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The relevance of systematics in choosing priority areas for global conservation

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Summary

While some researchers suggest that higher taxon richness be used for setting conservation priorities, others claim that even data on 'accepted species' are inadequate, and that documentation of the finest patterns of differentiation is needed. The significance of taxonomic resolution was assessed using distributional data for 798 Andean bird species, which were recorded in 15′ × 15′ grid cells. This dataset was used because of the fine spatial resolution and the complex biogeographic patterns in this region. The primary database served as a template for creating three new databases, namely for genera, broadly defined biospecies and phylogenetic species. With this spatial resolution, the taxic richness 'hotspots' were roughly the same on all taxonomic levels, but the ratio between generic and species richness increased towards the biologically-poor high plateaus. Richness 'hotspots' covered only a small fraction of the endangered species. 'Hotspots of endemism' provided better guidance, and complementarity was decidedly best, but with generic data neither of these approaches were effective. On the other hand, the recognition of phylogenetic species revealed few new areas of endemism which were not also apparent using 'accepted' species. The analyses drew attention to aggregates of endemic species which are often sited in areas immediately adjacent to areas with dense human populations, possibly because traditional human settlements relied on ecoclimatic conditions which also determined the peaks of endemism. Since data are available for some taxonomic groups for detailed analysis of species data, there is little reason to base the conservation planning on coarser surrogates.

Keywords: conservation priorities, systematics, 'hotspots', endemism, endangered species, South America, birds

Introduction

Actions to conserve biodiversity often conflict with human short or long-term interests, so it is essential to allocate land between conservation and development in the most effective way. Identification of priority sites for conservation requires good data about how the biodiversity involved is distributed. However, urgency and prohibitive costs of complete biodiversity inventories will force researchers and managers to search for compromises between complete accuracy and the use of proxy data.

Recent efforts to establish global conservation priorities have used endemic bird areas (ICBP 1992; Stattersfield *et al.* 1998), ecoregions (Olsen & Dinerstein 1998) and botanical 'hotspot' approaches (Myers 1990; Mittermeier *et al.* 1998). The two latter kinds of priority areas especially are substantial in size, so the precision and effectiveness are low. In reality, diversity hotspots and the threats towards them are often highly localized (Reid 1998), so conservation actions need to be precisely targeted. This in turn requires detailed distributional data and effective and flexible analytic algorithms (Church *et al.* 1996; Pressey *et al.* 1996; Williams 1999).

Data are indeed available for precise priority analysis for large parts of the world (e.g. Williams *et al.* 1999 for the European fauna; Burgess *et al.* 1997 and Williams *et al.* in press for African vertebrates; Fjeldså & Rahbek 1999 for South American birds). Several other studies are in progress.

Usually, an 'accepted' species level taxonomy is used. However, because of the amount of work involved, and incomplete and confused taxonomies even for higher vertebrates (Patterson 1996), several researchers have suggested the use of higher taxon richness (genera, families) for a shortcut (e.g. Prance 1994; Williams & Gaston 1994; Williams *et al.* 1994, 1997; Balmford *et al.* 1996*a*). However, most such studies use a very coarse geographical resolution and are concerned with richness patterns rather than the more efficient complementarity approach (except Balmford *et al.* 1996*b*). Others claim that the 'right' pattern for describing biological diversification, and for targeting conservation actions, will not emerge unless the smallest diagnosable evolutionary units are mapped (e.g. Daugherty & Triggs 1990; Cracraft 1992; Crowe & Brooke 1993 reviewing ICBP 1992). The widespread use of a broad (Mayrian) biospecies concept admittedly translates into a lack of conservation actions for distinctive forms which were disregarded as 'just subspecies' (Hazevoet 1996). Many conservationists now define management units using molecular markers (see Avise 1989; Moritz 1994), which may reveal deep phylogeo-

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graphic partitions of accepted species (Arctander *et al.* 1996) and processes relating to population viability (Loeschcke *et al.* 1994).

The viewpoints about the 'right' taxonomic level for conservation priority analysis are far apart, so we need to examine how much this matters. We may assume, *a priori*, that the most precise biosystematic information gives the best decisions. In a 'crisis discipline' such as conservation biology, we also need to consider what is feasible, what is too crude to be useful, and what is unnecessarily detailed.

