Conservation during times of change: correlations between birds, climate and people in South Africa

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Few studies have investigated the ability of national conservation networks to adapt to changes in underlying environmental drivers (such as precipitation) and their consequences for factors such as human density and species richness patterns. In this article, the South African avifauna is used as the basis for such analysis to ascertain the likely extent of current, and future, anthropogenic impacts on priority conservation areas. We show that human population pressure is high in or around most of these priority areas and is likely to increase, given the magnitude of post-climate change estimated from predicted changes in precipitation and relationships between species richness, human densities, and rainfall. Although additional conservation areas, such as the Important Bird Area (IBA) network, are likely to introduce valuable flexibility to conservation management, only limited options are available for such expansions, and the conservation value of these areas is likely to be compromised by changing climate. Ultimately, a more integrated conservation approach is needed for effective conservation policies. Such an approach should confer adequate protection on current reserves and emphasize sustainable utilization of non-reserve areas.

Introduction

Recent studies have shown that areas of high human activity and enhanced species richness are spatially congruent,[1–3] apparently because both variables respond similarly to increasing levels of primary productivity,[3–5] but see also ref. 6. This overlap has profound implications for conservation. First, in areas subjected to significant land transformation for human use, which correlates strongly with population pressure,[7,8] both wildlife population viability[9] and species richness are adversely affected.[10,11] Second, there is a tendency for human population densities to be high in areas surrounding current reserves, which in turn, are rich in species.[7,12–14] Reserves and the species they are designed to protect are therefore under considerable, and often mounting, external pressure.[7,12] Third, a correlation between species richness and human density generally means escalating conflict between economic development and conservation needs.[3,5]

These conservation conflicts are likely to grow as human populations increase.[2] This is especially true of countries such as South Africa where a population growth rate of 2.2% yr^{-1} (based on an estimated 40.6 million people in October 1996 and 44.8 million five years later)[15] is substantially higher than the corresponding growth rate for the rest of the world (1.3% yr^{-1}), and above that of most developing countries (1.6% yr^{-1}).[2] Changes in human population growth are therefore likely to alter the form of the relationship between species richness and human densities. Consequently, land-use planners will increasingly have to consider ways of incorporating these changes into their conservation strategies if they are to succeed in achieving long-term goals of sustainable development.[16,17]

An additional factor that is likely to modify the relationship between human density and species richness patterns, and therefore affect the conflict between conservation and human development needs, is climate change.[18,19] Recent evidence indicates that, in response to the latest climate trends, the northern distributional range limits of many species in both Europe and North America have extended northwards.[20–24] Such range shifts and other responses to climate change are affecting both species and communities in the northern hemisphere[23,25] and are also likely to influence those in the southern hemisphere.[26,27] Moreover, the extent of these shifts is likely to increase as climate change becomes more obvious.[26,28]

Conservation authorities will therefore have to make provision for the fact that changes in the underlying drivers of human population densities and species richness patterns will influence the value of conservation areas and, in turn, their impact on future human development options.[16–18,29] Incorporating system dynamics into conservation policy will require considerable flexibility, which will be difficult to achieve under reserve allocation procedures that rely on the *ad hoc* availability of space or of political convenience.[30–32] Recent studies have specifically addressed the issue of effective conservation responses to factors such as climate change, by advocating approaches based on regional reserve networks, landscape connectivity, and matrix management models.[18,33,34] In other words, conserving as much of the landscape outside the current conservation area network is one way partly to address these modifying patterns of human activity and species distributions.[35]

Approaches to identifying additional conservation areas vary widely. For example, for birds, the Important Bird Areas (IBAs) programme was established to create a global network of sites to protect the world's avian fauna over the long term.[36] Such IBAs are selected using four criteria devised by BirdLife International: the presence of globally threatened, restricted-range, or biome-restricted species, or the presence of substantial congregations of individuals.[36] A very different approach for setting geographical conservation priorities is systematic conservation planning.[37] This employs algorithms to identify seed areas for the development of regional conservation networks.[38,39] Nonetheless, the actual designation of such sites will depend on effective integration of these areas with competing land use.[3,39,40]

One major problem faced by all of these approaches is that the available options for expanding present conservation networks are limited in most regions, especially if among their aims the priority setting exercises seek to minimize conflict with other

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land-use requirements.[5,41] Therefore, as is the case in many countries (such as the United Kingdom),[42] conservation agencies are faced with limited scope to adapt. This makes the requirement for sustainable development[43] seem all the more difficult to achieve, at least if it means the maintenance of current biodiversity.

