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BIODIVERSITY ASSESSMENT AND CONSERVATION  
PLANNING: THE GRADSECT SURVEY METHOD AND THE  
USE OF LOCAL SCALE SURROGATE INFORMATION

MSc

UP

1997

**Biodiversity assessment and conservation planning: the  
gradsect survey method and the use of local scale surrogate  
information.**

by

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Submitted in partial fulfilment of the  
requirements for the degree of  
M.Sc.

in the Faculty of Biological and Agricultural Sciences  
University of Pretoria  
Pretoria

September 1997

## Acknowledgements

I would like to begin by thanking De Beers Consolidated Mines, Farms Department (Mr. Graham Main in particular) for their financial and logistical support. Thank you for a unique opportunity to test theories on data gathered in the African bush.

Many thanks to the Foundation for Research Development and the University of Pretoria for financial assistance which allowed me to embark on this study.

A special word of thanks to the staff of the Venetia-Limpopo Nature Reserve. Thank you to the game scouts for their company and timely advice on avoiding the lions and elephants. To Wayne Boyd, thank you for your assistance and friendship. My sincere thanks to Nigel and Merry Fairhead for their hospitality and for assuring that I did not end up as a hunter's trophy.

To Philip Richardson, thank you for initialising the project and allowing me to carry your fire arm in the field.

Thank you to Danita Hayes for helping me with figures and maps of the thesis. To my fellow students in the Conservation Planning Unit, thank you for adding some colour to the dullest days.

Dr. Mike van der Linde is acknowledged for the SAS programming of the bootstrap procedures and the generation of subsequent graphics. Jackie Grimbeek is acknowledged for refining and interpreting the statistical tests within the bootstrap procedures and writing the mathematical notation of the methods. To both these co-authors of Chapter 2, thank you for your endless patience and for believing in this project. Thanks to Dr. Endrödy-Younga and Dr. Adrian Davies for helping me with the identification of the dung beetles.

I would like to thank Chris Margules, Michael Austin, and Dan Faith (all of the Division of Wildlife and Ecology, CSIRO, Australia) for their advice and comments on drafts of the papers and particularly to Chris for his inputs into developing the ideas tested in Chapter 3.

I express my appreciation and thanks to Stefanie Freitag (co-author of Chapter 3) for writing the algorithms and providing indispensable guidance. Also, thanks to Prof. C.H. Scholtz who took up the task of co-supervisor at short notice.

My sincerest gratitude to my parents for their unconditional support during this study period.

Finally, my sincerest thanks and appreciation to my supervisor Albert van Jaarsveld for introducing me to conservation biology, for stimulating creative ideas, for his patience and for providing a very enjoyable learning experience.

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## **CHAPTER 1**

### **General Introduction**

## CHAPTER 1

# General Introduction

Biological diversity or “Biodiversity” is the number, variety and variability of all living organisms on earth (Groombridge, 1992). It encompasses diversity at all levels of the biological hierarchy, from genes to species to ecosystems and includes the ecological processes that support them. Our planet is currently experiencing an unprecedented decline in biodiversity due to anthropogenic forces (Wilson, 1988; UNEP, 1995). The current species extinction rate exceeds historical global extinction rates by between 1000 to 10 000 times (Wilson, 1988), which overshadows the ability of evolutionary processes to create new variation such as species (Groombridge, 1992). In contrast to many other forms of biological capital, biodiversity has therefore become a non-renewable resource (van Jaarsveld, In press).

Biodiversity provides goods (e.g. medicines) and services (e.g. providing clean air and water) essential to supporting human livelihoods and aspirations (Ehrlich and Ehrlich, 1992; Kunin and Lawton, 1996; van Jaarsveld and Chown, 1996). Despite the lack of a clear theoretical framework, there is general consensus that an intricate relationship exists between biodiversity and ecosystem function (Martinez, 1996). Species may have current or future *commodity value* if they are products with market value or *amenity value* when recreational activities such as eco-tourism revolve around them (Norton, 1988). Biodiversity also has *option value*, which maximises human capacity to adapt to changing environmental conditions by maximising the

evolutionary potential of other species (Reid, 1994). In addition, species also have *inherent value* (Norton, 1988) which is not dependent on the uses to which we put them and humankind therefore has a moral and ethical responsibility to care for life on earth.

One of the first measures countries should take to conserve their biodiversity is to establish a protected area network which represents all the species and/or communities of a particular region. Existing protected areas throughout the world were primarily proclaimed on an *ad hoc* basis and are highly ineffective at representing regional biotas (Pressey, 1994). In response, systematic reserve selection procedures were developed to identify priority conservation areas that complement one another in terms of their contributions towards protecting regional biodiversity, while ensuring that minimal land allocation is required (Pressey *et al.*, 1993). However, the usefulness of systematic reserve selection procedures is primarily determined by the availability and quality of species distribution data (Nicholls and Margules, 1993; Margules *et al.*, 1994; Freitag *et al.*, 1996; Nicholls, in press). Biological surveys are therefore an essential pre-requisite for effective conservation planning.

Most countries have not yet accumulated sufficient data on which to base reserve selection procedures (Belbin, 1993; Margules and Williams, in press) and there is an urgent need for biological surveys to be conducted globally (van Jaarsveld and Chown, 1996; Haila and Margules, 1996). Conventional “statistical” (random or systematic) survey methods have proven to be logistically demanding and expensive (Gillison and Brewer, 1985). The novel, swift and cost-effective “*gradsect*” survey method orientates sampling along the steepest environmental gradients in order to



detect the maximum number of species within an area (Gillison and Brewer, 1985). This thesis evaluated the efficiency of the gradsect biological survey method by comparing it to random, systematic and habitat-specific survey methods, during faunal field surveys of the Venetia-Limpopo Nature Reserve (target groups: birds and dung beetles)(Chapter 2).

Although the gradsect biological survey method offers a very effective method for gathering field records, conservation decisions often have to be made in the absence of adequate species distribution data. In such cases the best strategy would be to select areas that represent the entire range of environmental variation of a region, assuming that these areas contain all the species of that region (Belbin, 1993). Systematic reserve selection procedures could be used to identify a reserve network which is representative of all relevant environmental classes (Pressey and Tully, 1994; Margules *et al.*, 1994). These environmental classes thus serve as surrogates for species. The value of “*land facets*” (defined as the smallest distinct units of the landscape with uniform slope, soils and hydrological conditions; Lawrance *et al.*, 1993) as biodiversity surrogates was investigated by testing whether they represent distinct species assemblages (Chapter 3).

Since conservation has to compete with various other land uses, reserve selection procedures have to be as efficient as possible, i.e. represent all relevant biodiversity elements within the smallest possible area (Pressey, 1994). Recently there have been rapid advances in the development of methods identifying reserve networks to represent environmental surrogate classes (Bedward *et al.* 1992; Wionarski *et al.*, 1996). In the present study, a Geographic Information System (GIS) was used to overlay a land facets map of the study area with a grid and calculate the extent of each

land facet within every grid cell (selection unit). Based on these data three alternative reserve selection approaches were compared in terms of their efficiency at achieving specified conservation goals (Chapter 3). These approaches respectively aimed to: (i) represent a nominated percentage area of each feature; (ii) represent every species at least once within the smallest number of assemblages, thus avoiding representing assemblages that do not contain unique species; (iii) rapidly increase the diversity of a reserve network by first selecting areas containing diverse species assemblages. The advantages and disadvantages of each approach are discussed.

The thesis therefore initially presents the most effective means of gathering species distribution data (Chapter 2), then introduces surrogate measures for when these data are not available (Chapter 3) and finally compares different procedures which select reserve networks based on the surrogate information (Chapter 3). In the final chapter the current shortcomings of reserve selection procedures as well as their refinement and future role in biodiversity conservation are explored (Chapter 4).

#### **References:**

- Belbin, L. (1993) Environmental representativeness: Regional partitioning and reserve selection. *Biol. Conserv.* **66**, 223-30.
- Bedward, M., Pressey, R.L. and Keith, D.A. (1992) A new approach for selecting fully representative reserve networks: addressing efficiency, reserve design and land suitability with an iterative analysis. *Biol. Conserv.* **62**, 115-25.
- Ehrlich, P.R. and Ehrlich, A.H. (1992) The value of biodiversity. *Ambio* **21**, 219-26.

- Freitag, S., Nicholls, A.O. and van Jaarsveld, A.S. (1996) Nature reserve selection in the Transvaal, South Africa: what data should we be using? *Biodiv. Conserv.* **5**, 685-98.
- Gillison, A.N. and Brewer, K.R.W. (1985) The use of gradient directed transects or gradsects in natural resource surveys. *J. Environ. Mgmt* **20**, 103-27.
- Groombridge, B. (1992) *Global Biodiversity: Status of the Earth's Living Resources*. London: Chapman & Hall.
- Haila, Y. and Margules, C.R. (1996) Survey research in conservation biology. *Ecography* **19**, 323-31.
- Kunin, W.E. and Lawton, J.H. (1996) Does biodiversity matter? Evaluating the case for conserving species. In *Biodiversity: A Biology of Numbers and Difference* (K.J. Gaston, ed.) pp. 283-308. Oxford: Blackwell Science.
- Lawrance, C.J., Bryad, R.J. and Beavan, P.J. (1993) *Terrain Evaluation Manual*. London: HMSO.
- Margules, C.R., Cresswell, I.D. and Nicholls, A.O. (1994) A scientific basis for establishing networks of protected areas. In *Systematics and Conservation Evaluation* (P.I. Forey, C.J. Humphries and R.I. Vane-Wright, eds) pp. 327-50, Oxford: Clarendon Press.
- Martinez, N.D. (1996) Defining and measuring functional aspects of biodiversity. In *Biodiversity: A Biology of Numbers and Difference*. (K.J. Gaston, ed.) pp.114-48. Blackwell Science, Oxford.
- Nicholls, A.O. (in press) Integrating population abundance, dynamics and distribution into broad scale priority setting. In *Conservation in a Changing World*.

*Symposia of the Zoological Society of London* (A. Balmford, J. Ginsberg and G. Mace, eds)

Nicholls, A.O. and Margules, C.R. (1993) An upgraded reserve selection algorithm. *Biol. Conserv.* **64**, 165-69.

Norton, B. (1988). Commodity, Amenity, and Morality: the limits of quantification in valuing biodiversity. In *Biodiversity* (ed. E.O. Wilson) pp. 200-5, Washington: National Academy Press.

Pressey, R.L. (1994) *Ad hoc* reservations: Forward or backward steps in developing representative reserve systems? *Conserv. Biol.* **8**, 662-8.

Pressey, R.L. and Tully, S.L. (1994) The cost of *ad hoc* reservation: a case study in western New South Wales. *Aust. J. Ecol.* **19**, 375-84.

Reid, W.V. (1994) Setting objectives for conservation evaluation. In *Systematics and Conservation Evaluation*. (P.L. Forey, C.J. Humphries and R.I. Vane-Wright, eds) pp. 1-13. Oxford: Clarendon Press.

UNEP (1995) *Global Biodiversity Assessment*. Cambridge: Cambridge University Press.

Van Jaarsveld, A.S. (in press) Biodiversity: conserving the building blocks of environmental health. In: *Pulling together: the sustainability challenge for southern Africa*. (J. Whitman), ch. 12, London: McMillan Press.

Van Jaarsveld, A.S. and Chown, S.L. (1996) Strategies and time-frames for implementing the Convention on Biological Diversity: biological requirements. *S. Afr. J. Sci.* **92**, 1-6.

Wilson, E.O. (1988) The current state of biological diversity. In *Biodiversity*. (E.O. Wilson, ed.) pp.3-20. Washington: National Academic Press.

Woinarski, J.C.Z., Price, O. and Faith, D.P. (1996) Application of a taxon priority system for conservation planning by selecting areas which are most distinct from environments already reserved. *Biol. Conserv.* **76**, 147-59.

## **CHAPTER 2**

# **An Evaluation of the Gradsect Biological Survey**

## **Method.**

# **An Evaluation of the Gradsect Biological Survey Method.**

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Running title: **Gradsect Biological Survey Method**

Key words: gradsect survey, biological surveys, biodiversity, land facets.

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## Summary

Biological surveys are necessary to gather species distribution data for the identification of priority conservation areas. The rationale of the gradsect method is that sampling (transects) oriented along the steepest environmental gradient should detect the maximum number of species in an area. The efficiency of the gradsect survey method was evaluated by comparing it to random, systematic and habitat-specific survey methods, during faunal field surveys (target groups: birds and dung beetles). Three gradsects were positioned within the study area to follow the major physiographical characteristics, incorporate all environmental strata (land facets) and yet be as logistically convenient as possible. The efficiency of survey methods was expressed as the number of species recorded per sampling unit effort and illustrated using bootstrap estimations to plot species accumulation curves. The gradsect method proved to be as efficient as the habitat-specific survey method and consistently more efficient than the systematic and random surveys for both taxa sampled. The present study, therefore illustrates that the gradsect survey method provides a cost-effective and swift, representative sample of regional fauna. Moreover, the results indicate that land-form sequences, specifically “land facets” are useful surrogates when sampling environmental diversity where distinct environmental gradients such as altitude and rainfall are absent.



## Introduction

Biological diversity or "Biodiversity" is the number, variety and variability of living organisms and includes the total variety of life, as well as their accompanying ecological processes (Groombridge, 1992). Our planet is currently experiencing an unprecedented decline in biodiversity due to anthropogenic factors (Wilson, 1988; UNEP, 1995) and present ecological understanding dictates that the future health of the earth's ecological systems relies on the effective conservation of this biological diversity (Lubchenco *et al.*, 1991). In pursuit of this encompassing goal, conservation biologists have developed systematic procedures for selecting networks of conservation areas that represent natural features (e.g. species) efficiently (Usher, 1986; Margules *et al.*, 1988; Margules, 1989). The identification of priority conservation areas using criteria and principles such as species richness, rarity, endemism, representativeness and complementarity (Margules *et al.*, 1988; Pressey *et al.*, 1993; Lombard, 1995a; Williams *et al.*, 1996) requires data on the spatial distribution patterns of species (Lombard, 1995b). These distributional data are gathered as field records during biological surveys. Efficient biological surveys are therefore an essential prerequisite for the evaluation and identification of priority conservation areas (Huntley, 1989; Margules and Austin, 1991), since the value of iterative reserve selection procedures is primarily influenced by the quality of available biological data (Nicholls and Margules, 1993; Margules *et al.*, 1994; Freitag *et al.*, 1996; Nicholls, in press). Biological surveys thus constitute the most fundamental activity in the field of conservation biology. Most countries have not yet amassed adequate biogeographic data (Belbin, 1993) and there is an urgent need for comprehensive surveys to be conducted globally (Freitag, *et al.*, 1996; van Jaarsveld and Chown, 1996; Haila and Margules, 1996). Ehrlich (1992) concluded

that conservation biologists have about a decade to develop and deploy workable biodiversity sampling methods if they are to play any significant role in preventing the loss of more than half of terrestrial biodiversity.

### *Survey design*

Comprehensive biological surveys are expensive (Burbridge, 1991). Financial constraints and the increasing demand for living resource data both provide a strong incentive for optimising survey methods (Gillison, 1983; May, 1994). Historically, surveys were based on *ad hoc* random, systematic or simple stratified sampling (Lambert, 1972; Smartt and Grainger, 1974; Green, 1979; Greig-Smith, 1983). These “statistical” (probability) sampling procedures have proven to be logistically demanding and costly (Austin and Basinski, 1978; McKenzie and Austin, 1993). They also ignore the underlying non-random relationship between biota and their physical environment (Gillison and Brewer, 1985).

A novel, purposive or judgmental sampling strategy was subsequently introduced as a more efficient and cost-effective alternative (Gillison, 1983; Gillison and Brewer, 1985). This approach assumes that the greatest biological diversity in any region is associated with the maximum perceivable environmental gradients and allows the sampling of the most accessible areas. Therefore, sampling oriented along the steepest environmental gradient should detect the maximum number of species in an area. Transects oriented along environmental gradients are termed *gradsects* (Gillison, 1983). At the regional scale, such gradients include elevation, temperature and rainfall, while at finer local scales these gradients are topographical sequences

and changes in soil type (Gillison and Brewer, 1985; Currie, 1991). The gradsect approach therefore deliberately selects sampling sites to represent maximum variability and to be as accessible as possible (Austin and Heyligers, 1989).

Gillison and Brewer (1985) demonstrated that the gradsect method was swift, logistically far less demanding and detected more vegetation types than random transects. Austin and Heyligers (1989, 1991) refined and elaborated on Gillison and Brewer's sampling design and reported that the gradsects revealed new information on the diversity of *Eucalyptus* forests and proved to be representative of their entire study area. In addition, their gradsect sampling sites were restricted to areas accessible by vehicles, thus reducing travel time and survey costs (Austin and Heyligers, 1989, 1991). These studies illustrate that the gradsect method detected more elements of diversity per unit effort and was therefore more efficient than "statistical" sampling. To date, the effectiveness of gradsect sampling for animal surveys has only been tested by means of computer simulation (Austin and Adomeit, 1991; Belbin and Austin, 1991), where the gradsect method again proved to be more effective and practical than random and systematic sampling.

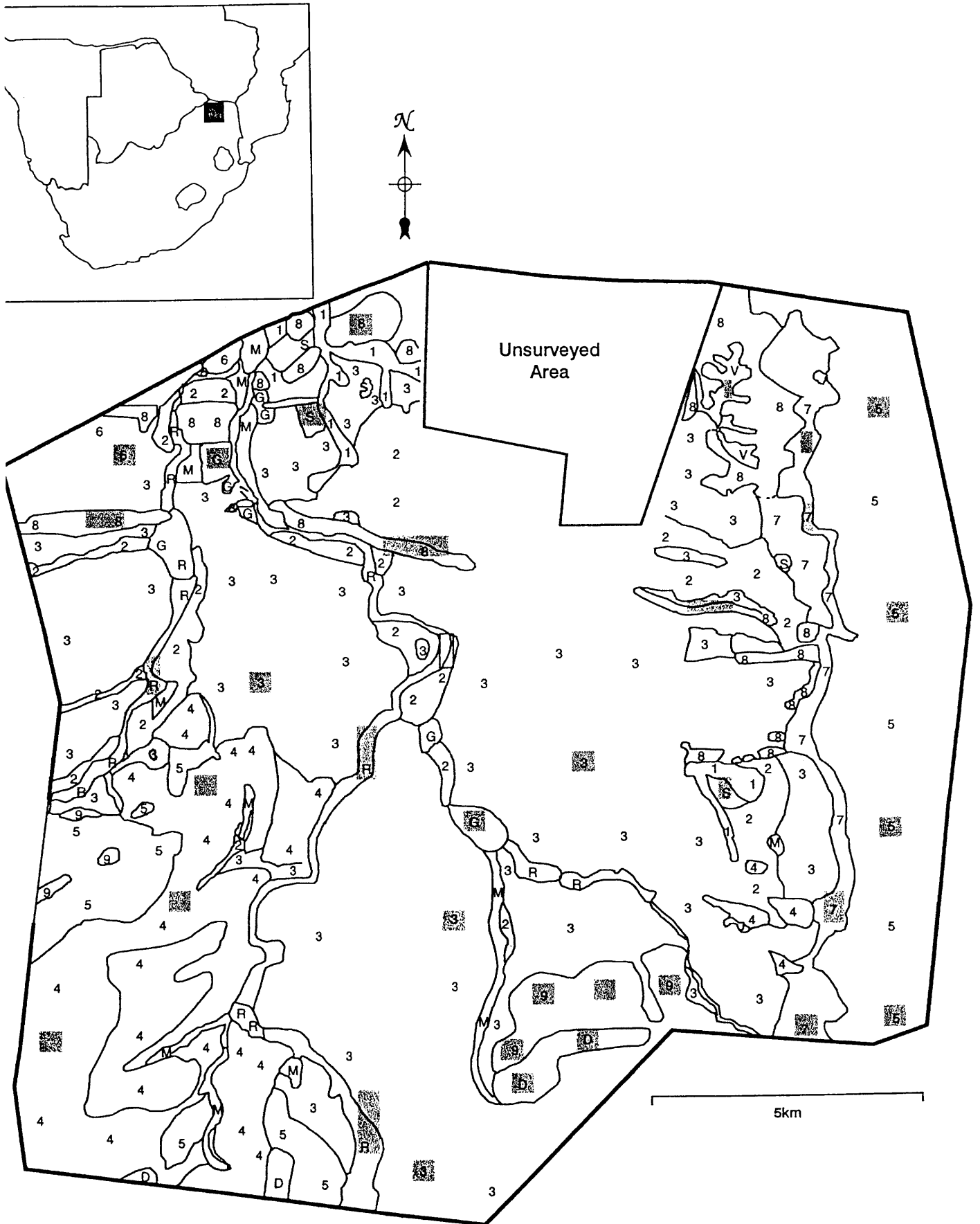
A habitat-specific survey generally provides the most appropriate stratification for animal surveys and should represent a comprehensive sample of an area (Austin and Basinski, 1978; Green, 1979). Detailed habitat-specific surveys are rarely feasible as areas under investigation are frequently biologically unknown (Margules and Redhead, 1995) and different vegetation types are unlikely to be mapped out. In the present study it was possible to compare the gradsect survey method to a comprehensive habitat-specific survey; the most stringent test for evaluating the relative efficiency of a gradsect faunal survey. Both gradsect and habitat-

specific surveys were conducted in the field, the habitat-specific method serving as a yardstick against which the efficiency of the gradsect method was measured. The objective was therefore not to contrast these two sampling strategies, but rather to rate the efficiency of the gradsect method against that of the habitat-specific survey method. The gradsect method was also compared to random and systematic surveys of the area. These two “statistical” surveys were not conducted in the field, but were based on simulated species data (Belbin and Austin, 1991; Austin and Adomeit, 1991). These hypothetical statistical surveys provided additional benchmark values for evaluating the relative efficiency of the gradsect method. Survey efficiency was expressed as the number of species detected per sampling effort (number of plots sampled) i.e. the rate at which the number of species recorded accumulates as effort is increased. Thus, the aim of the present study was to evaluate the efficiency of a gradsect faunal survey, by comparing it to simulated random and systematic survey methods, as well as a simultaneously conducted habitat-specific survey.

## **Methods**

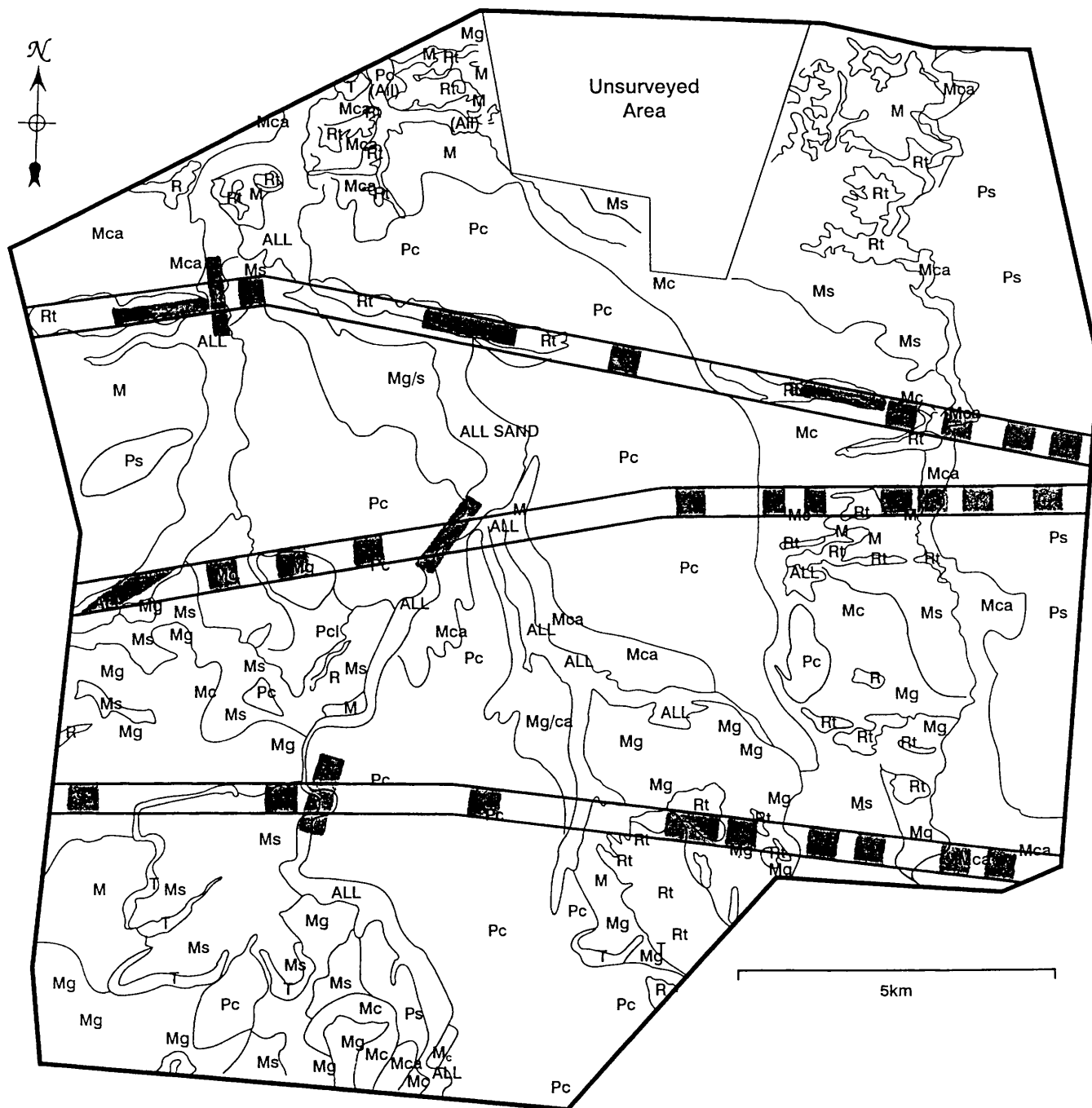
### *Study area*

Suitably documented areas for the evaluation and comparison of biodiversity survey techniques are rare (Gillison and Brewer, 1985; Belbin and Austin, 1991). The Venetia-Limpopo Nature Reserve was well suited for this study, since a comprehensive vegetation survey had been conducted (O'Connor, 1991) and extensive environmental information was readily available. The reserve is situated in the Northern Province of South Africa, close to the confluence of the Shashe and Limpopo rivers, which form the international boundaries between Zimbabwe,



**Figure 1.** Map of vegetation types of the Venetia-Limpopo Nature Reserve showing 25 ha plots (shaded areas) sampled by the habitat-specific survey method during field trip 1.<sup>1</sup>

<sup>1</sup> 1: *Acacia stuhlmannii*-*Salvadora angustifolia* open woodland; S: *Sesamothamnus lugardii* stands; G: grasslands; 2: *Colophospermum mopane*-*Salvadora angustifolia* open woodland; 3: *Colophospermum mopane* woodland on colluvial soils; 4: *Colophospermum mopane*-*Salvadora angustifolia* open woodland; 5: *Combretum apiculatum*-*Colophospermum mopane* open woodland; 6: fine sandveld; 7: escarpment vegetation; 8: rugged karoo hills; 9: *Combretum apiculatum* mixed woodland; D: mixed deciduous open woodland on diabase dykes; R: riverine forest; M: *Colophospermum mopane* tall riverine woodland; V: *Colophospermum mopane* woodland in valleys between rugged hills



**Figure 2.** Map of land facets of the Venetia-Limpopo Nature Reserve showing 25 ha plots (shaded areas) within three gradsects sampled by the gradsect survey method during field trip 1.<sup>2</sup>

<sup>2</sup> *all*: flat alluvial flood plains, rivers and stream channels with sandy soils; *mc*: moderate to gentle slopes with soil profiles containing sandy clays overlaying mudstone of the Karoo sequence; *mg*: moderate to gentle slopes with soil profiles containing gravel overlaying conglomerates and harder, weather resistant metamorphic rock; *ms*: moderate to gentle slopes with sandy soils associated with areas underlain by sandstone of the Karoo sequence; *mca*: crests of gentle slopes with calcrete rich soils; *ps*: pediplains with gentle to flat slopes and sandy soils; *pc*: pediplains with gentle to flat slopes and soils containing clay; *rt*: rugged topography, ridge plateaus with steep talus dominated slopes, boulders and rock outcrops.

Botswana and South Africa respectively (22°20' S, 29°20' E). This area falls within the Savanna biome and the Mopane Bushveld vegetation type (Louw and Rebelo, 1996). The reserve is approximately 35 000 ha (350 km<sup>2</sup>) in extent and is characterised by a low to moderate relief with an altitudinal variance of only 120m. The climate is semi-arid (mean annual rainfall = 350 mm) with rain falling during the hot summer months. The average maximum annual temperature is 30°C and the average minimum annual temperature is 13.2°C. The winters are dry and mild.

A comprehensive vegetation survey (based on the woody component) identified fourteen vegetation types (Appendix I) in the reserve (O'Connor, 1991). The spatial distribution of vegetation types is illustrated in Fig. 1. Three types of mopane (*Colophospermum*) woodland comprise the majority of the area. In addition, the *Acacia*, *Combretum* and riverine woodlands, as well as rugged Karoo hills and escarpment vegetation contribute to the habitat diversity within the reserve.

