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**THE DISTRIBUTION AND CONSERVATION OF
TERMITES (ISOPTERA) AND BUTTERFLIES (LEPIDOPTERA)
IN SOUTH AFRICA**

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**The distribution and conservation of termites (Isoptera) and butterflies (Lepidoptera) in
South Africa**

by

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Disclaimer

This MSc. dissertation comprises a number of chapters prepared for submission to a range of journals. Consequently, chapter formats and contents contain some inconsistencies and overlap in order to secure publishable entities.

Summary

In order to conserve maximum biological diversity and maintain entire ecosystems, the conservation of insect groups must be considered. Termites (Isoptera) and butterflies (Lepidoptera) were selected as study groups because of their well known taxonomy and as information on their distribution is more readily available than many other invertebrate groups. Accurate distribution data sets were compiled for the South African region and generalised to 15' X 15' grid cells. The conservation value of the two groups was determined by evaluating existing conservation practices. This thesis describes alternative methodologies for the preservation of these two taxa, using complementary-based iterative conservation area selection procedures. Existing reserve networks appear insufficient. The conservation strategy for termites must include production landscapes while threatened habitats for butterflies should receive the highest conservation priority. A sensitivity analysis was used to determine the spatial implications of utilising a poorly surveyed taxon. Perturbation of the well documented butterfly data set revealed that conservation area spatial configurations are compromised when less than 50% of the species are recorded in the input data set. The correlation between species richness and higher-taxon richness (genus and subfamilies) and the representation of species in higher taxon complementarity conservation networks was determined. There is a strong positive correlation between species and higher taxon richness but species are poorly represented in networks generated at higher taxonomic levels. The conservation area selection procedure adopted is strongly influenced by the taxon in question, their taxon-specific conservation requirements and the quality of the input data set.

Opsomming

Om die maksimum biodiversiteit te bewaar en ekosisteme in geheel te onderhou, moet insek-groepe ook in ag geneem word. Termiete (Isoptera) en skoenlappers (Lepidoptera) is takosomies welbekend en verspreidingsinligting geredelik bekombaar. Dis vir hierdie rede dat hulle as studiegroep gebruik is vir die projek. Akkurate verspreidingsdatastelle was opgestel vir Suid Afrika en na 15' X 15' ruitselle veralgemeen. Die bewaringswaarde van die twee groepe was bepaal deur 'n evaluasie van bestaande bewaringspraktyke. Hierdie tesis beskryf alternatiewe metodologieë vir die bewaring van hierdie twee taksa deur gebruik te maak van komplimentariteit-gebaseerde iteratiewe bewarings prosedures. Bestaande reservaatnetwerke blyk onvoldoende te wees. Die bewaringstrategie van termiete moet produksie landskappe insluit terwyl bedreigde skoenlapperhabitate die hoogste bewaringsprioriteit moet ontvang. 'n Sensitiwiteitsanalise was gebruik om die ruimtelike gevolge van 'n takson wat swak gedokumenteer vas te stel. Verstoring van 'n goed gedokumenteerde skoenlapper datastel dui daarop dat die ruimtelike konfigurasie van bewaringsnetwerke benadeel word wanneer minder as 50% van die spesies in die inset datastel gebruik word. Korrelasie tussen spesie rykheid en hoërtaksonrykheid (genus en subfamilie) en verteenwoordigheid van spesies in hoërtaksonnetwerke was bepaal. Daar is 'n sterk positiewe korrelasie tussen spesierykheid en hoërtaksonrykheid (genus en subfamilie), maar spesies word swak verteenwoordig in netwerke wat deur hoër taksonomiese vlakke gegeneer word. Die bewaringsareaseleksie prosedure wat hier gebruik word was sterk beïnvloed deur die takson wat gebruik word, hulle spesifieke bewaringsbehoefte sowel as die kwaliteit van die insetdatastel.

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Chapter One

Introduction

Biodiversity management

Biodiversity can be addressed at different levels, the diversity of species, habitats, genes and living systems (Margules & Redhead 1995). Three levels of biodiversity are commonly recognised; genetic diversity, species richness and the diversity of ecosystems. The most fundamental is species richness (Curtis *et al.* 1998). This refers to the variety of species within a region. The diversity of species within a set of areas is measured as the inventory of species occupying those areas (Margules & Redhead 1995; Pressey *et al.* 1993).

The preservation of biodiversity has become an important issue in conservation biology. Critical decisions concerning where biodiversity should be conserved are being made (Lombard 1995; Drinkrow and Cherry 1995; McNeely 1992). This is largely due to the recognition that nature conservation as a form of land use, is competing for limited land resources with forestry, agriculture, urban and industrial development (Freitag *et al.* 1995). Reserve systems need to encompass the full range of species if they are to maintain diversity and prevent extinctions (Austin and Margules 1986; Margules 1989) and issues such as the location and adequacy of the existing reserve networks urgently need to be addressed (Pressey *et al.* 1993).

How do we go about selecting nature reserves, assuming that they should encompass maximum biological diversity? Margules (1989) proposes the use of databases, and subsequently, the use of conservation evaluation procedures using these databases.

Databases

The selection of reserve networks depends on patterns in the distributions of species especially in relation to existing reserves. The first step is to map the distributions of species. This database will thus determine what species (communities etc.) exist, where they are and how many there are.

Richardson (1994) gives some guidelines on the set-up of a database, as well as some important parameters that should be included before making this information accessible to others.

Conservation evaluation

Historically, the identification or selection of nature reserves tended to be *ad hoc* (Siegfried 1989; Pressey 1994). It was subjective, often depended on what land was available and was influenced strongly by perceived threats to particular species. This is unsatisfactory because it results in a bias in the suite of species protected in reserves and species occupying environments not suitable for other exploitative uses tend to be over represented. There is an alternative, more systematic approach in which candidate sites are ranked by assigning them a range of variables (Bedward *et al.* 1992; Pressey *et al.* 1993). These variables are called criteria of conservation value and include such features as rarity, diversity, representativeness and naturalness (Margules and Usher 1981; Margules 1989).

Reserve selection

A major reason for systems of reserve¹ systems is to sustain biological diversity. This involves protecting examples of as many natural features as possible. In reality though, few reserves have been dedicated for their representativeness of features. The inefficient allocation of limited resources to these reserves can actually jeopardise the representation of all features (Pressey *et al.* 1993). In order for reserves to fulfil their role in conserving biodiversity, they need to be as representative as possible (Pressey *et al.* 1993). Severe habitat destruction (Lovejoy 1997) and increasing competition with alternative land use hamper this task. New reserves must therefore be selected carefully so that limited resources are utilised effectively. Three principles for selecting priority regions and regional reserves can be recognised, namely complementarity, flexibility and irreplaceability (Pressey *et al.* 1993).

¹ The term 'reserves' is used to describe areas under a range of *in situ* protection measures, from wilderness to managed extraction of resources for commerce or subsistence (Pressey *et al.* 1993).

Insect conservation

From a conservation point of view, insects may seem unimportant, but they contain a unique set of characteristics. The class Insecta makes up the largest group of terrestrial organisms. Their distribution is vast both within and outside protected areas. They show extreme sensitivity to climatic changes and habitat disturbance. Insects play a key role in maintaining healthy human-made (agricultural) and natural ecosystems and there are already well-documented impacts on human existence. Insect pests and pathogens are well known for their impact on humans and their livestock (Robinson *et al.* 1997a; Robinson *et al.* 1997b)

For this study two insect groups have been singled out namely the termites (Isoptera) and butterflies (Lepidoptera). Details of their distributions and importance (both ecological and economical) are provided below.

Termites (Isoptera) of Southern Africa are classified into 5 families namely;

Kalotermitidae: Dry-wood termites. 6 genera, 11 species.

Hodotermitidae: Harvester termites. 2 genera, 2 species.

Termopsidae: Damp-wood termites. 2 genera, 2 species.

Rhinotermitidae: Subterranean termites. 3 subfamilies, 3 genera, 7 species.

Termitidae: 'Higher' termites, nests arboreal, mounds or entirely subterranean. 4 subfamilies, 39 genera, 190 species (Howse 1970; Harris 1971; Ruelle 1996).

This study group is not only taxonomically relatively well described, but literature regarding their distribution is readily available. Termites are exceedingly abundant. They are found throughout the tropical and sub-tropical areas of the world (Howse 1970) and in some areas extending into the temperate regions (Hickin 1971). Only a few species are found in Europe (Howse 1970), and the nearer to the equator one travels, so the number of species and the total number of termites increase (Hickin 1971).

Generally speaking the number of different kinds of termites present in any locality is greatest in tropical rain forests, but the general level of their activity appears to be highest in deciduous woodlands and where farming has taken place. Both the number of species and of individual termites present fall rapidly outside the tropics, or where the elevation of the land leads to low minimum temperatures. In Africa, south of the Sahara, the number of termite species increases rapidly as one moves from the arid Sahara towards the tropical rain forest. The peak of visible termite activity is reached in the savannas and deciduous woodlands. The temperate southern tip of the continent has a limited fauna (Harris 1971).

Termites play a beneficial role. They function as scavengers, boring into, breaking up, and digesting woody tissue. The products of their activity are available, either directly or indirectly through the activities of other organisms, as a contribution toward the nutritional requirements of a succeeding generation of trees (Hickin 1971). They have had an enormous effect on the landscape of large areas in Africa. This applies mainly to the mound-building termites. When forest land is cleared they colonise it and later die off if the forest re-invades. Abandoned mounds in the savanna are rapidly colonised by vegetation; they have a higher mineral content than the surrounding soils, are better drained, and are less affected by grass fires because of their height. The colonisation begins with grasses and is followed by trees, resulting in islands of woodland in grassland, a so-called termite savanna (Howse 1970; Harris 1971). These islands eventually spread and coalesce to form continuous forest. While some species of termite can cause extensive damage to crops in tropical regions, it appears that others perform a valuable function in increasing the aeration and drainage of the soils. There is also evidence that the mound-builders may be responsible for the re-establishment of new soils in some areas after erosion has taken place (Howse 1970).

Much work has been done on the **butterflies** (Lepidoptera). Butterflies are taxonomically well described and it is estimated that only a few undescribed species remain (Owen 1971; Robbins & Opler 1997). There is also a great amateur interest in butterflies and this is largely due to their aesthetic value. This has contributed to them being more extensively collected than other insect

groups, and thus much more is known about the systematics and distribution of their species. Butterflies are good indicators of habitat health (New, 1991).

Most butterflies belong to the superfamily Papilionoidea of the order Lepidoptera. Members of another superfamily, the Hesperioidea, or skippers, are also usually regarded as butterflies, partly because like most butterflies and unlike most moths, they are day-flying, and partly because they share a number of features with the Papilionoidea. Butterflies occur in all parts of the world, but they are primarily tropical. About 13000 species are known of which 2674 occur in Africa south of the Sahara, and Madagascar.

The Hesperioidea has a single family in Southern Africa, while the superfamily Papilionoidea contains 4 families;

Hesperiidae: 3 subfamilies, 36 genera, 123 species.

Nymphalidae: 27 genera, 70 species.

 Danainae: 2 genera, 7 species.

 Satyrinae: 22 genera, 78 species.

 Acraeinae: 3 genera, 56 species.

 Charaxinae: 2 genera, 36 species.

 Libytheinae: 1 genus, 1 species

Lycaenidae: 6 subfamilies, 67 genera, 381 species.

Pieridae: 2 subfamilies, 13 genera, 53 species.

Papilionidae: 1 genus, 17 species.

(Henning 1996; Pennington 1994).

There is abundant evidence that the distribution of forest and savanna in Africa has changed markedly in the past million years and that in the past several hundred years the forest has become increasingly devastated by human activities. Derived savanna and cultivated land are fast becoming the most important butterfly habitats in Africa (Owen 1971).

The most striking variation in species diversity is latitudinal. There is a gradient of decreasing diversity from the equator to the poles. Many tropical species are relatively much rarer than temperate species. There are certainly more insect species in the tropics and butterflies are no exception to the rule. Animals such as butterflies depend largely on plants, and there is a marked tendency for species and genera to be confined to particular plants or groups of plants. There are more species of plants in the tropics than in the temperate regions (Robbins & Opler 1997) and thus it is not surprising that there are more species of animals all of which ultimately depend on plants. Tropical areas also offer a greater variety of habitats. The longer favourable season in tropical areas could allow more species to exploit the available resources: the edible parts of plants are available over longer periods in the tropics than in temperate areas (Owen 1971).

The present study centred around the distribution of selected termite and butterfly species in South Africa. The principle of complementarity is used throughout the study, the degree to which an area contributes unrepresented species to a network of areas (Pressey *et al.* 1993; Williams *et al.* 1996). Each chapter takes a different approach towards setting aside important conservation areas for invertebrates.

