Patterns of bird diversity in Welgevonden Game Reserve, South Africa: insights from distribution modelling using point count data in 2009

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Introduction

Welgevonden Game Reserve covers an area of around 34,200 hectares. It is situated in the Waterberg District of the Limpopo province of South Africa and forms part of a greater conservancy area of 100,000 hectares of game sanctuary with Marakele National Park. The biodiversity of Welgevonden has become a major draw for tourists, especially with over 50 different mammal species present, including the Big Five.

In this study we use a high-quality field monitoring dataset for an assemblage of birds integrated in GIS with readily available environmental data derived from remote sensing in order to model and validate the distributions of 13 bird species in Welgevonden.

Methods

Spatial sampling

Forty sample sites were chosen opportunistically across Welgevonden, their positions constrained by logistical factors.

Bird point counts took place at the centre of a 100m square sampling unit, from which habitat structure data was also collected.

Field data collection

Team of volunteers led by a guide completed 10 minute point counts on 3 occasions at the central point each of the sample sites. In order to reach the site the teams caused some disturbance in order to avoid an encounter with dangerous game. Upon getting to the site, they therefore waited for a 10 minute period to allow birds to return. On each bird point count occasion the team recorded the site code, the date, the start time, the name of the main observer and whether it was raining or windy.

After the settling down period the 10 minute point count began. When a cluster of individual birds was seen or heard the team recorded the species, number of individuals, their approximate distance (in 10m bands to 50m), the method of observation (seen, heard, seen and heard) and the time after the start of the point count.

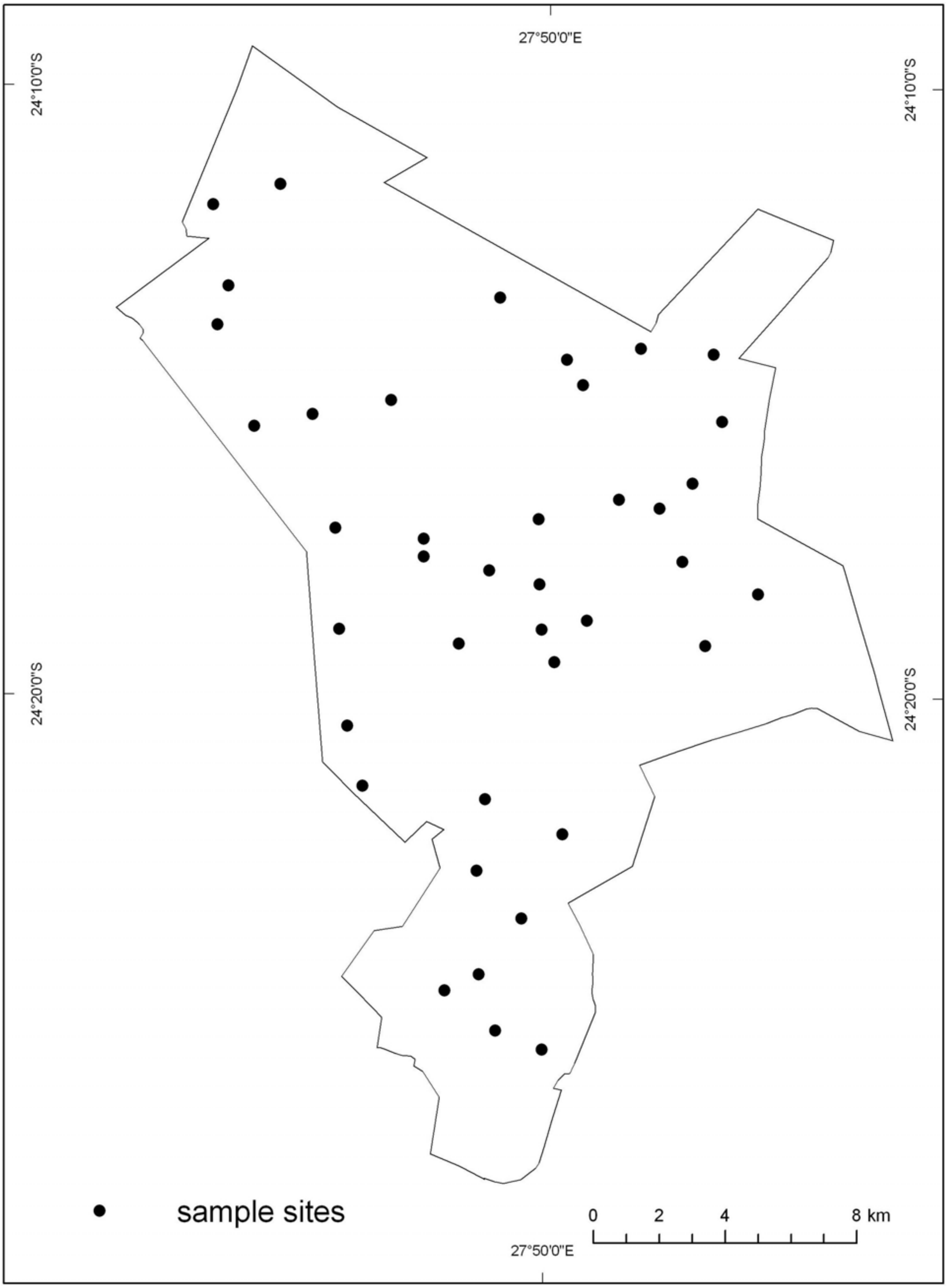

Fig 1. Distribution of 40 bird point count sites used in 2009.

Field data was recorded onto paper forms and then entered into a custom Access database on return to camp. The database is designed to reduce data entry errors and streamline analysis by folding together data from several tables (particularly bird species, sample sites, bird point count occasions and bird point count records) to produce queries which contain data prepared for analysis.

