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Endemism and important areas for representing European biodiversity : a preliminary exploration of atlas data for plants and terrestrial vertebrates

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Abstract

In order to represent as much as possible of European biodiversity for conservation, we need efficient, quantitative area-selection methods, which will also promote accountability. Some of the most widely valued biodiversity in Europe can be represented by combining data from recent atlases for vascular plants, amphibians, reptiles, breeding birds, and mammals. In a preliminary comparison of techniques we find that, at least when selecting up to 122 of the 50 × 50 km map cells (5% of the area), there is low (30/122) but significant coincidence between hotspots of richness and hotspots of narrow endemism. Despite this, the popular method of selecting hotspots of richness still represents no more species than choosing areas at random. When selecting more than 30 areas, hotspots of narrow endemism perform significantly better, although the best results come from using a method that targets the different species most directly: hotspots of complementary richness. When selecting more than ten areas, using complementary richness increases the representation of species over the other methods by nearly 20%. Quantitative methods using complementarity can be adapted to answer a variety of questions, and can be applied to area units of any shape and size, as well as accommodating additional constraints of viability, threat, cost, or any other quantifiable social and land-use factors that affect the suitability of areas for selection or their priority for conservation management.

Keywords : hotspots, complementarity, efficiency, species richness.

Introduction

Several international groups have recently asked the question: which are the important areas for biodiversity in Europe? (e.g. SMART, 1996; CE, 1997a; DEHARVENG, 1998; WOLTERS & BOUWMA, 1998; HEATH *et al.*, in press) One of these specifically concentrated on 'High Endemism Areas, Endemic Biota and the Conservation of Biodiversity in Western Europe' (DEHARVENG, 1998), because biodiversity is more likely to be well represented if the organisms with more restricted distributions are included. In a preliminary analysis of atlas data, we look at broad-scale patterns of endemism in Europe, and at how this information can be used to achieve a goal of representing the most biodiversity value for conservation.

Species (or other taxa) are said to be endemic if they are completely restricted to a specified region, whatever its size. Of most interest are narrow endemics, which have total global range sizes restricted to relatively small areas. This is a form of rarity as applied to range-size extent (RABINOWITZ, 1981; GASTON, 1994). Although rarity is often valued for its own sake (USHER, 1986), or for its relationship to extinction risk (JOHNSON, 1998), we are interested in it here mainly because it constrains the options for choosing areas that represent as much as possible of broader biodiversity.

Narrowly endemic species have been a popular focus for studies of important areas for biodiversity conservation, especially in the work of ICBP (1992). One reason for this is the belief that biodiversity will be especially high in areas where the presence of narrowly endemic species supplements a body of more widespread species (GENTRY, 1986).

In this paper, we examine the consequences of choosing hotspots of richness or hotspots of narrow endemism for representing the diversity of European vascular plants, amphibians, reptiles, breeding birds, and mammals, using recent atlas data. The assumption that widespread and narrowly endemic species of these groups tend to co-occur within hotspot areas of Europe is tested. We also use a method (hotspots of complementary richness) for maximising the representation of biodiversity by a technique of searching for the most narrowly restricted species. Representation of ecosystem and genetic diversity are discussed, as are the prospects of moving from simple representation of species to including viability, threat and social constraints in planning for the persistence of biodiversity.

Material and methods

Mapping biodiversity presents a philosophical problem: biodiversity can be seen as encompassing the entire and irreducible complexity of life, and not all of this complexity can be captured simultaneously in any single measure or map. Therefore particular aspects have to be chosen for mapping if the interpretation is to be clear. This amounts to selecting which aspect of

biodiversity is most valued (including non-monetary values), and the choice should depend on the purpose for which the measure is being made (NORTON, 1994). Here, only terrestrial biodiversity is included, and it is measured using the popular approach of counting the number of species. The number and variety of species may also reflect the underlying genetic diversity, which is important for the potential value of biodiversity for future use or evolution (reviewed by WILLIAMS, 1998).

Surveying biodiversity presents serious practical problems because it is almost always impossible to count all species, even in areas as small as a suburban garden (OWEN, 1991). If not all species can be counted, then one way of starting to make progress is to begin by mapping those groups of organisms that are the most valued part of biodiversity for most people. Information on other groups can be added later, when it becomes available. Empirically, the particular importance and value to people of terrestrial plants and vertebrates is evident from the strong bias in academic research and in conservation effort (WILLIAMS *et al.*, 1997). This bias is present even among biologists and continues despite the growing knowledge of the far greater numbers of smaller organisms within other groups, and of their roles in ecological processes. It is possible that vascular plants and vertebrates could also act as indicators for some of these other organisms, particularly if they share similar governing factors (PRENDERGAST, QUINN *et al.*, 1993; GASTON, 1996; WILLIAMS & GASTON, 1998). As a first step towards mapping the distribution of terrestrial biodiversity value across Europe, atlas data for some of the most valued groups can be added together as an estimate of their combined species richness (WILLIAMS *et al.* in DELBAERE, 1998). This reasoning provides the principal justification for choosing these groups, by linking plants and vertebrates most directly with a popular view of value in biodiversity. It is fortunate that these groups are also some of the best recorded, although this criterion has to be subordinate to the main aim of choosing what is most directly valued (for example, no matter how well recorded mosquitoes may be, they are not a widely valued part of biodiversity).

Terrestrial vertebrates and plants have been painstakingly mapped by European atlas projects from data collected largely by the many volunteer recorders across Europe. Vascular plants were mapped by the *Atlas Florae Europaeae* (AFE, c. 20% of the European species are mapped to date: JALAS & SUOMINEN, 1972-1994; JALAS *et al.*, 1996); amphibians and reptiles by the *Societas Europaea Herpetologica* (SEH: GASC *et al.*, 1997); breeding birds by the *European Bird Census Council* (EBCC: HAGEMEIJER & BLAIR, 1997); and mammals by the *Societas Europaea Mammalogica* (SEM: MITCHELL-JONES *et al.*, 1999).

The European atlases use the grid approach to map species' records. The grid used in Figs 1-5 is based on the AFE system of 50 × 50 km cells, with cell boundaries typically following the 50 km lines of the *Universal Transverse*

Mercator (UTM) grid, except near the border of the six-degree UTM zones and at coasts. The other atlases use slightly different grid systems, so that 40% of AFE grid cells differ to some degree from corresponding cells in the other atlases. This is unfortunate, although a common European *Chorological Grid Reference System* (CGRS) is now being prepared jointly by the atlas committees and the *European Topic Centre for Nature Conservation* (ETCNC: ROEKAERTS *et al.*, in prep.). In the interim, we have converted data from the vertebrate mapping grids to the AFE grid by identifying unique (though sometimes approximate) correspondence between cells in these grids. The largest mismatches between grids occur for cells on coasts and islands, although there are also differences in grid-cell boundaries near the borders of the six-degree UTM zones. Nonetheless, for exploring comparisons of area-selection methods, we believe that these differences are of not important.

The region of Europe mapped here (2435 grid cells) is restricted to the area where sampling effort has been relatively uniform and intensive (GASC *et al.*, 1997; HAGEMEIJER & BLAIR, 1997; LAHTI & LAMPINEN, 1999; MITCHELL-JONES *et al.*, 1999), and excludes the European part of the former Soviet Union, except for the Baltic countries and the Kaliningrad Region (Fig. 1). Available records for this area include 2362 vascular plant species, together with 58 amphibian, 91 reptile, 445 breeding bird, and 187 mammal species (Table 1). Where status is known, the data used include native records and established introductions, but exclude records where local populations are believed to have become extinct (e.g. for AFE data, they include only 'native', 'unknown' and 'introduced' records). Maps of 'European' endemics were prepared by searching the atlases for species that are recorded as being restricted to the particular part of Europe mapped here (the 2435 grid cells), and therefore excluded species restricted to larger definitions of Europe (for example, species of Madeira, Canary Islands, Crimea (Krym), Caucasus). Using different definitions of 'Europe' (or revisions of distribution data) could be accommodated and would be expected to result in different lists of endemic species.

Narrow endemics have been defined previously using thresholds of range size (TERBORGH & WINTER, 1983; ICBP, 1992; SÆTERSDAL *et al.*, 1993). In Europe, one proposal to the *Planta Europa* programme is that selection of 'Important Plant Areas' should favour areas with many species of plant with range sizes restricted to less than 20,000 km², a choice that was linked to the new IUCN Red List criteria for vulnerable species (OLDFIELD, 1998). This maximum area corresponds approximately to a threshold area of occupancy (in the sense of GASTON, 1994) of up to eight cells on the 50 km grid. Using other area thresholds (any size could be used) would be expected to result in different lists of narrowly endemic species.