An engineering geological survey of the area (A'Bear, 1994), conducted according to the methods proposed by Price (1981), investigated the underlying geology and topographical characteristics of the area. During this survey areas of common land form and geology were identified from aerial photographs. The identified zones were visited to examine the underlying geology and soil profiles (soil type and depth). The survey identified nine land facets, Fig. 2 (A'Bear, 1994). A land facet is defined as part of the landscape, with superform consisting of a particular rock or superficial deposit and with a soil and water regime that is either uniform over the whole facet or, if not, varies in a simple and consistent fashion (Price, 1981).

### *Survey schedules and methods*

Birds and dung beetles (Coleoptera: Scarabaeidae) were sampled during four field trips conducted from 1995 to 1996. Both these faunal groups have a high level of habitat specificity (Nealis, 1977; Doube, 1983; Liversidge, 1991) and are sampled and identified with relative ease. Each of the four field trips lasted seven weeks and approximated the four seasons of a year [1. July - August (winter), 2. October - November (spring), 3. January - February (summer), 4. April - May (autumn)]. Both gradsect and habitat-specific surveys were conducted concurrently yet independently during each field trip. During each field trip sampling spanned all 14 vegetation types (habitat-specific method) and 9 land facets (gradsect method). Two of the land facets, R (rugged topography) and T (steep talus slopes), were treated as a single environmental stratum, namely Rt (hills with rugged topography). As some of the vegetation types cover very small areas, these small, rare units were incorporated into and sampled together with adjacent and/or related units to form nine vegetation strata and eight environmental strata respectively (Appendix I and II).

Habitat-specific survey method: The habitat-specific sampling method followed the traditional approach of a stratified random sample (Silk, 1979; Barnett, 1991) of the nine vegetation strata defined in Appendix II (Taylor *et al.*, 1984). For each field trip four and three geographic replicates (25 ha plots), (Fig. 1) of each vegetation stratum were sampled for birds and dung beetles respectively. Different sampling plots were selected for each field trip.

Gradsect survey method: The gradsect method was based on environmental information provided by the engineering geological survey (A'Bear, 1994). Three 500 m wide gradsects



were laid out to accommodate the maximum range of environmental variation within the shortest geographical distance (Fig. 2). Physiographically the area comprises a plateau, a north-south running escarpment, an extensive level basin, undulating hills and a series of rugged, generally east-west running siltstone or sandstone hills (A'Bear, 1994). The gradsects were primarily directed to follow these physiographical characteristics and were specifically located to incorporate all environmental strata (Appendix II), complementing one another in terms of environmental strata intercepted. In addition, accessibility was enhanced by positioning the gradsects in the vicinity of roads or fire breaks. Before positioning the four sampling plots of each land facet, areas that would be logistically demanding to sample were identified and excluded. Where a specific land facet occurred within each of the three gradsects, one plot was positioned at random within each gradsect, with the fourth plot being randomly assigned to one of the three gradsects and then randomly positioned within that gradsect. Where a land facet occurred in only two of the gradsects, two sampling plots were positioned randomly within each gradsect. For each field trip four and three geographic replicates (25 ha sampling plots) of each environmental stratum were sampled for birds and dung beetles respectively. While the three gradsect were retained, different sampling plots were selected within them for each field trip. The gradsect sampling was therefore laid out to be as logistically convenient as possible, corepresentative of the environmental variation of the study area, stratified within each gradsect according to environmental strata and included both replication and randomisation to increase the effectiveness and objectivity of sampling (Austin and Heyligers, 1989, 1991).

*Field sampling techniques:* The following collecting and recording methods were employed for both the gradsect and habitat-specific survey methods. Within each chosen 25 ha plot of a particular stratum, birds seen and heard were recorded along a 1500m transect (3 x 500m sections at right angles to one another in square plots or sequentially in elongated plots along rivers and hills). Each plot was surveyed over approximately 150 minutes. Transects were of indefinite width and distances travelled along transects were estimated using a hand held counter (“tally”) to record the number of paces walked. The strata were sampled in a random order. Bird surveys were conducted twice daily, in one plot each of an environmental stratum, and a vegetation stratum. Morning and afternoon surveys commenced approximately ten minutes after sunrise and three hours before sunset respectively. When a gradsect plot was surveyed during the afternoon, the next gradsect plot was sampled the following morning. This temporal sampling sequence was rotated on alternate days to avoid possible time-of-day-effects (Friend and Taylor, 1984). During each field trip, a specific stratum was sampled twice during the morning and twice during the afternoon. Thus, a total of 32 (8 strata x 4) and 36 (9 strata x 4) plots were sampled for birds by the gradsect and habitat-specific methods respectively, during each fieldtrip.

Dung beetles were collected over 24 hour periods, using eight pitfall traps (diameter 140mm, height 250mm) baited with fresh cattle dung and laid out sequentially at 20 m intervals within each selected plot (Doubé, 1983). Sampling was restricted to sunny days to minimise the effect of weather on the number of beetles caught (Davis *et al.*, 1988). Plots were sampled according to the same schedule as the

birds, but only three geographic replicates of each stratum were sampled. As pitfall traps could not be used in strata with rocky substrates, only six environmental strata and six vegetation strata were sampled for dung beetles. This amounted to a total of eighteen plots (6 strata x 3) sampled by each of the gradsect and habitat-specific methods during every fieldtrip. Lists of bird or dung beetle species recorded within single plots, comprised the basic units of the data sets used to compare the survey methods.

Simulated statistical surveys (random and systematic): Random and systematic surveys were simulated for each field trip. A regular grid (25 hectare cells) was overlaid on the 1:50 000 vegetation map of the reserve. A random survey was generated by selecting 36 (birds) or 18 (dung beetles) cells (25 ha plots) at random from this grid (Silk, 1979; Barnett, 1991). The systematic survey method started from a random point and selected sampling plots at a calculated, regular interval from the grid (Silk, 1979; Taylor *et al.*, 1984; Barnett, 1991). The sampling interval (number grid cells between sampling plots) was calculated by dividing the total number of grid cells covering the entire study area by the number of plots (36 birds or 18 dung beetles) to be sampled (Silk, 1979; Barnett, 1991). After selecting cells, the spatially dominant vegetation type or land facet within each selected 25 ha plot was determined. Species presence data for a selected plot of a particular stratum were generated by drawing one plot's data at random from a pool of plots of the same stratum, as provided by the habitat-specific or gradsect field surveys. In this manner, the species that were expected to be recorded within each plot were allocated to a simulated survey. Complete data sets containing species lists of 36 plots (birds) and 18 plots (dung beetles), were generated for both the random and systematic surveys after each field trip.

### *Comparison of survey efficiencies*

The four field trips provided separate comparisons of the survey methods. The efficiency of gradsect, habitat-specific and simulated systematic and random survey methods were assessed by comparing species accumulation curves generated for each survey method of every field trip. Bootstrap estimations (Efron and Gong, 1983; Efron and Tibshirani, 1993) were used to plot species accumulation curves for each survey method; a methodology previously used to compare transects and point counts during bird surveys (Verner and Ritter, 1985).

For each field trip the data set of a specific survey method consisted of lists of species recorded within each of the plots  $\{x_1, x_2, x_3, \dots, x_n\}$  (birds:  $n = 32$  plots for gradsect method, or  $n = 36$  plots for habitat-specific, random and systematic methods; dung beetles:  $n = 18$  plots for all four methods). Therefore  $x_i$  is a list of species recorded within a plot. Each species accumulation curve plots the average number of species recorded by a specific survey method against the number of plots sampled (birds:  $l = 1, 2, 3, \dots, 32$  plots, dung beetles:  $l = 1, 2, 3, \dots, 18$  plots). To generate the average number of species detected after a specified number of plots sampled, e.g. ten ( $l = 10$ ), this number of plots was drawn 300 times at random, with replacement ( $x_i^*$ ), from the complete set of plots (36, 32 or 18) sampled by each survey method. A random set (bootstrap sample) being  $A_{li} = \{x_1^*, x_2^*, x_3^*, \dots, x_l^*\}$  ( $i = 1, 2, 3, \dots, 300$ ). This provided 300 sets of plots (e.g. ten,  $l = 10$ ) for which the total number of species recorded within each set of plots was tallied ( $t_{li}^*$ ).

The average number of species detected by the 300 sets of plots (e.g. 300 x 10) is represented

by one point on the species accumulation curve ( $\bar{x}_l^*$ ), with

$$\bar{x}_l^* = \frac{1}{300} \sum_{i=1}^{300} t_{li}^* .$$

Statistical significance of differences in the efficiency of the four survey methods was evaluated by sequentially comparing generated mean ( $\bar{x}_l^*$ ) numbers of species recorded by the appropriate number of plots sampled (birds:  $l = 1, 2, 3, \dots, 32$  plots, dung beetles:  $l = 1, 2, 3, \dots, 18$  plots). After following the above process to generate a new independent set of 300 values ( $t_{li}^*$ ), 300 differences ( $d_{li}^*$ ) in the number of species recorded were calculated for each of the six combinations of the survey methods.

Thus, for example gradsect (G) vs habitat-specific (H):

$$d_{li}^* = t_{li}^* (G) - t_{li}^* (H)$$

The standard deviation was derived as

$$s_l^* = \left[ \frac{1}{299} \sum_{i=1}^{300} (d_{li}^* - \bar{d}_l^*)^2 \right]^{1/2}, \text{ with}$$

$$\bar{d}_l^* = \frac{1}{300} \sum_{i=1}^{300} d_{li}^* .$$

The estimated “bootstrap” differences were standardised by :

$$z_i (G-H) = \frac{\bar{x}_i^*(G) - \bar{x}_i^*(H)}{s_i^*}$$

A normal approximation was used for the standardised bootstrap differences of these values ( $z_{ij}$ ) and the test was carried out at a 5 % significance level ( $P < 0.05$ ). All bootstrap analyses were conducted using mainframe based SAS Institute Inc. (Illinois, USA) software. The bootstrap methodology therefore enabled the simulation of descriptive statistics that were not readily available for this particular data set and the derivation of distributional characteristics of mathematically intractable sample statistics.

#### *Distances between sampling plots*

As gradsect and habitat-specific surveys were conducted simultaneously, actual distances travelled to and between the sampling plots of the respective survey methods could not be directly measured. The relatively uncharted territory also hampered initial attempts to do so. Instead, nearest neighbour distances between plots of the two respective survey methods (e.g. Figs 1, 2) were determined for each field trip. A Shapiro-Wilk test revealed that these data were not normally distributed. A non-parametric Wilcoxon Rank Sum test for two independent samples was used to test for significant differences in the nearest neighbour distances determined for the gradsect and habitat-specific methods. This test indicated whether the gradsect method would be logistically more convenient and potentially more cost-effective than the habitat-specific method.

## Results

### *Bird surveys*

A total of 146 terrestrial bird species was recorded during the study period (Appendix III). The total numbers of species recorded by each survey method during each field trip are provided in Table 1. These values are also expressed as a percentage of the total number of species available for detection (the combined number of species recorded by both the gradsect and habitat-specific methods) during each field trip. The two simulated “statistical” methods consistently recorded fewer species than the gradsect and habitat-specific surveys (Table 1) and were unable to record more than 77% of the available species during any field trip. The habitat-specific method detected nine and five species more than the gradsect method during field trips 2 and 3 respectively (Table 1). The gradsect method in turn recorded three and two bird species more than the habitat-specific method during field trips 1 and 4 respectively. The gradsect method therefore performed very well compared to the habitat-specific method, detecting more species on two occasions. The gradsect and the habitat-specific methods detected 87% (127) and 90% (131) of the total number of species (146) respectively, after four field trips. The systematic survey recorded 75% (110) and the random survey recorded 70% (102) of the total number of bird species (Table 1).

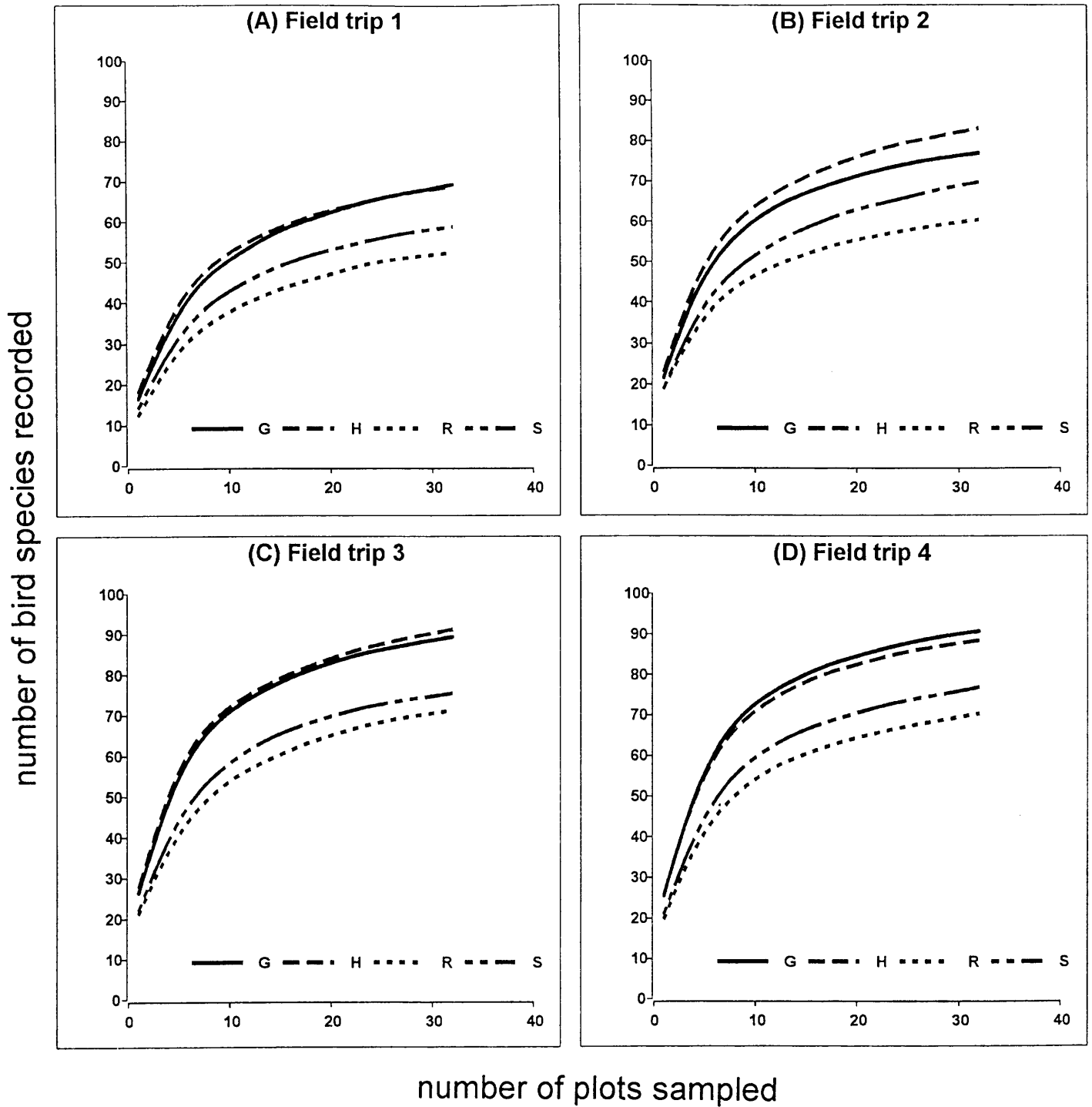
The species accumulation curves clearly illustrate that the gradsect and habitat-specific methods were consistently more efficient at detecting species than the simulated systematic and random surveys (Fig. 3a-d). (All the  $r^2$  values calculated for these curves, Fig. 3a-d, were above

98.9%.) The significance of differences between the number of species detected per number of plots sampled by the different survey methods, are summarized in Tables 2a-d. The gradsect and habitat-specific methods recorded significantly more species per number of plots sampled than the random survey, during all four the field trips. The differences between species accumulation curves, indicating efficiency, generally became significant after twelve plots sampled. Although the gradsect method recorded up to eleven species more than the systematic survey during fieldtrips 1 and 2, statistical significance was only reached at a single point along the curves (field trip 1, 31 plots). The gradsect method did however consistently record significantly more bird species than the systematic method during field trips 3 and 4 (Tables 2c,d).

**Table 1.** Numbers and percentage of available bird and dung beetle species recorded by the habitat-specific (H), gradsect (G), systematic (S) and random (R) survey methods, during four field trips.

		Total	field trip 1 (winter)	field trip 2 (spring)	field trip 3 (summer)	field trip 4 (autumn)
<b>Dung beetles</b>	<b>H</b>	51/56 (91%)	14/17 (82%)	-	45/48 (94%)	46/51 (90%)
	<b>R</b>	41/56 (73%)	12/17 (70%)	-	33/48 (68%)	36/51 (72%)
	<b>S</b>	48/56 (86%)	10/17 (58%)	-	39/48 (81%)	36/51 (72%)
	<b>G</b>	51/56 (91%)	12/17 (70%)	-	40/48 (83%)	44/51 (86%)
<b>Birds</b>	<b>H</b>	131/146 (90%)	77/91 (85%)	94/105 (90%)	103/116 (89%)	97/111 (87%)
	<b>R</b>	102/146 (70%)	60/91 (66%)	68/105 (65%)	79/116 (68%)	78/111 (70%)
	<b>S</b>	110/146 (75%)	68/91 (75%)	81/105 (77%)	82/116 (71%)	86/111 (77%)
	<b>G</b>	127/146 (87%)	80/91 (88%)	85/105 (81%)	98/116 (84%)	99/111 (89%)





**Figure 3.** Bird species accumulation curves of the gradsect (G), habitat-specific (H), systematic (S) and random (R) survey methods of four field trips.

The habitat-specific method recorded significantly more species per number of plots sampled, than the systematic survey during field trips 1, 2 and 3 (Tables 2a-c).

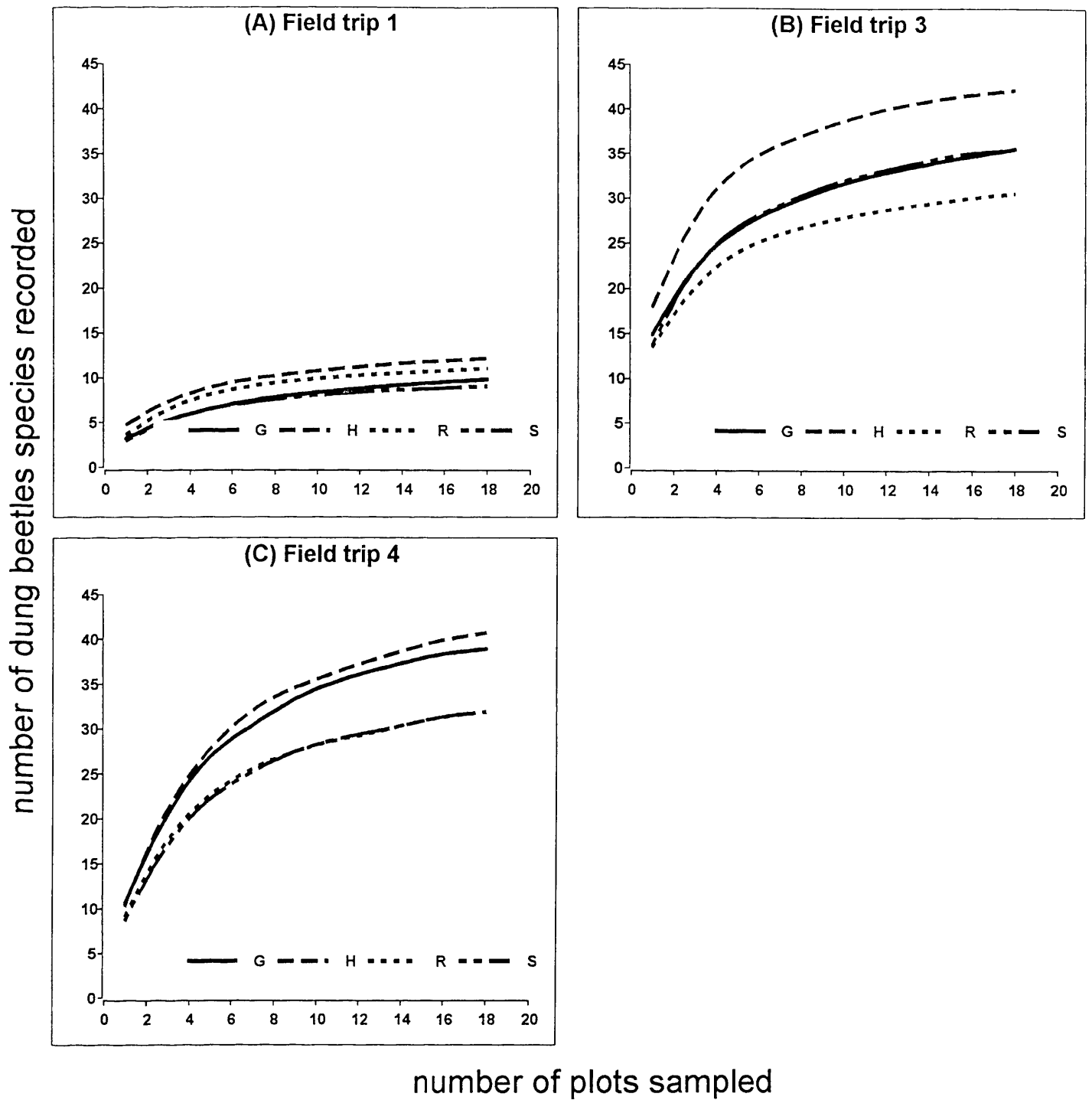
The species accumulation curves of the gradsect and habitat-specific survey methods were very similar for field trips 1 and 3 (Fig. 3a, c). The habitat-specific method showed a higher efficiency than the gradsect method in field trip 2 (Fig. 3b), whereas the gradsect approach performed slightly better than the habitat-specific method during field trip 4 (Fig. 3d). The difference between the number of species recorded by the gradsect and habitat-specific methods ranged from zero to three for the majority of the points along the curves (Tables 2a-d) and was never significant. The habitat-specific method did, however, record up to six species more than the gradsect method during field trip 2, but the differences again failed to reach statistical significance (Table 2b).

### *Dung beetle surveys*

A total of 56 species (11 morpho-species and 45 described species)\* of dung beetle was collected during the study period (Appendix IV). The numbers of species recorded by each survey method during the four field trips are provided in Table 1. The winter field trip (field trip 1) resulted in the collection of only seventeen species (Table 1) and consequently failed to provide an informative comparison of the survey methods (Table 3a). The species accumulation curves of the four survey methods were very similar for field trip 1 (Fig. 4a). The dry season extended into the second field trip, causing extremely low dung beetle abundances. Sampling was aborted and field trip 2 was therefore excluded from analyses regarding the dung beetles.

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\* identification was verified by Dr. A.L.V. Davis, Department of Zoology & Entomology, University of Pretoria, South Africa.



**Figure 4.** Dung beetle species accumulation curves of the gradsect (G), habitat-specific (H), systematic (S) and random (R) survey methods of four field trips

**Table 2.** The difference between the number of bird species recorded per number of plots sampled by the gradsect (G), habitat-specific (H), systematic (S) and random (R) surveys methods during four field trips. The standard deviation (SD) and statistical significance ( $p < 0.05$ , indicated with an asterisk \*) of the differences are provided for every third point along species accumulation curves.

**(a) field trip 1**

Number of plots sampled	Difference G - S $\pm$ SD	Difference G - R $\pm$ SD	Difference H - S $\pm$ SD	Difference H - R $\pm$ SD	Difference G - H $\pm$ SD
1	2.7 $\pm$ 6.5	3.7 $\pm$ 7.5	3.4 $\pm$ 6.0	4.4 $\pm$ 6.6	-0.7 $\pm$ 6.5
3	5.5 $\pm$ 8.7	7.7 $\pm$ 9.6	7.5 $\pm$ 8.1	9.7 $\pm$ 9.0	-1.9 $\pm$ 8.1
6	6.6 $\pm$ 8.8	9.2 $\pm$ 10.2	9.2 $\pm$ 8.4	11.8 $\pm$ 8.3	-2.6 $\pm$ 8.0
9	8.1 $\pm$ 8.9	11.9 $\pm$ 8.8	9.8 $\pm$ 8.6	13.4 $\pm$ 8.0	-1.7 $\pm$ 8.0
12	8.7 $\pm$ 8.1	13.5 $\pm$ 7.9	10.3 $\pm$ 7.5	15.1 $\pm$ 7.1 *	-1.6 $\pm$ 7.5
15	10.1 $\pm$ 7.4	14.3 $\pm$ 7.0 *	10.9 $\pm$ 6.9	15.1 $\pm$ 7.6 *	-0.8 $\pm$ 7.4
18	9.5 $\pm$ 6.8	14.4 $\pm$ 6.4 *	10.5 $\pm$ 6.5	15.3 $\pm$ 6.9 *	-0.9 $\pm$ 6.4
21	10.0 $\pm$ 6.3	15.9 $\pm$ 5.3 *	10.1 $\pm$ 5.9	15.9 $\pm$ 6.1 *	0.01 $\pm$ 6.1
24	10.7 $\pm$ 6.7	15.4 $\pm$ 5.9 *	10.9 $\pm$ 6.1	15.7 $\pm$ 5.9 *	-0.3 $\pm$ 5.7
27	11.0 $\pm$ 6.4	16.3 $\pm$ 5.7 *	10.4 $\pm$ 5.3 *	15.7 $\pm$ 5.4 *	0.6 $\pm$ 5.5
30	10.6 $\pm$ 6.2	15.9 $\pm$ 4.8 *	10.8 $\pm$ 5.5 *	16.1 $\pm$ 5.1 *	-0.2 $\pm$ 5.1
32	11.4 $\pm$ 5.9	17.2 $\pm$ 5.1 *	10.7 $\pm$ 5.3 *	16.5 $\pm$ 5.6 *	0.7 $\pm$ 5.3

**(b) field trip 2**

Number of plots sampled	Difference G - S $\pm$ SD	Difference G - R $\pm$ SD	Difference H - S $\pm$ SD	Difference H - R $\pm$ SD	Difference G - H $\pm$ SD
1	2.1 $\pm$ 5.4	1.7 $\pm$ 6.4	3.7 $\pm$ 7.5	3.4 $\pm$ 6.7	-1.6 $\pm$ 7.6
3	5.8 $\pm$ 8.5	7.5 $\pm$ 8.7	7.3 $\pm$ 10.3	8.9 $\pm$ 9.4	-1.4 $\pm$ 9.8
6	7.9 $\pm$ 9.8	10.8 $\pm$ 9.5	11.0 $\pm$ 11.8	13.9 $\pm$ 9.5	-3.1 $\pm$ 10.4
9	9.0 $\pm$ 9.1	13.1 $\pm$ 8.8	11.8 $\pm$ 10.8	15.8 $\pm$ 8.3	-2.8 $\pm$ 9.6
12	10.3 $\pm$ 8.5	15.2 $\pm$ 8.2	12.9 $\pm$ 9.9	17.8 $\pm$ 7.8 *	-2.6 $\pm$ 8.1
15	9.4 $\pm$ 8.6	15.1 $\pm$ 7.6 *	13.4 $\pm$ 9.4	19.2 $\pm$ 7.2 *	-4.0 $\pm$ 7.4
18	8.8 $\pm$ 8.3	15.2 $\pm$ 7.6 *	13.6 $\pm$ 9.0	19.9 $\pm$ 7.2 *	-4.8 $\pm$ 7.0
21	9.1 $\pm$ 7.3	16.0 $\pm$ 6.6 *	13.2 $\pm$ 8.4	20.1 $\pm$ 6.6 *	-4.1 $\pm$ 6.3
24	9.4 $\pm$ 6.5	16.6 $\pm$ 6.2 *	14.9 $\pm$ 7.4 *	22.8 $\pm$ 6.4 *	-5.4 $\pm$ 5.6
27	8.2 $\pm$ 6.3	15.9 $\pm$ 5.6 *	13.4 $\pm$ 6.8 *	21.1 $\pm$ 5.9 *	-5.2 $\pm$ 5.2
30	8.3 $\pm$ 5.8	15.8 $\pm$ 5.5 *	14.6 $\pm$ 6.6 *	22.0 $\pm$ 5.7 *	-6.3 $\pm$ 4.9
32	7.8 $\pm$ 5.5	16.5 $\pm$ 5.5 *	13.8 $\pm$ 6.7 *	22.6 $\pm$ 6.0 *	-6.1 $\pm$ 5.2

**Table 2. (Continued)**

<b>(c) field trip 3</b>					
<b>Number of plots sampled</b>	<b>Difference G - S ± SD</b>	<b>Difference G - R ± SD</b>	<b>Difference H - S ± SD</b>	<b>Difference H - R ± SD</b>	<b>Difference G - H ± SD</b>
1	3.12 ± 6.90	3.56 ± 7.87	4.19 ± 7.77	4.63 ± 6.69	- 1.07 ± 7.69
3	7.14 ± 8.41	9.66 ± 10.12	8.80 ± 10.06	11.32 ± 8.23	-1.66 ± 9.12
6	9.59 ± 8.20	13.81 ± 10.01	12.35 ± 9.00	16.57 ± 8.14 *	-2.75 ± 7.58
9	10.55 ± 7.72	16.46 ± 9.34	12.68 ± 8.36	18.59 ± 7.74 *	-2.13 ± 7.49
12	10.73 ± 6.38	16.88 ± 8.86	12.14 ± 6.78	18.29 ± 7.29 *	-1.41 ± 7.03
15	10.43 ± 5.98	17.04 ± 8.14 *	12.82 ± 6.78 *	19.43 ± 6.94 *	-2.38 ± 5.98
18	10.53 ± 5.54 *	17.27 ± 7.75 *	12.95 ± 6.03 *	18.43 ± 6.52 *	-2.41 ± 5.41
21	11.37 ± 5.36 *	17.27 ± 7.75 *	13.31 ± 5.96 *	19.21 ± 6.19 *	-1.96 ± 5.55
24	11.31 ± 4.90 *	17.29 ± 7.29 *	13.84 ± 5.46 *	19.82 ± 6.00 *	-2.53 ± 5.15
27	11.50 ± 4.60 *	16.74 ± 6.47 *	14.07 ± 5.38 *	19.31 ± 5.44 *	-2.57 ± 4.91
30	11.78 ± 4.31 *	17.13 ± 6.22 *	14.35 ± 4.75 *	19.70 ± 5.20 *	-2.57 ± 4.58
32	11.24 ± 4.50 *	17.17 ± 6.51 *	13.94 ± 4.58 *	19.87 ± 5.01 *	-2.70 ± 4.42

<b>(d) field trip 4</b>					
<b>Number of plots sampled</b>	<b>Difference G - S ± SD</b>	<b>Difference G - R ± SD</b>	<b>Difference H - S ± SD</b>	<b>Difference H - R ± SD</b>	<b>Difference G - H ± SD</b>
1	2.7 ± 7.5	3.4 ± 7.7	3.7 ± 8.3	4.4 ± 7.8	-1.0 ± 7.9
3	8.7 ± 9.4	10.1 ± 9.6	8.2 ± 10.2	9.7 ± 9.0	0.5 ± 10.2
6	11.6 ± 9.6	14.7 ± 9.3	11.5 ± 9.7	14.5 ± 9.0	0.2 ± 9.0
9	12.0 ± 9.3	17.1 ± 9.1	10.6 ± 9.1	15.7 ± 8.1	1.4 ± 8.1
12	12.3 ± 8.5	16.1 ± 8.4 *	11.7 ± 7.7	15.6 ± 8.0	0.5 ± 7.7
15	13.6 ± 7.9	18.2 ± 8.0 *	12.1 ± 7.6	16.7 ± 7.0 *	1.5 ± 6.7
18	14.7 ± 7.9	19.2 ± 7.8 *	12.6 ± 7.5	16.9 ± 6.8 *	2.1 ± 6.5
21	14.0 ± 7.0 *	18.1 ± 7.1 *	12.3 ± 6.7	16.5 ± 6.2 *	1.6 ± 5.4
24	13.9 ± 7.3 *	19.0 ± 6.8 *	12.5 ± 7.4	17.6 ± 6.2 *	1.4 ± 5.6
27	13.7 ± 6.7 *	18.7 ± 6.4 *	11.5 ± 6.6	16.4 ± 5.9 *	2.2 ± 4.8
30	14.7 ± 6.4 *	19.4 ± 5.6 *	12.2 ± 6.3	16.9 ± 5.1 *	2.5 ± 4.6
32	13.6 ± 6.2 *	19.0 ± 5.8 *	11.3 ± 6.0	16.7 ± 5.1 *	2.2 ± 4.5

Sufficient numbers of dung beetles were collected during field trips 3 and 4 to allow effective comparisons of survey methods.