Environmental data

In order to describe the environment of Welgevonden we prepared seven maps of environmental variables which were used as covariates in species distribution models. All maps were of the same resolution and spatial extent and perfectly geocoded to each other such that they are 'overlayable' in subsequent map algebra operations.

We used three Landsat 7 scenes collected in the summers of 2006 and 2009 to characterise land cover in the park (Table 1). The scenes were downloaded from the USGS, and the metadata was used to write macros to first correct all bands of all scenes to at-sensor radiance and then normalise this radiance in all bands of all scenes to top of atmosphere reflectance. These scenes were then overlaid in the sequence given in table 1 to simultaneously gapfill the SLC_off gaps in the Landsat 7 scenes and mosaic all scenes together to produce a complete coverage of Welgevonden. The six bands produced were then clipped to the outline of Welgevonden Game Reserve.

We then performed a tasselled cap (TC) transformation using ETM coefficients to reduce the dimensionality of this multispectral data set and produce three statistically orthogonal layers which are biologically meaningful: TC greenness represents the amount of healthy green vegetation, TC brightness represents the amount of bare soil, and TC moistness represents soil moisture (Figure 2).

We used a 30m digital elevation model derived by minimum curvature spline interpolation of 90m data from the shuttle radar tomography mission (Figure 2).

We used three spatially interpolated climate surfaces (Hijmans et al, 2005), Mean annual temperature, Total annual precipitation and Precipitation in the driest quarter (Figure 2).

Table 1. Landsat scenes used to derive environmental variables for Welgevonden

WRS path row	Date	Satellite	Sensor	Solar elevation (°)	Scene ID	Gapfill order
WRS-2 p171r077	13 August 2009	Landsat 7	ETM	38.4726340	LE71710772009225ASN00	1
WRS-2 p171r077	29 August 2009	Landsat 7	ETM	43.0598742	LE71710772009241ASN00	2
WRS-2 p171r077	18 June 2006	Landsat 7	ETM	32.0286457	LE71710772006169ASN00	3

Species distribution modelling

In this study we elected to make species distributions using generalised linear models (GLM). We used a bound query from our biodiversity monitoring database which unites all bird records with details of the occasion on which the record was made in order to select the species for which we have presence records in at least 10 unique spatial locations. We then selected only these records for further analysis, rarefied such that there were no spatially duplicated records for any species. We then created a set of randomly placed pseudo-absence points for each species within the boundary of Welgevonden such that for each species there was an equal number of pseudo-absences and presences.

In order to be able to validate our models, we used k-fold partitioning (Fielding & Bell 1997) and split the combined presence and pseudo-absence data for each species into 10 equal sized partitions. All points were then intersected with our seven maps of environmental covariates to create a complete dataframe for analysis.

In our study we began by attempting to identify the correct model structure for each species by using the full dataset, we then returned to validate our models using partitioning methods. All statistical analysis was performed in R.

All our models were GLMs with a logit link function and binomial error structure since the response variable in this study is a probability of species occurrence, which must be constrained to the range 0-1 and which exhibits non-constant variance across this range. Since some species had as few as 10 presences and thus only 20 cases in the full dataset once pseudo-absences had been generated and since there are seven covariates to analyse, there is potential for numerical problems due to the low case:variable ratio if maximal multivariate models were made for all species. Instead, we elected to first make a set of bivariate GLMs to identify the covariates which were significant for each species. Then we entered only these covariates into a full model for the species. We used a multi-model inference (Burnham & Anderson 2002) approach to simplify stepwise the full models by sequential deletion of the least significant term and compared models at each stage using the Akaike Information Criterion (AIC) to identify the structure of the minimum adequate model (Tables 2 and 6).

