial overlap among complementary sets, species richness (hotspots and coldspots), and areas containing rare taxa is expressed by the Jaccard coefficient (Table 1).

As in previous studies (*14*), we found little overlap within taxa using measures of richness (hotspots and coldspots) and rarity (*21*) (Fig. 1 and Table 1). The single exception was richness hotspots and rarity where the mean overlap was 50% (Table 1). This high value was due mostly to high overlap values in plants and in phytophagous insects (plants, buprestids, and butterflies all had overlap values exceeding 75%) (Table 1). Speciose plant regions in southern Africa include large numbers of rare plant species (*22*), and patterns in plant diversity are often a good predictor of patterns in insect diversity (*23*). This may account, at least to some extent, for the high overlap values of richness hotspots and rarity observed within each of these taxa.

Overlap among taxa for richness hotspots and coldspots is, respectively, highest between butterflies and plants (24%), and scarab and buprestid beetles (13%) (*24*). Overlap among areas containing rare taxa is most

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Table 1. Percentage overlap among types of priority conservation areas, species-based complementary sets for different taxa, and complementary sets representing different taxonomic levels. The overlap was calculated with the Jaccard coefficient [number of grids shared/(number of additional grids selected for taxon A + number of additional grids selected for taxon B)] × 100.

Comparisons/taxa	Mammals	Birds	Plants	Butterflies	Termites	Antlions	Scarab beetles	Buprestid beetles
Priority conservation areas								
Richness hotspots versus rare species	29.2	18.0	82.6	77.8	23.8	60.0	6.7	80.0
Richness coldspots versus rare species	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Complementary sets versus richness hotspots	8.1	20.0	8.6	16.3	11.1	16.7	32.1	19.7
Complementary sets versus richness coldspots	0.0	0.0	1.0	2.9	0.0	9.7	0.0	2.0
Complementary sets versus rare species	21.4	30.0	8.2	16.3	11.1	16.7	10.7	12.7
Complementary species sets								
Mammals		11.9	6.6	8.5	0.0	3.5	9.3	11.8
Birds			7.3	9.8	0.0	6.5	13.6	8.6
Plants				12.7	0.4	2.2	7.3	19.5
Butterflies					0.0	2.0	11.7	20.7
Termites						0.0	0.0	1.5
Antlions							10.0	2.9
Scarab beetles								14.3
Buprestid beetles								
Complementary sets representing different taxonomic levels								
Species versus genus	17.9	34.5	37.6	17.8	20.0	0.0	24.0	34.4
Species versus family	8.0	3.7	7.4	2.3	40.0	12.5	4.0	1.6

pronounced in mammals and birds (37%). Nonetheless, all of these overlap values are low, indicating that different taxa are speciose, species-poor, or have their rare species represented, in different grid cells (*24*).

The mean coincidence between complementary species sets and grids selected on the basis of richness (hotspots and coldspots), and between complementary sets and grids containing rare taxa, is well below 20% (Fig. 1 and Table 1). The highest overlap in complementary sets and richness hotspots is for scarab beetles (32%) and birds (20%); this overlap reached only 8% in mammals. Coincidence between complementary sets and rare taxa was highest in mammals (30%). Thus, grids selected for a single representation of each species tend not to be those with excessively high or unusually low species richness, nor do they include a disproportionate number of rare species (Table 1).

Pairwise comparisons of complementary species sets reveal a mean overlap of less than 10% (Fig. 2 and Table 1); maximum overlap (21%) is between butterflies and buprestid beetles. In multiple comparisons of complementary sets, no grid cell was shared by all taxa, and a maximum of six taxa shared complementary grids (coincidentally, $n = 6$ grids shared). This further emphasizes the lack of overlap of complementary sets across taxa. Thus, different conservation areas are required to conserve different taxa.

Complementary sets that represent genera and families show little overlap with species-based complementary sets across taxa (<30%) (Fig. 2 and Table 1). Maximum overlap between genus- and species-based sets is for plants (38%) and birds (35%), taxa that are well surveyed and systematically well known (*25*), and for buprestid beetles (34%), a group that has not been well surveyed and in which many species remain undescribed (*18*, *26*). Similarly, overlap between family- and species-based sets is highest for termites (40%) and antlions (13%), which are either poorly surveyed or represented by few species in this analysis. In contrast, the overlap between well-surveyed and taxonomically well-represented groups, namely plants, birds, and mammals, was minimal, at 7, 4, and 8% respectively (Table 1). Patterns of overlap based on complementary sets were also inconsistent between taxa with changing hierarchical levels (for plants, overlap declines from 38 to 7% from genus to family level, whereas for termites there was an increase from 20 to 40%). Thus, selecting conservation areas by genus- or family-level data cannot result in efficient species-level conservation.

Our results provide little support for the notion that species complementary sets are congruent across taxa or that complementary sets are congruent with richness (hotspots, coldspots, or both) or areas harboring rare taxa, or both. In addition, our results suggest that the use of higher taxa as surrogates (*27*) for species-based complementary set selection holds little promise at a scale relevant to practical conservation planning. This largely undermines hopes for using "indicator taxa" or higher taxon surrogate information as biodiversity planning tools. These data

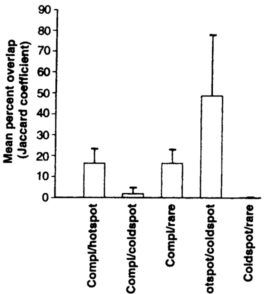

Fig. 1. The degree of spatial overlap (mean ± SD of Jaccard coefficient) between conservation areas generated by means of different prioritization criteria (species-based complementary areas, richness hotspots and coldspots, areas containing rare taxa).

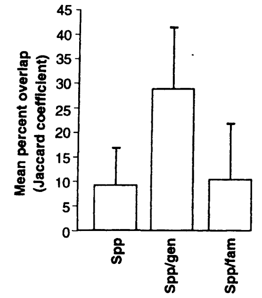

Fig. 2. The degree of spatial overlap (mean ± SD of Jaccard coefficient) among species-based complementary sets across higher taxonomic groupings (that is, species-based surrogacy) and overlap between the species-based priority conservation sets and sets generated by means of genus and family level data (that is, higher taxon surrogacy).

also support findings from a recent study that adopted a different approach and was conducted at a very different scale, yet also concluded that the prospects for indicator taxa are poor (*28*). Furthermore, conservation areas identified by means of traditional prioritization criteria [richness hotspots and coldspots and areas containing rare taxa (*21*)] are unlikely to be useful surrogates for representative complementary conservation networks. This lack of coincidence between taxa, hierarchical levels, and traditional criteria for priority conservation areas implies that all available species-based information should be incorporated into regional conservation assessments (*6*). Moreover, these results underscore the value of sound species-related distribution data for conservation planning and emphasize the necessity for survey research in conservation biology (*29*).

