REPORT

How large do reserve networks need to be?

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Abstract

Reserve networks are essential for the long-term persistence of biodiversity. To fulfil this goal, they need not only to represent all species to be conserved but also to be sufficiently large to ensure species' persistence over time. An extensive literature exists on the required size of individual reserves, but to date there has been little investigation regarding the appropriate size of entire networks. The IUCN's proposal that 10% of each nation be reserved is often presented as a desirable target, but concerns have been raised that this is insufficient and is dictated primarily by considerations of feasibility and politics.

We found that the minimum percentage of area needed to represent all species within a region increases with the number of targeted species, the size of selection units, and the level of species' endemism. This has important implications for conservation planning. First, no single universal target is appropriate, as ecosystems or nations with higher diversity and/or higher levels of endemism require substantially larger fractions of their areas to be protected. Second, a minimum conservation network sufficient to capture the diversity of vertebrates is not expected to be effective for biodiversity in general. Third, the 10% target proposed by the IUCN is likely to be wholly insufficient, and much larger fractions of area are estimated to be needed, especially in tropical regions.

Keywords

Biodiversity, complementarity, conservation targets, macroecology, protected areas.

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INTRODUCTION

Article 8 of the Convention on Biological Diversity (http://www.biodiv.org/) obliges contracting parties to establish networks of protected areas for conservation. As these areas cannot be expected to protect what they do not contain in the first place, the initial minimum requirement of such networks is that they represent all the species that are to be conserved. IUCN – The World Conservation Union advocates that at least 10% of the land area of each nation be set aside for this purpose (IUCN 1993). Although achieving this target would require nearly doubling the currently protected land area (Hobbs & Lleras 1995), recent concerns have been raised that even this is woefully insufficient and dictated more by considerations of feasibility and politics than of biology (Soulé & Sanjayan 1998). However, to date there has been little investigation of what would be an appropriate target from a biological perspective.

Complementarity-based methods provide a way to integrate political and biological considerations in the selection of networks of protected areas. They have been proposed in acknowledgement of the fact that resources available for conservation purposes are limited and should therefore be employed in efficient ways that maximize the diversity of biological features benefited (Pressey & Nicholls 1989; Pressey *et al.* 1993). When data on the distribution of all the species within a region are available, this is achieved by selecting areas that complement one another to the fullest possible extent in terms of their species composition. In the most widespread type of analyses applying these methods, minimum sets (i.e. sets of sites with minimum total area) are obtained which represent all of the target species at least once. These minimum networks are unlikely to be sufficient for ensuring the long-term persistence of the species represented (Rodrigues *et al.* 2000a,b), but they provide a lower bound to the size of an adequate network for conserving those species. These methods are therefore particularly suitable tools for determining the minimum percentage of a given region that needs to be reserved in order to ensure the representation of its species diversity.

In this study, complementary-based methods are used as a tool to explore the issue of how large reserve networks need to be. First, we examine patterns of variation in the sizes of minimum networks for a variety of assemblages.

Second, we test predictions for these patterns. Third, we analyse the implications of the patterns for conservation planning.

PREDICTIONS FROM PREVIOUS COMPLEMENTARITY STUDIES

We analysed 21 published and unpublished studies that found the minimum or near-minimum percentages of area required to represent each species in a region at least once (published studies: Rebelo & Siegfried 1992; Lombard *et al.* 1995; Castro Parga *et al.* 1996; Church *et al.* 1996; Freitag *et al.* 1996; Williams *et al.* 1996a,b; Willis *et al.* 1996; Csuti *et al.* 1997; Muriuki *et al.* 1997; Hacker *et al.* 1998; Nantel *et al.* 1998; Araújo 1999; Humphries *et al.* 1999; Lombard *et al.* 1999; Reyers *et al.* 2000; Williams *et al.* 2000a,b; unpublished studies: near-minimum area to represent plant species in the Northern Province of South Africa provided by B. Reyers, pers. comm.; minimum area to represent bird species in South Africa and Lesotho and in south-east Scotland calculated from data provided in published atlases – Harrison *et al.* 1997; Murray *et al.* 1998). These studies concern a diversity of geographical regions (in Europe, North America, Africa and the Neotropics), with scales varying from regional analyses (456 km^2) to entire continents (Africa, $\sim$ 20 million km^2) and with selection units sized between 1 km^2 and 1 degree grid cells ($\sim$ 12 000 km^2). In all cases, analyses were based on contiguous equal-sized selection units (grid cells, hexagons or rectangles), so that the solution to the problem of obtaining the minimum number of sites such that each species is represented at least once is equivalent to the problem of minimizing the area.