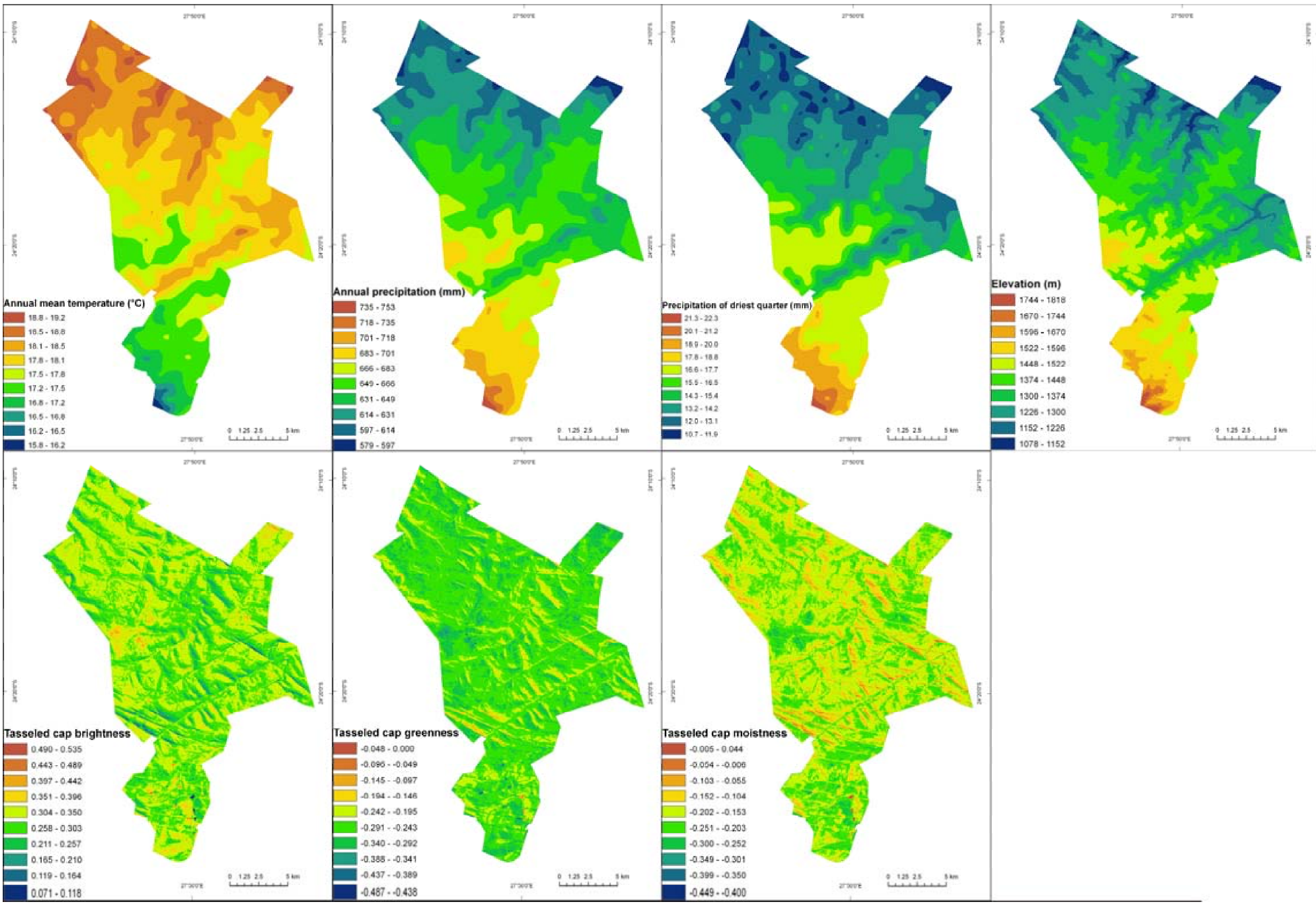

Figure 2. Environmental covariates used in species distribution models

We then created 10 partitioned MAMs for each species using the cases from 9 out of the 10 partitions and compared the predicted probability of occurrence with the 1 or 0 presence or pseudoabsence in the corresponding validation partition. In order to evaluate the performance of the 10 models across all possible thresholds of probability of occurrence with respect to the validation partition we used the program ROC_Kstats (Pearson 2004) which created 100 error matrices of model prediction versus validation data at every possible threshold (p.01, 0.02, 0.03 …) and then computes a Kappa statistic to measure model performance in terms of correct predictions, taking into account correct predictions that may be made by chance. It is also possible to use the error matrices to find the frequency of omission and commission errors in prediction at each threshold value and to identify the threshold at which Kappa is maximised. From this data we plotted a receiver operating characteristic curve (ROC) and found the area under the curve (AUC) by integration. This is an excellent threshold-independent metric of model performance. An AUC value of 1 is perfect whereas an AUC value of 0.5 denotes a model that performs no better than chance.

We then used the full dataset to estimate, with the greatest possible power, the parameter estimates for the covariates retained in the MAM and their uncertainties and used map algebra to evaluate the logistic function representing each species probability of occurrence across Welgevonden. We then used our Kappa maximising threshold to reclassify these maps to harden our predictions into areas of Welgevonden where each species is predicted to be present and absent.

Finally the thresholded validated distribution models for all species were added together to estimate species richness across space among the set of modelled birds. This map was then converted to 10 quantiles to represent the estimated spatial pattern of relative species richness of birds in Welgevonden.

Results

In summer 2009 bird point counts took place at 40 sample sites on 120 occasions. The mean number of sampling occasions at a site was 3 occasions. In total 1986 individual birds were observed in 1297 clusters of birds. During point counts in 2009 we recorded 90 species (table 5). 61 individual birds in 53 clusters were of unknown species (3.07% of individuals and 4.09% of clusters could not be identified).

In Welgevonden the bird community is dominated by a small number of common species and there is a long tail comprising very many rarer species. The most abundant two species (*Streptopelia capicola, Serinus mozambicus*) accounted for 25% of the individual birds recorded and with the subsequent five species (*Streptopelia semitorquata, Estrilda astrild, Pycnonotus barbatus, Turdoides jardineii, Francolinus natalensis*) accounted for 50% of the individual birds recorded during the surveys. Together with a further 11 species (*Oriolus larvatus, Zosterops pallidus, Turtur chalcospilos, Macronyx capensis, Francolinus shelleyi, Numida meleagris, Batis molitor, Francolinus swainsonii, Dicrurus adsimilis, Euplectes progne, Prinia subflava*), 75% of the individuals recorded during the surveys represented just 18 species. The final quartile of individuals birds recorded in the point counts comprised a further 71 species.

Of the 90 species of bird recorded at the point counts, 19 species met our criterion of providing records from at least 10 unique spatial locations. We attempted to make distribution models for this set of species. Subsequently, 6 of these species, *Batis molitor, Dicrurus adsimilis, Oriolus larvatus, Parus niger, Prinia subflava and Zosterops pallidus*, had to be dropped from the analysis as they exhibited no significant relationship with any environmental covariate, leaving 13 species which were modelled.

The minimum adequate models which we produced (summarised in Table 2, and in full in table 6) performed moderately well in explaining variation in probability of occurrence of our set of bird species.

We present a habitat suitability map and a thresholded habitat suitability map for a representative species: the African Hoopoe, *Upupa epops* (Figure 3), which is more likely to occur in areas that are less moist.

