

Conservation planning and viability: problems associated with identifying priority sites in Swaziland using species list data

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Abstract

Conservation planning assessments based on species atlas data are known to select planning units containing ecotones because these areas are relatively species-rich. However, this richness is often dependent on the presence of adjoining core habitat, so populations within these ecotones might not be viable. This suggests that atlas data may also fail to distinguish between planning units that are highly transformed by agriculture or urbanization with those from neighbouring untransformed units. These highly transformed units could also be identified as priority sites, based solely on the presence of species that require adjoining habitat patches to persist. This potential problem was investigated using bird and mammal atlas data from Swaziland and a landcover map and found that: (i) there was no correlation between planning unit species richness and proportion of natural landcover for both taxa; (ii) the priority areas that were identified for both birds and mammals were no less transformed than if the units had been chosen at random and (iii) an approach that aimed to meet conservation targets and minimize transformation levels failed to identify more viable priority areas. This third result probably arose because 4.8% of the bird species and 22% of the mammal species were recorded in only one planning unit, reducing the opportunity to choose between units when aiming to represent each species. Therefore, it is suggested that using species lists to design protected area networks at a fine spatial scale may not conserve species effectively unless population viability data are explicitly included in the analysis.

Key words: conservation planning, Marxan, presence/absence data

Résumé

On sait que les évaluations de planifications de la conservation qui se basent sur les données d'atlas des espèces choisissent des unités de planification qui contiennent des écotones parce que ces zones sont relativement riches en espèces. Cependant, cette richesse dépend souvent de la présence proche d'un habitat principal, de sorte que les populations de ces écotones pourraient en fait ne pas être viables. Cela signifie que les données des atlas pourraient aussi ne pas faire la distinction entre les unités de planification qui sont fortement modifiées par l'agriculture ou l'urbanisation et celles, voisines, qui ne sont pas modifiées. Des unités profondément modifiées pourraient aussi être identifiées comme sites prioritaires, si l'on se base seulement sur la présence d'espèces qui ont besoin des îlots d'habitats voisins pour subsister. Ce problème potentiel fut étudié en utilisant les données d'atlas sur des oiseaux et des mammifères du Swaziland et une carte de la couverture du terrain, et on a découvert que (i) il n'y avait pas de corrélation entre la richesse en espèces des unités de planification et la proportion de couverture naturelle pour les deux taxons; (ii) les zones prioritaires qui avaient été identifiées pour les oiseaux et pour les mammifères n'étaient pas moins transformées que si les unités avaient été choisies au hasard et (iii) une approche qui visait à atteindre des cibles de conservation et à minimiser le taux de transformation n'avait pas réussi à identifier les zones prioritaires les plus viables. Ce troisième résultat vient peut-être du fait que 4.8% des espèces d'oiseaux et 22% des espèces de mammifères avaient été rapportés pour une

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seule unité de planification, ce qui a réduit la possibilité de choisir entre les unités lorsque l'on a cherché à représenter chaque espèce. C'est pourquoi on attire l'attention sur le fait que l'utilisation des listes d'espèces pour concevoir les réseaux d'AP à petite échelle spatiale risque de ne pas préserver efficacement les espèces à moins que les données sur la viabilité de leur population ne soient explicitement incluses dans l'analyse.

Introduction

Species distribution records are frequently used in planning exercises to identify priority sites for conservation (Fjeldsa, 2000; Hopkinson *et al.*, 2000; Howard *et al.*, 2000; Tushabe & Fjeldsa, 2008). This generally involves dividing the study region into planning units, producing a species list for each unit based on the distribution data, setting targets for the minimum number of units in which each species should be represented and using algorithms to identify the portfolio of units that best meet these targets (Csuti *et al.*, 1997). These analyses have been used successfully to identify broad priority areas in a number of countries (Williams *et al.*, 1996; Brooks *et al.*, 2001), but the underlying algorithms tend to select ecotones. This is because ecotones generally have high levels of species richness, as they contain the interface between two or more habitat types (Branch, Benn & Lombard, 1995; Araújo & Williams, 2001; Gaston *et al.*, 2001). These ecotones may be important biological features that need conserving (Smith *et al.*, 2001) but their inclusion in portfolios can be problematic, as the populations they contain may be less viable than those in the adjoining core habitats (Araújo & Williams, 2001; Cabeza *et al.*, 2004).