Chapter two compares the efficiency of conservation areas based on species-rich areas versus various complementarity-based procedures. It also provides an experimental approach aimed at evaluating the impact of different land-use forms on the persistence of termite taxa

The taxonomic representation of the two data sets differed considerably. A sensitivity analysis allows us to evaluate the reliability and robustness of conservation area selection procedures. Chapter three aims to quantify the effects of implementing a species-poor data set (termites) through systematically perturbing the comprehensive butterfly data set and evaluating the performance of such conservation area networks.

Chapter four looks specifically at the status of butterfly conservation in South Africa. The contribution that formally protected areas make to the conservation of threatened species is addressed. The need for an alternate conservation strategy is explored.

Surrogacy, particularly higher-taxa surrogacy, is the focus of the fifth chapter. The objective is two-fold. First to determine the relationship between higher-taxon richness and species richness for butterflies and secondly to quantify if sets of areas set aside using higher taxonomic levels, adequately protect at the species level. The strengths and weaknesses of these disparate approaches for the development of an insect conservation strategy in South Africa is assessed.

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CHAPTER TWO

Termite (Isoptera) distributions, endemism, species richness and priority conservation areas: consequences for land-use planning in South Africa.[^]

Abstract

Spatial analyses of distribution patterns of selected termite surveyed during the National Survey of Isoptera were used to compare various procedures for determining priority conservation areas for termites. Species richness and endemism hotspots are spatially separated. Selecting species-rich areas is demonstrated to be extremely inefficient while the use of complementarity-based procedures requires less land for achieving species representativeness. In addition, different complementarity-based procedures (equal species weighting, endemism, taxonomic distinctiveness and a combination of endemism and taxonomic distinctiveness) vary in their land-use efficiency and in the extent to which they are congruent with areas containing formally protected areas as well as richness and endemism hotspots. As ecosystem engineers, termites are required for the maintenance of ecosystem functions in both conservation and production landscapes. Thus, the use of traditional protection strategies for termites appear insufficient and strategies that pursue production objectives within conservation constraints through adaptive management are required. Consequently we propose a dual strategy. The first aimed at the conservation of termite taxa in a core representative network. Secondly we propose the establishment of a supplementary network of sites, comprising multiple representations of each species, for the experimental monitoring of termite persistence under different land-uses (indicator taxa).

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Introduction

Termites (Isoptera) perform important and varied ecological roles. They function as scavengers and as degraders of woody tissue (Hicken 1971). The mound-building termites, in particular have an effect on the landscape. Termites temporarily colonise cleared forest lands and abandoned mounds in savannas are rapidly colonised by vegetation (Howse 1970). The soils of termite mounds contain elevated mineral concentrations, are better drained and, due to their height, termitaria are less affected by grass fires than surrounding soils. This results in islands of woodland in grasslands, so-called termite savannas which may spread to form continuous woodlands (Howse 1970; Harris 1971). While some termite species may cause extensive crop and pasture damage in tropical regions and they may contribute to 'greenhouse effects' through methane production, others perform an invaluable ecosystem function by increasing the aeration and drainage of soils and possibly even facilitating the re-establishment of soils after erosion (Howse 1970).

These roles of termites as ecosystem engineers (Jones *et al.* 1994), suggest a conservation approach which is fundamentally different from the traditional protected areas approach towards species conservation (Pressey *et al.* 1993; Lombard 1995). Traditionally, networks of protected areas are characterised by an estimated biodiversity set. This set is, however, not simply the sum of the biodiversity (*e.g.* the number of different species) contained within each area. As different areas within a region will overlap to some degree in their component species, the contribution of any one area to regional biodiversity depends on the species represented in other regional protected areas (Pressey *et al.* 1993; Faith 1995). This is the principle of complementarity. Complementarity is the degree to which an area contributes unrepresented species to a network of areas (Pressey *et al.* 1993; Williams *et al.* 1996).

With limited options and resources for conservation, an intelligent strategy would be to assess the content of any existing reserve system and then, in a stepwise fashion, to select at each step the site that is most complementary to the features already contained in the established reserve network. However, the key role played by termites in maintaining ecosystem functions suggests an approach that extends the traditional notion of formal protection and strives for the continued presence of

termite species in both conservation and production landscapes to ensure healthy and productive ecosystem functioning. Here we provide an approach that simultaneously provides room for the formal protection of termites (complementary set) and for an experimental approach aimed at evaluating the impact of different land-use forms on the persistence of termite taxa.

A global evaluation of termite distributions identified the Afrotropical Region as the global hotspot for termite genera (Eggleton *et al.* 1994). While the focus of that study concentrated on genera due to a lack of adequate species-based distribution data, the present paper evaluates published termite species distribution patterns, endemism and richness in South Africa. The use of conservation planning tools (minimum set and multi-criteria algorithms) for developing a conservation and land-use strategy to ensure the effective and continued deployment of termites as ecosystem engineers as well as the conservation of termite taxa is explored.

Material and methods

Termite distribution records for South Africa were extracted from published accounts of the National Survey of the Isoptera (Coaton & Sheasby 1972, 1973a, b, c, d, 1974a, b, 1975a, b, 1976a, b, 1977, 1978a, b, 1979, 1980, Ruelle *et al.* 1975, Ruelle 1979). Although not representative of all termite taxa, it does represent a unique country-wide survey that recorded both presence and absence of 28 of the 212 termite species recorded in southern Africa (Scholtz & Holm 1985) in 946 grids (4008 records, 1372 unique localities) throughout South Africa (Fig. 1). Only 25 of the 28 surveyed species were used in the final analyses as *Coptotermes* represent exotic species and were omitted from the analyses. The analyses included the following Families and genera: Kalotermitidae - *Bifiditermes* (Krishna), *Cryptotermes* (Banks); Termopridae - *Stolotermes* (Hagen), *Porotermes* (Hagen); Hodotermitidae - *Hodotermes* (Hagen), *Microhodotermes* (Sjöstedt); Rhonotermitidae - *Psammotermes* (Desneux), *Schedorhinotermes* (Silvestri); Termitidae - *Apicotermes* (Holmgren), *Baucaliotermes* (Sands), *Termes* (Linnaeus), *Ancistrotermes* (Silvestri), *Rhadinotermes* (Sands), *Fulleritermes* (Coaton), *Macrotermes* (Holmgren), *Allodontermes* (Silvestri) and *Pseudocanthotermes* (Sjöstedt).

As sampling localities were not identified with precise coordinates in survey documents, latitudes and longitudes were assigned to localities with the aid of the survey gazetteer. Sampled localities within a radius of 5 km from an identifiable landmark (*e.g.* town) were attributed to that landmark, localities closer than 3 km from one another were considered equivalent but recorded as separate records.

Species richness and endemism hotspots

Raw data were generalised to 15' x 15' grids (sixteenth degree square) to reflect the presence and absence of species in grids throughout South Africa (Fig. 1). The 5 % richest sites were designated richness hotspots (Prendergast *et al.* 1993). Five of the 25 species included in the study were considered established endemics to South Africa (*Stolotermes africanus* (Emerson), *Porotermes planiceps* (Sjöstedt), *Fulleritermes mallyi* (Fuller), *Termes winifredae* (Snyder & Emerson), *Cryptotermes merwei* (Fuller)). Potential endemics were *Baucaliotermes hainesi* (Fuller), *Fulleritermes coatoni* (Sands), *Macrotermes ukuzii* (Fuller) and *Microhodotermes viator* (Latreille). Endemism hotspots were determined as those grids richest in endemic species (2-3 endemics per grid).

Near minimum set and multi-criteria algorithm evaluations

The required near-minimum network (set of sites) required to represent all 25 termite taxa was determined following Nicholls & Margules (1993). Comparative near minimum sets which take species of regional conservation importance into account by giving higher weightings to endemic or taxonomically distinct species (Freitag & van Jaarsveld 1997; Freitag *et al.* 1997) were also generated.

For multi-criteria analyses each taxon was allocated a score using the relative taxonomic distinctiveness index (Freitag & van Jaarsveld 1997):

$$\text{Relative taxonomic distinctiveness} = \frac{1}{\sqrt{(f \times g \times s)}}$$

where f is the number of regionally 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 particular species belongs. For weighting species in terms of endemism, a distinction was made between species endemic to South Africa (score = 1.0), potential endemic species (score = 0.5) and non-endemics (score = 0) recorded in and outside South Africa. Potential endemics refer to the uncertainty of species distributions outside the borders of South Africa. The near-minimum set of sites required to represent the 25 termite species was determined (algorithm modified from Freitag *et al.* 1997) using taxonomic distinctiveness, endemism or both criteria in combination to determine priority termite conservation areas. In each instance the algorithm was altered from the standard Nicholls & Margules (1993) algorithm, which begins by selecting sites containing 'database rarest' species, to initially select taxonomically distinct taxa, endemic taxa or a combination of these criteria (multi-criteria) in the initial selection rules (Freitag *et al.* 1997). This approach emanates from procedures for prioritising species for regional conservation actions (Freitag & van Jaarsveld 1997) and ensures that sites selected initially represent those species of particular regional conservation importance. The use of multi-criteria weightings of species of regional conservation importance also makes it possible to rank the priority conservation areas (Freitag *et al.* 1997). These algorithms all employed the adjacency-constrained option which selects sites as close as possible to sites previously selected when the algorithm is faced with options (Nicholls & Margules 1993).

Efficiency

The efficiency of the algorithm was calculated using the equation defined by Pressey & Nicholls (1989) as follows:

$$Efficiency = 1 - \frac{X}{T}$$

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.

Conserved areas and termite distributions

The degree of overlap between termite richness and endemism hotspots, representative networks and existing conservation areas was evaluated. The degree of protection afforded grids was determined and deemed to be congruent with the distribution of species within that grid for different degrees of protection (some protection, 25 %, 50, 75, 100 % of grid cells protected; Table 1).

Compatible land-use monitoring

Following the selection of a core termite conservation network of grids these selected grids were excluded from further consideration. A network of sites representing five grid representations per species was subsequently selected (Freitag *et al.* 1997). These sites are intended as an experimental network for evaluating the impact of different land-uses on termite persistence outside core conservation areas.

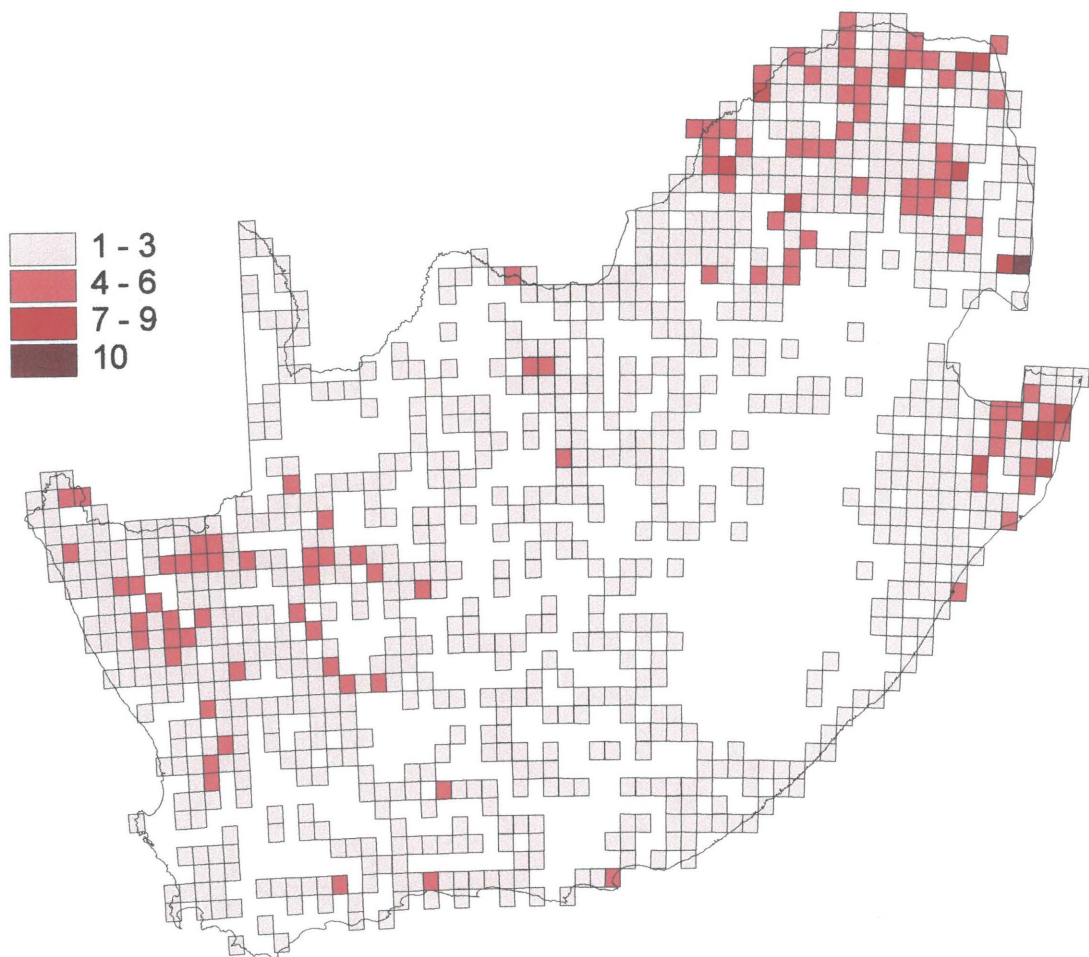


Figure 1. Species richness map indicating the number of Isoptera species recorded in each 15' x 15' grid square during the National Survey of Isoptera (1972 - 1980)

Table 1. The relative land-use efficiencies of different priority area selection procedures and their degree of congruence when applied to termite distribution data.

