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Atlas data indicate forest dependent bird species declines in South Africa

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Summary

Forest ecosystems in South Africa are at risk from a variety of anthropogenic threats impacting the faunal species dependent on them. These impacts often differ depending on species-specific characteristics. Range data on forest dependent bird species from the South African Bird Atlas Project (SABAP1 and SABAP2) were analysed to determine links between deforestation, species characteristics and range declines. Half of the species studied were found to have declining ranges. Range change data for these species were correlated with data on changes in land cover from 1990 to 2014. To determine which land cover changes affect extinction, occupancy was modelled for 30 sites across South Africa which experienced a loss of more than 10 species. Most species lost were birds of prey or insectivores. Indigenous forest decreased in 17% (n = 5) sites, while plantations/woodlots decreased in 60% (n = 18) sites. Occupancy modelling showed extinction to be mitigated by plantations in 6/28 species, and forest expansion mitigated extinction in 7/28 species. Responses to deforestation did not appear to be related to particular species characteristics. Half of South Africa's forest-dependent bird species have declining ranges, with the loss of these species most prominent in the Eastern Cape province. Four responses to changes in forest and plantation cover are discussed: direct effects, with forest loss causing species loss; matrix effects, where plantation loss resulted in species loss; degradation of indigenous forest; and the advent of new forest arising from woody thickening caused by carbon fertilisation, which may not result in optimal habitat for forest-dependent birds.

Introduction

Forest habitats make up approximately 0.56% of South Africa's landscape, but are home to some 14% of the country's terrestrial bird species (Geldenhuys and MacDevette 1989). Many of these are endemic, and seven are range-restricted endemics found only in South African forests (Low and Rebelo 1996, BirdLife International 2013). Natural fragmentation has occurred as a consequence of climate changes during the Quaternary which resulted in contractions and expansion of forests, so their biota has evolved under these conditions (Eeley *et al.* 1999, Kotze and Lawes 2007) and species distributions have been influenced by these fragmentation events (Lawes *et al.* 2004). Recently forest habitats have been extensively further fragmented by human activities, with most remaining forests being smaller than 1 km^2 (Eeley *et al.* 1999). Fragmentation is largely the result of deforestation, both for commercial plantations and by rural communities, with nearly 50% of indigenous forests in South Africa estimated to be degraded as a result of anthropogenic fragmentation (MacDonald 1989, Eeley *et al.* 1999, 2001). Forests are furthermore under continued pressure from rural communities, through collection for fuelwood, building materials, food and local medicine (Cocks and Wiersum 2003, Shackleton and Shackleton 2004). A large proportion of remaining forest has consequently been degraded, with some loss of ecosystem function (Berliner 2009).

In addition to the threats of deforestation to indigenous forests, habitats have been created in the form of commercial plantations of exotic trees. Plantations have had both positive and negative effects on bird assemblages within forests, and these effects are influenced by factors including tree species used, plantation age, and previous land uses (Bremer and Farley 2010), as well as species-specific characteristics such as mobility (Hinsley *et al.* 2009), degree of specialisation (Ewers and Didham 2006, Hinsley *et al.* 2009), trophic level and body size (Schoener 1968, Ewers and Didham 2006). Plantations can have the positive effects of aiding dispersal of some bird species by acting as corridors between forest patches (Wethered and Lawes 2003, 2005); providing a habitat for species tolerant of plantations (Estades and Temple 1999); and potentially increasing biodiversity if secondary forest or exotic pasture is transformed to plantations (Bremer and Farley 2010). Their negative effects include limiting indigenous forest distribution through the alteration of fire regimes and limiting the movement of some forest bird species between these fragments of indigenous forest (Geldenhuys 1991, Wethered and Lawes 2003). Studies link increased afforestation through plantations with the replacement of grassland bird assemblages by those traditionally found in wooded habitats, both in South Africa and globally (Allan *et al.* 1997, Azpiroz *et al.* 2012), and the replacement of grassland, shrubland and indigenous forests with plantations reduces biodiversity (Bremer and Farley 2010). The addition of plantations leads to species assemblages being altered, with few nectarivorous or hole-nesting insectivorous species being found in plantations (Armstrong and van Hensburgen 1995). There has been a loss of plantations nationally over recent years, with a decrease of 0.9% per annum between 1999 and 2009. Plantation loss could negatively impact those species utilising plantations, or even those in indigenous forest fragments linked by plantations.

In 2009, it was estimated that 10% of South African forest-dependent bird species were threatened (Berliner 2009). This number has since doubled, with 19% of forest-dependent bird species in South Africa listed as 'Near Threatened' or above on the IUCN Red List 2014 (BirdLife South Africa 2014). An understanding of these changes is essential. The South African Bird Atlas Project (SABAP), which incorporates volunteer surveying of quarter-degree grid cells from 1987 to 1992, and then again from 2007 onwards, allows the prospect of investigating changes in avian distribution over the last 20 years. When overlaid with data on changes in forest distribution and plantations over the same time period, the relationship between changes in forest distribution and changes in forest dependent bird distribution can be investigated.

The aims of this study were: (1) to determine changes in the distribution of forest dependent bird species; (2) to relate these changes to changes in land-use, specifically deforestation of indigenous forests and afforestation with alien plantations; and (3) to identify causal links between these changes, including species characteristics and responses.

It was predicted that deforestation would lead to the decline of forest-dependent bird species. It was expected that there would be a mixed response to plantations, with species that thrive in plantations responding negatively to a national loss of plantations, while species which are reliant exclusively on indigenous forests would respond negatively to any increases in plantation cover. It was also expected that suites of species would respond in similar ways to changes in indigenous forest and plantation extent.