When the models were validated by integration under their ROC curves to compute the AUC for each model, the mean AUC was 0.66 (range 0.52 – 0.84) indicating reasonable performance across all models (Table 3). The bootstrapped standard errors associated with each AUC estimate were small, mean = 0.06 (range 0.05 - 0.11), indicating that high confidence can be placed in the validation procedure. Kappa maximising thresholds (assuming equal costs associated with omission and commission errors) for each species are also reported. Note that the threshold for a particular species is independent of the performance of the model. It is simply a threshold at which the model's predictive power is optimised and varies depending on the prevalence of the species in the landscape.

We added the thresholded habitat suitability maps for each of the 13 modelled species to produce a map of species richness among the set of modelled bird species (Figure 4). It is critical to note that this map is not a prediction of bird alpha species richness across all bird species. For this reason we calculated bird relative species richness by slicing the richness map into ten quantiles (Figure 5). Our results suggest that the relatively drier areas of Welgevonden have higher relative species richness.

Table 2. Summary of minimum adequate models. For each species the symbols (+ and –) in the covariate columns denote the sign of the beta parameter associated with that covariate. These symbols only appear for the covariates which were retained in the minimum adequate model.

Species	Elevation(m)	Mean annual temperature (°C)	Total annual precipitation (mm)	Precipitation of the driest quarter (mm)	Tasseled cap brightness	Tasselled cap greenness	Tasseled cap moistness	n (presences and psudoabsences)	Deviance	AIC (MAM)	AIC (Full)	ΔAIC (MAM – Full)
Cercotrichas leucophrys	-							20	29.07	27.62	27.62	0.00
Dryoscopus cubla		+						29	41.59	42.18	42.18	0.00
Francolinus natalensis							-	23	33.27	28.88	28.88	0.00
Lanius collaris							-	21	30.50	25.20	25.19	0.01
Macronyx capensis							-	21	30.50	16.30	16.30	0.00
Pycnonotus barbatus							-	59	83.18	74.81	74.80	0.01
Serinus mozambicus							-	31	44.36	42.71	42.72	-0.01
Streptopelia capicola							-	79	110.90	104.28	104.30	-0.02
Streptopelia semitorquata							-	71	99.81	91.76	91.76	0.00
Tchagra senegala							-	39	55.45	56.21	56.21	0.00
Turdoides jardineii							-	21	30.50	27.52	27.52	0.00
Turtur chalcospilos	-							43	61.00	60.13	60.13	0.00
Upupa epops							-	25	36.04	32.51	32.51	0.00

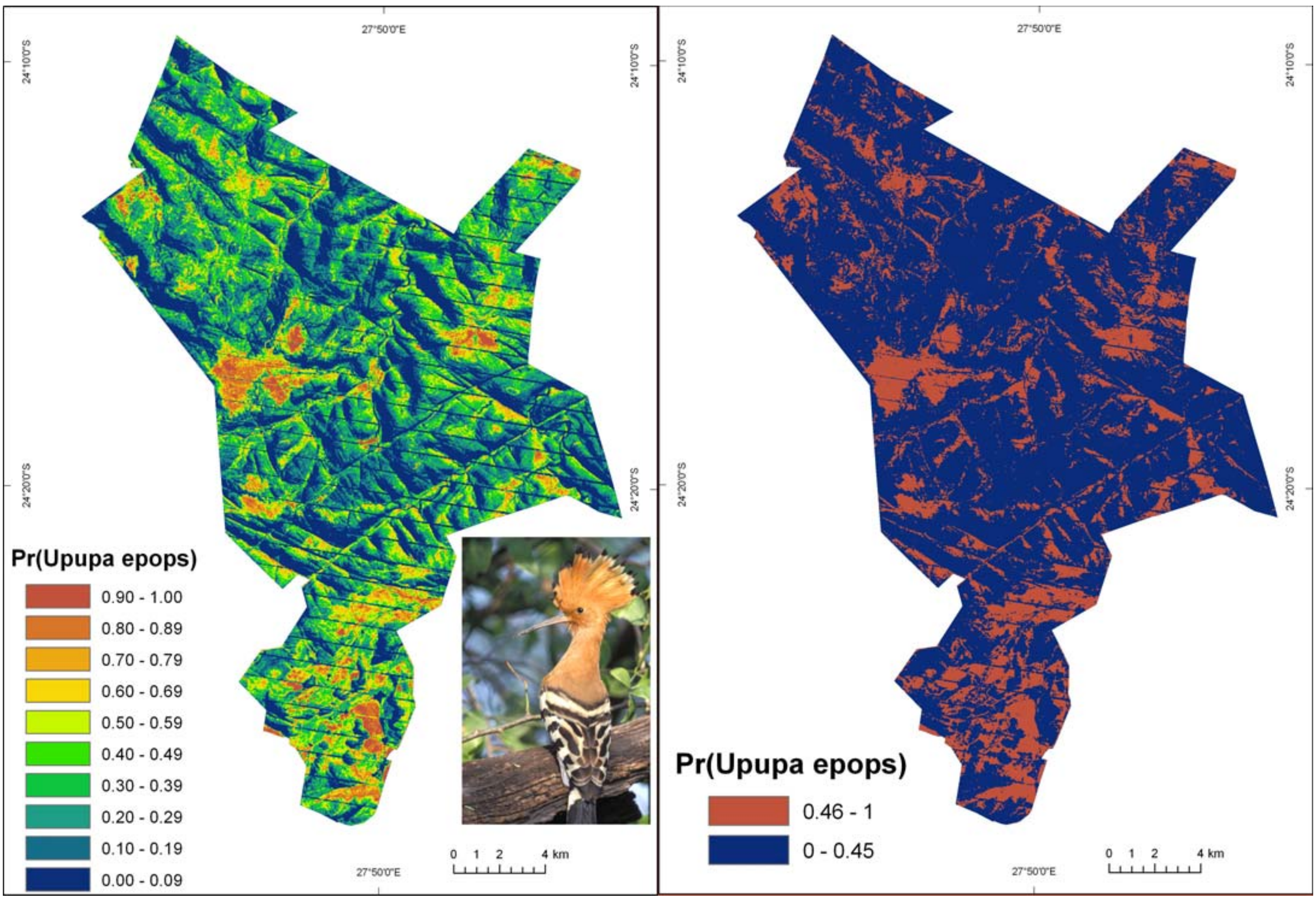

Figure 3. a) habitat suitability map and b) thresholded habitat suitability map for African Hoopoe

Table 3. Validation statistics. Area Under Curve (AUC) ± Standard Error, Kappa maximising threshold of probability of occurrence and the area (km^2) in Welgevonden which is modelled to be more suitable for the species than the Kappa maximising threshold.