	5% Richest grids	Equal species weighting ¹	Species prioritisation		
			Endemicity ²	Taxonomically distinct ² .	Endemic/Taxonomically distinct ² .
i. No. of grids selected	51	7	8	7	7
ii. Efficiency ³	0.946	0.993	0.992	0.993	0.993
iii. % of grids conserved ⁴	39	57	63	29	29
iv. No. additional grids required to represent all species ⁵	2	0	0	0	0
v. No. additional grids required to represent all species when pre-selecting grids					
a. 100% conserved	—	4	4	5	5
b. 75% conserved	—	2	2	2	2
c. 50% conserved	—	1	1	1	1
d. 25% conserved	—	1	1	1	1
e. containing any conservation area	—	0	0	0	0

1: Nicholls & Margules (1993).

2: adapted from Freitag *et al.* 1997.

3: Pressey & Nicholls (1989).

4: grids are considered conserved if they include any form of formal protection.

5: this measure assumes that the chosen algorithm continues to be applied.

Results

Species richness and endemism hotspots

The 5 % species richest sites are depicted in Fig. 2a. Fifty one sites were designated species richness hotspots, containing between five and 10 species per grid. Most of these, together with the most speciose grid (X), are concentrated in the northeastern region of South Africa. These top 5 % richest grids represented 88 % of the 25 species included in the analysis (Appendix 1). The endemism hotspots (2-3 endemics per grid cell) are shown in Fig. 2b. The five endemic species are represented in 148 grids within the study area. Only four grids contained the maximum of three endemic species per grid. The grids most rich in endemic species are clearly concentrated in the southwestern region of the country, particularly along the southern Cape coast. The species richness and endemism hotspots do not coincide, but rather occur in the two distinct groupings.

Priority areas (equal species weighting)

A near-minimum set of areas required to represent each species at least once (Nicholls & Margules 1993) is provided in Fig. 3a. Only seven grids were required to achieve total species representation, four in the northeast and three in the southwest of the country.



Figure 2. Hotspots indicating (a) the top 5 % richest termite grids ($n = 51$) where 'X' marks the most speciose grid in South Africa and (b) endemic species richness.

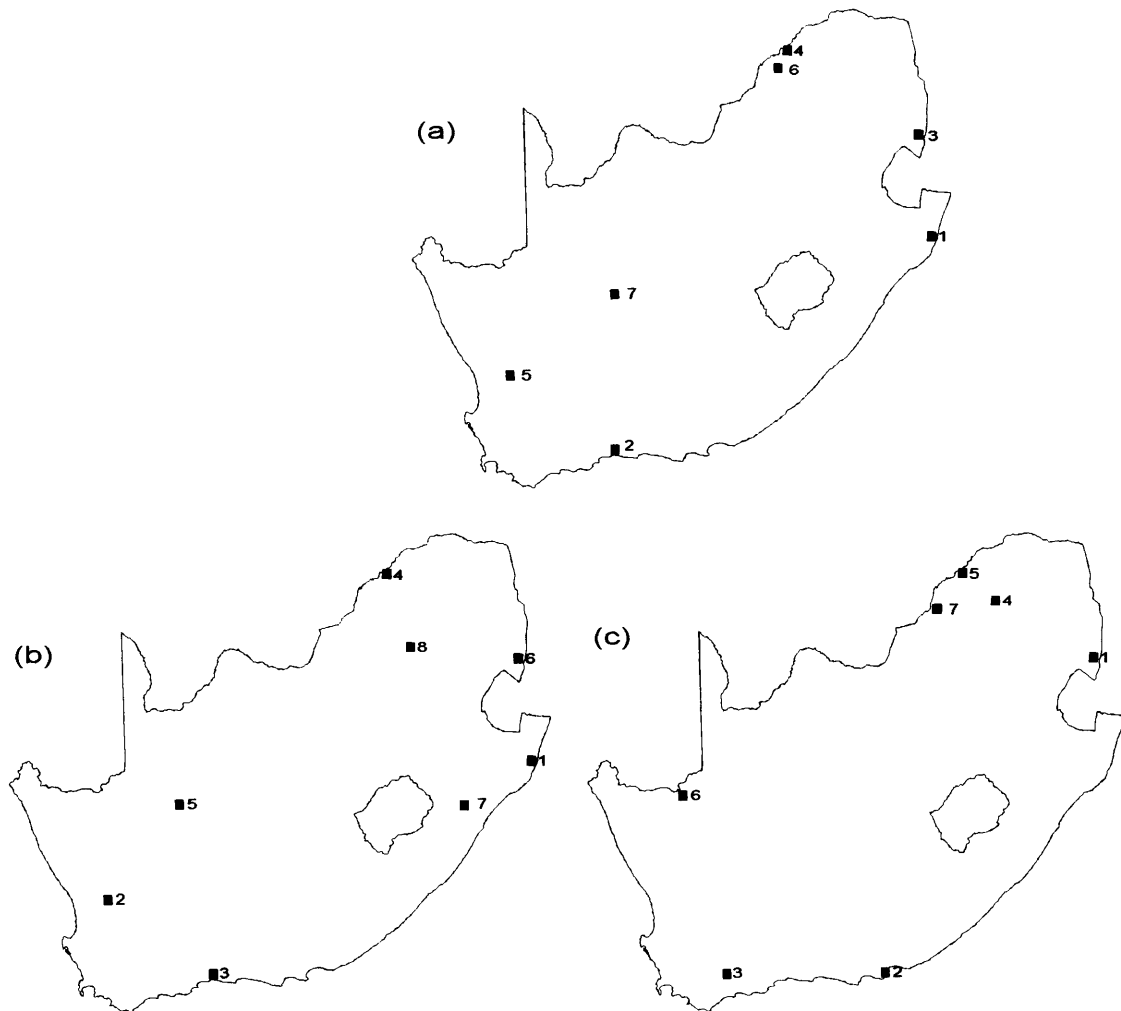


Figure 3. Generated priority conservation network when (a) species are afforded equal weighting (Nicholls & Margules 1993), (b) endemism is used as a criterion for prioritising species, (c) taxonomic distinctiveness is employed as a prioritisation criterion (Freitag *et al.* 1997). Numbers adjacent to grids indicate the sequence with which individual grids were added to the network.

Priority areas (endemicity/ taxonomic distinctiveness)

The network of priority sites that emerges when assigning priority to endemic species (Fig. 3b) required eight sites to achieve total species representation. To represent all species when prioritising by taxonomic distinctiveness required only seven grids (Fig. 3c). Using a multi-criteria approach (Freitag *et al.* 1997) and combining the prioritisation of endemic species with taxonomic distinctiveness also required seven grids to represent all species (Fig. 4). The order in which grids within the priority sets were selected is illustrated in Fig. 4 and Appendix 1.

The selected grids occur in two distinct groupings namely the northeastern region and the southwestern region of South Africa. The grids were not selected in any distinguishable pattern but grids higher up in the selection order (second and third on the priority list) have a tendency to group in the southwestern region of the country. The grid with the lowest priority in the sets (*i.e.* selected last) is found in the northeastern region and more specifically in the Northwest Province.

Comparative assessment of priority area networks

A comparative assessment of the various priority area networks is provided in Table 1 and the spatial details are provided in Appendix 1. From Table 1 it is clear that targeting species-rich areas is extremely inefficient in terms of land-use and that affording equal weightings to species results in greater efficiency as marginally fewer grids are required to represent all species. The complementarity-based algorithms differ marginally in their efficiencies (0.993 - 0.994), requiring between seven and eight grids to represent all species.

The spatial congruence among the various network sets is limited, ranging from 5.45 - 36.36 % with little overlap between the species richness network and the complementary networks (Table 2; 5.45 - 9.26 %). In addition, spatial congruence amongst the complementary networks was least (7.14 %) when the compared algorithms were based on prioritising taxonomic distinctiveness and the prioritisation of endemic species. The priority area networks also overlap with established

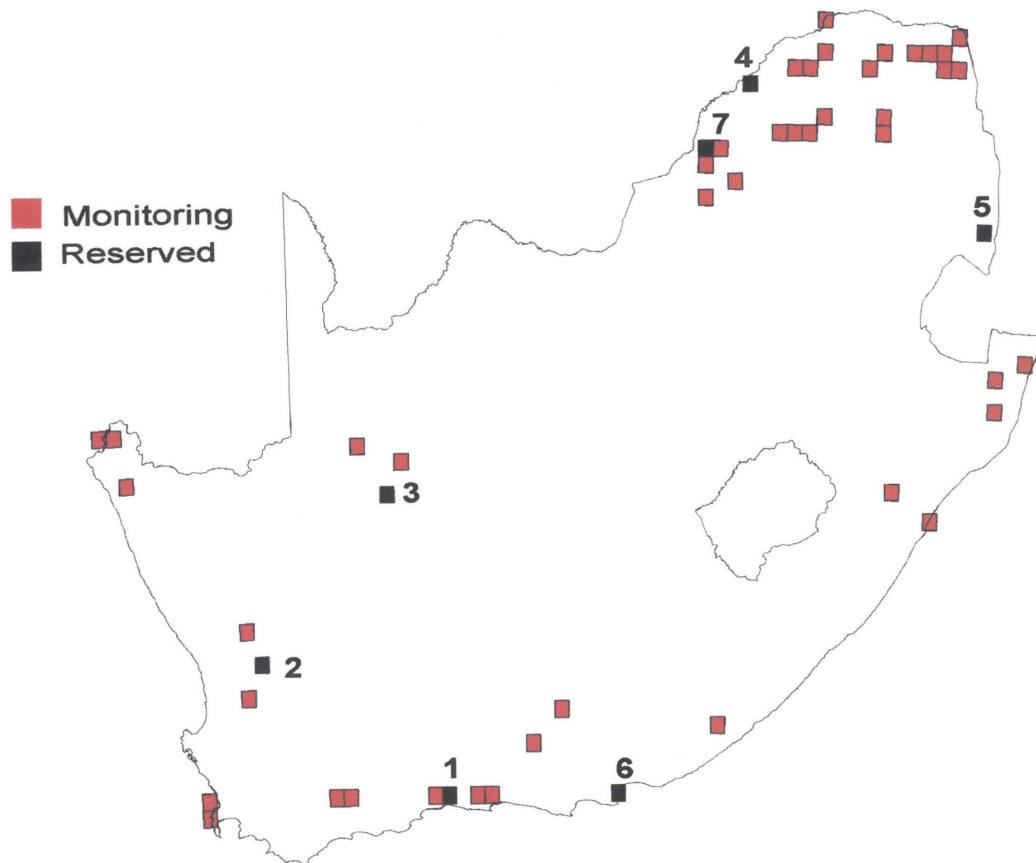


Figure 4. Priority area network using a combination of endemism and taxonomic distinctiveness (afforded equal weighting) as prioritization criteria (■; modified from Freitag *et al.* 1997). Numbers adjacent to grids indicate the sequence with which individual grids were added to the network and thus their regional termite conservation importance. The termite monitoring network depicts 5 grid representations per species (□) and could serve as an early warning system regarding the incompatibility of land-use forms with termite ecosystem engineering activity.

conservation areas to varying degrees (29 - 63 %; Table 1), while the number of additional grids required to complete the representative sets varies between zero and five.

Based on the limited overlap between the various priority area networks, the efficiency of the algorithms and the number of extra grids required in addition to already fully protected grids, and considering that not all grids can be secured at a single stroke of a brush (Vane-Wright 1996), the advantages associated with the prioritisation of selected sites that flows from the multi-criteria assessment is favoured as a core conservation network for termites (Fig. 4).