Methods

Species selection and range change

Selected species were listed as "forest-dependent" by Oatley (1989). In addition, species listed as having "high forest dependence" by BirdLife International (2014a) were selected. This resulted in a comprehensive list of 57 forest-dependent species. For the full list, see Appendix S1 in the online supplementary material. Forest-dependent in this study was defined as species depending on forest ecosystems for their ecological requirements, as used by Oatley (1989) and BirdLife International (2014a) in the creation of their respective species lists.

Species-specific information included red list status (IUCN 2013); habitat (BirdLife International 2014a, Sinclair *et al.* 2011); whether the species is found in plantations (BirdLife International 2014a); diet (Hockey *et al.* 2005, Sinclair *et al.* 2011); and whether a species is migratory or resident (Sinclair *et al.* 2011).

South African forest types have previously been categorised into three (Eeley *et al.* 2001), 10 (Cooper 1985), 12 (Mucina and Rutherford 2006), 15 (Acocks 1953) and 23 types (von Maltitz *et al.* 2003). Here we use the BirdLife International (2014b) global categories, which are based on the IUCN Habitats Classification Scheme (v 3.1), of which six categories (montane, lowland, dry, mangrove, riverine and swamp forest) occur in South Africa. These categories were used because information on which habitats bird species utilise were obtained from BirdLife International (2014b), and so the same categories were used in this paper to ensure continuity.

Changes in range size of the 57 species were determined using the South African Bird Atlas Project (SABAP). The first South African Bird Atlas Project (SABAP1), with data collection from 1987 to 1992, and SABAP2, with data collection from 2007 to September 2014, were compared. The protocol for both comprised volunteer surveying of birds within predetermined grid cells – quarter-degree grid cells were used in SABAP1, while 5-minute by 5-minute pentads were used in SABAP2. Accordingly, for each area covered by a quarter-degree grid cell in SABAP1, nine pentads were used in SABAP2. Comparisons of these datasets are thus possible by combining results from the nine pentads within each quarter-degree grid cell (Harebottle *et al.* 2010), provided that only presence/absence data, rather than those representing reporting rates, are used. Harebottle *et al.* (2010) provide further information on data acquisition and validation.

Range sizes for each species in SABAP1 and SABAP2 were compared to determine whether they were increasing, decreasing or stable. This resulted in a list of 28 decreasing species, 22 increasing species and seven stable species. The larger (and thus coarser) sampling units (quarter-degree grid cells: QDGC) used in SABAP1 compared to the finer scale (pentads) sampling in SABAP2 suggests that species might have been present but not detected in SABAP1, but it is far less likely that species would remain undetected within a given QDGC in SABAP2. Accordingly, a species could falsely be marked "absent" in SABAP1, and then seem to be increasing in SABAP2 when in reality this is a sampling artefact. Therefore, only species with decreasing ranges were used for quantitative analyses in this study (see full list in Table 1). Accordingly, the results of this study are conservative.

Percentage range change was used for analyses, and was calculated as the percentage of the range in SABAP1 lost by SABAP2. Previous studies using this technique include a study on fynbos birds in South Africa (Lee *et al.* 2015), and a prediction of Important Bird Areas in southern Africa (Coetzee *et al.* 2009).

Site selection and land cover change

We aimed to identify QDGCs in which more than 10 species (> 18% of the list of forest dependent species) were present in SABAP1 but not in SABAP2. This was determined by analysis of each QDGC known to contain either forest or plantation in the last 20 years (van den Berg *et al.* 2008, SANBI 2009, Schoeman *et al.* 2013). Only those QDGC with a sum of four or more SABAP2 report cards were used. Thirty QDGCs met these criteria, 17 of which were situated in the Eastern Cape province (Figure 1).

Two national land cover datasets were used to determine changes in forest and plantation/woodlot extent. The South African National Land Cover Dataset 1990 (GeoterraImage 2015a), was used to establish a baseline of forest and plantation cover. This was compared with the South African National Land Cover Database 2013/2014 (GeoterraImage 2015b), by calculating the percentage area covered by each category of land cover within each QDGC in ArcGIS 10.2 (ESRI 2011), and comparing the values for each category between 1990 and 2013/2014.

Table 1. Percentage range change throughout South Africa for all forest dependent bird species which experienced range declines between SABAP1 and SABAP2; as well as the number of report cards for each species across the country; and the number of report cards for each species within the thirty sites which experienced the loss of ten or more forest dependent species.

