Biodiversity and Conservation **12:** 1297–1320, 2003.

Integrating biodiversity priorities with conflicting socio-economic values in the Guinean–Congolian forest region

P.H. WILLIAMS[1,*], J.L. MOORE[2,3], A. KAMDEN TOHAM[4], T.M. BROOKS[2,3,5], H. STRAND[6], J. D'AMICO[6], M. WISZ[2], N.D. BURGESS[6], A. BALMFORD[2] and C. RAHBEK[3]

*[1]Biogeography and Conservation Laboratory, The Natural History Museum, Cromwell Road, SW7 5BD London, UK; [2]Conservation Biology Group, Department of Zoology, University of Cambridge, Downing Street, CB2 3EJ Cambridge, UK; [3]Zoological Museum, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark; [4]WWF Central Africa Regional Program Office, BP9144 Libreville, Gabon; [5]Center for Applied Biodiversity Science, Conservation International, 1919 M Street NW, Washington, DC 20036, USA; [6]WWF-US, Conservation Science Programme, 1250 24th Street NW, Washington, DC 20037, USA; *Author for correspondence (e-mail: worldmap@nhm.ac.uk; fax: +44-20-7942-5229)*

Received 31 October 2001; accepted in revised form 8 July 2002

Key words: Area selection, Biodiversity, Conservation priorities, Costs, Socio-economic values

Abstract. Identifying important areas for conserving biodiversity has attracted much discussion, but relatively few studies have dealt with conflicting socio-economic interests in a manner that is fully accountable. For the Guinean–Congolian forest region, we applied quantitative methods to select a network of coarse-scale areas sufficient to represent all forest mammal and bird species at least once. In a separate exercise, we prioritised 50% of the region to represent the same species as many times as possible. In both cases, we sought to minimise potential conflicts between conservation and other socio-economic imperatives by considering benefit-to-cost ratios. We found that by choosing areas to reduce conflicts, we were able to increase markedly the proportion of selected areas with low or medium conflict and decrease the proportion with high conflict. Nonetheless, we cannot expect that conservation goals will always be met unless some of these conflicts are faced and resolved. By working together with specialists from both the biological and socio-economic fields, we show that easily implemented quantitative tools could be useful for supporting the process of finding important areas for biodiversity conservation, while avoiding much of the conflict with other interests.

Introduction

Quantitative methods provide a transparent and accountable way of choosing areas with as much biodiversity for conservation as possible (Pressey et al. 1993; Margules and Pressey 2000). However, conservation is just one goal of landscape management, and has to be considered along with many other needs of people (McNeely 1997). The problem is that biodiversity conservation has been plagued by the absence of a workable cost-effectiveness framework (Metrick and Weitzman 1998). Previous studies seeking to integrate these other needs have tended to rely on conversions or trade-offs between biodiversity and other values that have no unique solutions and which are therefore easily challenged by people with other interests (e.g. Williams and Araújo 2002). In this paper, we demonstrate a simple quantitative method for reducing conflict with socio-economic interests that can avoid many of these problems. We illustrate this method using data and results generated at a recent workshop aimed at identifying conservation priorities in the Guinean–Congolian forest region of Africa. We do not intend to identify particular priorities for management action, but rather seek to explore approaches and the likely implications of incorporating socio-economic data within priority setting. Some of the strengths and weaknesses of quantitative methods are highlighted through a comparison with the expert-based priority areas identified at the workshop.

In March–April 2000, WWF-CARPO (Central African Regional Program Office) organised a workshop in Gabon to consider priorities for conserving biodiversity within the Guinean–Congolian forest region. The region extends from the Atlantic coastal forest in the west, to the foothills of the Albertine Rift in the east, and from the high mountains of Mount Cameroon to the lowlands of the Niger Delta. This includes several of WWF's 'Global 200' most biologically valuable ecoregions (Olson and Dinerstein 1998) as well as being one of the 'major tropical wilderness areas' (Mittermeier et al. 1998) with some of the largest intact blocks of rainforest. This wilderness holds a free-roaming megafauna, and the Congo River is still relatively undisturbed by dams and pollution. The Guinean–Congolian forests include areas with higher levels of endemism, for example in the Cameroon highlands, as well as areas of high species richness. Hence, this region is a high priority for conservation.

For the WWF-CARPO workshop, we measured biodiversity value as the representation of forest mammal and bird species among networks of selected areas. These groups comprise some of the most highly valued biodiversity within the region (Blom, in press). The most comprehensive biological database available for these organisms has been assembled by the Zoological Museum of the University of Copenhagen (ZMUC). Since 1995, data on the distribution of all Afro-tropical mammals and birds have been compiled on a 1° grid from information supplied by many experts in Africa and at institutions around the world (Burgess et al. 1997). Ideally, priority areas would be assessed at a finer scale by considering the viability of all species within smaller land management units. However, these data do not exist at present, so the ZMUC database represents the best available species-based distribution data for the region. This analysis serves to illustrate the principles of the method.

To make biodiversity area-selection methods more useful to decision makers formulating policy, we wished to include an appropriate treatment of some of the 'costs' associated with conservation as a form of land use. Our definition of cost is deliberately extremely broad, with the potential to include a combination of many different kinds of factors (e.g. purchase costs, management costs, opportunity costs), which need not be confined to monetary measures (e.g. including number of people affected; see Balmford et al. 2001). The WWF-CARPO workshop's socio-economic working group estimated the intensity of socio-economic activity in the region and its potential to affect the success of conservation initiatives. The conclusions were summarised in their maps of conservation opportunity (O'Hara, in press). Conservation opportunity ranks areas according to the predicted ease with which conservation initiatives could be implemented when socio-economic factors are taken into account. Factors considered included current and future land use patterns, human population density and the distribution of infrastructure.

Bringing this biodiversity and socio-economic information together, we see the area-selection problem as being one of selecting sufficient areas to meet an explicit conservation goal in terms of representing biodiversity, while improving the efficiency of uptake of conservation opportunities. This problem can be re-formulated by converting conservation opportunity to conservation 'conflict' (the reverse ranking; our use of this term is not necessarily intended to imply any form of civil disturbance or war). Networks of areas can then be selected to reduce conservation conflict. It is this second formulation that we consider. We converted data for conservation opportunity to conservation conflict by assuming that the potential for conflict with socio-economic interests is simply the reverse of conservation opportunity.

Conflicting socio-economic values have been accommodated in most area-selection studies only very crudely, by seeking to reduce the total area extent required to meet a conservation goal. This treats area extent as a surrogate for all other socio-economic costs. It has also led to an emphasis on 'efficiency', usually in terms of reducing the total area within a network of conservation areas that is required to meet a stated conservation goal (Pressey and Nicholls 1989a). In a few studies, costs have been addressed explicitly by incorporating within the area-selection algorithms some of the costs of areas as a way of breaking ties among alternative areas with otherwise identical contributions to biodiversity value (e.g. Pressey and Nicholls 1989b; Pressey et al. 1997; Nantel et al. 1998). However, this means that cost is considered only among those areas regarded as equivalent according to the other criteria, which are therefore given higher precedence. The result is that the cost of meeting the goal is unlikely to be minimised.

The simplest quantitative approach to integrating biodiversity value and socio-economic costs when making conservation decisions is to consider ideas of 'cost–benefit' (e.g. Dixon and Sherman 1990). Cost–benefit is usually considered as the difference ($B - C$) between benefit (B), in this case the biodiversity value protected, and costs (C), in this case the conservation conflicts. Calculating the difference requires that both terms be measured in the same currency (e.g. Faith 1995; Moran et al. 1997), which therefore depends on a conversion factor to 'price' biodiversity in terms of the cost currency. However, in situations where there is no uniquely justifiable conversion factor, no single 'best' solution can be identified.

When there is no clear cost constraint (such as a fixed budget) or when there is no complete countable set of species (or other biodiversity attributes), then the most direct approach to the problem of cost explicitly considers a range of different 'trade-offs' between cost and biodiversity value (Faith 1995, 1998; Faith and Walker 1996, 1997; Faith et al. 2001a). Trade-offs describe people's willingness to accept a decrease in one benefit (e.g. increasing management cost) when there is a compensatory increase in another benefit (e.g. biodiversity protected). Figure 1 illustrates how this has been applied to comparing many possible candidate networks of areas when we know the total cost of each network (in some sense, monetary or otherwise) and the amount of biodiversity foregone (e.g. the number of species not represented within each network). In this situation, simple trade-offs can be described on this graph as a family of straight lines, each with a negative slope *b* (i.e. increasing cost pays for reducing biodiversity value foregone at a constant rate). The best solution among candidate area networks for any particular trade-off is found by seeking the network intersected by the line of slope *b* that is as close to the origin of the graph as possible (in order to give the largest total net benefit in terms of biodiversity and cost, e.g. dashed lines in Figure 1). Therefore the 'curved' continuous line drawn to the left and below the sample of networks identifies the series of best networks (the 'non-dominated' solutions) when different trade-off slopes *b* in the range of 0–∞ are supplied. However, as discussed above, it may be difficult to justify the choice of any particular trade-off factor *b* (which amounts to a conversion factor between biodiversity and cost), so that no single 'best' network can be defended. Nonetheless, sensitivity analysis might be used to show which areas are always required or not (Faith and Walker 1996). This could be viewed as an extension of the idea of relative 'irreplaceability' among areas for representing biodiversity (Pressey et al. 1994).