Species	K maximising threshold	AUC±SE	Area Pr > K (km^2)
Cercotrichas leucophrys	0.54	0.65 ± 0.11	135.05
Dryoscopus cubla	0.44	0.53 ± 0.11	243.05
Francolinus natalensis	0.56	0.68 ± 0.10	118.90
Lanius collaris	0.41	0.78 ± 0.09	107.47
Macronyx capensis	0.87	0.84 ± 0.05	41.45
Pycnonotus barbatus	0.59	0.71 ± 0.06	99.50
Serinus mozambicus	0.49	0.61 ± 0.10	186.86
Streptopelia capicola	0.46	0.67 ± 0.06	169.15
Streptopelia semitorquata	0.59	0.67 ± 0.06	92.28
Tchagra senegala	0.47	0.52 ± 0.09	138.10
Turdoides jardineii	0.44	0.64 ± 0.11	192.81
Turtur chalcospilos	0.30	0.61 ± 0.08	269.57
Upupa epops	0.45	0.70 ± 0.09	82.09

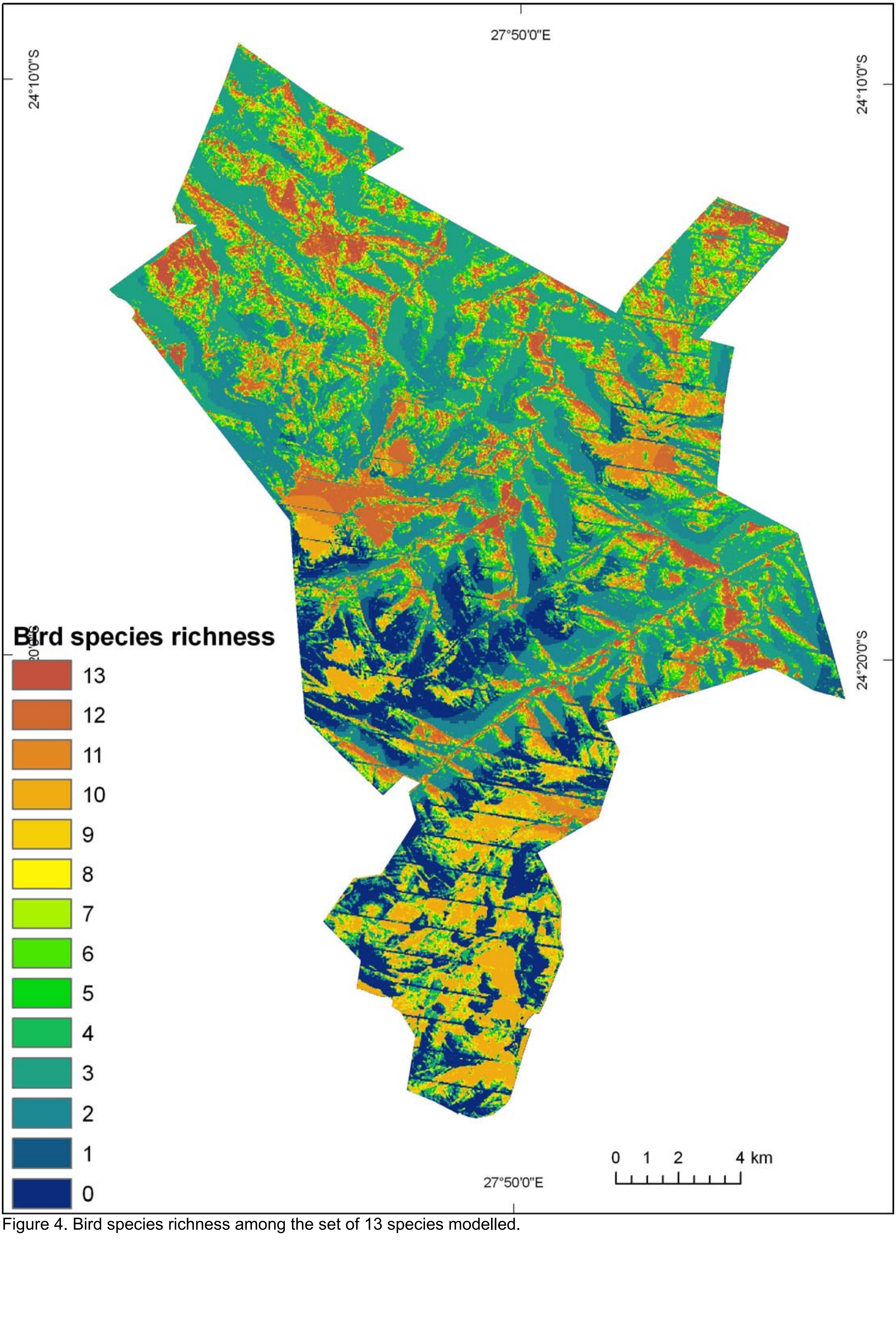

Figure 4. Bird species richness among the set of 13 species modelled.