The mean value of the minimum percentage of the area needed to represent all species in these studies is 13.6%, not far from the IUCN recommendation that 10% of land area be set aside for conservation; however, the range is very wide (0.3–66.0%). We tested a diversity of logistic regression models to look for the most parsimonious explanation of this variation. We found that the combined influences of the number of species considered in each study and the number of contiguous sites into which the study area was divided, expressed as a ratio of species per site, explains a highly significant part of this variation. This ratio is positively correlated with the minimum percentage of area required to represent all species (Fig. 1); this does not result from an intrinsic relationship between the number of species and the number of sites ($R^2 = 0.017$; $P = 0.57$). Moreover, a substantial proportion of the variability of the results seems to be explained by the nature of the biodiversity features considered: studies on plants and vertebrates lead to substantially different logistic regression curves when considered separately (Fig. 1).
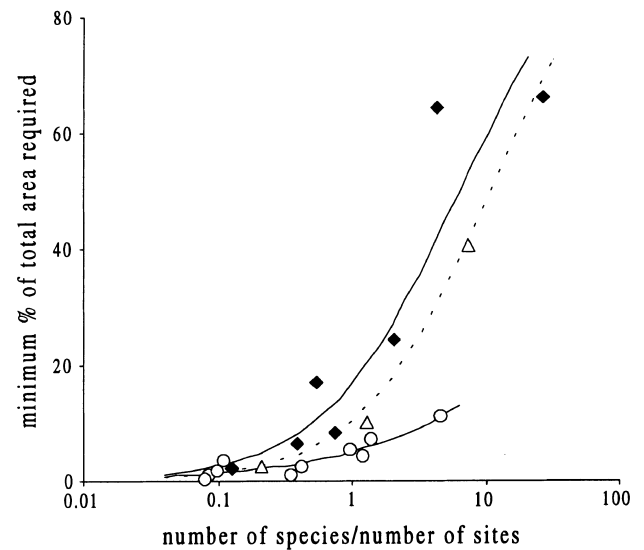
Figure 1 Relationship between the ratio of the number of species analysed to the number of sites into which the region has been divided and the minimum percentage of total area required to represent each species at least once (see text for details). The values were obtained from 21 published and unpublished studies that found the minimum (or near-minimum) percentage of area required to represent each species at least once. Logistic regression models were applied to determine the relationships for all studies (dashed line) and separately for plants (◆, upper continuous line) and vertebrates (○, lower continuous line). Highly significant relationships ($P < 0.001$) were obtained in all cases (all data: χ^2-test = 410.69, $n = 21$; plants: χ^2-test = 227.29, $n = 8$; vertebrates: χ^2-test = 20.71, $n = 10$). △ refer to studies based on multiple higher taxa (including plants and vertebrates).

These results suggest three mechanisms by which intrinsic properties of the data set affect the minimum percentage of area needed to represent all species within a region. First, everything else being equal (i.e. for the same geographical area and considering the same selection units), as more species are included in a reserve planning exercise, the minimum percentage of total area needed to ensure representation of all of those species will increase.

Second, an increase in the size of the selection units should result in an increase in the minimum percentage of the area required for representation of all species (see also Pressey & Logan 1998; Pressey *et al.* 1999).

Third, it seems probable that the different relationships for plants and vertebrates between the ratio of the number of species to the number of sites and the minimum percentage of total area required to represent each species at least once are derived from the larger mean geographical range sizes and greater distributional overlap of vertebrates compared to plants. If this is a general rule, then taxa that have higher levels of local endemism are expected to require

higher percentages of area in order to be fully represented (see also Soulé & Sanjayan 1998; Pressey *et al.* 1999).

Whilst logical and possibly obvious, these predictions have received little testing. This can be done by manipulating data sets in order to vary each one of the three variables mentioned (number of species, size of selection units and level of endemism) while controlling for the remaining ones. We used data on the distribution of birds in Southern Africa to perform these tests.

TEST OF THE PREDICTIONS

The Southern African Bird Atlas Project (Harrison *et al.* 1997) provides the most comprehensive information currently available on the distribution of birds in Southern Africa. Data were mainly collected between 1987 and 1992, at a spatial resolution of a quarter-degree grid for Lesotho, Namibia, South Africa, Swaziland and Zimbabwe, and on a half-degree grid for Botswana. Observers visiting each cell recorded the presence of identified species on checklists. A total of 909 species were recorded (for a more detailed description of the methodology used, see Harrison *et al.* 1997).