In this paper we consider instead situations where there is either a fixed goal or a

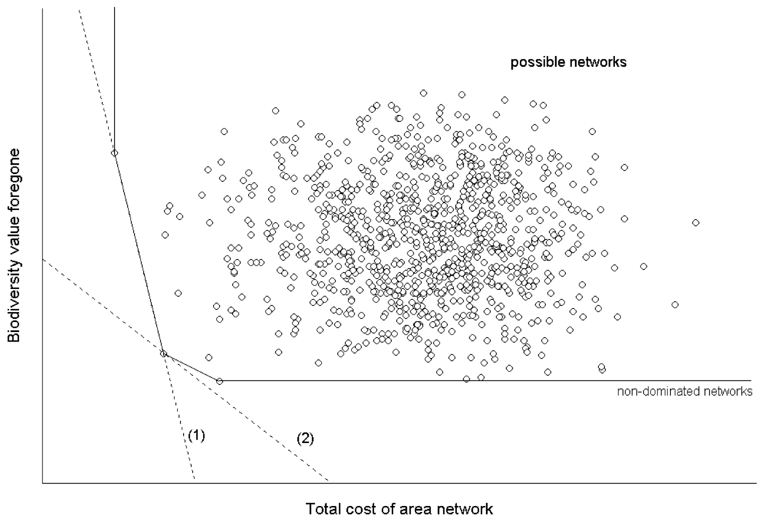


Figure 1. A hypothetical trade-off space in which the horizontal axis is the total cost of each area network and the vertical axis is the biodiversity value (the benefit) foregone (based on Faith and Walker 1996). Each circle represents one possible network. Networks giving results closer to the origin are 'better' in that they represent more biodiversity at lower cost. Any simple biodiversity-cost trade-off factor would describe a straight line on the graph, with negative slope (e.g. the dashed lines). When a range of different trade-offs is supplied, the corresponding range of 'best' networks (known as the non-dominated networks) are joined by the 'curved' solid line around the possible networks. For trade-off factor 1 there are two best solutions, whereas for trade-off factor 2 there is only one.

fixed cost budget for biodiversity representation. To address this case, we build on a related idea of increasing the 'cost-effectiveness' of area protection as described by Pressey and Bedward (1991). The most cost-effective solutions can be found using complex optimising algorithms that either (1) seek to represent predefined amounts of biodiversity for minimum cost, or (2) seek solutions that maximise biodiversity for a fixed cost (e.g. Ando et al. 1998; Balmford et al. 2000). However, simpler yet effective approximations are available. Cost-effectiveness can be measured using the benefit-to-cost ratio (B/C) between biodiversity value (B) and appropriate costs (C) (e.g. Moran et al. 1997; Metrick and Weitzman 1998), and because this is a ratio (retaining both kinds of units), no conversion factor between currencies is required. The principle is that at each step of area selection, the area is selected that gives the greatest increase in biodiversity protected relative to the increase in conservation conflicts that follow from selecting that area. This approach has been outlined previously (Williams 1996, 1998), and has been applied to area-selection problems (Balmford et al. 2001) because it is easily implemented within simple heuristic algorithms. The advantage of using quantitative cost-effectiveness methods that avoid conversion factors is that the results are accountable and uniquely justifiable (Williams and Araújo 2002).

We show how the benefit-to-cost ratio approach can be used to integrate information for a relatively large number of species with a layer of socio-economic information to prioritise areas, while making the process explicit, repeatable, and accountable. Many different kinds of socio-economic factors could be accommodated in this way if economists can find appropriate ways to combine them within a single cost variable (e.g. Faith et al. 2001a). The choice of factors to include may be unique, because it will depend on what is appropriate to each particular situation.

Methods

Data for biodiversity value: forest mammals and birds

The Guinean–Congolian forest region, as defined by the WWF-CARPO workshop, covers all or part of 228 1° grid cells of sub-Saharan Africa (each cell measures approximately 105 × 105 km). It includes large areas of undisturbed habitat, with relatively little forest fragmentation compared to many other areas of Africa. Unfortunately, little of this region has been surveyed for its biota. Therefore empirical knowledge of the biota reflects strongly the distribution of fieldwork effort, a problem that was recognised for all datasets at the workshop. The problem is addressed here by interpolating the expected distributions of species.

Data on the distribution of forest mammal and bird species have been entered into the ZMUC database in collaboration with an international network of experts (Brooks et al. 2001). For the larger and better-known species of mammals [following the taxonomy of Wilson and Reeder (1993)], the data are an estimate of distribution ranges in the period 1970–1989. For smaller and less well-known species, expected distribution ranges have been interpolated by assuming a continuous distribution between confirmed records within relatively uniform habitat, using available information on species' habitat associations, and taking into account specialist opinion, especially concerning any known gaps in distribution. For the least known species, records are plotted without interpolation because of lack of information, which would make interpolation very unreliable. These species with the fewest records are likely to have the least precisely known distributions. Data on the distribution of breeding bird species [following the taxonomy of Sibley and Monroe (1990, 1993)] have been entered on the same grid using similar methods and updated from published and unpublished sources (Burgess et al. 1997). For details of the methods and references used to construct the database see www.zmuc.dk/commonweb/research/biodata.htm. Of all species of sub-Saharan birds and mammals in the ZMUC database, 674 species were classified as forest species based on Burgess et al. (2000). Of these, 491 species have been recorded within the 228 1° grid cells of interest to this workshop (Figure 2a). Eleven species were then excluded because they are endemic to the mountains of the Albertine Rift, which are considered not to be part of the Guinean–Congolian forest region (mammals: *Crocidura montis, C. kivuana, C. stenocephala, Cephalophus rubidus, Delanymys brooksi, Dendromus kahuziensis, D. kivu, Dasymys montanus, Lophuromys cinereus*; birds: *Sylvietta chapini, Nectarinia prigoginei*), leaving 480 forest species in total.

Data for conservation conflicts: socio-economic opportunities

The socio-economic working group prepared a map of 'Conservation Opportunity in the Congo Basin' (O'Hara, in press). Opportunity was designated according to the presence or absence of remaining forest, forest concessions, roads and waterways, cities, and oil and gas-extraction pipelines. These elements were depicted on mapped overlays to help participants determine their extent. Areas of high human concentration (indicating potential human impact) were represented with mapped human population census data. The socio-economic working group was also asked to consider mining, hunting, non-timber forest exploitation, agriculture and fishing, although these elements were not mapped systematically. Where concentrations of these activities or phenomena occurred, the area is ranked as low opportunity or as 'high conflict'. Where these activities are absent, the area receives a rating of high opportunity or 'low conflict'. Several of the socio-economic factors represent likely future threats and it could be argued that these represent options for conservation intervention (see Discussion). However, for the purposes of this analysis, we accept the socio-economic working group's view that these factors are to be treated as increasing the costs of conservation management. Therefore, where the possibility exists, we prefer to select alternatives that reduce the likely conservation conflicts.

Just as with the biological assessment, the central Congo Basin is particularly deficient in data relating to socio-economic factors. An important feature of our approach is that areas were only classified as having conservation opportunity ('high', 'medium', 'low') where this is known to be the case. On the advice of the socio-economic working group, the 'unclassified' areas of the original map are