The network of grids representing the land-use compatibility monitoring experiment required an additional 37 grids for five representations per species (Fig. 4). All species successfully reached the target of five additional representations outside the core network. Consequently, none of the grid cells contained in the core conservation network can be considered irreplaceable (Pressey *et al.* 1994).

Table 2. Percentage of selected grids shared (Jaccard coefficient: Gotelli & Graves 1996) by the various algorithms.

	Equal species weighting ¹	Species prioritisation		
		Endemicity ²	Taxonomically distinct ² .	Endemic./ Taxonomically distinct ² .
5% richest sites	5.5	9.3	7.4	7.4
Equal species weight.	—	15.4	7.7	27.3
Endemicity	—	—	7.1	36.4
Tax distinct.	—	—	—	40.0

1: Nicholls & Margules (1993)

2: adapted from Freitag *et al.* 1997

Discussion

The spatial congruence between species richness areas, endemism and complementary areas has not been investigated extensively (Gaston 1996). Lombard (1995) and Williams *et al.* (1996) reported spatial disparities between richness hotspots, rarity hotspots and complementary areas for South African vertebrates and British birds respectively but did not quantify the degree of spatial congruence. In addition, a limited number of studies suggest a lack of congruence between complementarity-based richness and endemism sets (Kershaw *et al.* 1994; Williams & Humphries 1994; Gaston 1996). In contrast, considerable spatial congruence (50-77 %) resulted from employing complementary algorithms that assign equal weightings to species (Nicholls & Margules, 1993) and algorithms that incorporate principles of taxonomic distinctiveness, endemism, vulnerability and rarity for mammalian species in South Africa (Freitag *et al.* 1997). The basis for these conflicting patterns needs to be investigated further as they may have significant conservation planning implications.

The outcome of various priority conservation area selection procedures applied to termite distribution data in the present study (Table 1) underscores the relative inefficiency of selecting for species-rich areas *vs* applying the principle of complementarity in near minimum set selection procedures (Williams *et al.* 1996). In the present study the 5 % richest sites required some 500 % more land than any complementary network. The degree of land-use inefficiency of this conservation strategy is further emphasised by the additional two grids (total = 53) required to represent all species should the species richness selection criterion continued to be applied (Table 1).

The complementary-based algorithms differ marginally in terms of their efficiency. The most important disparity between the different complementary-based algorithms is the number of additional grids that need to be conserved (4 or 5) when pre-selecting grids that are 100 % conserved before running the algorithm (Table 1). In this regard the equal species weighting and endemism algorithms provided the best outcome. When applying the various complementary

algorithms the priority areas network always occurred in two distinct groupings, the northeastern and southwestern regions. This can be attributed to the fact that these two regions contain the top 5 % species rich and endemic hotspots respectively. These two areas were subsequently prioritised during the network selection procedures.

Spatial congruence analyses revealed less than 10 % overlap between the 5 % richest sites and complementary-based spatial networks (Table 2). Similarly, among the complementary-based procedures, little overlap was evident when species were assigned equal weights compared to prioritisation of taxonomically distinct species. The degree of spatial congruence between complementary priority area networks varied between 7.14 and 36.36 % (Table 2) and the basis for this variance appeared to revolve around the low degree of overlap between algorithms based on taxonomic distinctiveness and those based in prioritising endemic species. Higher degrees of spatial congruence were evident when the multi-criteria algorithm was compared to the other priority setting procedures. This raises questions about the generality of this pattern which should be evaluated using other taxa and / or combinations of procedures for prioritising species within priority area selection algorithms. The distinct spatial separation between endemic hotspots (southwest) and richness hotspots (northeast) can be ascribed to the endemic fynbos vegetation types found in the Western Cape Province and the southernmost limits of many subtropical and tropical species in the northeast of the country. A similar pattern was described for vertebrate taxa in South Africa (Lombard 1995).

The presence of a species in a protected area network does not mean that it is adequately conserved (van Jaarsveld 1995). This is particularly true for termites that perform important roles as ecosystem engineers (Jones *et al.* 1994). Termites need to be conserved on a broader front, within production landscapes, to maintain ecosystem processes. Considering the varied ecological roles played by termites (Scholtz & Holm 1985) it is also important to conserve all termite species. Thus we propose the implementation of a core termite conservation network which represents all taxa incorporated in the present study (Fig. 4). In addition, we suggest that the influence of various forms of land-use on the persistence of termite species be evaluated in a supplementary network of

sites that represents each species multiple times (Fig. 4). In essence this amounts to the establishment of an experimental set of sites for monitoring the impact of various forms of land-use on termite species, where the termites are used as indicator taxa for ecosystem processes. Moreover, to derive maximum ecological benefit from the varied ecosystem processes facilitated by termites, land-use strategies should strive to exploit their capabilities wherever feasible. This would require adaptive management in production landscapes. Naturally, formal protection is likely to be the most compatible form of land-use and intensive crop production, that requires significant insecticide application, the least. Extensive livestock production or pastoralism may be more acceptable (but see Scholtz & Chown 1993).

In conclusion, a conservation strategy aimed purely at the preservation of termite species appears to be an inadequate goal for this group of organisms. Their role as ecosystem engineers requires their conservation on a broader front within production landscapes. We propose a dual conservation strategy for these taxa: a core conservation area and a supplementary termite monitoring network where the compatibility of land-use types with the persistence of termite taxa will be experimentally evaluated (indicator taxa). The objective in the production landscapes would therefore be to pursue production objectives within conservation constraints (Faith 1995) through adaptive management.

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Appendix 1. Spatial distribution and selection order of priority area conservation sites emanating from the application of a number of algorithms on selected termite data from South Africa.

15' x 15' grid square	5% Richest grids	Equal species weighting ¹	Species prioritisation ²		
			Endemicity	Tax distinct.	Endem./ Tax distinct.
2531BD	1	3		1	5
2231CA	2				
2229DD	3				
2327BB	4		4	5	4
2430BB	5				
2531BC	6		6		
2732CA	7				
2732CB	8				
2230DB	9				
2427AB	10	4			
2428CB	11				
2732BC	12				
2831AB	13				
2832AB	14		1		
2229CA	15				
2328CD	16				
2330CA	17				
2428CC	18				
2430AC	19				
2430CA	20				
2527DB	21				
2732AA	22				
2732AD	23				
2732DA	24				
2832AC	25				
2228CB	26				
2228DC	27				
2229AA	28				
2229CD	29				
2230AC	30				
2230DC	31				
2327CA	32				
2328DC	33				
2329AA	34				
2427AA	35			7	
2429AD	36				7
2430AD	37				
2430BA	38				
2430CB	39				

Appendix 1 (continued)

2527CA	40				
2528BA	41		8		
2731BC	42				
2731DC	43				
2832AA	44	1			
2919AB	45			6	
2921AC	46				
2921BC	47		5		3
2931CC	48				
3018BA	49				
3018BD	50				
2227DD	51				
2328DD				4	
2426BD		6			
2922DC		7			
2930AD			7		
3119CD		5	2		2
3320DC				3	
3322DC		2	3		1
3325DC				2	6

1: Nicholls & Margules (1993)

2: modified from Freitag *et al.* 1997.

CHAPTER THREE

Sensitivity analysis to evaluate input data set quality: butterfly and termite conservation planning. [^]

Abstract

The paucity of global distribution data poses special challenges to conservation biology. We use a well documented taxon (butterflies) and a poorly documented taxon (termites) to evaluate the consequences of using partial (species poor) data sets for identifying conservation areas. A comprehensive butterfly species distribution data set from South Africa is systematically perturbed to levels equivalent to the termite data set. The land-use efficiency and the degree of spatial overlap among conservation networks identified at different levels of data perturbation was quantified. Furthermore, the implementation of conservation areas identified using species poor data sets on subsequent land additions indicate that increased network variability and inefficient land-use is likely. The implications of this analysis for the species poor termite data set suggest that conservation area selection procedures are spatially compromised when less than 50% of the species are recorded in an input data set. Thus, the taxonomic extent of an input data set should be evaluated prior to implementing conservation area networks and there is an urgent need to develop a predictive capability regarding the spatial implications of utilising poorly documented taxa in conservation planning.

[^] MS submitted: Muller, C., Freitag, S., van Jaarsveld, A.S., & Krüger, M. Sensitivity analysis to evaluate input data set quality : butterfly and termite conservation planning.

Introduction

The efficacy of biodiversity conservation efforts will ultimately depend on the quality of biodiversity information at our disposal (Freitag & van Jaarsveld 1995; Haila & Margules 1996; Lawton *et al.* 1998; van Jaarsveld *et al.* 1998; Freitag & van Jaarsveld, 1998). While acknowledging the need to continually improve biodiversity data sets (Margules & Nicholls 1993; Freitag & van Jaarsveld 1995; Haila & Margules 1996), conservation decisions need to be made now, by making the best possible use of existing data sets (Davis *et al.* 1990) before there is little left worth conserving (Lawton *et al.* 1994). Although poor survey extent and survey intensity may partially be compensated for using established data interpolation techniques (Austin & Margules 1986; Margules & Redhead 1995), poor taxonomic representation is more problematic and can only be overcome at considerable expense (Cracraft 1995; Freitag & van Jaarsveld, 1998). Thus, there appears to be little prospect of imminent or useful substitutes for biological surveys for improving the planning value of regional biodiversity data (Haila & Margules 1996; Lawton *et al.* 1998; van Jaarsveld *et al.* 1998).

An alternative pragmatic approach towards dealing with species poor data sets in conservation area selection procedures is to develop a quantitative understanding of the risks associated with using limited data sets. Sensitivity analyses can be used to evaluate the reliability of and robustness of conservation area selection procedures by comparing outputs derived from systematically perturbed data sets (Lodwick *et al.* 1990; Stoms *et al.* 1992; Freitag & van Jaarsveld 1998). The present study evaluates the performance of priority area networks derived from a systematically perturbed butterfly data set (initially containing 94% of known species) up to levels equivalent to a termite data set containing only 12% of known species from the region. Consequently, the risks associated with implementing the poor termite data set can quantitatively be assessed. We find that systematic species deletions may result in smaller conservation area networks but poorer long-term land use efficiency.

Methods

Butterfly and termite distribution data

An extensive butterfly distribution data set for South Africa was collated from the Transvaal Museum. Sampling localities were transformed to 15' x 15' grid squares with the aid of a gazetteer. Much work has been conducted on the systematics and distribution of the group and only a few undescribed species remain (<5%; Owen 1971). Untraceable and/or ambiguous localities were discarded and these data reflect presence data only. The 10196 distribution records reflect the presence of 613 species in 600 grid squares throughout the country (total 2014 grid squares).

Termite distribution records from South Africa were extracted from published accounts of the National Survey of Isoptera (Muller *et al.* 1997). Although comprising only 12% of the indigenous species from the region (25 of 212; Scholtz & Holm, 1985), it does represent a unique country wide survey that recorded both presence and absence of species in 946 grid cells throughout South Africa (4008 records). As sampling localities were not identified with precise co-ordinates in all survey documents, latitudes and longitudes were assigned to localities with the aid of a gazetteer. Sampled localities within a radius of 5km from an identifiable landmark (e.g. town) were attributed to that landmark, localities closer than 3 km to one another were considered equivalent but recorded as separate records (Muller *et al.* 1997).

Sensitivity analysis

The sensitivity of a routinely employed conservation area selection algorithm (Nicholls & Margules 1993) to variations in butterfly species numbers was determined by randomly deleting a pre-determined percentage of the total number of species (n = 613). Deletions were systematically performed beginning with the random deletion of 25% of the species and subsequently increased to 50, 80 and 88% of the total number of species (Table 1). This latter database therefore contained only 12% of the known butterfly species and was ultimately comparable to the termite input database. The algorithm (Nicholls & Margules 1993) was employed on the original database as well

as after each random deletion event to identify representative conservation area networks. The complete process (deletion and algorithm) was carried out 500 times per deletion level (25 - 88%).

Priority area networks were compared in terms of the:

(a) number of grid cells required from the perturbed database to achieve complete species representativeness, i.e. priority area network size and efficiency (Pressey *et al.* 1993) (n = 500);

(b) degree of spatial overlap between a random subset of selected networks (n = 30 of 500) per deletion level. Spatial congruence measures the degree of spatial overlap of each of the 30 runs with one another (Van Jaarsveld *et al.* 1998; Freitag & van Jaarsveld 1998), and

(c) number of additional grid cells required to complete full species representation after pre-selecting the grid cells chosen from the perturbed data sets (n = 30 per deletion level). This takes into consideration the grid cells chosen for the perturbed data sets and estimates the total network sizes required to finally represent the complete database. This procedure mimics future additions to a conservation area network implemented today and using data from a poorly surveyed taxon.