I will explore here to what extent the effectiveness for conservation planning is influenced by the level of systematic resolution. Since the value of higher taxon richness has been discussed elsewhere, albeit mainly on a very coarse spatial scale, I will pay more attention to what can be achieved by recognizing the smallest diagnosable units. This is particularly relevant since the data-gathering effort is essentially the same, whether we record these separately or combine them in broad biospecies.

The analysis will be done for a tropical region characterized by complex biogeographic patterns, namely the tropical Andes region. I used bird data because of the detailed distributional data and large literature dealing with the different taxonomic opinions on these animals. I used one primary distributional database (Fjeldså *et al.* 1999*b*) as a template for creating three new databases which differ in taxonomic resolution but not in spatial scale. In this way, the consequences of taxonomic decisions could be determined explicitly.

Methods

Computer software and analytic tools

Computer programmes have been developed for automated analyses that accommodate distribution data for large numbers of species and provide gridded maps showing various taxic diversity measures. I used the WORLDMAP software (P.H. Williams, ongoing personal communication), a PC-based graphical tool designed for fast, interactive handling of distributional data for large numbers of taxa. The following functions were used: (1) 'richness', expressed as numbers of taxa per grid cell, and (2) endemism, expressed as inverse range-size, either the sum of inverse range-sizes for all taxa present in a grid cell ('range-size rarity' hereafter), or the mean value per taxon ('mean range-size rarity'). The latter measure may be biased towards isolated and biologically poor areas, and is therefore sensitive to presence or absence of single taxa of very localized distribution.

Effective site-selection must, in addition to taxic richness, take into account the complementarity among sites. 'Near-minimum sets' of areas are determined using a heuristic search option for complementarity of areas and a redundancy back-check. Complementarity explicitly describes the degree to which an area contributes otherwise unrepresented taxa to a set of areas (Humphries *et al.* 1996; Pressey *et al.* 1996; Williams 1999). A minimum set is the smallest number of grid cells which covers all taxa; however, additional information, for example about population viability and costs, is needed to form a definite conservation plan.

The effectiveness of different kinds of priority areas was assessed by pre-selecting these areas in the database with the finest taxonomic resolution to see how many populations were covered. I also examined how well the different 'conservation plans' covered the 78 species which are listed as endangered and vulnerable (Collar *et al.* 1994).

Distribution data

Distributional data were compiled for 789 'accepted' species of birds breeding in the highlands (the 'temperate zone', in most districts corresponding to land above 2500 m) of the tropical Andes region (Fig. 1). I focused on the highland avifauna since it is known in much greater detail than that of the tropical foothills and lowlands. The highlands are also