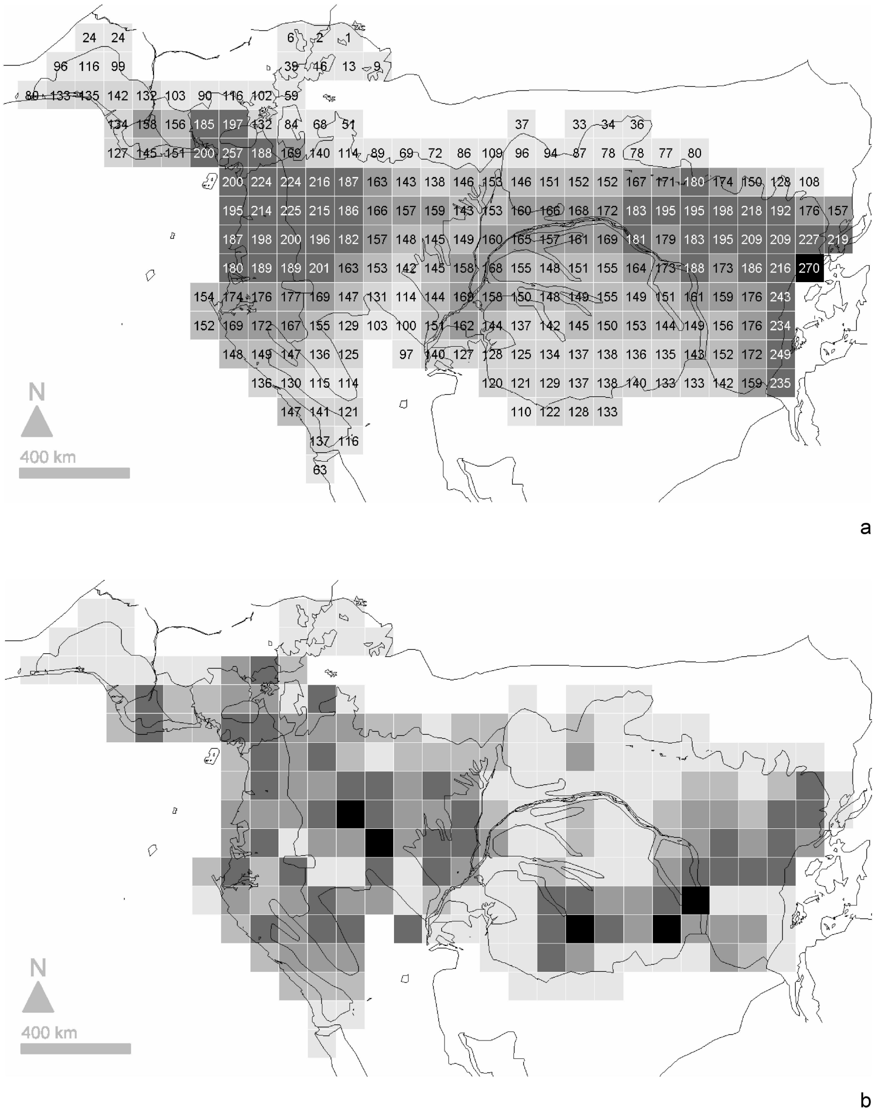


Figure 2. Data for biodiversity value and socio-economic opportunity. (a) Species richness per 1° grid cell for the 480 species of forest mammals and birds within the Guinean–Congolian forest region from interpolated records in the ZMUC database. Lines delimit WWF ecoregions. Grid cells are approximately 105 × 105 km. The grey scale shows high species richness in black, low richness in light grey, and numbers within cells are the number of recorded forest bird and mammal species per grid cell. (b) Map of 'Conservation Opportunity in the Congo Basin' from the socio-economic working group, re-sampled at 16 points per grid cell for the region of interest on a 1° grid and WWF ecoregions. The grey scale uses black for high, dark grey for medium, and light grey for low opportunity scores (for conservation conflict defined by Equation 1, read map (b) as black for low conflict, dark grey for medium conflict, and light grey for high conflict).

treated as presenting the lowest conservation opportunity, reflecting the highest potential conflict between resource use and biodiversity potential (Equation 1). We converted polygon data from the original map to grid-cell data (Figure 2b) by re-sampling the map at 16 points per grid cell and calculating a mean conservation conflict score for each cell (Equation 1).

$$\text{conservation conflict} = (\text{high opp} + (\text{medium opp} \times 2) + (\text{low opp} \times 3) + (\text{unclassified} \times 4))/16 \qquad (1)$$

Quantitative area-selection methods

We used quantitative methods to identify two kinds of priority-area networks: minimum-cost networks and maximum-coverage networks. Minimum-cost networks identify sets of areas that represent all species *at least once* while minimising the total cost (measured as area or as conservation conflict). Maximum-coverage networks identify sets of areas for a pre-defined total cost (e.g. 50% of the area of the region) that maximise the number of species representations. The cost can be counted in number of areas or as conservation conflict. Thus we compare two kinds of minimum-cost networks: *minimum-area networks* to represent all species within the minimum total area, and *minimum-conflict networks* that represent all species but minimise total conservation conflicts. The quantitative methods used here have been implemented in the WORLDMAP software (Williams 1996). For details and references see www.nhm.ac.uk/science/projects/worldmap/.

Minimum-cost networks of areas are selected using a progressive rarity algorithm based on the idea of complementarity (adapted from Margules et al. 1988; for details see Williams et al. 2000). The simple algorithm used here has been demonstrated to give a close approximation to the mathematically optimal solution (Csuti et al. 1997; Moore et al. in preparation; henceforth assumed to be effectively optimal). It begins by choosing those cells containing species found nowhere else, then the cell with the highest ratio of unrepresented rarest species to cost (the benefit-to-cost ratio rule), and so on, until all species are represented at least once. Using WORLDMAP, it is also easy to generate tables of results for accountability, to show why each area is chosen and which species are represented where.

For maximum-coverage networks, areas are selected initially using the same method described above for minimum-cost networks (for representing species one or more times). Selected areas are re-ordered by the algorithm by choosing at each successive step the area with the highest unrepresented-species-richness-to-cost ratio (a benefit-to-cost ratio rule). The required number of areas, or areas with the required cumulative cost, are then chosen from the top of this list (Williams et al. 2000).

Flexibility of area-selection solutions

The algorithms described above find a single approximate solution to the problem of discovering minimum-cost networks or maximum-coverage networks. However, it is often the case that there are many possible solutions, all of which are equally efficient. Priority networks that have many equivalent solutions are considered to have high flexibility, while those with few solutions have low flexibility.

The contribution that each area makes towards the flexibility of the entire network can be assessed as follows. Some selected areas are completely *irreplaceable*, in that no alternatives exist to represent one or more of their species (Rebelo and Siegfried 1992). Therefore, the location of these irreplaceable areas is fixed by their unique possession of records for certain species. Other areas are *flexible*, in that other alternative areas (or combinations of alternative areas) exist for representing the species that they contribute towards complete species representation. Only these flexible areas can be affected by the change of objective from minimising number of areas to minimising the sum of conservation conflicts. There are two kinds of flexible areas. An area is *fully flexible* if it can be exchanged for at least one other area (one-for-one) while still managing to represent all species the required number of times within the same number or total cost of areas. In contrast, *partly flexible* areas are areas within the network that could be exchanged for others outside the network while still allowing the network to represent all of the species, although the substitutes would require a larger number of areas, larger total area extent, or higher total cost of areas.

Flexibility can be explored inter-actively within even a large biodiversity database using computer software such as WORLDMAP. Exploring flexibility may be useful when some socio-economic factors (or other factors that may affect area selection) cannot be quantified for the analysis, or when the final selection of areas is to be negotiated with parties with conflicting needs.

Priorities from expert working groups

The WWF-CARPO workshop prepared a map of ‘Final Priorities’, which combined results from all expert working groups for not only birds and mammals, but also reptiles, amphibians, plants, invertebrates, and fish. This map represents the areas identified as most important for biodiversity conservation by this workshop. Priority was assigned among areas according to their biological distinctiveness as perceived by the expert groups. To use this information, we converted polygon data from the expert priorities map to grid-cell data by re-sampling at 16 points per grid cell. ‘High’ priority points are given a score of 3, ‘medium’ points a score of 2, ‘low’ points a score of 1, and ‘unclassified’ points a score of 0. These scores are averaged for each grid cell (Equation 2). The 114 grid cells with the highest priority scores (i.e. 50% of the region) were ranked by their scores in order to represent their relative priority for comparison with the quantitative results.

$$\text{priority} = ((\text{high priority} \times 3) + (\text{medium priority} \times 2) + \text{low priority})/16 \tag{2}$$