Order	Scientific name	Common name	Author	Percentage range change	Country-wide		Sites	
					S1	S2	S1	S2
Accipitridae	*Accipiter rufiventris*	Rufous-chested sparrowhawk	Smith 1830	-36.33	1227	737	52	5
Accipitridae	*Accipiter tachiro*	African goshawk	Daudin 1800	-4.69	5907	5369	187	69
Accipitridae	*Buteo trizonatus*	Forest buzzard	Rudebeck 1957	-8.05	1571	1893	48	0
Accipitridae	*Circaetus fasciolatus*	Southern banded snake-eagle	Kaup 1850	-16.00	140	186	3	2
Accipitridae	*Stephanoaetus coronatus*	African crowned eagle	Linnaeus 1766	-14.12	3278	2550	98	28
Bucerotidae	*Bycanistes bucinator*	Trumpeter hornbill	Temminck 1824	-3.96	6542	4801	163	136
Campephagidae	*Coracina caesia*	Grey cuckooshrike	Lichtenstein 1823	-16.29	1165	1292	54	15
Columbidae	*Aplopelia larvata*	Lemon dove	Temminck 1809	-27.72	1275	1185	84	4
Fringillidae	*Crithagra scotops*	Forest canary	Sundevall 1850	-10.23	2376	3204	123	61
Malaconotidae	*Telophorus olivaceus*	Olive bush-shrike	Shaw 1809	-2.23	2720	5246	84	67
Motacillidae	*Motacilla clara*	Mountain wagtail	Sharpe 1908	-29.61	1794	1223	79	14
Muscicapidae	*Batis capensis*	Cape batis	Linnaeus 1766	-1.30	6756	10533	297	97
Muscicapidae	*Trochocerus cyanomelas*	Blue-mantled crested-flycatcher	Vieillot 1818	-6.36	1529	2090	75	24
Muscophagidae	*Tauraco corythaix*	Knysna turaco	Wagler 1827	-4.08	11266	5863	820	58
Nectariniidae	*Nectarinia chalybea*	Southern double-collared sunbird	Linnaeus 1766	-12.28	10388	17415	285	60
Oriolidae	*Oriolus oriolus*	Eurasian golden oriole	Linnaeus 1758	-34.62	1277	549	21	8
Psittacidae	*Poicephalus robustus*	Cape parrot	Gmelin 1788	-58.33	1725	391	43	25
Rallidae	*Sarothrura elegans*	Buffspotted flufftail	Smith 1839	-28.57	954	653	76	12
Strigidae	*Strix woodfordii*	African wood-owl	Smith 1834	-12.32	2958	963	143	22
Sylviidae	*Bradypterus barratti*	Barratt's warbler	Sharpe 1876	-4.48	570	819	21	21
Sylviidae	*Camaroptera brachyura*	Green-backed camaroptera	Vieillot 1820	-13.17	12635	15207	262	367
Timaliidae	*Lioptilus nigricapillus*	Bush blackcap	Vieillot 1818	-10.71	286	429	10	5
Trogonidae	*Apaloderma narina*	Narina trogon	Stephens 1815	-4.27	2344	1832	123	25
Turdidae	*Cossypha dichroa*	Chorister robin-chat	Gmelin 1789	-19.53	2710	2556	161	16
Turdidae	*Phylloscopus ruficapilla*	Yellow-throated woodland-warbler	Sundevall 1850	-20.69	945	10533	24	18
Turdidae	*Pogonocichla stellata*	White-starred robin	Vieillot 1818	-23.02	823	701	22	7
Turdidae	*Zoothera gurneyi*	Orange ground-thrush	Hartlaub 1864	-8.33	197	241	10	0
Turdidae	*Zoothera guttata*	Spotted ground-thrush	Vigors 1831	-27.59	185	188	3	2

Figure 1. Sites across South Africa that experienced a loss of 20% or more of forest-dependent bird species between the two South African Bird Atlas Project (SABAP) periods of 1987–1992 and 2007–present. Filled in sites indicate those that experienced a loss of indigenous forest during this period. The grey shaded area represents the former East Griqualand.

Occupancy modelling

Reporting rate was not used as a proxy for abundance in this study due to the inherent flaws in this method when species have low detectability, as with most forest bird species (see MacKenzie *et al.* 2002). Occupancy modelling, using presence/absence data, was used to determine the effects of land cover change on species across the 30 identified QDGCs (sites). Data for all species were extracted from the SABAP database of the Animal Demography Unit of the University of Cape Town using R (R Core Team 2014). SABAP1 data were extracted from the start of 1 January 1987 to 31 December 1991, and for SABAP2 from 1 July 2007 to 30 September 2014, from the 30 sites. Data formatting was done as per MacKenzie *et al.* (2006).

Single species, multi-season occupancy models were run on PRESENCE (Hines 2006), with SABAP1 as the first season and SABAP2 as the second. Four parameterizations were used to determine best fit, by holding all parameters constant and adding appropriate covariates sequentially for ψ, γ, ε and ρ. These covariates were percentage land cover in 1990 for ψ, and land cover change for γ and ε. ρ was kept constant due to the sampling technique, but seasonal effects were allowed. Additional covariates were then added into a single model to determine best fit. A logistic link was used to calculate probabilities, with 10,000 bootstraps performed. Models with a delta AIC (Akaike's Information Criterion) of less than 2.00 were selected as fitting best. Significance at $P = 0.05$ was determined using standard errors and 95% confidence intervals.

Statistical analyses

T-tests were performed on the number of cards and reports per species and per site to ensure that the numbers for SABAP1 and SABAP2 were comparable. Species characteristics on all 57 forest dependent species were transformed to a binary matrix for statistical analysis, as per Okes *et al.* (2008). Although some variables could have been recorded as categorical, a binary index was used for all characteristics to allow comparison. Species were categorised by response, as having an increasing range (increasers), having a decreasing range (decreasers), or having a stable range

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with a change of fewer than two quarter-degree grid squares (stable) before analyses. Data on species characteristics were subsequently grouped by response, and characteristics analysed as a percentage of the whole to identify patterns. Chi-squared tests for homogeneity were performed to determine significant differences in characteristics among responses, with the hypothesis that species with a similar response to land cover change would exhibit similar characteristics. Chi-square tests were then performed on the characteristics data to determine the prevalence of each category of each characteristic within response groups.

Results

The changes in range size across South Africa for each declining forest dependent species can be seen in Table 1. The average change in range size was -16.39%. Species with the largest changes are the Rufous-chested Sparrowhawk, *Accipiter rufiventris* (-36.33%), Eurasian Golden Oriole, *Oriolus oriolus* (-34.62%), and Cape Parrot, *Poicephalus robustus* (-58.33%). The thirty sites analysed in this study, and the forest-dependent bird species which were lost from each, can be seen in Table 2.