The habitat-specific survey method recorded the highest number of species during all field trips (Table 1). During field trip 3 the gradsect method recorded only one species more than the simulated systematic survey (Table 1). The habitat-specific and gradsect methods respectively recorded ten and eight species more than the two “statistical” methods during field trip 4 (Table 1). The habitat-specific method detected two, five and two species more than the gradsect method during the three respective field trips (Table 1). The gradsect and the habitat-specific methods both recorded 91% (51), the random method 73% (41) and systematic method 86% (48) of the total number of species (56) after the three field trips (Table 1).

The species accumulation curves of field trip 4 illustrates a higher efficiency of the habitat-specific and gradsect methods compared to the two “statistical” methods (Fig. 4c). (All the  $r^2$  values calculated for these curves, Figs 4a-c, are above 99.1%.) The curves of the gradsect and systematic surveys for field trip 3 were, however, almost identical (Fig. 4b). The gradsect method recorded up to five species more than the random method of field trip 3, but the difference did not reach significance (Table 3b). The habitat-specific method detected significantly more species than the random survey during field trip 3 (Table 3b). During field trip 4 the gradsect method detected more species than the systematic and random methods, the difference with the systematic method reaching significant levels (Table 3c). During field trip 4 the habitat-specific method recorded significantly more species than both “statistical” methods towards the latter portions of the curves. The habitat-specific method showed a higher efficiency than the gradsect method during field trip 3 (Fig. 4b). However, there was no statistically

**Table 3.** The difference between the number of dung beetle species recorded per number of plots sampled by the gradsect (G), habitat-specific (H), systematic (S) and random (R) surveys methods during three field trips. The standard deviation (STD) and statistical significance ( $p < 0.05$ , indicated with an asterisk \*) of the differences are provided for every second point along the species accumulation curves.

**(a) field trip 1**

Number of plots sampled	Difference G - S $\pm$ SD	Difference G - R $\pm$ SD	Difference H - S $\pm$ SD	Difference H - R $\pm$ SD	Difference G - H $\pm$ SD
2	0.1 $\pm$ 1.4	-1.8 $\pm$ 3.0	1.1 $\pm$ 2.7	1.4 $\pm$ 2.6	-1.5 $\pm$ 2.1
4	0.2 $\pm$ 1.2	-1.1 $\pm$ 2.4	1.8 $\pm$ 2.6	1.6 $\pm$ 2.0	-1.8 $\pm$ 2.1
6	0.1 $\pm$ 1.4	-1.8 $\pm$ 1.6	1.7 $\pm$ 2.6	1.8 $\pm$ 2.3	-2.1 $\pm$ 2.1
8	0.4 $\pm$ 1.9	-1.2 $\pm$ 1.5	2.5 $\pm$ 2.9	1.5 $\pm$ 1.0	-2.3 $\pm$ 2.0
10	0.4 $\pm$ 1.6	-1.8 $\pm$ 1.4	2.7 $\pm$ 1.3	1.1 $\pm$ 1.1	-2.4 $\pm$ 1.7
12	0.5 $\pm$ 1.3	-1.3 $\pm$ 1.1	2.7 $\pm$ 2.0	0.6 $\pm$ 1.5	-2.4 $\pm$ 1.6
14	0.6 $\pm$ 1.2	-1.6 $\pm$ 1.1	3.7 $\pm$ 1.4	1.5 $\pm$ 1.6	-2.4 $\pm$ 1.5
16	0.8 $\pm$ 1.2	-1.7 $\pm$ 1.9	3.5 $\pm$ 1.2	1.3 $\pm$ 2.0	-2.3 $\pm$ 1.7
18	0.9 $\pm$ 1.6	-1.1 $\pm$ 1.8	3.7 $\pm$ 1.7	1.9 $\pm$ 1.1	-2.3 $\pm$ 1.3

**(b) field trip 3**

Number of plots sampled	Difference G - S $\pm$ SD	Difference G - R $\pm$ SD	Difference H - S $\pm$ SD	Difference H - R $\pm$ SD	Difference G - H $\pm$ SD
2	-0.1 $\pm$ 6.4	1.8 $\pm$ 5.0	4.1 $\pm$ 8.7	4.4 $\pm$ 6.6	-4.2 $\pm$ 5.9
4	-0.2 $\pm$ 6.2	2.1 $\pm$ 3.4	5.8 $\pm$ 7.6	9.7 $\pm$ 9.0	-6.0 $\pm$ 5.5
6	-0.1 $\pm$ 5.4	2.8 $\pm$ 3.6	6.7 $\pm$ 6.6	11.8 $\pm$ 8.3	-6.8 $\pm$ 5.3
8	-0.4 $\pm$ 4.9	3.2 $\pm$ 3.5	6.5 $\pm$ 5.9	13.5 $\pm$ 8.0	-6.9 $\pm$ 5.0
10	-0.4 $\pm$ 4.6	3.8 $\pm$ 3.4	6.7 $\pm$ 5.3	15.1 $\pm$ 7.1 *	-7.1 $\pm$ 4.3
12	-0.5 $\pm$ 4.3	4.3 $\pm$ 3.1	6.7 $\pm$ 4.9	15.1 $\pm$ 7.6 *	-7.3 $\pm$ 4.4
14	-0.3 $\pm$ 4.2	4.6 $\pm$ 3.1	6.7 $\pm$ 4.4	11.6 $\pm$ 3.6 *	-7.0 $\pm$ 3.8
16	-0.4 $\pm$ 4.2	4.7 $\pm$ 2.9	6.5 $\pm$ 4.2	15.3 $\pm$ 7.0 *	-6.8 $\pm$ 3.6
18	0.2 $\pm$ 3.6	5.1 $\pm$ 2.8	6.7 $\pm$ 3.7	15.9 $\pm$ 6.1 *	-6.5 $\pm$ 3.4

**(c) field trip 4**

Number of plots sampled	Difference G - S $\pm$ SD	Difference G - R $\pm$ SD	Difference H - S $\pm$ SD	Difference H - R $\pm$ SD	Difference G - H $\pm$ SD
2	1.85 $\pm$ 5.30	0.79 $\pm$ 8.39	3.38 $\pm$ 7.98	2.68 $\pm$ 9.14	-1.70 $\pm$ 10.02
4	4.52 $\pm$ 6.62	3.61 $\pm$ 8.88	4.73 $\pm$ 7.02	4.11 $\pm$ 8.43	0.38 $\pm$ 9.72
6	5.18 $\pm$ 5.06	3.50 $\pm$ 7.84	6.50 $\pm$ 6.94	6.23 $\pm$ 7.49	-1.51 $\pm$ 8.47
8	5.48 $\pm$ 4.58	4.70 $\pm$ 6.88	7.16 $\pm$ 5.86	6.98 $\pm$ 6.47	-1.56 $\pm$ 7.25
10	6.49 $\pm$ 4.31	5.30 $\pm$ 6.52	7.17 $\pm$ 5.67	6.97 $\pm$ 5.86	-1.26 $\pm$ 6.56
12	6.71 $\pm$ 3.66	6.74 $\pm$ 6.38	7.55 $\pm$ 5.12	7.99 $\pm$ 5.89	-0.56 $\pm$ 5.93
14	6.86 $\pm$ 3.32 *	5.83 $\pm$ 5.78	8.14 $\pm$ 4.55	8.07 $\pm$ 5.18	-1.88 $\pm$ 5.64
16	6.96 $\pm$ 3.12 *	5.83 $\pm$ 5.78	8.56 $\pm$ 4.04 *	8.65 $\pm$ 4.52	-1.48 $\pm$ 5.56
18	7.09 $\pm$ 2.74 *	6.60 $\pm$ 4.87	8.87 $\pm$ 3.80 *	8.82 $\pm$ 4.47 *	-1.73 $\pm$ 4.92

significant difference between the number of species recorded by the gradsect and habitat-specific methods after any number of plots sampled, for any of the three field trips.

#### *Distances between sampling plots*

The mean nearest neighbour distances between sampling plots of the gradsect and habitat-specific survey methods are provided in Table 4. These distances were significantly ( $p < 0.05$ ) shorter for the gradsect survey method during all four field trips (Table 4).

**Table 4.** The mean nearest neighbour distances between the sampling plots ( $\pm$  SD) recorded for the gradsect and habitat-specific surveys methods during four field trips. P-values resulting from a Wilcoxon Rank Sum test are all significant ( $p < 0.05$ ).

	<b>field trip 1</b>	<b>field trip 2</b>	<b>field trip 3</b>	<b>field trip 4</b>
Gradsect	1071 $\pm$ 1268 m	1108 $\pm$ 1289 m	1015 $\pm$ 1247 m	1076 $\pm$ 1227 m
Habitat-specific	2133 $\pm$ 1107 m	1914 $\pm$ 1605m	1838 $\pm$ 1243 m	1838 $\pm$ 1344 m
p-value	0.0007	0.0004	0.0002	0.0007

#### **Discussion**

The *a priori* identification of environmental gradients contains a level of subjective bias which has been regarded as unacceptable for surveys following a strict statistical design protocol. However, it has been suggested that randomisation is largely irrelevant where the principle



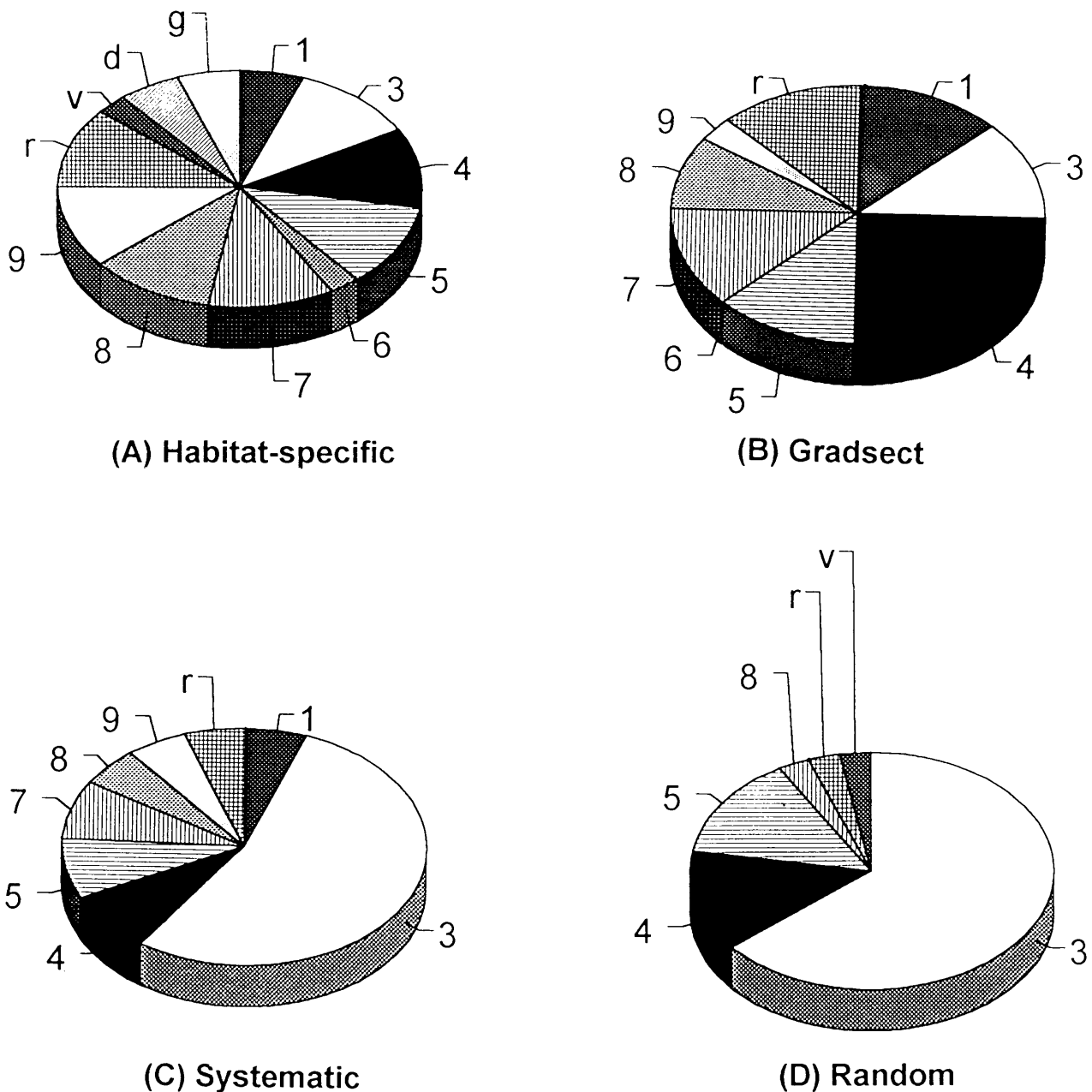
survey objective is the detection of maximum diversity (Gillison and Brewer, 1985). Austin and Adomeit (1991) added that where constraints such as cost and access already cause bias, and where the goal is to obtain a representative sample rather than an unbiased estimate of a mean, the gradsect survey method is the best available option. In accordance with previous studies (Gillison and Brewer, 1983, 1985; Austin and Heyligers, 1989, 1991; Austin and Adomeit, 1991) the results presented here confirm the high efficiency of the gradsect method compared to the random and systematic survey methods (Figs 3a-d; 4b,c ). The gradsect method recorded significantly more bird species per number of plots sampled than the simulated random surveys, during all four the fieldtrips. The gradsect surveys consistently recorded an average of ten bird species more than the simulated systematic surveys (Tables 2a-d) and this difference reached statistical significance during two field trips. For dung beetles, the species accumulation curves of the gradsect method showed a higher efficiency than that of the random survey during field trip 3 and a higher efficiency compared to both “statistical” methods during field trip 4 (Fig. 4b,c). The gradsect method recorded up to six dung beetle species more than the random surveys and recorded significantly more species per number of plots sampled than the systematic method of field trip 4. The gradsect method was therefore more efficient at sampling both birds and dung beetles than the “statistical” methods.

It is important to note that the purpose of the bootstrap curves was not to illustrate how many species each survey method would have recorded if each survey was designed to sample fewer numbers of plots e.g. only ten sampling plots. If the gradsect survey of the present study area was *a priori* limited to sampling e.g. only ten plots, the survey would have been designed in a very different fashion. This would have resulted in the efficiency of the gradsect method

being much higher after e.g. ten plots sampled, than indicated by the current bootstrap curves (Fig. 3a-d; 4a-c). The species accumulation curves presented here rather took a retrospective view of the total number of plots (18, 32) sampled and illustrate that there was larger variation between the species compositions of the plots sampled by the gradsect method, which resulted in higher efficiency.

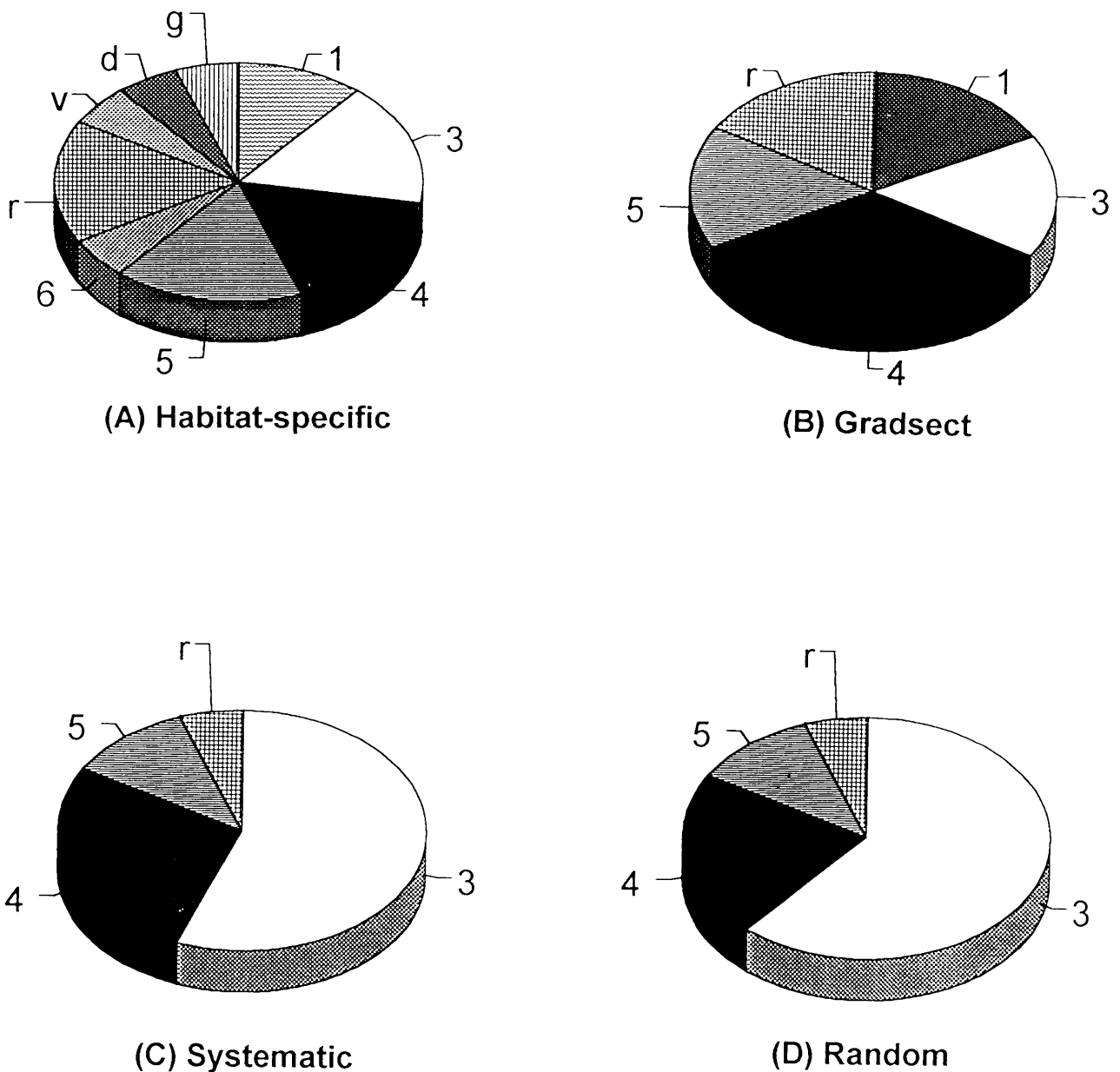
The simulation process treated the random and systematically positioned plots as if they sampled only the spatially dominant vegetation type or land facet within it. Subsequently, this may have eliminated potential variation within plots which contained more than one stratum. This procedure could therefore have underestimated the efficiency of the two “statistical” survey methods. On the other hand, the bootstrap procedures also under represented the efficiency of the gradsect method relative to the “statistical” methods: this was due to the drawing of sampling plots at random with replacement from the complete number of plots sampled. In practice, the gradsect method would avoid repeatedly sampling the same conditions. Assuming that the aforementioned underestimations would nullify one another, we suggest that the bootstrap estimates provide dependable indications of relative survey efficiency.

Since the gradsect survey sampled a range of sites that were representative of the environmental variation of the reserve, this approach maximised the variation between plots (Austin and Basinski, 1978; Austin and Adomeit, 1991) and consistently detected more species within a given number of plots than the systematic and random surveys. Figures 5a,b illustrate that more than half of the plots sampled by the two “statistical” methods were located within the most abundant vegetation type in the study area,



**Figure 5.** The average proportions of vegetation types encountered in bird survey sampling plots are shown for the different survey methods (A-D).<sup>3</sup>

<sup>3</sup> 1: *Acacia stuhlmannii*-*Salvadora angustifolia* open woodland; 3: *Colophospermum mopane* woodland on colluvial soils; 4: *Colophospermum mopane*-*Salvadora angustifolia* open woodland; 5: *Combretum apiculatum*-*Colophospermum mopane* open woodland; 6: fine sandveld; 7: escarpment vegetation; 8: rugged karoo hills; 9: *Combretum apiculatum* mixed woodland; d: mixed deciduous open woodland on diabase dykes; v: *Colophospermum mopane* woodland in valleys between rugged hills; g: grasslands; r: riverine forest; m: *Colophospermum mopane* tall riverine woodland.



**Figure 6.** The average proportions of vegetation types encountered in dung beetle survey sampling plots are shown for the different survey methods (A-D).<sup>4</sup>

<sup>4</sup> 1: *Acacia stuhlmannii-Salvadora angustifolia* open woodland; 3: *Colophospermum mopane* woodland on colluvial soils; 4: *Colophospermum mopane-Salvadora angustifolia* open woodland; 5: *Combretum apiculatum-Colophospermum mopane* open woodland; 6: fine sandveld; d: mixed deciduous open woodland on diabase dykes; v: *Colophospermum mopane* woodland in valleys between rugged hills; g: grasslands; r: riverine forest; m: *Colophospermum mopane* tall riverine woodland.

the *Colophospermum mopane* woodland (Fig.1 vegetation type 3), which also contains the lowest number of bird and dung beetle species. As a result the two “statistical” survey methods repeatedly recorded the same species during the simulations and were therefore less efficient (Figs 3a-d, 4a-c). It may be argued that the sampling of additional plots in the *C. mopane* woodland could have detected more species than could be allocated from the plots sampled using the gradsect and habitat-specific methods; potentially resulting in the underestimation of the “statistical” methods’ efficiency. However, the field surveys in the *C. mopane* woodland illustrated that the species accumulation curve for this species-poor vegetation type swiftly (after four plots sampled) approached an asymptote. The sporadic detection of additional species by the two “statistical” methods within a few plots of *C. mopane* woodland is expected to have a limited effect on the robust bootstrap estimations, since these were based on the average of 300 plots drawn at random. Consequently, we suggest that the simulation process provides a reliable reflection of the species accumulation curve that would result from sampling the different vegetation types in the field, according to the ratios illustrated in Figs 5, 6.

Although the present study clearly illustrates that the gradsect method is more efficient than “statistical” sampling, another aim was to ascertain how well it compares to an optimal sampling strategy, the habitat-specific survey method. The species accumulation curve of the gradsect method showed an apparent lower efficiency than the habitat-specific method in only two cases (both the bird and dung beetle surveys of field trip 3, Figs. 3b, 4b), however, this difference did not reach statistical significance (Table 3b). In the remaining comparisons, the gradsect and habitat-specific surveys’ species accumulation curves were very similar. In general, the results illustrate that the gradsect survey method recorded as many species as the

habitat-specific method, after any given amount of survey effort (number of plots sampled). The efficiency of the gradsect method therefore measured up very well to that of the “yardstick” habitat-specific method. The gradsect and habitat-specific methods both recorded substantially more species over the complete study period than the two “statistical” methods (Table 1). Limited difference between the total number of species detected by the gradsect and habitat-specific methods after all four field trips, illustrates that the gradsect survey provided a representative sample of both the bird and the dung beetle species in the study area.

Gillison and Brewer (1985) predicted that long, thin corridors of vegetation such as riverine forests, which occupy relatively small areas, are more likely to be intercepted by gradsect than random or systematic sampling. This was true in the present study where the “statistical” survey methods rarely sampled within riverine areas (Figs 5,6), and subsequently did not record species restricted to this habitat e.g. *Lagonosticta senegala* (Redbilled firefinch), *Streptopelia semitorquata* (Redeyed dove), *Turdus libonyana* (Kurrichane thrush) and *Cossypha humeralis* (African whitethroated robin). The gradsects did not intercept and therefore did not sample within the following vegetation types: fine sandveld (6), mixed deciduous open woodland on diabase dykes (D), *Colophospermum mopane* woodland in valleys between rugged cave and sandstone hills (V), *Sesamothamnus lugardii* stands (S), grasslands (G) (Fig. 5). Certain bird species, e.g. *Cisticola fulvicapilla* (Neddicky), *Eremomela usticollis* (Burntnecked eremomela) and *Cisticola juncidis* (Fantailed cisticola), that were only recorded by the habitat-specific surveys, occurred in small isolated patches of *Acacia* thickets within grasslands (G), a rare vegetation type within the reserve. The available environmental information could not predict the presence of these small isolated habitat patches. Thus,

although the gradsect method improves the chances of detecting rare elements, there will always be a residual probability of their non-location in the field (Gillison and Brewer, 1985). Awareness of this potential limitation of the gradsect survey method, particularly in regions where such small habitat patches may be of high conservation value, is important. Remote sensing techniques should prove useful for the detection of such rare habitats (Gillison and Brewer, 1985) before gradsects are laid out.

#### *Inferred costs and survey logistics*

The high efficiency of the gradsect method provides for a rapid and representative sample of a region's fauna. In turn, this should ensure the cost-effectiveness of the method, since less time is required in the field to sample the diversity of an area (Gillison and Brewer, 1985; Austin and Heyligers, 1989, 1991). The results presented here imply that the chosen level of stratification within the gradsects was appropriate and that the gradsect sampling plots were positioned in the most suitable locations to maximise the number of species recorded within a given number of plots.

The mean nearest neighbour distances between the gradsect sampling plots were between 70 % and 100 % closer than those measured between plots sampled by the habitat-specific survey method (Table 4). This once again illustrates how logistically demanding stratified random surveys (habitat-specific method) of widely-distributed sites are (Gillison and Brewer, 1985) (Fig. 1). In contrast to this, the sampling plots of the gradsect method were in close proximity to one another, so successive plots could be sampled with short distances

to travel between them (Fig. 2) (Table 4). To ensure the effectiveness of the rendered data for spatial modelling and avoid possible spatial autocorrelation between sampling plots, the gradsect method should include appropriate stratification, geographical replication and randomisation (Austin and Heyligers, 1989, 1991). By sampling the most accessible areas and restricting the distribution of sampling plots to transects, the gradsect approach should always reduce the required travelling distances and should further reduce survey costs (Austin and Basinski, 1978).