In this study, we used presence-absence data collected for South Africa and Lesotho (1858 quarter-degree grid cells), and excluded marine, vagrant, marginal and escaped species from the analysis (651 species were analysed). We manipulated the data properties in order to test each one of the predictions presented above. All optimization problems referred to below have been solved optimally using CPLEX software (ILOG 1999).

Prediction 1. An increase in the number of species should result in an increase in the minimum percentage of area required

This prediction was tested using data subsets for Lesotho (329 species, 46 quarter-degree grid cells) and for the South African provinces of Northern Cape (401 bird species, 542 cells), Northern Province (555 species, 174 cells) and Mpumalanga (561 species, 118 cells). These were used rather than the entire data set in order to obtain a priori higher values for the ratio between the number of species and the number of sites.

For each political unit separately, data subsets were created with variable numbers of species while keeping the number of sites constant (for example, for Lesotho, subsets were obtained with 10, 30, 50, 100, 150, 200, 250 and 300 species, all with 46 cells). In this way, a wide range of values for the ratio between the number of species and the number of sites was obtained, which was necessary to cover the variability (across the x axis) of the data points plotted in Fig. 1.

The species included in each subset were selected randomly, and 10 replicates with the same number of species were created in each case. For each subset, the minimum percentage of area needed to represent each species at least once was obtained, and the average values across the 10 replicates were then calculated.

The results support the first prediction. For each unit separately, the minimum percentage of total area needed to represent all species increased steadily for increasing numbers of species (Fig. 2a). The values obtained are very accurately described by logistic regression curves (Fig. 2a).

Prediction 2. An increase in the size of the selection units considered should result in an increase in the minimum percentage of area required
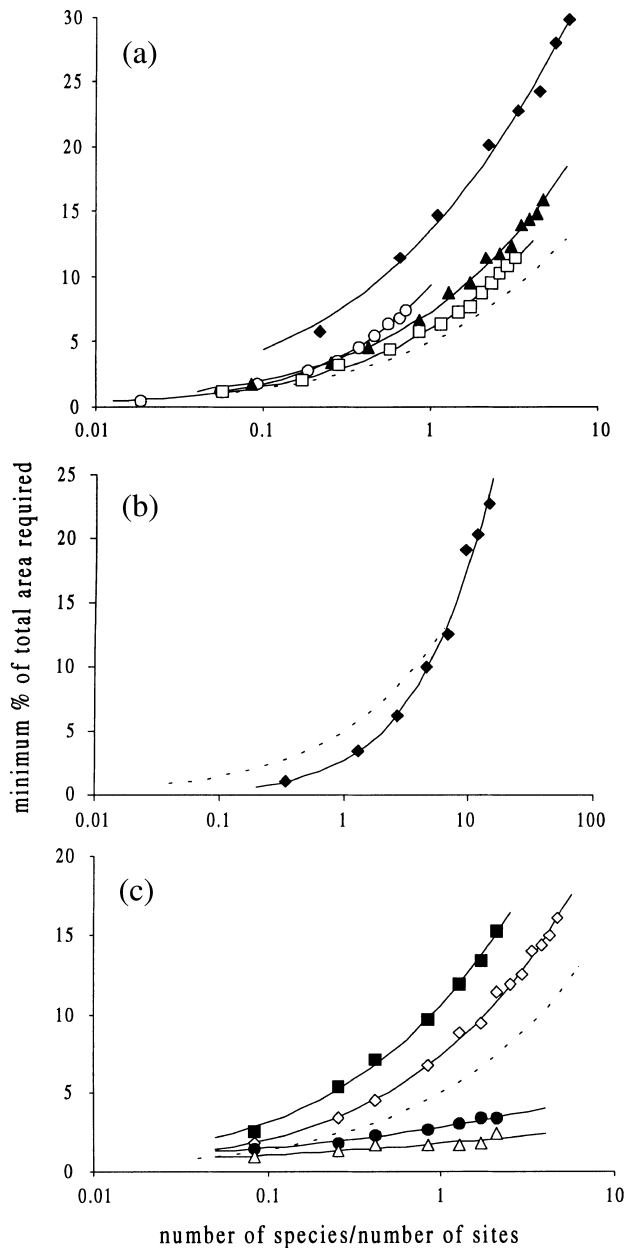
Using the entire data set on the distribution of bird species in South Africa and Lesotho we manipulated the size of the selection units while keeping the number of species constant (651 species) by re-sampling the data at different spatial resolutions. Unit sizes employed were of 1 × 1 (the original 1858 quarter-degree grid cells), 2 × 2 (498 half-degree cells), 3 × 3 (240 cells), 4 × 4 (139 one-degree cells), 5 × 5 (95 cells), 6 × 6 (68 cells), 7 × 7 (54 cells) and 8 × 8 (44 two-degree cells) grid cells. A species was considered to be present in a given cell at a given resolution if it occurred in at least one of the quarter-degree grid cells that composes the larger cell. For each unit size, the minimum percentage of area needed to represent each species at least once was obtained.