REFERENCES AND NOTES

1. P. B. Landres, J. Verner, J. W. Thomas, *Conserv. Biol.* **2**, 316 (1988).
2. R. F. Noss, *ibid.* **4**, 355 (1990).
3. J. Curnutt, J. Lockwood, H.-K. Luh, P. Nott, G. Russel, *Nature* **367**, 326 (1994).
4. D. L. Pearson, *Philos. Trans. R. Soc. London Ser. B* **345**, 75 (1994).
5. P. H. Williams and C. J. Humphries, in *Biodiversity*, K. J. Gaston, Ed. (Blackwell, Oxford, 1996), pp. 54–76.
6. K. J. Gaston, *Progr. Phys. Geogr.* **20**, 105 (1996).
7. ______, in (*5*), pp. 77–113.
8. ______ and P. H. Williams, in (*5*), pp. 202–229.
9. J. M. Scott *et al.*, *Wildl. Monogr.* **123**, 41 (1993).
10. R. L. Pressey, C. J. Humphries, C. R. Margules, R. I. Vane-Wright, P. H. Williams, *Trends Ecol. Evol.* **8**, 124 (1993).
11. C. R. Margules, I. D. Cresswell, A. O. Nicholls, in *Systematics and Conservation Evaluation*, P. L. Forey, C. J. Humphries, R. I. Vane-Wright, Eds. (Clarendon, Oxford, 1994), pp. 327–350.
12. A. O. Nicholls and C. R. Margules, *Biol. Conserv.* **64**, 165 (1993).
13. D. P. Faith and P. A. Walker, *Biodiv. Conserv.* **5**, 399 (1996).
14. J. R. Prendergast, R. M. Quinn, J. H. Lawton, B. C. Eversham, D. W. Gibbons, *Nature* **365**, 335 (1993).
15. A. T. Lombard, *S. Afr. J. Zool.* **130**, 145 (1995).
16. A. P. Dobson, J. P. Rodriguez, W. M. Roberts, D. S. Wilcove, *Science* **275**, 550 (1997).
17. J. R. Prendergast and B. C. Eversham, *Ecography* **20**, 210 (1997).
18. C. H. Scholtz and E. Holm, *Insects of Southern Africa* (Butterworth, Durban, South Africa, 1995).
19. C. Muller, S. Freitag, C. H. Scholtz, A. S. van Jaarsveld, *Afr. Entomol.* **5**, 261 (1997).
20. K. J. Gaston, *Oikos* **61**, 434 (1991).
21. International Council for Bird Preservation (ICBP), *Putting Biodiversity on the Map: Priority Areas for Global Conservation* (Birdlife International, Cambridge, UK, 1992); World Conservation Union (IUCN), *Centres of Plant Diversity: A Guide and Strategy for Their Conservation* (IUCN, Richmond, VA, 1987).
22. A. G. Rebelo, *Strelitzia* **1**, 231 (1994).
23. K. J. Gaston, *Funct. Ecol.* **6**, 243 (1992).
24. A detailed list providing the degree of overlap between different taxa for complementary sets, richness hotspots, coldspots, and rare taxa is available at www.sciencemag.org/feature/data/975464.sh/.
25. J. A. Harrison *et al.*, Eds., *The Atlas of Southern African Birds* (Birdlife South Africa, Johannesburg, 1997); R. M. Cowling and C. Hilton-Taylor, *Strelitzia* **1**, 31 (1994); A. S. van Jaarsveld and S. L. Chown, *S. Afr. J. Sci.* **92**, 459 (1996).
26. C. H. Scholtz and S. L. Chown, *S. Afr. J. Sci.* **91**, 124 (1995).
27. P. H. Williams and K. J. Gaston, *Biol. Conserv.* **67**, 211 (1994).
28. J. H. Lawton *et al.*, *Nature* **391**, 72 (1998).
29. Y. Haila and C. R. Margules, *Ecography* **19**, 323 (1996).

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APPENDIX 2

The use of vegetation types as surrogates for the conservation of five South African insect taxa*

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INTRODUCTION

Although attempts to identify priority sites for conserving biodiversity are hindered by the lack of sound data (Margules & Austin 1991; Lombard 1995; Balmford *et al.* 1996; Freitag *et al.* 1997), pressures arising from land transformation rates demand that existing biodiversity data be used as effectively as possible to make conservation decisions (Davis *et al.* 1990). This is particularly important for insect conservation strategies, because their high species' richness by its very nature virtually precludes any other conservation options (Samways 1994; Scholtz & Chown 1995). However, existing data may embody substantial flaws associated with collector bias, low collection effort and taxonomic impediments (Samways 1994; Siegfried & Brooke 1994; Drinkrow & Cherry 1995; Lombard 1995; Freitag *et al.* 1998)

One way in which to address this problem is to conduct reserve selection using surrogate measures for biodiversity (Vane-Wright *et al.* 1994; Andersen, 1995; Wessels *et al.* 1999). Information on the distribution of surrogates is potentially easier and cheaper to acquire than species distribution data (Pressey & Logan 1994; Williams & Humphries 1994) and is usually available at a more consistent, although generalised, level of detail (Pressey 1990; Belbin, 1993; Wright *et al.* 1993; Williams & Humphries 1994; Andersen, 1995; Wessels *et al.* 1999). Nonetheless, identifying the appropriate surrogate is often problematic (Vane-Wright *et al.* 1994). Environmental surrogates such as climatic attributes, edaphic variables, landscapes, vegetation classes, land systems, landscape ecosystems (Belbin 1993), physico-chemical variables (such as energy flux - Currie & Paquin (1987), Currie (1991) and Turner *et al.* (1988)), environmental groups and environmental domains have all been investigated as possible surrogates (Wessels *et al.* 1999). The same is true of species richness or endemism patterns across taxa (Thirgood & Heath 1994; Williams & Humphries 1994; Dobson *et al.* 1997; Howard *et al.* 1998; Van Jaarsveld *et al.* 1998a), richness at higher taxonomic levels (Pearson & Cassola 1992; Williams & Gaston 1994; Andersen 1995), and indicator taxa (Chapin *et al.* 1992; Kellert 1993; New 1993; Heywood 1994; Hunter 1996). Unfortunately, conclusive support for the use of hotspots of species' richness, endemism or higher taxon richness has not been forthcoming and may hold little promise at a scale relevant to practical conservation planning (Flather *et al.* 1997), performing better at broader (e.g. global) scales of analysis (Reid 1998). Species-rich areas for indicator groups are only likely to represent other organisms if the members of the group occur over a wide habitat range (Faith & Walker 1996). In addition, Prendergast *et al.* (1993) and Van Jaarsveld *et al.* (1998a) noted that high diversity hotspots of certain taxa did not represent rare species to a great extent and Dobson *et al.* (1997) found little coincidence for hotspots of endangered taxa in the United States.

On the other hand, vegetation types (see Low & Rebelo 1996 for a definition), have been regarded as promising surrogates at finer scales by Purdie *et al.* (1986), Woinarski *et al.* (1988), Davis *et al.* (1990), Woinarski & Braithwaite (1993), Oliver & Beattie (1994), Kiester *et al.* (1996) and Rushworth (1997). This is because vegetation is an easily identifiable and important landscape feature representing the integration of many less visible ecological and physical factors, such as climate, soil type, elevation and aspect (Davis *et al.* 1990; Scott *et al.* 1992). It is also composed of the ecosystem's primary producers and serves as a habitat for animal communities (Scott *et al.* 1992).

In the present study, the efficiency of vegetation types (identified for South Africa, Lesotho and Swaziland - Low & Rebelo (1996)) as a surrogate for insect conservation planning in South Africa, Lesotho and Swaziland was evaluated. The insect groups used were the buprestid beetles (569 species), scarab beetles (482 species) (Coleoptera: Buprestidae, Scarabaeidae respectively), butterflies (Lepidoptera) (614 species), antlions (Neuroptera: Myrmeleontidae) (43 species) and termites (Isoptera) (28 species). These taxa were chosen because they have previously been examined with regard to reserve selection using a species-based approach (Hull *et al.* 1998; Freitag & Mansell 1997; Muller *et al.* 1997) and because they are representative of a variety of insect taxa with different habitat requirements. (It should be noted here that the numbers of species used did not consist of all the species comprising the taxa occurring in the study area, but consisted only of those that were documented for inclusion in the respective databases at the time.)

The evaluation of vegetation types as surrogates for these taxa was accomplished by generating representative networks for the protection of target areas of vegetation types in South Africa, Lesotho and Swaziland, and exploring the degree to which these insect taxa were represented as a consequence. In addition, the distributional characteristics of the species that are not represented by the broad-scale vegetation types approach that could explain the reasons for this omission, was evaluated.

MATERIAL & METHODS

Species – vegetation type affinities.

Species' point distributions of all taxa, besides butterflies, were projected onto a vegetation map of the Low & Rebelo (1996) vegetation types in order to determine the number of vegetation types and the most common vegetation types occupied by each taxon (see Woinarski & Braithwaite 1993), using ARCVIEW®, (Version 3.0a, ESRI Inc., Redlands, California, USA). This latter procedure was not possible for the butterflies, as these data were not recorded as point localities, but as grid cell (15 ' X 15 ') specific data.

The vegetation type classification used is that of Low & Rebelo (1996), in which the study area was divided into 68 distinct vegetation types. Cropland, dams, urban areas and other land transformations have been ignored (Low & Rebelo 1996). This classification therefore differs from the more frequently used Acocks Veld Types (Acocks 1988), which evaluates vegetation types from a purely agricultural perspective (Low & Rebelo 1996).