This viability problem can be reduced by using larger planning units in priority setting exercises, as these are more likely to contain core habitat for the associated species (Pressey & Logan, 1998). However, it still implies that analyses based on species list data may be insensitive to issues of population viability (Araújo, 2002) and this has serious implications. In particular, it suggests that species list data may be poor at distinguishing between transformed and untransformed habitats, as these fragmented landscapes could be seen as ecotones between natural and anthropogenic habitats. If this is the case then species lists for units containing transformed and fragmented habitat patches may be indistinguishable

from those containing relatively undisturbed core areas, making it less likely that conservation planning algorithms will identify viable priority sites. Alternatively, it may be that highly transformed units are not affected by this phenomenon and their associated species lists reflect the amount of available habitat (Gaston & Spicer, 2003). Here, this potential problem is investigated by comparing landcover patterns with results from a priority setting exercise for Swaziland, based on bird and mammal species list distribution data.

This Swaziland dataset allows an analysis of the relationship between species list data and transformation levels because it is unaffected by several factors that might mask any pattern. First, all of the mammal and bird species that were listed in the Swaziland dataset are affected by levels of agricultural and urban transformation (Monadjem *et al.*, 2003) and previous work has shown that the presence of mammal species at the site level is affected by transformation levels (Monadjem, 1999). Second, the distribution data have been collected for a series of 12.5×12.5 km planning units and these are not generally large enough for individual highly transformed units to contain viable populations of the recorded species. In addition, the range of habitat transformation in these units is broad enough to allow useful comparisons with species richness to be made. Third, the biodiversity and landcover data were collected concurrently (Parker, 1994; Thompson, 1996; Monadjem, 1998), thus avoiding problems caused when distribution records are collected over a number of years and fail to reflect recent patterns of habitat encroachment (Wessels, Reyers & Van Jaarsveld, 2000). Finally, an equal amount of time was spent sampling in each planning unit for both datasets. This is important because transformed areas tend to be more accessible and so *ad hoc* sampling regimes can lead to highly transformed units being more heavily sampled, increasing their recorded species richness (Freitag *et al.*, 1998).

This meant that the Swaziland dataset could be used to investigate whether: (i) bird and mammal species list data are sensitive to levels of habitat transformation; (ii) these relationships affect the results of a conservation planning exercise and (iii) incorporating data on levels of habitat transformation improves the results of the planning process, as previous work found that including similar information on human population density can improve the ecological viability of the identified priority areas (Luck *et al.*, 2004; Carwardine *et al.*, 2008).

Materials and methods

Study area

Swaziland is a landlocked country in southern African that covers an area of 17,290 km² (Fig. 1). Despite its small size, Swaziland is topographically diverse with altitude ranging from 150 to 1860 m above sea level (Goudie & Price-Williams, 1983). The mean annual rainfall range is 500–1500 mm and the daily mean temperature range is 16–22°C. Almost 60% of Swaziland falls under Swazi Nation Land, which is communally managed and where subsistence agriculture is typically practiced. There are eight protected areas (PAs) that range in size from 3.7 to 217 km² and 3.8% of Swaziland has PA status (Fig. 1).

Producing the datasets

Bird distribution data were obtained from the Swaziland Bird Atlas project (Parker, 1994), which collected data in 101 1/8th degree grid squares (12.5 × 12.5 km). These grid squares were then used as the planning units in the subsequent conservation assessments. Each planning unit was visited at least 12 times during different seasons and the presence of each bird species was recorded (Parker, 1994). Distributional data on the mammals were collected by sampling 50 of the same units for 4–5 days (Monadjem, 1998). These were located throughout the country and previous analyses found that sampling showed no bias with respect to land use or land tenure system (Monadjem, 1999). All of the species that were used in the analysis are native to Swaziland and associated with natural habitats.

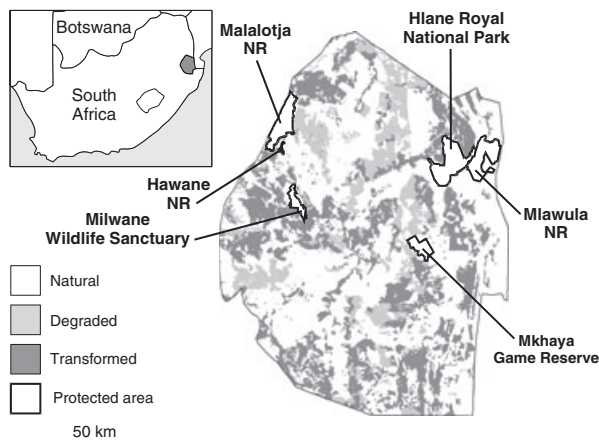


Fig 1 The landcover types and six main PAs of Swaziland

The land cover data were derived from the Council for Scientific and Industrial Research (CSIR) landcover map of southern Africa (Thompson, 1996). These data were imported into the ArcVIEW v3.2 GIS software and the land cover classes used in the original coverage were combined into three broader categories. Forest, woodland, grassland and wetlands were re-classified as 'natural'; degraded forest, degraded woodland and degraded grassland were re-classified as 'degraded' and urban and cultivated land was re-classified as 'transformed'. The PA coverage was digitized from a 1:50,000 paper map and ArcView was used to find the area of each broad landcover type and PA extent within each of the planning units. In subsequent analyses it was assumed that degraded and transformed landcover types were unsuitable for conserving the species used in the analyses, based on field guides of the region (Skinner & Smithers, 1990; Parker, 1994).