The results support the second prediction, as the minimum percentage of total area needed to represent all species increased steadily with increasing size of the unit (Fig. 2b). The values obtained are again very accurately described by a logistic regression curve.

Prediction 3. Steeper slopes are expected for taxa with higher levels of endemism

One way of measuring the level of endemism in a data set is by calculating the average range of the species, which can be presented in a standardized way (comparable across different data sets) as the average percentage of sites in the study area occupied by each species. The smaller the average range, the higher the level of endemism.

This prediction was tested using data for the Mpumalanga province (561 species, 118 cells). Four levels of endemism were analysed by creating data subsets with a variable number of species randomly extracted from: (i) all the 561 species (average range 43% of the total area); (ii) the 50% most common species in terms of range size (measured as the number of cells occupied by a given species; average range 69%); (iii) the 50% rarest species (average range 18%);

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Figure 2 Variation in the minimum percentage of total area required to represent all species when data are manipulated to vary (a) the number of species, (b) the spatial resolution, and (c) the level of endemism (see text for details). For reference, the dashed line is that obtained for studies on vertebrates, as plotted in Fig. 1. (a) Variation in the minimum percentage of total area required as the number of bird species increases in Lesotho (◆), Northern Cape (○), Mpumalanga (▲), and the Northern Province (□). Each data point corresponds to the average minimum percentage of area obtained across 10 replicates. All relationships are well described ($P < 0.001$) by logistic regression models (Lesotho: χ^2-test = 33.6, $n = 8$; N. Cape: χ^2-test = 16.1, $n = 10$; Mpumalanga: χ^2-test = 33.1, $n = 13$; N. Province: χ^2-test = 24.6, $n = 13$). (b) Variation in the minimum percentage of total area required to represent all species as size of selection units increases for data in South Africa and Lesotho. The leftmost data point corresponds to the smallest selection units (quarter-degree grid cells) and the rightmost to the largest (two-degree grid cells). The relationship is well described by a logistic regression model (χ^2-test = 50.2, $n = 8$, $P < 0.001$). (c) Variation in the slopes of the relationship between the ratio of the number of species to the number of sites and the minimum percentage of total area needed to represent all species for four levels of endemism: (i) all species (◇); (ii) the 50% most common species (△); (iii) the 50% rarest species (◆); and (iv) the 50% 'middle' species (●). Highly significant relationships ($P < 0.001$) were found in (i) (χ^2-test = 33.1, $n = 13$) and (iii) (χ^2-test = 15.8, $n = 7$). The lack of significant relationships in (ii) and (iv) reflects the limited variation in the minimum percentage of total area required in these cases.

species (iv) have quite different slopes, despite having similar average range sizes. The first one is much closer to the level obtained for the rare species (iii), whereas the second is closer to the level for the common species (ii). This is probably due to the disproportionate influence of the very rare species (excluded from level (iv) but still present in level (i)) on the number of sites selected (Rodrigues & Gaston in press). If so, then the average range size may not be the most adequate measure of the data property that is influencing the slope of the regression curves obtained. A more sensitive measure of the influence of very rare species is the average range size for the 10% rarest species amongst the ones considered in each data set. The corresponding values for the different levels are: (i) 1.9%; (ii) 42.4%; (iii) 1.1%; and (iv) 19.3%. These are more consistent with the relative position of the curves in Fig. 2(c).

The relative position of the curves in Fig. 2(a) also supports the prediction that higher levels of endemism result in higher slopes when the measure of endemism is the average range size for the 10% rarest species (Lesotho: 0.85%; N. Cape 1.04%; Mpumalanga: 1.88%; N. Province: 2.27%), but not when the measure is the average range for all species (Lesotho: 30%; N. Cape: 22%; Mpumalanga: 43%; N. Province: 40%). These results support the idea that

and (iv) the 50% 'middle' species (excluding the 25% rarest and the 25% most common species; average range 40%). Ten replicates were obtained for each number of species (between 10 and 550 in (i) and between 10 and 250 in (ii), (iii) and (iv)) and each of the four levels of endemism. The minimum percentage of area needed to represent each species at least once was found for each subset, and average values were calculated across the 10 replicates.