Within the 30 study sites, there were 1,225 report cards submitted for SABAP1 (mean 40.83), and 1,192 report cards submitted for SABAP2 (mean 39.73). No significant difference was found ($P = 0.4678$), indicating that the number of cards is comparable. Within the study sites, the number of reports of all declining forest dependent species was 3,371 for SABAP1 and 1,168 for SABAP2 ($P = 0.0096$). This decrease in the number of reports (by almost two thirds) is indicative of a true loss of occupancy of these species within these sites. Table 1 shows a breakdown of the number of report cards submitted for SABAP1 and SABAP2 per species.

Table 3 shows the number of report cards submitted for each QDGC (site) which experienced a loss of 10 or more bird species between SABAP1 and SABAP2, as well as the number of species lost and gained within each site between SABAP1 and SABAP2. In exactly half of the 30 sites, sampling effort was improved or equal between SABAP2 and SABAP1, and the other half it was

Table 2. Patterns of forest dependent bird species loss between SABAP1 and SABAP2. Red cells indicate sites from which a species was lost, blue cells indicate a site that a species newly colonized, yellow cells indicate sites within which a species was stable, and grey sites indicate a site in which the species was not found. The extinction parameters of the species as per occupancy modelling are indicated in the final column, where F indicates a relationship between forest extent and extinction; P indicates a relationship between plantation extent and extinction, (-) indicates a negative relationship and (+) indicates a positive relationship.

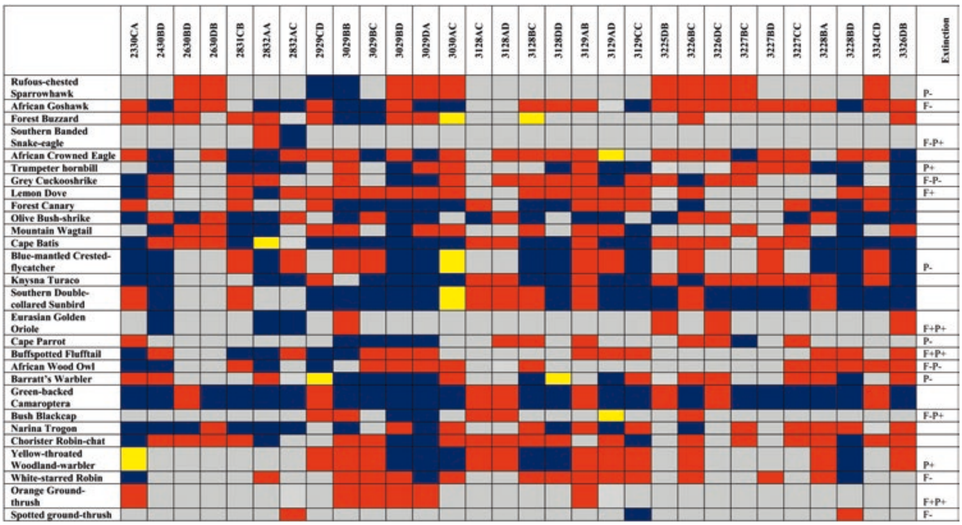

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Table 3. The number of report cards for each of 30 sites experiencing a loss of 10 or more forest dependent bird species between SABAP1 (1987–1992) and SABAP2 (2007–present), and the number of bird species gains (where a species was not found in a site in SABAP1 but was found there in SABAP2) and bird species losses (where a species was found in a site in SABAP1 but not in SABAP2) from that site between the two atlas periods.

Province	QDGC site	SABAP1	SABAP2	Species gains	Species losses
Northern Province	2330CA	76	19	4	11
	2430BD	103	256	3	11
Mpumalanga	2630BD	35	9	0	10
	2630DB	53	5	1	10
KwaZulu-Natal	2831CB	39	45	3	10
	2832AA	48	180	3	10
	2832AC	39	93	2	10
	2929CD	114	186	1	13
	3029BB	50	133	2	15
	3029BC	30	20	3	11
	3029BD	5	22	1	11
	3029DA	20	15	1	11
	3030AC	7	30	4	19
Eastern Cape	3128AC	5	5	0	10
	3128AD	13	6	0	14
	3128BC	3	4	2	13
	3128DD	6	7	2	10
	3129AB	2	5	0	23
	3129AD	1	11	2	11
	3129CC	9	19	2	12
	3225DB	38	5	0	11
	3226BC	8	4	0	18
	3226DC	104	8	0	15
	3227BC	27	7	1	12
	3227BD	8	4	1	10
	3227CC	10	6	1	14
	3228BA	6	5	0	13
	3228BD	17	13	0	10
	3324CD	7	19	0	14
	3326DB	342	51	0	11

lower (Table 3). In terms of sites which had lost more than 10 forest dependent species, losses were most prevalent in the Eastern Cape ($n = 17$ sites) and KwaZulu-Natal ($n = 9$ sites). The sites with the greatest loss of species were 3129AB (18 species lost), and 3226BC (15 species lost) (Table 2), both of which are in Eastern Cape province (Figure 1).

Within the Eastern Cape, 10/17 sites had a decreased sampling effort in SABAP2. Two of these (3225DB and 3326DB) fall outside of the former homelands. Five are in the former Ciskei, all of which had a decreased sampling effort in SABAP2. The remaining three are in the former Transkei, but the remaining six sites in this region had improved sampling effort in SABAP2. Six of the KwaZulu-Natal sites fall within East Griqualand, each of which fell partially in the former Transkei and partially in the former Natal province (Figure 1); again only two (one third) of these sites had a decreased sampling effort in SABAP2, while the other four (two thirds) had improved sampling. Hence, in the former Ciskei reduced sampling effort may have resulted in an overestimation of species loss.