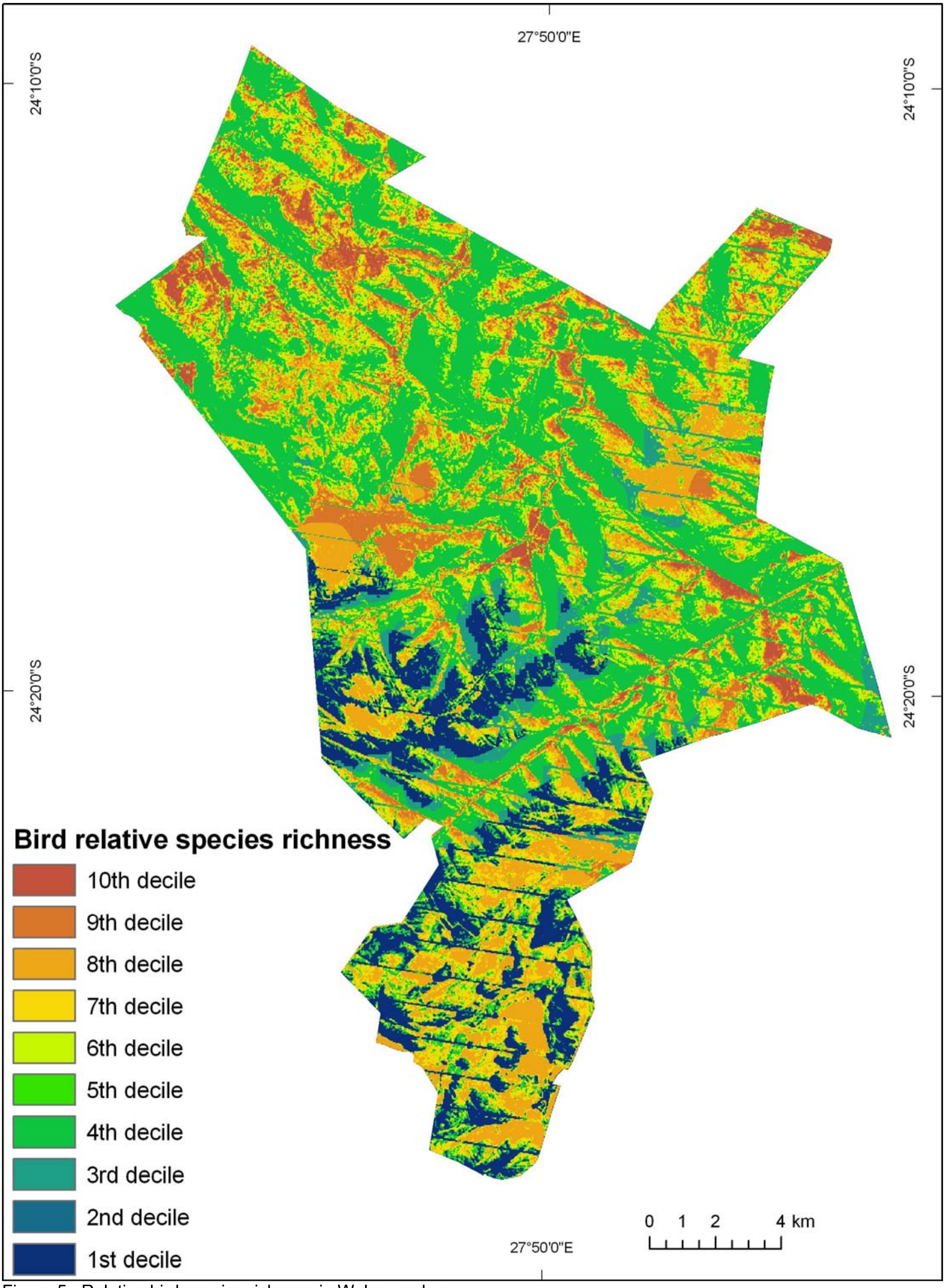

Figure 5. Relative bird species richness in Welgevonden.

Discussion

In this study we demonstrate the value of volunteer-led monitoring for collecting data which may be used to inform management. We believe our result provide a reasonable estimation of spatial trends in diversity across a taxonomic group in Welgevonden. It would be fascinating to apply this approach to other groups in the reserve as well and extend the study temporally and spatially, possibly even to include the greater conservancy area which Welgevonden forms with Marakele National Park.

Although the validation statistics show that across all species the models have reasonable predictive power, it is important that the distribution models are interpreted critically. It is possible that the spatial and temporal distribution of sampling has not allowed us to measure the full variation in all covariates across the park. Additionally a species may not be found in a landscape unit predicted to be suitable by a model due to processes including exploitation (unlikely in Welgevonden), competition or meta-population dynamics.

Taken together though, our results suggest that appropriately constructed and validated distribution models can be useful in exploring patterns of diversity across many species in Welgevonden. However it would be possible to refine this approach by using multi-year monitoring data and temporally referenced covariates to create a synoptic monitoring tool for biodiversity in Welgevonden.

The biodiversity database associated with the bird point counts has not yet been fully exploited. It should be possible to use distance sampling to estimate densities of the most abundant bird species in Welgevonden and, given that we have estimated distributions, estimate population sizes – a potentially very powerful approach to monitoring. Such data would also permit more sophisticated maps of diversity indices (not just richness) to be calculated.