The results support the third prediction, as steeper slopes are obtained for increasing levels of endemism (Fig. 2c). However, the curves for the levels obtained by selection from the entire set of 561 species (i) and from the 'middle'

it is the range of the rarest species that determines the slope of the relationship between the ratio of the number of species to the number of sites and the minimum percentage of total area needed to represent all species.

IMPLICATIONS FOR CONSERVATION PLANNING

Our results demonstrate that the minimum percentage of area that would need to be reserved simply to represent all species within a region is highly variable and depends upon the diversity and endemism of the taxa of concern, and on the size of the selection units considered. This is supported by our analyses of data from various taxa and geographical regions (Fig. 1), as well as by analyses manipulating data on the distribution of birds in Southern Africa (Fig. 2).

Plainly, conservation requires more than just representation; however, these results have three important implications for practical conservation planning. First of all, they demonstrate that no single universal target for the minimum percentage of area that should be reserved (such as the 10% proposed by IUCN) can be appropriate. Instead, ecosystems or nations with higher species diversity and/or higher levels of endemism, such as the tropical ones, are expected to require substantially larger fractions of their areas to be reserved. This need is acknowledged in the main proposals of priority areas for global conservation (16 out of the 25 biodiversity hotspots, comprising 75% of the overall area proposed, include tropical biomes: Mittermeier *et al.* 1999; Myers *et al.* 2000; 76% of all Endemic Bird Areas are in the tropics: ICBP 1992; Stattersfield *et al.* 1998), but, unfortunately, is the opposite of the current situation (Pimm & Lawton 1998). For example, a higher percentage of the area of the species-poor tundra communities (7.5%) or mixed mountain systems (8.0%) is protected than of the rich tropical humid forests (5.1%), tropical dry forests/woodlands (4.7%) or tropical grasslands/savannahs (5.5%) (Hobbs & Lleras 1995).

Second, these results confirm that a minimum conservation network sufficient to capture the diversity of vertebrates will not be an effective umbrella for biodiversity in general (Howard *et al.* 1998; Kerr 1997), because many other more diverse groups with higher levels of local endemism (including plants and many groups of invertebrates) are expected to require considerably larger areas to be fully represented. Because in practice it is unlikely that data on the distribution of all species of concern in a given region will be available in the near future, this provides another reason why reserve networks must not be based solely on a minimum representation target of the well-studied species. The finding that higher levels of endemism result in the need to select larger areas supports the emphasis given by international conservation organizations to areas of exceptional concentrations of endemic species (as in the

biodiversity hotspots, Mittermeier *et al.* 1999; Myers *et al.* 2000; in the Endemic Bird Areas & ICBP 1992; Stattersfield *et al.* 1998).

The third implication of these results is that considerable variation in the minimum percentage of the area required for representation of all species results from changing the size of the selection units. Conservation plans that consider the smallest possible selection units would greatly reduce the minimum percentage of area needed to represent all species: carried to an absurd extreme, the cheapest reserve network would adopt a Noah's Ark approach, by reserving only a few square metres to represent one pair of each species (Pimm & Lawton 1998). However, representation is not the same as conservation, and in order to ensure that the reserve networks selected fulfil their role of maintaining biodiversity over time, the size of selection units must be one at which the populations of species are likely to persist (recognizing that for many species more than one unit in which they occur will be selected, which may be adjacent or not). This reinforces both the need for caution in the interpretation and implementation of the results obtained when selecting minimum complementary sets, and the belief that complementary reserve planning must take viability considerations into account (e.g. Rodrigues *et al.* 2000a,b; Gaston *et al.* 2001; see also Fahrig 2001).

Treating the relationships in Fig. 1 as representative, they can be used to predict what would be the minimum percentage of land area required to represent each species of terrestrial plant and higher vertebrate in a global or a tropical rain forest conservation network considering selection units of different sizes (Fig. 3). In order to do so, the parameters of the corresponding logistic model obtained from the empirical data (Fig. 1) have been used, and it was assumed that 24 500 higher vertebrates (mammals, birds, reptiles and amphibians) and 240 000 seed plants have been described (WCMC 1992), that at least 50% of all species exist in tropical rain forests (WCMC 1992; Wilson 1988), and that the area of land surface on earth (excluding Antarctica) is 133 149 000 km^2 (Good 1974) and of the remaining rain forest is *c.* 12 008 000 km^2 (WCMC 1992).