Conservation assessments

The bird and mammal data were analyzed separately using the Marxan conservation planning software (Ball & Possingham, 2000), together with the CLUZ ArcView Extension (Smith, 2004). Marxan uses a simulated annealing process to identify a number of near-optimal portfolios that meet conservation targets while minimizing the combined cost of the planning units. This planning unit cost can reflect a range of factors, such as the cost of purchasing the land or the opportunity costs from agriculture (Carwardine *et al.*, 2008), but in this analyses two different cost metrics were used. The first used planning unit area as the cost, so that Marxan acted to minimize the total extent of the portfolios. The second used 'transformation level' as the cost, which was defined as the proportion of that unit covered by degraded and transformed landcover types, so that Marxan acted to minimize how much transformed land was contained within the portfolios. Thus four assessments were undertaken: bird data with the two different cost metrics and mammal data with the two different cost metrics. For each assessment, we set a target that each species had to be represented at least once.

Marxan was run 1000 times, producing a different near-optimal solution each time, with each run consisting of 1,000,000 iterations (Ball & Possingham, 2000). Marxan identifies the 'best' portfolio, defined as the one with the lowest cost, but it also produces a 'summed score' output which counts the number of times that each planning unit appeared in the 1000 portfolios produced. For the area cost

analyses it was noted from the summed score output that there was more than one portfolio that would meet all the targets with the same low combined planning unit cost. Thus, some planning units were 'irreplaceable', because they were required to meet the targets, whereas some were 'flexible' and could be swapped for another unit containing the same key species without increasing the planning unit costs. It was decided to include all flexible planning units in subsequent analyses because each one could potentially appear in a portfolio, even though only half these units would be included in any one portfolio. This problem did not arise for the assessments based on the transformation level cost because the range of cost values varied between the planning units, so that no flexible planning units existed.

Statistical analysis

The number of species in each planning unit was counted and all of the relevant data were imported into the SPSS statistical analysis software. The recorded bird and mammal species richness was calculated for each planning unit and corrected for the nonlinear relationship between species number and area by dividing species number by Az , where A is unit area and z is set as 0.2 (Rosenzweig, 1995). Data from units that had less than 50% of their area within Swaziland were excluded to avoid information from very small planning units disproportionately influencing the results. Spearman's rank tests were then used to find whether species richness and proportion of natural landcover was correlated for both birds and mammals.

The analyses to investigate habitat transformation levels consisted of three parts. First, the mean proportion of natural landcover was calculated in each of the best portfolios identified by the four assessments (named the 'selected portfolio'), including any flexible planning units. Second, to determine whether the four selected portfolios were less transformed than would be expected by chance, an Excel spreadsheet-based algorithm was used to choose an equal number of units at random, calculated their

mean proportion of natural landcover and repeated this process 1000 times. Third, for each selected portfolio an equal number of the least transformed planning units (named 'the least transformed portfolio') were chosen and their mean proportion of natural landcover was calculated. This was done in order to determine whether it was possible to select any portfolio of planning units that were significantly less transformed than random, as this would be impossible if all the planning units had similar levels of habitat loss. Z-tests were then used to determine whether the selected portfolio and the least transformed portfolio for each of the four assessments were significantly less transformed than random.

Results

The Swaziland bird database contains 18,255 records that describe the distribution of 476 species in 101 1/8th degree planning units (Table 1). The recorded distribution of species ranges between 1 and 101 planning units, with 23 species having a recorded distribution of only one unit. The mammal database contains 905 records that describe the distribution of 122 species in 50 planning units. The recorded distribution of each species ranges between 1 and 43 planning units, with 27 species having a recorded distribution of only one unit. The units that contain the largest number of species records are generally found in the north and east of the country (Fig. 2). Twenty of the planning units overlap one or more PAs and seven of these have more than 25% of their area within a PA. If it were assumed that all of these 20 units conserve all of their associated species then 94% of the bird and 94% of the mammal species would be represented in the present PA system, although five of these units were not sampled as part of the mammal survey.