Indigenous forest decreased in five of 30 sites between 1990 and 2014, while plantation/woodlot cover decreased in 18 of 30 sites over the same time period (Figure 2). Of the five sites

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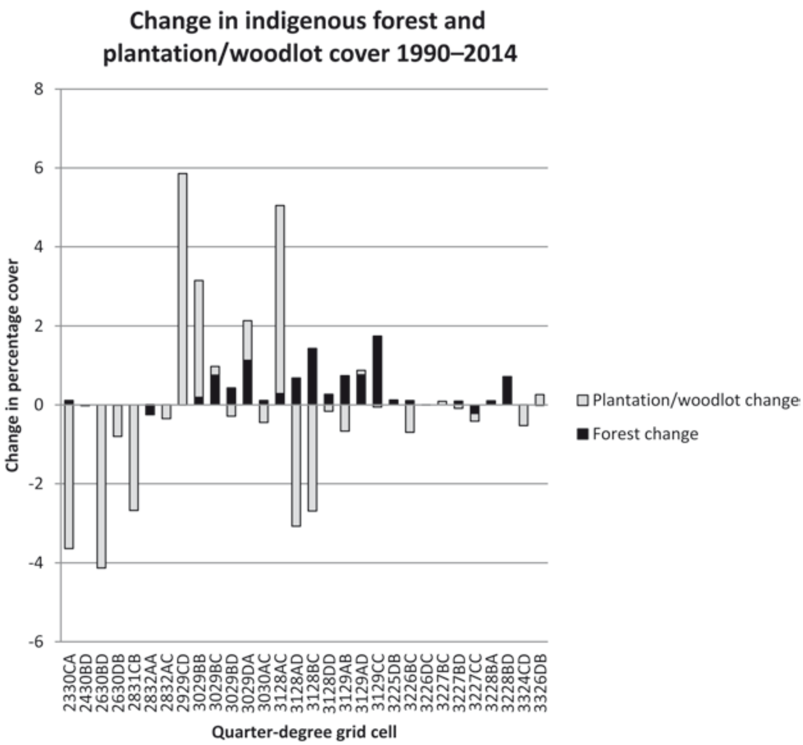

Figure 2. Changes in indigenous forest and plantation/woodlot for each of the 30 sites that experienced a loss of 20% or more of forest dependent bird species between SABAP1 (1987–1992) and SABAP2 (2007–2014).

experiencing a loss of indigenous forest, three are located in KwaZulu-Natal (2630DB, 2832AA, 2929CD), and two are located in the Eastern Cape (3227CC, 3326DB). The largest change in indigenous forest was an increase of 1.7% (mean 0.3%), while the largest change in plantation/woodlot cover was an increase of 5.8% (mean -1.2%).

Forest extent determined initial occupancy (i.e. occupancy in SABAP1) for 14 species, while for one species occupancy was more likely in sites with less forest cover (Rufous-chested Sparrowhawk). Plantation extent determined initial occupancy for eight species, while for five species it was limited by plantation extent (Table 4).

Increases in forest-mitigated extinction in seven species (African Goshawk *Accipiter tachiro*, Southern Banded Snake-eagle *Circaetus fasciolatus*, Grey Cuckooshrike *Coracina caesia*, Bush Blackcap *Lioptilus nigricapillus*, White-starred Robin *Pogonocichla stellata*, African Wood Owl *Strix woodfordii*, and Spotted Ground-thrush *Zoothera guttata*). Increases in forest extent contributed towards local extinction in four species (Lemon Dove *Aplopelia larvata*, Eurasian Golden Oriole, Buff-spotted Flufftail *Sarothrura elegans*, and Orange Ground-thrush *Zoothera gurneyi*) (Table 4).

Increases in plantation extent mitigated extinction in six species (Rufous-chested Sparrowhawk, Barratt's Warbler *Bradypterus barratti*, Grey Cuckooshrike, Cape Parrot, African Wood Owl, and Blue-mantled Crested-flycatcher *Trochocerus cyanomelas*). Increases in plantation extent contributed towards local extinction in six species (Trumpeter Hornbill *Bycanistes bucinator*, Southern Banded Snake-eagle, Bush Blackcap, Eurasian Golden Oriole, Yellow-throated Woodland-warbler *Phylloscopus ruficapilla*, and Orange Ground-thrush) (Table 4).

Table 4. Summary of significant land cover factors affecting initial occupancy and extinction of forest-dependent bird species, as well as whether this effect was positive (+) or negative (-). Positive effects indicate that with a larger covariate value the probability of initial occupancy or extinction was greater; negative effects indicate that a larger covariate value led to a smaller probability of initial occupancy or extinction.

Species	Common name	Initial occupancy	Extinction
Accipiter rufiventris	Rufous-chested Sparrowhawk	Forest-	Plantations-
Accipiter tachiro	African Goshawk	Forest+	Forest-
Coracina caesia	Grey Cuckooshrike	Forest+, plantations-	Forest-, plantations-
Telophorus olivaceus	Olive Bush-shrike	Forest+, plantations+	
Stephanoaetus coronatus	African Crowned Eagle	Forest+, plantations+	
Aplopelia larvata	Lemon Dove		Forest+
Motacilla clara	Mountain Wagtail	Forest+	
Circaetus fasciolatus	Southern Banded Snake-eagle		Forest-, plantations+
Trochocerus cyanomelas	Blue-mantled Crested-flycatcher	Plantations+	Plantations-
Telophorus olivaceus	Olive Bush-shrike	Forest+, plantations+	
Nectarinia chalybea	Southern Double-collared Sunbird	Forest+, plantations+	
Stephanoaetus coronatus	African Crowned Eagle	Forest+, plantations+	
Trochocerus cyanomelas	Blue-mantled Crested-flycatcher	Plantations+	Plantations-
Oriolus oriolus	Eurasian Golden Oriole		Forest+, plantations+
Poicephalus robustus	Cape Parrot		Plantations-
Strix woodfordii	African Wood Owl	Forest+, plantations-	Forest-, plantations-
Bycanistes bucinator	Trumpeter Hornbill	Forest+, plantations-	Plantations+
Crithagra scotops	Forest Canary	Forest+	
Tauraco corythaix	Knysna Turaco	Plantations+	
Buteo trizonatus	Forest Buzzard		
Batis capensis	Cape Batis	Forest+, plantations+	
Sarothrura elegans	Buff-spotted Flufftail		Forest+
Pogonocichla stellata	White-starred Robin		Forest-
Zoothera gurneyi	Orange Ground-thrush		Forest+, plantations+
Zoothera guttata	Spotted Ground-thrush	Plantations-	Forest-