Results

The results of the butterfly database perturbation are provided in Table 1. As more species are excluded from the database mean network size decreased from 84 to 21. Thus, by increasing species deletions, a logical decrease in the number of grids required to form representative networks is observed (Fig. 1). However, the suite of grid cells selected among successive runs also becomes increasingly variable (171 – 274 grid cells) as the number of species is reduced by 25% - 88% of the original number of species (Table 1).

The mean percentage of grid cells shared (i.e. the degree of spatial overlap) across 30 random networks is reflected in Fig. 2. Increased species deletions result in decreased spatial congruence among successive runs (75% - 23% mean overlap).

Finally, the number of additional grid cells required for total species representation increases dramatically following the pre-selection of grid cells required by reduced databases. As more species are deleted (n = 461 - 74), more additional grid cells are subsequently required to complete species representation (16 - 67) - (Fig. 3). Consequently, the total number of grid cells required in the final network also increased from 84 to 91. The impact (%) of this pattern relative to the scale of the study (original network size) reveals a near proportional response in both butterfly and mammal studies (Fig. 4).

Table 1. Results of sensitivity analysis showing averages of (i) numbers of species and grids used, (ii) mean network size and (iii) network size range after random species exclusions.

% of data set remaining	No. of species included	No. of grids used	Mean network size	Network size range	No. of runs
100	614	–	84	–	1
75	461	171	71	60 - 80	500
50	307	215	55	46 - 65	500
20	123	267	31	22 - 41	500
12	74	274	21	14 - 28	500

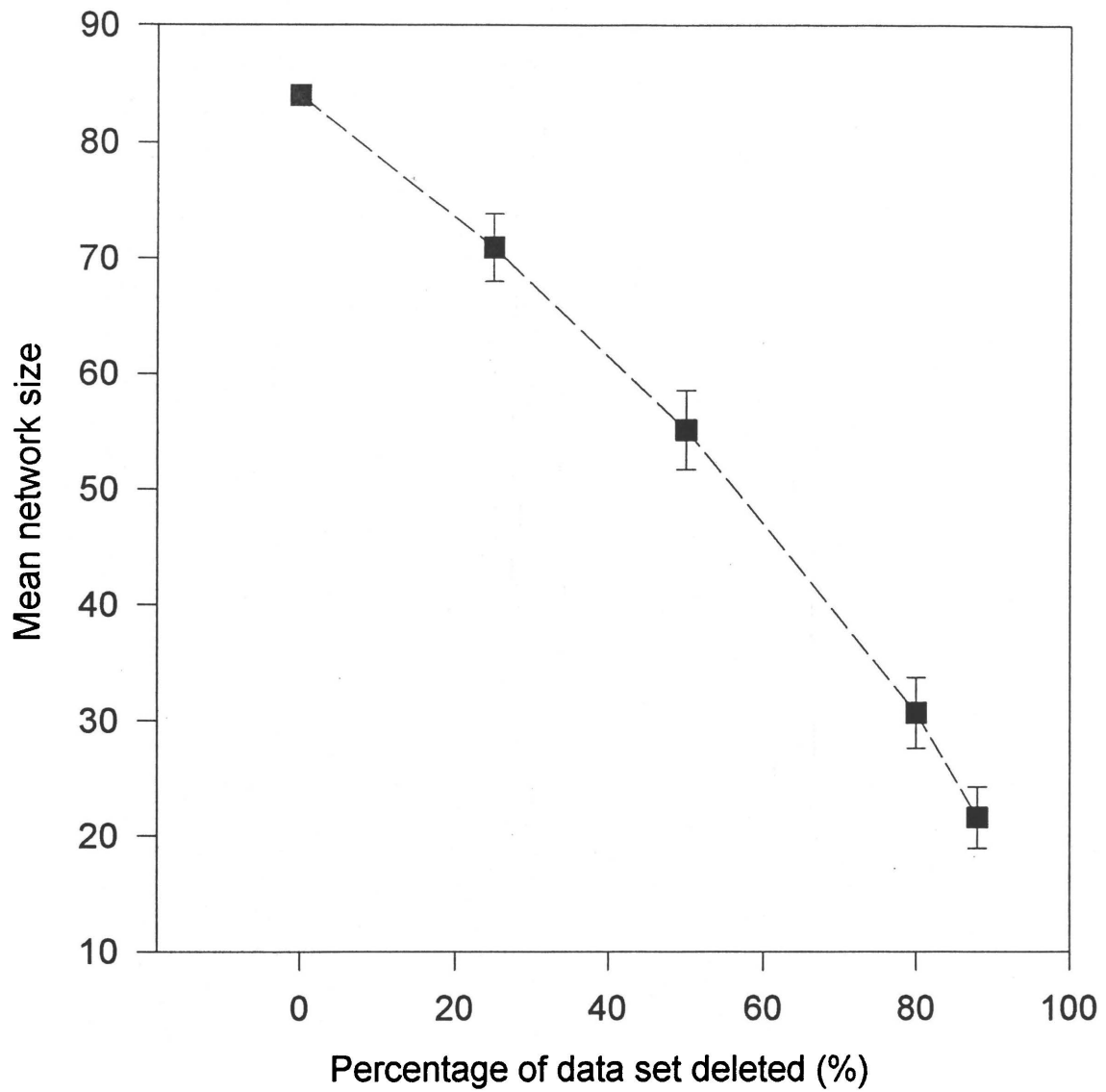


Figure 1. Mean network size selected as representative networks at different levels of species deletions

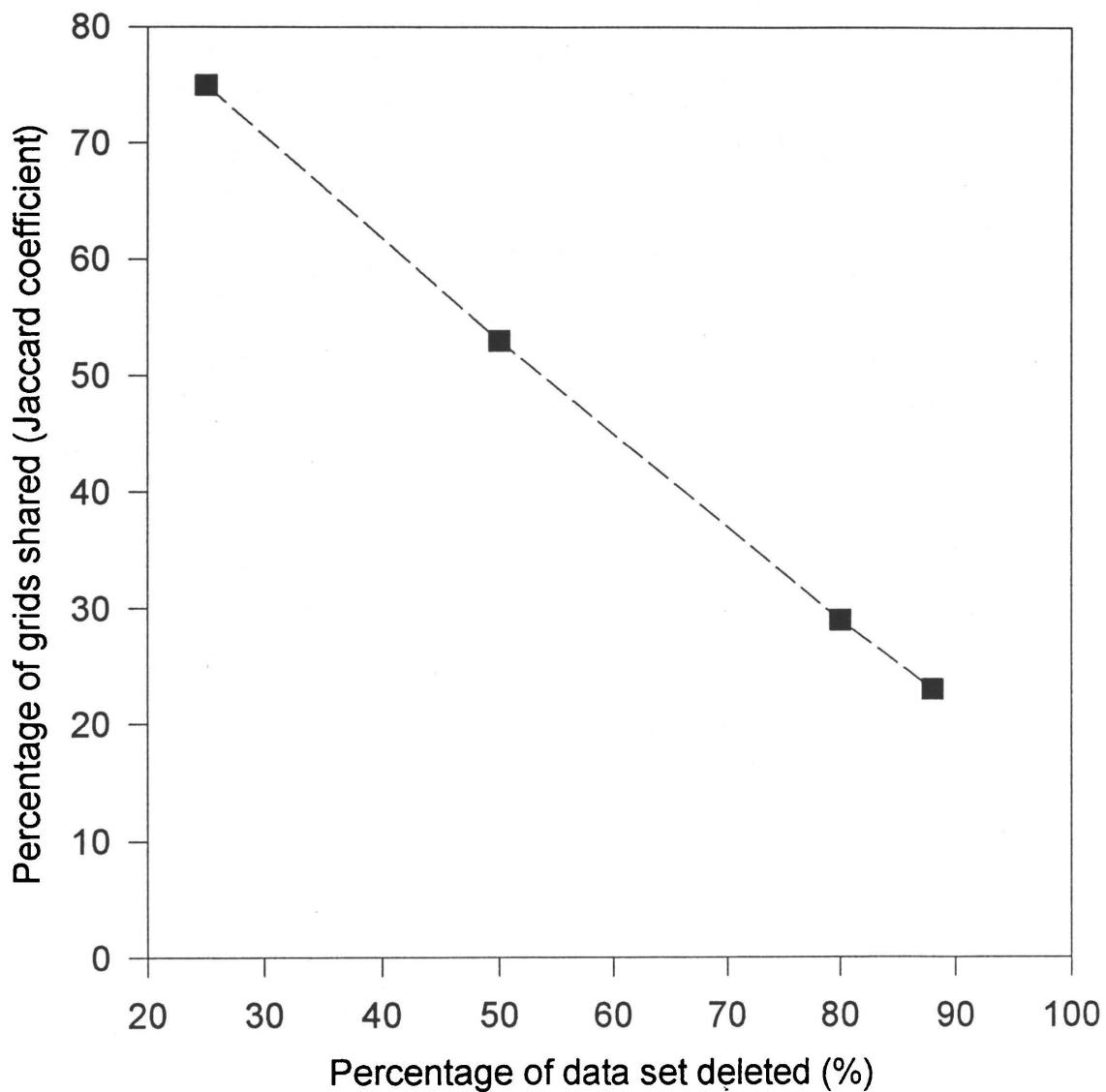


Figure 2. Degree of spatial congruence (in terms of % grid cells shared) among multiple networks (n = 30) random networks selected at different species deletion levels

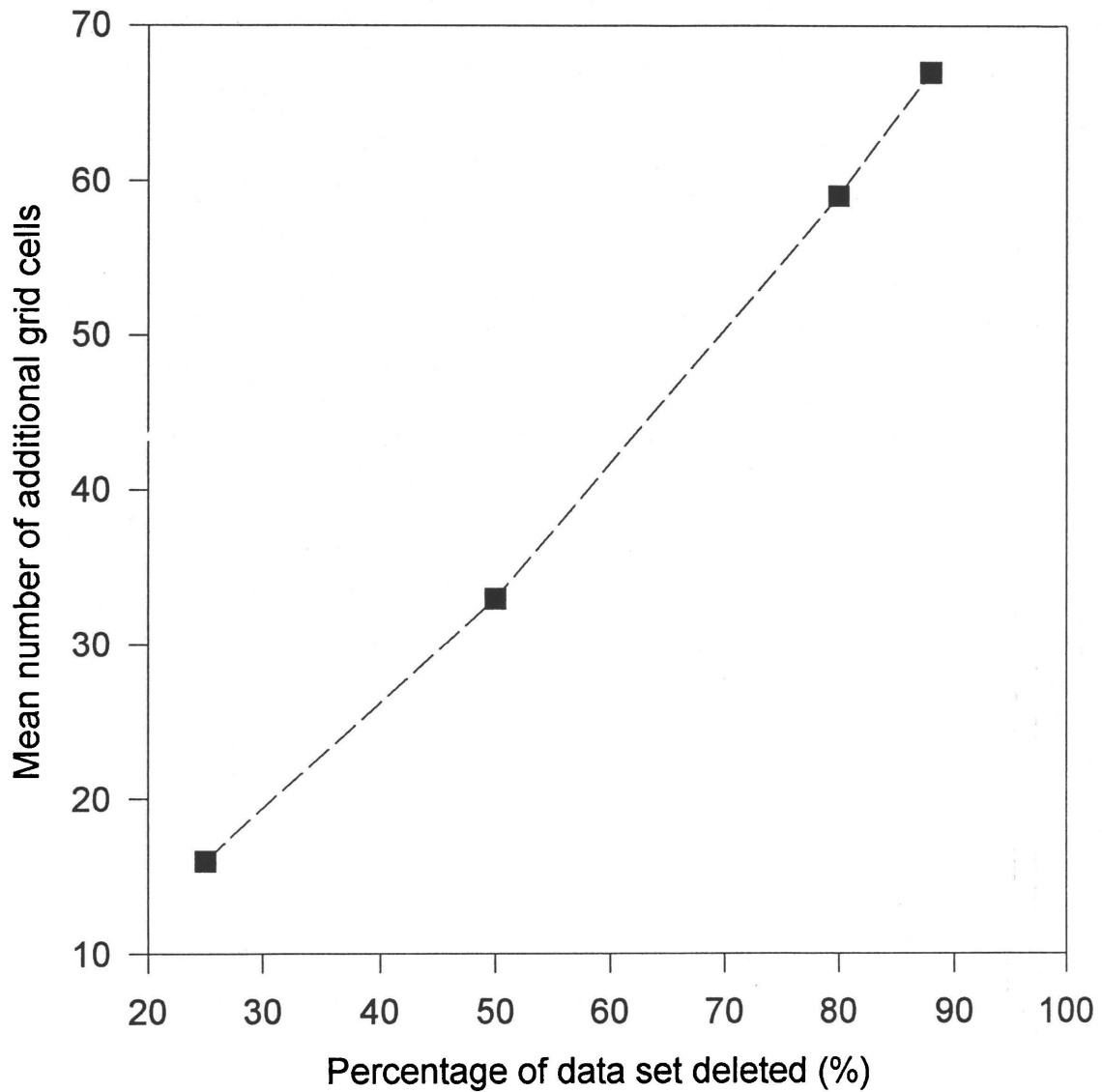


Figure 3. Mean number of additional grid cells required to complete species representation after pre-selection of grids selected in sensitivity analysis