Hotspots have often been considered as important areas for conserving biodiversity. The term 'hotspots' was used by MYERS (1988, 1990) for regions of the world that combine particularly high species richness, endemism and

Table 1. Data sources and characteristics. Numbers of records refer to the data matched to the 2435 cells in the region of Europe mapped in Fig. 1 from the *Atlas Florae Europaeae* 50 × 50 km grid. Endemic species are defined arbitrarily as species with their total range restricted to the area with records in Fig. 1. Narrowly endemic species are defined as the subset of endemic species that are recorded from eight or fewer of these grid cells.

Taxon	Source	No. of species	No. of species-in-grid-cell records	Median range size (no. of cells)	Percentage endemic species	Percentage narrowly endemic species
vascular plants	*Atlas Florae Europaeae* JALAS *et al.*, 1972-1996	2362	463,009	28	32	16
amphibians	*Societas Europaea Herpetologica* GASC *et al.*, 1997	58	17,094	79	57	17
reptiles	*Societas Europaea Herpetologica* GASC *et al.*, 1997	91	17,043	86	41	8
breeding birds	*European Bird Census Council* HAGEMEIJER & BLAIR, 1997	445	291,178	389	2	0.4
mammals	*Societas Europaea Mammalogica* MITCHELL-JONES *et al.*, 1999	187	80,724	187	4	0
total		3143	869,049	47	27	13

threat. However, hotspots have often been used in the sense of areas of highest total species richness, and often at the scale of continents or countries. To apply hotspots of (total) richness as an area-selection method, the most species-rich areas are selected (e.g. SCOTT *et al.*, 1987; PRENDERGAST, QUINN *et al.*, 1993; MITTERMEIER *et al.*, 1998; REID, 1998). Here we follow some earlier authors (e.g. PRENDERGAST, QUINN *et al.*, 1993) in choosing as a target 5% of the mapped area (122 grid cells) for a convenient illustration of the method, although any number of areas could be used. To apply hotspots of narrow endemism as an area-selection method based on OLDFIELD's (1998) 20,000 km² range-size criterion, we can begin by identifying the species with ranges restricted to eight grid cells or less, map richness in these species, and then select the 5% of areas with the highest richness (WILLIAMS *et al.* in DELBAERE, 1998).

There is another method that builds on the importance of endemism in order to represent even more of biodiversity. Hotspots of narrow endemism often represent more species than hotspots of richness, because the narrowly endemic species should differ more among areas. This pattern of difference

can be exploited most directly by using complementarity. In this context, complementary richness measures the degree to which an area contributes different and previously unrepresented species to a set of areas (VANE-WRIGHT *et al.*, 1991). For example, the (heuristic) area-selection rules introduced by MARGULES *et al.* (1988) begin by selecting the area richest in the most narrowly distributed (or endemic) species in the data, moving to progressively less rich areas (using complementarity), and then to less narrowly distributed species (Table 2). Two steps have been added to these rules by WILLIAMS *et al.* (in press): (1) a test to reject any areas that in hindsight are redundant to the goal of representing all species; and (2) a final re-ordering of selected areas by complementary richness. The second step is needed in order to find area sets that give nearly maximum biodiversity for any number of areas or for any level of investment (a trial of this procedure has shown that it is equal to or better than the most efficient of the other heuristic algorithms, see 'algorithm 8' in CSUTI *et al.*, 1997).

We need to be able to assess how well different methods of selecting areas perform at representing biodiversity in Europe (SMART, 1996). One approach is to compare the results of these methods with the consequences of choosing areas at random (e.g. REBELO & SIEGFRIED, 1992; WILLIAMS *et al.*, in press). To simulate choosing areas at random, the data were sampled 1000 times (without replacement), in order to estimate the number of species that we would expect to see represented by chance. An important refinement for maximum coverage sets is the need to move from a measure of absolute efficiency (PRESSEY & NICHOLLS, 1989) to one of relative efficiency. The problem is that the ease with which high absolute efficiency can be attained depends on patterns of species coincidence within the data, as shown by differences in the shape of species-accumulation curves as more areas are selected (VANE-WRIGHT *et al.*, 1991). To standardise comparisons against this effect, the relative efficiency of any set of n areas ($E_{\text{observed},n}$) can be expressed as the diversity of species represented relative to the upper and lower bounds of performance that would be expected for those particular data:

$$E_{\text{observed},n} = 100.(s_{\text{observed},n} - s_{\text{random},n}) / (s_{\text{maximum},n} - s_{\text{random},n})$$

where a lower bound is provided by the median species representation expected by chance ($s_{\text{random},n}$), and the upper bound is approximated by the species representation that can be achieved with the complementarity method ($s_{\text{maximum},n}$). Note that this index can take negative values. Alternatively, it would be possible to use the representation associated with the upper 5% tail of the simulated random distribution for the lower bound in order to make the

Table 2. A heuristic maximum-coverage algorithm from Williams *et al.* (in press). This is a set of rules for selecting a given number (n) of hotspots of complementary richness in order to provide a near-maximum coverage of species. In this context, 'areas' are grid cells, and the 'rarest species' is taken to be the one with the fewest grid-cell records.

Step	Rule
1	select all areas for species that are more restricted than the representation goal (for representing all species at least once, this means selecting all areas with unique species records)
2	the following rules are applied repeatedly until all species are represented -
	A select areas with the greatest complementary richness in just the rarest species (ignoring less rare species), if there are ties (areas with equal scores), then:
	B select areas among ties with the greatest complementary richness in the next-rarest species and so on, if there are persistent ties, then:
	C select areas among persistent ties with the lowest grid-cell number (this is an arbitrary rule, used rather than random choice among ties in order to ensure repeatability in tests; other criteria, such as proximity to previously selected cells, or number of records in surrounding cells, can be substituted)
	(repeat steps A-C until all species are represented)
3	identify and reject any areas that in hindsight are unnecessary to represent all species
4	repeat steps 1-3 for representing every species at least once, twice and so on, until the required number of areas, n, is attained or exceeded, disregarding the results of one iteration of steps 1-3 before moving on to the next
5	the following rules are applied repeatedly until all selected areas are re-ordered by complementary richness -
	a choose the previously selected area with the greatest complementary richness, then:
	b if before all areas are re-ordered the maximum complementary richness increment declines to 0, continue to re-order areas (step a above) after re-setting the cumulative richness to 0 but starting scoring complementary richness again from the current position on the area list (ignoring: previously re-ordered areas, species more restricted than the current multiple representation target, and species that are already represented the required number of times within a smaller number of areas) (repeat steps a-b until all previously selected areas are re-ordered)
6	choose the first n areas from the re-ordered area list

comparison relative to significantly higher representation than expected by chance (substituting $s_{p<0.05,n}$ for $s_{\text{random},n}$). The problem with this is that it would tie the measure to a particular probability level, which might make comparisons between studies difficult (although there may still be uncertainties in the estimates of $s_{\text{maximum},n}$ and $s_{\text{random},n}$). Instead, for our analysis the significance threshold is included by substituting the representation associated with the upper 5% tail ($s_{p<0.05,n}$) for ($s_{\text{observed},n}$) in the formula above, in order to calculate

a separate threshold efficiency ($E_{p<0.05,n}$) expected for n areas. For the upper bound, the results of heuristic complementarity methods provide an estimate of the maximum representation efficiency possible ($s_{maximum,n}$) (CHURCH *et al.*, 1996). The degree to which these heuristic methods are suboptimal is usually small (CSUTI *et al.*, 1997; PRESSEY *et al.*, 1997).

All of the procedures described here are automated within the WORLDMAP software for personal computers (WILLIAMS, 1996). This is a simple, specialised, geographic information system (GIS). Specialisation allows the analysis in this paper to be completed within a few minutes, so that many variations on a question can be explored interactively, and in the future, the results could be re-assessed routinely as new data become available.

Results

Distribution of diversity

Fig. 1 shows how combined species richness for the atlas records of vascular plants, amphibians, reptiles, breeding birds and mammals (total 3143 species) varies across the mapped area of Europe. Recorded diversity for these terrestrial groups is high in and around the mountains of central Europe (Pyrenees, Alps, Carpathians, Balkans (Stara mountains)), and low in both the north and the south of Europe.