Species characteristics were analysed within each response group. Chi-squared tests for homogeneity found no significant difference in characteristics among response groups. Pearson's chi-square tests (Table 5) showed increasing species to occur more frequently in lowland and dry forest ($P < 0.005$), while decreasing and stable species occurred most frequently in montane and lowland forest ($P < 0.005$ in both cases) (Figure 3). More decreasing than increasing species were monogamous ($P < 0.005$; 96% of decreasing species as opposed to 86% of increasing species). Solitary nest dispersion was prevalent in both increasing ($P = 0.05$) and decreasing species ($P < 0.005$). A higher proportion of decreasing species have built nests ($p < 0.005$) than other nest categories. A higher proportion of stable species were insectivores ($P = 0.025$). Stable species also had a significantly lower body size (< 20 cm, $P = 0.025$) and body mass (< 100 g, $P = 0.025$), and have a tendency to breed in summer ($P = 0.025$).

Discussion

The results of this study suggest that at least 50% of forest-dependent birds in South Africa are experiencing range declines (Table 1). In terms of sites which had lost more than 10 forest dependent species, losses were most prevalent in the Eastern Cape ($n = 17$ sites) and KwaZulu-Natal ($n = 9$ sites). The forests of the former homelands were transferred from the former Ciskei and Transkei conservation authorities to the national forestry department post-1994. The inland forests of the Eastern Cape and former East Griqualand (the latter now forms part of the province

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Table 5. Results of the Chi-square test on species characteristics of South African forest dependent birds. Significance is marked at the 0.05 (*), 0.025 (**) and < 0.005 (***) level.

Characteristic	Increasing	Decreasing	Stable
Plantation occurrence	0.995	0.99	0.9
Forest dependency	0.995	0.995	0.9
Threatened	0.995	0.995	0.9
Response to afforestation	0.95	0.995	0.9
Forest type	<0.005***	<0.005***	<0.005***
Specialist/Generalist	0.995	0.995	0.995
Mobile/Sedentary	0.99	0.995	0.9
Migrant/Resident	0.9	0.9	0.95
Endemicity	0.95	0.99	0.9
Gregarious/Solitary	0.995	0.995	0.975
Location in forest	0.995	0.995	0.995
Diet level 1	0.995	0.975	0.9
Diet level 2	0.9	0.9	0.025**
Body size (cm)	0.9	0.95	0.025**
Nest type	0.1	<0.005***	0.1
Breeding system	0.9	<0.005***	0.9
Nest dispersion	0.05*	<0.005***	0.9
Nest site fidelity	0.995	0.995	0.975
Body mass (g)	0.9	0.9	<0.005***
Precocial/Altricial	0.9	0.9	0.9
Number of eggs	0.995	0.975	0.95
Breeding season length	0.95	0.99	0.9
Breeding season	0.9	0.9	0.025**

of KwaZulu-Natal, and can be seen in Figure 1) are associated with plantations, granting them some measure of protection as a result of this proximity, as forestry companies police them. However, the majority of the coastal forests (most of which fall within the former Transkei) are not associated with plantations, have not been uniformly effectively conserved post-1994, resulting in alien floral invasion, deforestation, and some illegal harvesting of trees (J. Feely pers. comm.). This may have led to differences in the response of species to these changes.

Local extinction of forest dependent birds was influenced almost equally by changes in indigenous forest and plantation/woodlot cover (Table 4). The mean change in indigenous forest was a very small increase (0.3%), while the mean decrease in plantation cover, although still small (1.2%) was four times larger. In terms of particular grid squares, 60% ($n = 18$) experienced plantation loss while only 17% ($n = 5$) experienced deforestation of indigenous forest (Figure 2). There were four main responses to changes in forest and plantation/woodlot extent occurring between the SABAP1 and SABAP2 surveys.

Species which suffered a direct impact of changes in forest extent were the African Goshawk, Southern Banded Snake-eagle, Grey Cuckooshrike, Bush Blackcap, White-starred Robin, African Wood Owl, and Spotted Ground-thrush. These species went extinct from sites where indigenous forest was lost ($n = 5$ sites, Figure 2), and remained in sites where forest extent increased. Further deforestation of indigenous forest should be avoided in order to conserve these species.