Representation of target areas of vegetation types.

The proportion of each vegetation type occupying every quarter degree grid cell (15 ' X 15 ') in South Africa, Lesotho and Swaziland was obtained by projecting a map of the 2013 grid cells constituting the study area onto the Low & Rebelo (1996) vegetation map in ARC/INFO® GIS, Version 7.1.2 (ESRI, Inc., Redlands, California, USA). A modified version of the Percentage Area Selection algorithm of Wessels *et al.* (1999) (hereafter referred to as PAR_2) was run on the resultant table of vegetation type areas per grid cell, to determine the number of grid cells required to represent a specified target area of each vegetation type. These target areas were 5, 10, 15, 20, 25, 30, 40 and 50 % of the total areas of each vegetation type.

The rules for the original algorithm (referred to hereafter as PAR), as well as for PAR_2 are provided in Appendices A and B, respectively. The major difference between these algorithms lies in the initiation procedure. The PAR algorithm starts at the vegetation type with the smallest total area (i.e. the rarest vegetation type), representing as much of it as possible by choosing the grid cell with the largest area of that type, and then by choosing other grid cells containing that vegetation type until it is fully represented. The areas of any other vegetation types occurring in the grid cells are subtracted from the target area required for each of these vegetation types. The next rarest vegetation type (in terms of area) is the next to be fully represented. This process is repeated until all types have reached the target representation level. Although this algorithm is land-use efficient, it provides an inflexible result with the same outcome at each run. For this reason, it is necessary to use an algorithm that will perform a specified number of iterations at each representation level in order to generate alternative networks of grid cells for each target level of vegetation type representation.

The PAR_2 algorithm was used for this purpose, which requires a randomly arranged list of vegetation types and a pre-specified random initiation grid cell. All of the vegetation types occurring in that grid cell are represented fully to their required target levels in the same manner as above. The next vegetation type to be fully represented is the top-most occurring type in the randomly arranged list of types.

Twenty iterations of the PAR_2 algorithm were run at each specified target level. The same randomly arranged vegetation type reference file and initial random grid cell was used for each target level of area representation, but different files were used for each iteration.

Species' overlap with the chosen grid cells.

The number of the species in each taxon captured by the grid cells selected by the PAR_2 algorithm were calculated. The number of species having at least one record, as well as those having at least three records were assessed. The latter scenario was modified for species with only two or one record(s). They were included in the category of having three representations if the species with two records were fully represented, and the species with one record were fully represented. The percentage species represented at least once and the percentage represented at least three times for each level of representation and for each database were compared using the Mann-Whitney U test at the 95 % significance level. The requirement of independence of data for this test may not have been satisfied, given that the two representation levels used the same data, and the degrees of freedom of the test are likely to be over-estimated. For this reason, the statistical significance of the two percentages that were numerically closest to one another was noted. If the difference was highly significant ($p < 0.01$), it was predicted that any other comparisons were also significantly different.

Characteristics (in terms of species' representation in databases) shared by species not represented by vegetation types.

The number of grid cells in which species occurred was determined for each taxon (i.e. number of records per species at the grid cell scale), and these numbers were ranked in descending order and split into quartiles (25 % rarest, 25 % next most scarce, 25 % next most abundant, and 25 % most common species). The number of species within each quartile range that were represented at least once in grid cells chosen by representing vegetation types at each target level of area representation (5 - 50 %), using the PAR algorithm, was assessed. This was done to determine how the representation of species by a surrogate is affected by the species' abundance within the database (see Scott *et al.* 1992). The PAR algorithm was used in this case as no iterations were required.

Furthermore, the approximate percentage of species out of the total number in South Africa, median value of number of records per species, number of species with five or less records, and percentage of grids surveyed out of the total number in the study area were summarised for each database. These are all linked to the phenomenon of rare species, survey bias and efficiency.

Extra grids required to fully represent "database rare" taxa.

The Nicholls & Margules (1993) rarity based algorithm was employed to demonstrate the number of extra grids required to represent the species out of the 25 % "database rarest" species that are not represented by vegetation type surrogacy, or occur at least once in a protected area. This algorithm represents species at least once, starting at the rarest species, and proceeding until all species are represented.

A protected areas map of South Africa which included national reserves and some of the larger private reserves was obtained from the Council for Scientific Industrial Research (CSIR), Pretoria, South Africa. The point localities of all species were projected onto this map, in order to determine the number of species that have at least one record in a protected area. As the butterfly database was not mapped to point localities, no assumptions about the protected species in this database was made. The Low & Rebelo (1996) vegetation map and a map of the grid cells were then projected onto the protected areas map to determine the percentage area of each vegetation type that was protected, per grid cell (Fearnside & Ferraz 1995).

The PAR algorithm was used to select 15 % of each vegetation type, after subtracting the areas of those types that were already protected. The number of additional grid cells required to represent all vegetation types to the 15 % target level was thus determined. The 15 % minimum was chosen as the frequently cited goal for protecting biodiversity is between 10 and 12 % (IUCN 1992), and in Australia, a proposal has been put forward to raise this level to 15 % (Pressey & Logan 1997). The number of species occurring at least once in the network obtained was calculated (excluding those species already present in reserves). Thereafter, the Nicholls & Margules (1993) rarity species selection algorithm was run only for those species for each taxon that were not represented in protected areas or in grids selected by the PAR algorithm and fell into the 25 % database rarest species category.

RESULTS

Species – vegetation type affinities.

Recorded antlion distributions overlapped with 54 out of the 68 vegetation types, buprestids with 66, scarabs with 67 and termites with 65.

Representation of target levels of vegetation types.

The number of grids chosen by the PAR_2 algorithm showed an increase as the degree of representation increased (Table 1). From the table it can be seen that the standard deviations between the number of grid cells chosen increased as the representation increased.

Table 1. Mean number of grids, and standard deviations from mean, selected by the PAR_2 algorithm at each level of representation of vegetaton types.

Level of representation (%)	**Average number of grids selected by algorithm**	**Standard deviation from mean of grids selected**
5	114.4	2.3
10	209.1	2.5
15	306.8	2.8
20	402.4	2.5
25	500.1	3.6
30	600.2	4.2
40	800.0	6.1
50	1003.5	6.6

Species' overlap with the chosen grid cells.

As the level of protection of vegetation types increased, more species were represented, both a minimum of once, and thrice. The percentage species represented varied between 20.8 % (of buprestid species at the 5 % vegetation representation level) and 91.9 % (of the butterfly species at the 50 % level) for a minimum of one representation per species (Fig. 1b,c). The results for at least 3 representations of each species were lower than those for one representation (Fig, 1a-e). Percentage representation of species varied between 2.79 (of buprestid species at the 5 % vegetation representation level) and 69.5 % (of the butterfly species at the 50 % level) (Fig. 1b,c). Significantly higher numbers of species were represented at least once, compared to at least three times at the 95 % significance level, for all taxa. The lowest level of significance was for the termites at 50 % representation ($z = -2.978$; $p = 0.003$). In general, the percentage representation of species at least once compared to at least three times was the closest numerically for the termites than for any other taxon (Fig. 1a-e).

Characteristics (in terms of species' representation in databases) shared by species not represented by vegetation types.

There was a clear decrease in the number of species protected within each quartile range towards the rarest of these ranges. This was evident for all taxa, and thus the results for all species were combined and represented in Fig. 2 .

The Buprestidae, although being relatively well collected and surveyed, have few records per species and large numbers of grids containing relatively rare species (Fig. 3). On the other hand, the termites are poorly represented in the database in terms of species' numbers, but those species that are present are relatively well surveyed, and there are few rare species (Fig. 3).

Extra grids required to fully represent "database rare" taxa.

Relatively high percentages of species occurred in already protected areas: 53.3 % of antlions, 42.7 % of buprestids, 68.5 % of scarabs and 85.7 % of termites (Table 2). The inclusion of these mandatory sites into the PAR algorithm run at a representation level of 15 % resulted in 242 additional grid cells being selected.