#### *The future role of the gradsect survey method in conserving Biodiversity*

Biological surveys form a fundamental component of any scientific effort to conserve biodiversity and the Convention on Biological Diversity specifies that signatory countries have to identify and monitor components of biodiversity (CBD, 1992). The quantity, geographic coverage and consistency of biological data determines the value and reliability of Geographic Information Systems (GIS) (Cocks and Baird, 1991; Lombard *et al.*, 1992) and iterative reserve selection procedures in identifying priority conservation areas (Nicholls and Margules, 1993; Margules, *et al.*, 1994; Miller, 1994; Lombard, 1995a; Trinder-Smith *et al.*, 1996; Freitag *et al.*, 1997). Biological surveys are also required to “ground truth” identified priority areas and to establish the distribution patterns of species on a local scale (Lombard *et al.*, 1995c). Furthermore, continued surveys are essential to monitor whether priority area networks are indeed protecting the biodiversity elements which were initially targeted (Baird and Cocks, 1983; Burbridge, 1983; Noble and Norton, 1991). The gradsect survey method can be employed



in each instance to provide the necessary biological information required for conservation planning.

Austin and Heyligers (1989, 1991) conducted a gradsect survey in a 20 000 km<sup>2</sup> area and stratified their sampling within plots according to local topography. In contrast to this regional scale survey, the present study employed the gradsect method at a local scale ( 350 km<sup>2</sup> area). Even though appropriate stratification is scale-dependent, the general principles of gradsect sampling are therefore not confined to any particular scale (Gillison, 1983).

Recently the Rapid Appraisal of Biodiversity Resource Project (BioRap Project) (Margules and Redhead, 1995) was launched to provide the World Bank's client countries with tools and methods to assist in the identification of priority areas in response to the Convention on Biological Diversity. Many countries however do not yet have sufficient biogeographic data on which to base reserve selection procedures (Belbin, 1993). The BioRap methodology includes and strongly recommends the use of the gradsect survey method for gathering all new biological data (Margules and Redhead, 1995; van Jaarsveld and Chown, 1996), as it provides species distribution data in association with environmental data which may then be used in statistical models (Nicholls, 1989; Margules and Austin; 1994), and empirical models e.g. BIOCLIM (Busby, 1991; Hutchinson *et al.*, 1996) to predict species occurrences within unsampled areas (Margules and Stein, 1989; Margules and Redhead, 1995). Such predictive modelling can further aid in the selection of reserve networks that encompass the range of environmental variability needed to represent a region's biodiversity (Nicholls, 1991). Regional reserve networks could then be identified within biologically unsampled regions, using remote

sensing techniques, such as satellite imagery to gather predictive environmental information (Miller, 1994).

## **Conclusion**

The present study illustrates that the gradsect method is more effective than the traditional random and systematic methods for faunal surveys. More importantly, the study shows that the gradsect method is as effective as a comprehensive habitat-specific faunal survey and can be employed with confidence in areas for which very little or no vegetation information exists. Surveys could then sample various combinations of environmental variables as a means of obtaining representative samples. Where vegetation information is available, it can be used to refine and improve the gradsect sample design to include specific vegetation associations. Although the appropriate environmental attributes to be sampled are related to scale, the general principle of gradient oriented sampling is scale-free and flexible. The results presented here furthermore illustrate that land-form sequences, specifically “land facets” are useful surrogates when sampling environmental diversity where distinct environmental gradients such as altitude and rainfall are absent at finer regional scales.

## **Acknowledgements**

We would like to thank De Beers Consolidated Mines for permission, financial and logistical support to conduct field work; Nigel Fairhead and the rest of the Venetia-Limpopo Nature Reserve staff for their assistance; Chris Margules, Micheal Austin, Ken Brewer and Stefanie Freitag for commenting on drafts of this paper and the University of Pretoria and the Foundation for Research Development for financial support.

## References

- A'Bear, A.G. (1994) Report on the engineering geological map of the Limpopo-Venetia Reserve. Unpublished report, Kimberley: De Beers Farms Department.
- Austin, M.P. and Adomeit, E.M. (1991) Sampling strategies costed by simulation. In *Nature Conservation: Cost Effective Survey and Data Analysis*. (C.R. Margules and M.P. Austin, eds) pp. 167-75. Australia: CSIRO.
- Austin, M.P. and Basinski, J.J. (1978) Bio-physical Survey Techniques. In *Land Use of the South Coast of New South Wales*. (M.P. Austin and K.D. Cocks, eds) pp. 34-54. Australia: CSIRO.
- Austin, M.P. and Heyligers, P.C. (1989) Vegetation survey design for conservation: gradsect sampling of forests in North-eastern New South Wales. *Biol. Conserv.* **50**, 13-32.
- Austin, M.P. and Heyligers, P.C. (1991) New approaches to vegetation survey design: gradsect sampling. In *Nature Conservation: Cost Effective Survey and Data analysis*. (C.R. Margules and M.P. Austin, eds) pp. 31-37. Australia: CSIRO.
- Baird, I.A. and Cocks, K.D. (1983) The role of plant and animal survey in park management. In *Survey Methods for Nature Conservation* (K. Meyers, C. R. Margules & I. Musto, eds) Vol. 2, pp. 349-70. Canberra: CSIRO.
- Barnett, V. (1991) *Sample Survey: Principles and Methods*. London: Edward Arnold.
- Belbin, L. & Austin, M.P. (1991) ECOSIM - A Simulation model for training cost-effective survey methods. In *Nature Conservation: Cost Effective Survey and Data Analysis*. (C.R. Margules & M.P. Austin, eds) pp. 159-68. Australia: CSIRO.

- Belbin, L. (1993) Environmental representativeness: regional partitioning and reserve selection. *Biol. Conserv.* **66**, 223-30.
- Burbridge, A.A. (1983) Selecting and managing parks and reserves: interpretation and communication of survey data. In *Survey Methods for Nature Conservation*. (K. Meyers C.R. Margules & I. Musto, eds) Vol. 2, pp. 387-402., Canberra: CSIRO.
- Burbridge, A.A. (1991) Cost constraints on surveys for nature conservation. In *Nature Conservation: Cost Effective Survey and Data Analysis*. (C.R. Margules & M.P. Austin, eds) pp. 1-3. Australia: CSIRO.
- Busby, J.R. (1991) BIOCLIM - a bioclimatic analysis and prediction system. In *Nature Conservation: Cost Effective Survey and Data Analysis*. (C.R. Margules & M.P. Austin, eds) pp. 64-8. Australia: CSIRO.
- CBD (1992) *Convention on Biological Diversity*, Rio de Janeiro: UNCED.
- Cocks, K.D. and Baird, I.A. (1991) The role of geographic information systems in the collection, extrapolation and use of survey data. In *Nature Conservation: Cost Effective Survey and Data Analysis*. (C.R. Margules and M.P. Austin, eds) pp. 74-80. Australia: CSIRO.
- Currie, D.J. (1991) Energy and large-scale patterns of animal- and plant-species richness. *Am. Nat.* **137**, 27-49.
- Davis, A.L.V., Doube, B.M. & McLennan, P.D. (1988) Habitat associations and seasonal abundance of coprophilous Coleoptera in the Hluhluwe region of South Africa. *Bull. Ent. Res.* **78**, 425-34.

- Doube, B.M. (1983) The habitat preference of some bovine dung beetles (Coleoptera: Scarabaeidae) in Hluhluwe Game Reserve, South Africa. *Bull. Ent. Res.* **73**, 351-71.
- Efron, B. and Gong, G. (1983) A leisurely look at the bootstrap, the jackknife, and cross-validation. *Am. Stat.* **37**, 36-48.
- Efron, B. and Tibshirani, R.J. (1993) *An Introduction to the Bootstrap*. New York: Chapman & Hall.
- Ehrlich, P.R. (1992) Population biology of checkerspot butterflies and the preservation of global biodiversity. *OIKOS* **63**, 6-12.
- Freitag, S., Nicholls, A.O. and van Jaarsveld, A.S. (1996) Nature reserve selection in the Transvaal, South Africa: what data should we use? *Biodiv. Conserv.* **5**, 685-98.
- Freitag, S. and van Jaarsveld, A.S. (1997) Relative occupancy, endemism, taxonomic distinctiveness and vulnerability: prioritizing regional conservation actions. *Biodiv. Conserv.* **6**, 211-32.
- Friend, G.R. and Taylor, J.A. (1984) Ground surface features attributable to feral buffalo, *Bubalus bubalis*. II. Their relationship to the abundance of small animal species. *Aust. Wildl. Res.* **11**, 311-23.
- Gillison, A.N. (1983) Gradient orientated sampling for resource surveys - The gradsect method. In *Survey Methods for Nature Conservation*. (K. Meyers, C. R. Margules & I. Musto, eds) Vol. 2, pp. 349-70. Canberra: CSIRO.
- Gillison, A.N. and Brewer, K.R.W. (1985) The use of gradient directed transects or gradsects in natural resource surveys. *J. Envir. Mngt* **20**, 103-27.

- Green, R.H. (1979) *Sampling Design and Statistical Methods for Environmental Biologists*. New York: John Wiley.
- Greig-Smith, P. (1983) *Quantitative Plant Ecology* (3rd Edition). London: Blackwell Scientific Publications.
- Groombridge, B. (1992) *Global Biodiversity: Status of the Earth's Living Resources*. London: Chapman & Hall.
- Haila, Y. and Margules, C.R. (1996) Survey research in conservation biology. *Ecography* **19**, 323-331.
- Huntley, B.J. (1989) Conserving and monitoring biotic diversity - some South African examples. In *Biodiversity*. (E.O. Wilson, ed.) pp. 248-60. Washington: National Academic Press.
- Hutchinson, M.F., Belbin, L., Nicholls, A.O., Nix, H.A., McMahon, J.P. and Orb, K.D. (1996) *BioRap: Rapid Assessment of Biodiversity. Vol.2 Spatial Modelling Tools*. Australia: CSIRO.
- Lambert, J.M.L. (1972) Theoretical models for large-scale vegetation survey. In *Mathematical Models in Ecology*. (J.N.R. Jeffers, ed.) pp.87-109. Oxford: Blackwell.
- Liversidge, R. (1991) *The Birds Around Us*. Cape Town: Fontein Books.
- Lombard, A.T. (1995a) Introduction to an evaluation of the protection status of South Africa's vertebrates. *S. Afr. J. Zool.* **30**, 63-70.
- Lombard, A.T. (1995b) Problems with multi-species conservation: do hotspots, ideal reserves and existing reserves coincide? *S. Afr. J. Zool.* **30**, 145-63.

- Lombard, A.T., Nicholls, A.O. and August, P.V. (1995c) Where should nature reserves be in located in South Africa? A snakes perspective. *Conserv. Biol.* **9**, 363-72.
- Lombard, A.T., August, P.V. and Siegfried, W.R. (1992) A proposed Geographic Information System for assessing the optimal dispersion of protected areas in South Africa. *S. Afr. J. Sci.* **88**, 136-37
- Lubchenco, J., Olson, A.M., Brubaker, L.B., Carpenter, S.R., Holland, M.M., Hubbell, S.P., Levin, J.A. (1991) The sustainable biosphere initiative: an ecological research agenda. *Ecology* **72**, 371-412.
- Low, A.B. and Rebelo, A.G. (1996) *Vegetation of South Africa, Lesotho and Swaziland*. Department of Environmental Affairs and Tourism, Pretoria.
- Margules, C.R. (1989) Introduction to some Australian developments in conservation evaluation. *Biol. Conserv.* **50**, 1-11.
- Margules, C.R. and Austin, M.P. (1991) *Nature Conservation: Cost Effective Survey and Data Analysis*. Australia: CSIRO.
- Margules, C.R. and Austin, M.P. (1994) Biological models for monitoring species decline: the construction and use of databases. *Phil. Trans. R. Soc.* **344**, 69-75.
- Margules, C.R. and Redhead, T.D. (1995) *BioRap: Guidelines for Using the BioRap Methodology and Tools*. Australia: CSIRO.
- Margules, C.R. and Stein, J.L. (1989) Patterns in the distribution of species and the selection of nature reserves: an example from *Eucalyptus* forests in south-eastern New South Wales. *Biol. Conserv.* **50**, 219-38.



- Margules, C.R., Cresswell, I.D. and Nicholls, A.O. (1994) A scientific basis for establishing networks of protected areas. In *Systematics and Conservation Evaluation* (P.I. Forey, C.J. Humphries and R.I. Vane-Wright, eds) pp. 327-350. Oxford: Clarendon Press.
- Margules, C.R., Nicholls, A.O. and Pressey, R.L. (1988) Selecting networks of reserves to maximise biological diversity. *Biol. Conserv.* **43**, 63-76.
- May, R.M. (1994) Conceptual aspects of the quantification of the extent of biological diversity. *Phil. Trans. R. Soc. Lond. B* **345**, 13-20.
- McKenzie, N.J. and M.P. Austin (1993) A quantitative Australian approach to medium and small scale surveys based on soil stratigraphy and environmental correlation. *Goederma* **57**, 329-55.
- Miller, R.I. (1994) Setting the scene. In *Mapping the Diversity of Nature*. (R.I. Miller, ed.) pp.1-15. London: Chapman & Hall.
- Nealis, V.G. (1977) Habitat associations and community analysis of South Texas dung beetles. *Can. J. Zool.* **55**, 138-147.
- Nicholls, A.O. (1989) How to make biological surveys go further with generalised linear models. *Biol. Conserv.* **50**, 51-75.
- Nicholls, A.O. (1991) Examples of the use of Generalised Linear Models in analysis of survey data for conservation evaluation. In *Nature Conservation: Cost Effective Survey and Data Analysis*. (C.R. Margules & M.P. Austin, eds) pp. 54-63. Australia: CSIRO.

- Nicholls, A.O. (In press) Integrating population abundance, dynamics and distribution into broad scale priority setting. In *Conservation in a Changing World. Symposia of the Zoological Society of London* (A. Balmford, J. Ginsberg and G. Mace, eds)
- Nicholls, A.O. and Margules, C.R. (1993) An upgraded reserve selection algorithm. *Biol. Conserv.* **64**, 165-69.
- Noble, I. and Norton, G. (1991) Economic aspects of monitoring for National Park management. In *Nature Conservation: Cost Effective Survey and Data Analysis*. (C.R. Margules & M.P. Austin, eds) pp. 69-74. Australia: CSIRO.
- O'Connor, T.G. (1991) The vegetation types of the Venetia-Limpopo Nature Reserve. Unpublished report, Kimberley: De Beers Farms Department.
- Pressey, R.L. (1994) *Ad hoc* reservations: forward or backward steps in developing representative reserve systems? *Conserv. Biol.* **8**, 662-8.
- Pressey, R.L., Humphries, C.R., Margules, C.R., Vane-Wright, R.I. and Williams, P.H. (1993) Beyond opportunism: key principles for systematic reserve selection. *TREE* **8**, 662-8.
- Price, G.V. (1981) *Methods of Engineering Geological Mapping and their Application on a Regional Scale in South Africa*. M.Sc. Thesis, Univ. of Pretoria.
- Silk, J. (1979) Random sampling procedures. In *Statistical Concepts in Geography*. (J. Silk, ed.) pp. 133-46. London: George Allen & Unwin.
- Smartt, P.F.M. and Grainger, J.E.A. (1974) Sampling for vegetation survey: some aspects of the behaviour of unrestricted, restricted, and stratified techniques. *J. Biogeogr.* **1**, 193-206.

- Taylor, J.A., Friend, G.R. and Dudzinski, M.L. (1984) Influence of sampling strategy on the relationships between fauna and vegetation structure, plant lifeform and floristics. *Austr. J. Ecol.* **9**, 281-7.
- Trinder-Smith, T.H. Lombard, A.T. and Picker, M.D. (1996) Reserve scenarios for the Cape Peninsula: high-, middle- and low-road options for conserving the remaining biodiversity. *Biodiv. Conserv.* **5**, 649-69.
- UNEP (1995) *Global Biodiversity Assessment*. Cambridge University Press.
- Usher, M.B. (1986) *Wildlife Conservation Evaluation*. London: Chapman & Hall.
- Van Jaarsveld, A.S. and Chown, S.L. (1996) Strategies and time-frames for implementing the Convention on Biological Diversity: biological requirements. *S. Afr. J. Sci.* **92**, 459-64.
- Verner, J. and Ritter, L. V. (1985) A comparison of transects and point counts in oak-pine woodlands of California. *The Condor* **87**, 47-68.
- Williams, P., Gibbons, D., Margules, C.R., Rebelo, A., Humphries, C. and Pressey, R. (1996) A comparison of richness hotspots, rarity hotspots, and complementary areas for conserving diversity of British birds. *Conserv. Biol.* **10**, 155-74.
- Wilson, E.O. (1988) The current state of biological diversity. In *Biodiversity*. (E.O. Wilson, ed.) pp. 3-20. Washington: National Academic Press.

## APPENDIX I

**Vegetation types of the Venetia-Limpopo Nature Reserve (O'Connor, 1991) grouped into  
vegetation strata sampled by the habitat-specific survey method .**

**(labels used in Fig.1 are given in parentheses)**

stratum	vegetation types
1.	<i>Acacia stuhlmannii</i> - <i>Salvadora angustifolia</i> open woodland (1); <i>Sesamothamnus lugardii</i> stands (S); Grasslands (G)
2.	<i>Colophospermum mopane</i> - <i>Salvadora angustifolia</i> open woodland (4)
3.	<i>Colophospermum mopane</i> woodland on colluvial soils (3)
4.	Riverine forest (R); <i>Colophospermum mopane</i> tall riverine woodland (M)
5.	<i>Combretum apiculatum</i> - <i>Colophospermum mopane</i> open woodland (5)
6.	Fine sandveld (6); Mixed deciduous open woodland on diabase dykes (D); <i>Colophospermum mopane</i> woodland in valleys between rugged hills (V)
7.	Escarpment vegetation (7)
8.	Rugged karoo hills (8)
9.	<i>Combretum apiculatum</i> mixed woodland (9)

## APPENDIX II

### Engineering geological land facets of the Venetia-Limpopo Nature Reserve (A'Bear, 1994) sampled by the gradsect survey method.

- 
- All.* Flat alluvial floodplains, river and stream channels. Sandy soils are located in the river channels and banks. Clayed soils are located in the floodplains of the rivers and streams.
- Mc.* Moderate to gentle slopes with sandy clays overlaying mudstone of the Karoo sequence.
- Mg.* Moderate to gentle slope with gravel rich profiles developed over conglomerates and harder, weather resistant metamorphic rock.
- Ms.* Moderate to gentle slopes with sandy profiles associated with areas underlain by Karoo sequence sandstones.
- Mca.* Crests of gentle slopes with calcrete rich profile.
- Ps.* Pediplains with gentle to flat slopes and sandy soils, wind blown.
- Pc.* Pediplains with gentle to flat slopes and soils containing clay, alluvial and sheetwash in origin.
- Rt.* Rugged topography, a ridge plateau, with steep talus dominated slopes. Abundant gravel, boulders and rock outcrop occasionally covered with thin soil.
-

**APPENDIX III.**  
**Bird species recorded in Venetia-Limpopo Nature Reserve.**

Scientific name	Common name	Scientific name	Common name
<i>Accipiter badius</i>	Little banded goshawk	<i>Eremomela usticollis</i>	Burntnecked eremomela
<i>Accipiter minullus</i>	Little sparrowhawk	<i>Eremopterix leucotis</i>	Chestnutbacked finchlark
<i>Accipiter tachiro</i>	African goshawk	<i>Erythropygia leucophrys</i>	White browed robin
<i>Amadina erythrocephala</i>	Redheaded finch	<i>Erythropygia paena</i>	Kalahari robin
<i>Amadina fasciata</i>	Cut-throat finch	<i>Eupodotis ruficrista</i>	Redcrested korhaan
<i>Anaplectes rubriceps</i>	Redheaded weaver	<i>Eurocephalus anguitimens</i>	Whitecrowned shrike
<i>Anthoscopus caroli</i>	Grey penduline tit	<i>Falco biarmicus</i>	Lanner falcon
<i>Anthus vaalensis</i>	Buffy pipit	<i>Falco tinnunculus</i>	Rock kestrel
<i>Ardeotis kori</i>	Kori bustard	<i>Francolinus natalensis</i>	Natal francolin
<i>Batis molitor</i>	Chin-spot batis	<i>Francolinus sephaena</i>	Crested francolin
<i>Bubalornis niger</i>	Redbilled buffalo weaver	<i>Francolinus swainsonii</i>	Swainsons francolin
<i>Bubo africanus</i>	Spotted eagle owl	<i>Glaucidium perlatum</i>	Pearlspotted owl
<i>Bubo lacteus</i>	Giant eagle owl	<i>Halcyon chelicuti</i>	Striped kingfisher
<i>Buphagus erythrorhynchus</i>	Redbilled oxpecker	<i>Halcyon albiventris</i>	Brownhooded kingfisher
<i>Burhinus capensis</i>	Spotted dikkop	<i>Halcyon senegalensis</i>	Woodland kingfisher
<i>Camaroptera brevicaudata</i>	Greybacked bleat warbler	<i>Indicator indicator</i>	Greater honeyguide
<i>Camaroptera fasciolata</i>	African barred warbler	<i>Ispidina picta</i>	Pygmy kingfisher
<i>Camator jacobinus</i>	Jacobin cuckoo	<i>Lagonosticta rubricata</i>	Bluebilled firefinch
<i>Campephaga flava</i>	Black cuckooshrike	<i>Lagonosticta senegala</i>	Redbilled firefinch
<i>Campethera abingoni</i>	Goldtailed woodpecker	<i>Lamprotornis nitens</i>	Glossy starling
<i>Centropus burchelli</i>	Burchell's coucal	<i>Lamprotornis mevesii</i>	Longtailed starling
<i>Cercomela familiaris</i>	Familiar chat	<i>Lanarius aethiopicus</i>	Tropical boubou
<i>Chrysococcyx caprius</i>	Diederik cuckoo	<i>Lanarius atrococcineus</i>	Crimsonbreasted Shrike
<i>Chrysococcyx klaas</i>	Klaas's cuckoo	<i>Lanius minor</i>	Lesser grey shrike
<i>Cinnyricinclus leucogaster</i>	Plumcoloured starling	<i>Lanius collurio</i>	Redbacked shrike
<i>Cisticola aberrans</i>	Lazy cisticola	<i>Lybius leucomelas</i>	Pied barbet
<i>Cisticola chiniana</i>	Rattling cisticola	<i>Malaconotus blanchoti</i>	Greyheaded bush shrike
<i>Cisticola fulvicapilla</i>	Neddicky	<i>Melaenornis mariquensis</i>	Marico flycatcher
<i>Cisticula juncidis</i>	Fantailed cisticola	<i>Melierax canorus</i>	Pale chanting goshawk
<i>Clamator glandarius</i>	Greater spotted cuckoo	<i>Melierax metabates</i>	Dark chanting goshawk
<i>Clamator levaillantii</i>	Striped cuckoo	<i>Merops pusillus</i>	Little bee-eater
<i>Colius indicus</i>	Redfaced mousebird	<i>Merops apiaster</i>	European bee-eater
<i>Columba guinea</i>	Rock pigeon	<i>Merops nubicoides</i>	Carmine bee-eater
<i>Coracias naevia</i>	Purple roller	<i>Micronisus gabar</i>	Gabar goshawk
<i>Coracias caudata</i>	Lilacbreasted roller	<i>Mirafra africana</i>	Rufousnaped lark
<i>Corvinella melanoleuca</i>	Longtailed shrike	<i>Mirafra passerina</i>	Monotonous lark
<i>Corythaixoides concolor</i>	Grey lourie	<i>Mirafra sabota</i>	Sabota lark
<i>Cossypha humeralis</i>	Whitethroated robin	<i>Muscicapa striata</i>	Spotted flycatcher
<i>Creatophora cinerea</i>	Wattled starling	<i>Nectarinia mariquensis</i>	Marico sunbird
<i>Cuculus gularis</i>	African cuckoo	<i>Nectarinia talatala</i>	White bellied sunbird
<i>Cursorius temminckii</i>	Temminck's courser	<i>Nilaus afer</i>	Brubru
<i>Dendropicos fuscescens</i>	Cardinal woodpecker	<i>Oena capensis</i>	Namaqua Dove
<i>Dicrurus adsimilis</i>	Forktailed drongo	<i>Oenanthe pileata</i>	Capped wheatear
<i>Dryoscopus cubla</i>	Puffback	<i>Oriolus larvatus</i>	Blackheaded oriole
<i>Emberiza flaviventris</i>	Goldenbreasted bunting	<i>Oriolus oriolus</i>	European golden oriole
<i>Emberiza impetuari</i>	Larklike bunting	<i>Parus niger</i>	Southern black tit
<i>Emberiza tahapisi</i>	Rock bunting	<i>Passer domesticus</i>	House sparrow
<i>Eremomela icteropygialis</i>	Yellowbellied eremomela	<i>Passer griseus</i>	Greyheaded sparrow

APPENDIX III (Continued)

Scientific name	Common name	Scientific name	Common name
<i>Petronaria superciliaris</i>	Yellow throated sparrow	<i>Sylcietta rufescens</i>	Longbilled Crombec
<i>Phoeniculus purpureus</i>	Redbilled woodhoopoe	<i>Tchagra australis</i>	Threestreaked tchagra
<i>Phylloscopus trochilus</i>	Willow warbler	<i>Tchagra senegala</i>	Blackcrowned tchagra
<i>Pinarocorys nigricans</i>	Dusky lark	<i>Telophorus sulfureopectus</i>	Orangebreasted bush shrike
<i>Plocepasser mahali</i>	Whitebrowd sparrow-weaver	<i>Terpsiphone viridis</i>	Paradise flycatcher
<i>Ploceus velatus</i>	Southern masked weaver	<i>Thamnolaea cinnamomeiventris</i>	Mocking chat
<i>Poicephalus meyeri</i>	Meyer's parrot	<i>Thripias namaquus</i>	Bearded woodpecker
<i>Polyboriodes typus</i>	Gymnogene	<i>Tockus alboterminatus</i>	Grey hornbill
<i>Prinia flavicans</i>	Blackchested prinia	<i>Tockus erythrorhynchus</i>	Redbilled hornbill
<i>Prinia subflava</i>	Tawnyflanked prinia	<i>Tockus flavirostris</i>	Yellowbilled hornbill
<i>Prionops plumatus</i>	White helmetshrike	<i>Trachyphonus vaillantii</i>	Crested barbet
<i>Prionops retzii</i>	Redbilled helmetshrike	<i>Turdoides bicolor</i>	Pied babbler
<i>Prodotiscus regulus</i>	Sharpbilled honeyguide	<i>Turdoides jardineii</i>	Arrowmarked Babbler
<i>Pterocles bicinctus</i>	Doublebanded sandgrouse	<i>Turdus libonyana</i>	Kurrichane thrush
<i>Pycnonotus barbatus</i>	Blackeyed bulbul	<i>Turdus litsitsirupa</i>	Groundscraper thrush
<i>Pytilia melba</i>	Melba finch	<i>Turdus olivaceus</i>	Southern olive thrush
<i>Rhinopomastus cyanomelas</i>	Greater scimitarbill	<i>Turtur chalcospilos</i>	Greenspotted dove
<i>Rhinoptilus chalcopterus</i>	Bronzewinged courser	<i>Upupa epops</i>	Hoopoe
<i>Sagittarius serpentarius</i>	Secretarybird	<i>Uraeginthus angolensis</i>	Blue waxbill
<i>Serinus atrogularis</i>	Blackthroated canary	<i>Uraeginthus granatinus</i>	Violet eared waxbill
<i>Serinus flaviventris</i>	Yellow eyed canary	<i>Vanellus coronatus</i>	Crowned plover
<i>Sporopipes squamifrons</i>	Scalyfeathered finch	<i>Vidua chalybeata</i>	Steelblue widowfinch
<i>Streptopelia capocola</i>	Cape turtle dove	<i>Vidua paradisaea</i>	Paradise whydah
<i>Streptopelia semitorquata</i>	Redeyed dove	<i>Vidua regia</i>	Shaft-tailed whydah
<i>Streptopelia senegalensis</i>	Laughing Dove		

**APPENDIX IV**  
**Dung Beetle species recorded in the Venetia-Limpopo Nature Reserve**

genus	species	genus	species
<i>Aphodius</i>	<i>sp. 1</i> <i>sp. 2</i> <i>moestus</i> <i>sp. 6</i> <i>sp. 7</i> <i>sp. 8</i> <i>impurus</i>	<i>Onthophagus</i>	<i>depressus</i> <i>pallidipennis</i> <i>quadraticeps</i> <i>vinctus</i> <i>nanus</i> <i>variegatus</i> <i>aeruginosus</i> <i>signatus</i> <i>flavolimbatus</i> <i>rasipennis</i> <i>sp. 1</i> <i>sp. 3</i> <i>sp. 17</i> <i>sp. 18</i>
<i>Anachalcos</i>	<i>convexus</i>		
<i>Allogymnopleurus</i>	<i>thalassinus</i>		
<i>Copris</i>	<i>mesacanthus</i> <i>elephenor</i> <i>amyntor</i>		
<i>Cleptocaccobius</i>	<i>viridicollis</i>	<i>Oniticellus</i>	<i>formosus</i>
<i>Chironitis</i>	<i>scabrosus</i>	<i>Pedaria</i>	<i>sp. 1</i>
<i>Digitonthophagus</i>	<i>gazella</i>	<i>Phalops</i>	<i>ardea</i> <i>boschas</i>
<i>Euoniticellus</i>	<i>intermedius</i>	<i>Pachylomerus</i>	<i>femoralis</i>
<i>Euonthophagus</i>	<i>carbonarius</i>	<i>Scarabaeus</i>	<i>zambesianus</i> <i>satyrus</i> <i>bohemani</i>
<i>Gymnopleurus</i>	<i>aenescens</i> <i>ignitus</i> <i>thelwalli</i>	<i>Sisyphus</i>	<i>goryi</i>
<i>Garetta</i>	<i>nitens</i>		
<i>Heliocopris</i>	<i>andersoni</i>		
<i>Kheper</i>	<i>nigroaeneus</i> <i>lamarcki</i> <i>cupreus</i>		
<i>Metacatharsius</i>	<i>opacus</i> <i>troglydites</i> <i>sp. 1</i>		
<i>Neosisyphus</i>	<i>calcaratus</i>		
<i>Onitis</i>	<i>obenbergeri</i> <i>uncinatus</i> <i>alexis</i>		



## **CHAPTER 3**

# **The use of Land Facets as Biodiversity Surrogates during Reserve Selection at a Local Scale.**

# **The use of land facets as biodiversity surrogates during reserve selection at a local scale.**

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**Running title:** Land facets as biodiversity surrogates.