Distribution of narrow endemism

Of the species in the plant and vertebrate atlases, approximately one quarter (847 species, 27%) are endemic to the area of Europe plotted in the main map (Fig. 2). Of these, approximately one half (402 species, 13%) are narrowly restricted to eight or fewer cells (Fig. 3). The percentages vary strongly among the atlas groups (Table 1) for both endemics (2-57%) and narrow endemics (0-17%). With the possible exception of plants and amphibians, these percentages are likely to be lower than for many invertebrate groups in Europe (DEHARVENG, 1998). Fig. 2 shows that richness in endemics is highest in the Pyrenees, Alps and Dalmatian mountains, is generally high in south-western Europe, and generally low in north-eastern Europe. Fig. 3 shows that areas rich in narrowly endemic plants and vertebrates by this definition are located much further to the south than are areas rich in overall diversity (Fig. 1). Areas of high narrow endemism for these species are concentrated particularly in the mountains of Greece and the Sierra Nevada, and on the islands of Majorca, Corsica, and Crete, with very few narrowly endemic species recorded from northern Europe.

Comparing hotspots of richness and narrow endemism

Fig. 4 shows that, whereas the top 5% hotspots of richness are concentrated in central Europe, the top 5% hotspots of narrow endemism (as defined here) are concentrated further south, around the Mediterranean. Therefore, the two sets of 122 hotspots are largely non-coincident, with only 30 grid cells (25%) held in common (this is unaffected by area flexibility: there are no alternatives for the 122 hotspots of richness and only two alternatives for one of 122 hotspots of narrow endemism, neither of which coincides with a hotspot of richness).

At first sight, the low match between hotspots of richness and of narrow endemism does not appear to support the assumption that widespread species tend to co-occur within hotspots with narrowly endemic species. However, 30/122 coincident cells is a high proportion when considered in the context of 2435 mapped cells. To test this, the narrowly endemic species were excluded from the data before recalculating hotspots of richness (with no detectable effect on the results). The hotspots for the two sets of species were found to be coincident significantly more frequently than would be expected by chance if the two sets of hotspots were distributed independently of one another ($G = 58, p < 0.001$).

A more direct assessment of the performance of the areas selected by the different methods is to compare the total numbers of species that they succeed in representing. The top 5% hotspots of richness include at least some representation of 63% of the 3143 plant and vertebrate species, and the hotspots of narrow endemism include at least some representation of 78% of these species. However, if the same number of areas were chosen at random, then the expected median representation would be 69%, and any representation above 72% would be greater than expected by chance ($p = 0.05$). Therefore, hotspots of richness fail to represent more species than expected by chance, whereas hotspots of narrow endemism perform significantly better.

Hotspots of complementary richness

Fig. 5 shows that hotspots of complementary richness are more broadly and evenly scattered across Europe than are either hotspots of (total) richness or hotspots of narrow endemism. Some complementary areas with unique species (within the area set) are irreplaceable. Other complementary areas have many alternative areas for the species they contain, so that there is plenty of flexibility for planners. For example, to represent every species in these data at least once requires a minimum of 247 grid cells, although the method used here estimates 2×10^{27} alternative sets of 247 fully representative areas. However, because both irreplaceable areas and all alternative fully flexible areas for these sets can be mapped simultaneously (not shown), it is possible to confirm that all of the 2×10^{27} sets are broadly scattered across Europe.

Therefore, the arbitrary choice of one particular area set for Fig. 5 is not misleading in showing such broadly scattered areas.

Hotspots of complementary richness perform better than either of the other methods, by representing 94% of the 3143 plant and vertebrate species in the same number (122, or 5%) of areas. This is significantly better than the maximum expected by chance (72%). Fig. 6 shows how the methods compare when choosing different numbers of areas from 1 to 122 grid cells. That the heuristic procedure in Table 2 gives only an approximation to the true optimum is shown by the hotspots of richness apparently narrowly exceeding the hotspots of complementary richness when only a single area is selected. A common limitation of heuristic procedures is that their relative efficiency depends in part on the particular data. Therefore, to provide a more reliable upper bound for Fig. 7, the representation by hotspots of complementary richness is taken from the maximum between the Table 2 procedure and another heuristic, simple greedy richness (e.g. VANE-WRIGHT *et al.*, 1991). Although area sequences from these methods cannot be combined or interchanged without re-calculation at each step, it is legitimate to choose the better solution for any particular number of areas. Fig. 7 then shows the standardised comparison of the results of the hotspots of richness and hotspots of narrow endemism, expressed relative to the boundaries of performance that would be expected with these particular data.

Discussion

Mapping diversity

The degree to which the combined atlas data are representative of all European biodiversity is unknown. They include all of the terrestrial vertebrates, but only about 20% of the vascular flora of Europe (LAHTI & LAMPINEN, 1999), and none of the more diverse invertebrates and microorganisms. If data on any other species were available from other sources for the same areas, then they could easily be incorporated into the database for assessment. We might expect that the broad variety of different ecological groups already included should help to ensure that the patterns obtained are representative of many other groups with similar ecology (e.g. PRENDERGAST, QUINN *et al.*, 1993; GASTON, 1996; WILLIAMS & GASTON, 1998). However, when data become available for invertebrates and for other plant families, such as umbellifers and composites, then the apparent relative richness of southern areas may be expected to increase.

The degree to which distribution data are representative of species' true distributions is a question that hangs over all mapping studies (e.g. GASTON, 1998). When interpreting the combined richness map in Fig. 1, two problems are particularly important to consider. First, for each group the recording effort may vary among different parts of Europe, which could produce trends in species richness that are artefacts of patterns in recording activity (e.g.

PRENDERGAST, WOOD *et al.*, 1993). In particular, many of the least abundant or most cryptic species (including some narrow endemics) may be recorded only in those areas that have been sampled most intensively (e.g. NELSON *et al.*, 1990). Second, recording effort may vary among species and among groups, causing some to be better known than others. This could also result in regional bias in the combined scores, if different groups have different regional distributions. Low apparent richness in some areas, particularly in the south and east, is known to be due in part to low recording effort (GASC *et al.*, 1997; HAGEMEIJER & BLAIR, 1997; LAHTI & LAMPINEN, 1999; MITCHELL-JONES *et al.*, 1999).

Data can be treated in a variety of ways to try to reduce the effects of small or uneven sample sizes. To begin, atlas data can be thought of as forming a table or matrix of species by areas. This table can be approached either by considering species lists for areas, or from the other direction, by considering the distributions of each species in turn. Taking the first approach, if the sampling effort could be measured in some way, then there are a range of techniques for estimating the 'total' (or at least a standardised) species richness of an area (e.g. COLWELL & CODDINGTON, 1994), or for comparing recorded species richness among areas (PRENDERGAST, WOOD *et al.*, 1993). The problem is that these techniques lose all information on the identities of which species are recorded where, without which endemism and complementarity cannot be measured. The second approach takes the form of modelling to estimate the expected distribution of each species. These techniques range from simple 'range filling' of maps, to statistical procedures using environment-response surfaces (e.g. AUSTIN & HEYLIGERS, 1991; BUSBY, 1991; CARPENTER *et al.*, 1993). An example that models distributions of plant species across Europe as a response to climate is described by HUNTLEY *et al.* (1995). A similar approach is now being explored using WORLDMAP (ARAÚJO & WILLIAMS, in press). If interpolated data were used in area selection, local surveys would become even more important, to verify the conservation value of these areas. Naturally, any study based on 50 × 50 km grid cells would need to be followed with more detailed studies of the biota and of factors such as social constraints at a local scale.

Nevertheless, despite some deficiencies in the data, atlas maps still present by far the best empirical summaries of species' distributions that are available to date.

Mapping endemism

Richness in endemic species (Fig. 2) shows a tendency to be lower in the east than in the west. Although not tested here, we believe this part of the pattern to be in part an artefact caused by the imposition of a biologically arbitrary eastern boundary on the mapped region. The most narrowly distributed species could occur almost anywhere within the mapped area, whereas broadly distributed species could only be recorded as endemic if they do not cross the artificial eastern boundary. This effectively excludes many of

the more broadly distributed species from the eastern part of the map, reducing apparent richness in endemics in the east. COLWELL & HURTT (1994) have described other kinds of richness patterns that result from similar, non-biological effects. This kind of artefact should be much less important when considering narrow endemics, because it may then only be apparent when very close to the eastern boundary.