Addition of the percentage of species represented in protected areas to the percentage species represented by the grid cells selected by the PAR algorithm run with these mandatory sites always resulted in over 50 % species represented (Table 2). The number of grid cells selected by the Nicholls & Margules (1993) algorithm to represent those 25 % "database" rarest species not found in protected areas or by overlap with grid cells chosen by the PAR algorithm amounted to 162 grid cells (after accounting for overlap of grid cells chosen for different taxa) (Fig. 4). Table 3 compares this to the numbers required in other studies for species-based algorithms.

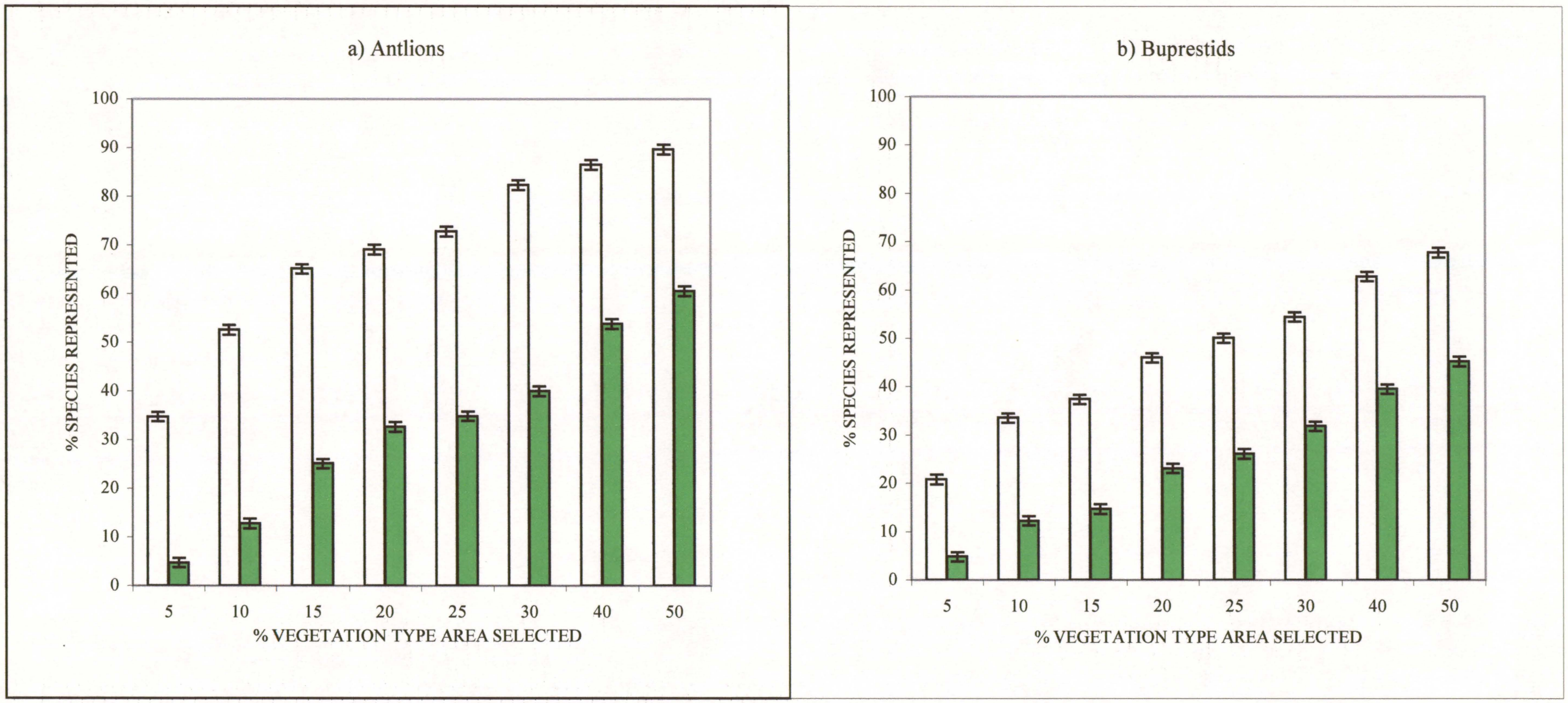
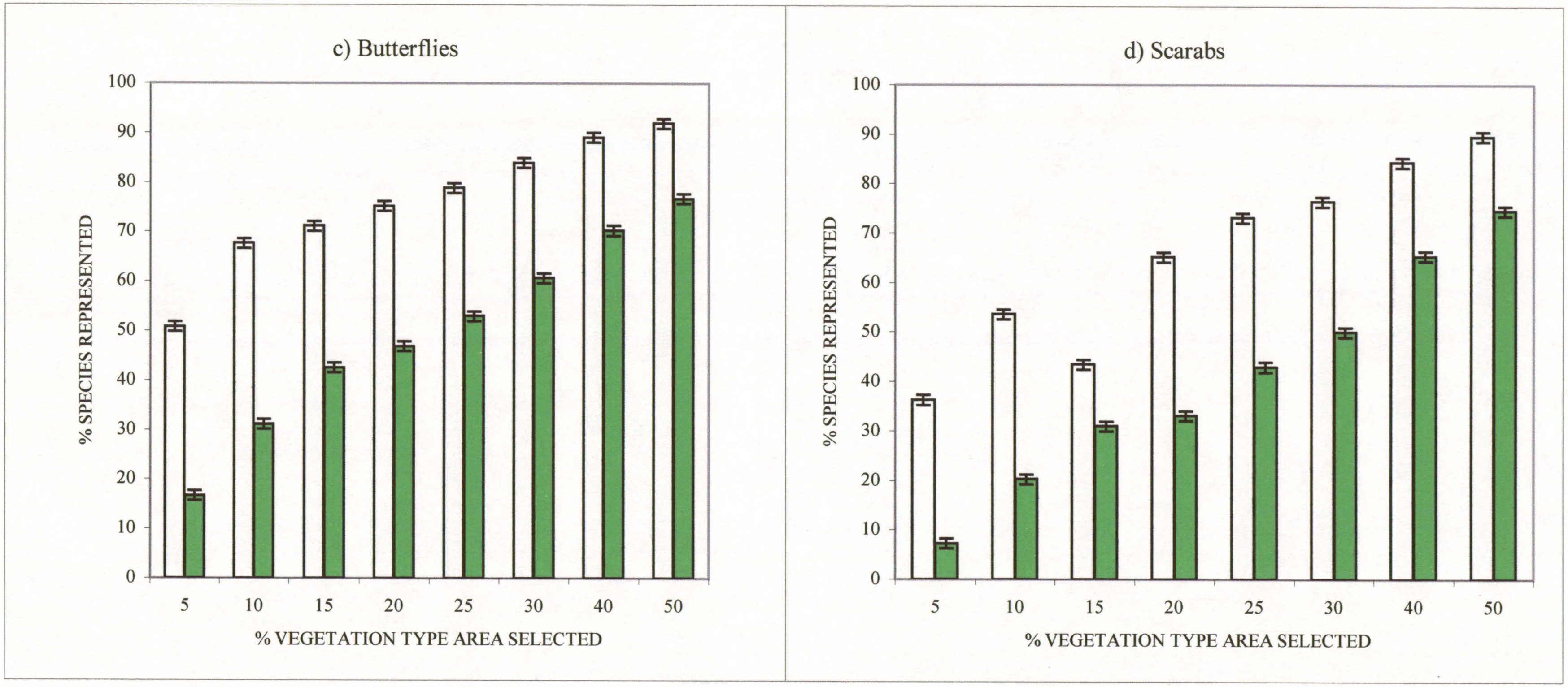
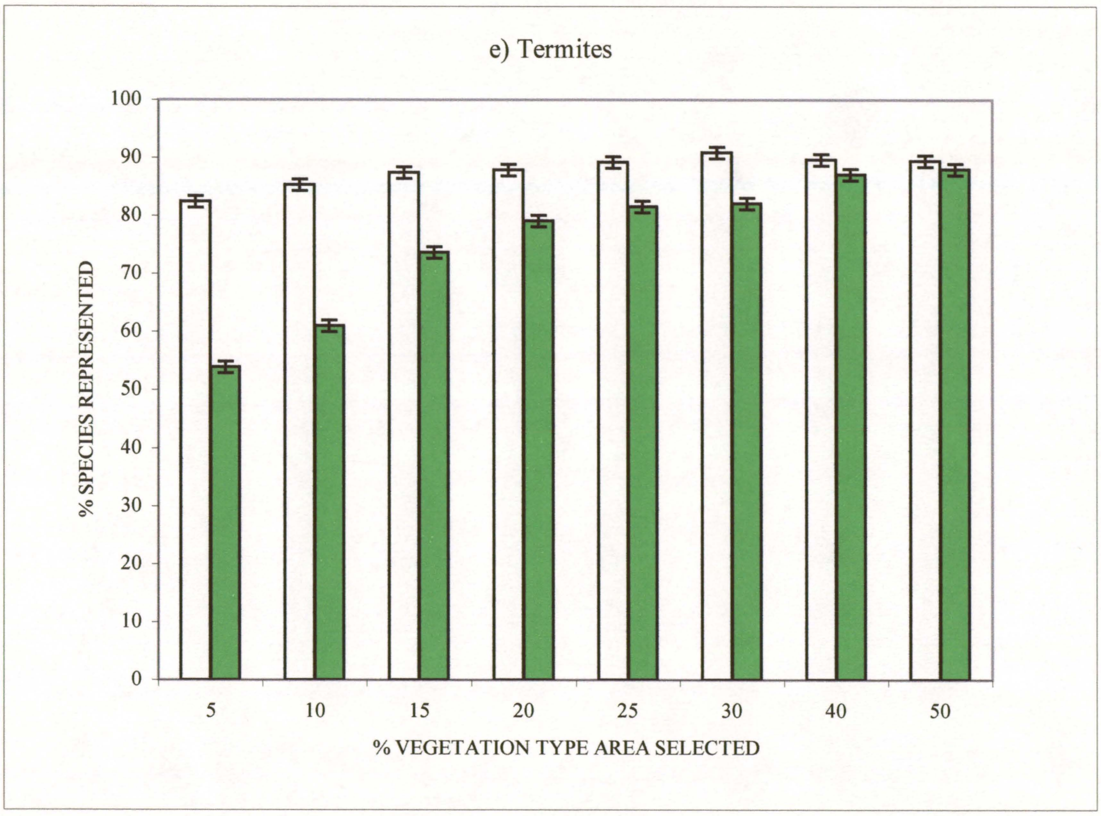