**Key words:** Biodiversity, Surrogates, Land facets, Reserve selection, Priority conservation areas

## Summary

Where species distribution data are inadequate reserve selection procedures have to rely on surrogate measures of biodiversity. The informativeness of land facets (the simplest units of a landscape with uniform slope, soils and hydrological conditions) as a local scale environmental surrogate was investigated in the Venetia-Limpopo Nature Reserve, South Africa. Multivariate analysis (MDS, ANOSIM) revealed that the land facets adequately represent distinct bird and dung beetle assemblages and are therefore useful surrogates. These land facets/assemblages were subsequently used as attributes in the following reserve selection procedures: (i) *Percentage Area Representation* (PAR - represent a nominated percentage area of each assemblage); (ii) *Species-Assemblage Representation* (SAR - represent each species within the smallest number of assemblages); (iii) *Assemblage Diversity* (AD - maximising diversity by first selecting areas containing most dissimilar assemblages). The influence of grid cell size, target representation percentages and an over-representation constraint on the efficiency of the algorithms were illustrated. The SAR procedure did not represent assemblages lacking distinguishing species and were thus more efficient in terms of total area selected. The AD procedure selected a slightly larger area than the PAR procedure, but was highly effective at rapidly increasing the diversity of the reserve network.

## Introduction

The identification of a representative and complementary network of areas with high conservation value requires extensive information on the distribution of species (Pressey *et al.*, 1993). However, regions under evaluation often have inadequate databases on species distributions (Belbin, 1993; Haila and Margules, 1996) and systematic reserve selection procedures have to rely on surrogate measures of biodiversity. Surrogate classes at higher levels of the biological hierarchy (e.g. communities, landscape types, or environmental domains) can be used as the attributes of candidate conservation areas during reserve selection (Margules and Williams, in press; Williams and Humphries, 1996). Information on the distribution of surrogates is easier and cheaper to acquire than species distribution data and is available at a more consistent level of detail (Belbin, 1993; Pressey, 1994; Margules and Redhead, 1995; Pressey and Logan, 1995; Margules and Williams, 1996). Such information incorporate attributes like soil properties, climatic data, terrain data (Miller *et al.*, 1989; Hutchinson *et al.*, 1996) and may be derived using remote sensing techniques such as aerial photography and satellite imagery (Austin and Margules, 1986; Margules and Redhead, 1995).

Priority area selection to represent all surrogate classes and therefore the entire range of regional environmental variation, assumes that these areas contain all the species found in that region (Purdie *et al.* , 1986; Belbin, 1993; Nicholls and Margules, 1993; Faith and Walker, 1996). This pattern-based approach links species variation to environmental variation as summarised in an environmental pattern (Walker and Faith, 1996). Using this rationale, the environmental representativeness

of reserve networks have been assessed using the following surrogate measures: climatic attributes (Austin and Nix, 1978), climatic and edaphic variables (Belbin, 1993), landscapes (Noss, 1983, 1987; Scott *et al.*, 1987; Pressey and Nicholls, 1989), landform-vegetation classes (Awimbo *et al.*, 1996), land systems (Purdie *et al.*, 1986; Pressey and Nicholls, 1989; Bull *et al.*, 1993 in Margules and Redhead, 1995; Pressey and Tully, 1994), landscape ecosystems (Lapin and Barnes, 1995), land classes (Pressey and Logan, 1995), physico-chemical variables (Faith and Norris, 1989), environmental groups (Mackey *et al.*, 1989), environments (Margules *et al.*, 1994) and environmental domains (Richards *et al.*, 1990 in Margules and Redhead, 1995; Bedward *et al.*, 1992). It has however also been argued that the predictive relationship between surrogates and the target elements (e.g. species) should be demonstrated, not simply assumed (Bedward *et al.*, 1992; Pressey, 1994; Landres *et al.*, 1988; Noss, 1990; Margules and Williams, in press; Williams and Humphries, 1996). In other words, do different taxa show the same pattern in relation to surrogates and should particular *a priori* classes be merged or subdivided before using them as attributes to be represented within a reserve network? (Pressey, 1994) The latter is essential, as the amalgamation or subdivision of surrogate classes has a profound influence on the apparent efficiency and representativeness of reserve systems (Pressey and Logan, 1994).

The present study therefore investigated the informativeness of *land facets* as biodiversity surrogates at the local scale, by testing whether these land facets represent different bird and dung beetle communities. These two target groups were chosen because (1) they are not expected to be ecologically linked, have very different nutritional roles, longevities and habitat requirements, and therefore represent two

independent evaluations; (2) they are relatively easy to sample and are systematically well described.

### *Reserve selection based on surrogates*

The goal of iterative reserve selection procedures is to represent each of the attributes in the data set, i.e. species or biodiversity surrogates (e.g. land facets), a nominated number of times (Margules *et al.*, 1988) or quantitatively with a nominated proportion of total area (Margules and Redhead, 1995). These systematic approaches are termed iterative because they proceed stepwise with all successive steps taking into account the attributes of sites already selected (Pressey and Nicholls, 1989). The efficiency of reserve selection algorithms means minimising (or near minimising) the number and area of selected sites needed to achieve conservation goals (e.g. representing 10 % of every surrogate class) and is thus an essential property given the need to defend reserve proposals against competing land uses (Bedward *et al.*, 1992). Efficiency is achieved by maximizing complementarity (Vane-Wright, 1996). The efficiency of various algorithms in representing species a nominated number of times, have been extensively evaluated (for review see Pressey *et al.*, 1996; Csuti *et al.*, 1997; Freitag *et al.*, 1996). However, only a limited number of studies (Bedward *et al.*, 1992; Nicholls and Margules, 1993; Pressey and Tully, 1994; Pressey and Logan, 1995) have done similar comparative analyses involving quantitative representation targets (Pressey *et al.*, 1996). The novel “Phylogenetic Diversity” approach (PD; Faith, 1992; Walker and Faith, 1995) differs from the traditional minimum-set approach (Bedward *et al.*, 1992) in that it does not treat all surrogate classes as equal, since they are not equally distinct in

multivariate space (Vane-Wright *et al.*, 1991; Belbin, 1993). Woinarski *et al.* (1996) adapted the “P D” model to prioritise sites that are environmentally most dissimilar to those environments already protected. The order of site selection is therefore aimed at rapidly increasing the diversity of a reserve network (Woinarski *et al.*, 1996).

In the present study we investigated: (1) the influence of selection unit size (grid cells) and different representation target levels (5, 10, 20 and 30% of total area of each feature) on the outcome of a reserve selection algorithm; (2) the contribution made to overall efficiency by incorporating an “over-representation constraining” (ORC) rule into algorithms and (3) the results of three very different reserve selection approaches:

- (i) *Percentages Representation (PR) approach* - represents a nominated percentage area of each feature (land facets or identified species assemblages);
- (ii) *Species-Assemblages Representation (SAR) approach* - represents every species at least once within the smallest number of assemblages, thus avoiding representing assemblages that do not contain unique species;
- (iii) *Assemblage Diversity (AD) approach* - rapidly increases the diversity of a reserve network by first representing areas containing species assemblages which are most dissimilar, i.e. cover the largest distances within a hierarchical classification.

## Materials and methods

### *Study area*

The Venetia-Limpopo Nature Reserve is situated in the Northern Province of South Africa, close to the confluence of the Shashe and Limpopo Rivers, which form the international boundaries between Zimbabwe, Botswana and South Africa respectively (22°20' S, 29°20' E). This area falls within the Savanna biome and the Mopane Bushveld vegetation type (Louw and Rebelo, 1996). The reserve is approximately 35 000 ha (350 km<sup>2</sup>) in extent and is characterised by a low to moderate relief with an altitudinal variance of only 120m. The climate is arid (mean annual precipitation = 350 mm), with rain falling during the hot summer months, while the winters are dry and mild. The average maximum annual temperature is 30°C and the average minimum annual temperature is 13.2°C. Three types of mopani woodland (*Colophospermum mopane*) comprise the majority of the area. In addition, the *Acacia*, *Combretum* and riverine woodlands, as well as rugged Karoo hills and escarpment vegetation contribute to the habitat diversity within the reserve.

### *Land facets*

A *land system* is a large area with a recurring pattern of land forms, soils and hydrological regimes which can be identified from air or space due to the regular arrangement of surface features at a 1: 150 000 to 1: 1 000 000 scale (Brink *et al.*, 1968; Lawrence *et al.*, 1993). *Land facets* are the basic units, the “building blocks”

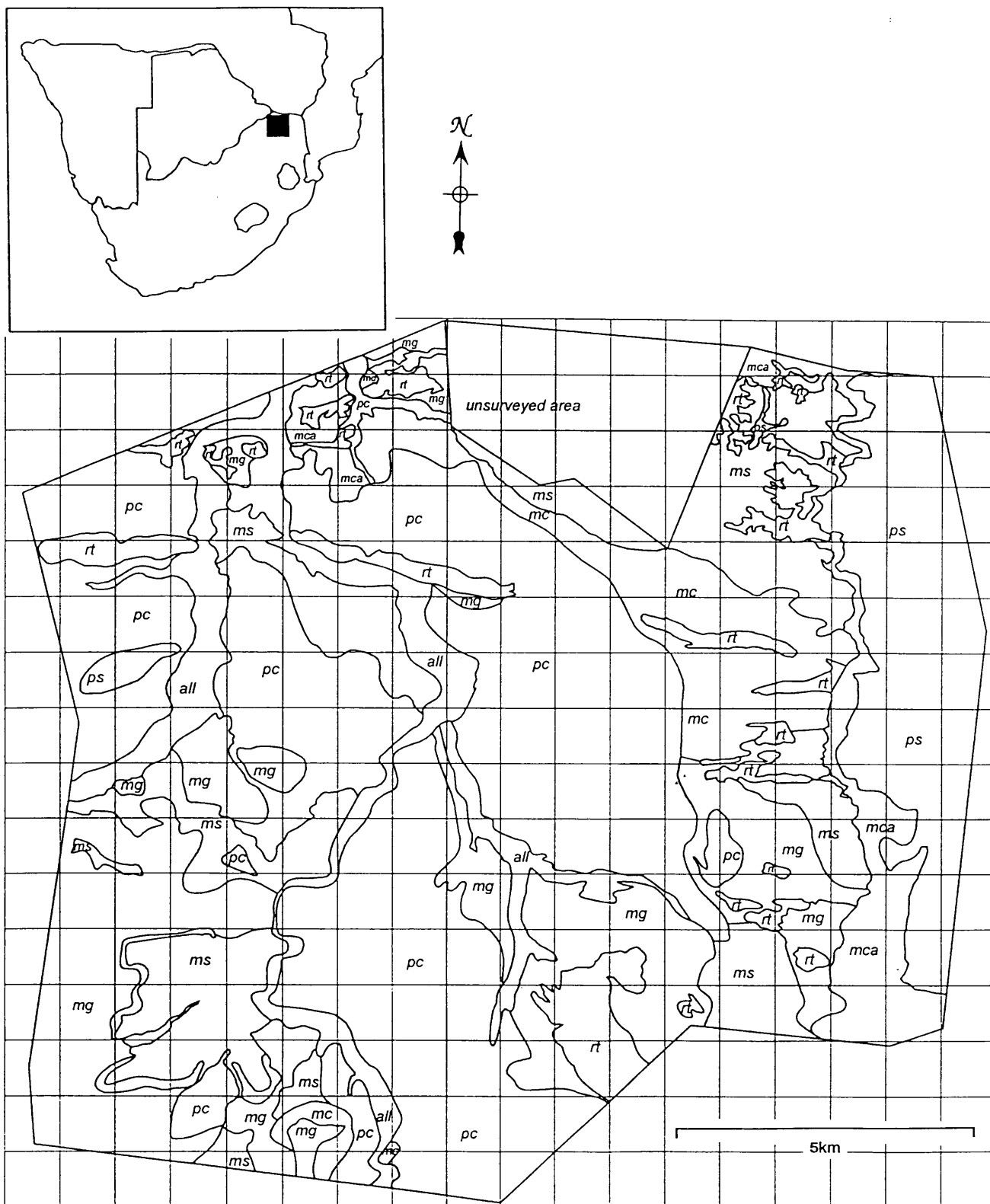


that make up a land system and are mapped at a 1: 10 000 to 1: 50 000 scale (Brink *et al.*, 1968). A land facet is defined as a the simplest terrain unit of uniform slope, parent material, soils and hydrological conditions identifiable from aerial pattern (Christian and Steward, 1968; Galloway, 1978; Price, 1981; Lawrence *et al.*, 1993). Land systems have been extensively used as environmental surrogates during reserve network evaluation at broad regional scales (Purdie *et al.*, 1986; Pressey and Nicholls, 1989; Bull *et al.*, 1993 in Margules and Redhead, 1995 ; Pressey and Tully, 1994). The present study was concerned with the use of land facets as a biodiversity surrogate at a local scale.

An engineering geological survey of the area (A'Bear, 1994), conducted according to the methods proposed by Price (1981), investigated the underlying geology, soil profiles and topographical characteristics of the area. The survey was used to identify and map nine land facets, Fig. 1 (Appendix I). Two land facets, *R* (rugged topography) and *T* (steep talus slopes), were treated as a single land facet *Rt* (hills with rugged topography) during field sampling and analyses.

### *Field sampling techniques*

Surveys were conducted during four field trips that approximated the four seasons of a year (field trip 1: July - August, winter; field trip 2: October - November, spring; field trip 3: January - February, summer; field trip 4: April - May, autumn). Sampling plots (25 ha) were located at random within every land facet. Within plots, visual bird surveys were conducted along a 1500m transect (3 x 500m sections at right angles to one another in square plots or sequentially in elongated plots along rivers and hills).



**Figure 1.** Land facet map of the Venetia-Limpopo Nature Reserve overlaid with a 1 km<sup>2</sup> gradicule.\*

\* *all*: flat alluvial flood plains, rivers and stream channels with sandy soils; *mc*: moderate to gentle slopes with sandy clays overlaying mudstone of the Karoo sequence; *mg*: moderate to gentle slopes with soil profiles containing gravel overlaying conglomerates and harder, weather resistant metamorphic rock; *ms*: moderate to gentle slopes with sandy soils associated with areas underlain by sandstone of the Karoo sequence; *mca*: crests of gentle slopes with calcrete rich soils; *ps*: pediplains with gentle to flat slopes and sandy soils; *pc*: pediplains with gentle to flat slopes and soils containing clay; *rt*: rugged topography, ridge plateaus with steep talus dominated slopes, boulders and rock outcrops.

Each plot was surveyed for approximately 150 minutes. Transects were of indefinite width and distances travelled along transects were estimated using a hand held counter (“tally”) to record the number of paces walked. The total number of individuals counted per bird species, within one plot, served as measures of abundance. Strata were sampled in a random order and bird surveys were conducted twice daily. Morning and afternoon surveys commenced approximately ten minutes after sunrise and three hours before sunset respectively. During each of the four field trip, a specific land facet was sampled four times during the morning and four times during the afternoon. Thus, a total of 64 plots (8 strata x 8 plots) were sampled for birds.

Dung beetles were collected over 24 hour periods, using eight pitfall traps baited with fresh cattle dung and laid out sequentially at 20 m intervals within each plot (Doube, 1983). Sampling was restricted to sunny days to minimise the effect of weather on the number of beetles caught (Davis *et al.*, 1988). As pitfall traps could not be used in strata with rocky substrates, only six land facets were sampled for dung beetles. This amounted to a total of 36 sampled plots (6 strata x 6 plots).

### *Multivariate analyses*

Multidimensional scaling (MDS) ordinations based on a rank Bray-Curtis similarity matrix (Bray and Curtis, 1957) were used to visualise the community compositions of the sampling plots in two dimensional space (Kruskal and Wish, 1978; Faith and Norris, 1989, Clarke, 1993). The stress values calculated for each MDS plot indicate how well rank similarity is presented in the reduced dimensions (Fig. 2, 3) (Clarke and Warwick, 1994). For dung beetles, the average number of individuals per species caught within eight traps was used as the abundance estimate for that sampling plot.

In all cases fourth root transformed abundance data were used to reduce the potentially large contribution of a few common species to the dissimilarity. A one-way analysis of similarity (ANOSIM) was used to test for significant differences in community composition between different land facets (Clarke, 1993). The method uses the ratio of the mean within- to between group (land facets) distances (scaled to fall between -1 and 1) to calculate the test parameter R. The significance of the calculated R-values are assessed using randomisation procedures, consisting of 1000 random permutations of distances between samples. The null hypothesis of no difference in community composition of the different land facets, is rejected at a significance level of 3% ( $p < 0.03$ ) (Clarke and Warwick, 1994). The global test indicated whether there were any community differences between land facets in the data. A pair-wise test (ANOSIM) subsequently tested for significant differences in the community composition of land facets in a pairwise fashion. All multivariate analyses were conducted using PRIMER (Plymouth Routines In Multivariate Ecological Research; Clarke and Warwick, 1994).

#### *Reserve selection procedures*

The study area was overlaid with a 1km<sup>2</sup> grid (Fig. 1) and 4km<sup>2</sup> grid respectively and the extent of the eight land facets within each grid cell (1km<sup>2</sup> or 4km<sup>2</sup>) calculated using the Geographic Information System ReGIS<sup>TM</sup>. The percentage of the total study area covered by the different land facets is provided in Appendix I.

An obvious weakness of the earliest reserve selection algorithms was that they generally selected a diffuse scatter of sites (Bedward *et al.*, 1992). An “adjacency constraint” rule was incorporated in all the algorithms used in the present study in

order to select adjacent grid cells and create larger contiguous areas where options were available (Nicholls and Margules, 1993; Lombard *et al.*, 1995; Freitag *et al.*, 1996; Willis *et al.*, 1996). The explicit selection rules for the algorithms used are provided in Appendix II.

### 1. Percentages Representation (PR) approach

This approach follows Pressey and Nicholls (1989) and Pressey and Tully (1994), as it attempts to select the smallest set of grid cells that together sample a nominated percentage area (5, 10, 20, 30%) of each land facet or each of the identified species assemblage areas. The algorithm begins by selecting for the feature covering the smallest total area and thus conforms to a “rarity-based” algorithm (Margules *et al.*, 1988). Reserve selection procedures often overshoot initial target representation levels (Bedward *et al.*, 1992; Nicholls and Margules, 1993). To curb this inefficiency, an “over-representation constraint” (ORC) rule (Appendix II) was designed to restrict over-representation of features and reduce the total area selected (Nicholls and Margules, 1993). This algorithm was used with (PR+ORC) and without the ORC rule (PR) to alternatively represent land facets and identified species assemblage areas.

### 2. Species-Assemblages Representation (SAR) approach

This approach is similar to that used by Margules *et al.* (1988) and identifies the smallest number of species assemblages that are required to represent each species at least once and then represents the areas associated with these identified assemblages to a nominated level. The algorithm begins by representing the assemblage containing the largest number of “unique” species (i.e. species not found in other assemblages) to the required level and then progresses to represent the assemblage which is most

complementary, in terms of species to that already represented. This approach does not represent assemblages which do not contain unique species. The ORC rule was incorporated into this algorithm. Only bird assemblage data were used to compare this approach to the others, since dung beetles could not be collected within two land facets (*Mca* and *Rt*).

### 3. Assemblage Diversity (AD) approach

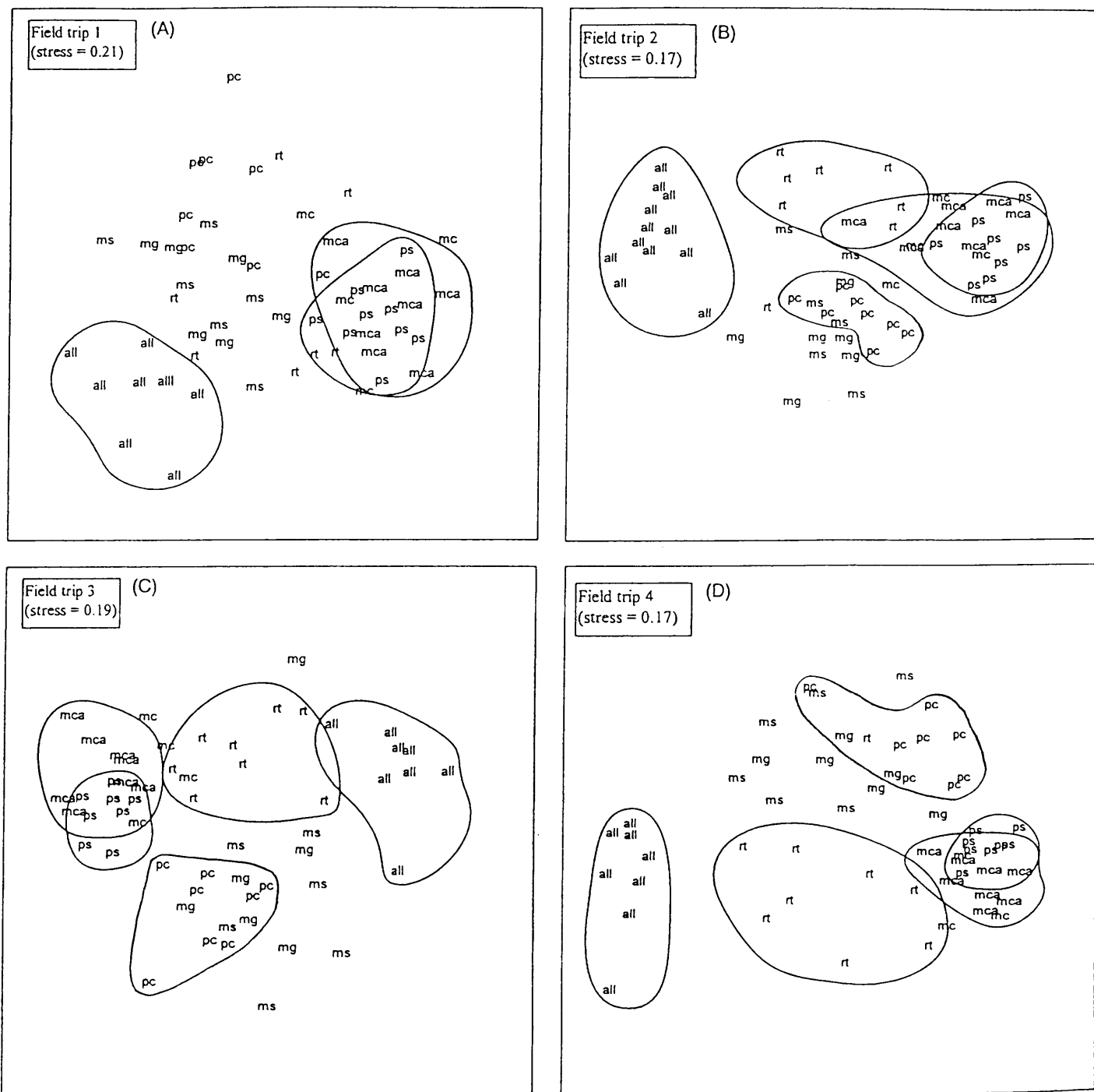
Measures of “Phylogenetic Diversity” (PD; Faith and Walker, 1995; Walker and Faith, 1995) were used to prioritise the selection of grid cells according to the diversity of bird species assemblages within each cell, while representing areas containing assemblages to nominated levels (5, 10, 20, 30%). The order of grid cell selection was therefore aimed at rapidly increasing the diversity of the resulting priority area network (Wionarski *et al.*, 1996).

The average untransformed bird species abundances were calculated for each assemblage over all four field trips. A hierarchical classification based on these averages was used to produce a dendrogram illustrating cluster relationships between assemblages (Fig. 5). The PD program of the “Diversity” software package (Faith and Walker, 1995, Walker and Faith, 1995) was used to calculate the contribution to overall diversity made by each grid cell. The program gave equal weighting to every assemblage in a cell regardless of their extent, although assemblages covering less than 10 000 m<sup>2</sup> (1% of 1km<sup>2</sup>) of one cell were excluded from the calculation of the PD value, since very small patches of an assemblage have limited conservation value in the context of this analysis. The PD value of each grid cell was calculated as the sum of the pair-wise classification branch lengths that connect all assemblages occurring within that cell.

The AD procedure starts by selecting the cell(s) with the highest PD value. If a number of cells score the same PD value, this list of ties is given as input to the PR+ORC algorithm (Appendix II). Selecting from this list of ties the PR+ORC algorithm attempts to reach the target representation percentage of the assemblage covering the smallest total area. If this initial target is not reached, it starts selecting cells containing the largest area of the next smallest assemblage. Should the target percentage of any assemblage not be reached within a list of ties, the next highest scoring list of ties is entered into the algorithm. When the target percentage of an assemblage is reached, the PD gains of all the remaining grid cells are recalculated, excluding assemblages already represented to the nominated level. The selection rules of the PR+ORC algorithm is therefore used to prioritise cell selection within lists of PD ties and increase the efficiency of assemblage representation. This iterative process of recalculating PD gains, selecting cells with the highest PD gains, selecting cells within lists of PD ties and adding newly represented assemblages to the secured list, is repeated until all assemblages are represented to the specified target level. The efficiency of the different priority area selection approaches were assessed in terms of total reserve area selected, spatial configuration of grid cells and the area of each land facet or assemblage represented in relation to target values.

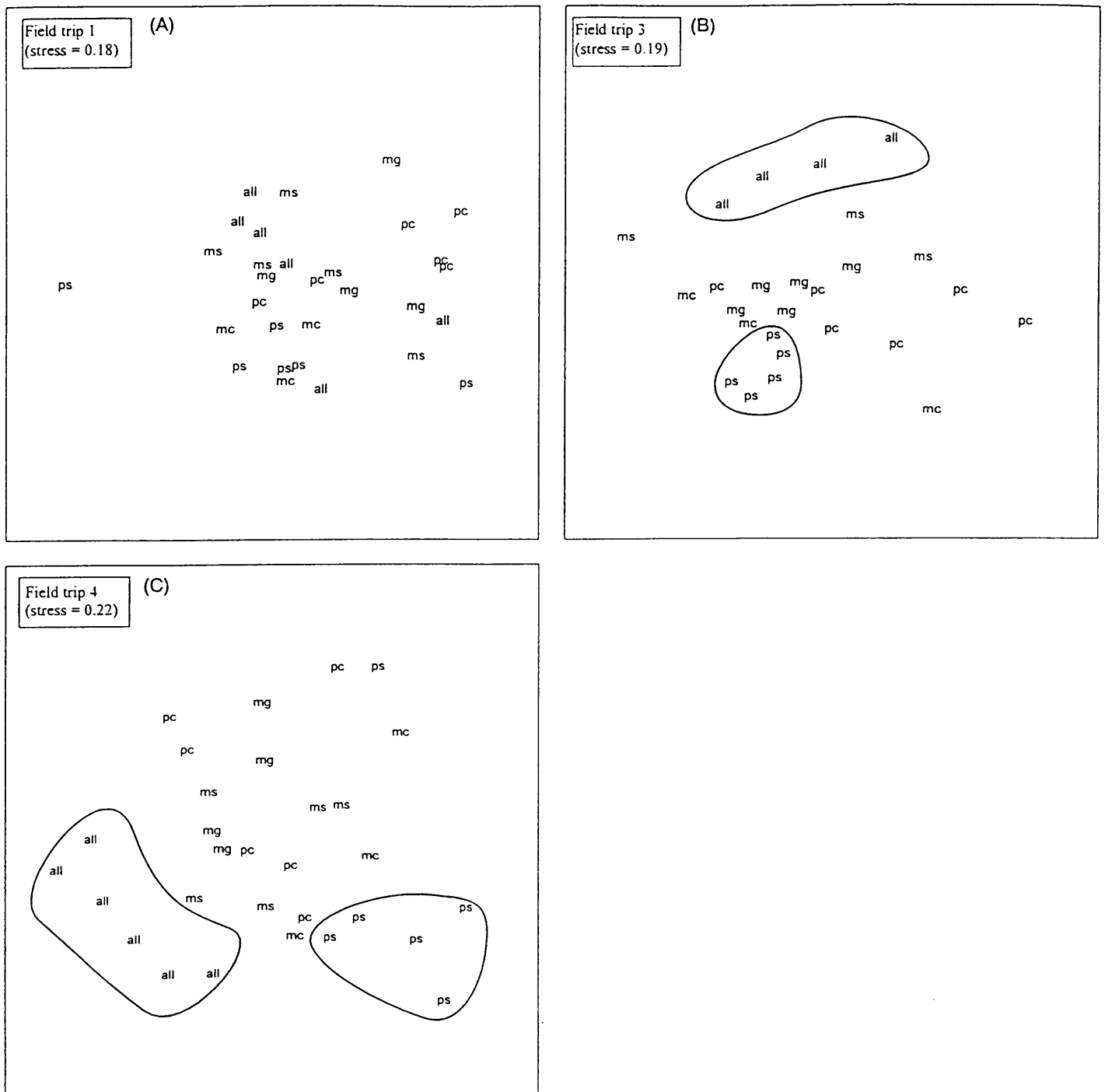
## **Results**

A non-metric MDS ordination of the sampling plots within land facets is presented for each field trip in Figure 2 (birds) and Figure 3 (dung beetles). Each point in these ordinations represents the community composition recorded within a single sampling



**Figure 2.** Non-metric multidimensional scaling (MDS) ordination (four field trips, A-D) of sampling plots within land facets, as defined by Bray-Curtis distances calculated from fourth-root transformed bird species abundances. Distinct clusters are circled. Land facets are described in Appendix I.