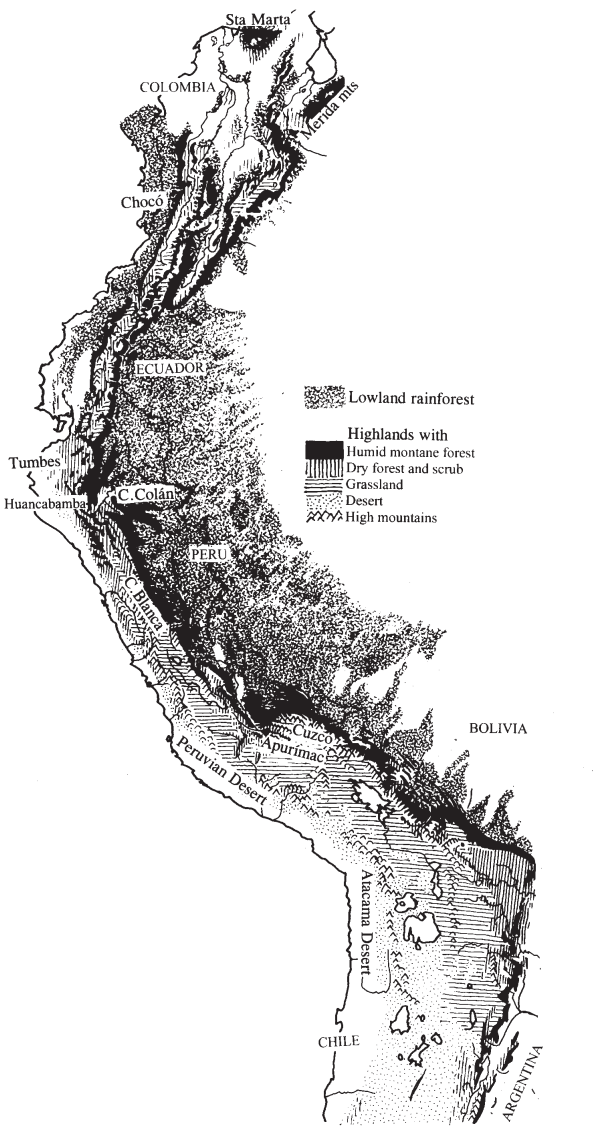


Figure 1 Map of the study region with the main life zones and geographical names mentioned in the text.

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characterized by some distinctive biogeographic patterns with marked local peaks of endemism and some areas that are biologically very uniform. The data compiled for the *Birds of the High Andes* (Fjeldså & Krabbe 1990) were supplemented with recent surveys to fill in gaps (e.g. Fjeldså & Kessler 1996; Fjeldså *et al.* 1999*a*), standard effort studies (e.g. Poulsen & Krabbe 1997), working maps prepared by R.S. Ridgely and W.L. Brown for *The Birds of South America* (Ridgely & Tudor 1989, 1994), all records of rare or endangered South American birds in the databases of BirdLife International (Collar *et al.* 1992; Wege & Long 1995) and data from numerous recent trip reports and personal communications.

The data were entered into a geographical projection grid of 0.25° (729 km^2 at the equator), a compromise between sampling unevenness and the need for a resolution which is fine enough for conservation planning. This is probably the finest geographical resolution permissible for a tropical region using data available today. In order to reduce the sampling bias, range maps were made by interpolation within areas of uniform macrohabitat. Assuming some connectivity of populations and possibilities for recolonization where there is suitable habitat between the collecting points, I considered this to be a realistic approach. The existence of suitable habitat in the individual grid cells was determined using numerous topographic and ecological maps and satellite imagery (e.g. Mapas planimetrico de imagines de satelite 1:250 000 for Peru [Republica del Peru 1984], LANDSAT scenes and GIS data available on the Internet). The interpolation was conservative and distribution gaps were included where a species was un-recorded in a well-researched site with appropriate macrohabitats. Examples of species maps are shown in García-Moreno *et al.* (1998).

The estimate of range-size rarity required that I include the global distribution of a taxon. In practice, species which inhabit hundreds or thousands of cells will contribute very little to the total rarity score. To secure a reasonably accurate endemism scoring, I therefore included extensive adjacent lowland areas in the database (with coarse range-maps). The southern cut-off limit was in an arid and species-poor region, and it did not create substantial artefacts.

Three new databases were created by copying the original database, defining new taxon identification cards and then moving the original records between these cards as appropriate, and finally deleting cards which had been made obsolete in the process. The new databases were:

(1) Split. There is no consistent classification of the smallest diagnosable clusters of individual birds within which there is a parental pattern of ancestry and descent (Cracraft 1983). I therefore used the finest species splitting that has been suggested in publications which postdate the typological 'oversplitting' of morphospecies which characterized the post-Darwinian period (see Haffer 1992 for a history of concepts). I reviewed taxonomic and regional handbooks, group revisions and papers dealing with single species, and also dealt with statements such as 'probably represents more than one species'. I also followed new molecular studies which showed some species to be para- or polyphyletic or contain units which are equally distinctive as some other 'accepted' species (Arctander & Fjeldså 1994; García-Moreno *et al.* 1998, 1999; García-Moreno & Fjeldså 1999, in press). The number of highland species was raised from 789 (in the initial database, which followed Sibley & Monroe 1990) to 902. As these are monotypic or composed of rather subtle or intergrading subspecies, they represent, overall, phylogenetic species.

(2) Lump. Here I combined all distributional data for taxa which have been lumped under one species name by some authority in the post-Darwinian period (viz., para- and allopatric populations, or in some cases altitudinal subspecies, under a broad biological species concept, which would even include megaspecies as defined by Crawford-Cabral 1986). Six hundred and seventy-two species were recognized in this way.