Fig. 1. Graphs depicting the average percentage of species of each taxon present in grids selected by the twenty iterations of the PAR2 algorithm at each level of area representation for at least one representation (in white) and for at least three representations (in green). Error bars indicate the standard deviations of the average percentage species selected at each level of representation (graphs of the remaining taxa are depicted on the following two pages).



c) Butterflies

d) Scarabs


e) Termites
% SPECIES REPRESENTED
100
90
80
70
60
50
40
30
20
10
0
5
10
15
20
25
30
40
50
% VEGETATION TYPE AREA SELECTED

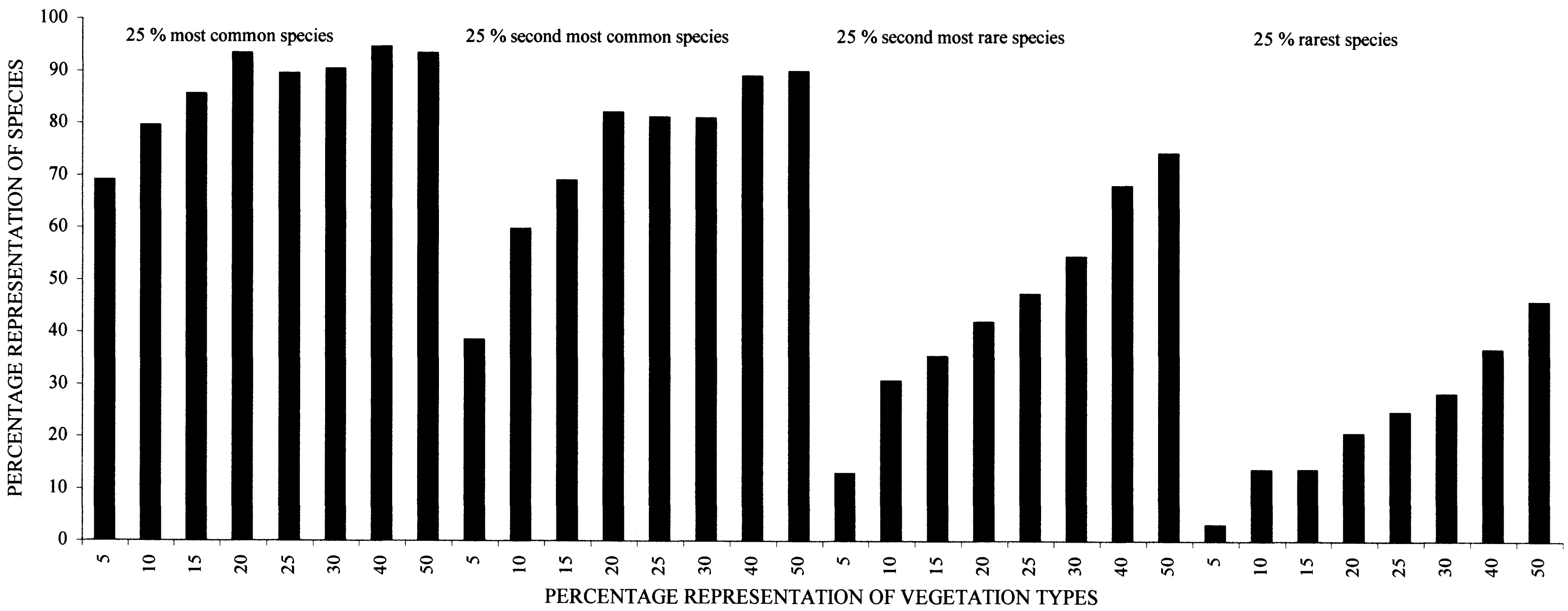


Fig. 2. Graph showing the quartile distribution of abundances of species in the database, represented at least once at each level of area representation by the PAR algorithm (Wessels *et al.* 1999). Note that as the rarest quartile is approached, fewer species are represented.