The CSIR land cover data showed that 59.5% of Swaziland is covered by natural landcover types, 12.8% is covered by degraded types and 27.7% is covered by transformed types. Most of the natural landcover (91%) is found in one large patch that covers 54% of the country

Table 1 Details of the distribution datasets for birds and mammals in Swaziland

	Number of records	Number of species	Planning units sampled	Range of distributions in units	Number of species found in only one unit	Range of unit species richness
Birds	18,255	476	101	1–101	23	108–307
Mammals	905	122	50	1–43	27	2–65

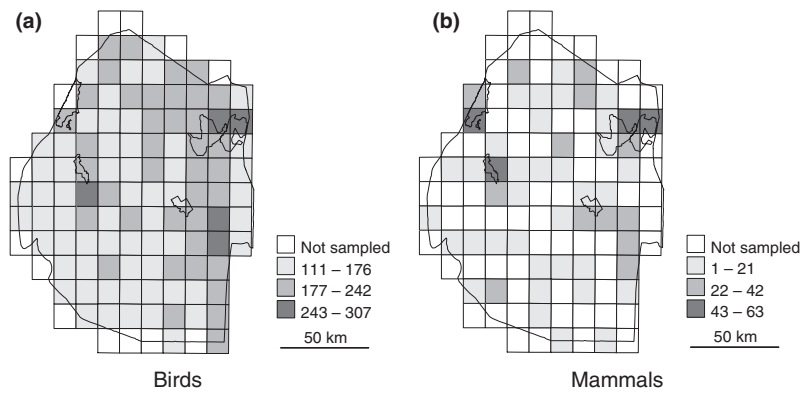


Fig 2 Species richness of birds and mammals across Swaziland together with protected area boundaries

(Fig. 1). The proportion of natural landcover found in these planning units ranged between 0.218 and 1, with a median of 0.564. There was no correlation between species richness and proportion of natural landcover for birds ($n = 101$, $r_s = 0.09$, $P = 0.353$) or mammals ($n = 50$, $r_s = -0.05$, $P = 0.971$), although there was a significant correlation between bird and mammal species richness ($n = 48$, $r_s = 0.70$, $P < 0.001$). There was also no correlation between species richness and combined proportion of natural and degraded landcover types for both taxa (birds: $n = 101$, $r_s = 0.03$, $P = 0.745$; mammals: $n = 50$, $r_s = 0.03$, $P = 0.853$).

The portfolio of planning units required to represent each bird species at least once while minimizing planning unit area contained 17 irreplaceable and three sets of two flexible units, whereas thirteen irreplaceable units and one set of two flexible units were needed to represent each mammal species (Fig. 3). The majority of the irreplaceable units were found in the north and east of the country, with eight of the irreplaceable bird units and nine of the mammal species containing parts of an existing PA. The portfolios that met the targets while minimizing habitat

transformation levels contained 30 planning units for birds and fifteen for mammals (Fig. 4).

All four portfolios were not significantly less transformed than the equivalent number of units chosen at random (Area as cost: birds: $n = 22$, $P = 0.744$; mammals: $n = 15$, $P = 0.277$; Transformation level as cost: birds: $n = 25$, $P = 0.277$; mammals: $n = 15$, $P = 0.226$; Table 2) but the least transformed portfolios were significantly less transformed than random (Area as cost: birds: $n = 22$, $P < 0.001$; mammals: $n = 15$, $P < 0.001$; Transformation level as cost: birds: $n = 25$, $P < 0.001$; mammals: $n = 15$, $P < 0.001$; Table 2). Therefore, there was potential for including significantly fewer transformed planning units in the portfolios if these had contained associated distribution records for the target species.

Discussion

Approximately 4% of Swaziland has PA status but this network is unlikely to conserve the nation's biodiversity effectively (Soulé & Sanjayan, 1998; Pressey, Cowling & Rouget, 2003). Therefore, systematic conservation

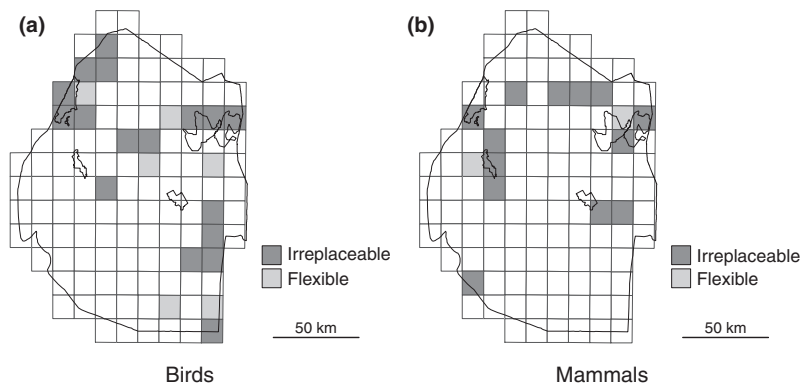


Fig 3 Near-minimum sets for representing Swaziland's bird and mammal species together with protected area boundaries