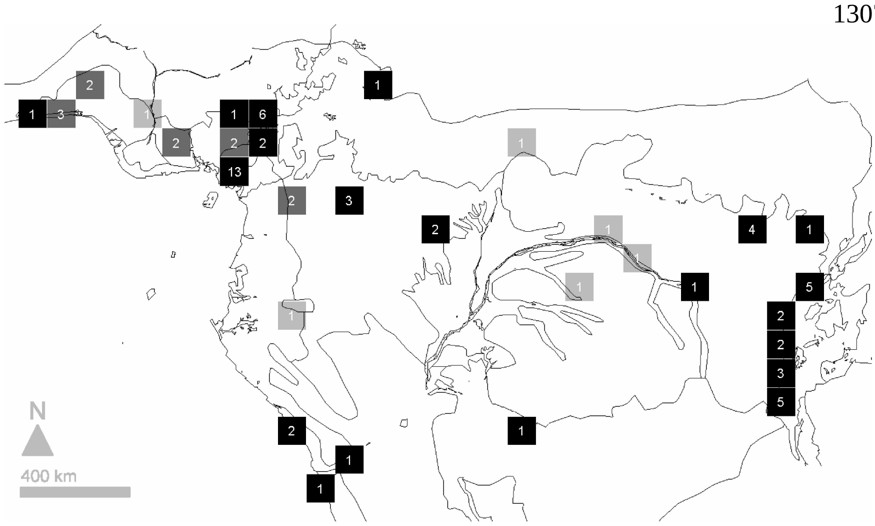
Results

Reducing conservation conflicts

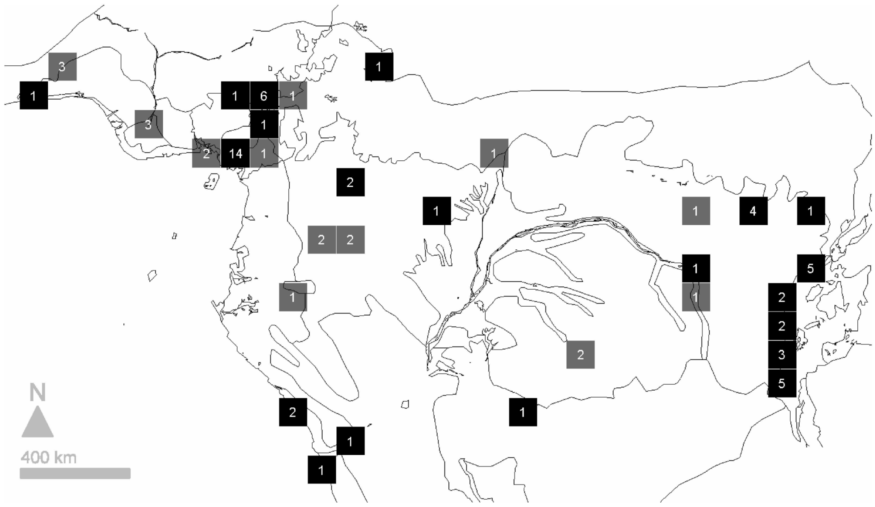
We identified two minimum networks of areas for representing all of the forest mammal and bird species using the benefit-to-cost ratio algorithm. The first network minimised the number of areas required to be selected, identifying a network of 31 areas to represent all of the forest mammal and bird species at least once (Figure 3a). The second network minimised the total amount of conservation conflict, identifying a network of 32 areas to represent all mammals and birds at least once (Figure 3b). In line with the map for conservation opportunities identified by the socio-economic working group (Figure 3b), the minimum-conflict network gives priority to slightly fewer areas along the Congo River.

Using the conservation conflict information from the socio-economic working group resulted in reducing the total cost of conflict by 5.8% from 27.38 units for the minimum-area network to 25.77 units for the (3% larger) minimum-conflict network. Although this change may seem rather modest, it may correspond to a considerable reduction in conflict. The advantage of using socio-economic data in priority setting studies is illustrated in Figure 4. This figure shows that compared to minimising area (Figure 4a), explicitly setting out to make the best use of conservation opportunities (Figure 4b) results in choosing a much higher proportion of the available cells with high and medium conservation opportunity (i.e. low conservation conflict) and a lower proportion of cells with lowest opportunity (i.e. high conservation conflict). Utilising areas with high conservation opportunity does not result in a marked decrease in the area efficiency of the network (Pressey and Nicholls 1989a) – only one more area is required in the conflict-minimising than in the area-minimising network.

Another way of assessing the consequences of using the benefit-to-cost algorithm is to examine the results within a trade-off framework (e.g. Faith and Walker 1996; see the Introduction). This can be illustrated by examining a maximum-coverage problem as an example. For maximum-coverage networks that cover 10% of the total extent of the region (23 grid cells), Figure 5 plots the biodiversity value foregone (the number of forest mammal and bird species unrepresented in a network, although without considering which species or what their relative value might be) against the total cost (as conservation conflict from Equation 1). The circles in the figure represent a sample of 1000 networks of 23 grid cells that were selected at random (without replacement within networks, but with replacement among networks). The data point for the network of the top 23 cells from the expert group lies close to the non-dominated line on the left edge of the distribution of sample networks. Therefore compared to this random sample, the expert network shows relatively low conservation conflict but misses many species. In comparison, networks obtained using the quantitative methods are significantly better at reducing the number of unrepresented species. Unfortunately, the network of the top 23 cells from the algorithm that seeks to minimise area for complete representation has a relatively high cost in conservation conflict. However, the network of the top 23 cells from the algorithm that seeks to minimise conflict is shown to perform particularly well, because it is close to the origin of the graph, with low cost and yet with few species foregone. From Figure 5, only if a trade-off between biodiversity and cost were extremely steep could a small proportion of networks (maximum 7 out of the random sample of 1000 networks, to the left of the dashed line) be marginally



a



b

Figure 3. Area networks to represent on a 1° grid all forest mammal and bird species within the Guinean–Congolian forest region selected using quantitative methods. (a) A minimum-area network of areas (31 areas), one of an estimated 15530 alternative solutions, and (b) the single minimum-conflict network of areas (32 areas). The numbers in the squares show how many species the selected area contributes uniquely to the representation of all species by the area network – these are the species that justify selection of each area. Where some of these species are not known to occur anywhere else within the region, these areas are irreplaceable to achieving the goal, and the cells are shown in black. Where all of these species occur in other areas, these other areas could be substituted as flexible alternatives. There are two kinds of flexible areas. First, if there are no flexible alternatives for the same cost (i.e. for the same level of conflict), then they are maximally efficient and only partly flexible (by increasing cost). These are shown in dark grey. Second, if there were flexible alternatives for the same cost, then the areas selected are fully flexible. These are shown in light grey (with these data, fully flexible alternatives exist only when cost is measured in number of areas, as in map a).

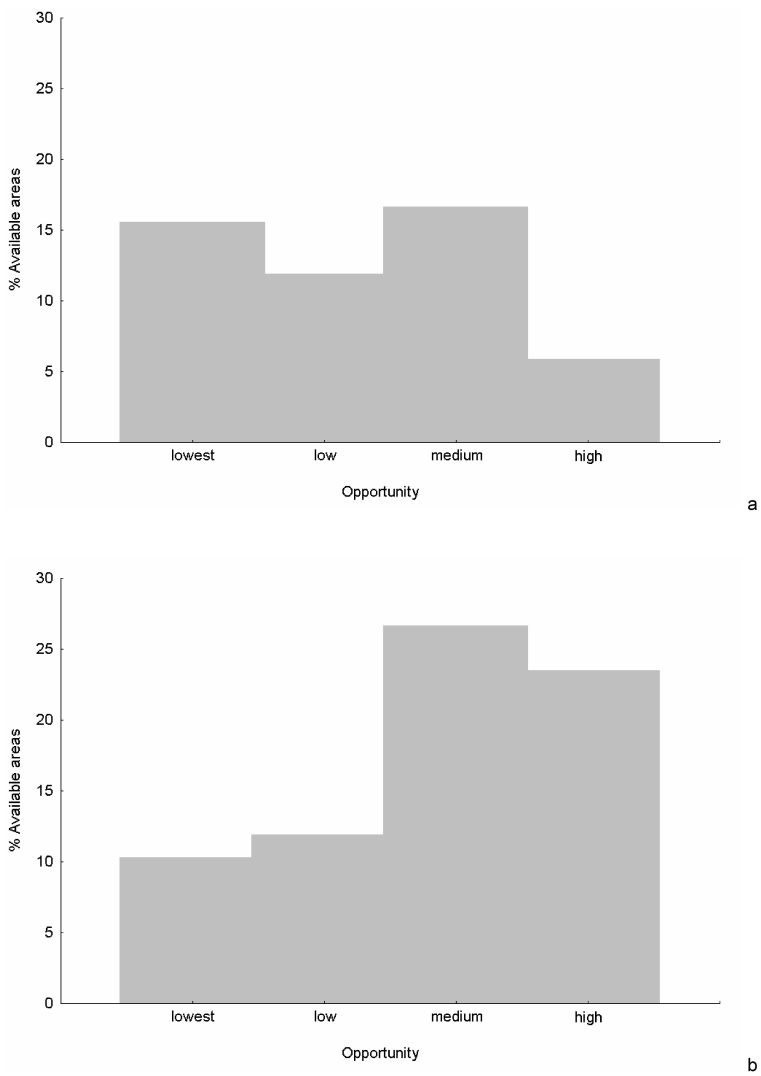


Figure 4. Assessing the effects of including conservation conflict. Selected areas plotted by conservation opportunity class (scores from Equation 1: lowest 1, low 1–2, medium 2–3, high 3–4) as a percentage of areas available in each class (lowest 97, low 84, medium 30, high 17). (a) Minimum-area network to represent all forest mammals and birds (Figure 3a). (b) Minimum-conflict network to represent all forest mammals and birds (Figure 3b).

more cost-effective than the ‘minimum-cost’ network. This makes intuitive sense, because such a steep slope for the trade-off gives a very low price to biodiversity, so that the seven apparently ‘better’ area networks would really only be chosen for their slightly lower socio-economic cost and only if their biodiversity contribution were not valued. Therefore we interpret our heuristic near-minimum-cost solutions to be good approximations to the true mathematical minima for situations where biodiversity is given any substantial value (the case of interest to conservationists).