**Figure 3.** Non-metric multidimensional scaling (MDS) ordination (three field trips, A-C) of sampling plots within land facets, as defined by Bray-Curtis distances calculated from fourth-root transformed dung beetle species abundances. Distinct clusters are circled. Land facets are described in Appendix I.

plot. The stress values of each MDS ordination provided in Figures 2 and 3 are moderately high (0.17 - 0.22), indicating some difficulty in displaying relationships between this large number of samples. However, the values suggest that the 2-dimensional representations are useful and informative (Clarke and Warwick, 1994).

### *Bird assemblages*

The global ANOSIM test revealed that there were significant differences ( $p < 0.001$ ) between the community compositions of the land facets, for all four field trips (Table 1). The samples of land facet *All* formed distinct clusters in the MDS ordinations for all four the field trips (Fig. 2a-d) and the pair-wise ANOSIM revealed that this facet was consistently significantly different from all other land facets ( $p < 0.03$ ; Table 1). Samples of land facet *Rt* grouped together in the MDS ordinations of fields trip 1, 2 and 3 (Fig. 2a-c) and were significantly different from all other facets during all four field trips (Table 1). Samples of land facet *Mc* clustered relatively close together for all four field trips, but showed considerable overlap with the *Mca* facet, with which it displayed no significant difference ( $p > 0.03$ ) on two occasions (Table 1). Samples of facets *Ps* and *Mca* formed overlapping clusters, that were clearly distinguishable from all other land facets. The pair-wise ANOSIM revealed that the *Ps* and *Mca* facets were significantly different ( $p < 0.03$ ) in field trips 2, 3 and 4 (Table 1) and that both these facets differed significantly from all others (Table 1). Samples of the *Pc*, *Ms* and *Mg* land facets did not form distinguishable groups (Fig. 2a-d). No differences were found between land facets *Ms* and *Mg*, but *Pc* differed significantly from these two facets

**Table 1.** R-statistic and significance level (p-values) of global and pair-wise analysis of similarity (ANOSIM) between the bird community compositions of land facets, for four field trips.

Pairs of land facet	Field trip 1		Field trip 2		Field trip 3		Field trip 4	
	R	p <	R	p <	R	p <	R	p <
<b>Global</b>	0.57	0.001*	0.77	0.001*	0.75	0.001*	0.72	0.001*
Ps - Mc	0.71	0.001*	0.61	0.002*	0.84	0.002*	0.75	0.006*
Ps - Mg	0.77	0.001*	0.98	0.001*	0.85	0.001*	0.89	0.001*
Ps - Ms	0.89	0.001*	0.94	0.001*	0.87	0.001*	0.82	0.002*
Ps - Pc	0.74	0.001*	0.95	0.001*	0.89	0.001*	0.65	0.001*
Ps - Rt	0.63	0.002*	0.84	0.001*	0.79	0.001*	0.83	0.001*
Ps - All	0.95	0.001*	1.00	0.001*	0.99	0.001*	1.00	0.001*
Ps - Mca	0.02	0.347	0.19	0.017*	0.21	0.025*	0.22	0.014*
Mc - Mg	0.60	0.010*	0.69	0.005*	0.50	0.005*	0.68	0.012*
Mc - Ms	0.59	0.010*	0.62	0.005*	0.64	0.005*	0.58	0.024*
Mc - Pc	0.47	0.008*	0.76	0.002*	0.86	0.002*	0.76	0.006*
Mc - Rt	0.42	0.015*	0.47	0.010*	0.34	0.020*	0.61	0.006*
Mc - All	0.92	0.020*	1.00	0.002*	0.99	0.002*	1.00	0.006*
Mc - Mca	0.36	0.032	0.30	0.059	0.36	0.018*	0.67	0.006*
Mg - Ms	0.03	0.355	0.18	0.963	0.09	0.818	0.08	0.779
Mg - Pc	0.11	0.144	0.26	0.013*	0.28	0.008*	0.39	0.005*
Mg - Rt	0.27	0.024*	0.76	0.001*	0.67	0.001*	0.49	0.002*
Mg - All	0.30	0.011*	0.93	0.001*	0.85	0.001*	0.88	0.001*
Mg - Mca	0.81	0.001*	0.92	0.001*	0.86	0.001*	0.90	0.002*
Ms - Pc	0.16	0.073	0.40	0.006*	0.35	0.002*	0.38	0.006*
Ms - Rt	0.41	0.004*	0.66	0.001*	0.60	0.001*	0.40	0.002*
Ms - All	0.36	0.003*	0.93	0.001*	0.87	0.001*	0.94	0.002*
Ms - Mca	0.88	0.001*	0.76	0.002*	0.89	0.001*	0.82	0.002*
Pc - Rt	0.63	0.001*	0.84	0.001*	0.91	0.001*	0.78	0.001*
Pc - All	0.66	0.001*	0.96	0.001*	0.99	0.001*	1.00	0.001*
Pc - Mca	0.73	0.001*	0.83	0.001*	0.92	0.001*	0.81	0.001*
Rt - All	0.68	0.001*	0.95	0.001*	0.97	0.001*	0.89	0.001*
Rt - Mca	0.62	0.002*	0.63	0.001*	0.67	0.001*	0.77	0.001*
All - Mca	0.96	0.001*	0.99	0.001*	0.99	0.002*	1.00	0.001*

\* difference significant at a level of 3% (p < 0.03)

**Table 2.** R-statistic and significance level (p-values) of global and pair-wise analysis of similarity (ANOSIM) between the dung beetle community compositions of land facets, for three field trips.

Pairs of land facest	Field trip 1		Field trip 3		Field trip 4	
	R	p <	R	p <	R	p <
<b>Global</b>	0.06	0.170	0.35	0.001*	0.53	0.001*
Ps - Mc			0.68	0.018*	0.65	0.018*
Ps - Mg			0.53	0.008*	0.83	0.008*
Ps - Ms			0.85	0.018*	0.72	0.008*
Ps - Pc			0.40	0.009*	0.55	0.006*
Ps - All			0.84	0.008*	0.97	0.002*
Mc - Mg			0.46	0.036	0.22	0.171
Mc - Ms			0.15	0.300	0.21	0.214
Mc - Pc			0.15	0.190	0.04	0.440
Mc - All			0.65	0.029*	0.95	0.012*
Mg - Ms			0.51	0.018*	-0.23	0.929
Mg - Pc			0.02	0.335	-0.14	0.810
Mg - All			0.39	0.024*	0.80	0.005*
Ms - Pc			0.09	0.34	0.01	0.424
Ms - All			0.26	0.114	0.69	0.002*
Pc - All			0.55	0.005*	0.67	0.002*

\* difference significant at a level of 3% ( $p < 0.03$ )

during field trips 2, 3 and 4 (Table 1). The *Ms* and *Mg* land facets were consequently grouped into one bird assemblage, *Ms+Mg*.

#### *Dung beetle assemblages*

The MDS plot for field trip 1 (winter) showed no clustering of sampling plots (Fig. 3a). The global ANOSIM test of field trip 1 showed no significant differences in the communities from the different land facets ( $p < 0.17$ ; Table 2) and therefore the pair-wise tests were not carried out. Field trip 1 was conducted during the dry winter and as a result only 16 dung beetle species were caught. Consequently, no pattern was displayed by the dung beetles during field trip 1. The drought extended into field trip 2 and dung beetle sampling was abandoned for this field trip.

The global test for field trips 3 and 4 displayed significant differences ( $p < 0.001$ ) between land facets. Samples of land facets *All* and *Ps* formed distinct clusters (Fig. 3 b, c) and were both significantly different ( $p < 0.03$ ) from all other facets, with the exception of the *All* - *Ms* pair from field trip 3 (Table 2). Samples of *Pc*, *Mc*, *Ms* and *Mg* land facets did not form any distinct groupings (Fig. 2b, c) and the pair-wise ANOSIM test showed no differences between these four facets (Table 2).

*Reserve selection procedures: grid cell size, target representation percentage and the over-representation constraint (ORC).*

The number of grid cells and percentage of the total study area selected using the various algorithms and the 1 km<sup>2</sup> or 4 km<sup>2</sup> grid cells for representation levels

**Table 3.** Percentage of total study area and number of grid cells (in parentheses) selected by different algorithms for various nominated representation targets, using 1 km<sup>2</sup> or 4 km<sup>2</sup> grid cells.

Target percentage	PR 1 km <sup>2</sup>	PR+ORC 1 km <sup>2</sup>	PR+ORC on assemblages 1 km <sup>2</sup>	PR 4 km <sup>2</sup>	PR+ORC 4 km <sup>2</sup>	SRA 1 km <sup>2</sup>	AD 1km <sup>2</sup>
5%	6.20% (13)	5.36% (12)	5.41% (12)	12.68% (7)	7.93% (5)	2.34% (5)	5.51% (13)
10%	11.94% (25)	10.85% (23)	10.47% (23)	14.62% (8)	11.98% (8)	4.68% (10)	10.79% (25)
20%	21.68% (46)	20.60% (44)	20.83% (46)	23.35% (14)	23.18% (13)	8.14% (18)	21.19% (48)
30%	32.39% (69)	30.90% (67)	31.16% (69)	36.85% (22)	32.78% (20)	12.39% (27)	32.54% (74)

**Table 4.** Percentage of each land facet selected by each algorithm for various representation targets.

Land facet	PR	PC+ORC	SRA	AD	PR	PC+ORC	SRA	AD	PR	PR+ORC	SRA	AD	PR	PR+ORC	SRA	AD
	5%				10%				20%				30%			
All	5.37	7.31	6.71	7.37	13.87	13.17	10.01	12.96	21.86	20.00	20.03	22.92	32.49	32.96	30.11	44.03
Mc	7.67	5.07	5.07	5.70	14.61	10.19	10.19	14.88	21.25	20.97	20.39	27.65	34.88	31.58	30.43	44.28
Mca	9.65	5.06	5.42	9.47	19.34	10.01	10.01	10.36	29.07	24.26	23.81	25.97	34.45	30.62	33.73	31.47
Mg (Ms+Mg)*	5.83	5.09	1.49*	9.65*	11.64	10.49	1.83*	18.97*	21.01	20.13	2.95*	36.60*	31.64	30.01	5.32*	55.52*
Ms	6.60	5.05	0	0	11.78	10.07	0	0	22.17	20.15	0	0	31.65	30.13	0	0
Pc	5.58	5.01	0.28	5.01	10.18	10.00	2.35	10.01	20.24	20.00	1.49	20.01	30.59	30.00	2.23	30.00
Ps	5.13	5.13	5.00	5.01	11.01	10.13	10.13	10.13	21.53	20.04	20.04	20.12	31.80	30.02	30.08	30.43
Rt	8.70	7.77	5.17	5.30	14.93	18.59	10.02	12.35	26.26	24.91	20.08	24.46	44.56	39.64	30.01	38.52

\* Where algorithms targeted identified species assemblages, areas of Ms and Mg are joined into one assemblage.

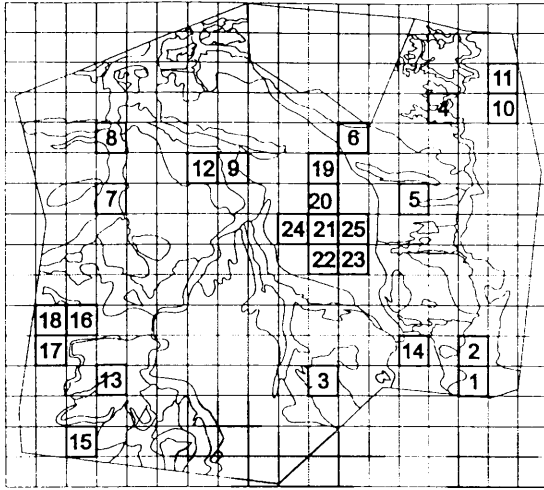
of 5, 10, 20 and 30% of areas are provided in Table 3. The configuration and selection order of grid cells chosen by algorithms for various representation targets are illustrated in Figure 4 (a-l). Figure 1 provides additional detail on the land facets occurring within each grid cell. The use of 1 km<sup>2</sup> grid cells as selection units resulted in little difference between the representation target and the percentage area selected to represent each feature, while the use of the 4km<sup>2</sup> grid cells (Fig. 4 i,j) reduced the efficiency of the algorithms (Table 3; Fig. 6).

Incorporation of the ORC rule reduced the selected area by approximately 1% and 3% of the total study area for the 1 km<sup>2</sup> and 4 km<sup>2</sup> grid cell sizes respectively (Table 3). Over-representation was highest for the lowest representation level (5%) using 4 km<sup>2</sup> grid cells (Table 3; Fig. 6). The PR algorithm using 4 km<sup>2</sup> grid cells was least efficient, while the PR+ORC algorithm using 1 km<sup>2</sup> grid cells was most efficient (Fig. 6).

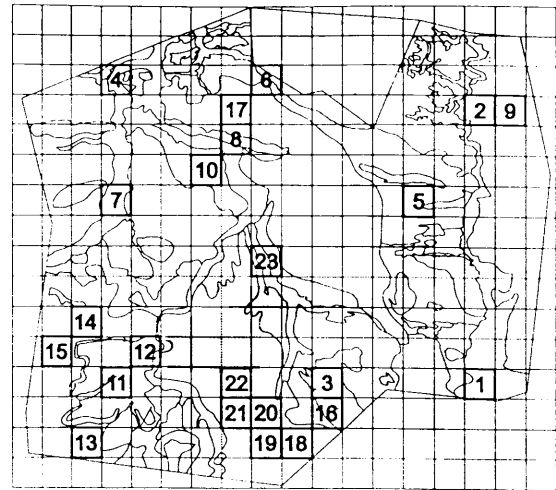
The ORC rule reduced over-representation of each land facet effectively to result in the representation being very close to the nominated level (Table 4). The operation of the ORC rule can be demonstrated with reference to Figure 4 a and b. The standard PR algorithm first selected cell No. 1 (Fig. 4a), containing the largest area of the rarest land facet (*Mca*, covering the smallest area), followed by cell No. 2 (Fig. 4a), containing the second largest area of *Mca*. The PR algorithm consequently overshoot the nominal 10% target (Table 4). In contrast the second cell (No. 2, Fig 4b) selected by the PR+ORC algorithm, contained only a small area of *Mca* required to reach the target representation level (Appendix I). This cell (No. 2, Fig. 4b) also contained a large area of land facet *Ps*, which ultimately resulted in only one additional cell (No. 9) being chosen by PR+ORC to reach the *Ps* representation target. The standard PR algorithm had to select two cells (No. 10 and 11, Fig. 4a) covered exclusively by *Ps* to reach the 10% area target for *Ps*.



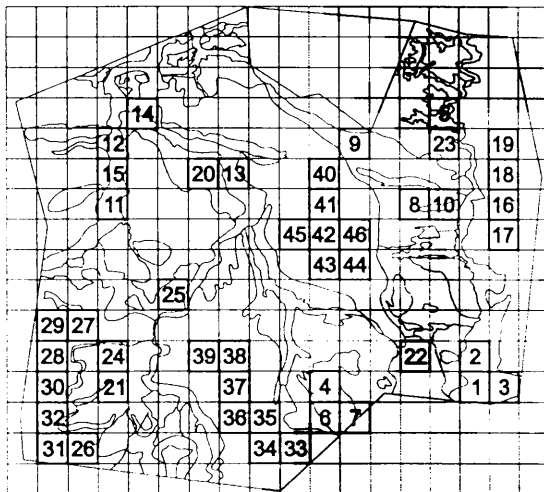
a. PR 10%



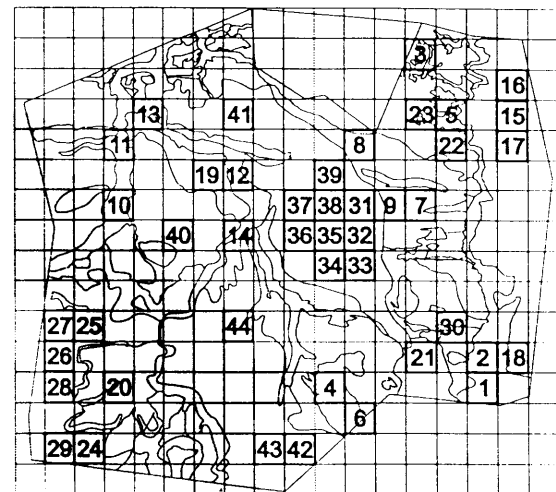
b. PR+ORC 10%



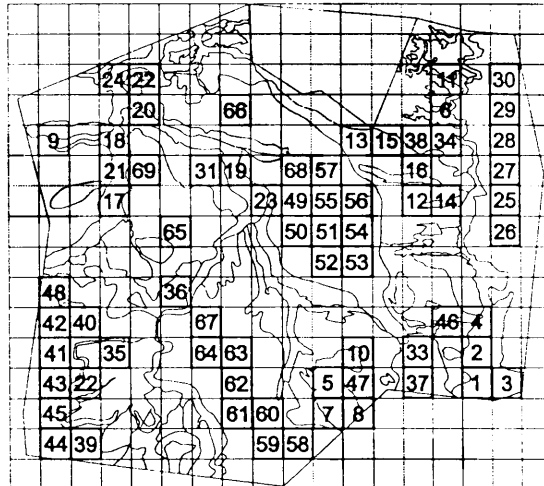
c. PR 20%



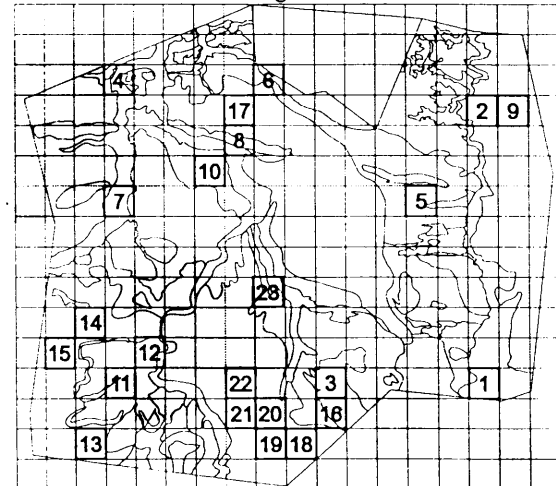
d. PR+ORC 20%



e. PR 30%

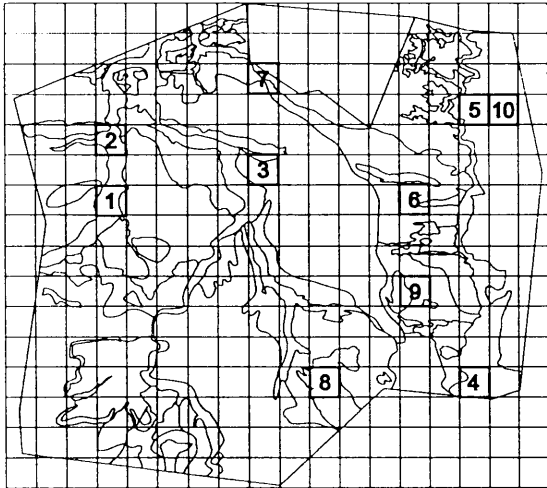


f. PR+ORC assemblages 10%

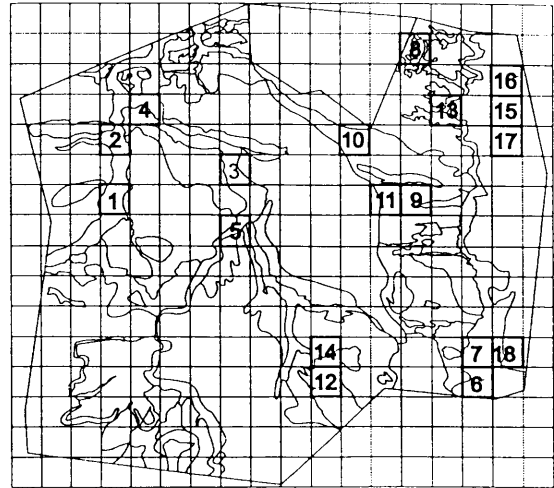


**Figure 4.** Land facet maps of the Venetia-Limpopo Nature Reserve overlaid with a 1 km<sup>2</sup> (a-h, k, l) or 2 km<sup>2</sup> gradicule (i, j). Numbers within grid cells indicate the order in which they were selected. PR: Percentage Representation, PR+ORC: Percentage Representation with over-representation constraint, SAR: Species-Assemblages Representation, AD: Assemblage Diversity. Representation target percentages are indicated for each map.

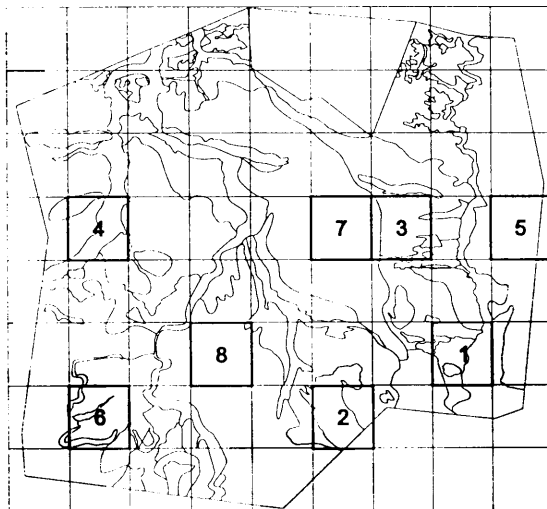
g. SAR 10%



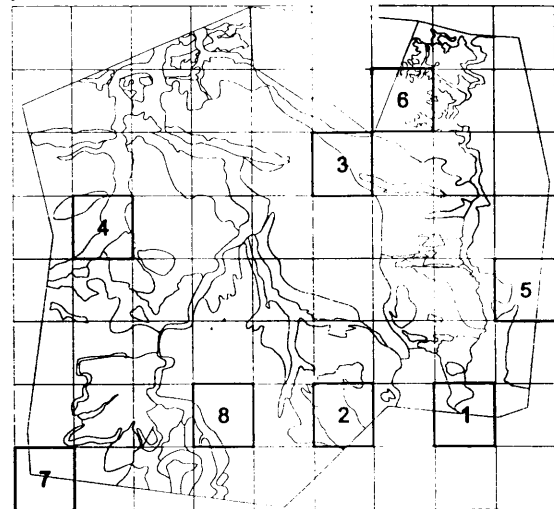
h. SAR 20%



i. PR 10%



j. PR+ORC 10%



k. AD 10%



l. AD 20%

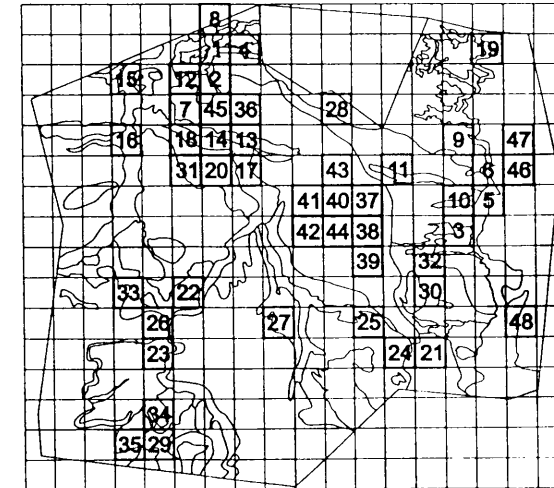
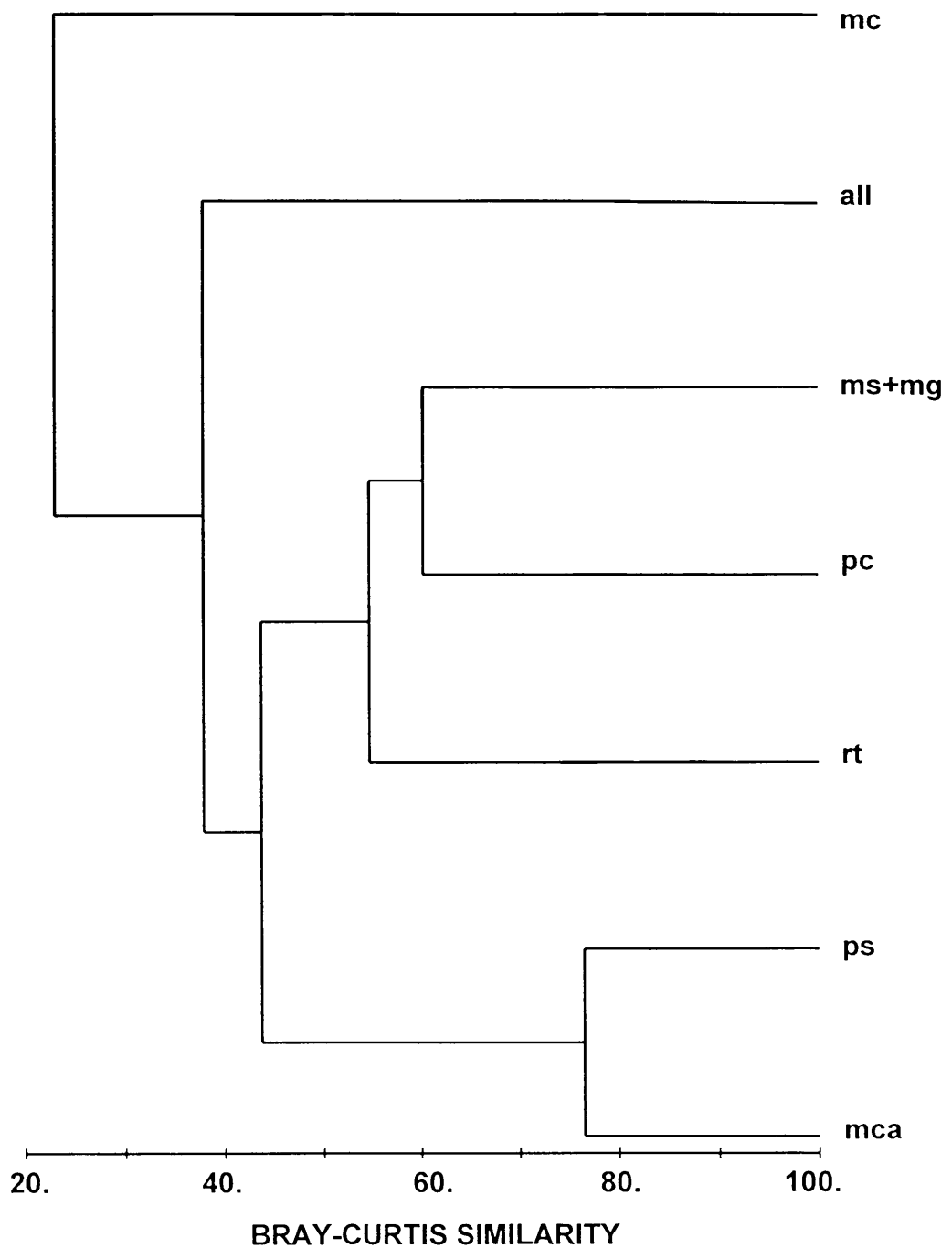


Figure 4. continued

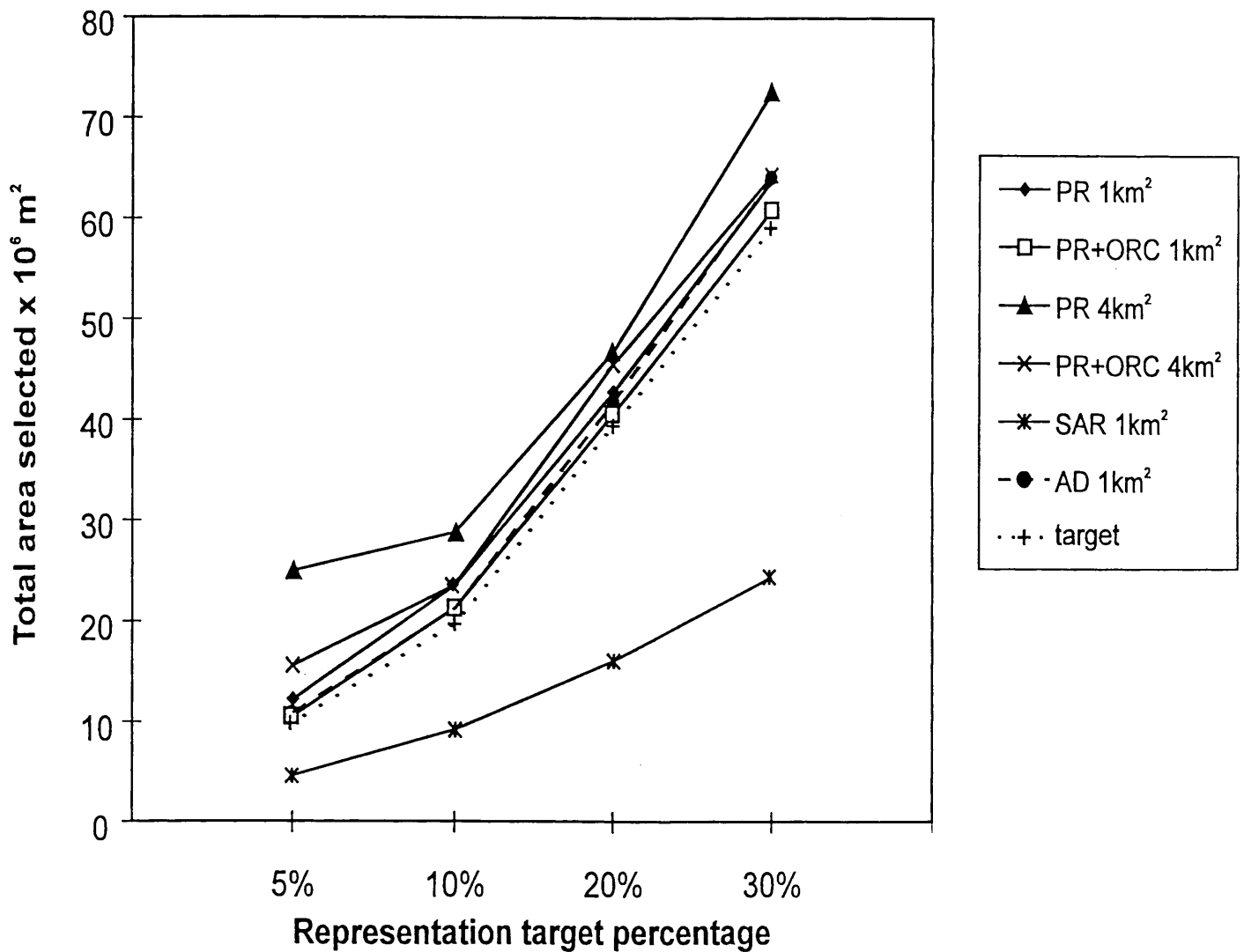
In the same manner the ORC rule also caused the selection of  $4\text{km}^2$  grid cells (No. 1, 7; Fig. 4 j) that included relatively small land facet areas required to meet target levels and large areas that fell outside the study area boundaries. Although this illustrates a potentially undesirable influence of the ORC rule, this could be attributed to the large  $4\text{km}^2$  selection units.