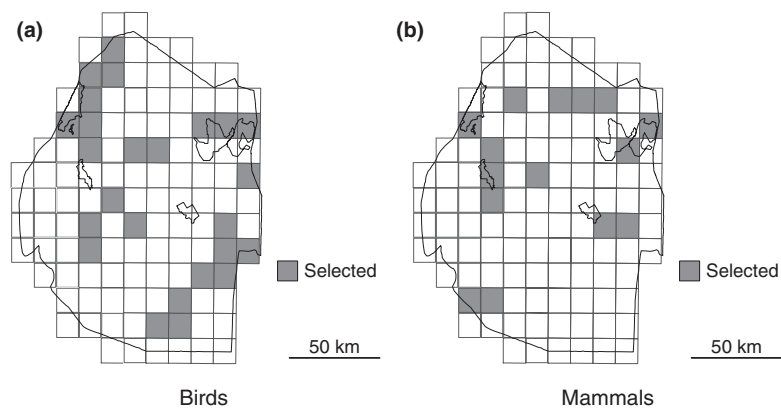


Fig 4 Priority areas for representing species of birds and mammals, and maximizing proportion of natural landcover in Swaziland together with protected area boundaries

Table 2 The proportion of natural landcover in portfolios selected using different techniques

	Portfolio based on meeting targets				Portfolio based on meeting targets and maximizing natural landcover			
	Not selected	Selected	Random	Most natural	Not selected	Selected	Random	Most natural
Birds								
N	79	22	22	22	76	25	25	25
Mean	0.598	0.583	0.595	0.881	0.586	0.621	0.597	0.869
SD	0.208	0.182	0.037	0.070	0.195	0.223	0.035	0.073
Mammals								
N	35	15	15	15	35	15	15	15
Mean	0.572	0.634	0.590	0.828	0.569	0.641	0.590	0.828
SD	0.175	0.218	0.040	0.085	0.176	0.212	0.040	0.085

assessments are needed to identify with accountability and efficiency how Swaziland's PA system should be developed. However, our results suggest that these plans should not be based solely on the available species presence/absence distribution data. This is because these data fail to reflect patterns of land transformation, despite the entire set of target species only being associated with untransformed habitats. One reason for this may be the time lag that can occur between habitat loss and local extinction (Brooks, Pimm & Oyugi, 1999), but one might still expect to observe some relationship, given that many of the target species are wide ranging and therefore sensitive to patterns of habitat transformation (Monadjem *et al.*, 2003). A lack of correlation might also be expected if habitats with low species richness were also the least transformed (Fjeldsa & Burgess, 2008) but both the species richness patterns and the distribution of transformed land in Swaziland make this unlikely.

Instead, this pattern probably arose because many highly transformed planning units contain the edges of

large patches of natural vegetation. Thus, the recorded species lists for a unit containing habitat edge and a unit containing core habitat may be identical, despite the presence of species in the former depending on contiguous habitat in neighbouring planning units. This mirrors previous results showing that ecotones tend to contain species associated with both sets of habitats, even though populations within these ecotones would not be viable if conserved in isolation (Branch *et al.*, 1995; Araújo & Williams, 2001; Gaston *et al.*, 2001). This problem may have arisen partly because the survey regime aimed to produce accurate distribution maps for each species and so sampling effort tended to focus on patches of natural landcover in highly transformed units. However, this is likely to be the case for other biodiversity distribution datasets and so this measured lack of correlation between species richness and ecological viability is probably more widespread. Moreover, many of these other datasets are affected by sampling bias between planning units (Kress *et al.*, 1998), which would further weaken any correlation.

A lack of correlation between species richness and land transformation helps explain why the near-minimum sets of planning units identified to conserve bird and mammal species were not significantly less transformed than a random selection. Not surprisingly, analyses based on species list data can only distinguish between highly transformed and untransformed planning units if this is reflected in the species distribution patterns, which was not the case for the Swaziland datasets. One approach to overcoming the problem is to incorporate landcover data explicitly into the planning methodology (Wessels *et al.*, 2000), or use other data, such as human population density, that are likely to affect habitat viability (Luck *et al.*, 2004). However, this approach did little to improve the priority sites identified for Swaziland, as these planning units were also no less transformed than would be expected from random.