Here, we use the South African avifauna as a means to examine current and future human resource demands on (i) established conservation areas and (ii) priority conservation areas identified both inside and outside existing conservation area networks. To date, studies on the relationship between human activity and areas important for bird conservation have received little attention at a national scale. We address this gap by examining, at a quarter-degree resolution, whether areas important for bird conservation are located in areas of unusually high human population pressure, before and after human density and avian richness patterns alter in response to climate change. This approach provides a broad indication of the extent to which previously identified priority bird areas are subjected to the threat of land-use conflict owing to high current or future human densities in their vicinity. If, for example, priority bird areas outside protected areas are not threatened by large numbers of people, these parts may be identified as potential new reserve areas. Huston[29] argued that priority conservation areas should maximize species conservation and minimize the negative effects of proposed conservation areas on human welfare and economics.

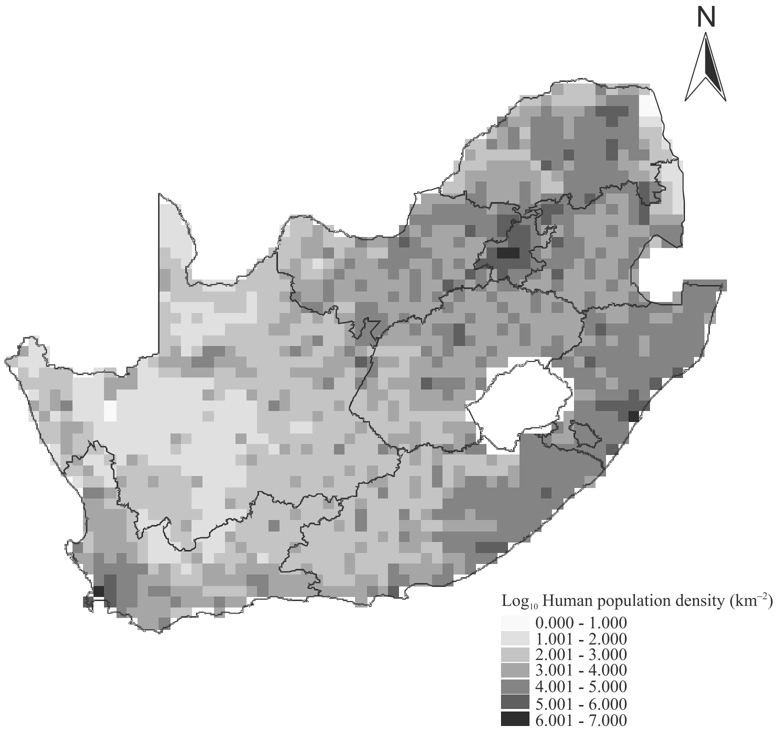

Fig. 1. Human population density variation across South Africa.

Methods

Avian species richness data and human population figures for South Africa (excluding Lesotho) were obtained from the Southern African Bird Atlas Project (SABAP)[44] and from the latest South African population census data,[45] respectively (Fig. 1). This information gave species occurrences and the numbers of humans per quarter-degree grid cell (1796 cells that varied in area from 635 km^2 in the south to 712 km^2 in the north). Data on human population density were obtained after information on the number of people in 80 000 landscape units, or enumeration areas, were mapped and combined with a quarter-degree grid cell using ArcView GIS.[46] In the case of the birds, marine, vagrant, marginal (species with only one occurrence in the study area and substantial populations outside of it) and escaped species were excluded from the analysis; 651 species were included.