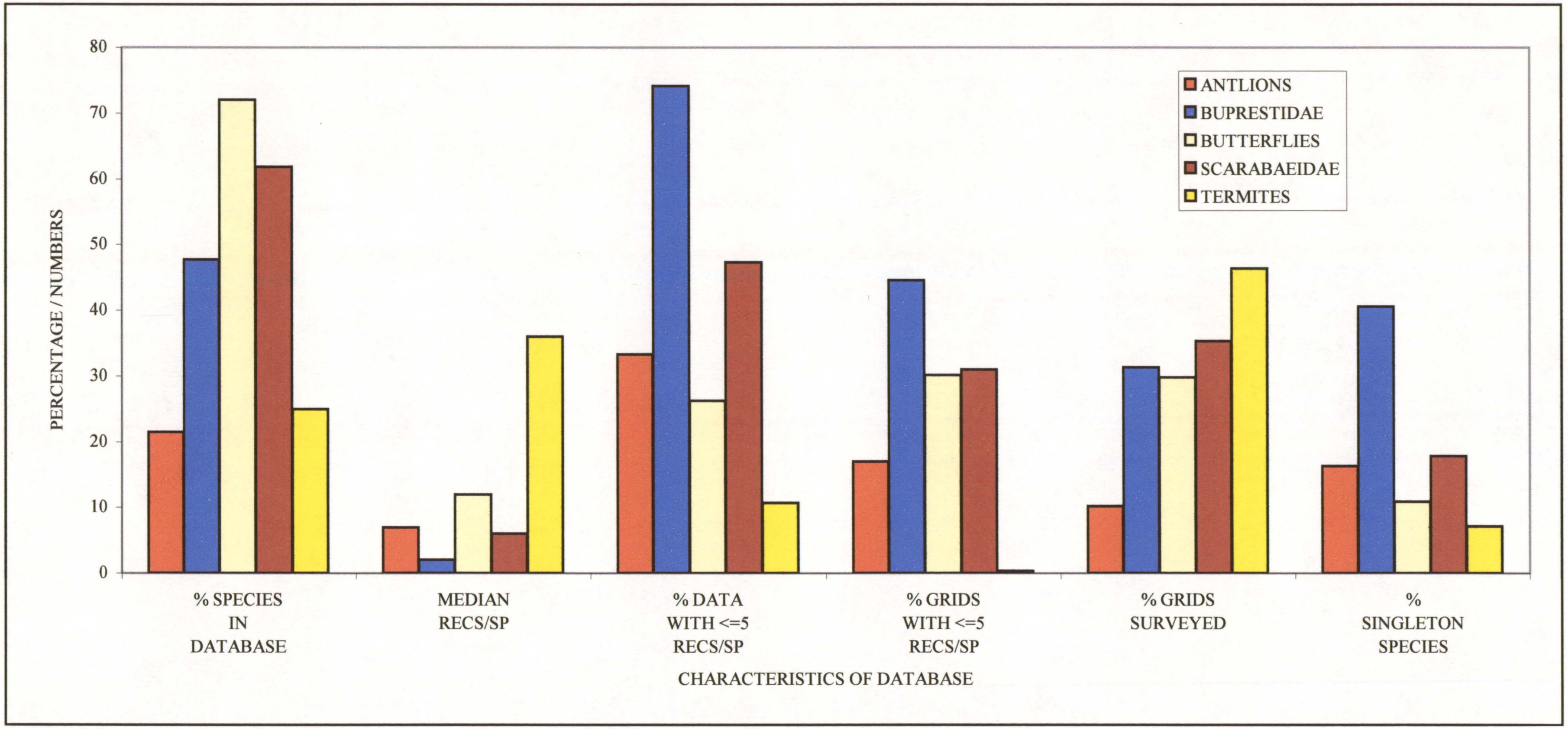


Fig. 3. Graph showing certain characteristics for each database. Comparing the Buprestidae database to the termite one, it can be seen that there are many species represented, with a small median record number per species, many species with few records and a small number of grid cells surveyed in the former. The opposite holds true for the termite database.

Table 2. Species represented at the 15 % area representation level using the PAR algorithm (Wessels *et al.* 1999), including already protected areas as mandatory sites.

Taxon	**% species in protected areas**	**Total % species represented (including those already in protected areas**
Antlions	53.5	58.1
Buprestidae	42.7	51.1
Butterflies	N/A	79.6*
Scarabaeidae	68.5	79.7
Termites	85.7	89.3

* Only those species occurring in grid cells chosen to represent vegetation types to 15 %

Table 3. Number of grid cells required to represent all species of each taxon, as noted in other studies (Cells_before), compared to the number of cells required to represent the species in each database out of the 25 % rarest species that have not been represented in already protected areas or by overlap with cells chosen by the PAR algorithm run at a protection level of 15 % (Cells_after).

Taxon	**Cells_before**	**Cells_after**
Antlions	14 (Freitag & Mansell 1997)	6
Buprestidae	133 (Hull *et al.* 1998)	62
Butterflies	84 (unpublished data)	66
Scarabaeidae	85 (unpublished data)	48
Termites	6 (Muller *et al.* 1997)	0

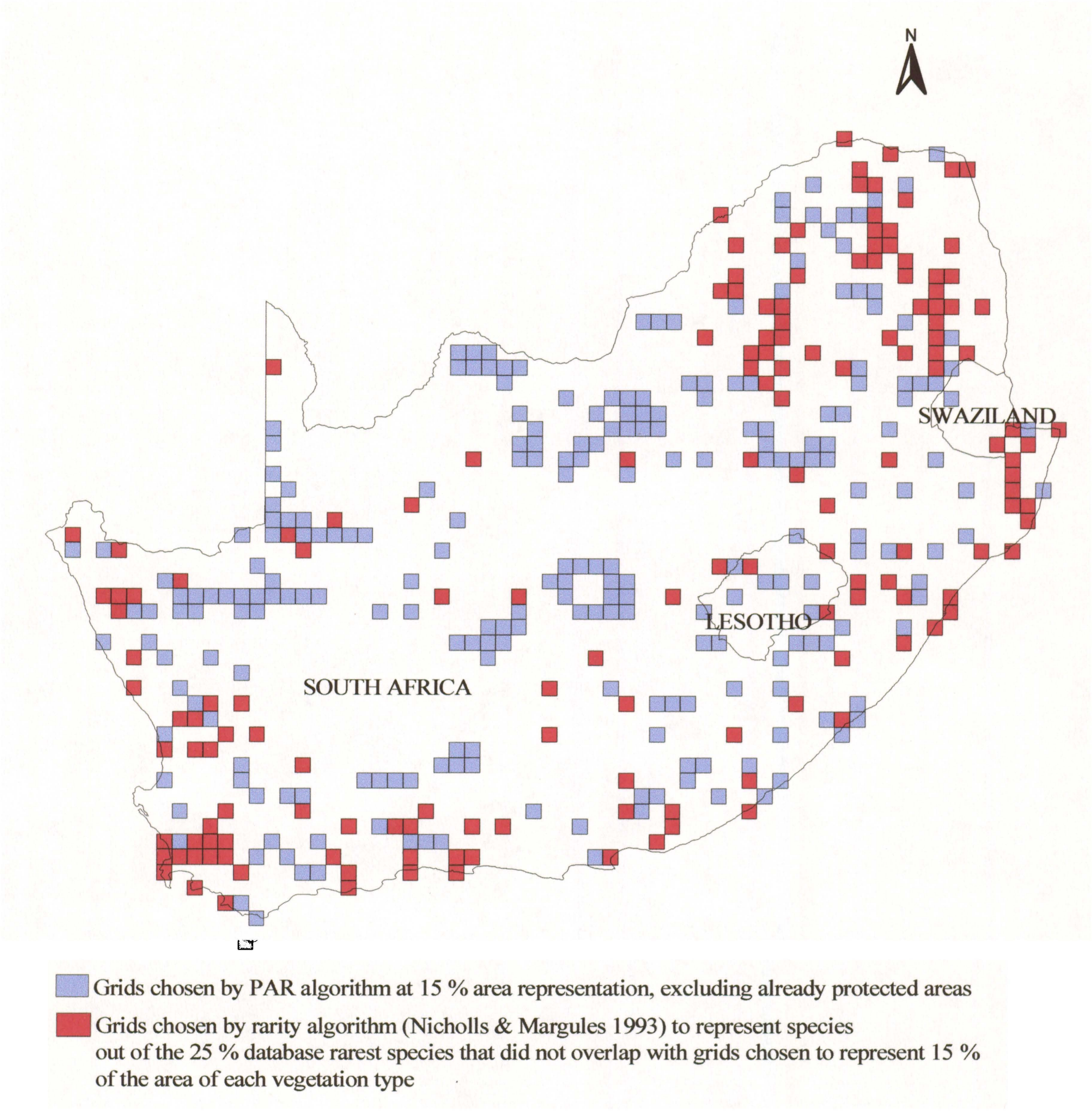


Fig. 4. Map of the sudy area showing the number of grid cells required to represent 15 % of the area of each vegetation type, after accounting for the areas already represented in protected areas. Also represented are the grid cells required to represent the 25 % rarest insect taxa at least once that did not have at least one record occurring in the above selected grid cells.

DISCUSSION

The top 5 % richest vegetation types for buprestids were Mixed Bushveld in the Northern and Mpumalanga Provinces and Mountain Fynbos and Upland Succulent Karoo in the Southern and Northern Cape provinces. For Scarabaeidae the top 5 % richest vegetation types included Coastal Bushveld/Grassland in northern Kwa-Zulu Natal, Lowveld Bushveld in Mpumalanga and NE Mountain Grassland in the north eastern highlands of Mpumalanga. In the case of the termites, Coastal Bushveld/Grassland was the richest, followed by Sweet Bushveld and Mopane Bushveld in the Northern Province. Antlion top 5 % richest vegetation types were Mixed Bushveld, Mopane Bushveld and shrubby Kalahari Dune Bushveld, occurring largely in the Kalahari Gemsbok National Park.