Richness in narrow endemics is mapped in Fig. 3 using the threshold approach. This has been the most popular technique (e.g. ICBP, 1992) and is widely understood. However, it has several disadvantages. First, an absolute area threshold is scale-dependent. This can be overcome by using a consistent proportion of species by range size (GASTON, 1994), such as the rarest quartile (an example for Europe is mapped by HUMPHRIES *et al.*, 1999: fig. 7). Second, any choice of threshold must be arbitrary and in consequence is likely to exclude marginally more widespread species that are of particular value to some people (CROWE & SIEGFRIED, 1993). Third, no comparative information is presented for many of the grid cells.

If information were available on the global range sizes of all of the species, then it would become possible to address the problems of thresholds for narrow endemism by using alternative approaches, in which all species make some contribution. The simplest measure is to map the median range size among species for each grid cell (SMITH *et al.*, 1994). A disadvantage with this measure is that it is influenced as much by the widespread species as by the very restricted species. To concentrate on the more restricted species, a species' contribution can be weighted according to its range size. The most common form of weighting is to sum, for each grid cell, the inverse of the range sizes of all of the species present (an example for European plants, but using ranges measured only within Europe, is mapped by HUMPHRIES *et al.*, 1999: fig. 6). Arbitrariness (comparing with threshold approaches) is not entirely avoided, because it remains in the choice of formula for weighting (a few examples are listed in Table 3), and there is no obvious 'natural' choice (WILLIAMS, 1998). The greatest problem is that data on global range sizes are as yet unavailable for all of the species mapped here.

Table 3. Examples of measures of range-size rarity using continuous functions of range size. In effect, the relative weighting given to the most restricted species increases in the functions towards the bottom of the table. Range size is measured as the number of occupied cells (c_i) for species (i) in the grid. C is the total number of cells in the grid and S the total number of species. The score for a grid cell is the sum of the scores from all of the species recorded as present. Symbols have been changed from original references in order to standardise formulae.

Formula	Examples of authors
$\sum_{(i:\, c_i \neq 0,\, 1 \leq i \leq S)} (C - c_i)$	DANIELS *et al.*, 1991
$\sum_{(i:\, c_i \neq 0,\, 1 \leq i \leq S)} (1 / c_i)$	JEFFERSON, 1984; USHER, 1986; AVERY & LESLIE, 1990; WILLIAMS *et al.* 1996
$\sum_{(i:\, c_i \neq 0,\, 1 \leq i \leq S)} (1 / c_i^2)$	WILLIAMS, 1996

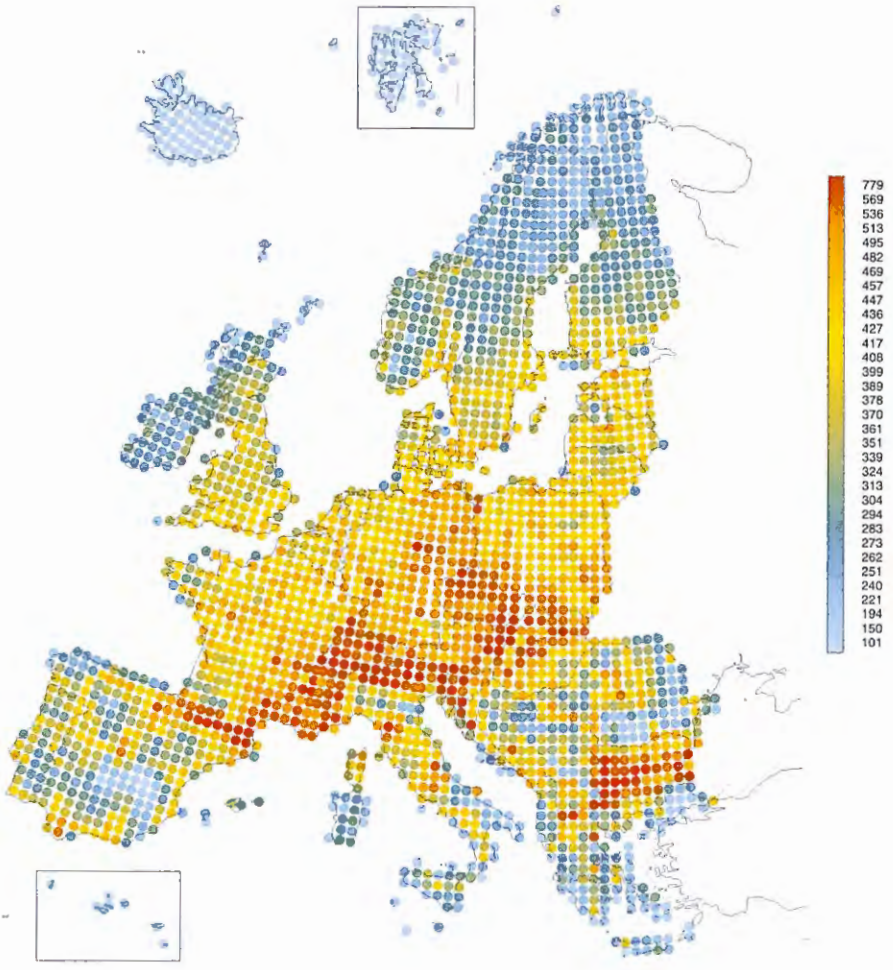


Fig. 1. Map of species richness. Plot of combined records from atlas data for vascular plants, amphibians, reptiles, breeding birds and mammals among 50 × 50 km grid cells (total 3143 species, 2435 grid cells). Species richness counts are divided into 33 colour-scale classes (shown right) of approximately equal size by numbers of grid cells, with maximum richness shown in red and minimum richness in light blue. This equal-frequency colour scale is used for comparability among maps. Svalbard and the Azores are shown displaced relative to the mainland and in boxes.

Hotspots in Europe

There have been few previous studies of hotspots in Europe, and most of the work that has been done is at much coarser spatial scales. This is important, because as STOMS (1994) has shown, apparent patterns of species richness can change dramatically when measured on grids of different sizes. This effect has inevitable consequences, not only for the distribution of hotspots of richness, but also for hotspots of narrow endemism and complementary richness, because all three depend on patterns of co-occupancy by species within areas of a particular size.

In their global reviews of hotspots, MYERS (1988, 1990) and ICBP (1992) listed none within the area of Europe mapped in Fig. 1, and MITTERMEIER *et al.* (1998) listed only the 'Mediterranean Basin.' Of more interest, AKEROYD & HEYWOOD (1994) listed 23 centres of plant diversity and endemism in greater detail within the region of Fig. 1, concentrated primarily in the mountains of south-eastern Spain, the Pyrenees, Alps, and Balkan peninsula. In a consistently quantitative analysis, GASTON & DAVID (1994) used equal-area cells of approximately 152,000 km² and found that most of the groups they looked at had hotspots of richness in the Pyrenees, Alps, Balkans and neighbouring areas. Despite the very much larger size of their grid cells, these results agree broadly with the maps in Figs 1-4. More recently, WCMC (1998) have produced a semi-quantitative map of 100 hotspots of widely varying size for the WWF European Forest team, using a mixture of information and criteria from the Dobris Assessment, BirdLife's Important Bird Areas database, CORINE Landcover and Biotopes Programmes, and the WWF European Programme (OLDFIELD, 1998). Of these 100 hotspots, 70 are broadly scattered within the region of Fig. 1. It would be useful to locate these areas on the 50 km grid in order to look for any particularly important areas that might be added, as a form of 'gap' analysis (see SCOTT *et al.* 1993).

Important Biodiversity Areas in Europe

For any practical implementation of conservation areas, we recognise that an analysis of priorities should require consideration of at least three other factors. First, detailed data will be needed at a local scale, more appropriate to management decisions (PRESSEY *et al.*, 1993; FREITAG *et al.*, 1996). This is likely to require consideration of candidate areas of very different shapes and sizes (polygons), a capability already supported by the methods used here. Second, it would require consideration of local viabilities of species, which are expected to be not the same for a species in all parts of its distribution. Third, it would need local threats to the survival of species to be taken into account (as well as other social and land use factors affecting the suitability of areas for selection, and their priority for conservation management). All of these factors, if quantified, could be accommodated by quantitative area-selection methods (reviewed by WILLIAMS, 1998; ARAÚJO & WILLIAMS, in press). In the meantime, we can begin to discern some patterns of biological value from the atlas data for the broad-scale distribution of terrestrial plants and vertebrates across Europe.