Appendix

Table 4. Sample sites used for bird point counts in 2009

Sample site	X	Y
WE1	589872	7316941
WE2	587408	7319155
WE3	585664	7318052
WE4	585175	7318831
WE5	584309	7314002
WE6	582815	7312443
WE8	580828	7312868
WE9	578268	7310680
WE10	581891	7310240
WE13	580830	7313408
WE15	574583	7319908
WE16	574913	7321077
WE19	589619	7318980
WE21	579840	7317615
WE22	577462	7317190
WE23	584339	7312023
WE24	584406	7310652
WE25	585776	7310926
WE26	588673	7312703
WE27	589359	7310152
WE28	578515	7307748
WE29	582687	7305528
WE31	585033	7304462
WE32	583794	7301912
WE33	582493	7300223
WE34	587983	7314318
WE38	576490	7324151
WE40	578159	7313749
WE42	586746	7314583
WE43	582430	7303362
WE44	590955	7311723
WE48	575692	7316824
WE49	578975	7305935
WE51	581454	7299740
WE52	583146	7320703
WE54	588977	7315069
WE55	574457	7323533
WE56	584789	7309667
WE58	584403	7297942
WE60	582995	7298513

Table 5. All bird species observed during point counts in 2009

Common name	Latin name
African Goshawk	Accipiter tachiro
Egyptian Goose	Alopochen aegyptiacus
Yellow-billed Duck	Anas undulata
Cape Penduline Tit	Anthoscopus minutus
Bush pipit	Anthus caffer
Plain-backed Pipit	Anthus leucophrys
Striped Pipit	Anthus lineiventris
Marsh Owl	Asio capensis
Chinspot Batis	Batis molitor
Hadada Ibis	Bostrychia hagedash
Red-billed Oxpecker	Buphagus erythrorhynchus
Green-backed Camaroptera	Camaroptera brachyura
Golden-tailed Woodpecker	Campethera abingoni
White-browed Coucal	Centropus superciliosus
Desert Cisticola	Cisticola aridulus
White-browed Scrub-Robin	Cercotrichas leucophrys
Pied Kingfisher	Ceryle rudis
Lazy Cisticola	Cisticola aberrans
Desert Cisticola	Cisticola aridulus
Rattling Cisticola	Cisticola chinianus
Neddicky	Cisticola fulvicapilla
Levaillant's Cisticola	Cisticola tinniens
White-throated Robin-Chat	Cossypha humeralis
Common House-Martin	Delichon urbicum
Cardinal Woodpecker	Dendropicos fuscescens
Bearded Woodpecker	Dendropicos namaquus
Fork-tailed Drongo	Dicrurus adsimilis
Black-backed Puffback	Dryoscopus cubla
Black-shouldered Kite	Elanus axillaris
Golden-breasted Bunting	Emberiza flaviventris
Common Waxbill	Estrilda astrild
Long-Tailed Widowbird	Euplectes progne
Coqui Francolin	Francolinus coqui
Natal Francolin	Francolinus natalensis

Shelley's Francolin	Francolinus shelleyi
Swainson's Spurfowl	Francolinus swainsonii
Red-knobbed Coot	Fulica cristata
Pearl-spotted Owlet	Glaucidium perlatum
Brown-hooded Kingfisher	Halcyon albiventris
Striped Kingfisher	Halcyon chelicuti
African Hawk-Eagle	Hieraaetus spilogaster
Jameson's Firefinch	Lagonosticta rhodopareia
African Firefinch	Lagonosticta rubricata
Cape Glossy Starling	Lamprotornis nitens
Orange-breasted Bushshrike	Laniarius brauni
Southern Boubou	Laniarius ferrugineus
Common Fiscal	Lanius collaris
Black-collared Barbet	Lybius torquatus
Cape Longclaw	Macronyx capensis
Grey-headed Bushshrike	Malaconotus blanchoti
Southern Black Flycatcher	Melaenornis pammelaina
Fawn-colored Lark	Mirafra africanoides
Bronze Mannikin	Munia lonchura
Grey Tit-Flycatcher	Myioparus plumbeus
Mocking Cliff-Chat	Myrmecocichla cinnamomeiventris
White-bellied Sunbird	Nectarinia talatala
Brubru	Nilaus afer
Helmeted Guineafowl	Numida meleagris
Ant-eating Chat	Nyrmecocichla fornicivora
Capped Wheatear	Oenanthe pileata
Red-winged Starling	Onychognathus morio
Black-headed Oriole	Oriolus larvatus
African Quail Finch	Ortygospiza atricollis
Southern Black Tit	Parus niger
House Sparrow	Passer domesticus
Reed Cormorant	Phalacrocorax africanus
Green Woodhoopoe	Phoeniculus purpureus
Tawny-flanked Prinia	Prinia subflava
White Helmetshrike	Prionops plumatus
Groundscraper Thrush	Psophocichla litsipsirupa
Dark-capped Bulbul	Pycnonotus barbatus
African Stonechat	Saxicola torquatus
Streaky-headed Seedeater	Serinus gularis
Yellow-fronted Canary	Serinus mozambicus
Cape Turtle-Dove	Streptopelia capicola
Red-eyed Dove	Streptopelia semitorquata
Long-billed Crombec	Sylvietta rufescens
Brown-crowned Tchagra	Tchagra australis
Black-crowned Tchagra	Tchagra senegala
African Grey Hornbill	Tockus nasutus
Crested Barbet	Trachyphonus vaillantii
Arrow-marked Babbler	Turdoides jardineii
Kurrichane Thrush	Turdus libonyanus
Emerald-spotted Wood-Dove	Turtur chalcospilos
African Hoopoe	Upupa epops
Blue Waxbill	Uraeginthus angolensis
Blacksmith Lapwing	Vanellus armatus
Crowned Lapwing	Vanellus coronatus
Wattled Lapwing	Vanellus senegallus
Cape White-eye	Zosterops pallidus

Table 6. Minimum adequate models

Response variable	Explanatory variable	Beta	z	P
Pr(Cercotrichas leucophrys)	Intercept	16.865	2.018	0.0436
	Elevation	-4.556	-2.019	0.0435