Changes in flexibility

Comparison between the two minimum-cost networks shows that flexibility decreases if conflict rather than area is minimised. For the minimum-area network, six of the selected areas (shown in light grey in Figure 3a) have fully flexible alternatives. For each of these areas, any one of the fully flexible alternatives can be substituted one-for-one while still managing to represent all of the species at least once. This flexibility per cell gives an upper estimate ($2 \times 3 \times 4 \times 4 \times 13 \times 17$ alternatives) of up to 21 216 possible alternative solutions. The complication is that changing more than one fully flexible area can cause the representation of some species to change, so that more areas are needed in the network. Therefore we need to check how many of these networks are indeed fully representative (see Williams

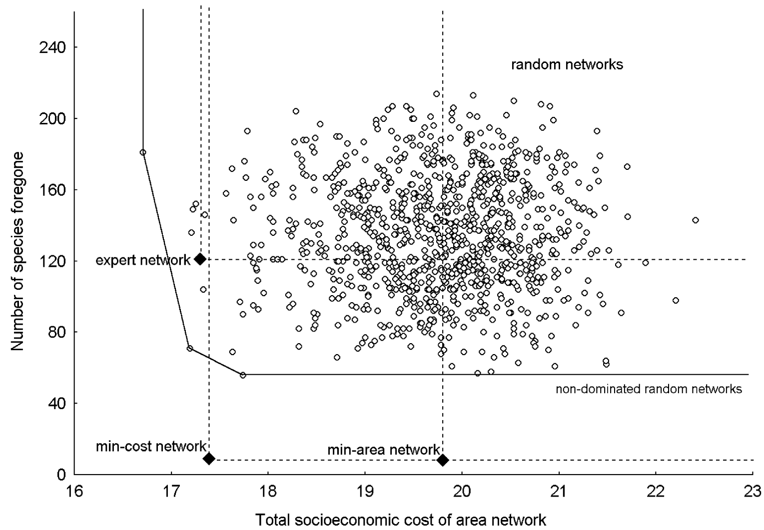


Figure 5. A trade-off space for the Guinean–Congolian forest region (see Figure 1). The horizontal axis is total socio-economic cost expressed as the conflict with biodiversity conservation. The vertical axis is the biodiversity value foregone expressed as the number of forest mammal and bird species not represented within area networks. All points represent different networks of 10% of the total area (23 1° grid cells) selected by different methods. Each circle represents one of 1000 networks selected as a random sample of all possible networks of 23 grid cells. The 'curved' line drawn around the randomly generated solutions links the 'best' of the sample of networks (the 'non-dominated' solutions) when the complete range of different values for the trade-off factor between biodiversity value and socio-economic cost is supplied (see Figure 1). For comparison, three networks of 23 grid cells are shown from selections: (1) by the expert working groups from the WWF-CARPO Workshop; (2) by maximum coverage, using numbers of areas as the cost; and (3) by maximum coverage, using conservation conflict (from Equation 1) as the cost. For each of these three cases, any circles below or to the left of the dashed lines identify randomly selected networks that could be better within the range of possible trade-offs (see Results).

et al. 2000). Drawing at random a sample of 1000 alternatives from among these 21 216 networks, we find that 732 represent all 480 forest mammal and bird species, so we estimate that $21\,216 \times 0.732 = 15\,530$ alternative fully representative networks exist. However, in comparison, only one network was found that minimises conservation conflict (Figure 3b). This decrease in flexibility is expected when costs differ among areas that otherwise make an equal contribution to biodiversity representation.

For the single minimum-conflict network (Figure 3b), there are still many other alternative solutions for representing all of the species when a slightly higher cost in terms of conflict is permitted. These areas can be identified by exploiting those alternative partly flexible areas (dark grey areas in Figure 3b) that could still represent all species. However, none of the alternative areas would minimise the potential conservation conflicts, because in each case at least one more costly area would have to be substituted. The irreplaceable areas (black areas in Figure 3) are potentially much more of a problem, simply because for them no alternatives exist. Fortunately, for the Congo data we find that the 20 irreplaceable areas do not have significantly higher conservation conflict than would be expected for areas drawn at random ($P = 0.54$).

Networks of different sizes

To explore issues of number of species representations and of benefit-to-cost ratios further, we selected maximum-coverage networks of up to 50% of the region to represent all of the species as many times as possible while minimising conservation conflict (Figure 6a). A network covering 50% of the region (114 grid cells, with no fully flexible alternatives) is just slightly smaller than would be required to represent the forest mammal and bird species at least nine times (122 grid cells).

The 114 highest priority grid cells identified by the expert working groups (Figure 6b) represent 459 (95.6%) of the 480 forest mammal and bird species from the ZMUC data. The 21 species not represented in the expert-derived priority network (Table 1) are recorded primarily from the eastern and northwestern parts of the region (areas less well represented among the expert priorities, Figure 6). Among these species, two are globally threatened birds (Collar and Stuart 1985): *Ploceus aureonucha* and *Malimbus flavipes*. Both of these unrepresented species are endemic to the Guinean–Congolian forest region.

Comparison of these results with those from random selection shows the greater efficiency of quantitative methods. We compared the cumulative percentage of species represented as the number of selected areas increased between the quantitative and expert-derived priority networks (Figure 7a). This shows that the quantitative approach represents consistently more species per area selected, although for larger number of areas the difference decreases as the number of areas chosen increases. In addition, the quantitative approach was always significantly more efficient than choosing areas at random, while at no stage is the representation of species in the expert-derived network significantly greater than the representation expected if areas were selected at random.

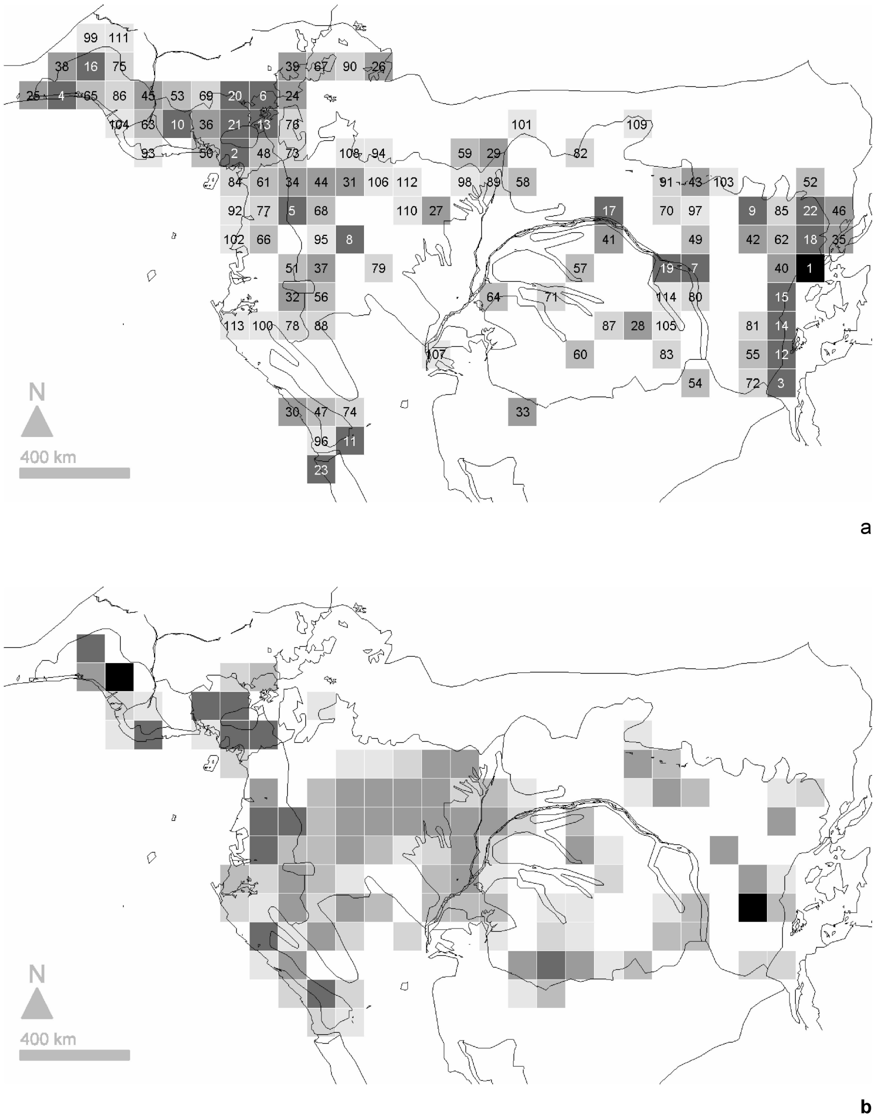


Figure 6. Priorities from expert and quantitative methods when selecting (in priority order) from 1 to 114 1° grid cells (50% of the region). (a) Maximum-coverage network of areas, prioritising areas selected to represent forest birds and mammals within the Guinean–Congolian forest region (black for high priority, light grey for low priority, white for unselected). The selection method seeks to maximise the ratio between representation of forest bird and mammal species relative to conservation conflict (from Equation 1). Areas are prioritised (re-ranked) by their contribution to representing biodiversity: the shades of grey show the order for choosing areas so as to maximise the combined species representation at each step relative to conservation conflict (a series of maximum-coverage solutions). Therefore, if only a few areas can be chosen, these should be taken from the black cell, then the dark grey cells, and so on. Numbers in grid cells are the cell priority rankings. (b) The expert-selected priority network from the WWF-CARPO Workshop, scored for the 1° grid. Areas have been prioritised according to their perceived biological value (black for high priority, light grey for low priority, white for unselected).