We have shown that choosing hotspots of richness is not always better than choosing areas at random (Figs 6-7), at least when selecting up to 5% of the total area for these data. Hotspots of narrow endemism perform better, but using hotspots of complementarity (which also depend on patterns of endemism and rarity) is distinctly and consistently the most efficient approach to area selection when we are forced to make choices. When selecting more than ten areas, the result of using complementarity is to increase species representation over the other two methods by nearly 20%. The ranking of the three methods with these European data is consistent with results from many other analyses, including those using other taxonomic groups, other regions, and other spatial scales (e.g. PRESSEY & NICHOLLS, 1989; WILLIAMS *et al.*, 1996; REID, 1998; ARAÚJO, 1999).

Some of the reasons for the differences in species representation we find from applying different criteria may be seen by looking at the geographical distribution of the top 5% of hotspots in Figs 4-5. The hotspots of richness are strongly clustered around the mountains of central Europe, where altitudinal zonation ensures that many different habitats with many different species occur within the same grid cells. However, clustered areas also tend to share many of the same species, which reduces the cumulative number of species represented. Consequently, many species are left unrepresented, particularly those from distant areas of the Iberian Peninsula, in the Arctic, and in south-eastern Europe. If instead, hotspots of richness were selected for each of the European countries separately, then this would increase the geographical coverage of areas, and with it the number of species (although using hotspots of complementary richness should always do better). The hotspots of narrow endemism are slightly less clustered, including for example areas further to the west in Spain and further to the east, next to the Black Sea (Fig. 4). Unfortunately, particularly many northern species remain unrepresented in these more southern areas. Unlike the hotspots of richness and narrow endemism, the hotspots of complementary richness are more widely scattered, which may be important politically, including cells in the Azores, Svalbard, Fennoscandia, central Europe and the Mediterranean islands (Fig. 5). The numbers of species remaining unrepresented by hotspots of complementary richness are lower, and these species are more evenly scattered across Europe.

Hotspots of richness and hotspots of narrow endemism remain biologically interesting, even though they are less efficient than hotspots of complementarity at representing the maximum biodiversity. Therefore, their use in area-selection may only be fully justified under a narrow range of circumstances. In particular, for hotspots of richness, these are situations where only the numbers of species in each area are known, without knowing the identities of species. For hotspots of narrow endemism, these are situations when only the numbers of narrowly distributed or narrowly endemic species are known, or when these are the only species that are valued.

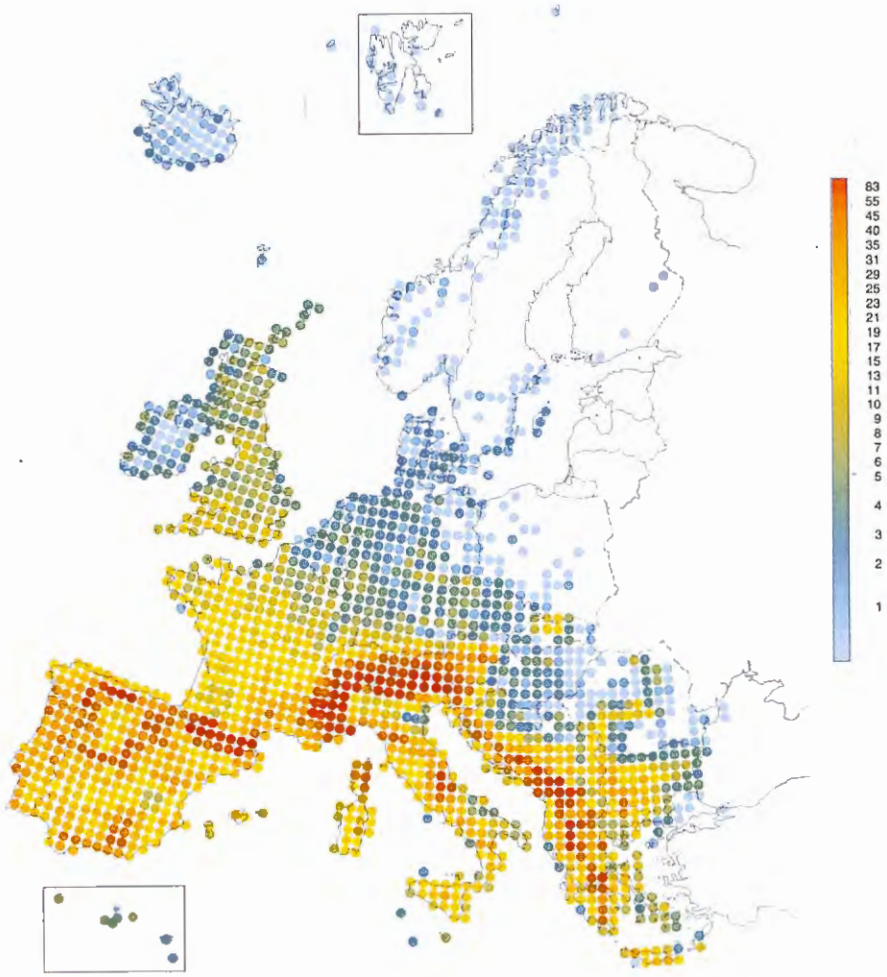


Fig. 2. Map of endemic species richness. Plot of richness in species restricted to the region of Europe with records in Fig. 1, from combined atlas data for vascular plants, amphibians, reptiles, breeding birds and mammals among 50 × 50 km grid cells (total 847 species). Colour scale as for Fig. 1.

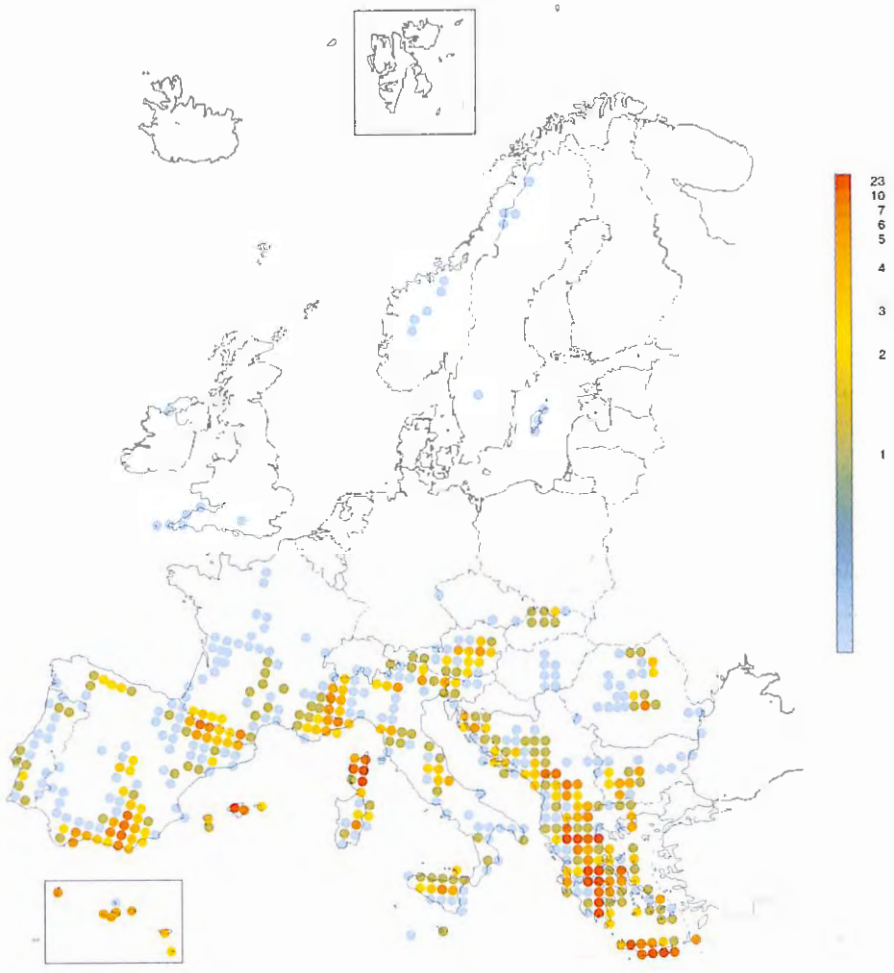
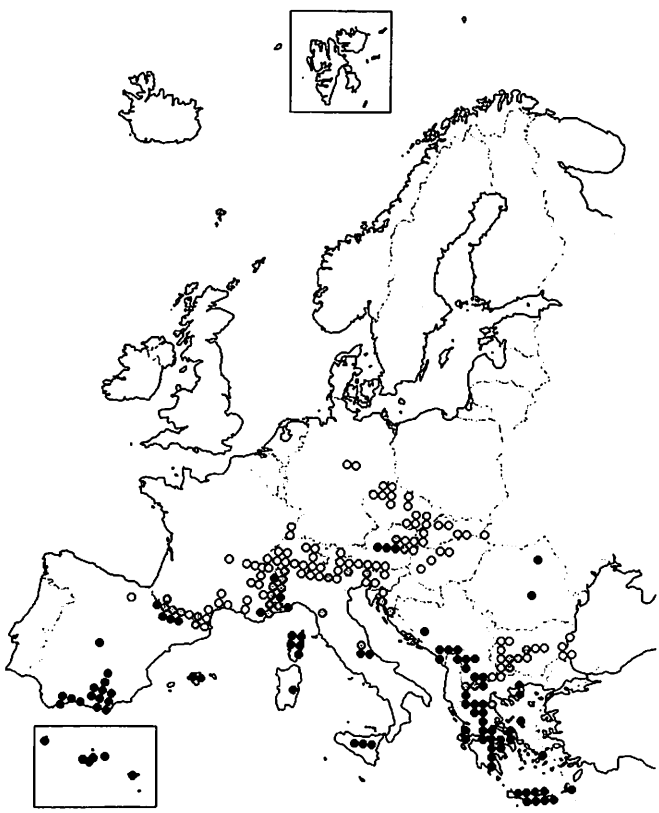