3) Genus. Here all congeneric taxa (following Sibley & Monroe 1990) were transferred to the same map. Three hundred and seven generic taxa were recognized.

Some species generated by splitting do not inhabit highland habitat, and were deleted. On the other hand, the lumping of para- and allospecies, and of congeneric species, means an inclusion of lowland records. The richness in the lowlands therefore differs between the three datasets.

Results

Taxon richness

The 150 top-scoring cells (Fig. 2*b*, each with 164–250 species) were found on high altitude gradients facing the Amazon rainforest (compare with Fig. 1). Because a large proportion of the genera of the upper montane forest and treeline zone are differentiated as allo- or parapatric forms which replace each other along the Andes, species and genus level diversity showed very similar patterns here at this geographical scale. The lumping of congeneric highland and lowland forms in the Genus database meant that the richness peak might move one or two cells downslope.

With all datasets (Fig. 2), the highest scoring cell was at the head of the Huancabamba valley, which is a northern branch of the North Peru low (Fig. 1) and combined humid and dry zones. The rather low ridges in Colombia and in central Peru house fewer species, as do slopes which are adjacent to savanna-like lowlands (mainly in Colombia), or which are disturbed by occasional winter freezes (in the south; Fjeldså *et al.* 1999*b*). The Pacific slope is more species-poor, except for a small area in northern Ecuador and southern Colombia. Within the highlands, the species richness varies from up to 150 species per grid cell in areas with complex landscapes to 25–60 species per grid cell in the driest parts of the Altiplano.

While the ratio between species and genus level richness per cell was quite constant around 1.31 in the upper montane forest, it was variable (1.1–1.5) in the montane basins, around 1.5 in the humid parts of the Altiplano, and increased to 2.0

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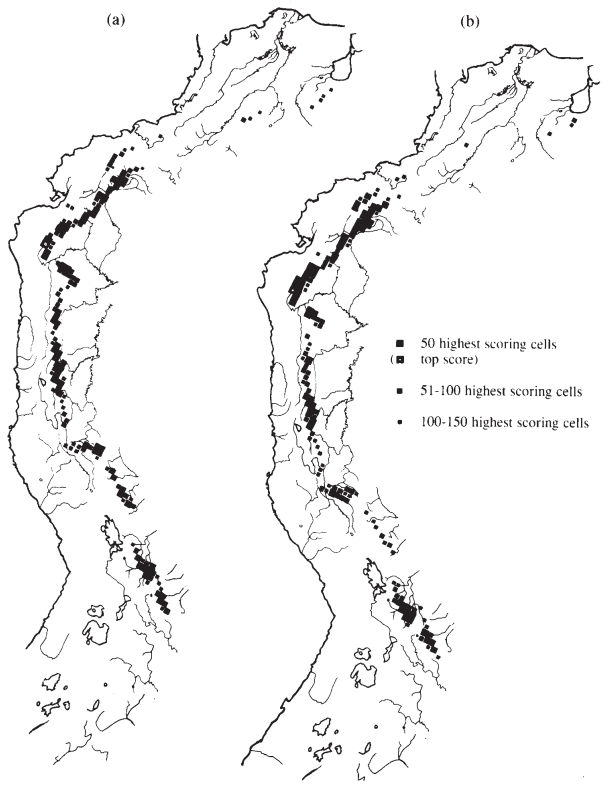


Figure 2 Areas with highest taxon richness: (a) genera, based on the database Genus, (b) 'phylogenetic species', based on the database Split (the database Lump gave virtually the same pattern as shown in (b), because the lumping consisted of re-combining closely related populations which are allo- or parapatric).

in the driest zones of western Bolivia and northern Argentina. This difference reflected the strong dominance on the Altiplano of a few genera with many broadly overlapping species, namely *Anas*, *Geositta*, *Upucerthia*, *Asthenes*, *Muscisaxicola*, *Anthus*, *Sicalis*, *Phrygilus* and *Carduelis*.

The 'richness hotspot' (defined here as the 50 top scoring cells) covered the fauna of the humid montane forests well with all three datasets. However, the approach paid no attention to the rather isolated and biologically-unique mountains of Colombia, namely the scarp west of the Bogotá plateau, the Perija and Merida mountains and Nevado de Santa Marta. Also, the species of deciduous woodlands and xeric habitats, and those of the high Andean plateaus, were left out. With all three databases the 'hotspot' approach missed one third of the regional fauna and three quarters of the species which are currently classified as endangered and vulnerable (Tables 1 & 2).