To evaluate the conflict between human development needs and areas important for bird conservation, we made use of seven categories of previously identified priority bird areas. First, based on Barnes's[47] list of 104 Important Bird Areas located within the 1796 quarter-degree grid cells used, we made use of GIS to map information on the size of each IBA. From this we obtained the number of quarter-degree cells occupied by each IBA (406 cells). Second, we used 30 previously identified optimal solutions which represent each bird species in at least one grid cell across South Africa and Lesotho, each one requiring 19 quarter-degree cells (overlapped, these 30 solutions occupy 44 quarter-degree cells in South Africa).[48] Third, based on the 1997 United Nations list of protected areas for South Africa,[49] we mapped information on the size of 423 protected areas using GIS and obtained the percentage of protected area in each quarter-degree cell that included some extent of protected area (474 cells). IBAs and protected areas are, with a few exceptions, generally smaller in size than an entire quarter-degree grid cell, although only two (0.4%) and three (0.6%) cells, respectively, were smaller that 10 ha. Fourth, the number of quarter-degree cells that contain IBAs, but without any degree of formal protection, was calculated (hereafter referred to as IBAs outside protected areas) (119 cells). Fifth, the number of minimum complementary grid cells identified previously[48] that do not include formally protected areas was calculated (hereafter referred to as minimum complementary cells outside protected areas) (24 cells). Sixth, the number of quarter-degree cells with both IBAs and protected area in the grid cell was calculated (hereafter referred to as IBAs inside protected areas) (287 cells). Seventh, the number of minimum complementary grid cells identified previously[48] with some protected areas in them was calculated (hereafter referred to as minimum complementary cells inside protected areas) (20 cells).

Quantifying human densities in priority bird areas

To address the question of whether cells representing priority bird areas are likely to be characterized by large numbers of people, we first calculated the human population of the 406 cells representing all IBAs (that is, cells corresponding to the first priority bird area category listed above). This value was then compared with the mean population size found in 10 000 random draws of 406 cells. These cells were selected from a pool of all possible grid cells, that is, the 1796 cells covering South Africa. Similarly, we then determined whether each of the remaining six categories of priority bird areas had higher values of human density than expected by chance. Finally, using the same priority bird areas, we repeated these analyses after taking the effect of climate change on human distribution patterns into account.

Climate change

The effects of climate change on the form and the strength of the relationship between human density and avian species

Table 1. Results indicating whether grid cells within each priority bird area category have significantly greater values of human density than expected by chance based on 10 000 permutations. Analyses were conducted using both current human density values and corresponding climate-adjusted values calculated from predicted precipitation.

Priority bird area categories	Mean human population density	Climate-adjusted mean human population density
IBA* cells	Greater (0.043)	Greater (0.003)
Minimum complementary cells	n.s. (0.944)	Greater (0.033)
Protected area cells	Greater (0.015)	Greater (0.0001)
IBA cells outside protected areas	n.s. (0.176)	n.s. (0.074)
Minimum complementary cells outside protected areas	n.s. (0.783)	n.s. (0.077)
IBA cells inside protected areas	Greater (0.024)	Greater (0.0001)
Minimum complementary cells inside protected areas	n.s. (0.056)	Greater (0.002)

*IBA, Important Bird Area. Significance value (*P*) in brackets. Significance was calculated at $P < 0.05$. n.s. = value not significantly greater than the mean value.

richness across South Africa were investigated in terms of mean annual precipitation (PPT in mm yr^{-1}) predicted for each of the 1796 grid cells given a doubling in pre-industrial CO_2 levels using the HadCM2 (no sulphates) model.[27,50] Precipitation, which sets the upper limit to net primary productivity, and therefore the amount of available environmental energy for a given area,[51,52] has been identified as an important correlate of spatial variation of both human density patterns[5] and avian species richness patterns[53] across South Africa.

Incorporating the same species richness and human density values as used by Chown *et al.*[5] at a quarter-degree resolution, the predicted PPT amounts were used to calculate new, climate-adjusted avian species richness and human densities for each grid cell covering South Africa (excluding Lesotho). This was done by substituting the climate-adjusted PPT values into the regression equations representing avian species richness and human density values as a function of current precipitation (Avian species richness = $64.49 + .2128 \times \text{PPT}$, $r^2 = 0.47$; and $\log_{10}$ human density = $2.707 + 0.00218 \times \text{PPT}$, $r^2 = 0.44$). The human density data for grid cells entirely protected by nature reserves and therefore with ostensibly zero value were not modified by the climate-adjusted PPT values.