Table 1. Species of forest mammals and birds unrepresented in expert-group selected areas together with their range sizes measured as numbers of occupied 1° grid cells.

Species unrepresented in expert-group areas	No. of grid cells in Guinean–Congolian forest region with records	No. of grid cells in subSaharan Africa with records	Globally threatened species (Collar and Stuart 1985)
Mammals			
Crocidura manengubae	3	3	
Crocidura caliginea	2	2	
Crocidura congobelgica	2	2	
Crocidura luna	2	73	
Crocidura polia	1	1	
Crocidura tarella	1	3	
Sylvisorex granti	1	7	
Sylvisorex oriundus	1	1	
Rhinolophus maclaudi	2	9	
Chalinolobus superbus	1	2	
Pipistrellus inexspectatus	1	6	
Scotophilus viridis	2	120	
Cercopithecus petaurista	1	66	
Otomys typus	1	34	
Lophuromys eisentrauti	1	1	
Praomys mutoni	1	1	
Birds			
Francolinus nahani	5	7	
Platysteira albifrons	1	5	
Apalis pulchra	5	21	
Ploceus aureonucha	2	2	✓
Malimbus flavipes	4	4	✓

The comparisons in Figure 7a are based on the cumulative number of species represented at least once. Hence, these comparisons are only strictly valid when both methods have achieved <100% representation of species (i.e. for <13.6% of the total area of the region). Beyond this, the single-representation comparison takes no account of the ability of the quantitative approach to maximise the number of multiple representations per species. If multiple representations are considered (Figure 7b), then the difference in efficiency between the quantitative and expert approaches shows consistently large differences as the area of the region selected increases. (Initially, cases where median representations per species are zero occur because medians are counted among all 480 species. This comparison is chosen so that comparability is maintained when number of species represented varies among networks.)

The quantitative approach can be seen to represent consistently more diversity for a broad range of number of areas selected (Figure 7b). This remains true irrespective of whether these budgets are measured in terms of numbers of areas, or in terms of the conservation conflicts (not shown). It can also be seen by plotting the benefit-to-cost ratio in Figure 7c: the vertical separation of the lines shows that the quantitative

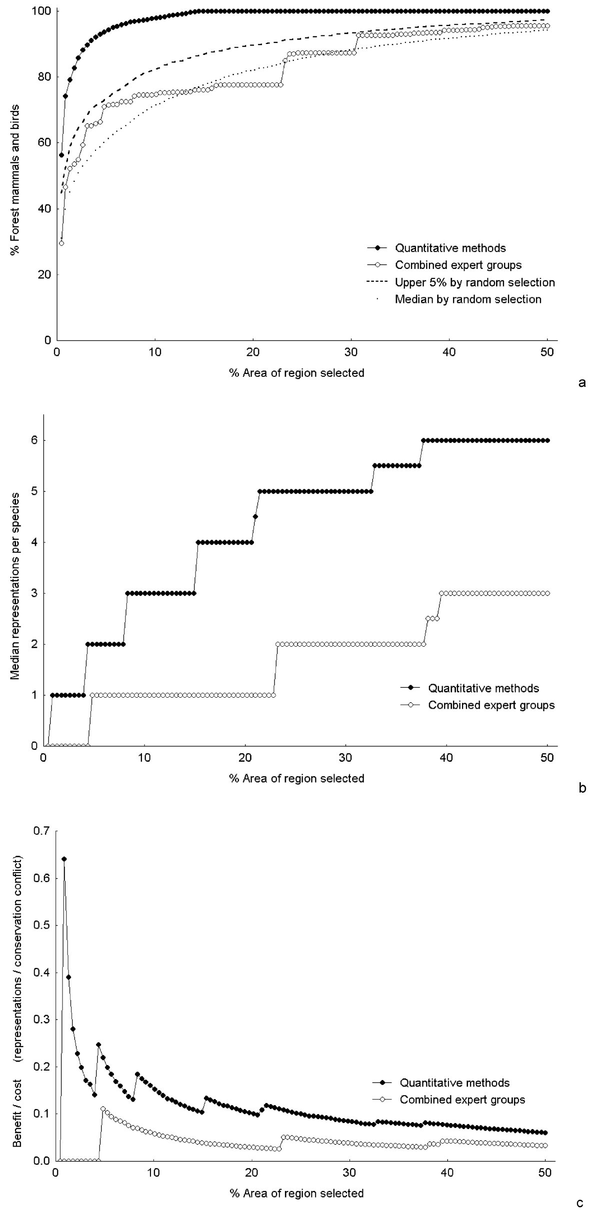


Figure 7. Comparing cost-effectiveness of priorities from expert and quantitative methods for representing the diversity of forest mammals and birds in the ZMUC database. (a) Comparison of the percentages of species represented at least once. (b) Comparison of the median number of representations per species. (c) Comparison of benefit-to-cost as the ratios between cumulative diversity as the median number of representations per species and the cumulative conservation conflict. The first selection method uses the maximum-coverage relative to conservation conflict, as mapped in Figure 6a. The second method is the combined selections from the expert working groups, prioritised by biological distinctiveness, as mapped in Figure 6b. The third method in (a) is to select networks of areas 1000 times at random without replacement and identify the threshold to the top 5% of network scores.

approach is consistently accumulating more multiple representations of species per unit of conservation conflicts. The apparent oscillation in Figure 7c is an artefact of the interaction between the stepwise increase in median representation (an integer) and the continuous increase in cost (a real number). The broader trend to declining plots in Figure 7c shows that for both methods the rate at which biodiversity benefit increases tends to be lower than the rate of increase in conservation conflicts as the proportion of the total area selected increases.

Discussion

Conflicting socio-economic values

Incorporating socio-economic information into conservation planning is likely to improve greatly the chances of success in achieving conservation goals if it can help avoid conflicts with people's other needs. This socio-economic information may come from expert analysis, as in our example, but this could and should include the values, concerns and participation of local people (Newmark and Hough 2000). Understanding the extent of potential conflicts for conservation can help direct the timing and amount of resources for implementing a conservation plan. Hopefully, there will be several alternatives for many area choices, so that a selection can be made according to existing conservation opportunities. Nonetheless, some areas will be highlighted in which conflict appears inevitable and where the cost of conservation is likely to be high.

For the region considered here, the scope for avoiding conflict is reasonably modest. This can be attributed to the large proportion of areas that combine high conflicting values with being irreplaceable to any priority network that meets the conservation goal. Clearly, the proportion of irreplaceable areas within a priority network, and so the scope for conflict avoidance, will depend on the characteristics of species' distributions within the region, the scale of the study, and the precise conservation goals. Although much conflict can be avoided, conflict cannot be avoided entirely: some areas that are necessary to meet conservation goals are also valuable for other uses. This pattern has been found in other similar studies (Ando et al. 1998; Balmford et al. 2001). In these areas, conflicts will have to be faced and resolved.

Our scores for the socio-economic costs of conservation-area networks combine several different factors. In time, it might be better to separate some of these factors within the selection process by considering them as threats rather than as costs. One way of dealing with threats to areas is by using threat scores to re-order selected areas by urgency for conservation management (Williams 1998). Separating threats would also allow for differences among species in their vulnerabilities to be treated more appropriately (see comments below on persistence), and would allow the costs of ameliorating the threats to be considered directly. This approach will have to wait until much more information on species' individual threats and vulnerabilities becomes available. To date, much of the work on costs and trade-offs has concentrated on capital, recurrent and opportunity costs of particular alternative land uses such as forestry (e.g. Faith 1995; Faith et al. 2001a). However, the same approach could be extended to explore potential conservation instruments including environmental levies, subsidies, carbon offsets, and biodiversity offsets (Faith et al. 2001b).