As expected, all databases exhibited an increase in percentage species represented with an increase in the areas of each vegetation type selected by the PAR_2 algorithm. The reason for this was simply that as more grid cells were selected, more species were likely to be targeted. Also to be expected was the fact that the standard deviations from the mean percentage of species of each taxon that were represented showed a decrease, noted in Figs 1a-e, as the level of area representation increased. This was probably because the choices of grid cells available for selection decreased as the target for representation increased, resulting in the same grid cells being chosen in each case, and thus the same species.

The marked differences between the numbers of species represented (either at least once or more than three times) could be related to the number of database rare species in each database (Fig. 2). (In this case "rare species" signifies the 25 % rarest species within each database).

The termite database consists of only a small representative group of the termites of South Africa (approximately 25 %), but the species that are present are known to be well represented, evidenced by the large number of grids surveyed, and by the presence of many records per species. There are consequently, few rare species, and these rare species occur in relatively few grid cells, meaning that few extra grids would be required to represent them (Fig. 3).

On the other spectrum of the scale, the buprestid database has many species, which have in general been poorly sampled, with few records per species (although a comparatively large proportion of grids were sampled), a very high proportion of rare species, and a large proportion of the database consisting of grid cells containing rare species (Fig. 3). It was noted in Freitag & Van Jaarsveld (1998) in their sensitivity analysis that the more records a species has, the fewer grid cells are needed to fully represent all species.

The presence of large numbers of rare species thus pose a problem, as there are a limited number of sites in which to represent them. How many of these species are really rare, and genuinely have localised distributions, or are range-restricted? The only manner in which this can be ascertained is through further surveys, and to save money and time, perhaps to only concentrate on those species that are database rare. The present situation demands an extra 162 grid cells to conserve the 25 % database rarest species not yet represented by vegetation type conservation or already protected areas (Fig. 4). If all of these areas were proclaimed as reserves, or at least areas that should be monitored for conservation purposes, even more money may be wasted compared to the cost of further surveys, and a situation may ultimately develop that is little different than at present - with many *ad hoc* reserves that serve little purpose.

Although there are still many problems to be overcome in the search for a good surrogate, this paper provides the most promising result thus far, and certainly better than results obtained previously for attempts at finding surrogates for the representation of these taxa. Van Jaarsveld *et al.* (1998a) obtained from 0 - 20.7 % overlap of complementary sites and higher taxon overlap from 0 - 37.6 % for these taxa with one another and with plants in the Transvaal region of South Africa.

Furthermore, the percentage species covered by representing from 5 - 15 % of vegetation type area was usually much higher than that added by conserving percentages greater than this. This means that around 10 - 15 % vegetation type conservation provides an optimal solution, and there may be reason to consider the guidelines set down by the IUCN (1992). In fact, an average of 60.9 % of all species were represented at least once at the 15 % level, and 37.4 % three or more times. The prospects for vegetation types acting as surrogates for the representation of these species is therefore good, and additional surveying is crucial only for species which have small amounts of data.

The decrease in percentages of species represented at least thrice may prove to be worrisome. The prospect for conserving as many records as possible of a species seems to be significantly lower than for only one representation, although the better the collection efficiency, the closer the numbers of species represented once, and those represented three or more times becomes (Fig. 1e), until the numbers are not significantly different. Additional surveys should, therefore, improve the results further.

REFERENCES

Acocks, J. P. H. (1988). Veld types of South Africa. *Mem. Bot. Soc. S. Afr.* **57**: 1-146.

Andersen, A. (1995). Measuring more of biodiversity: Genus richness as a surrogate for species richness in Australian ant faunas. *Biol. Conserv.* **73**: 39-43.

Balmford, A., Green, M. J. B. & Murray, M. G. (1996). Using higher-taxon richness as a surrogate for species richness: I. Regional tests. *Proc. R. Soc. Lond. B.* **263**: 1267-1274.

Belbin, L. (1993). Environmental representativeness: Regional partitioning and reserve selection. *Biol. Conserv.* **66**: 223-230.

Chapin III, F. S., Schulze, E.-D. & Mooney, H. A. (1992). Biodiversity and ecosystem processes. *Trends Ecol. Evol.* **7**: 107-108.

Currie, D. J. (1991). Energy and large-scale patterns of animal and plant-species richness. *Am. Nat.* **137**: 27-49.

Currie, D. J. & Paquin, V. (1987). Large-scale biogeographical patterns of species richness of trees. *Nature* (Lond.) **329**: 326-327.

Davis, F. W., Stoms, D. M., Estes, J. E., Scepan, J. & Scott, J. M. (1990). An information systems approach to the preservation of biological diversity. *Int. J. G.I.S.* **4**: 55-78.

Dobson, A. P., Rodriguez, J. P., Roberts, W. M. & Wilcove, D. S. (1997). Geographic distribution of endangered species in the United States. *Science* (Wash.) **275**: 550-553.

Drinkrow, D. R. & Cherry, M. I. (1995). Anuran distribution, diversity and conservation in South Africa, Lesotho and Swaziland. *S. Afr. J. Zool.* **30**: 82-89.

Faith, D. P. & Walker, P. A. (1996). How do indicator groups provide information about the relative biodiversity of different sets of areas?: On the hotspots, complementarity and pattern-based approaches. *Biodiversity Letters* **3**: 18-25.

Fearnside, P. M. & Ferraz, J. (1995). A conservation Gap analysis of Brazil's Amazonian vegetation. *Conserv. Biol.* **9**: 1134-1147.

Flather, C. H., Wilson, K. R., Dean, D. J. & McComb, W. C. (1997). Identifying gaps in conservation networks: Of indicators and uncertainty in geographic-based analyses. *Ecol. Appl.* **7**: 531-542.

Freitag, S. & Mansell, M. W. (1997). The distribution and protection of selected antlion species (Neuroptera: Myrmeleontidae) in South Africa. *Afr. Entomol.* **5**: 205-216.

Freitag, S. & Van Jaarsveld, A. S. (1998). Sensitivity of selection procedures for priority conservation area to survey extent, survey intensity and taxonomic knowledge. *Proc. R. Soc. Lond. B.* **265**: 1-8.

Freitag, S., Van Jaarsveld, A. S. & Biggs, H. C. (1997). Ranking priority biodiversity areas: An iterative conservation value-based approach. *Biol. Conserv.* **82**: 263-272.

Freitag, S., Hobson, C., Biggs, C. & Van Jaarsveld, A. S. (1998). Testing for potential survey bias: The effect of roads, urban areas and nature reserves on a southern African mammal dataset. *Anim. Conserv.* **98**: 119 - 127.

Heywood, V. H. (1994). The measurement of biodiversity and the politics of implementation. In *Systematics and Conservation Evaluation.* 15-22. Forey, P. I., Humphries, C. J. & Vane-Wright, R. I. (Eds). Oxford: Clarendon Press.

Howard, P. C., Viskanic, P., Davenport, T. R. B., Kigenyi, F. W., Baltzer, M., Dickinson, C. J., Lwanga, J. S., Matthews, R. A. & Balmford, A. (1998). Complementarity and the use of indicator groups in reserve selection in Uganda. *Nature* (Lond.) **394**: 472-475.

Hull, H. E., Freitag, S., Chown, S. L. & Bellamy, C. L. (1988). Identification and evaluation of priority conservation areas for Buprestidae (Coleoptera) in South Africa, Lesotho, Swaziland and Namibia. *Afr. Entomol.* **6**: 265-274.

Hunter, M. L. (1996). *Fundamentals of Conservation Biology.* Cambridge, Massachusetts: Blackwell Scientific Publications.

Kellert, S. R. (1993). Values and perceptions of invertebrates. *Conserv. Biol.* **7**: 845-855.

Kiester, A. R., Scott, J. M., Csuti, B., Noss, R. F., Butterfield, B., Sahr, K. & White, D. (1996). Conservation prioritisation using GAP data. *Conserv. Biol.* **10**: 1332-1342.