This lack of improvement was probably because the Swaziland analyses included data on 50 species that were recorded in only one planning unit. This meant that many of the units had to be selected to meet the representation targets and some of these were highly transformed. This is best illustrated by the planning unit containing the southernmost tip of Milwane Game Reserve (Fig. 1), which was the third most transformed unit used in the analysis. Despite being highly transformed, this unit contains records for 280 bird and 28 mammal species and was one of the mammal priority areas because it contained the only record for the dusky pipistrelle *Pipistrellus hesperidus*. This suggests that the mammal and, to a lesser extent, the bird datasets were affected by under-sampling, as it is unlikely that the actual ranges of all of the species recorded in one unit are so limited. Underscoring this point is the fact that *P. hesperidus* has now been shown to have a wider distribution in Swaziland (Monadjem & Reside, 2008; Monadjem *et al.*, in press) than previously thought. However, collecting both datasets involved a large amount of effort and so improving the quality of data to avoid this problem would be costly. Moreover, combining the datasets or including information on other species would probably exacerbate the problem.

Another alternative would have been to exclude the single-record species from the analysis but this approach would have been problematic for two reasons. First, these species may not have been represented in priority areas based on the more widely recorded species. Consequently, excluding records from any conservation planning exercise needs to be done with caution. Second, the importance of

the distributions of the single-record species in determining the locations of the priority areas was only due to setting the target of representing each species at least once. This target was arbitrary and could have been increased, but this would have also increased the number of irreplaceable units and the likelihood that more highly transformed units would have been identified as priority sites. Moreover, it is not uncommon for conservation planning datasets to include large numbers of single-record species (Kress *et al.*, 1998; Brooks *et al.*, 2001), so this problem is unlikely to be limited to this Swaziland analysis.

More successful techniques could involve using planning algorithms that contain species that have been repeatedly recorded in a unit (Araújo, Williams & Fuller, 2002) but it is still probable that some highly transformed units will be selected. Therefore, it is suggested that fine-scale conservation planning exercises should model the distribution of the target biodiversity elements, rather than relying on field records. Such modelling has been used successfully elsewhere (Ferrier *et al.*, 2002) and the data it produces allows the use of algorithms that are less prone to select highly transformed areas or ecotones because they use probability of occurrence, abundance or occupancy data (Ferrier, Pressey & Barrett, 2000; Araújo *et al.*, 2002; McDonnell *et al.*, 2002). It is also suggested that species list data should be restricted to analyses that use planning units that are large enough to contain viable populations of each target species. However, such coarse scale analyses make it difficult to determine whether species found in a planning unit are also found in any associated PA (Lombard, 1995; Fjeldsa *et al.*, 2004; Oldfield *et al.*, 2004), so it is suggested that such analyses should focus on identifying broad-scale priority regions that should then be the focus of finer-scale assessments (De Klerk *et al.*, 2004; Smith *et al.*, 2008).

Acknowledgements

We are grateful to the British Council, the British Government's Darwin Initiative for the Survival of Species and the University of Kent for funding this work. We would also like to thank all of the people involved in collecting the biodiversity data, Ian Ball and Hugh Possingham for providing Marxan, as well as Matt Linkie, Matt Walpole and Paul Williams for commenting on earlier work. We are particularly grateful to Ian Swingland for establishing the link project between DICE (University of Kent) and the Department of Biological Sciences, University of Swaziland.