Ordinary least-squares regression was used to investigate the relationship between human density and avian species richness after patterns of both had been altered to take account of predicted climate change. Tabulated results were subjected to sequential Bonferroni corrections, a nonparametric technique used to calculate table-wide significance levels and therefore the better to control the group-wide type-I error rate.[54] The regression equation obtained from this relationship was then compared with that for the relationship between human density and avian species richness before taking climate change into account, using analysis of covariance (ANCOVA).[55] We predicted that increasing conflict between human development needs and avian conservation requirements, as a consequence of climate change, would be indicated by a rise in the y-intercept value (that is, for a given value of avian richness there would be more humans per grid cell) and/or the regression coefficient (that is, areas of high species richness will have even greater human densities than before, although areas of low richness might not be affected to the same extent).[27]

Results

Human densities in priority bird areas before climate change

The 406 quarter-degree grid cells representing IBAs had significantly greater human densities than expected by chance ($P < 0.05$, 10 000 permutations; Table 1). This was also true for the cells representing formal protected areas (474 cells), and for the cells representing IBAs inside protected areas (287 cells) (Table 1). There was considerable spatial overlap (48%) between the cells representing protected areas and those representing IBAs. It is reasonable, therefore, to suggest that a large number of protected areas and IBAs are either located relatively close to one another (within a ~25 km radius of each other), show some spatial overlap, or tend to be represented by the same cells. Thus, several IBAs were affected by factors similar to those that result in high human densities in protected area cells (see Discussion).

Population pressure generally leads to enhanced land transformation. This explains our finding that 402 (85%) of the 474 cells containing protected areas were also transformed to some degree by anthropogenic activities, and 179 (45%) of these transformed cells were more than 25% modified (mean land transformation value across the 1796 grid cells was *c.* 19%), based on Fairbanks and Thompson's[56] National Land-Cover database for South Africa. This was also true for the grid cells representing IBAs, where 336 (83%) of the 406 cells were transformed to some degree, and 154 (46%) of these transformed cells were more than 25% modified. This was because protected areas and/or IBAs are often smaller in area than an entire quarter-degree grid cell, which means that human land transformation, conservation activities, and areas important for conservation often occur within the same grid cell.

Moreover, as has been found for protected areas elsewhere in Africa[7] and in the United States,[12] small protected areas are likely to be more prone to the effects of high human population densities than larger ones. This follows from a significant negative relationship between human density and the size of protected areas ($r = -0.32$, $P < 0.0001$, d.f. = 1, 263),[5] and human density and size of the IBAs ($r = -0.13$, $P < 0.007$, d.f. = 1, 404). In addition, there was a significant relationship between the perimeter to area ratio (larger protected areas have smaller values) and human density for both protected areas ($r = 0.22$, $P < 0.005$, d.f. = 1, 263) and IBAs ($r = 0.21$, $P < 0.005$, d.f. = 1, 404). For these reasons, and because areas important for bird conservation in South Africa are generally small (protected areas: 70% <5000 ha; IBAs: 36% <5000 ha) avian conservation would benefit considerably from an increase in the size and/or number of priority bird areas under protection.

Quarter-degree grid cells representing IBAs outside protected areas did not support significantly greater human densities than expected by chance (Table 1). This suggests that some of these IBAs may be favourable for conservation. However, this conclusion would be enhanced if it were possible to identify a subset of IBAs outside protected areas with significantly lower human densities than expected by chance. Using a random draw technique (see Methods), we examined the IBA grid cells outside protected areas (119 cells) by comparing the mean human density value of these cells with the mean human density found for 10 000 sets of (n) randomly selected grid cells after eliminating the IBA grid cell with the highest human density. The elimination of such a cell is necessary to identify the largest subset of

Table 2. Pearson correlation coefficients between human population density and avian species richness before and after the values for both were calculated from predicted precipitation values.

Variables	Before climate change	After climate change
Species richness vs. Log$_{10}$ population density	0.61***	0.98***

***$P < 0.001$. Significance was calculated after a sequential Bonferroni correction was applied (d.f. = 1, 1794).

IBAs possible while still maintaining lower human densities than expected by chance. In other words, the number of randomly selected grid cells within each set (n) was equivalent to the number of IBA cells minus the cell with the highest human density. After several eliminations, to identify the maximum number of IBA cells (found outside protected areas) with significantly lower human densities than expected by chance, a total of 108 grid cells was identified (see Fig. 2).