Range-size rarity

The sum of rarity scores is generally high along the species-rich eastern Andean ridges, reflecting the small average rangesize of the species inhabiting such a narrow habitat band (Graves 1988). However, the high scores were somewhat concentrated near the equator (using Genus data, Fig. 3*a*), or

Table 1 Effectiveness of different datasets and methods for making conservation priorities, in terms of what percentages of the smallest taxonomic units (defined in the Split database) are covered.

	Genus	*Lump*	*Split*
Richness, 50 top scores	66.8%	66.2%	67.7%
Rarity, 50 top scores	37.7%	71.5%	79.5%
Mean rarity, 50 top scores	58.7%	74.1%	83.1%
Near-minimum set	13 cells = 70.4%	39 cells = 91.4%	57 cells = 100%

Table 2 Effectiveness of different datasets and methods for making conservation priorities, in terms of what percentages of the 78 threatened and vulnerable taxa are covered.

	Genus	*Lump*	*Split*
Richness, 50 top scores	25.6%	25.6%	28.2%
Rarity, 50 top scores	26.9%	44.9%	46.2%
Mean rarity, 50 top scores	34.6%	43.6%	61.5%
Near-minimum set	13 cells = 28.2%	39 cells = 83.3%	57 cells = 100%

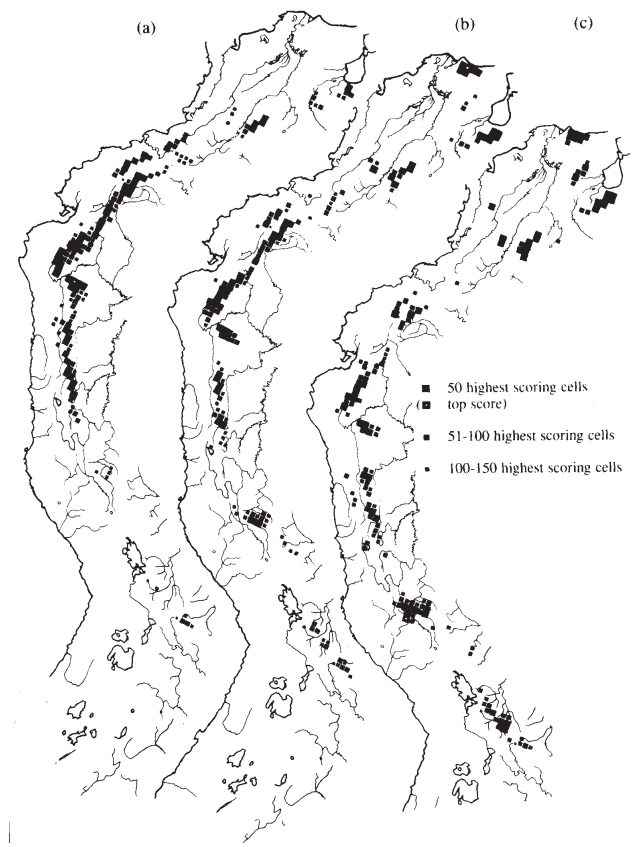


Figure 3 Areas with the highest rarity (sum of range-size rarity scores for all species present): (a) genera, based on the database Genus, (b) broad biospecies, based on the database Lump, and (c) 'phylogenetic species', based on the database Split.