Fig. 3. Map of narrowly endemic species richness. Plot of those species with 8 or fewer grid-cell records and restricted also to the region of Europe with records in Fig. 1, from combined atlas data for vascular plants, amphibians, reptiles, breeding birds and mammals among 50 × 50 km grid cells (total 402 species). Colour scale as for Fig. 1.

Representation of a broad variety of habitat types (e.g. CEC, 1989) and biotic provinces (e.g. UDVARDY, 1975) is a concern for many conservationists. For example, selecting hotspots of complementary richness achieves a higher representation of the Natura 2000 biogeographic provinces (Fig. 8). This occurs because hotspots of complementary richness are used to seek the largest numbers of different species for each included area, and these different

species tend to occur in different habitats and in different biogeographic provinces. If required, habitats and provinces could be entered into the analysis explicitly as area attributes for representation in place of species, or possibly even alongside them. The advantage of this kind of approach would be to place much of the knowledge of unique local features and conditions into a Europe-wide context for explicit and accountable assessment.

A third level of biodiversity that is often valued is genetic diversity. There may be concern that hotspots of complementarity will fail to recognise important areas for representing aspects of variation below the rank of species. Representation at this level can be ensured by including different populations or genotypes (when known) as separate entities for representation.



Hotspots of ●narrow endemism, ●narrow endemism & richness, Orichness

Fig. 4. Top 5% hotspots of richness and of narrow endemism. Hotspots of richness (open circles) are 122 areas with the highest numbers of species from Fig. 1. Hotspots of narrow endemism (black spots) are 122 areas with the highest numbers of species from Fig. 3. Grey spots are areas in both sets. Each area is a grid cell measuring approximately 50 × 50 km.

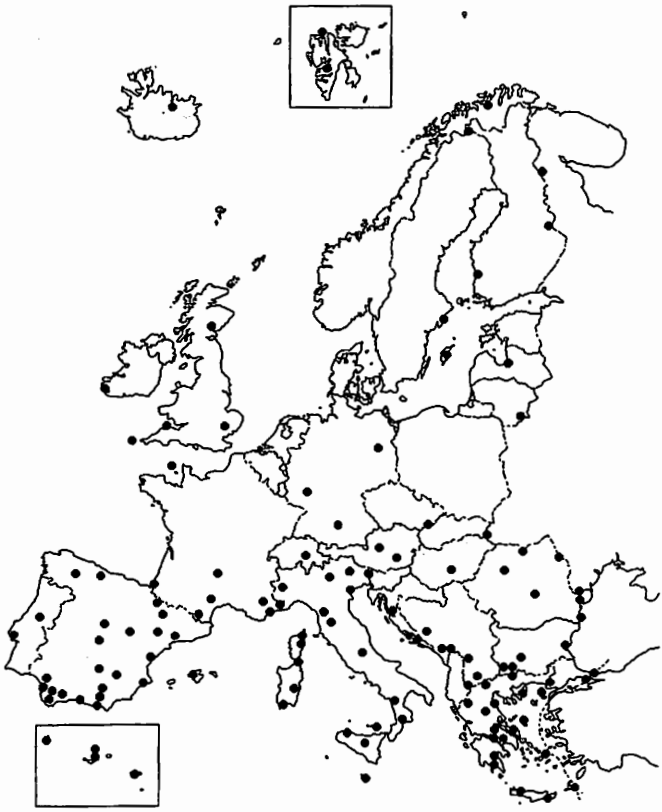


Fig. 5. Top 5% hotspots of complementary richness. Hotspots of complementary richness (black spots) are 122 areas selected using the rules in Table 2 (this is one of many possible such sets). Each area is a grid cell measuring approximately 50 × 50 km.

Complementarity is particularly well suited to 'gap analysis'. In its broadest sense, gap analysis is any method used to answer questions of the form 'what is the best way to complement a set of existing conservation areas?' (SCOTT *et al.*, 1993). This kind of problem has begun to be tackled in Europe by using hotspots of complementary richness (CASTRO PARGA *et al.*, 1996; ARAÚJO, 1999), and the complementarity approach has already helped to influence the establishment of one new protected area in the Sierra Nevada of Spain (MORENO *et al.*, 1998). Much could be done to maximise conservation of European biodiversity if biologists and planners were to use quantitative methods. This can be achieved by implementing complementarity-based rules (e.g. Table 2) within geographical information systems (GIS), as in WORLDMAP. Conservationists could then focus on the 'gaps' in the coverage of organisms that are left beyond existing conservation measures.

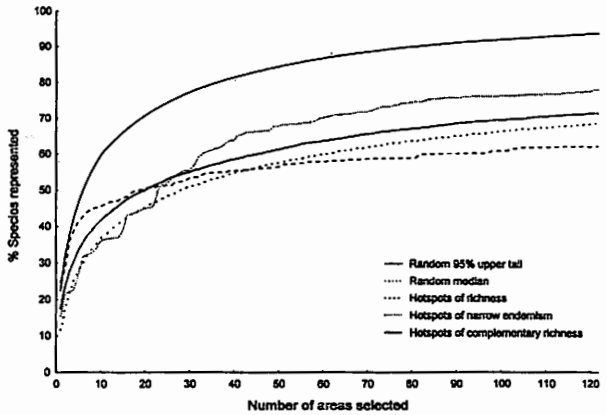


Fig. 6. Cumulative percentage of all recorded plant and vertebrate species represented within increasing numbers of areas selected by three quantitative methods and by choosing areas at random. Hotspots of richness (dashed black line) are areas with the highest numbers of species from Fig. 1. Hotspots of narrow endemism (dotted black line) are areas with the highest numbers of species from Fig. 3. Hotspots of complementary richness (solid black line) are areas selected using the rules in Table 2. Scores above the solid grey line are significantly better than expected when choosing areas at random (the percentage threshold score to the top 5% within 1000 randomly drawn scores). Each area is a grid cell measuring approximately 50 × 50 km.

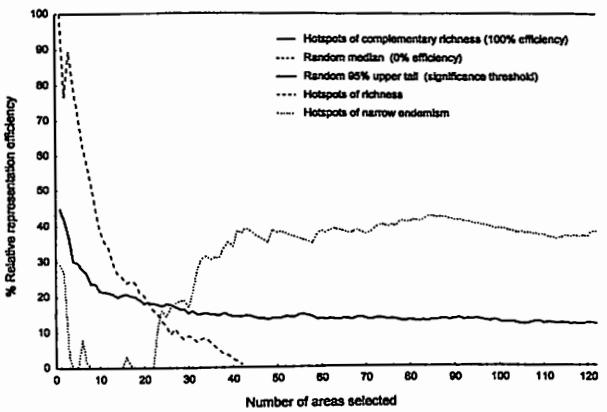


Fig. 7. Relative efficiency of species representation for hotspots of richness and hotspots of narrow endemism among all recorded plant and vertebrate species. This is a transformation of the results in Fig. 6, re-scaled between an estimate of the maximum that can be achieved (from hotspots of complementary richness), and the median representation expected from selecting areas at random (relative representation efficiency $E_{observed,n} = 100.(s_{observed,n} - s_{random,n}) / (s_{maximum,n} - s_{random,n})$). Scores above the solid grey line are significantly better than expected when choosing areas at random (the percentage threshold score to the top 5% within 1000 randomly drawn scores). Each area is a grid cell measuring approximately 50 × 50 km.