Considering selection units of 1° × 1° (*c.* 12 000 km^2), the finest resolution that has been considered practical for mapping bird species (the best known group) across an entire continent spanning the tropical zone (Fjeldså & Rahbek 1998), it is predicted that 74.3% of the global land area and 92.7% of the tropical rain forests would be required to represent every plant species once, and 7.7% and 17.8% for higher vertebrates (Fig. 3). Although the values obtained for plants may seem high, they simply mean that, for example, in 92.7% of all 1° × 1° cells across the tropical rain forest it is expected that at least one plant species exists that requires that cell or part of it to be selected. This may not be unrealistic, given that high
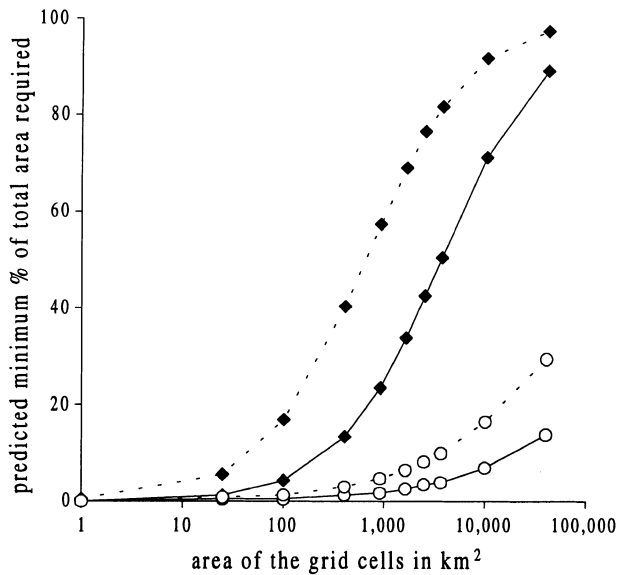
Figure 3 Relationship between the size of the selection units and the predicted minimum percentage of area required to represent each species at least once, for seed plants (◆) and higher vertebrates (○), at a global scale (continuous lines) or in the tropical rain forest (dashed lines; see text for details).

percentages of the tropical plant species described are known from single localities (e.g. 33.8% of neotropical plants in Andersen *et al.* 1997). The values obtained for the higher vertebrates are probably underestimated. The sites selected by complementarity tend to be highly scattered (e.g. Lombard 1995), and therefore isolated, and even reserves of this size ($1° \times 1°$) may not be sufficiently large for maintaining viable populations of many species. For example, even very large reserves such as Kruger National Park in South Africa (19 485 km^2) and Yellowstone in the United States (8992 km^2) have lost or are in danger of losing some of their mammal species (e.g. Newmark 1987, 1996; Mattson & Reid 1991; Nicholls *et al.* 1996); and Manne *et al.* (1999) showed that a high percentage of American bird species with range of the size of a $1° \times 1°$ cell are threatened with imminent extinction.

Conversely, if the target was to reserve 10% of the total area, as suggested by the IUCN guidelines, selection units of 16.5×16.5 km for the world, or of 7.0×7.0 km for the tropical rain forest, would have to be considered to represent all plant species. Reserves of this size would undoubtedly be inadequate for maintaining viable populations of many (probably most) species, demonstrating that 10% of land area is indeed an insufficient target. Especially for species-rich areas with high levels of endemism, such as the tropical rain forest, a much larger fraction of the total area is needed if a significant fraction of species diversity is to be conserved into the future.

Further empirical data are needed to test how realistic are the values obtained in this study. Meanwhile, our results reinforce the need for urgent conservation action, particularly in the tropical regions, where the protected area network needs to be large, few biological data exist to support decisions about the appropriate location of sites, little national political will and economic resources exist to invest in reserve acquisition and which continue to suffer high rates of habitat destruction.

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REFERENCES

Andersen, M., Thornhill, A. & Koopowitz, H. (1997). Tropical forest disruption and stochastic biodiversity losses. In: *Tropical Forest Remnants – Ecology, Management and Conservation of Fragmented Communities* (eds Lawrence, W.F. & Bierregaard, R.O. Jr). University of Chicago Press, Chicago, pp. 281–291.