The human population contained in the quarter-degree cells representing all 30 of the different minimum complementary set solutions (44 cells) was no different from that of the randomly drawn cells (Table 1). This was true also of those complementary cells found outside the current protected area network (24 cells) and for those complementary cells inside the current protected area network (20 cells, Table 1). However, the collection of 30 complementary solutions contains a sub-set of solutions that were equally efficient (representing all species in 19 cells), but which differed in terms of the specific sites they require. This provides some flexibility[16] for minimizing the human population in reserve networks while still representing all species. After taking this limited flexibility into account by examining whether each of the optimal complementary sets representing all species had significantly higher values of human density than expected by chance, the human population in the 30 complementary solution sets was either slightly higher than (significantly so for 18 out of 30 cases) or not different from randomly drawn cells.[5]

Avian richness and human density before and after climate change

Bird species richness showed a strong, significant positive correlation with human density (Table 2), with strong non-linear or asymptotic effects (checked using a quadratic term). Much of the correlation between richness and human density was a consequence of spatially structured environmental variation, largely the result of a strong east–west moisture gradient in southern Africa,[52] to which both birds and humans respond.[5,53] While several studies have indicated that climate is likely to contribute most to changes in richness in the region, vegetation heterogeneity has a second-order effect on changes in species identity, a major component of turnover.[51–53,57] As expected, when using human density and species richness calculated from the climate-affected PPT values, the correlation between species richness and human density remained positive (Table 2). More interestingly, the linear regressions between human densities and avian species richness before and after climate change revealed significant differences in both the y-intercept values ($P < 0.0001$, $F = 41.7$, d.f. = 1, 3589) and in the regression coefficients ($P < 0.001$, $F = 249.1$, d.f. = 1, 3588) (Fig. 3). Based on these linear regressions, a relative decrease in conflict between human development and bird species richness can be expected in areas with values of the latter presently lower than *c.* 170 species (corresponding to the x-axis value at the point where the two linear regressions intersect each other; see Fig. 3), and consequently, a relative increase in conflict between human development and bird species richness can be expected in areas with the latter values presently higher than *c.* 170 species (see Fig. 4 for these areas).

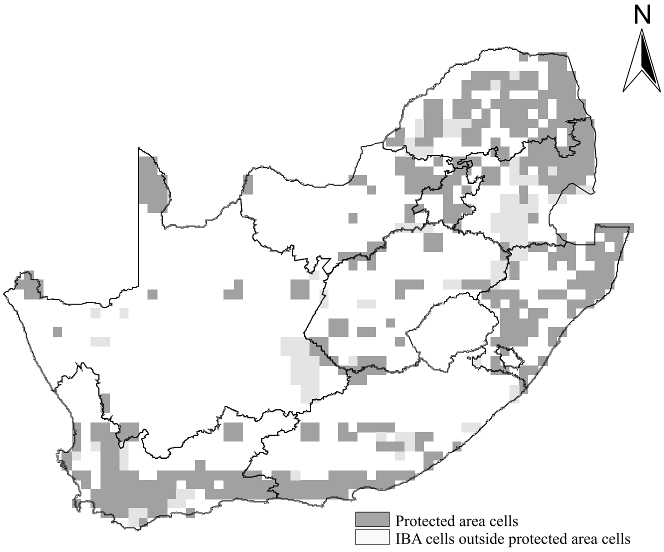

Fig. 2. Spatial distribution of protected area cells across South Africa in relation to Important Bird Area (IBA) cells outside the current protected area network with lower than expected human density values.

Human densities in priority bird areas after climate change

The likely increase in conflict between people and birds in some areas of South Africa, following climate change, raised the question of whether the cells that currently represent priority bird areas are likely to support larger numbers of people as a consequence of climate change.