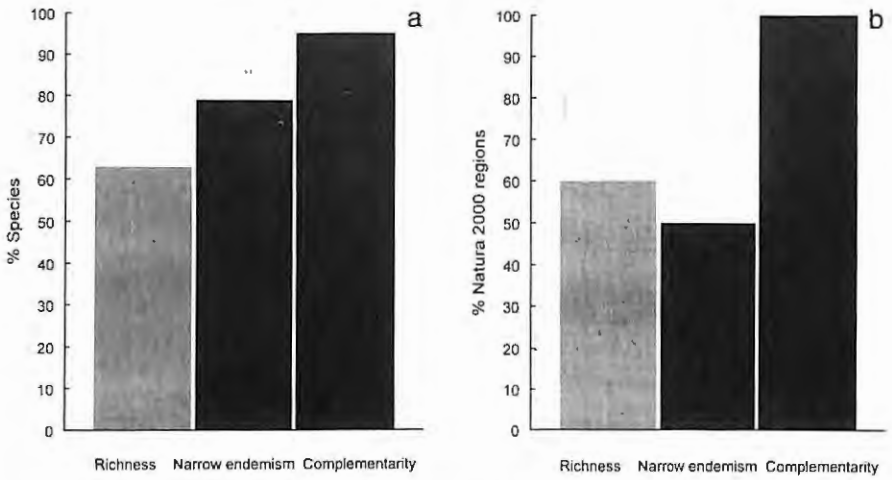


Fig. 8. Consequences of selecting 5% of areas by each of three quantitative methods (hotspots of richness and hotspots of narrow endemism from Fig. 4; hotspots of complementary richness from Fig. 5) for representing the diversity of: (a) species of plants and vertebrates from Fig. 1; and (b) biogeographical regions from the extended Biogeographical Regions map of Natura 2000 (CE, 1997b) (excluding the Anatolian region, which does not extend to the region mapped here).

Conclusions

(1) Atlas data permit direct assessment of provisional criteria for selecting important areas for biodiversity based on species. Although only part of the biota is mapped to date (even at the relatively coarse scale of the 50 × 50 km grid), in principle any further information on any taxa could be included when it becomes available.

(2) WORLDMAP provides an example of an interactive system for assessing the criteria used to select important areas for biodiversity, and for assessing the consequences of selecting particular areas. The explicit, quantitative approach provides rigour and accountability.

(3) The preliminary assessment in this paper shows that selection of areas by the criterion of exceptional richness may, on its own, be no better for conserving biodiversity in Europe than choosing areas at random. Hotspots of narrow endemism perform significantly better, but the most biodiversity, whether assessed at the level of species or at the level of Natura 2000 biogeographic provinces, is represented by choosing hotspots of complementary richness.

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References

AKEROYD J.R. & HEYWOOD V.H., 1994. - Regional overview: Europe. Pages 39-54. *In: Centres of plant diversity.* S.D. DAVIS, V.H. HEYWOOD & A.C. HAMILTON (eds). IUCN, Cambridge.

ARAÚJO M.B., 1999. - Distribution patterns of biodiversity and the design of a representative reserve network in Portugal. *Diversity and Distributions*, 5 : 151-163.

ARAÚJO M.B. & WILLIAMS P.H., in press. - Selecting areas for species persistence from occurrence data. *Biological Conservation.*

AUSTIN M.P. & HEYLIGERS P.C., 1991. - New approach to vegetation survey design: gradsect sampling. Pages 31-36. *In: Nature conservation: cost effective biological surveys and data analysis.* C.R. MARGULES & M.P. AUSTIN (eds). CSIRO, Melbourne.

AVERY M. & LESLIE R., 1990. - *Birds and forestry.* Poyser, London.

BUSBY J.R., 1991. - BIOCLIM - a bioclimatic analysis and prediction system. Pages 64-68. *In: Nature conservation: cost effective biological surveys and data analysis.* C.R. MARGULES & M.P. AUSTIN (eds). CSIRO, Melbourne.

CARPENTER G., GILLISON A.N. & WINTER J., 1993. - DOMAIN: a flexible modelling procedure for mapping potential distributions of plants and animals. *Biodiversity and Conservation*, 2: 667-680.

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. *Botanical Journal of the Linnean Society*, 121: 189-206.

CHURCH R.L., STOMS D.M. & DAVIS F.W., 1996. - Reserve selection as a maximal covering location problem. *Biological Conservation*, 76: 105-112.

COLWELL R.K. & CODDINGTON J.A., 1994. - Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society* (B), 345: 101-118.

COLWELL R.K. & HURTT G.C., 1994. - Nonbiological gradients in species richness and a spurious Rapoport Effect. *American Naturalist*, 144: 570-595.

COMMISSION OF THE EUROPEAN COMMUNITIES, 1989. - *CORINE database and manual version 2.2.* KUL University, Brussels.

COUNCIL OF EUROPE, 1997a. - *The EMERALD Network - a network of areas of special conservation interest for Europe.* Council of Europe, Strasbourg.

COUNCIL OF EUROPE, 1997b. - *Extension of the biogeographical regions map of Natura 2000 to pan-Europe, in the framework of the Emerald network of Areas of Special Conservation Interest.* Council of Europe, Strasbourg.

CROWE T.M. & SIEGFRIED W.R., 1993. - Conserving Africa's biodiversity: stagnation versus innovation. *South African Journal of Science*, 89: 208-210.

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. *Biological Conservation*, 80: 83-97.

DANIELS R.J.R., HEGDE M., JOSHI N.V. & GADGIL M., 1991. - Assigning conservation value: a case study from India. *Conservation Biology*, 5: 464-475.

DEHARVENG L. (ed.), 1998. - *Endemism. Final report of the programme on High Endemism Areas, Endemic Biota and the Conservation of Biodiversity in Western Europe.* Laboratoire d'Ecologie Terrestre, Toulouse.

DELBAERE B.C.W. (ed.), 1998. - *Facts & figures on Europe's biodiversity. State and trends 1998-1999.* ECNC Technical Report Series. European Centre for Nature Conservation, Tilburg.

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 and Conservation*, 5: 685-698.

GASC J.-P., CABELA A., CRNOBRNJA-ISAILOVIC J., DOLMEN D., GROSSENBACHER K., HAFFNER P., LESCURE J., MARTENS H., MARTÍNEZ RICA J.P., MAURIN H., OLIVEIRA M.E., SOFIANIDOU T.S., VEITH M. & ZUIDERWIJK A. (eds), 1997. - *Atlas of amphibians and reptiles in Europe.* Societas Europaea Herpetologica & Muséum National d'Histoire Naturelle, Paris.

GASTON K.J., 1994. - *Rarity.* Chapman & Hall, London.

GASTON K.J., 1996. - Biodiversity - congruence. *Progress in Physical Geography*, 20: 105-112.

GASTON K.J., 1998. - Biodiversity - the road to an atlas. *Progress in Physical Geography*, 22: 269-281.

GASTON K.J. & DAVID R., 1994. - Hotspots across Europe. *Biodiversity Letters*, 2: 108-116.

GENTRY A., 1986. - Endemism in tropical versus temperate plant communities. Pages 153-181. *In: Conservation biology, the science of scarcity and diversity.* M. SOULÉ (ed.). Sinauer, Sunderland, Massachusetts.

HAGEMEIJER W.J.M. & BLAIR M.J. (eds), 1997. - *The EBCC atlas of European breeding birds, their distribution and abundance.* Poyser, London.

HEATH, M.F., PAYNE, A.J. & EVANS, M.I. (in press). - *Important Bird Areas in Europe.* BirdLife International, Cambridge.

HUMPHRIES C., ARAÚJO M., WILLIAMS P., LAMPINEN R., LAHTI T. & UOTILA P., 1999. - Plant diversity in Europe: Atlas Florae Europaeae and WORLDMAP. *Acta Botanica Fennica*, 162: 11-21.

HUNTLEY B., BERRY P.M., CRAMER W. & MCDONALD A.P., 1995. - Modelling present and potential future ranges of some European higher plants using climate response surfaces. *Journal of Biogeography*, 22: 967-1001.

INTERNATIONAL COUNCIL FOR BIRD PRESERVATION, 1992. - *Putting biodiversity on the map: priority areas for global conservation.* International Council for Bird Preservation, Cambridge.

JALAS J. & SUOMINEN J. (eds), 1972, 1973, 1976, 1979, 1980, 1983, 1986, 1989, 1991, 1994. - *Atlas Florae Europaeae.* Vols 1-10. The Committee for Mapping the Flora of Europe & Societas Biologica Fennica Vanamo, Helsinki.