Araújo, M.B. (1999). Distribution patterns of biodiversity and the design of a representative reserve network in Portugal. *Diversity Distributions*, 5, 151–163.

Castro Parga, I., Moreno-Saiz, J.C., Humphries, C.J. & Williams, P.H. (1996). Strengthening the Natural and National Park system of Iberia to conserve vascular plants. *Bot. J. Linnean Soc.*, 121, 189–206.

Church, R.L., Stoms, D.M. & Davis, F.W. (1996). Reserve selection as a maximal covering location problem. *Biol. Conservation*, 76, 105–112.

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. Conservation*, 80, 83–97.

Fahrig, L. (2001). How much habitat is enough? *Biol. Conservation*, 100, 65–74.

Fjeldså, J. & Rahbek, C. (1998). Continent-wide conservation priorities and diversification processes. In: *Conservation in a Changing World* (eds Mace, G.M., Balmford, A. & Ginsberg, J.R.). Cambridge University Press, Cambridge, pp. 139–160.

Freitag, S., Nicholls, A.O. & van Jaarsveld, A.S. (1996). Nature reserve selection in the Transvaal, South Africa: What data should we be using? *Biodiversity Conservation*, 5, 685–989.

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.

Good, R. (1974). *The Geography of Flowering Plants*. Longman, White Plains, N.Y.

Hacker, J.E., Cowlishaw, G. & Williams, P.H. (1998). Patterns of African primate diversity and their evaluation for the selection of conservation areas. *Biol. Conservation*, 84, 251–262.

Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. & Brown, C.J., eds. (1997). *The Atlas of Southern African Birds*. BirdLife South Africa, Johannesburg.

Hobbs, R. & Lleras, E. (1995). Protecting and restoring ecosystems, species, populations and genetic diversity. In: *Global Biodiversity Assessment* (eds Heywood, V.H. & Watson, R.T). UNEP, Cambridge University Press, Cambridge, pp. 981–1017.

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

Humphries, C., Araújo, M., Williams, P., Lampinen, R., Lahti, T. & Uotila, P. (1999). Plant diversity in Europe: Atlas Florae Europaeae. *Acta Bot. Fennica*, 162, 11–21.

ICBP (1992). *Putting Biodiversity on the Map: Priority Areas for Global Conservation*. International Council for Bird Preservation, Cambridge.

ILOG (1999). *CPLEX 6.5*, ILOG, Gentilly, France.

IUCN (1993). *Parks for Life – Report of the 4th World Conference on Natural Parks and Protected Areas*. IUCN, Gland, Switzerland.

Kerr, J.T. (1997). Species richness, endemism, and the choice of areas for conservation. *Conservation Biol.*, 11, 1094–1100.

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

Lombard, A.T., Hilton-Taylor, C., Rebelo, A.G., Pressey, R.L. & Cowling, R.M. (1999). Reserve selection in the Succulent Karoo, South Africa: coping with high compositional turnover. *Plant Ecol.*, 142, 35–55.

Lombard, A.T., Nicholls, A.O. & August, P.V. (1995). Where should nature-reserves be located in south Africa – a snakes perspective. *Conservation Biol.*, 9, 363–372.

Manne, L.L., Brooks, T.M. & Pimm, S.L. (1999). Relative risk of extinction of passerine birds on continent and islands. *Nature*, 399, 258–261.

Mattson, D.J. & Reid, M.M. (1991). Conservation of the Yellowstone grizzly bear. *Conservation Biol.*, 5, 364–372.

Mittermeier, R.A., Myers, N., Robles Gil, P. & Mittermeier, C.G. (1999). *Hotspots – Earth's Biologically Rich and Most Endangered Terrestrial Ecoregions*. CEMEX, Mexico City, Mexico.

Muriuki, J.N., De Klerk, H.M., Williams, P.H., Bennun, L.A., Crowe, T.M. & Berge, E.V. (1997). Using patterns of distribution and diversity of Kenyan birds to select and prioritize areas for conservation. *Biodiversity Conservation*, 6, 191–210.

Murray, R.D., Holling, M., Dott, H.E.M. & Vandome, P. (1998). *The Breeding Birds of South-East Scotland – a Tetrad Atlas 1988–94*. The Scottish Ornithologists Club, Edinburgh.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403, 853–858.

Nantel, P., Bouchard, A., Brouillet, L. & Hay, S. (1998). Selection of areas for protecting rare plants with integration of land use conflicts: a case study for the west coast of Newfoundland, Canada. *Biol. Conservation*, 84, 223–243.