The PR+ORC algorithm was also used to represent the seven identified bird species assemblage areas. The procedure treated the land facets  $Mg$  and  $Ms$  as a single species assemblage,  $Ms+Mg$ . This had little influence on the total size of the selected area (Table 3), since the effective representation target remained the same and no assemblage areas were excluded from this representation. In addition, it had minimal influence on the identity of the grid cells selected (facets: Fig. 4 b,d; assemblages: Fig. 4 f).

The adjacency constraint (Rule 3, Appendix II) resulted in the selection of contiguous clusters of grid cells (Fig. 4 a-f). Rules 4 and 5 (Appendix II) are the same for all the algorithms, however, for this particular data set, these two rules were never employed. Rule 6, which selected the first cell in a list of cells that still remained tied after applying the five preceding rules, was rarely applied, only where a number of homogenous cells (containing only one land facet or assemblage) were encountered close to one another within the  $Pc$  and  $Ps$  land facets / assemblages (e.g. cell No. 11 Fig. 4a ; cell No. 16 Fig. 4d).



**Figure 5.** Dendrogram for hierarchical classification based on Bray-Curtis similarities calculated from average bird species abundances of the identified species assemblages. Land facets comprising assemblages are described in Appendix I.



**Figure 6.** Efficiency of the different reserve selection approaches in relation to the target representation percentages. PR: Percentage Representation, PR+ORC: Percentage Representation with over-representation constraint, SAR: Species-Assemblages Representation, AD: Assemblage Diversity.

### *Species-Assemblages Representation (SAR)*

The *Pc* and *Ms+Mg* assemblages did not contain unique species and were subsequently not targeted by the SAR algorithm (Table 4)(Fig. 4i,j). Since these two assemblages, covering 67.7% of the study area (Appendix I) were not targeted (Table 4), the total selected area was substantially less than that selected by the PR and PR+ORC algorithms (Table 3)(Fig. 6). The SAR algorithm was effective at avoiding the representation of the assemblages *Pc* and *Ms+Mg* and also restricted the over-representation of the assemblages selected to represent all species (Table 4). To maximise complementarity in terms of species representativeness, the SAR algorithm selected assemblages in the following order: (1) *All*, (2) *Mca*, (3) *Mc*, (4) *Rt*, (5) *Ps*.

### *Assemblage Diversity (AD) vs. PR+ORC approaches*

The PD values of the first five grid cells chosen by the AD approach were considerably higher than those selected by the PR+ORC algorithm (Table 5). The AD approach initially selected areas (Fig. 4 k,l) where the landscape is very complex or disparate landscape features meet e.g. rivers run next to hills (Fig. 1). However, the AD approach selected between one and seven grid cells more than the PR+ORC approach to reach the representation percentages (Table 3), which resulted in a slight increase in over-representation and decreased efficiency (Fig. 6).

**Table 5.** PD gain values of the first five grid cells selected by the AD and PR+ORC approaches for 10% representation target.

grid cell selection order	AD	PR+ORC
1	136	57
2	122	68
3	117	52
4	109	71
5	98	68

## Discussion

The majority of studies that followed pattern-based approaches and used surrogates in reserve selection did not attempt to demonstrate a relationship between fauna and the appropriate surrogate classes (e.g. Pressey and Nicholls, 1989; Bedward *et al.*, 1992; Pressey and Logan, 1995; Pressey and Tully, 1994; McKey *et al.*, 1989). Pressey (1994) questioned the actual informativeness of environmental surrogates such as land systems and like others (Bedward *et al.*, 1992; Landres *et al.*, 1988; Noss, 1990; Margules and Williams, in press) suggested that the relationship between surrogate classes and the distribution and abundance of species should be investigated. With a few exceptions (e.g. Woinarski and Braithwaite, 1993; McKenzie and Robinson, 1987) little work has been conducted on how well distributional patterns exhibited by one taxon are reflected by another (Pressey, 1994; Faith and Walker, 1995). In the present study the MDS ordinations in conjunction with the results of the analysis of similarity illustrate that all land facets, with the exceptions of the *Ms* - *Mg* pair, have significantly different bird communities. The reason for this may be that although land facets *Ms* and *Mg* differ slightly in their soil profiles (Appendix I), both have gentle to

moderate slopes and are covered by the same vegetation type (*Colophospermum mopane* shrubland). Seven of the eight land facets therefore formed distinct bird assemblages, whereas the five land facets sampled for dung beetles grouped into three distinct assemblages. The three distinct dung beetle communities identified in these analyses correspond with the three major topographical features of the area, namely alluvial river courses (land facet *All*), sandy soils of the eastern plateau (land facets *Ps*) and the extensive level basin (land facets *Mg*, *Ms*, *Mc* and *Pc*; Fig. 1). If the land facets *Rt* and *Mca* (which were not sampled for dung beetles) are ignored in Figs 2 a-d, it becomes evident that the birds show the same three general groupings as the dung beetles Fig3 b,c. In both Figs 2 and 3 the two clusters on opposite sides of the ordinations are formed by samples taken from the alluvial river courses (land facet *All*) and sandy soils of the eastern plateau (land facets *Ps*) respectively, while samples from the extensive level basin (land facets *Mg*, *Ms*, *Mc* and *Pc*; Fig. 1) are grouped between these two clusters. Birds and dung beetles thus displayed the same general patterns in relation to the land facets, with the birds forming two additional distinct assemblages for the *Pc* and *Mc* facets of the extensive level basin.

Faith (1991) emphasised that the usefulness of pattern analysis, e.g. ordinations and hierarchical classification, for conservation depends upon the application of robust hypothesis testing procedures (e.g. ANOSIM: Clarke and Warwick, 1994; Monte Carlo tests: Faith and Norris, 1989; Faith, 1991; Saetersdal and Birks, 1993) to test the statistical significance of apparent patterns. In the present study, analysis of similarity (ANOSIM) warranted the rejection of the null hypothesis that the observed community pattern could have arisen by chance alone. Temporal change in the habitat relationships of fauna e.g. birds (Woinarski and Tidemann,



1991; Woinarski *et al.* 1992) could complicate the use of surrogate classes for priority area selection (Pressey, 1994). The four seasonal field trips conducted in the present study enabled us to investigate the temporal consistency of these patterns. Besides the dung beetle data from the winter field trip 1, which showed no pattern, no seasonal variation in the relationship between the species assemblages and land facets were observed. Results presented here illustrate that although the *Ms* and *Mg* land facets can be merged into one assemblage, the land facets represent meaningful biological entities which can serve as attributes to be represented within a reserve network (Pressey and Logan, 1994).

There is little evidence that the spatial variation in the diversity of any taxonomic sub-set actually predicts, or can act as a surrogate for, that of other taxa (Vane-Wright, 1978; Majer, 1983; Yen, 1987; Gaston, 1996 and references within). Patterns in the similarity of species compositions (classification groupings) between different habitat classes of the Kakadu National Park were reasonably consistent for different animal groups (birds, reptiles, frogs, mammals; Woinarski and Braithwaite, 1993). McKenzie *et al.* (1987, 1989, 1991) concluded that community types identified within the Nullabor region represent useful surrogates for conservation evaluation, since these classes encompassed patterning by very different taxa (perennial plants, mammals, birds and reptiles). In the present study, birds and dung beetles displayed an informative level of congruence in the variation of their distributions and abundances in relation to land facets. Since these two taxa are phylogenetically and ecologically unrelated, general patterns displayed by them may therefore be representative of other unsampled taxa, within this particular region (Gaston, 1996; Csuti *et al.*, 1997). Furthermore it may be argued that distinct communities of

vascular plants or vertebrates, for example, are nested ecologically within interactions between smaller organisms such as nematodes, arthropods, fungi, protozoa and bacteria (Margules and Redhead, 1995). In the present study the reasonably strong relationship between the communities of these two taxa and land facets suggests that land facets are indeed useful biodiversity surrogates. The patterns shown by birds and dung beetles in relation to land facets is largely due to the fact that land facets are highly homogeneous components of the landscape which did not subdivide natural communities of our study area. It should be realised that the juxtaposition of land facets should vary throughout a large region, altering their landscape context and most likely their biota (Braithwaite, 1991). However, since the land facets are defined within a specific land system, this variation should be limited. Although the extent of the land system covering the study area has not yet been quantified, the topographical pattern within the reserve is regarded as typical of the regional landscape. This region's fauna could therefore be effectively represented by conserving areas of all land facets.

Land systems have been mapped within many territories of the world, including amongst others Australia, Indonesia, Nepal, Iran, Ghana, Nigeria, Kenya, Malawi, Botswana, Belize, Colombia and South Africa (Lawrance *et al.*, 1993). Although the constituent land facets within all these land systems have not necessarily been mapped, the facets have been defined and described for each land system. The present study illustrates the importance of including all, or the majority of land facets of each land system within a reserve network to ensure maximal species or community representativeness. In some cases it might be possible to further subdivide land facets into land elements, e.g. a plateau facet may consist of a flat crest and a

convex margin (Brink *et al.*, 1968). However, since mapping at finer scales increases costs (Pressey and Bedward, 1991) and may subdivide natural communities, land facets are most likely the smallest proficient biodiversity surrogates.

### *Reserve selection approaches*

Bedward *et al.* (1992) reported that a reserve network identified at a 5% feature representation level occupied 26% of the study area, whereas an addition of only 5% of their study area was required to satisfy the higher representation target of 20%. The percentage of the total area ultimately selected to represent all features at a nominated level is largely influenced by the scale at which the attributes (e.g. land facets) are defined, the number of attributes and the size of the selection units (e.g. grid cells) (Bedward *et al.*, 1989; Nicholls and Margules, 1993; Pressey and Logan, 1995).

In the present study, the larger 4km<sup>2</sup> grid cells increased incidental over-representation of land facets (Fig. 4i,j) because selected cells often contained untargeted replication of land facets (Pressey and Logan, 1995). This over-representation effect was most pronounced at the lowest representation level (5%) using 4km<sup>2</sup> grid cells (Table 3). Using the 1km<sup>2</sup> grid cells as selection units increased the efficiency of the algorithms (Fig. 6; Table 3) because the smaller grid cells more neatly fit into the polygons of land facets (Pressey and Logan, 1995). It may prove essential to employ analytical techniques (e.g. blocking techniques, spectral analysis) on remotely sensed data to first detect the scale of the regional landscape patterns (Turner *et al.*, 1991; Quattrochi *et al.*, 1991) before defining the appropriate scales of

the surrogate classes (e.g. land facets), selection units and the resulting reserve network.

The identified bird assemblage along the alluvial river courses (land facet *All*) was chosen first by the SAR algorithm as it contained 18 species which were not recorded within any other assemblage. Although the bird community of the rocky hills (land facet *Rt*) had the second highest number of unique species ( $n=6$ ), the SAR algorithm selected the bird community of the escarpment (land facet *Mca*) since its species list was most complementary to the *All* assemblage. Despite the fact that the *Pc* and *Ms+Mg* bird assemblages were distinct from all others (Table 1), these assemblages of the extensive level basin proved to be mere subsets of the other assemblages, lacking distinguishing species. McKenzie *et al.* (1989) argued that for a reserve network to maintain ecological processes and evolutionary opportunities it should encompass not only the individual native species, but various alternative combinations of species that form naturally occurring assemblages. Simple numerical classification of communities may produce classes consisting of simple subsets of the species represented within other classes. Representing such sub-set classes would reduce efficiency, if measured as the number of species represented per area (Margules and Williams, in press; Williams and Humphries, 1996). By representing each species within a nominated proportion of at least one assemblage, the SAR approach consistently selected areas that were less than half the size of the areas selected by the PR+ORC (on assemblages) approach (Table 3; Fig. 6). Choosing to represent all assemblages instead of individual species, as suggested by McKenzie *et al.* (1989), would therefore substantially increase the total area required (Margules and Williams, in press). However, the weakness of the SAR approach is that it may lead to the

“representation” of species within marginal, ecotone habitats where they occasionally occur, without offering protection to their core habitats.

The subdivision of the landscape to exclude specific features (e.g. *Pc*, *Ms* and *Mg* land facets) may not be feasible at the local scale, especially when considering the home range sizes of large mammals, such as elephants occurring in our study area. Noss and Harris (1986) also suggested that conservation strategies should expand beyond simple communities, targeting unique combinations or patterns of communities while preserving natural processes within functional landscapes and promoting species and gene flow within regional habitat mosaics. In the context of the present study a good option might be to select sites that include large areas of landscape features that are most complementary in terms of species composition as long as the resulting reserve network does not fragment populations and thus jeopardise ecosystem viability.

The AD approach was effective at prioritising relatively small areas containing highly dissimilar species assemblages (Table 5) within diverse landscapes (Fig. 4 k,l). Since the *Mc* assemblage represents the largest portion (24%) of the total diversity (Fig. 5), all the high PD-scoring cells initially selected included *Mc* areas (Fig. 4 k,l cell No. 1,2,3; Fig 1). Consequently *Mc* was consistently the first assemblage to be represented to the nominated levels (5-30%). In contrast, the PR+ORC approach first targeted assemblage *Mca* (Fig. 4 b, d; cell No. 1) because it covers the smallest total area (Appendix I). As opposed to the *Mc* assemblage, *Mca* is distinguished from other assemblages at a low level of classification (Fig. 5). This difference in selection priorities of AD and PR+ORC clearly illustrates the contrast in the underlying rationale of these two approaches (Wionarski *et al.*, 1996).

The cost of the AD approach is reduced efficiency (Woinarski *et al.*, 1996). However, in the present study AD only required between 0.2 (at 5% target level) and 2% (at 30% target level) more of the study area than the PR+ORC approach (Table 3). This minor loss of efficiency (Fig. 6) is negligible in the light of the potential benefits of rapidly increasing the diversity of a reserve network. The main limitation of the traditional minimum-set approach, such as PR, is that it presents a highly integrated solution that can only be realised if the entire selected set can be protected (Woinarski *et al.*, 1996). Where economic constraints restrict the total conservation area that can be acquired to less than that required to satisfy minimum-set algorithms, the AD approach can prioritise priority areas which rapidly represents the diversity of a region (Woinarski *et al.*, 1996). The AD approach can potentially be complemented by the novel approach of using satellite image pixel analysis to quantify landscape diversity (Nøhr and Jørgensen, 1997).

Pressey *et al.* (in press) as well as Willis *et al.* (1996) illustrated how optimising algorithms (linear programming) (Church *et al.*, 1996) failed to solve quantitative target area problems involving large data sets, whereas these problems were easily resolved using heuristic algorithms. All the algorithms used in the present study proved to be very efficient with a low level of over-representation. However, this may be the result of the few features (eight land facets) that had to be represented. This study nevertheless reaffirms the value and flexibility of heuristic algorithms in providing real time answers to exploring various conservation planning options.

## Conclusion

Land facets proved to represent distinct species assemblages and are therefore useful biodiversity surrogates at a local scale (1: 50 000 to 1: 100 000). If species assemblages prove to be mere subsets of others, containing no unique species, it may be decided not to target them during reserve selection as long as this does not fragment populations or jeopardise ecological processes within the landscape. Where species distribution data are inadequate, the representation of land facets may provide the most reliable “fine grain filter” (Noss, 1987) available for capturing species within a reserve network. The efficiencies of heuristic reserve selection algorithms are influenced by the number of surrogate classes, the relative size of the selection units and the target percentage of each feature to be represented. The Assemblage Diversity (“Phylogenetic Diversity”) approach provides an effective method for rapidly increasing the diversity of a reserve network and for prioritising priority areas that are unlikely to be secured at a single stroke of the brush (Vane-Wright, 1996).

## References:

- A'Bear, A.G. (1994) *Report on the Engineering Geological map of the Limpopo-Venetia Reserve*. De Beers Farms Department.
- Austin, M.P. and Margules, C.R. (1986) Assessing representativeness. In *Wildlife Conservation Evaluation* (M.B. Usher, ed.) pp.45-67. London: Chapman & Hall.
- Austin, M.P. and Nix, H.A. (1978) Regional classification of climate and its relation to Australian rangelands. In *Studies of Australian Arid Zone. III. Water in Rangelands* (K.M.W. Howse, ed.) pp. 9-17, Melbourne: CSIRO.
- Awimbo, J.A., Norton, D.A. and Overmars, F.B. (1996) An evaluation of representativeness for nature conservation, Hokitika ecological district, New Zealand. *Biol. Conserv.* **75**, 177-86.
- Bedward, M., Pressey, R.L. and Keith, D.A. (1992) A new approach for selecting fully representative reserve networks: addressing efficiency, reserve design and land suitability with an iterative analysis. *Biol. Conserv.* **62**, 115-25.
- Belbin, L. (1993) Environmental representativeness: Regional partitioning and reserve selection. *Biol. Conserv.* **66**, 223-30.
- Belbin, L. (1995) A multivariate approach to the selection of biological reserves. *Biodiv. Conserv.* **4**, 951-63.
- Braithwaite, L.W. (1991) Fauna and habitat surveys as ecological pathfinders. In *Cost Effective Biological Surveys and Data Analysis*. (C.R. Margules and M.P. Austin, eds) pp. 23-8. Canberra: CSIRO.



- Braithwaite, L.W., Austin, M.P., Clayton, M., Turner, J. and Nicholls, A.O. (1989)  
 On predicting the presence of birds in Eucalyptus forest types. *Biol. Conserv.* **50**, 33-50.
- Bray, T.R. and Curtis, T.J. (1957) An ordination of the upland forest communities of Western Wisconsin. *Ecol. Monogr.* **27**, 325-49.
- Brink, A.B.A., Partridge, T.C., Webster, R. and Williams, A.A.B. (1968) Land classification and data storage for engineering usage of natural materials. In *Proceedings of the Forth Conference of the Australian Road Research Board.* pp. 1624-47.
- Christian, C.S and Steward, G.A. (1968) Methodology of integrated surveys. In *Proceedings of the Toulouse Conference on Aerial and Integrated Studies.* pp. 233-80. Paris: UNESCO.
- Church, R.L. Stoms, D.M. and Davis, F.W. (1996) Reserve selection as a maximal covering location problem. *Biol. Conserv.* **76**, 105-12.
- Clarke, K.R. (1993) Non-parametric multi-variate analyses of changes in community structure. *Aust. J. Ecol.* **18**, 117-43.
- Clarke, K.R. and Warwick, R.M. (1994) *Changes in Marine Communities: An Approach to Statistical Analysis and Interpretation.* UK: Plymouth Marine Laboratory.
- Csuti, B., Polasky, S., Williams, P.H., Pressey, R.L., Camm, J.D., Kershaw, M., Kiestler, A.R., Downs, B., Hamilton, R., Huso, M. and Sahr, K. (1997) A comparison of reserve selection algorithms using data on terrestrial vertebrates in Oregon. *Biol. Conserv.* **80**, 83-97.

- Davis, A.L.V., Doube, B.M. and McLennan, P.D. (1988) Habitat associations and seasonal abundance of coprophilous Coleoptera in the Hluhluwe region of South Africa. *Bull. Ent. Res.* **78**, 425-34.
- Doube, B.M. (1983) The habitat preference of some bovine dung beetles (Coleoptera: Scarabaeidae) in Hluhluwe Game Reserve, South Africa. *Bull. Ent. Res.* **73**, 351-71.
- Faith, D.P. (1991) Effective pattern analysis models for nature conservation. In *Cost Effective Biological Surveys and Data Analysis*. (C.R. Margules and M.P. Austin, eds) pp. 47-54. Canberra: CSIRO.
- Faith, D.P. (1992) Conservation evaluation and phylogenetic diversity. *Biol. Conserv.* **61**, 1-10.
- Faith, D.P. and Norris, R.H. (1989) Correlation of environmental variables with patterns of distribution and abundance of common and rare freshwater macroinvertebrates. *Biol. Conserv.* **50**, 77-99.
- Faith, D.P. and Walker, P.A. (1995) *Diversity: a software package for sampling phylogenetic and environmental diversity*. Canberra: CSIRO.
- Faith, D.P. and Walker, P.A. (1996) Environmental diversity: on the best-possible use of surrogate data for assessing the relative biodiversity of sets of areas. *Biodiv. Conserv.* **5**, 399-415.
- Faith, D.P. and Walker, P.A. (1996) How do indicator groups provide information about the relative biodiversity of different sets of areas? : on hotspots, complementarity and pattern-based approaches. *Biodiv. Letters.* **3**, 18-25.

- Freitag, S. Nicholls, A.O. and van Jaarsveld, A.S. (1996) Nature reserve selection in the Transvaal, South Africa: what data should we be using? *Biodiv. Conserv.* **5**, 685-98.
- Galloway, R.W. (1978) Landforms. In *Land Use of the South Coast of New South Wales*. (M.P. Austin and K.D. Cocks, eds) pp. 20-6. Australia: CSIRO.
- Gaston, K.J. (1996) Biodiversity - congruence. *Progress in Physical Geography.* **20**, 105-12.
- Haila, Y. and Margules, C.R. (1996) Survey research in conservation biology. *Ecography* **19**, 323-31.
- Hutchinson, M.F., Belbin, L., Nicholls, A.O., Nix, H.A., McMahon, J.P. and Orb, K.D. (1996) *BioRap: Rapid Assessment of Biodiversity. Vol.2 Spatial Modelling Tools*. Australia: CSIRO.
- Kruskal, J.B. and Wish, M. (1978) *Multidimensional scaling*. California: Sage Publications.
- Landres, P.B., Verner, J. and Thomas, J.W. (1988) Ecological uses of vertebrate indicator species: a critique. *Conserv. Biol.* **2**, 316-28.
- Lapin, M. and Barnes, B.V. (1995) Using the landscape ecosystem approach to assess species and ecosystem diversity. *Conserv. Biol.* **9**, 1148-58.
- Lawrance, C.J., Byard, R.J. and Beavan, P.J. (1993) *Terrain Evaluation Manual*. London: HMSO.
- Lombard, A.T., Nicholls, A.O., and August, P.V. (1995) Where should nature reserves be located in South Africa? A snake's perspective. *Conserv. Biol.* **9**, 363-72.
- Low, A.B. and Rebelo, A.G. (1996) *Vegetation of South Africa, Lesotho and Swaziland*. Department of Environmental Affairs and Tourism, Pretoria.

- Mackey, B. G., Nix, H.A., Stein, J.A., Cork, S.E. and Bullen, F.T. (1989) Assessing representativeness of the wet tropics of Queensland World Heritage Property. *Biol. Conserv.* **50**, 279-303.
- Majer, J.D. (1983) Ants: bio-indicators of minesite rehabilitation, land use and land conservation. *Environ. Mgmt* **7**, 375-83.
- Margules, C.R. and Redhead, T.D. (1995) *BioRap: Guidelines for Using the BioRap Methodology and Tools*. Australia: CSIRO.
- Margules, C.R. and Williams, P.H. (in press) Identifying biodiversity priority areas: the State of the Art. *Ambio*
- Margules, C.R., Cresswell, I.D. and Nicholls, A.O. (1994) A scientific basis for establishing networks of protected areas. In *Systematics and Conservation Evaluation* (P.I. Forey, C.J. Humphries and R.I. Vane-Wright, eds) pp. 327-50. Oxford: Clarendon Press.
- Margules, C.R., Nicholls, A.O. and Pressey, R.L. (1988) Selecting networks of reserves to maximise biological diversity. *Biol. Conserv.* **43**, 63-76.
- McKenzie, N.L., Belbin, D.L., Gunjko, A. and Robinson, A.C. (1987) Biological patterns in the Nullarbor study area. In *A biological survey of the Nullarbor region South and Western Australia in 1984*. (N.L. McKenzie and A.C. Robinson eds) pp. 211-30. Adelaide: Department of Environment and Planning.
- McKenzie, N.L., Belbin, L., Margules, C. R. and Kieghery, G.J. (1989) Selecting representative reserve systems in remote areas: A case study in the Nullarbor region, Australia. *Biol. Conserv.* **50**, 239-61.

- McKenzie, N.L., Robinson, A.C. and Belbin, L. (1991) Biogeographic survey of the Nullarbor district, Australia. In *Cost Effective Biological Surveys and Data Analysis*. (C.R. Margules and M.P. Austin, eds) pp. 109-26. Canberra: CSIRO.
- Miller, R.I., Stuart, S.N. and Howell, K.M. (1989) A methodology for analyzing rare species distribution patterns utilizing GIS technology: the rare birds of Tanzania. *Landsc Ecol.* **2**, 173-89.
- Nicholls, A.O. (in press) Integrating population abundance, dynamics and distribution into broad scale priority setting. In *Conservation in a changing world. Symposia of the Zoological Society of London*. (A. Balmford, J.Ginsberg and G.Mace, eds)
- Nicholls, A.O. and Margules, C.R. (1993) An upgraded reserve selection algorithm. *Biol. Conserv.* **64**, 165-9.
- Nøhr, H. and Jørgensen, A.F. (1997) Mapping of biological diversity in Sahel by means of satellite image analyses and ornithological surveys. *Biodiv. Conserv.* **6**, 545-66.
- Noss, R.F. (1983) A regional landscape approach to maintaining diversity. *BioScience*, **33**, 700-6.
- Noss, R.F. (1987) From plant communities to landscapes in conservation inventories: A look at The Nature Conservancy (USA). *Biol. Conserv.* **41**, 11-37.
- Noss, R.F. (1990) Indicators for measuring biodiversity: a hierarchical approach. *Conserv. Biol.* **4**, 355-64.
- Noss, R.F. and Harris, L.D. (1986) Nodes, Networks, and MUMs: Preserving diversity at all scales. *Environ. Mgmt* **10**, 299-309.