Quantitative methods

Comparisons of the priorities for the Guinean–Congolian forest region selected by expert opinion and by quantitative methods show that both methods represent the majority of species (we have not considered differences in the identities or threatened status of the particular species that are missed in any detail, but see Table 1). Consequently, there might appear to be little advantage in using the more demanding formal quantitative approach when the effectiveness of the priority networks is evaluated as the number of each species represented at least once. Indeed, not only do the results of quantitative methods and of expert opinion converge as the area coverage becomes large (Figure 7a), but so too do the results obtained when selecting areas at random. This might appear to remove any justification for expensive survey and analysis in conservation evaluation. However, the higher efficiency of quantitative methods is highlighted when the number of multiple representations per species is considered (Figure 7b). Multiple representations of species are likely to improve the probability of selecting an area that will maintain a viable population of each species (e.g. Nicholls 1998), as well as providing redundant populations as insurance against catastrophes. Hence, maximising multiple representations should improve the effectiveness of the network of areas selected.

It is important to note that the apparent inefficiency of the expert-selected network can be attributed in part to their different representation goals. The expert groups identified areas to represent not only birds and mammals, but also reptiles, amphibians, plants, invertebrates and fish, as well as considering the viability of some of these species within the selected areas. In addition, we have converted the irregular areas chosen by experts into priority scores for 1° grid squares. This conversion will reduce the apparent efficiency of the expert approach when compared to an evaluation based on the original area polygons, because the grid cells extend beyond the polygons. This constraint of working with 1° grid cells is imposed not by our methods or computer software, but by the available data for species.

Clearly, both the expert approach and the quantitative approach suffer from biases and errors. Expert opinion may vary depending on who is present in a working group and who is outspoken. Furthermore, the number of factors that people can keep track of in their heads at one time is limited. This makes it difficult to find the 'best' results in terms of conservation conflicts when dealing with complex biodiversity data (Dixon and Sherman 1990). On the other hand, experienced specialists can make excellent judgements for particular species when few data are available. Ideally, the strengths of both approaches would be combined within a single process. For example, the best procedures according to experts can be incorporated into quantitative modelling methods (Fonseca et al. 2000), to make the benefit of their expertise more widely available.

However, quantitative methods can be implemented only when suitable data are available. Hence, data availability will determine the scale at which areas can be chosen and the taxonomic breadth of species considered. We were restricted by data availability to considering grid cells of 1° in size. These data have low spatial resolution, but were nonetheless expensive to acquire. Fortunately, data for the entire world at a similar scale will soon be widely available as work on mapping projects progresses. But in our study, only for mammals and birds was it known which species were associated with forests, the ecosystem of interest. Ideally, data for viable biodiversity and for socio-economic costs would be available at the scale of realistic land-management units. We do not expect priorities identified at a finer spatial scale to fall necessarily within the larger area units that we have identified in this study. Patterns of co-occurrence and richness among species are well known to change with spatial scale (e.g. Stoms 1994), as are the total number or extent of area units required to meet particular species-representation goals (Pressey and Logan 1998). Nevertheless, in the absence of comprehensive data at finer scales, our analysis allows us to identify which areas make an important contribution at the larger scale and which species within those areas are in need of particular attention for subsequent analysis at a finer scale (Vane-Wright 1996). In addition, quantitative methods would be more useful if species' viability and predicted threat could also be incorporated to provide an estimate of overall persistence. All of these factors could and should be included within quantitative assessments when appropriate data become available (e.g. Pressey et al. 1993; Witting and Loeschcke 1993; Lombard 1995; Freitag et al. 1996; Howard et al. 1997; Nicholls 1998; Williams 1998; Cowling et al. 1999; Araújo and Williams 2000; Margules and Pressey 2000). Quantitative methods then make it possible to identify precisely why each area is seen to be valuable. This is useful because the information can assist further assessment and negotiations, as well as ensuring that all conservation goals are met despite the inevitable compromises that will result in changes to the priority network of areas. One of the most valuable properties of these methods is that they are rigorous and repeatable, so that the priority-setting process can be transparent and accountable.

Conclusions

Our results show that the quantitative approach applied here could be a useful tool for assessing and refining expert-based priority networks. This kind of support role could be applied even within a workshop environment (e.g. Finkel 1998). Because quantitative methods can maximise species representation and can accommodate other vital factors, we suggest that they have the potential to make a useful contribution to the development of regional conservation priorities. Looking ahead, the quantitative approach has the potential to integrate biological and socio-economic concerns in an accountable and straightforward way. We have illustrated some possibilities by examining how priority setting based on biological criteria might be modified to take account of patterns of conservation conflict with socio-economic factors. We are very keen to work more closely with socio-economic specialists (working, in turn, with local people), to explore more of the possibilities for estimating quantitative measures of conservation threats, costs and opportunities. For example, estimates of the costs of acquiring areas for conservation, costs of management to ameliorate threat, lost opportunities to exploit incompatible land uses, as well as costs associated with the effects of other social and political factors (e.g. Faith et al. 2001b; Wilkie et al. 2001), are all needed for realistic priority setting. Note that for costs to be used by quantitative methods, they need to be measured neither in a monetary value, nor in an absolute measure, so that any index that represents the relative costs associated with each site could be useful. The barrier to including these factors stems more from a lack of suitable data than from a lack of quantitative methods for handling them.

Acknowledgements

We thank J. Fjeldså for support and encouragement, and P. Agnelli, J.L. Amiet, the late W.F.H. Ansell, E. Baker, N. Baker, P. Bates, S. Bearder, W. Bergmans, L. Boitani, B. Branch, D. Broadley, G. Bronner, C. Cabral, M.D. Carleton, A. Channing, C. Claessen, M. Colyn, W. Cotterill, G. Cowlishaw, T. Crowe, C. Dardia, G. Davies, F. Dieterlen, N. Dippenaar, B. Dowsett, F. Dowsett-Lemaire, J.M. Duplantier, H.M. de Klerk, J.-P. d'Huart, J. Fahr, M.B. Fenton, C. Fitzgibbon, S. Galster, C. Gans, L. Granjon, P. Grubb, T. Halliday, D.C.D. Happold, R. Hoffman, M.E. Holden, P. Howard, B. Hughes, R. Hutterer, N.H.G. Jacobsen, P. Jenkins, W. Jetz, D. Koch, A.J.L. Lamberis, M. Languy, M. Largen, H. Leirs, A. Linzey, J. Mutke, J. Oates, B. Patterson, J.-L. Perret, J.C.K. Peterhans, J.C. Poynton, P.A. Racey, J.B. Rasmussen, G.B. Rathburn, L. Robbins, V. Salewski, A. Schiøtz, D. Schlitter, A.M. Simonetta, J.D. Skinner, S. Spawls, W. Stanley, M.E. Taylor, P. Taylor, V. van Cakenberghe, E. van der Straeten, E. van Dijk, H. van Rompaey, W. Verheyen, V. Wallach, N. Winser, R. Wirth, D. Yalden, and BirdLife International for providing data. We also thank S. Galster, L.A. Hansen, A. Jakobsen, J.B. Larsen, T. Lehmberg, P.V. Nielsen, T.S. Romdal, L.L. Sørensen, and M.M. Westergaard for entering data, J. Oglethorpe for discussion, and A. Blom, D.P. Faith, L.A. Hansen, L.L. Manne and B.A. Walther for comments on the manuscript. Funding was provided by WWF, the Danish Research Council, the Danish Council for Development Research, the Isaac Newton Trust of the University of Cambridge, and Conservation International's Center for Applied Biodiversity Science.

References

Ando A., Camm J., Polasky S. and Solow A. 1998. Species distributions, land values, and efficient conservation. Science 279: 2126–2128.

Araújo M.B. and Williams P.H. 2000. Selecting areas for species persistence from occurrence data. Biological Conservation 96: 331–395.

Balmford A., Gaston K.J. and Rodrigues A.S.L. 2000. Integrating costs of conservation into international priority setting. Conservation Biology 14: 597–605.

Balmford A., Moore J.L., Brooks T., Burgess N., Hansen L.A., Williams P. et al. 2001. Conservation conflicts across Africa. Science 291: 2616–2619.

Blom A. 2003. The extraordinary biodiversity of the Guinean–Congolian Forest Region. In: Toham A.K., Olson D., Abell R., D'Amico J., Burgess N., Thieme M. et al. (eds), Biological Priorities for Conservation in the Guinean–Congolian Forest and Freshwater Region. Proceedings of Workshop held on March 30–April 2, 2000 in Liberville, Gabon., pp. 13–16 (in press).

Brooks T., Balmford A., Burgess N., Fjeldså J., Hansen L.A., Moore J. et al. 2001. Toward a blueprint for conservation in Africa. BioScience 51: 613–624.

Burgess N.D., de Klerk H., Crowe T.M. and Rahbek C. 2000. A preliminary assessment of congruence between biodiversity patterns in Afrotropical forest birds and forest mammals. Ostrich 71: 286–290.

Burgess N.D., de Klerk H., Fjeldså J., Crowe T.M. and Rahbek C. 1997. Mapping Afrotropical birds: links between atlas studies and conservation priority analyses. Bulletin of the African Bird Club 4: 93–98.