Newmark, W.D. (1987). A land-bridge island perspective on mammalian extinctions in western North American parks. *Nature*, 325, 430–432.

Newmark, W.D. (1996). Insularization of Tanzanian parks and the local extinction of large mammals. *Conservation Biol.*, 10, 1549–1556.

Nicholls, A.O., Viljoen, P.C., Knight, M.H. & van Jaarsveld, A.S. (1996). Evaluating population persistence of censused and unmanaged herbivore populations from the Kruger National Park, South Africa. *Biol. Conservation*, 76, 57–67.

Pimm, S.L. & Lawton, J.H. (1998). Planning for biodiversity. *Science*, 279, 2068–2269.

Pressey, R.L., Humphries, C.J., Margules, C.R., Vane-Wright, D. & Williams, P. (1993). Beyond opportunism – key principles for systematic reserve selection. *Trends Ecol. Evol.*, 8, 124–128.

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. Conservation*, 85, 305–319.

Pressey, R.L. & Nicholls, A.O. (1989). Efficiency in conservation evaluation – scoring versus iterative approaches. *Biol. Conservation*, 50, 199–218.

Pressey, R.L., Possingham, H.P., Logan, V.S., Day, J.R. & Williams, P.H. (1999). Effects of data characteristics on the results of reserve selection algorithms. *J. Biogeogr.*, 26, 179–191.

Rebelo, A. & Siegfried, W.R. (1992). Where should nature reserves be located in the Cape Floristic Region, South Africa? Models for the spatial configuration of a reserve network aimed at maximizing the protection of floral diversity. *Conservation Biol.*, 6, 243–252.

Reyers, B., van Jaarsveld, A.S. & Krüger, M. (2000). Complementarity as a biodiversity indicator strategy. *Proc. Roy. Soc. Lond. B*, 267, 505–513.

Rodrigues, A.S.L. & Gaston, K.J. (in press). Rarity and conservation planning across geopolitical units. *Conservation Biol.*, in press.

Rodrigues, A.S.L., Gaston, K.J. & Gregory, R. (2000a). Using presence-absence data to establish reserve selection procedures which are robust to temporal species turnover. *Proc. Roy. Soc. Lond. B*, 267, 1–6.

Rodrigues, A.S.L., Gregory, R. & Gaston, K.J. (2000b). Robustness of reserve selection procedures under temporal species turnover. *Proc. Roy. Soc. Lond. B*, 267, 49–55.

Soulé, M.E. & Sanjayan, M.A. (1998). Ecology – conservation targets: do they help? *Science*, 279, 2060–2061.

Stattersfield, A.J., Crosby, M.J., Long, A.J. & Wege, D.C. (1998). *Endemic Bird Areas of the World – Priorities for Biodiversity Conservation*. BirdLife International, Cambridge.

WCMC (1992). *Global Biodiversity – Status of the Earth's Living Resources*. Chapman & Hall, London.

Williams, P.H., Burgess, N.D. & Rahbek, C. (2000a). Flagship species, ecological complementary and conserving the diversity of mammals and birds in sub-Saharan Africa. *Anim. Conservation*, 3, 249–260.

Williams, P., Humphries, C., Araújo, M., Lampinen, R., Hagemeijer, W., Gasc, J.-P. & Mitchell-Jones, T. (2000b). Endemism and important areas for representing European biodiversity: a preliminary exploration of atlas data for plants and terrestrial vertebrates. *Belgian J. Entomol.*, 2, 21–46.

Williams, P.H., Prance, G.T., Humphries, C.J. & Edwards, K.S. (1996b). Promise and problems of applying quantitative complementary areas for representing the diversity of some Neotropical plants (families Dichapetalaceae, Lecythidaceae, Caryocaraceae, Chrysobalanaceae and Proteaceae). *Biol. J. Linnean Soc.*, 58, 125–143.

Williams, P.H., Gibbons, D., Margules, C., Rebelo, A., Humphries, C. & Pressey, R. (1996a). A comparison of richness hotspots, rarity hotspots, and complementary areas for conserving diversity of British birds. *Conservation Biol.*, 10, 155–174.

Willis, C.K., Lombard, A.T., Cowling, R.M., Heydenrych, B.J. & Burgers, C.J. (1996). Reserve systems for limestone endemic flora of the Cape lowland fynbos: iterative vs. linear programming. *Biol. Conservation*, 77, 53–62.

Wilson, E.O., ed. (1988). *Biodiversity*. National Academy Press, Washington D.C.

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