An apparent paradox is that four species suffered a decline in areas with increased indigenous forest: Lemon Dove, Eurasian Golden Oriole, Buff-spotted Flufftail, and Orange Ground-thrush. This could be for one of two reasons, both related to the fact that remote sensing techniques fail at identifying the three-dimensional structure of forests (Martinuzzi *et al.* 2009). First, carbon fertilisation leads to the increased occurrence of woody thickening (Buitenwerf *et al.* 2012) of savannah or thicket, producing a forest-like habitat which although categorised as forest by NLC

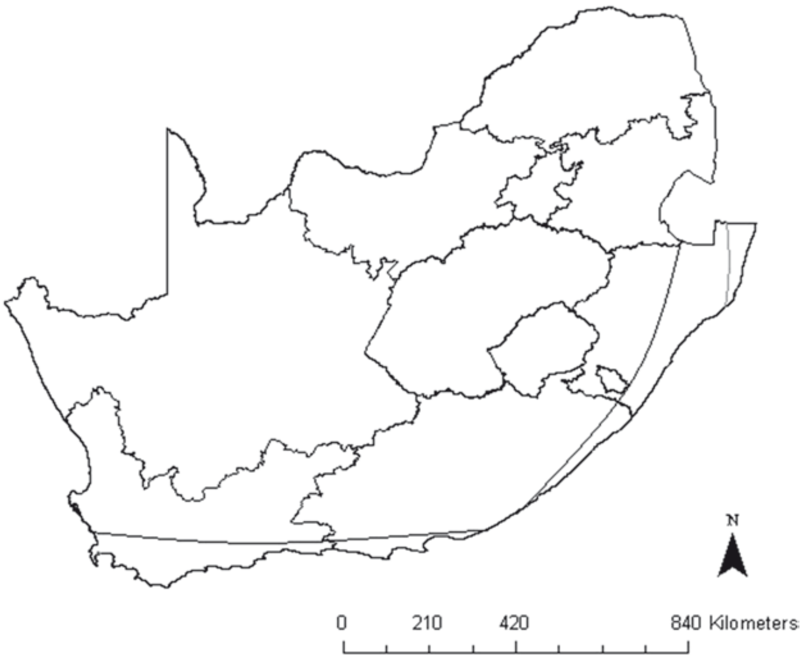

Figure 3. The delineation of forest types found to be most critical for forest-dependent bird species in this study. Dry forest occurs to the right of the grey line; lowland forest occurs below the black lines, and montane forest occurs above the black lines. Other forest types were not included here due to their limited extent.

datasets may not be ecologically suitable for some forest specialists such as these four species (compared to primary forest). An alternative explanation is that there is a decline in forest quality derived from human harvesting even in areas where forest cover appears to be expanding.

Some species likely suffered local extinction (Figure 2) in areas where plantations were lost: Rufous-chested Sparrowhawk, Barratt's Warbler, Grey Cuckooshrike, Cape Parrot, African Wood Owl, and Blue-mantled Crested-flycatcher. Birds of prey have long been known to utilise plantations for nesting and feeding (Prestt 1965), explaining why the Rufous-chested Sparrowhawk and African Wood Owl were found to benefit from plantations. In addition, a matrix effect could be occurring, whereby species in areas already deforested of indigenous forest utilised plantations/woodlots for survival. The decline in plantations/woodlots which occurred in many areas between 1990 and 2014, if not yet replaced by indigenous forest, could leave these species with no suitable habitat. Internationally it has been shown that plantations may act as a refuge for certain species tolerant of this habitat type (e.g. in Mauritius, Carter and Bright 2002; and in Malaysia, Mitra and Sheldon 1993), and plantations may act as a corridor between small forest fragments, allowing a rescue effect (Wethered and Lawes 2003).

Those species which cannot survive in plantations were lost from areas where plantations increased. These include the Trumpeter Hornbill, Bush Blackcap, Yellow-throated Woodland-warbler, and Orange Ground-thrush. Plantations are unsuitable habitats for species that build nests in the undergrowth; Bush Blackcap, Yellow-throated Woodland-warbler and Orange Ground-thrush all fall into this category (Tarboton 2001). The Trumpeter Hornbill is a habitat specialist (Harrison *et al.* 1997) which does not occur in plantations (BirdLife International 2014b). The Eurasian Golden Oriole, a non-breeding migrant, is also negatively affected by plantation cover, despite being known to occur in plantations elsewhere in the world (e.g. tea plantations and palm plantations in India; Sinu 2011, Basheer and Aarif 2013). The Southern Banded Snake-eagle was also lost from a single cell in which plantations increased (Table 2, Table 4), and deforestation of indigenous forest occurred. The only site in which it was found in SABAP2 had an increase in indigenous forest and a decrease in plantations (Table 2).

The species found to be experiencing the greatest loss in range were the Eurasian Golden Oriole, Rufous-chested Sparrowhawk and Cape Parrot. It is important to note that range declines do not necessarily correspond to population declines. A study by Downs *et al.* (2014) on the long-term population trends of the Cape Parrot in South Africa found that, while the proportion of locations in which Cape Parrots were observed decreased over a 15-year period, the abundance of the species increased. These data were not included in the SABAP2 data used for the present study, perhaps explaining the disparity in results. The Cape Parrot is large and mobile, and frequently forages long-distance in flocks (Wirminghaus *et al.* 2002).