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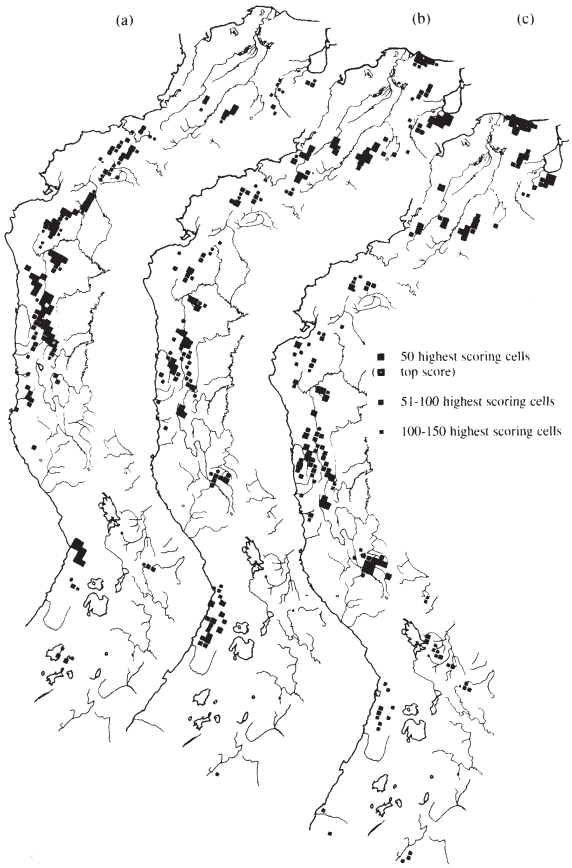


Figure 4 Areas with the highest mean rarity (mean range-size rarity score per species present): (a) genera, based on the database Genus, (b) broad biospecies, based on the database Lump, and (c) 'phylogenetic species', based on the database Split.

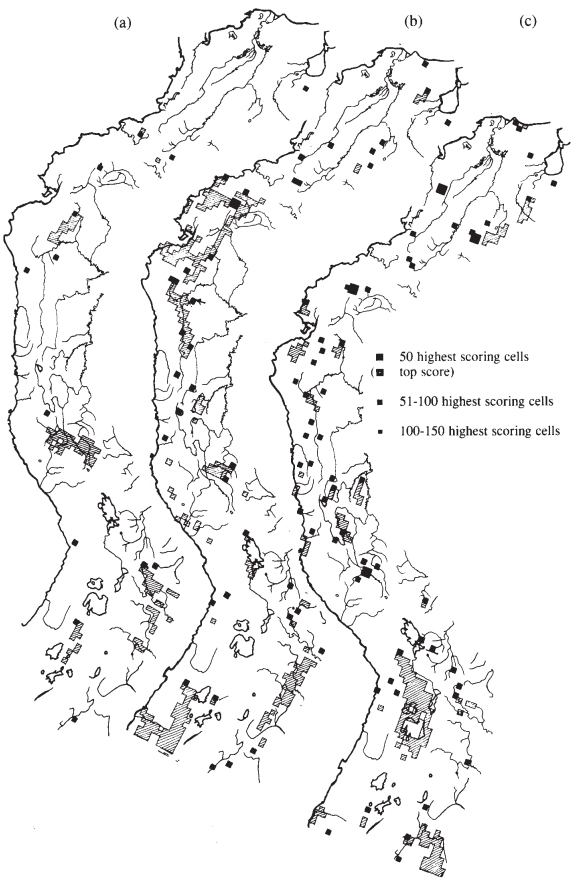


Figure 5 Near-minimum sets of areas needed to cover all taxa: (a) all genera, (b) all broadly-defined biospecies and (c) all 'phylogenetic species'. The irreplaceable cells were determined by the presence of a taxon which was recorded nowhere else, while the flexible cells could be replaced by other cells although this might require a larger total area.

locally aggregated, even in the relatively species-poor and isolated mountains of Colombia, and away from the humid slopes (Lump and Split data Fig. 3*b*, *c*; see Stattersfield *et al.* 1998 and Fjeldså *et al.* 1999*b* for detailed descriptions of patterns of endemism). Using the Genus data, the 'range-size rarity hotspot' of 50 top-scoring cells covered only a small fraction of the regional fauna (Table 1) and of the endangered species (Table 2). The other datasets provided a considerably better coverage, including nearly half of the threatened species (Table 2). Yet, the faunas of the deciduous forest formations of Bolivia and Argentina, and of the Altiplanos and the dry Pacific slope, received no coverage.

Mean range-size rarity

Here, the highest-scoring cells formed several aggregates in intermontane areas and even in some isolated and species-poor and arid environments in the west (Fig. 4). These included the woodland mosaics in Cordillera Blanca, mist vegetation above the Peruvian deserts and even the oases in the Atacama Desert. Using the Split data, the deciduous Tumbesian forests were recognized as fairly important, even though most of the 55 Tumbesian endemics inhabit elevations which are too low for inclusion in this database. The Genus dataset showed a peculiar pattern as there were some narrowly-endemic (monotypic) genera inhabiting montane basins and adjacent humid ridges in southern Ecuador and northern Peru, and in the mist vegetation above the Peruvian coastal desert.