Lombard, A. T. (1995). The problems with multi-species conservation: Do hotspots, ideal reserves and existing reserves coincide? *S. Afr. J. Zool.* **30**: 145-160.

Low, A. B. & Rebelo, A. G. (1996). *Vegetation of South Africa, Lesotho, and Swaziland.* Pretoria: Dept. Environmental Affairs and Tourism.

Margules, C. R. & Austin, M. P. (1991). Nature conservation: Cost effective survey and data analysis. Australia: CSIRO.

Muller, C., Freitag, S., Scholtz, C. H. & Van Jaarsveld, A. S. (1997). An assessment of termite distributions, endemism, species richness and priority conservation areas in South Africa. *Afr. Entomol.* **5**: 261-271.

New, T. R. (1993). Angels on a pin: Dimensions of the crisis in invertebrate conservation. *Am. Zool.* **33**: 623-630.

Nicholls, A. O. & Margules, C. R. (1993). An upgraded reserve selection algorithm. *Biol. Conserv.* **64**: 165-169.

Oliver, I. & Beattie, A. J. (1994). A possible method for the rapid assessment of biodiversity. In *Systematics and Conservation Evaluation.* 133-136. Forey, P. I., Humphries, C. J. & Vane-Wright, R. I. (Eds). Oxford: Clarendon Press.

Pearson, D. L. & Cassola, F. (1992). World-wide species richness patterns of tiger beetles (Coleoptera: Cicindelidae): Indicator taxon for biodiversity and conservation studies. *Conserv. Biol.* **6**: 376-391.

Prendergast, J. R., Quinn, R. M., Lawton, J. H., Eversham, B. C. & Gibbons, D. W. (1993). Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature* (Lond.) **365**: 335-337.

Pressey, R. L. (1990). Reserve selection in New South Wales: Where to from here? *Austr. Zool.* **26**: 70-75.

Pressey, R. L. & Logan, V. S. (1994). Level of geographical subdivision and its effects on assessments of reserve coverage: A review of regional studies. *Conserv. Biol.* **8**: 1037-1046.

Pressey, R. L. & Logan, V. S. (1997). Inside looking out: Findings of research on reserve selection relevant to off-reserve nature conservation. In *Conservation Outside Nature Reserves.* 407-418. Hale, P. & Lamb, D. (Eds). Brisbane: University of Queensland.

Purdie, R. W., Blick, R. & Bolton, M. P. (1986). Selection of a conservation reserve network in the Mulga biogeographic region of south-western Queensland, Australia. *Biol. Conserv.* **38**: 369-384.

Reid, W. V. (1998). Biodiversity hotspots. *Trends Ecol. Evol.* **13**: 275-279.

Rushworth, I. (1997). Aiming for Persistence: An Approach to Prioritising the Allocation of Conservation Resources in Northern KwaZulu-Natal. MSc Thesis, University of Cape Town, Cape Town.

Samways, M. J. (1994). *Insect Conservation Biology.* London: Chapman & Hall.

Scholtz, C. H. & Chown, S. L. (1995). Insects in southern Africa: How many species are there? *S. Afr. J. Sci.* **91**: 124-126.

Scott, J. M., Davis, F., Csuti, B., Noss, R., Butterfield, B., Groves, C., Anderson, H., Caicco, S., D'Erchia, F., Edwards, T. C., Ulliman, J. & Wright, R. G. (1992). GAP Analysis: A geographic approach to protection of biological diversity. *Wildl. Monogr.* **123**: 1-41.

Siegfried, W. R. & Brooke, R. K. (1994). Santa Rosalia's blessing: Cryptic and underrecognised species in southern Africa. *S. Afr. J. Sci.* **90**: 57 - 58.

Thirgood, S. J. & Heath, M. F. (1994). Global patterns of endemism and the conservation of biodiversity. In *Systematics and Conservation Evaluation* 207 - 227. Forey, P. I., Humphries, C. J. & Vane-Wright, R. I. (Eds). Oxford: Clarendon Press.

Turner, J. R. G., Lennon, J. J. & Lawrenson, J. A. (1988). British bird species distributions and the energy theory. *Nature* (Lond.) **335**: 539-541.

Van Jaarsveld, A. S., Freitag, S., Chown, S. L., Muller, C., Koch, S., Hull, H., Bellamy, C., Kruger, M., Endrody-Younga, S., Mansell, M. W. & Scholtz, C. H. (1998a). Biodiversity assessment and conservation strategies. *Science* (Wash.) **279**: 2106-2108.

Vane-Wright, R. I., Smith, C. R. & Kitching, J. J. (1994). Systematic assessment of taxic diversity by summation. In *Systematics and Conservation Evaluation.* 309-326. Forey, P. I., Humphries, C. J. & Vane-Wright, R.-I. (Eds). Oxford: Clarendon Press.

Wessels, K. J., Freitag, S. & Van Jaarsveld, A. S. (1999). The use of land facets as biodiversity surrogates during reserve selection at a local scale. *Biol. Conserv.* **89**: 21-38.

Williams, P. H. & Gaston, K. J. (1994). Measuring more of biodiversity: Can higher-taxon richness predict wholesale species richness? *Biol. Conserv.* **67**: 211-217.

Williams, P. H. & Humphries, C. J. (1994). Biodiversity, taxonomic relatedness, and endemism in conservation. In *Systematics and conservation evaluation.* 269-287. Forey, P. I., Humphries, C. J. & Vane-Wright, R.-I. (Eds). Oxford: Clarendon Press.

Woinarski, J. C. Z., Tidemann, S. C. & Kerin, S. (1988). Birds in a tropical mosaic: The distribution of bird species in relation to vegetation patterns. *Austr. Wildl. Res.* **15**: 171-196

Woinarski, J. C. Z. & Braithwaite, R. W. (1993). The distribution of terrestrial vertebrates and plants in relation to vegetation and habitat mapping schemes in stage III of Kakadu National Park. *Wildl. Res.* **20**: 355-370.

World Conservation Union (IUCN). (1992). *IUCN Bulletin* **43**: 10

Wright, R. G., MacCracken, J. G. & Hall, J. (1993). An ecological evaluation of proposed new conservation areas in Idaho: Evaluating proposed Idaho National parks. *Conserv. Biol.* **8**: 207-216.

Appendix A

Percentage Area Representation (PAR) algorithm (Wessels *et al.* 1999).

Written by Stefanie Freitag (1996 - 1997).

Selection rules are as follows:

1. Choose a grid cell containing an occurrence of the smallest (in terms of area) vegetation type. If more than one type is equally small, choose the one which is also "database rarest" (i.e. there are fewest polygons (records) of that type).
2. If there is a choice of grid cells to represent this type, choose the one containing the biggest area of the type required to bring the representation of the type to the required level (i.e. the site which contains either the smallest % area necessary to achieve the required representation, or the one that contributes the largest % area of that type if no one site will achieve the representation target).
3. If there is a choice, select the grid cell that is nearest in space to one that is already selected (adjacency constraint).
4. If there is still a choice, select the grid cell that also contributes the largest area of the next smallest under-represented type.
5. If there is still a choice, select the grid cell that will add the most under-represented types.
6. If there is still a choice, select the first in the list of types.

Appendix B

Percentage Area Representation Algorithm for iterative selections (PAR_2).
This algorithm was modified from the previous algorithm (Wessels *et al.* (1999), by Heath Hull (1998).
Selection rules are as follows:

1. Select a grid cell at random.
2. If there is only one vegetation type present in the grid, select further grids until the required target level is reached using the methods described for "rule 2" in Appendix A. If there is more than one vegetation type in the grid, select all vegetation types present in that grid (one at a time, but in no specific order) by adding further grids until all target levels are met, using the methods described in Appendix A (rules 2 - 6).
3. Go to the top of the file containing a list of all vegetation types (randomly arranged). Select the vegetation type to be fully represented next by choosing the type occurring on the top of the list.
4. Select all types using the rules described in Appendix A (rules 2 - 6). Each time a type is fully represented, the next to be represented is the one occurring on the top of the vegetation type list.

All areas of vegetation types that are present in the grid cell chosen, other than the type for which the algorithm was selecting, are subtracted from the areas required to fully represent them.