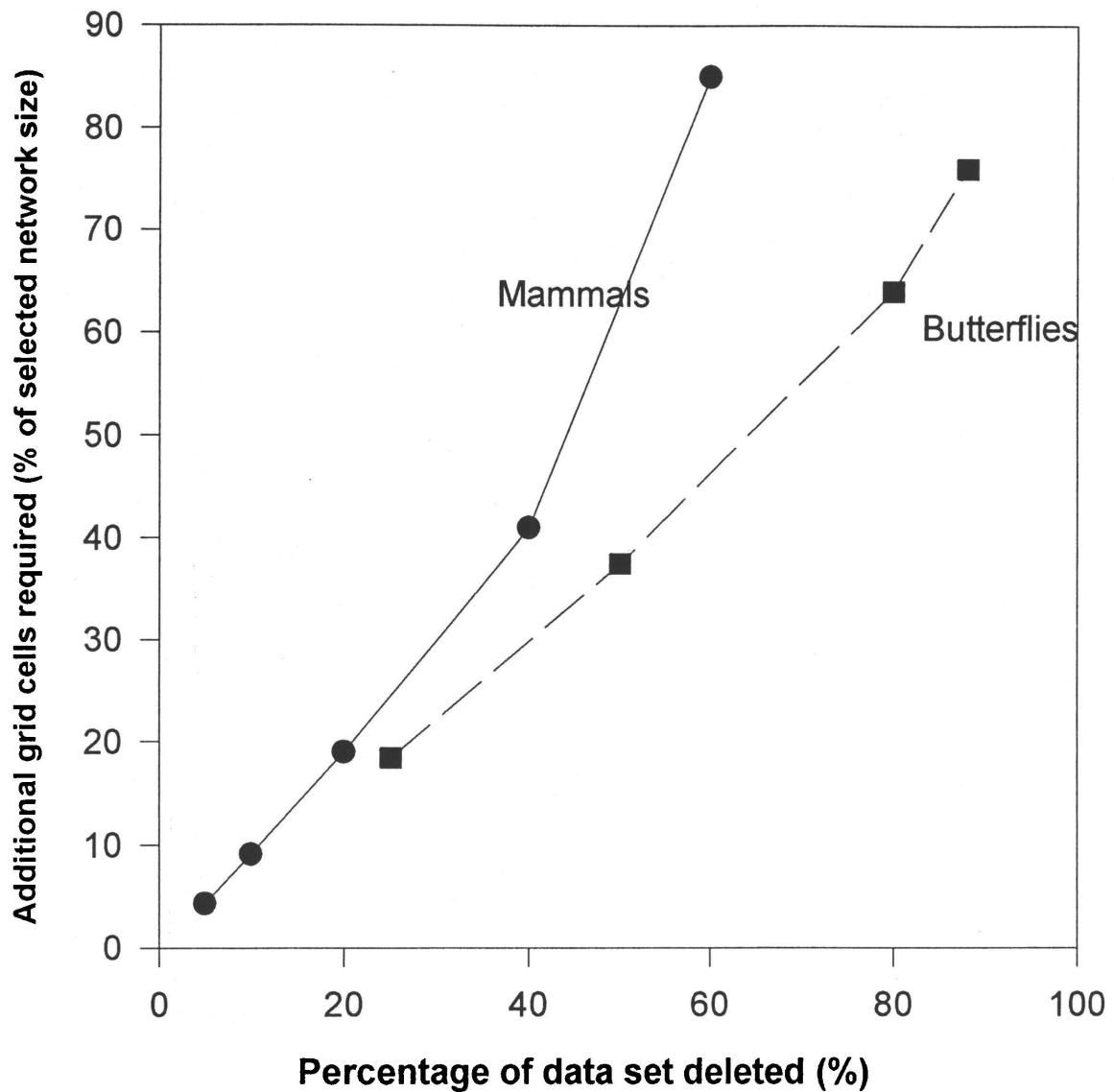


Figure 4. Observed relationships between data deletion levels the additional grid cells required, expressed as a percentage of the selected network size at that deletion level. Mammal data extracted from Freitag & van Jaarsveld (1998).

Discussion

When making critical conservation decisions, use is often made of input databases that are less than complete. Although the importance of using adequate databases and the use of data interpolation techniques have been frequently discussed (Nicholls & Margules 1993; Margules & Redhead 1995), iterative reserve selection algorithms do not make adequate provision for databases poor in species resolution. As improving the taxonomic knowledge of taxa requires considerable inputs (Cracraft 1995), it is important that we develop an understanding of the consequences of using input databases of varying taxonomic resolution in conservation planning (Freitag & van Jaarsveld 1998).

Freitag & van Jaarsveld (1998) observed that the systematic perturbation of a mammal database from South Africa resulted in predictable responses by conservation area selection procedures. Increased species deletion levels led to increased conservation network land-use efficiency, increased variability in the specific sites selected and decreased spatial overlap among potential conservation network options. The butterfly database used in the present study responded in a similar fashion, with the degree of spatial overlap declining below 50% once 50% of the species database had been deleted (Fig. 2; Freitag & van Jaarsveld 1998). Ideally, therefore, the input data set should not be less than 85% complete (Fig. 3).

In addition, the use of databases poor in species also impacted negatively on the long-term land-use efficiency of conservation planning by requiring more additional grids in order to finally completely the representation of all species (Fig. 3). This outcome indicated that the implementation of a conservation network based on groups where species are poorly known is detrimental to the long-term land-use efficiency of conservation (Freitag & van Jaarsveld, 1998).

In terms of the number of additional grid cells required, the most important differences between the two studies conducted to date, is the spatial extents of the studies (butterflies 3 x area) and the degrees of data deletion (butterflies 88% vs 60% for mammals). These factors, obviously affect the absolute short falls in grid cells. However, the additional grid cells required expressed as a

percentage of network size at that deletion level, followed the degree of database deletion is a near proportional manner, with some variation between the two studies (Fig. 4). If these preliminary findings prove to be robust in studies across different scales and taxa, it may provide a basis for predicting the numbers of additional grid cells required to complete reserve networks, currently generated from incomplete data sets. Expert-derived estimates about the numbers of potential species expected in certain taxa (Scholtz & Chown 1995) could form the basis for such predictions.

More specifically, the results of this sensitivity analysis have important implications for the termite database. When a database containing 12% of established species is used in determining conservation area networks, the initial network size is obviously relatively small. However, under these conditions the spatial congruence among multiple network options is low (Freitag & van Jaarsveld 1998; present study). If priority areas are implemented based on the termite database (Muller *et al.* 1997) and the available distribution data increases to include more species, a large number of additional grids will be required to represent these additional species. This acquisition process may be difficult given current land-transformation trends.

In conclusion, although implementing priority areas based on data that represents all species is ideal, practical, logistic and financial constraints do not always allow for this. The present study confirms that implementing priority areas based on data that represent less than 50% of the species affects long-term conservation land-use efficiency. Thus, ideally only databases containing not less than 50% of the species should be used in conservation network determinations. On the other hand, ignoring available data, even for a limited number of species may condemn them to extinction, and may require sensitive trade-offs between immediate biodiversity gains versus long-term land-use efficiency/ availability. Consequently, a predictive capacity about the land-use implications of alternative conservation strategies, reflecting degrees of data completeness, could prove invaluable.

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CHAPTER FOUR

The status of butterfly conservation in South Africa – a two-tiered and species assemblage approach.[♣]

The amateur collector, ease of sampling, and conspicuous nature of butterflies have all contributed to them being an extensively surveyed taxonomic group (Williams & Gaston, 1994; Owen, 1971). Butterflies have also been suggested to be valuable biodiversity indicator taxa (Samways, 1993; Prendergast *et al.* 1993).

Approaches to butterfly conservation have been varied. Red Data books are useful tools for the identification of species at risk of extinction (Warren *et al.* 1997). These Red Data lists are drawn up based on IUCN criteria (endangered, vulnerable, rare and indeterminate) and although these criteria have been revised (IUCN, 1994) it does result in species orientated conservation efforts (Larsen 1995). Unfortunately these lists exclude a large proportion of species because of limited available information. The Ruimsig Entomological Reserve established to protect the Roodepoort Copper *Aloeides dentatis* (Swiestra) is a good example of just such a species-specific conservation action. Another relevant conservation initiative is the South African National Heritage Program which aims to protect endangered species like the Karkloof Blue *Orachrysops ariadne* (Butler) and Brenton Blue *Orachrysops niobe* (Trimen) (see New, 1991 for international case histories).

[♣] Short communication submitted: Muller, C., Krüger, M., Scholtz C.H. & van Jaarsveld, A.S. The status of butterfly conservation in South Africa – a two-tiered and species assemblage approach.

Single species conservation plans for invertebrate species require a great deal of time and input because it requires a thorough knowledge of distribution and population dynamics (Erlich, 1992). The majority of such conservation areas were allocated on a species-specific *ad hoc* basis (Gotmark *et al.* 1986) and this resulted in an uneven representation of biodiversity in most reserves. Many South African National Parks are able to preserve some butterfly species but it is those species that fall outside their boundaries that are our main concern. This paper assesses the distribution of butterfly species within formally protected areas and proposes an alternative conservation strategy that aims to protect all species, regardless of their conservation status. This is in line with recent developments in the field of conservation planning and conservation area delimitation (Pressey *et al.* 1993; Williams *et al.* 1996; van Jaarsveld *et al.* 1998).

A butterfly distribution database was obtained from the Transvaal Museum. Raw data were collated and untraceable and / or ambiguous localities were excluded from the final analysis. Sampling localities were transformed to 15' X 15' grid cells with the aid of a gazetteer. The input database reflects presence only data and the 10196 distribution records reflect the presence of 613 species (94% of estimated total) in 600 grids cells throughout the country (total 2014 grid cells).

A conservation area network was identified using an iterative adjacency-constrained algorithm (Nicholls & Margules, 1993). This algorithm identifies the nearest minimum set of areas which represents each species at least once (Gaston & Williams, 1993). Species that occur in grids which fall partially or completely within existing conservation areas were identified to establish how many species were currently being represented in protected areas. The extent of protection afforded each grid cell was determined (<25 %, 25, 50, 75 and 100 % of the total area) and the degree of species representation based on these calculations evaluated.

The extent of formal protection afforded endangered, vulnerable or rare species was evaluated to determine how many threatened species are found in unprotected areas. Additional grid cells required to conserve all species outside formally protected areas were also determined by preselecting protected grids prior to running the algorithm.

The near minimum set of grid cells required to represent each butterfly species at least once is illustrated in figure 1. Eighty-four grid cells were required for total butterfly species representation. These grid cells are scattered around the entire country but are conspicuously absent from the south-central regions. Only 27 of the 84 grid cells (32%) are partially protected in formally protected areas (table 1).

Eighty-four percent of the 613 species considered were found within grid cells that have some degree of formal protection (243 grids). Sixty-three percent, 53, 19, and 25 % of butterfly species were found in grid cells with 25%, 50, 75, and 100 % formal protection respectively. This translates into a quarter of the species with guaranteed protection while some 224 protected grid cells overlap with other forms of land use. Twenty-seven species from the selected Red Data categories were limited to unprotected grid cells (Appendix 1). The distribution of endangered subspecies within protected areas as well as any recent conservation measures is still under investigation. Fourteen Red Data species occur in at least partially protected grid cells. When preselecting grid cells within existing conservation areas, the number of additional grid cells required to complete species representation varied between 18 and 208 (table 1).

The principal threat to many butterfly populations throughout the world is habitat destruction (Henning & Henning 1996; Warren *et al.* 1997; Grundel *et al.* 1998; New, 1991; Robbins & Opler 1997). Unfortunately this is not easily avoided given the nature of human requirements and activities (Cohen 1997).

National Parks and provincial conservation areas do contribute to the protection of species found within their borders but often it is the rare or threatened species which occur outside these boundaries. Two hundred and twenty four 'protected' grid cells share their area with other forms of land use. It must not be ruled out that some species may occur outside the boundaries of the reserves and are experiencing habitat destruction.