Deviance = 29.07, n = 20 presences and pseudo-absences, AIC = 27.62
Excluded variables: Tasseled cap brightness, Tasseled cap greenness, Tasseled cap moistness, Annual mean temperature, Annual precipitation, Precipitation of the driest quarter

Response variable	Explanatory variable	Beta	z	P
Pr(Dryoscopus cubla)	Intercept	-23.956	-1.726	0.0843
	Annual mean temperature	5.053	1.728	0.0840

Deviance = 41.59, n = 29 presences and pseudo-absences, AIC = 42.18
Excluded variables: Elevation, Tasseled cap brightness, Tasseled cap greenness, Tasseled cap moistness, Annual precipitation, Precipitation of the driest quarter

Response variable	Explanatory variable	Beta	z	P
Pr(Francolinus natalensis)	Intercept	-12.349	-2.169	0.0301
	Tasseled cap moistness	-61.672	-2.170	0.0300

Deviance = 33.27, n = 23 presences and pseudo-absences, AIC = 28.88
Excluded variables: Elevation, Tasseled cap brightness, Tasseled cap greenness, Annual mean temperature, Annual precipitation, Precipitation of the driest quarter

Response variable	Explanatory variable	Beta	z	P
Pr(Lanius collaris)	Intercept	-9.956	-2.193	0.0283
	Tasseled cap moistness	-46.647	-2.214	0.0268

Deviance = 30.50, n = 21 presences and pseudo-absences, AIC = 25.20
Excluded variables: Elevation, Tasseled cap brightness, Tasseled cap greenness, Annual mean temperature, Annual precipitation, Precipitation of the driest quarter

Response variable	Explanatory variable	Beta	z	P
Pr(Macronyx capensis)	Intercept	-23.43	-2.264	0.0236
	Tasseled cap moistness	-112.59	-2.271	0.0231

Deviance = 30.50, n = 21 presences and pseudo-absences, AIC = 16.30
Excluded variables: Elevation, Tasseled cap brightness, Tasseled cap greenness, Annual mean temperature, Annual precipitation, Precipitation of the driest quarter

Response variable	Explanatory variable	Beta	z	P
Pr(Pycnonotus barbatus)	Intercept	-5.817	-2.875	0.00404
	Tasseled cap moistness	-29.686	-2.923	0.00347

Deviance = 83.18, n = 59 presences and pseudo-absences, AIC = 74.81
Excluded variables: Elevation, Tasseled cap brightness, Tasseled cap greenness, Annual mean temperature, Annual precipitation, Precipitation of the driest quarter

Response variable	Explanatory variable	Beta	z	P
Pr(Serinus mozambicus)	Intercept	-4.125	-2.071	0.0384
	Tasseled cap moistness	-21.629	-2.103	0.0355

Deviance = 44.36, n = 31 presences and pseudo-absences, AIC = 42.71
Excluded variables: Elevation, Tasseled cap brightness, Tasseled cap greenness, Annual mean temperature, Annual precipitation, Precipitation of the driest quarter

Response variable	Explanatory variable	Beta	z	P
Pr(Streptopelia capicola)	Intercept	-4.614	-2.916	0.00355
	Tasseled cap moistness	-23.131	-2.949	0.00319

Deviance = 110.90, n = 79 presences and pseudo-absences, AIC = 104.28
Excluded variables: Elevation, Tasseled cap brightness, Tasseled cap greenness, Annual mean temperature, Annual precipitation, Precipitation of the driest quarter

Response variable	Explanatory variable	Beta	z	P
Pr(Streptopelia semitorquata)	Intercept	-5.333	-2.909	0.00362
	Tasseled cap moistness	-27.152	-2.948	0.00319

Deviance = 99.81, n = 71 presences and pseudo-absences, AIC = 91.76
Excluded variables: Elevation, Tasseled cap brightness, Tasseled cap greenness, Annual mean temperature, Annual precipitation, Precipitation of the driest quarter

Response variable	Explanatory variable	Beta	z	P
Pr(Tchagra senegala)	Intercept	-5.541	-1.688	0.0914
	Tasseled cap moistness	-27.256	-1.702	0.0887

Deviance = 55.45, n = 39 presences and pseudo-absences, AIC = 56.21
Excluded variables: Elevation, Tasseled cap brightness, Tasseled cap greenness, Annual mean temperature, Annual precipitation, Precipitation of the driest quarter

Response variable	Explanatory variable	Beta	z	P
Pr(Turdoides jardineii)	Intercept	-7.675	-1.850	0.0643
	Tasseled cap moistness	-39.450	-1.889	0.0589

Deviance = 30.50, n = 21 presences and pseudo-absences, AIC = 27.52
Excluded variables: Elevation, Tasseled cap brightness, Tasseled cap greenness, Annual mean temperature, Annual precipitation, Precipitation of the driest quarter

Response variable	Explanatory variable	Beta	z	P
Pr(Turtur chalcospilos)	Intercept	8.907	2.057	0.0397
	Elevation	-2.405	-2.061	0.0393

Deviance = 61.00, n = 43 presences and pseudo-absences, AIC = 60.13
Excluded variables: Tasseled cap brightness, Tasseled cap greenness, Tasseled cap moistness, Annual mean temperature, Annual precipitation, Precipitation of the driest quarter

Response variable	Explanatory variable	Beta	z	P
Pr(Upupa epops)	Intercept	-10.382	-1.850	0.0643
	Tasseled cap moistness	-48.159	-1.867	0.0619

Deviance = 36.04, n = 25 presences and pseudo-absences, AIC = 32.51
Excluded variables: Elevation, Tasseled cap brightness, Tasseled cap greenness, Annual mean temperature, Annual precipitation, Precipitation of the driest quarter