References

- ARAÚJO, M.B. (2002) Biodiversity hotspots and zones of ecological transition. *Conserv. Biol.* **16**, 1662–1663.
- ARAÚJO, M.B. & WILLIAMS, P.H. (2001) The bias of complementarity hotspots toward marginal populations. *Conserv. Biol.* **15**, 1710–1720.
- ARAÚJO, M.B., WILLIAMS, P.H. & FULLER, R.J. (2002) Dynamics of extinction and the selection of nature reserves. *Proc. R. Soc. B* **269**, 1971–1980.
- BALL, I. & POSSINGHAM, H. (2000) *Marxan (v1.8.2) – Marine Reserve Design using Spatially Explicit Annealing*. University of Queensland, Brisbane, Australia.
- BRANCH, W.R., BENN, G.A. & LOMBARD, A.T. (1995) The tortoises (Testudinidae) and terrapins (Pelomedusidae) of southern Africa: their diversity, distribution and conservation. *S. Afr. J. Zool.* **30**, 91–102.
- BROOKS, T.M., PIMM, S.L. & OYUGI, J.O. (1999) Time lag between deforestation and bird extinction in tropical forest fragments. *Conserv. Biol.* **13**, 1140–1150.
- BROOKS, T., BALMFORD, A., BURGESS, N., FJELDSA, J., HANSEN, L.A., MOORE, J., RAHBEK, C. & WILLIAMS, P. (2001) Toward a blueprint for conservation in Africa. *Bioscience* **51**, 613–624.
- CABEZA, M., ARAÚJO, M. B., WILSON, R.J., THOMAS, C.D., COWLEY, M.J. R. & MOILANEN, A. (2004) Combining probabilities of occurrence with spatial reserve design. *J. Appl. Ecol.* **41**, 252–262.
- CARWARDINE, J., WILSON, K.A., CEBALLOS, G., EHRLICH, P.R., NAIDOO, R., IWAMURA, T., HAJKOWICZ, S.A. & POSSINGHAM, H.P. (2008) Cost-effective priorities for global mammal conservation. *PNAS* **105**, 11446–11450.
- CSUTI, B., POLASKY, S., WILLIAMS, P.H., PRESSEY, R.L., CAMM, J.D., KERSHAW, M., KIESTER, A.R., DOWNS, B., HAMILTON, R., HUSO, M. & SAHR, K. (1997) A comparison of reserve selection algorithms using data on terrestrial vertebrates in Oregon. *Biol. Conserv.* **80**, 83–97.
- DE KLERK, H.M., FJELDSA, J., BLYTH, S. & BURGESS, N.D. (2004) Gaps in the protected area network for threatened Afrotropical birds. *Biol. Conserv.* **117**, 529–537.
- FERRIER, S., PRESSEY, R.L. & BARRETT, T.W. (2000) A new predictor of the irreplaceability of areas for achieving a conservation goal, its application to real-world planning, and a research agenda for further refinement. *Biol. Conserv.* **93**, 303–325.
- FERRIER, S., WATSON, G., PEARCE, J. & DRIELSMA, M. (2002) Extended statistical approaches to modelling spatial pattern in biodiversity in northeast New South Wales. I. Species-level modelling. *Biodivers. Conserv.* **11**, 2275–2307.
- FJELDSA, J. (2000) The relevance of systematics in choosing priority areas for global conservation. *Environ. Conserv.* **27**, 67–75.
- FJELDSA, J. & BURGESS, N.D. (2008) The coincidence of biodiversity patterns and human settlement in Africa. *Afr. J. Ecol.* **46**, 33–42.
- FJELDSA, J., BURGESS, N.D., BLYTH, S. & DE KLERK, H.M. (2004) Where are the major gaps in the reserve network for Africa's mammals? *Oryx* **38**, 17–25.
- FREITAG, S., HOBSON, C., BIGGS, H.C. & VAN JAARSVELD, A.S. (1998) Testing for potential survey bias: the effect of roads, urban areas and nature reserves on a southern African mammal data set. *Anim. Conserv.* **1**, 119–127.
- GASTON, K.J. & SPICER, J. (2003) *Biodiversity: An Introduction*. Wiley-Blackwell, Oxford, UK.
- GASTON, K.J., RODRIGUES, A.S.L., VAN RENSBURG, B.J., KOLEFF, P. & CHOWN, S.L. (2001) Complementary representation and zones of ecological transition. *Ecol. Lett.* **4**, 4–9.
- GOUDIE, A. & PRICE-WILLIAMS, D. (1983) *The Atlas of Swaziland*. Swaziland National Trust Commission, Mbabane, Swaziland.
- HOPKINSON, P., TRAVIS, J.M.J., PRENDERGAST, J.R., EVANS, J., GREGORY, R.D., TELFER, M.G. & WILLIAMS, P.H. (2000) A preliminary assessment of the contribution of nature reserves to biodiversity conservation in Great Britain. *Anim. Conserv.* **3**, 311–320.
- HOWARD, P.C., DAVENPORT, T.R.B., KIGENYI, F.W., VISKANIC, P., BALTZER, M.C., DICKINSON, C.J., LWANGA, J., MATTHEWS, R.A. & MUPADA, E. (2000) Protected area planning in the tropics: Uganda's national system of forest nature reserves. *Conserv. Biol.* **14**, 858–875.
- KRESS, W.J., HEYER, W.R., ACEVEDO, P., CODDINGTON, J., COLE, D., ERWIN, T.L., MEGGERS, B.J., POGUE, M., THORINGTON, R.W., VARI, R.P., WEITZMAN, M.J. & WEITZMAN, S.H. (1998) Amazonian biodiversity: assessing conservation priorities with taxonomic data. *Biodivers. Conserv.* **7**, 1577–1587.
- LOMBARD, A.T. (1995) The problems with multi-species conservation: do hotspots, ideal reserves and existing reserves coincide? *S. Afr. J. Zool.* **30**, 145–163.
- LUCK, G.W., RICKETTS, T.H., DAILY, G.C. & IMHOFF, M. (2004) Alleviating spatial conflict between people and biodiversity. *Proc. Natl Acad. Sci. USA* **101**, 182–186.
- MCDONNELL, M.D., POSSINGHAM, H.P., BALL, I.R. & COUSINS, E.A. (2002) Mathematical methods for spatially cohesive reserve design. *Environ. Model. Assess.* **7**, 107–114.
- MONADJEM, A. (1998) Distributional patterns and conservation status of mammals of Swaziland, southern Africa. *Koedoe* **41**, 45–59.
- MONADJEM, A. (1999) Geographic distribution patterns of small mammals in Swaziland in relation to abiotic factors and human land-use activity. *Biodivers. Conserv.* **8**, 223–237.
- MONADJEM, A. & RESIDE, A. (2008) The influence of riparian vegetation on the distribution and abundance of bats in an African savanna. *Acta Chiropterol.* **10**, 339–348.
- MONADJEM, A., BOYCOTT, R.C., PARKER, V. & CULVERWELL, J. (2003) *Threatened Vertebrates of Swaziland. Swaziland Red Data Book: Fishes, Amphibians, Reptiles, Birds and Mammals*. Ministry of Tourism, Environment and Communication, Mbabane, Swaziland.
- MONADJEM, A., TAYLOR, P., COTTERILL, F.P.D. & SCHOEMAN, M.C. (in press) *Bats of Southern Africa: A Biogeographic and Taxonomic Synthesis*.
- OLDFIELD, T., SMITH, R., HARROP, S. & LEADER-WILLIAMS, N. (2004) A gap analysis of terrestrial protected areas in England and its