- Pressey, R.L. (1994) Land classifications are necessary for conservation planning but what do they tell us about fauna? In *Future of the fauna of western New South Wales* (D. Lunney, S. Hand, P. Reed and D. Butcher, eds) pp. 33-41. Mosman: Royal Society of NSW.
- Pressey, R.L. and Bedward, M. (1991) Mapping environment at different scales: Benefits and costs for Nature Conservation. In *Cost Effective Biological Surveys and Data Analysis*. (C.R. Margules and M.P. Austin, eds) pp. 7-13. Canberra: CSIRO.
- Pressey, R.L. and Logan, V.S. (1994) Level of geographical subdivision and its effects on assessments of reserve coverage: A review of regional studies. *Conserv. Biol.* **8**, 1037-46.
- Pressey, R.L. and Logan, V.S. (1995) Reserve coverage and requirements in relation to partitioning and generalization of land classes: Analyses for Western New South Wales. *Conserv. Biol.* **9**, 1506-17.
- Pressey, R.L. and Nicholls, A.O. (1989) Application of a numerical algorithm to the selection of reserves in semi-arid New South Wales. *Biol. Conserv.* **50**, 263-78.
- Pressey, R.L. and Tully, S.L. (1994) The cost of *ad hoc* reservation: A case study in western New South Wales. *Aust. J. Ecol.* **19**, 375-84.
- Pressey, R.L. Possingham, H.P. and Day, J.R. (1997) Effectiveness of alternative heuristic algorithms for identifying indicative minimum requirements for conservation reserves. *Biol. Conserv.* **80**, 207-19.
- Pressey, R.L. Possingham, H.P. and Margules, (1996) Optimality in reserve selection algorithms: When does it matter and how much? *Biol. Conserv.* **76**, 259-67.

- Pressey, R.L., Humphries, C.L., Margules, C.R., Vane-Wright, R.I., and Williams, P.H. (1993) Beyond opportunism: Key principles for systematic reserve selection. *TREE*, **8**, 124-8.
- Price, G.V. (1981) *Methods of Engineering Geological Mapping and their Application on a Regional Scale in South Africa*. M.Sc. Thesis, Univ. of Pretoria.
- Purdie, R.W., Blick, R. and Bolton, M.P. (1986) Selection of a conservation reserve network in the Mulga Biogeographic Region of South-Western Queensland, Australia. *Biol. Conserv.* **38**, 369-84.
- Quattrochi, D.A. and Pelletier, R.E. (1991) Remote sensing for analysis of landscapes: An introduction. In *Quantitative Methods in Landscape Ecology: The Analysis and Interpretation of Landscape Heterogeneity*. (M.G. Turner and R.H. Gardener, eds) pp. 51-76. London: Springer-Verlag.
- Saetersdal, M. and Birks, H.J.B. (1993) Assessing the representativeness of nature reserves using multivariate analysis: Vascular plants and breeding birds in deciduous forests, western Norway. *Biol. Conserv.* **65**, 121-32.
- Scott, M.J., Csuti, B., Jacobi, J.D. and Estes, J.E. (1987) Species richness: A geographic approach to protecting future biological diversity. *BioScience* **37**, 783-8.
- Turner, S.J., O'Neill, R.V., Conley, W., Conley, M.R. and Humphries H.C. (1991) Pattern and Scale: Statistics for Landscape Ecology. In *Quantitative Methods in Landscape Ecology: The Analysis and Interpretation of Landscape Heterogeneity*. (M.G. Turner and R.H. Gardener, eds) pp. 17-50. London: Springer-Verlag.

- Vane-Wright, R.I. (1978) Ecological and behavioural origins of diversity in butterflies. In *Diversity of Insect Faunas*. (L.A. Mound and N. Waloff, eds) pp. 56-70. Oxford: Blackwell Science.
- Vane-Wright, R.I. (1996) Identifying priorities for the conservation of biodiversity: systematic biological criteria within a socio-political framework. In *Biodiversity: A Biology of Numbers and Difference* (K.J. Gaston, ed.) pp. 309-38. Oxford: Blackwell Science.
- Vane-Wright, R.I., Humphries, C.J. and Williams, P.H. (1991) What to Protect? - Systematics and the agony of choice. *Biol. Conserv.* **55**, 235-54.
- Walker, P.A. and Faith, D.P. (1995) Diversity - PD: Procedures for conservation evaluation based on phylogenetic diversity. *Biodiv. Letters* **2**, 132-139.
- Williams, P.H. and Humphries, C.J. (1996) Comparing character diversity among biotas. In *Biodiversity*. (K.J. Gaston, ed.) pp. 54-76. Oxford: Blackwell Science.
- Willis, C.K., Lombard, A.T., Cowling, R.M., Heydenrych, B.J. and Burgers, C.J. (1996) Reserve systems for limestone endemic flora of the Cape lowland fynbos: Iterative versus linear programming. *Biol. Conserv.* **77**, 53-62.
- Woinarski, J.C.Z. and Braithwaite, R.W. (1993) The distribution of terrestrial vertebrates and plants in relation to vegetation and habitat mapping schemes in stage III of Kakadu National Park. *Wildl. Res.* **20**, 355-70.
- Woinarski, J.C.Z. and Tidemann, S.C. (1991) The bird fauna of a deciduous woodland in the wet-dry tropics of northern Australia. *Wildl. Res.* **18**, 479-500.
- Woinarski, J.C.Z., Price, O. and Faith, D.P. (1996) Application of a taxon priority system for conservation planning by selecting areas which are most distinct from environments already reserved. *Biol. Conserv.* **76**, 147-59.



Woinarski, J.C.Z., Whitehead, P.J., Bowman, D.M.S. and Russell-Smith, J. (1992)

Conservation of mobile species in a variable environment: the problem of reserve design in the Northern Territory, Australia. *Glob. Ecol. Biogeogr. Let.* **2**, 1-10.

Yen, A.L. (1987) A preliminary assessment of the correlation between plant, vertebrate and Coleoptera communities in the Victorian mallee. In *The Role of Invertebrates in Conservation and Biological Survey*. (J.D. Majer, ed.) pp. 73-88. Perth: Dept. of Conservation and Land Management.

## APPENDIX I

### Description of land facets and percentage of the study area covered by each land facet within the Venetia-Limpopo Nature Reserve.

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<i>All.</i> 6.9%	Flat alluvial floodplains, river and stream channels. Sandy soils are located in the river channels and banks. Clayed soils are located in the floodplains of the rivers and streams.
<i>Mc.</i> 5.8%	Moderate to gentle slopes with sandy clays overlaying mudstone of the Karoo sequence.
<i>Mg.</i> 17.3%	Moderate to gentle slope with gravel rich profiles developed over conglomerates and harder, weather resistant metamorphic rock.
<i>Ms.</i> 14.3%	Moderate to gentle slopes with sandy profiles associated with areas underlain by Karoo sequence sandstones.
<i>Mca.</i> 4.5%	Crests of gentle slopes with calcrete rich profile.
<i>Ps.</i> 9.3%	Pediaplains with gentle to flat slopes and sandy soils, wind blown.
<i>Pc.</i> 36.1%	Pediaplains with gentle to flat slopes and soils containing clay, alluvial and sheetwash in origin.
<i>Rt.</i> 5.7%	Rugged topography, a ridge plateau, with steep talus dominated slopes. Abundant gravel, boulders and rock outcrop occasionally covered with thin soil.

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## APPENDIX II

### Selection rules of algorithms

#### *Percentages Representation (PR) algorithm*

1. Choose grid cell with unique occurrence of the land facet covering the smallest area. If more than one land facet is equally small, choose the one which is also "database rarest". If there are no unique occurrences, establish the smallest unrepresented land facet.
2. option 1 (PR)- If there is a choice of cells to represent this land facet, always choose the cell with the biggest area of the facet under consideration.  
option 2 (PR+ORC)- If there is a choice of cells to represent this land facet, choose the cell with the particular land facet/assemblage area which is closest in size to that required to bring the representation of the land facet up to the required level, i.e. the cell which contains either (a) the largest area of that land facet if no one cell will achieve the representation target, or (b) the smallest area necessary to achieve the required target.
3. If there is a choice, i.e. more than one cell with the same largest area, select the cell that is nearest in space to a cell that is already selected (adjacency constraint).
4. If there is still a choice, select the cell that also contains the largest area of the next smallest under-represented land facet.
5. If there is still a choice, select the cell which will add the most additional under-represented facets.
6. If there is still a choice, select the first cell in the list of ties (order dependency).

*Species Representation within Assemblages (SRA) algorithm*

1. Choose the assemblage which contains the largest number of unique unrepresented species. If there is a choice, select the cell with a unique occurrence of the assemblage covering the smallest total area. If more than one assemblage is equally small, choose the one which is also "database rarest".
2. If there is a choice of cells to represent this assemblage, choose the cell with the particular assemblage area which is closest in size to that required to bring the representation of the assemblage up to the required level, i.e. the site which contains either (a) the largest area of that land facet if no single cell will achieve the representation target, or (b) the smallest area necessary to achieve the required target representation percentage (ORC rule).
3. If there is a choice, select the cell that is nearest in space to a cell that is already selected (adjacency constraint).
4. If there is still a choice, select the cell that also contains the largest area of the next smallest under-represented assemblage.
5. If there is still a choice, select the cell which will add the most additional under-represented assemblages.
6. If there is still a choice, select the first in the list of ties (order dependency).

## **CHAPTER 4**

# **Current Obstacles and the Way Forward for Biodiversity Conservation.**

## CHAPTER 4

# Current Obstacles and the Way Forward for Biodiversity Conservation.

### Elements of Biodiversity: Species vs. Surrogates

Where biotic data are sparse, spatially biased or completely lacking, surrogates have to be used as more practical measures of biodiversity (Margules and Williams, in press). Surrogate measures include sub-sets of taxa, also referred to as indicator groups, higher taxa such as genera or families and higher order or environmental surrogates e.g. communities or landscape classes (Margules and Redhead, 1995). There is very little evidence, either theoretical or empirical, that any taxonomic subset actually represents or can act as a surrogate for all other taxa (Margules and Redhead, 1995). Although family richness has been proven to be a good predictor of species richness for a variety of groups and regions (Williams and Gaston, 1994), this was found not to be true in all instances (Prance, 1994). Higher taxon richness furthermore plays no role in the identification of representative and complementary sets of conservation areas.

Environmental surrogates provide the most appropriate option, since information on their distribution is easier and cheaper to acquire than biotic data and these surrogates may also integrate more of the functional processes that are important for maintaining ecosystem viability and species (Williams and Humphries, 1996).

Representation of environmental surrogate classes is likely to encompass some unknown species and known species with unknown distribution patterns (Margules and Redhead, 1995). It is however possible that representing surrogate classes could miss certain species that “fall through the coarse filter” (Noss, 1987; Bedward *et al.*, 1992; Stokland, 1997). Rare species are particularly vulnerable if they are confined to small patches of habitat that can not be identified as distinct environmental classes, when using broad scale (e.g. 1: 250 000) environmental data. Conservation planners should therefore attempt to base their decisions on data that include as much biological information as possible and may use a combination of indicator-group and environmental surrogates (Margules and Williams, in press). Limited funds would be well spent if future biological surveys are directed towards previously under sampled areas to improve the geographical coverage of species distribution data. In addition, the gradsect survey method will provide a highly efficient means for gathering new biological data (Chapter 2).

In the present thesis the value of land facets as local scale biodiversity surrogates would have been better illustrated if the study area was three to five times larger (100 000 to 200 000 ha). However, logistic demands may have been prohibitive. Since neighbouring land is the property of a number of different farmers and land facets have not been mapped in these areas, surveys could not be conducted over a larger area. However, from geological and land type maps (1: 250 000 scale) it is clear that Venetia-Limpopo Nature Reserve is representative of the surrounding regional landscape. The observed relationship between the distribution and abundance of species (birds and dung beetles) and the land facets should therefore be applicable to a larger area.

The only potential biodiversity surrogates that have been mapped for the entire South Africa are *land types*. A land type denotes an area that can be delineated at 1:250 000 scale and that displays a marked degree of uniformity with respect to terrain form, soil pattern and climate (MacVicar *et al.*, 1974; Land Type Survey Staff, 1986). Since these land types may provide useful regional scale biodiversity surrogates, future research should investigate the relationship between these land units and vegetation, as well as faunal communities (Pressey, 1994). Land systems are per definition very similar to land types (Lawrence *et al.*, 1993) and have been extensively used as environmental surrogates during reserve network evaluation at broad regional scales in Australia (Purdie *et al.*, 1986; Pressey and Nicholls, 1989; Pressey and Tully, 1994). The present thesis does however illustrate that, as expected, there is a certain amount of variation within these broad scale land types and that all their sub-units, namely terrain types (which are similar to land facets) should be represented to maximise the probability of sampling all species.

### **Limitations of priority area selection methods**

Grid squares as well as hexagons (Csuti *et al.*, 1997) of various sizes are the most frequently used priority area selection objects. Although units of land tenure are more practical selection objects (Pressey and Nicholls, 1989), these units are essentially artificial. Selection units such as vegetation remnants (Margules and Nicholls, 1987) or water catchments (Bedward *et al.*, 1992) could be used in some instances, since they are more likely to represent natural, ecologically functional units.



The target levels to which surrogate classes are represented, are essentially arbitrary (Pressey and Logan, 1995), since they do not take into account the long term viability of “reserved” populations (Trinder-Smith *et al.*, 1995; Stokland, 1997; Nicholls, in press, Margules and Williams, in press), the status of source and sink areas (Pulliam, 1988), landscape context and disturbance regimes (Noss, 1983, 1986, 1987; Bourgeron, 1988), or the ability of protected area networks to maintain species following climatic changes (Hunter *et al.*, 1988). A minimum set of sites identified by current reserve selection algorithms are therefore indicative rather than prescriptive and is not the ultimate goal of a conservation effort within a region (Nicholls and Margules, 1993; Lombard *et al.*, 1995; Pressey *et al.*, 1997). The application of a basic reserve selection algorithm is merely the first step in alleviating the inefficiency of past *ad hoc* reserve selection practices (Pressey, 1994; Stokland, 1997) in representing a region’s biodiversity elements (e.g. species, vegetation types or landscape types).

### **Refined priority area selection for future land-use planning**

Efforts are underway to refine reserve selection procedures to be more practical within a “real world” context by taking into account economic parameters, population abundances and measures of threat. In an attempt to ensure the economic sustainability of regional reserve networks, priority area selection algorithms have been refined to make trade-offs between conservation value and the costs of forgone development opportunities (Faith and Walker, 1996). Population abundance data are also being integrated into priority area selection procedures for the identification of a

set of sites that should contain a user defined minimum number of individuals per species (Nicholls, in press). The problem with this approach is however that comprehensive abundance data, such as the Kruger National Park annual census data, are mostly unavailable for areas under evaluation. Studies on the incorporation of abundance into selection algorithms will nevertheless enable us to set surrogate representation targets (percentage area of each attribute) that are most likely to ensure the long-term survival of species.

To quantify threat, the transformation of natural habitats by various land uses, e.g. agriculture and forestry, can be monitored with the aid of remote sensing (Graetz *et al.*, 1992). From the spatial data rendered the degree of habitat fragmentation (Skole *et al.*, 1993; Hollander *et al.*, 1994) as well as indices such as irreplaceability and vulnerability (Pressey *et al.*, 1996) can be calculated for each vegetation type or any other surrogate class. As we have illustrated with the “PD gain” scores (Chapter 3), the aforementioned measures can be incorporated into reserve selection algorithms to direct conservation efforts towards high priority threatened habitats. Since remote sensing in a GIS environment can deliver the required information in a timely manner it opens up the door for dynamic and flexible integrated land-use planning.

In fulfilment of South Africa’s obligations to the Convention on Biological Diversity the South African government has expressed their intent to (amongst other actions):

*“Investigate, formulate and implement integrated land-use planning approaches that include multiple natural resource activities which are compatible with and which complement the conservation and sustainable use of biodiversity.”* (DEAT, 1996; DA,1997)

If species are to be maintained within an ever-changing landscape mosaic, conservation needs to be recognised as a competing “land use” and included in future land use planning exercises (White *et al.*, 1997). As reserve selection algorithms evolve into more realistic priority area selection procedures, the goal of conservation biologists should be to have these procedures incorporated into land use planning decision support systems. Although this intention might currently seem naive, it represents our only viable option and the inevitable way forward. One should not however, lose sight of the fact that the implementation of sustainable integrated land-use systems would ultimately be a social and political exercise.

## References

- Bedward, M., Pressey, R.L. and Keith, D.A. (1992) A new approach for selecting fully representative reserve networks: addressing efficiency, reserve design and land suitability with an iterative analysis. *Biol. Conserv.* **62**, 115-25.
- Bourgron, P.S. (1988) Advantages and limitations of ecological classification for the protection of ecosystems. *Conserv. Biol.* **2**, 218-20.
- Csuti, B., Polasky, S., Williams, P.H., Pressey, R.L., Camm, J.D., Kershaw, M., Kiester, A.R., Downs, B., Hamilton, R., Huso, M. and Sahr, K. (1997) A comparison of reserve selection algorithms using data on terrestrial vertebrates in Oregon. *Biol. Conserv.* **80**, 83-97.
- DEAT (1996) *Green Paper on the Conservation and Sustainable use of South Africa's Biological Diversity*. Department of Environmental Affairs and Tourism.

- DA (1997) *White Paper: Policy on Sustainable Resource Use*. Department of Agriculture.
- Faith, D.P. and Walker, P.A. (1996) Integrating conservation and development: effective trade-offs between biodiversity and cost in the selection of protected areas. *Biodiv. Conserv.* **5**, 431-46.
- Graetz, D., Fisher R. and Wilson M. (1992) *Looking back: the changing face of the Australian Continent 1972-1992*. Australia: CSIRO.
- Hunter, M.L., Jacobsen, G.L. and Webb, T. (1988) Paleocological and coarse-filter approach to maintaining biological diversity. *Conserv. Biol.* **2**, 375-85.
- Land Type Survey Staff. (1986) Land types of the map 2730 Vryheid. *Mem. Agric. Nat. Resour. S.Afr.* No. 7.
- Lawrance, C.J., Byard, R.J. and Beavan, P.J. (1993) *Terrain Evaluation Manual*. London: HMSO.
- Lombard, A.T., Nicholls, A.O., and August, P.V. (1995) Where should nature reserves be located in South Africa? A snake's perspective. *Conserv. Biol.* **9**, 363-72.
- MacVicar, C.N., Scotney, D.M., Skinner, T.E., Niehaus, H.S. and Loubser, J.H. (1974) A classification of land (climate, terrain form, soil) primarily for rainfed agriculture. *S. Afr. J. Agric. Extensions.* **3**, 21-4.
- Margules, C.R. and Nicholls, A.O. (1987) Assessing the conservation value of remnant habitat islands: mallee patches on the western Eyre Peninsula, South Australia. In *Nature Conservation, the Role of Remnants of Native Vegetation*. (D.A. Saunders, G.W. Arnold, A.A. Burbidge and A.J.M. Hopkins, eds) pp. 89-102. Sydney: Surrey Beatty and Sons.

- Margules, C.R. and Redhead, T.D. (1995) *BioRap: Guidelines for Using the BioRap Methodology and Tools*. Australia: CSIRO.
- Margules, C.R. and Williams, P.H. (in press) Identifying Biodiversity priority areas: the State of the Art. *Ambio*.
- Nicholls, A.O. (in press) Integrating population abundance, dynamics and distribution into broad scale priority setting. In *Conservation in a changing world. Symposia of the Zoological Society of London*.(A. Balmford, J.Ginsberg and G.Mace, eds)
- Nicholls, A.O. and Margules, C.R. (1993) An upgraded reserve selection algorithm. *Biol. Conserv.* **64**, 165-9.
- Noss, R.F. (1983) A regional landscape approach to maintaining diversity. *BioScience*, **33**, 700-6.
- Noss, R.F. (1987) From plant communities to landscapes in conservation inventories: A look at The Nature Conservancy (USA). *Biol. Conserv.* **41**, 11-37.
- Noss, R.F. and Harris, L.D. (1986) Nodes, Networks, and MUMs: Preserving diversity at all scales. *Environ. Mgm.* **10**, 299-309.
- Prance, G.T. (1994) A comparison of the efficacy of higher taxa and species numbers in assessment of biodiversity in the neotropics. *Phil. Trans. R. Soc. Lond., B.* **345**, 89-99.
- Pressey, R.L., Ferrier, S., Hager, T.C., Woods, C.A., Tully, S.L. and Weinman, K.M. (1996) How well protected are the forests of north-eastern New South Wales? Analyses of forest environments in relation to formal protection measures, land tenure and vulnerability to clearing. *Forest Ecol. Mngmt* **85**, 311-33.

- Pressey, R.L. (1994) Land classifications are necessary for conservation planning but what do they tell us about fauna? In *Future of the fauna of western New South Wales* (D. Lunney, S. Hand, P. Reed and D. Butcher, eds) pp. 33-41. Mosman: Royal Society of NSW.
- Pressey, R.L. and Logan, V.S. (1995) Reserve coverage and requirements in relation to partitioning and generalization of land classes: Analyses for Western New South Wales. *Conserv. Biol.* **9**, 1506-17.
- Pressey, R.L. and Tully, S.L. (1994) The cost of *ad hoc* reservation: A case study in western New South Wales. *Aust. J. Ecol.* **19**, 375-84.
- Pressey, R.L. and Nicholls, A.O. (1989) Application of a numerical algorithm to the selection of reserves in semi-arid New South Wales. *Biol. Conserv.* **50**, 263-78.
- Pressey, R.L., Possingham, H.P. and Day, J.R. (1997) Effectiveness of alternative heuristic algorithms for identifying indicative minimum requirements for conservation reserves. *Biol. Conserv.* **80**, 207-19.
- Pulliam, H.R. (1988) Sources, sinks, and population regulation. *Am. Nat.* **132**, 652-661.
- Purdie, R.W., Blick, R. and Bolton, M.P. (1986) Selection of a conservation reserve network in the Mulga Biogeographic Region of South-Western Queensland, Australia. *Biol. Conserv.* **38**, 369-84.
- Skole, D.L. and Tucker, C.J. (1993) Tropical deforestation and habitat fragmentation in the Amazon: a case study for the Paragominas region of the state of Para. *Biotropica* **21**, 98-106.

- Stokland, J.N. (1997) Representativeness and efficiency of bird and insect conservation in Norwegian boreal forest reserves. *Conserv. Biol.* **11**, 101-11.
- Trinder-Smith, T.H., Lombard, A.T. and Picker, M.D. (1996) Reserve scenarios for the Cape Peninsula: high-, middle- and low-road options for conserving the remaining biodiversity. *Biodiv. Conserv.* **5**, 649-69.
- White, D., Minotti, P.G., Barczak, M.J., Sifneos, J.C., Freemark, K.E., Santelmann, M.V., Steinitz, C.F., Kiester, A.R. and Preston, E.M. (1997) Assessing risk to Biodiversity from future landscape change. *Conserv. Biol.* **11**, 349-60.
- Williams, P.H. and Gaston, K.J. (1994) Measuring more of biodiversity: can higher-taxon richness predict wholesale species richness? *Biol. Conserv.* **67**, 211-17.
- Williams, P.H. and Humphries, C.J. (1996) Comparing character diversity among biotas. In *Biodiversity*. (K.J. Gaston, ed.) pp. 54-76. Oxford: Blackwell Science.

## **Summary**



## Summary

Biological surveys are necessary to gather species distribution data for the identification of priority conservation areas. The rationale of the *gradsect* method is that sampling (transects) oriented along the steepest environmental gradient should detect the maximum number of species in an area. The efficiency of the *gradsect* survey method was evaluated by comparing it to random, systematic and habitat-specific survey methods, during faunal field surveys (target groups: birds and dung beetles). Three *gradsects* were positioned within the study area to follow the major physiographical characteristics, incorporate all environmental strata (land facets) and yet be as logistically convenient as possible. The efficiency of survey methods was expressed as the number of species recorded per sampling unit effort and illustrated using bootstrap estimations to plot species accumulation curves. The *gradsect* method proved to be as efficient as the habitat-specific survey method and consistently more efficient than the systematic and random surveys for both taxa sampled. The present study, therefore illustrates that the *gradsect* survey method provides a cost-effective and swift, representative sample of regional fauna.

Where species distribution data are inadequate, surrogate measures of biodiversity have to be established. Surrogate classes at higher levels of the biological hierarchy (e.g. communities, landscape types, or environmental domains) can be used as attributes of candidate conservation areas during reserve selection. Information on the distribution of surrogate classes is easier and cheaper to acquire than species distribution data. The present study investigated the informativeness of land facets as

a biodiversity surrogate in the Venetia-Limpopo Nature Reserve. Land facets are defined as the simplest units of a landscape with uniform slope, soils and hydrological conditions. Multivariate analysis (MDS) and analysis of similarity (ANOSIM) revealed that the land facets adequately represent distinct bird and dung beetle assemblages and are therefore useful surrogates. These land facets were subsequently used as attributes in the following reserve selection procedures: (i) *Percentage Area Representation* (PAR - represent a nominated percentage area of each assemblage); (ii) *Species-Assemblage Representation* (SAR - represent each species within the smallest number of assemblages); (iii) *Assemblage Diversity* (AD - maximising diversity by first selecting areas containing most dissimilar assemblages, i.e. cover the largest distances within a hierarchical classification). The influence of grid cell size (selection units), target representation percentages and a “over-representation constraint” on the efficiency of the algorithms were illustrated.

The efficiency of the three procedures were compared. The SAR procedure did not represent two of the seven assemblages, since they lacked distinguishing species. The SAR procedure subsequently selected a total area that was 50% smaller than that selected using the PAR approach. The AD procedure selected a slightly larger area than the PAR procedure, but was highly effective at rapidly increasing the diversity of the reserve network. Where economic constraints restrict the total conservation area that can be currently acquired, the AD approach provides a method that first secures the most diverse priority areas.

# **Opsomming**

## Opsomming

Spesies verspreidingsdata, wat versamel word tydens biologiese opnames, is nodig vir die identifikasie van prioriteitsbewaringsareas. Die beredenering van die “*gradsect*” metode is dat monsterneming wat langs die steilste omgewingsgradiënt geöriënteer is, die maksimum aantal spesies binne ‘n area sal oplewer. Die effektiwiteit van die “*gradsect*” opnamemetode is geëvalueer deur dit te vergelyk met ewekansige, sistematiese en habitat-spesifieke opnamemetodes, gedurende fauna veldopnames (teiken groepe: voëls en miskruiers). Drie “*gradsects*” (gerigte transekte) is in posisie gestel om die vernaamste topografiese eienskappe in die studie area te volg, al die omgewingsstrata te inkorporeer en ook logisties so gerieflik as moontlik te wees. Die effektiwiteit van die opnamemetodes is uitgedruk as die aantal spesies wat waargeneem is per eenheid monsteringsinsette. Die effektiwiteit is geïllustreer d.m.v. spesie akkumulasiekurwes wat op “bootstrap” beramings gebaseer is. Die “*gradsect*” metode was net so effektief soos die habitat-spesifieke metode en deurgaans meer effektief as die sistematiese en ewekansige opnames vir beide teiken taksa. Die huidige studie illustreer dus dat die “*gradsect*” biologiese opname metode ‘n vinnige, koste-effektiewe en verteenwoordigende monster van die fauna in ‘n spesifieke area kan lewer.

In die afwesigheid van voldoende spesieverspreidingsdata moet plaasvervangende of surrogaat maatstawwe van biodiversiteit gebruik word. Surrogaat klasse, byvoorbeeld by hoër ordes in die biologiese hiërargie (bv. gemeenskappe, landskaptipes, of omgewingseenhede) kan gebruik word as die attribute van kandidaat

bewaringsareas gedurende reservaatseleksie. Inligting oor die verspreiding van surrogaatklasse is makliker en goedkoper om in te samel as spesieverspreidingsdata. Die huidige studie het die waarde van landfasette as biodiversiteits surrogaat ondersoek in die Venetia-Limpopo Natuurresewaat. Landfasette word gedefiniër as die eenvoudigste eenhede van die landskap met eenvormige gradiënt, grond en hidrologiese toestande. Meerveranderlike analise (MDS) en “ooreenkoms analises” (ANOSIM) het aan die lig gebring dat landfasette tot ‘n groot mate verskillende voël- en miskruiergemeenskappe verteenwoordig en dus waardevolle surrogaat is. Die landfasette is ook gebruik in die volgende reservaat seleksieprosedures: (i) *Persentasie Area Verteenwoordiging* (PAR - verteenwoordig ‘n genomineerde persentasie area van elke gemeenskap); (ii) *Spesies-Gemeenskappe Verteenwoordiging* (SAR - verteenwoordig elke spesie binne die minste moontlike gemeenskappe); (iii) *Gemeenskap Diversiteit* (AD - selekteer vir maksimum diversiteit deur aanvanklik areas wat die mees verskillende gemeenskappe bevat te selekteer, d.w.s. die grootste afstand binne die hiërargiese klassifikasie verteenwoordig). Die invloed van roosterselgrootte (seleksie eenhede), teiken verteenwoordigings persentasies en ‘n oorvertteenwoordigingsbeperking op die effektiwiteit van die verskillende algoritmes is ondersoek.

Die effektiwiteit van die prosedures is vergelyk. Die SAR prosedure het twee van die sewe gemeenskappe nie verteenwoordig nie, aangesien hul geen kenmerkende spesies bevat wat nie in ander gemeenskappe voorkom nie. Die SAR prosedure het dus ‘n area geselekteer wat 50% kleiner is as die area geselekteer deur die PAR benadering. Die AD prosedure het ‘n area geselekteer wat slegs marginaal groter was as die area wat deur die PAR prosedure geselekteer is, maar was uiters effektief in die

seleksie van areas wat vinnig die diversiteit van die reservaatnetwerk verhoog. Waar ekonomiese realiteite die totale bewaringsarea wat aangekoop kan word beperk, bied die AD benadering 'n metode wat die mees diverse prioriteitsareas eerste beveilig.