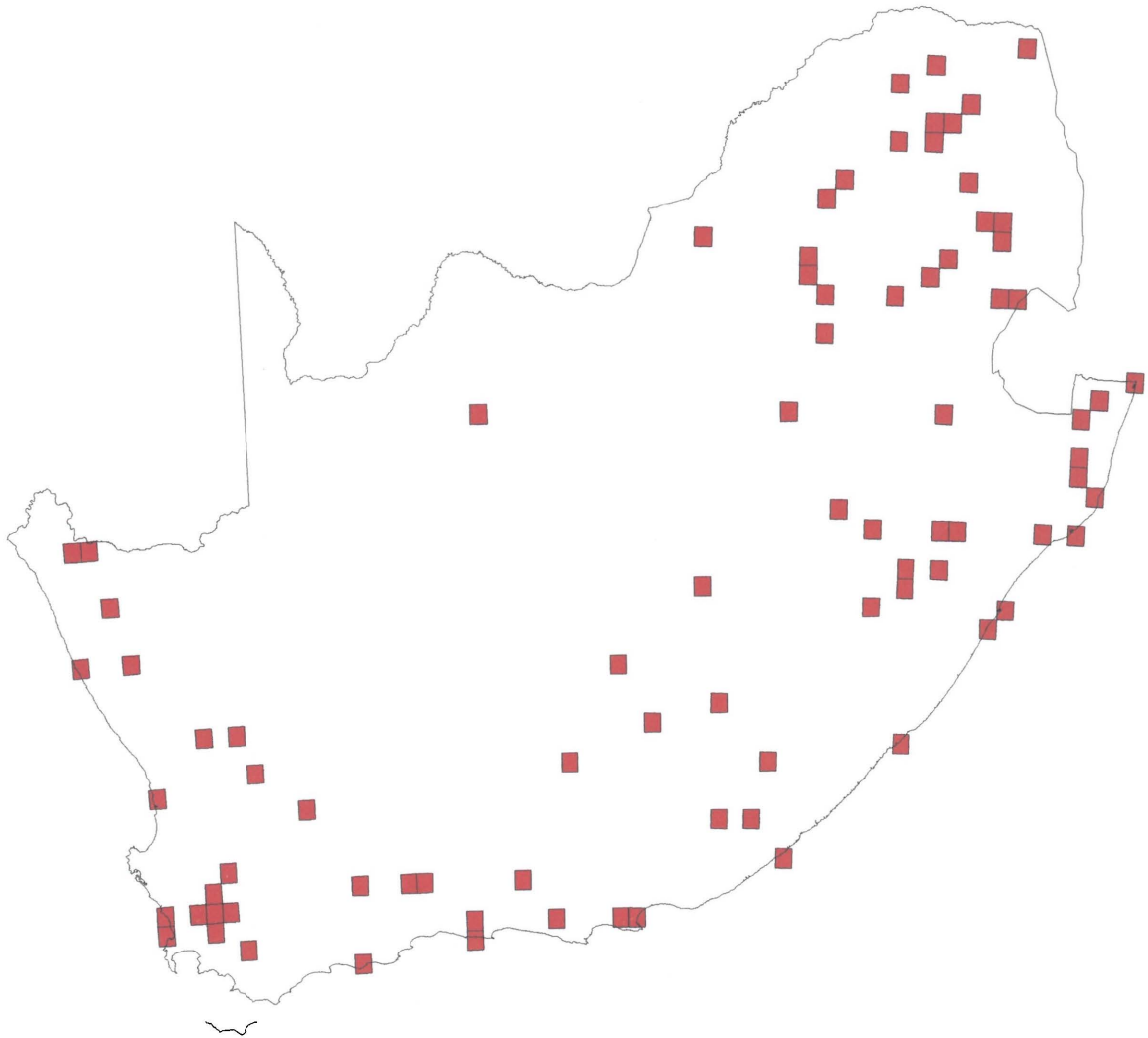


Figure 1. Priority conservation areas network for butterflies in South Africa

Table 1. The number of grids from a priority areas network afforded formal protection and percentage species representation (n = 613) within varying conservation categories

Degree of formal protection	Species occurrence (%)	No. of grids in priority areas network ¹ (total 84)	Number of additional grids required after preselection
any protection	84	27	208
25%	63	11	80
50%	53	3	45
75%	19	1	32
100%	25	1	18

1: Nicholls & Margules (1993)

Only 25 % of all butterfly species are found in grid cells where the entire area is under formal protection; 59 % are found in grid cells that are partially protected and 16 % occur in 'unprotected' grid cells. Nine unprotected species are considered as threatened and have high priority conservation status.

By employing the adjacency constrained algorithm a priority areas network is identified which encompasses all species regardless of conservation status. Only 84 grids are required for complete species representation. Forty-three of the 84 grids from the network benefit from some degree of formal protection. When these protected grid cells are preselected, the number of additional grids required increases dramatically (table 1) and leads to a decrease in land-use efficiency. The findings are consistent with Hull *et al.* 1998 and Muller *et al.* 1997, using Buprestid and termite data respectively.

A two-tiered conservation strategy will fulfil two roles:

- a) provide crisis management for species with the highest conservation priority (e.g. endangered species in unprotected / threatened habitats). Conservation initiatives are already in place which support finer-scale habitat protection.
- b) select a broad scale conservation area network. This aim of this network is to represent maximum diversity and a monitoring programme for the slower decline of less threatened and / or abundant species.

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Appendix 1. Red Data list species limited to unprotected grid cells in South Africa.

Species	Red Data category
<i>Oxychaeta dicksoni</i> (Gabriel)	V
<i>Dingana alaedeus</i> Henning & Henning	R
<i>Toryensis orangica</i> Vári	R
<i>Pseudonympha paragaika</i> Vári	R
<i>Charaxes pondoensis</i> Van Someren	R
<i>Auslauga australis</i> Cottrell	R
<i>Thestor kaplani</i> Dickson & Stephen	R
<i>Thestor pringlei</i> Dickson	R
<i>Aloeides dentatis dentatis</i> (Swiestra)	R
<i>Aloeides clarki</i> Tite & Dickson	R
<i>Poecilmitis lyncurium</i> (Trimen)	R
<i>Poecilmitis aureus</i> Van Son	R
<i>Poecilmitis wykehami</i> Dickson	R
<i>Poecilmitis penningtoni</i> Riley	R
<i>Poecilmitis kaplani</i> Henning	R
<i>Poecilmitis stepheni</i> Dickson	R
<i>Poecilmitis adonis</i> Pennington	R
<i>Bowkeria phosphor phosphor</i> (Trimen)	R
<i>Lepidochrysops badhami</i> Van Son	R
<i>Lepidochrysops jamesi jamesi</i> Swanepoel	R
<i>Lepidochrysops littoralis</i> Swanepoel & Vári	R
<i>Lepidochrysops oosthuizeni</i> Swanepoel & Vári	R
<i>Orachrysops ariadne</i> (Butler)	R
<i>Colotis doubledayi angolanus</i> (Talbot)	R
<i>Coeliades anchises</i> (Gerstaecker)	R
<i>Metsisella syrinx</i> (Trimen)	R
<i>Platylesches tina</i> Evans	R

CHAPTER FIVE

Higher-taxon surrogacy: implications for the conservation of South African butterflies. †

Abstract

Biodiversity management requires detailed inventories of the distribution of species. Limited financial and human resources do not allow us to count all species in a region. Higher-taxon surrogacy is one method for estimating species richness that has drawn much attention but the implication for site selection is poorly documented. The correlation between higher-taxon richness (subfamily and genus levels) and species richness was determined for butterflies in South Africa. Sets of priority areas were generated using the higher-taxon data sets. The representation of species in these networks was quantified. There is a strong positive correlation between higher-taxon richness and species richness. However between 34% and 76% of species will not be represented in higher-taxon networks. Thus higher-taxon surrogacy is not an effective tool for the conservation of butterfly species in South Africa.

† MS submitted: Muller, C., van Jaarsveld, A.S., & Krüger, M. & Scholtz, C.H. Higher-taxon surrogacy: implications for the conservation of South African butterflies.

Introduction

Biodiversity is not only the diversity of species but the diversity of life at various levels of nature's hierarchy (Noss, 1990; Stork, 1994; Heywood, 1994; McNaughton, 1994). However, species diversity (richness) is a frequently employed measure for estimating the biodiversity value of areas and is routinely used to identify conservation areas (Myers, 1990; Prendergast *et al.*, 1993; Reid, 1998). This is despite frequently expressed reservations about the use of species richness for identifying potential conservation areas in favour of a more rational approach towards representing species (Pressey *et al.*, 1993; Williams *et al.*, 1996).

One case for including areas rich in species in conservation networks comes from adopting an evolutionary-ecological perspective to conservation (Soulé & Wilcox, 1980, Frankel & Soulé, 1981, Soulé, 1986). This view essentially extends a strictly pragmatic representation conservation goal (Pressey *et al.*, 1993) to incorporate an added goal to reduce the risks of extinction (Fjeldså, 1994). Here areas that are comparatively rich in species are viewed as regions: (1) containing larger numbers of restricted range species, (2) where large numbers of species accumulate, or (3) that act as centres of diversification (see Fjeldså, 1994). In each of these instances a case can be made for conserving species rich areas that underpin such evolutionary-ecological processes.

Moreover, species are an accepted fundamental unit of conservation evaluation (Peet, 1974; Crow *et al.*, 1994; Gaston *et al.*, 1995) and it is impossible to count all species in a region (Gaston & Williams, 1993; Faith & Walker, 1995; Gaston, 1996). Consequently, conservation biologists continue to explore methods for estimating species richness. One approach is to use higher taxon richness as a surrogate for species richness but requires a strong correlation between these parameters (Andersen, 1995). This has been investigated at regional (Prance, 1994; Beccaloni & Gaston, 1995; Andersen, 1995; Balmford *et al.*, 1996a; 1996b) and global (Eggleton *et al.*, 1994; Williams *et al.*, 1994; Gaston *et al.*, 1995; Gaston & Blackburn, 1995; Williams *et al.*, 1997) scales, with varying results.

Studies that support the higher-taxon approach are mostly from temperate data sets (but see Balmford *et al.*, 1996a; 1996b). However, there is some concern regarding the value of this technique for identifying richness hotspots in the tropics (Prance, 1994; Anderson, 1995; Balmford *et al.*, 1996a).

The present paper explores the spatial relationships between (1) richness patterns and (2) complementary-based representative networks generated for butterflies species and higher systematic groupings from South Africa. The region represents a transition zone from sub-tropical to temperate areas (Low & Rebelo, 1997).

Material and Methods

The butterfly data set was selected as they are well surveyed and the group is systematically well known in South Africa (some 94% of known species – Owen, 1971). Moreover, butterflies are frequently recommended indicator taxa (Brown, 1991; Samways, 1993). Presence only distribution data obtained and collated from the Transvaal Museum were generalized to 15' x 15' grid cells (approx. 25 km x 25 km) for the entire South African region. The 10196 distribution records included 613 species, 155 genera, 17 subfamilies (Hesperiinae, Pyrginae, Coeliadinae, Polyommatainae, Lipteninae, Theclinae, Lycaninae, Miletinae, Liphyrinae, Nymphalinae, Acraeinae, Satyrinae, Danainae, Charaxinae, Libythinae, Papilioninae and Pierinae) and five families. Records were standardized to recent taxonomies (Pennington, 1994). Butterfly distributions were examined at species and higher taxonomic levels (subfamily and genus).

Species, genus and subfamily richness was summed within each of the 600 data-containing grid cells. The species distribution database was not evaluated for spatial autocorrelation because biologically interesting patterns are inadvertently disregarded when removing the autocorrelation (Williams & Gaston, 1998).

The relationship between higher-taxon richness and species richness was tested for the entire study region using product-moment correlation following log₁₀-transformation of data. The relationship between selection order (rank) of the grid cells was tested using Spearman's rank correlation (Sokal & Rohlf, 1981).

Three separate distribution databases that reflect the distributions of species, genera and subfamilies were generated. At each taxonomic level, complementary sets of areas were identified using a routinely employed area selection algorithm (Nicholls and Margules, 1993). The generated conservation area networks represent their respective species, genera or sub-families at least once using the principle of complementarity.

In addition, individual grids from the higher-taxon complementary sets (Genus and sub-family levels) were evaluated for the numbers of species they inadvertently sampled. The degree of spatial congruence among the three conservation area networks was also assessed using the Jaccard coefficient (Gotelli and Graves, 1996; van Jaarsveld *et al.*, 1998; Freitag and van Jaarsveld 1998).

Results

The observed relationship between species richness ($n = 600$) and higher taxon richness is illustrated in Fig. 1, and was statistically significant at each taxonomic level (Fig. 1. Subfamily: $r^2 = 0.90$, $p < 0.05$, genus: $r^2 = 0.958$, $p < 0.05$). The strength of this relationship was strongest between species richness and genus richness and less so between species richness and sub-family richness.