There is some disagreement on the effects of plantations on biodiversity, with two conflicting views presented in the literature: that plantations improve biodiversity of adjacent indigenous forests (Estades and Temple 1999, Bremer and Farley 2010), or that plantations reduce biodiversity of adjacent indigenous forests (Geldenhuys 1991, Wethered and Lawes 2003, 2005), and alter species assemblages (Armstrong and van Hensburgen 1995, Allan *et al.* 1997). The results of this study show that of the 12 species affected by plantations, half are affected positively and half are affected negatively (Table 4). It has previously been postulated that certain guilds or groups of species exhibit the same reaction to plantations (e.g. Prestt 1965, Armstrong and van Hensburgen 1995); however, this was not evident in our study, with no particular guild appearing to benefit from or be impaired by plantations. Plantations may act as a refuge for those species tolerant to them (e.g. Carter and Bright 2002), where indigenous forests are lost. Some species have developed such a tolerance that they prefer to breed and feed in plantations, such as many birds of prey (Tarboton 2001, BirdLife International 2014a). Some relative specialists, such as the Cape Parrot, also feed in plantations (Wirminghaus *et al.* 2002). South Africa experienced an increase in plantations towards the end of the last century (Berliner 2009), before decreasing over the last 20 years (Forestry Economics Services CC 2014). This decrease in plantation cover could be leading to a loss of species which feed and breed in plantations, as well as those which use plantations to buffer the effects of indigenous forest loss. In addition, the forests themselves may be buffered by plantations from local harvesting pressure (Berliner 2009, J. Feely pers. comm.) and loss to fire (Geldenhuys 2002). If a loss of plantations leads to a loss of this protection of indigenous forests, even those species which do not occur in plantations may be negatively affected. Lantschner *et al.* (2008), in a study of birds in pine plantations in Argentina, suggested that species which evolved in a fragmented forest biome may be pre-adapted to surviving in plantations, as they have evolved to withstand some level of disturbance. The long history of natural fragmentation of forests in South Africa (Berliner 2009) could enable some South African forest birds to do the same.

Of the 28 species with declining ranges, 24 were secondary consumers (birds of prey, insectivores or omnivores which feed on insects or invertebrates). Higher trophic levels are more at risk from habitat destruction, alteration and fragmentation (Schoener 1968, Ewers and Didham 2006), leading to a trophic bias in response to human-mediated habitat loss (Duffy 2003). Hunting and harvesting of local resources is common in South African rural communities (Shackleton and Shackleton 2004), and species utilised often comprise birds (Shackleton *et al.* 2002, Twine *et al.* 2003, Shackleton and Shackleton 2006), including birds of prey (Asibey 1974). Other threats to birds of prey in areas utilised by humans include deliberate and accidental poisoning, gin traps, drowning in farm reservoirs, electrocution by, and collision with, power lines, and road casualties (Anderson 2000). Insectivorous birds are known to decrease with increasing urbanisation (Chace and Walsh 2006), and this decline is attributed to a loss of invertebrate food resources (Wilson *et al.* 1999, Benton *et al.* 2002).

The occurrence of 37/57 species in montane and 45/57 species in lowland forests suggests that these forest subtypes should enjoy the highest conservation priority. This is especially true for montane forests, as most decreasing species occur here (Appendix S2), indicating that this vegetation type is most at risk; lowland forests had a mixture of increasing and decreasing species, while dry forests (22/57) tended to contain increasing species.

Maintaining the diversity of species guilds present in a natural environment is vital to the functional processes of ecosystems. Healthy plant populations are maintained by insectivorous birds through insect predation, and this guild is more prominent in heterogeneous forests (Sekercioglu 2010, Bereczki *et al.* 2014). Cavity nesters are the most important of these insectivores, and are the first to disappear from exploited forests, with the removal of dead wood changing resource availability (Du Plessis 1995, Bereczki *et al.* 2014). Likewise, forest regeneration through the plant-frugivore network, can be affected by a loss of dispersers reducing tree recruitment (Cordeiro and Howe 2001, Chama *et al.* 2013). Frugivores generally subsist on only a subset of the fruiting species available, and therefore conserving forest heterogeneity and fragment size is important for their persistence (Cordeiro and Howe 2001, Bleher *et al.* 2003). Frugivores can also be affected indirectly, as pollination by bird species is restricted in a fragmented landscape, which can lead to lower fruit sets and thus limit frugivore food sources (Cunningham 2000). A loss of frugivores in a community will inevitably lead to the vulnerability of more specialised plant species, potentially altering species richness (Chama *et al.* 2013). Where forest fragments do possess a high amount of fruit availability, they can be instrumental in maintaining the connectivity of forest fragments and patches in a matrix, if the forest community is one tolerant of fragmentation (Berens *et al.* 2014). This resource availability is a crucial determinant in the health of the plant-frugivore network (Chama *et al.* 2013).

Seed dispersal is recognised as one of the most important ecological functions of birds, and loss of forest habitats has been linked to losses of bird dispersers and resultant lower tree recruitment (Howe and Smallwood 1982, Cordeiro and Howe 2001). The Cape Parrot is dependent on *Podocarpus* spp (yellowwood tree species) for both food and reproduction, nesting in holes in large yellowwood trees often utilised in logging (Wirminghaus *et al.* 2001b, Downs 2005). As *Podocarpus* species are dispersed by birds (Adie and Lawes 2011), a reduction in trees due to logging and deforestation would lead to a reduction in the bird species dependent on them, which would in turn limit dispersal of remaining trees. Hornbills, such as the Trumpeter Hornbill documented here to be undergoing a range decline, are keystone species within forests and vital for seed dispersal (Trail 2007). Trumpeter Hornbills have been found to be important dispersers of seeds within and between South African forest patches, where seed removal rates decline with increasing degradation of forests and deforestation (Kirika *et al.* 2008, Lenz *et al.* 2011).

The bird diversity of South African forests is under threat from changes in plantation/woodlot extent and changes in forest quality resulting from forest degradation and/or from the prevalence of woody thickening as a result of carbon fertilisation, caused by anthropogenic climate change. Plantations seem to be acting as a refuge for some species, particularly in areas already denuded of indigenous forest. Further loss of plantations may lead to local species extinctions if these plantations are not replaced by indigenous forest. The response of species to deforestation or plantation loss does not appear to be determined by particular characteristics. The Eastern Cape province is of particular concern, as the majority of species losses appear to be occurring here. Range declines in forest dependent species will be arrested only through active efforts to conserve the remaining South African forest fragments.

Supplementary Material

To view supplementary material for this article, please visit https://doi.org/10.1017/S095927091600040X

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