The 'mean rarity hotspots' covered a large total number of species (Table 1) and also a significant portion of the endangered species, except in the case of the Genus data (Table 2). However, the faunas of the Argentinean and Bolivian forest and woodland formations, and of the dry southern parts of the Altiplanos, were still neglected. Also some endemics of the humid Andes of southern Ecuador were left out.

Near-minimum sets

Fifty-seven cells (corresponding to 2.5% of the area of the tropical Andes region) were needed to cover all taxa in the Split database. Thirty-nine areas were needed using the Lump database, and 13 areas using the Genus database (Fig. 5). Only one of the latter areas matched a cell in each of the two other near-minimum sets. The Lump near-minimum set

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matched 17 cells in the Split set. However, a direct count of matching cells underestimated the overlap, since adjacent cells were sometimes equally good choices. When the Lump minimum set was pre-selected in the Split database, 91.5% of all taxa and 83.3% of the endangered species were covered.

The Genus minimum set catered for a large fraction of all taxa (Table 1), but provided very little 'protection' for the endangered taxa (Table 2). This was only partly a consequence of the small size of this near-minimum set. Fifty complementary cells which provided triplicate representation of all genera would cover 85.4% of all taxa but still only 52.5% of the endangered species. If, for comparison, the network of complementary areas based on Split data were reduced to 50 cells, by removing the seven cells which contributed least to the total goal, 99.1% of all taxa and 94.9% of all endangered species were covered.

The Split minimum set was clearly better than the Lump set, but differed little from a set based on the 789 currently-accepted species (Sibley & Monroe 1990). This latter minimum set of 55 cells missed only two taxa recognized in the Split database.

Discussion

This paper does not consider the usefulness of bird data for biodiversity conservation, but deals explicitly with the relevance of the taxonomic resolution. Higher-taxon richness has been suggested as a useful biodiversity surrogate because it can be rapidly compiled, but this advantage is partly related to the extremely coarse spatial resolution of most studies (e.g. Gaston & Williams 1993; Williams *et al.* 1994; Gaston & Blackburn 1995). On this coarse scale, the approach is useful for comparing the biodiversity of different areas, and for theoretical studies. Balmford *et al.* (1996*b*) suggest that higher-taxon data may also be useful for prioritizing forest sites on a local scale.

The present study, which covered a complex tropical habitat mosaic with an intermediate spatial resolution, did not convincingly demonstrate the usefulness of the higher-taxon approach. Only for a 'richness hotspot approach' was the taxonomic resolution unimportant. While the higher-taxon data efficiently identified the biologically richest area, they did not predict well the variation in species richness across different ecological zones. This is partly because the species of poor ecoregions tend to be clumped within particularly large genera (Williams & Gaston 1994). Roy *et al.* (1997) pointed out that some ecoregions are characterized by rapid diversification, while others, such as lowland floodplains, are dominated by widespread and geographically-overlapping species which represent deeper phylogenetic branches. The Andean slopes have a large number of genera composed of allopatric species, while the high Andean plateaus are dominated by a few genera with several broadly-overlapping species. Such differences lead to complex and scale-dependent variations in richness on different taxonomic levels. For Australian ants, Andersen (1995) found that generic richness was a poor predictor of species-level richness.

The 'hotspot approach' provided poor guidance for reducing extinction risks (Table 2), irrespective of the taxonomic resolution. In the Andes, high species richness is correlated well with conditions which do not promote high human pressures, namely high rainfall, steep landscapes and frequent landslides causing high local-habitat turnover. Since the majority of biospecies inhabiting this zone are distributed along a few thousand kilometres of Andean slopes, the risks of global extinction are low. Even local endemics in this zone are mostly in the lower threat categories, unlike in the biologically-poorer montane basins, where aggregates of narrowly-endemic species are often found closer to densely populated areas (Fjeldså & Rahbek 1999).