Collar N.J. and Stuart S.N. 1985. Threatened Birds of Africa and Related Islands. ICBP/IUCN Red Data Book, Part 1. 3rd edn. International Council for Bird Preservation, Cambridge, UK.

Cowling R.M., Pressey R.L., Lombard A.T., Desmet P.G. and Ellis A.G. 1999. From representation to persistence: requirements for a sustainable system of conservation areas in the species-rich mediterranean-climate desert of southern Africa. Diversity and Distributions 5: 51–71.

Csuti B., Polasky S., Williams P.H., Pressey R.L., Camm J.D., Kershaw M. et al. 1997. A comparison of reserve selection algorithms using data on terrestrial vertebrates in Oregon. Biological Conservation 80: 83–97.

Dixon J.A. and Sherman P.B. 1990. Economics of Protected Areas. Earthscan Publications, London.

Faith D.P. 1995. Biodiversity and Regional Sustainability Analysis. CSIRO Publications, Lyneham, Australia.

Faith D.P. 1998. Some considerations in the design of a national biodiversity monitoring system for Brazil's protected areas. In: Baker D.S., Ferreira L.M. and Saile P.W. (eds), Proceedings and Papers of the International Workshop on Biodiversity Monitoring in Federal Protected Areas: Defining the Methodology. IBAMA/GTZ, Pirenopolis, Brazil, pp. 51–65.

Faith D.P. and Walker P.A. 1996. Integrating conservation and development: effective trade-offs between biodiversity and cost in the selection of protected areas. Biodiversity and Conservation 5: 431–446.

Faith D.P. and Walker P.A. 1997. Regional sustainability and protected areas – biodiversity protection as part of regional integration of conservation and production. In: Pigram J.J.J. and Sundell R.C. (eds), National Parks and Protected Areas: Selection, Delimitation, and Management. University of New England Press, Armidale, Australia, pp. 297–314.

Faith D.P., Margules C.R. and Walker P.A. 2001a. A biodiversity conservation plan for Papua New Guinea based on biodiversity trade-offs analysis. Pacific Conservation Biology 6: 304–324.

Faith D.P., Walker P.A. and Margules C.R. 2001b. Some future prospects for systematic biodiversity planning in Papua New Guinea – and for biodiversity planning in general. Pacific Conservation Biology 6: 325–343.

Finkel E. 1998. Software helps Australia manage forest debate. Science 281: 1789–1791.

Fonseca G., Balmford A., Bibby C., Boitani L., Brooks T., Burgess N. et al. 2000. Following Africa's lead in setting priorities. Nature (London) 405: 393–394.

Freitag S., Nicholls A.O. and van Jaarsveld A.S. 1996. Nature reserve selection in the Transvaal, South Africa: what data should we be using? Biodiversity and Conservation 5: 685–698.

Howard P., Davenport T. and Kigenyi F. 1997. Planning conservation areas in Uganda's natural forests. Oryx 31: 253–264.

Lombard A.T. 1995. The problems with multi-species conservation: do hotspots, ideal reserves and existing reserves coincide? South African Journal of Zoology 30: 145–164.

Margules C.R. and Pressey R.L. 2000. Systematic conservation planning. Nature (London) 405: 243–253.

Margules C.R., Nicholls A.O. and Pressey R.L. 1988. Selecting networks of reserves to maximise biological diversity. Biological Conservation 43: 63–76.
McNeely J.A. 1997. Assessing methods for setting conservation priorities Investing in Biological Diversity: the Cairns Conference, OECD Proceedings. OECD, Paris, pp. 25–55.
Metrick A. and Weitzman M.L. 1998. Conflicts and choices in biodiversity preservation. Journal of Economic Perspectives 12: 21–34.
Mittermeier R.A., Myers N., Thomsen J.B. and da Fonseca G.A.B. 1998. Biodiversity hotspots and major tropical wilderness areas: approaches to setting conservation priorities. Conservation Biology 12: 516–520.
Moore J., Folkmann M., Balmford A., Brooks T., Burgess N., Hansen L. et al. in preparation. Heuristic and optimal solutions for set-covering problems in conservation biology. .
Moran D., Pearce D. and Wendelaar A. 1997. Investing in biodiversity: an economic perspective on global priority setting. Biodiversity Conservation 6: 1219–1243.
Nantel P., Bouchard A., Brouillet L. and Hay S. 1998. Selection of areas for protecting rare plants with integration of land use conflicts: a case study for the west coast of Newfoundland, Canada. Biological Conservation 84: 223–234.
Newmark W.D. and Hough J.L. 2000. Conserving wildlife in Africa: integrated conservation and development projects and beyond. BioScience 50: 585–601.
Nicholls A.O. 1998. Integrating population abundance, dynamics and distribution into broad-scale priority setting. In: Mace G.M., Balmford A. and Ginsberg J.R. (eds), Conservation in a Changing World. Cambridge University Press, Cambridge, UK, pp. 251–272.
O'Hara D. 2003. Socio-economic context. In: Kamdem Toham A., Olson D., Abell R., D'Amico J., Burgess N., Thieme M. et al. (eds), Biological Priorities for Conservation in the Guinean-Congolian Forest and Freshwater Region. Proceedings of Workshop held on March 30–April 2, 2000 in Libreville, Gabon., pp. 17–29 (in press).
Olson D.M. and Dinerstein E. 1998. The global 200: a representation approach to conserving the Earth's most biologically valuable ecoregions. Conservation Biology 12: 502–515.
Pressey R.L. and Bedward M. 1991. Mapping the environment at different scales: benefits and costs for nature conservation. In: Margules C.R. and Austin M.P. (eds), Nature Conservation: Cost Effective Biological Surveys and Data Analysis. CSIRO, Canberra, Australia, pp. 7–13.
Pressey R.L. and Logan V.S. 1998. Size of selection units for future reserves and its influence on actual vs targeted representation of features: a case study in western New South Wales. Biological Conservation 85: 305–319.
Pressey R.L. and Nicholls A.O. 1989a. Efficiency in conservation evaluation: scoring versus iterative approaches. Biological Conservation 50: 199–218.
Pressey R.L. and Nicholls A.O. 1989b. Application of a numerical algorithm to the selection of reserves in semi-arid New South Wales. Biological Conservation 50: 263–278.
Pressey R.L., Humphries C.J., Margules C.R., Vane-Wright R.I. and Williams P.H. 1993. Beyond opportunism: key principles for systematic reserve selection. Trends in Ecology and Evolution 8: 124–128.
Pressey R.L., Johnson I.R. and Wilson P.D. 1994. Shades of irreplaceability: towards a measure of the contribution of sites to a reservation goal. Biodiversity and Conservation 3: 242–262.
Pressey R.L., Possingham H.P. and Day J.R. 1997. Effectiveness of alternative heuristic algorithms for identifying indicative minimum requirements for conservation reserves. Biological Conservation 80: 207–219.
Rebelo A.G. and 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.
Sibley C.G. and Monroe B.L. Jr 1990. Distribution and Taxonomy of Birds of the World. Yale University Press, New Haven, Connecticut.
Sibley C.G. and Monroe B.L. Jr 1993. A Supplement to Distribution and Taxonomy of Birds of the World. Yale University Press, New Haven, Connecticut.
Stoms D.M. 1994. Scale dependence of species richness maps. Professional Geographer 46: 346–358.
Vane-Wright R.I. 1996. Identifying priorities for the conservation of biodiversity: systematic biological

criteria within a socio-political framework. In: Gaston K.J. (ed.), Biodiversity: a Biology of Numbers and Difference. Blackwell Science, Oxford, UK, pp. 309–344.

Wilkie D.S., Carpenter J.F. and Zhang Q. 2001. The under-financing of protected areas in the Congo Basin: so many parks and so little willingness-to-pay. Biodiversity and Conservation 10: 691–709.

Williams P.H. 1996. Worldmap 4 windows: software and help document 4. London: distributed privately and from http://www.nhm.ac.uk/science/projects/worldmap/.

Williams P.H. 1998. Key sites for conversation: area-selection methods for biodiversity. In: Mace G.M., Balmford A. and Ginsberg J.R. (eds), Conservation in a Changing World. Cambridge University Press, Cambridge, UK, pp. 221–249.

Williams P.H. and Araújo M.B. 2002. Apples, oranges, and probabilities: integrating multiple factors into biodiversity conservation with consistency. Environmental Modeling and Assessment 7: 139–151.

Williams P.H., Burgess N.D. and Rahbek C. 2000. Flagship species, ecological complementarity, and conserving the diversity of mammals and birds in sub-Saharan Africa. Animal Conservation 3: 249–260.

Wilson D.E. and Reeder D.M. 1993. Mammal Species of the World: a Taxonomic and Geographic Reference. Smithsonian Institution, Washington, DC.

Witting L. and Loeschcke V. 1993. Biodiversity conservation: reserve optimisation or loss minimisation? Trends in Ecology and Evolution 8: 417.