Quarter-degree grid cells representing IBAs had significantly greater human densities than expected by chance after taking climate change effects into account (Table 1). Although this was also the case before taking climate change into account, the difference between the climate-adjusted density values for the IBAs and those of the randomly drawn cells was more pronounced (larger) in this case (Table 1). This means that elevated human numbers are likely to have a pronounced effect on the IBAs following climate change. A similar result was obtained for the grid cells representing protected areas and for cells representing IBAs inside protected areas (Table 1). In the case of grid cells representing all combinations of the 30 different minimum complementary site solutions (the 44 cells occupied by these 30 solutions), significantly greater human densities than expected by chance were found after taking climate change into account (Table 1). Moreover, because the densities were higher than expected from a random draw, it was clear that these minimum complementary cells were likely to be characterized by higher numbers of humans following climate change. A similar result was obtained for the grid cells representing minimum complementary cells inside protected areas (Table 1).

Finally, the total climate-adjusted human population in the IBA cells outside protected areas, and the total climate-adjusted human population in the minimum complementary cells outside protected areas, were no different from those of randomly drawn cells (Table 1). However, both here and in previous analyses, the overall number of people in the cells generally increased. Thus, like the regression analyses, the random draw results also suggested that conflict between human requirements and avian conservation needs is likely to escalate considerably under a climate change scenario.

Discussion

Human population density and avian species richness were strongly and positively related, indicating that areas with the most species are associated with the greatest human population density. This means that there is substantial scope for conservation conflicts in the region, as has been demonstrated elsewhere.[1,3,4] This conflict is likely to affect conservation areas for two main reasons. First, human population densities are higher immediately adjacent to all protected areas in the region than they are elsewhere.[5] Protected areas generally provide access to improved resources such as bush meat and/or fuelwood, and to employment opportunities from tourism.[7,13,58] In consequence, reserves in developing countries such as South Africa are considered centres of economic opportunity within an otherwise impoverished economic landscape.[59–61] Such centres could therefore enhance human settlement around protected areas and partly be responsible for the positive correlation found between human population density and avian species richness. Second, small reserves, which represent most formally protected areas in the region (70% <5 000 ha),[62] are more prone to intense edge effects caused by human land transformation than large reserves.[7,12] This is mostly because smaller reserves tend to be surrounded by higher human population densities than larger ones. Thus, in southern Africa conflicts between human requirements and conservation needs are a feature both of conservation areas and their setting.[31,62–64]

One way in which the conflict between human needs and conservation requirements might be reduced is to expand the existing reserve network with additional protected areas.[35] However, whether expansion of the reserve network would alleviate the conflict depends on which of the areas identified as important for conservation are selected. Conservation is more feasible in thinly populated areas than in those dominated by people.[65]

In the case of the 30 different optimal complementary networks, we find that although the maximum achievable population (that is, the complementary set with the highest human population) found in these sets is more than twice that of randomly selected cells, the minimum possible human population (the complementary set with the lowest human population) encountered is only slightly smaller. This suggests that there is some, but not much, flexibility for avoiding human conflict in the most efficient complementary sets.[5] Moreover, the potential for these optimal complementary networks to be treated as acquisition areas is also limited. The primary reason for their limited utility is that many of these cells reflect areas of ecological transition,[48] and therefore represent species at the edge of their distribution ranges. Such representations are unlikely to provide long-term security for the species involved.[39]

By contrast, the options for increasing the conservation network by adding IBAs with low human population density seem more promising. Indeed, 108 IBA cells (found outside protected areas) with human densities that are lower than expected by chance were identified in our analysis (Fig. 2). Formal protection of these areas would certainly minimize conflicts between human development and conservation needs, although in some cases only a few species might be involved owing to the ways in which IBAs are selected.[47] Because of the location of IBAs that have no formal protection, but lower human densities than expected by chance, at least some, and perhaps most of these IBAs could contribute towards increasing the size of formally protected areas. The incorporation of cells containing IBAs adjacent to protected areas would be most advantageous. However, it is important that cells containing high human population densities, situated adjacent to established conservation areas, and that could undermine effective conservation management, be avoided whenever possible.