The relatively poor performance of 'hotspots' in terms of representing all features of interest is well established, and it is also well known that endemism and complementarity are better performing principles (e.g. Pressey & Nicholls 1989; Lombard *et al.* 1995; Williams 1999). It is less well known how poorly the latter principles work with higher-taxon data. Generic range-size rarity data gave attention mainly to humid slopes near the equator, but not to unique faunas which are found in other parts of the region. Where the use of a crude (genus and mega-species) taxonomy is not a complete failure, this is because of a certain aggregation of patterns of endemism. Thus, density peaks for isolated relict populations (recent isolates) correlate with aggregates of endemic species in recently-diversified groups, and also often have some generic endemics (Fjeldså 1995). The Central Andes of Colombia-Ecuador and Cordillera Colán in northern Peru have endemic genera aggregated within areas with many recently differentiated endemics, a fact which is reflected in some matching and near-matching cells in Figure 5. More often, there are too few narrowly-endemic genera for making clear priorities. The only endemic genus of the central Peruvian montane basins, namely *Oreonympha*, was for some reason 'captured' by a flexible cell 250 km west of the main peak of endemism in Figure 3*b* and *c*. The main problem is posed by those biologically-unique areas which are geologically too young to have any endemism on the generic level. Thus, the Nevado Santa Marta has no endemic genera. The Tumbes region, which is globally one of the most critical areas for conservation (Stattersfield *et al.* 1998), appears unimportant using Genus data. The area has only two endemic genera, namely *Myrmia* and *Piezorhina*, both restricted to lowland habitats.

While Genus data may be useful for identifying areas of high biological diversity, they fail to indicate how extinction risks might be reduced, or to guide large enterpreneurs and donors (e.g. the World Bank) who might try to avoid damaging unique environments. In these respects, it would probably be more effective to selectively map narrowly-endemic and endangered species (Stattersfield *et al.* 1998). Tables 1 and 2 suggest that Lump data are also more effective than Genus data.

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It is sometimes suggested, although rarely in the literature, that by using the phylogenetic species concept, a number of new areas of endemism will be revealed. This is not very apparent from Figures 3 and 4. While the endemism in the cordilleras near Cuzco, Peru, is apparent even with Lump data, the finer taxonomic splitting permits recognition of a finer local differentiation and additional marginal conservation targets in small forest isolates deeper into the highland (Fig. 5*c*). Virtually all diagnosable local populations fell within areas of endemism which are apparent using currently accepted species. A near-minimum set based on 'accepted' species missed only two taxa in the Split database. This reflects the aggregated distribution of endemic taxa (Fjeldså 1995).

Comparing the avian distribution data with remote sensing data on interannual ecological variability, Fjeldså *et al.* (1999*b*) provided statistical evidence for linking peaks of endemism with local stability. Thus, most narrow endemics, whether generic or distinctive subspecies, are relict populations whose local persistence is related to orographic moderation of extreme weather. Perhaps because of the predictable local climates, these areas are densely populated and were important population centres also in the past (Fjeldså & Rahbek 1999). Because the unique biological communities of these places are threatened by traditional rural populations who have few alternatives, it is difficult to establish traditional national parks without people. We need instead to manage a political process, looking for links and connections within cultural landscapes, and providing incentives for new kinds of land-use which are more environmentally sustainable. This is probably the most critical issue today relating to risks of global extinctions in the Andes.

In conclusion, it seems that higher-taxon richness can be used to define areas of high biological diversity; however, these could probably also be defined using climatic-topographic models or evapo-transpiration data. The higher-taxon richness did not help us to identify unique local faunas or to make an effective plan for reducing extinction risks. The main advantage of the approach may therefore be for more theoretical macro-ecological studies. It is difficult to see the value of using surrogate data which cannot effectively help us reduce extinction risks when better data actually exist. Species-level data reveal other patterns which help to draw attention to the most endangered local faunas. Finer taxonomic splitting may lead to some refinement of the area selection, but 'accepted' species seem, overall, to be an adequate unit for conservation priority analysis (except perhaps for islands; Hazevoet 1996).

Good conservation strategies require good understanding of these relationships. We need good data, and it is important to note that such data do exist for large parts of the world, or can be compiled within a reasonable time-frame. It should of course be assessed what are the best taxa for such analyses, but good candidates would be birds, amphibians, snakes, butterflies and some groups of flowering plants.

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