There was also a significant positive rank correlation between species and higher-taxon richness (Fig. 1: (a) $r_s = 0.95$, $n = 600$; $p < 0,001$ (b) $r_s = 0.99$, $n = 600$; $p < 0,001$). This suggests that when identifying richness hotspots using higher-taxa the set of grid cells selected was not altered

significantly. An assessment of congruence between richness hotspots indicated that species and genera hotspots overlap by 88% while species and family hotspots overlap by 69% (Table 1). Thus, the relationship between species and subfamily richness is influenced by grid cells other than the top 5% species rich grid cells.

The number of grid cells required to represent each taxon in a conservation area network is provided in Table 1 together with the maximum number of species each network could potentially represent. Consequently, representing each subfamily or genus at least once will increase efficiency in terms of sites required but effectively means that between 34 and 76% of butterfly species will not be included in priority networks. The spatial congruence was minimal at 0.05% and 0.21% between species and subfamilies and species and genera respectively due to these different network sizes required.

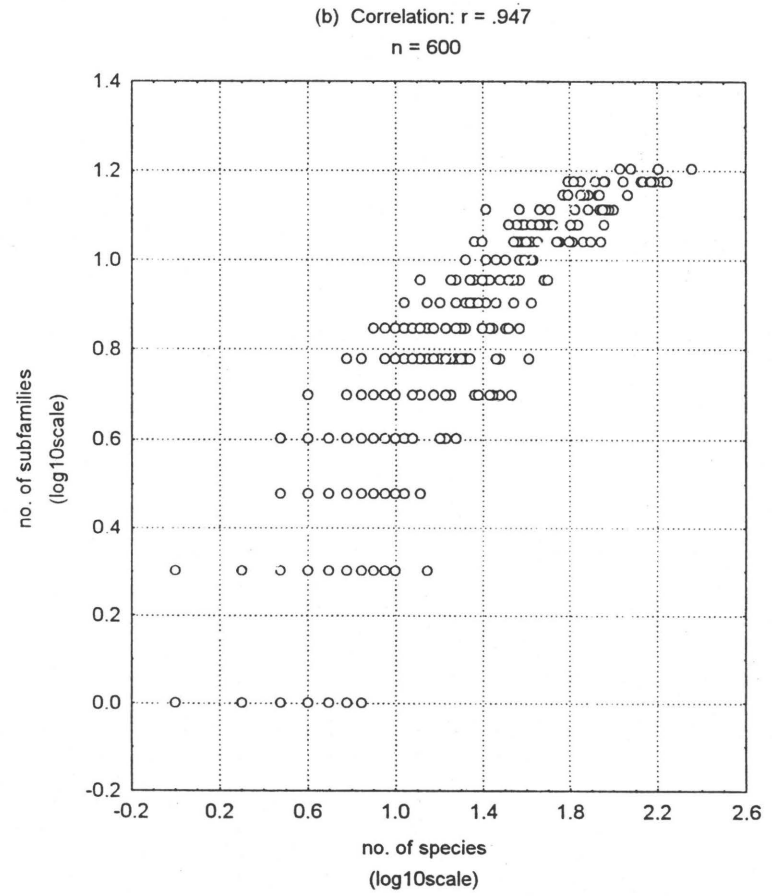
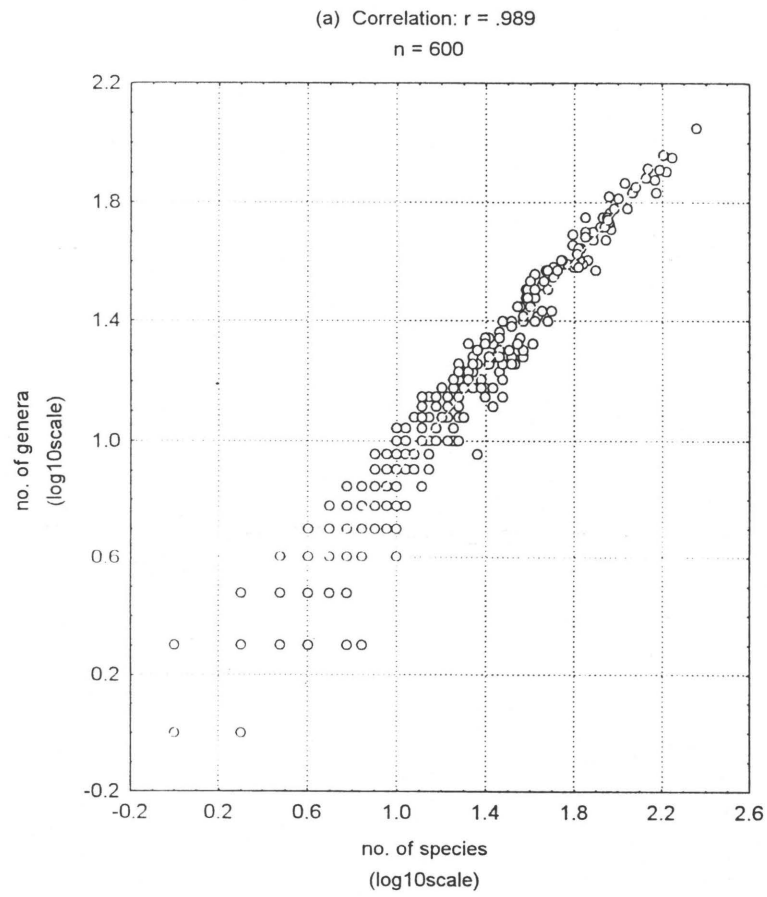


Figure 1. Species richness in relation to a) genus richness and b) subfamily richness for butterflies in South Africa

Table 1. Comparison of priority area networks generated at three taxonomic levels

	Taxonomic level		
	Species	Genus	Subfamily
Total number of grids selected	84	13	2
Jaccard coefficient of overlap with species complementary set	–	0.21	0.05
Jaccard coefficient of overlap with species hotspots	–	88	69
Max. number of species represented	613	403	150

1: Jaccard coefficient: Gotelli & Graves (1996)

Discussion

Despite the positive correlation between species and higher-taxon richness for butterflies in South Africa, this approach to surrogacy holds little promise for strategic conservation planning. Higher-taxon surrogacy at the genus level appears to be more efficient than subfamily-based surrogacy when predicting overall richness. This is consistent with findings of McAllister *et al.* (1993) in coral reef fishes, but Andersen (1995) found that the number of Australian ant genera were poor predictors of species level richness. This inconsistency suggests that the usefulness of the taxonomic level used as a substitute is case-specific (Balmford *et al.* 1996a).

Rank correlation behaved in much the same way, with neither subfamily or genus richness significantly altering the sequence in which grids would be prioritised. This result would prove to be significant if the goal of higher-taxon surveys were merely to rank the relative richness of sites (Balmford *et al.* 1996a). It is impractical to assume that all sites will receive priority attention during conservation planning and hotspots (defined here as the top 5% taxa rich sites) are often targeted (Prendergast *et al.* 1993). This implies that one third of the sites that would have been targeted for their species diversity may receive little or no attention if we set aside subfamily hotspots. Richness is not an effective tool for conservation planning (Williams *et al.* 1996). Complementary sets generated at the three taxonomic levels showed little spatial overlap and spatial congruence of networks across groups does not improve (Van Jaarsveld *et al.* 1998).

Balmford *et al.* (1996b) found that for woody plants in Sri Lankan forests higher-taxon surrogacy does perform well during priority-setting (species loss of 7-10%). However the effect that higher-taxon data has on possible species loss has received little attention in the past and further assessment is required.

For the purpose of the present study we are primarily concerned with protecting the species component of diversity. Selecting priority areas at higher taxonomic levels will have severe implications and possibly lead to the loss of many butterfly species. This study reveals that while protecting higher taxa diversity up to 76% of the species will be at risk. Higher-taxon surveys will prove more cost effective but for conservation purposes species data are preferable if we want to minimize the risk of losing valuable butterfly species in South Africa.

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CHAPTER SIX

Synthesis

Insects make up approximately three-quarters of all terrestrial species and are therefore considered important components of biodiversity. Comparatively, little work has been done on the total insect fauna of any one geographical region. For the purpose of biodiversity studies, the best groups to consider should be taxonomically well described and their distribution data readily available. In this way different areas can be compared and the appropriate conservation areas selected (Samways, 1993). The termites and butterflies were selected as study groups based on these criteria.

In order to develop methodologies for the preservation of termite and butterfly species the following factors must be taken into consideration: (i) conservation goal, (ii) site selection procedures, (iii) taxonomic level and (iv) data set quality.

Both termites and butterflies were found to be good candidates for conservation initiatives, however their conservation requirements differ. Termites (as ecosystem engineers; Jones *et al.* 1994) form an important component of both conserved and production landscapes. It is therefore impractical to set aside conservation areas solely for the protection of termite species. A more practical approach is a core conservation network based on a multi-criteria algorithm (chapter one) and a second network which will facilitate the monitoring of the relationship between termite species and other forms of land-use.

The importance of butterflies include their roles as pollinators, indicators of habitat health and their high esthetic value (New, 1991). They require a more explicit conservation strategy because of their intimate relationship with their habitat. To secure the continuation of species the protection of individual habitats is required. In chapter 4, I propose a dual conservation strategy. A priority areas

network will strive to represent maximum species diversity while species orientated conservation gives highest priority to threatened species.

Unfortunately the existing reserve network does not adequately contribute to the protection of either termites or butterflies (chapter 1 and 4). This is largely due to the fact that reserves were allocated on an *ad hoc* basis (Gotmark *et al.* 1986). Preselecting conserved grids and subsequently adding unrepresented species to the priority network results in low land-use efficiency. Acquiring large numbers of additional grids will be difficult given current land-transformation trends (chapter 1 & chapter 4).

In chapter 1 a comparison was made of different site selection procedures. Applying the principle of complementarity proved to be more land-use efficient than selecting sites based on species richness (Williams *et al.* 1996). Complementary-based algorithms differed marginally in terms of their efficiency, but this should be evaluated using other taxa.

The effectiveness of higher-taxon surrogacy (chapter 5) was tested using the butterfly data. Higher-taxon surrogacy at the genus and subfamily proved to be an efficient tool for predicting overall species richness but priority area networks generated using higher-taxa data failed to represent a large proportion of species.

The sensitivity analysis in chapter 3 highlights the risks associated with implementing conservation areas based on species-poor data sets. The butterfly data set was systematically perturbed and the spatial congruence at the different deletion levels quantified. The implications for the species-poor termite data set was evaluated. Implementing conservation area selection procedures using data that represents less than 50% of the species will spatially compromise future site selection procedures. It is suggested that a sensitivity analysis form an integral part of conservation planning.

In conclusion, insect conservation requires an approach that moves away from traditional conservation strategies. From this study it is evident that different insect taxa have different conservation requirements. Further studies of a broad range of insect taxa will enable us to develop suitable conservation approaches.

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Biodiversity Assessment and Conservation Strategies

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Biodiversity Assessment and Conservation Strategies

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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 (Mymeleontidae), 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
<i>Priority conservation areas</i>								
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
<i>Complementary species sets</i>								
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								
<i>Complementary sets representing different taxonomic levels</i>								
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 species-poor, 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

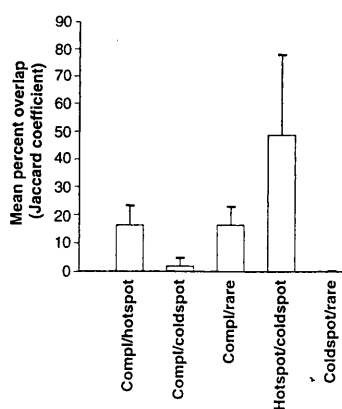


Fig. 1. The degree of spatial overlap (mean ± SD of Jaccard coefficient) between conservation areas generated by means of different prioritization criteria (species-based complementary areas, richness hotspots and coldspots, areas containing rare taxa).

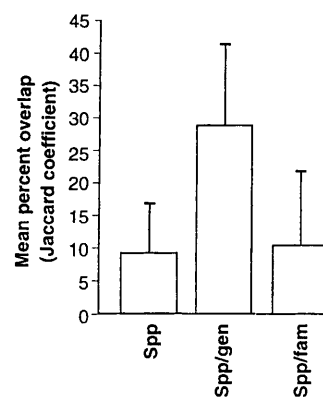


Fig. 2. The degree of spatial overlap (mean ± SD of Jaccard coefficient) among species-based complementary sets across higher taxonomic groupings (that is, species-based surrogacy) and overlap between the species-based priority conservation sets and sets generated by means of genus and family level data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

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