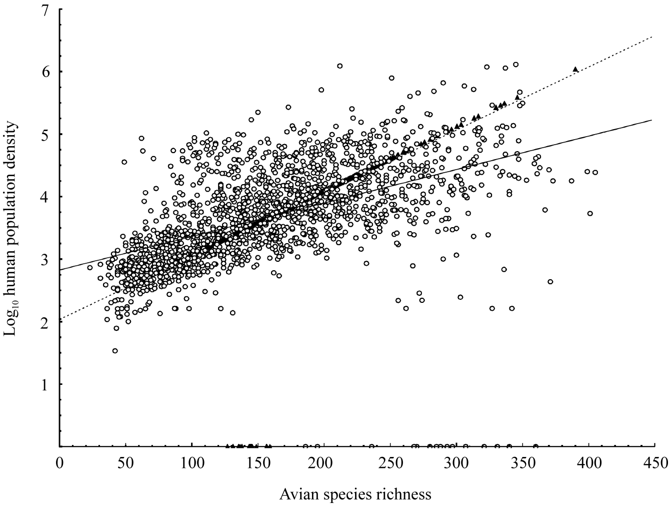

Fig. 3. Linear regressions between Log$_{10}$ human population densities and avian species richness (—; ○) before variable values were calculated based on climate-adjusted PPT (Log$_{10}$ human density = 2.83 + 0.005 × Avian species richness; r^2 = 0.25), and (-----; ▲) after variable values were calculated based on climate-adjusted PPT (Log$_{10}$ human density = 2.03 + 0.010 × Avian species richness; r^2 = 0.71).

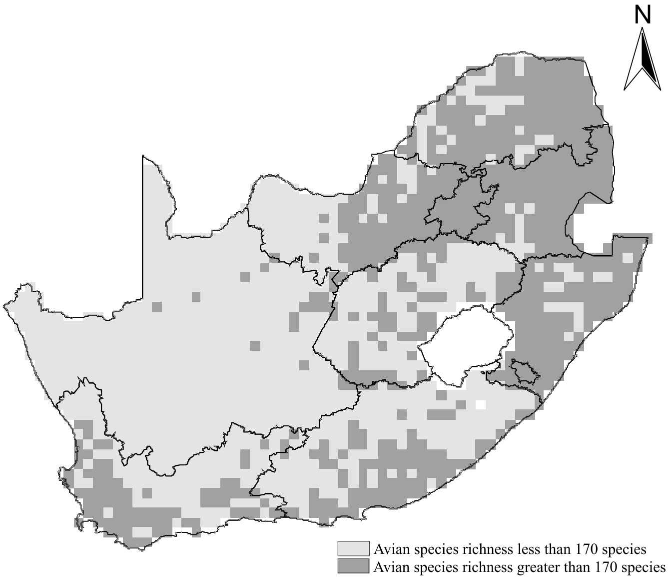

Fig. 4. The spatial distribution of quarter-degree grid cells across South Africa, with avian species richness values presently less than, and greater than, 170 species per cell.

Under a climate change scenario it seems likely that conservation conflicts will increase, mainly because both human numbers and species richness change markedly in the same grid cells, owing to similar responses to changes in water availability (Fig. 3). In southern Africa, water availability is an important correlate of species richness and is probably responsible for much of its variation.[51–53] Moreover, human population density increases with water availability[5] Any change in water availability might therefore be translated into a corresponding alteration in both richness and population density,[27,66] although humans can partially mitigate these changes by hydraulic engineering. However, this, in turn, has knock-on effects on biodiversity. Water availability in southern Africa is likely to decline,[27,67] and so fewer areas across the country will harbour both high species richness and greater population density than is presently the case (Fig. 5).[67] These are mostly areas that currently have a high rainfall and an avifauna greater than about 170 species. If the estimated annual population growth continues at 2.2%, then the high species richness cells will have even higher human population densities than estimated by the simple forecast adopted here. There is thus likely to be a substantial increase in conflict between conservation and other landuse requirements. This conflict is also likely to be exacerbated by future human demands for agricultural resources, especially water, as human population continues to grow.[68] Indeed, anthropogenic desertification and competition between human and animal needs for water have been identified as forces leading to the extinction of mammal populations in Africa,[11] and there seems to be no reason why this should not also be the case for the avifauna, or at least some major avian groups.