- implications for conservation policy. *Biol. Conserv.* **120**, 307–313.
- PARKER, V. (1994) *Swaziland Bird Atlas*. Websters, Mbabane.
- PRESSEY, R.L. & LOGAN, V.S. (1998) Size of selection units for future reserves and its influence on actual vs targeted representation of features: a case study in western New South Wales. *Biol. Conserv.* **85**, 305–319.
- PRESSEY, R.L., COWLING, R.M. & ROUGET, M. (2003) Formulating conservation targets for biodiversity pattern and process in the Cape Floristic Region, South Africa. *Biol. Conserv.* **112**, 99–127.
- ROSENZWEIG, M.L. (1995) *Species Diversity in Space and Time*. Cambridge University Press, Cambridge, UK.
- SKINNER, J.D. & SMITHERS, R.H.N. (1990). The mammals of the Southern African subregion. University of Pretoria, South Africa.
- SMITH, R.J. (2004) Conservation Land-Use Zoning (CLUZ) software. <http://www.mosaic-conservation.org/cluz>. Durrell Institute of Conservation and Ecology, Canterbury, UK.
- SMITH, T.B., KARK, S., SCHNEIDER, C.J., WAYNE, R.K. & MORITZ, C. (2001) Biodiversity hotspots and beyond: the need for preserving environmental transitions. *TREE* **16**, 431–431.
- SMITH, R.J., EASTON, J., NHANCALE, B.A., ARMSTRONG, A.J., CULVERWELL, J., DLAMINI, S., GOODMAN, P.S., LOFFLER, L., MATTHEWS, W.S., MONADJEM, A., MULQUEENY, C.M., NGWENYA, P., NTUMI, C.P., SOTO, B. & LEADER-WILLIAMS, N. (2008) Designing a transfrontier conservation landscape for the Maputaland centre of endemism using biodiversity, economic and threat data. *Biol. Conserv.* **141**, 2127–2138.
- SOULÉ, M.E. & SANJAYAN, M.A. (1998) Conservation targets: do they help? *Science* **279**, 2060–2061.
- THOMPSON, M. (1996) A standard land-cover classification scheme for remote-sensing applications in South Africa. *S. Afr. J. Sci.* **92**, 34–42.
- TUSHABE, H. & FJELDSA, J. (2008) Identifying suitable conservation targets: can GIS-based modeling serve to link coarse-scale complementarity to local selection of conservation sites? *Afr. J. Ecol.* **46**, 109–117.
- WESSELS, K.J., REYERS, B. & VAN JAARSVELD, A.S. (2000) Incorporating land cover information into regional biodiversity assessments in South Africa. *Anim. Conserv.* **3**, 67–79.
- WILLIAMS, P.H., PRANCE, G.T., HUMPHRIES, C.J. & EDWARDS, K.S. (1996) Promise and problems in applying quantitative complementary areas for representing the diversity of some neotropical plants (families Dichapetalaceae, Lecythidaceae, Caryocaraceae, Chrysobalanaceae and Proteaceae). *Biol. J. Linnean Soc.* **58**, 125–157.

(Manuscript accepted 18 May 2009)

doi: 10.1111/j.1365-2028.2009.01168.x