JALAS J., SUOMINEN J. & LAMPINEN R. (eds), 1996. - *Atlas Florae Europaeae.* Vol. 11. The Committee for Mapping the Flora of Europe and Societas Biologica Fennica Vanamo, Helsinki.

JEFFERSON R.G., 1984. - Quarries and wildlife conservation in the Yorkshire Wolds, England. *Biological Conservation*, 29: 363-380.

JOHNSON L.N., 1998. - Species extinction and the relationship between distribution and abundance. *Nature*, London, 394: 272-274.

LAHTI T. & LAMPINEN R., 1999. - From dot maps to bitmaps: Atlas Florae Europaeae goes digital. *Acta Botanica Fennica*, 162: 5-9.

MARGULES C.R., NICHOLLS A.O. & PRESSEY R.L., 1988. - Selecting networks of reserves to maximise biological diversity. *Biological Conservation*, 43: 63-76.

MITCHELL-JONES A.J., AMORI G., BOGDANOWICZ W., KRYŠTUFEK B., REIJNDERS P.J.H., SPITZENBERGER F., STUBBE M., THISSEN J.B.M., VOHRALÍK V. & ZIMA J., 1999. - *Atlas of European Mammals*. Academic Press, London.

MITTERMEIER R.A., MYERS N., THOMSEN J.B., DA FONSECA G.A.B. & OLIVIERI S., 1998. - Global biodiversity hotspots and major tropical wilderness areas. *Conservation Biology*, 12: 516-520.

MORENO J.C., CASTRO I., HUMPHRIES C.J. & WILLIAMS P.H., 1998. - Conservación de la biodiversidad en la Península y Baleares: ¿qué hacer a partir de los datos florísticos? *Quercus*, 144: 19-22.

MYERS N., 1988. - Threatened biotas: "hot spots" in tropical forests. *Environmentalist*, 8: 187-208.

MYERS N., 1990. - The biodiversity challenge: expanded hot-spots analysis. *Environmentalist*, 10: 243-256.

NELSON B.W., FERREIRA C.A.C., DA SILVA M.F. & KAWASAKI M.L., 1990. - Endemism centres, refugia and botanical collection density in Brazilian Amazonia. *Nature*, London, 345: 714-716.

NORTON B.G., 1994. - On what we should save: the role of culture in determining conservation targets. Pages 23-39. *In: Systematics and conservation evaluation.* P.L. FOREY, C.J. HUMPHRIES, & R.I. VANE-WRIGHT (eds). Oxford University Press, Oxford.

OLDFIELD S., 1998. - *Criteria, methodology and information requirements for the selection of the Important Plant Areas of Europe.* Discussion paper for *Planta Europa* Workshop on Important Plant Areas of Europe, 29-30 January 1998, Cambridge. Plantlife, London.

OWEN J., 1991. - *The ecology of a garden: the first fifteen years.* Cambridge University Press, Cambridge.

PRENDERGAST J.R., QUINN R.M., LAWTON J.H., EVERSHAM B.C. & GIBBONS D.W., 1993. - Rare species, the co-incidence of diversity hotspots and conservation strategies. *Nature*, London, 365: 335-337.

PRENDERGAST J.R., WOOD S.N., LAWTON J.H. & EVERSHAM B.C., 1993. - Correcting for variation in recording effort in analyses of diversity hotspots. *Biodiversity Letters*, 1: 39-53.

PRESSEY R.L., HUMPHRIES C.J., MARGULES C.R., VANE-WRIGHT R.I. & WILLIAMS P.H., 1993. - Beyond opportunism: key principles for systematic reserve selection. *Trends in Ecology and Evolution*, 8: 124-128.

PRESSEY R.L., & NICHOLLS, A.O., 1989. - Efficiency in conservation evaluation: scoring versus iterative approaches. *Biological Conservation*, 50: 199-218.

PRESSEY R.L., POSSINGHAM H.P. & MARGULES C.R., 1997. - Optimality in reserve selection algorithms: when does it matter and how much? *Biological Conservation*, 76: 259-267.

RABINOWITZ D., 1981. - Seven forms of rarity. Pages 205-217. *In: The biological aspects of rare plant conservation.* H. SYNGE (ed.). Wiley, New York.

REBELO, A.G. & 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 Biology*, 6: 243-252.

REID W.V., 1998. - Biodiversity hotspots. *Trends in Ecology and Evolution*, 13: 275-280.

ROEKAERTS M., CONDÉ S., DA COSTA H., HAGEMEIJER W., LAHTI T., LAMPINEN R. & THISSEN J., (in preparation). - Proposal for a common European Chorological Grid System (CGRS). Report to the European Environment Agency, Copenhagen.

SÆTERSDAL M., LINE J.M. & BIRKS H.J.B., 1993. - How to maximize biological diversity in nature reserve selection: vascular plants and breeding birds in deciduous woodlands, western Norway. *Biological Conservation*, 66: 131-138.

SCOTT J.M., CSUTI B., JACOBI J.D. & ESTES J.E., 1987. - Species richness. A geographic approach to protecting future biological diversity. *BioScience*, 37: 782-788.

SCOTT J.M., DAVIS F., CSUTI B., NOSS R., BUTTERFIELD B., GROVES C., ANDERSON H., CAICCO S., D'ERCHIA F., EDWARDS JR T.C., ULLIMAN J. & WRIGHT R.G., 1993. - Gap Analysis: a geographic approach to protection of biological diversity. *Wildlife Monographs*, No. 123: 1-41.

SMART J., 1996. - The need to identify Important Plant Areas in Europe. Pages 226-228. *In: Planta Europa.* Proceedings of the First European Conference on the Conservation of Wild Plants, 2-8 September 1995, Hyères. J. NEWTON (ed.). Plantlife, London.

SMITH F.D.M., MAY, R.M. & HARVEY, P.H., 1994. - Geographical ranges of Australian mammals. *Journal of Animal Ecology*, 63: 441-450.

STOMS D.M., 1994. - Scale dependence of species richness maps. *Professional Geographer*, 46: 346-358.

TERBORGH J. & WINTER B., 1983. - A method for siting parks and reserves with special reference to Colombia and Ecuador. *Biological Conservation*, 27: 45-58.

UDVARDY M.D.F., 1975. - *A classification of the biogeographical provinces of the world.* IUCN occasional paper no. 18. IUCN, Morges.

USHER M.B., 1986. - Wildlife conservation evaluation: attributes, criteria and values. Pages 3-44. *In: Wildlife conservation evaluation.* M.B. USHER (ed.). Chapman & Hall, London.

VANE-WRIGHT R.I., HUMPHRIES C.J. & WILLIAMS P.H., 1991. - What to protect? - Systematics and the agony of choice. *Biological Conservation*, 55: 235-254.

WILLIAMS P.H., 1996. - WORLDMAP 4 WINDOWS: software and help document 4.1. Distributed privately, London & http://www.nhm.ac.uk/science/projects/worldmap.

WILLIAMS P.H., 1998. - Key sites for conservation: area-selection methods for biodiversity. Pages 211-249. *In: Conservation in a changing world.* G.M. MACE, A. BALMFORD & J.R. GINSBERG (eds). Cambridge University Press, Cambridge.

WILLIAMS P., BURGESS N. & RAHBEK C., (in press). - Flagship species, ecological complementarity, and conserving the diversity of mammals and birds in sub-Saharan Africa. *Animal Conservation.*

WILLIAMS P.H. & GASTON K.J., 1998. - Biodiversity indicators: graphical techniques, smoothing and searching for what makes relationships work. *Ecography*, 21: 551-560.

WILLIAMS P.H., GASTON K.J. & HUMPHRIES C.J., 1997. - Mapping biodiversity value world-wide: combining higher-taxon richness from different groups. *Proceedings of the Royal Society (B)*, 264: 141-148.

WILLIAMS P., GIBBONS D., MARGULES C., REBELO A., HUMPHRIES C. & PRESSEY R., 1996. - A comparison of richness hotspots, rarity hotspots and complementary areas for conserving diversity using British birds. *Conservation Biology*, 10: 155-174.

WOLTERS, R. & BOUWMA I., 1998. - Stepping stones towards the future. *European Nature*, 1: 6-8.

WORLD CONSERVATION MONITORING CENTRE, 1998. - Forest hotspots in Europe. WCMC, Cambridge & http://www.wcmc.org.uk/forest/hotspots.htm.