Unfortunately, much of the flexibility required to expand the current conservation network, which might alleviate some of the conflict, also disappears under a climate-change scenario. Although the conservation of IBAs with lower than expected human population density does provide some scope for alleviating the conflict, human population pressure generally increases both in the IBAs and in the minimum complementary site solutions. Moreover, the value of the complementary set solutions and IBAs is likely to change as species assemblages are re-arranged when climate changes.[27] Nonetheless, low human population densities in the grid cells within which IBAs are found means that they are likely to form valuable conservation areas in an otherwise highly transformed landscape.[1,10,69]

Conservation conflict might also become less in some regions, especially the western parts, as both human populations and species richness decline with reduced rainfall.[5,27] However, whether conservation and other priority bird areas (such as IBAs) would retain their utility in these parts is not clear, largely because it is not possible to forecast exact changes in species composition for these areas.[27]

In sum, our analyses show that conservation conflicts are set to escalate in southern Africa and that there is little flexibility to ensure conservation simply by the designation of new dedicated areas. Rather, a more integrated approach, emphasizing the value of existing conservation areas, the designation of additional sites based on rational area selection principles,[70] and the sustainable development of the land surrounding these sites needs to be adopted.[64,71] This means a focus on safeguarding protected areas to ensure that they do not suffer the same fate as many of those elsewhere.[58] High population densities surrounding protected areas mean that formal protection will be increasingly difficult, though necessary. The litany of examples of adverse effects of even low-level human exploitation of resources on many species[9,72] is sufficient to show that formally protected areas should be just that. Finally, an integrated strategy also implies the careful and sustainable utilization of the non-reserve lands[71] so that the several options can be exercised for ensuring that species continue to have a future under scenarios of human population growth, increasing per capita consumption,[73] and climate change.

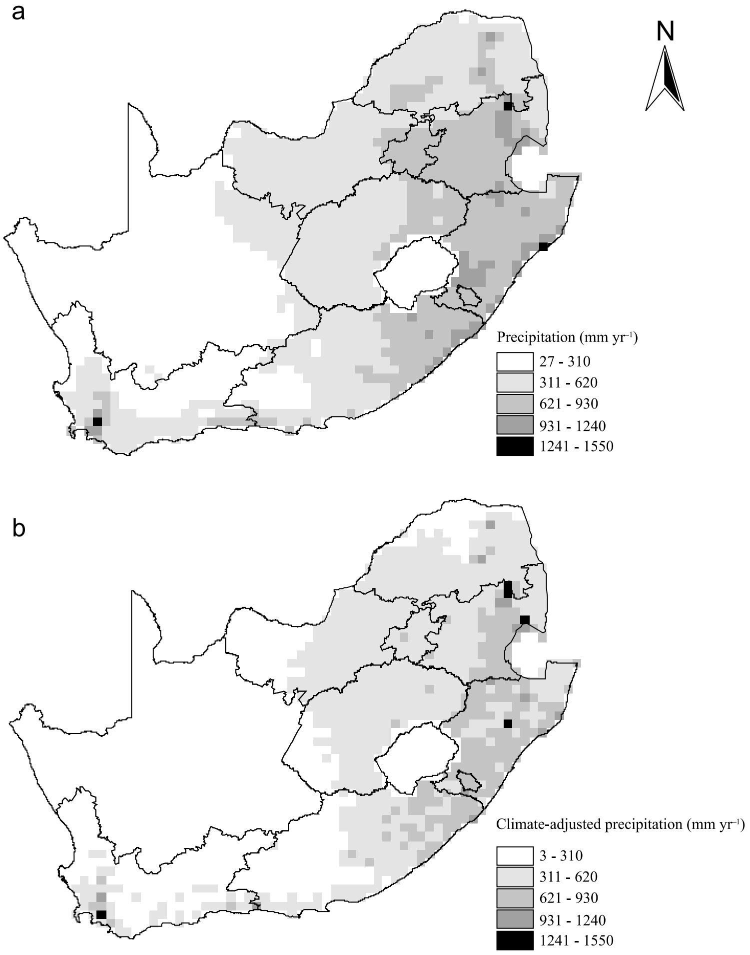

Fig. 5. Variation in precipitation values across South Africa (**a**) before and (**b**) after taking climate-adjusted precipitation values into account as predicted by Shannon.[50]

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