



The use of habitat suitability models and species–area relationships to predict extinction debts in coastal forests, South Africa

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ABSTRACT

Aim Predicting extinctions before they are realized has proven difficult, yet is increasingly important for biodiversity conservation as habitat destruction continues unabated around the world. We evaluated whether habitat suitability models can be used in conjunction with species–area relationships (SAR) to detect apparent extinction debts as implicated by the conservation status assigned to bird species.

Location KwaZulu-Natal province, South Africa.

Methods We modelled historic distributions of coastal forests using MaxEnt, a presence-only technique for modelling species distributions. The model provided an estimate of forest loss. We then conducted 293 point counts to survey birds within remaining forest fragments and employed an information-theoretic framework to test for the best fit SAR model. Extinction debts were calculated using the estimate of forest loss and the empirical SAR data.

Results Our model suggests extensive forest loss (82%) within a naturally fragmented landscape. The power function provided the best fit for bird SAR. Fourteen bird species are predicted to go extinct from coastal forests. Predicted extinctions closely matched the number of threatened species locally but not globally. Predicted extinctions also only matched globally threatened species that reach their northernmost distribution limit within coastal forests, but not species that reach their southernmost distribution limit here.

Main conclusions We found that habitat suitability models could be used in conjunction with SAR to estimate extinction debt implied by conservation statuses of extant species. Our approach assumed that forest loss drives extinction debts but also provided the opportunity to link forest loss and the likelihood of extinction. Models of historical forest distribution may provide guidelines of where to implement restoration actions. Maintaining matrix habitats that link forest fragments and targeted landscape level restoration that increases fragment area and link isolated fragments will be important to prevent predicted extinctions.

Keywords

Conservation, forest loss, fragmentation, MaxEnt, metapopulation, restoration.

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INTRODUCTION

Extinction debt is the expected future losses of species in response to present habitat loss, yet it is a phenomenon that can easily go unnoticed (Kuussaari *et al.*, 2009). Predicting extinction debts has important implications for conservation

planning, as the associated time delay provides the opportunity to enact conservation measures which may mitigate future species losses (Wearn *et al.*, 2012). Because habitat loss is the main driver of species extinction (Pimm & Raven, 2000), mitigation measures often relate to habitat restoration or preservation (Hanski, 2000; Lamb *et al.*, 2005). These

proactive initiatives protect species from extinction (Brooks *et al.*, 1999). However, even though extinction debts may be common in many remaining natural communities, verifying the existence of extinction debts remains problematic (Hanski & Ovaskainen, 2002; Kuussaari *et al.*, 2009).

Species–area relationships (SAR) have been used to estimate extinction debt and depend on four variables: (1) the habitat area prior to loss, (2) the number of species that occurred within the habitat prior to loss, (3) the area of habitat that remains, and (4) an estimate of z that is determined by the slope of the power law that describes the SAR (e.g. Pimm & Askins, 1995; Brooks *et al.*, 1997; Cowlshaw, 1999; Wearn *et al.*, 2012). The problem, however, is that many threatened habitats are poorly studied with limited data on historic land cover and land use (Brooks *et al.*, 2002; Trimble & van Aarde, 2012). Therefore, estimates of the original habitat area and the number of species that occurred there prior to habitat loss are rarely available. In such instances, indirect approaches based on modelling may provide a way to delineate habitat area and evaluate species responses to habitat loss.

Habitat suitability models entail the geographical modelling of biospatial patterns in relation to environmental gradients. These models can contribute to conservation (Hirzel & Lay, 2008) and have been used to select sites for ecological restoration (e.g. Franklin *et al.*, 2005), predict the biological effects of climate change and invasive species (e.g. Thomas *et al.*, 2004; Ficetola *et al.*, 2007) and design corridors (e.g. Roever *et al.*, 2013). However, despite their wide range of applications, their usefulness in predicting extinction debts has not been evaluated. Combining spatially explicit modelling with empirical data may prove a potentially powerful approach to predict extinction debt (Kuussaari *et al.*, 2009). In the absence of historical data that describe land use history, habitat suitability models can be used to estimate the original area covered by a habitat. The effect of a reduction in habitat area on species occupancy can then be investigated with SAR.

Here, we test this idea by studying a coastal forest along the east coast of South Africa. Coastal forests fall into two critically endangered ecoregions: the Maputland Coastal Forest Mosaic and the KwaZulu-Cape Coastal Forest Mosaic which both support exceptionally high levels of floristic endemism as well as a high number of narrowly endemic species, including relict species (Burgess *et al.*, 2004). Anecdotal evidence (e.g. McCracken, 2008; Skead, 2009) and published reports (e.g. Cooper, 1985; Avis, 1992; Lawes, 2002; Thompson, 2002) suggest that coastal forests were once more widespread than they are today. However, we do not know to what extent. Current estimates of forest loss vary widely because they are not derived from consistent methodologies, but depend on expert opinion and their definitions of forest types (Berliner, 2009). For example, estimates of coastal forest loss vary from ‘greater than 35%’ (Berliner, 2009), 65% (Lawes, 2002) and 90% (Cooper, 1985). Yet despite more than two centuries of intensifying human disturbances,

species have not gone extinct from coastal forests in the region. Could these forests therefore harbour an unpaid extinction debt?

We used habitat suitability models that include information on remaining coastal forest distribution to model past forest distribution under assumed similar environmental conditions (e.g. Guisan & Zimmermann, 2000; Elith & Leathwick, 2009; Franklin, 2009). We compared modelled and current distributions of coastal forests to quantify forest loss and fragmentation. We then used our modelled estimate of forest loss to calculate extinction debts based on the SAR. Studies have shown that the number of extinctions predicted from deforestation, and the number of species actually threatened are in many instances strikingly similar (Brooks *et al.*, 1997; Wearn *et al.*, 2012). Therefore, the number of species classified as threatened may represent the extinction debt of the habitat if these species match the number of species predicted to have become extinct based on SAR (e.g. Brooks *et al.*, 1997). We therefore compared the extinction debt based on our estimate of forest loss with the number of species listed as conservation concern in a) South Africa (locally) and b) on the IUCN Red List of Threatened Species (globally). We assumed that our estimate of modelled forest loss can be used to calculate extinction debt if the number of species predicted to go extinct matched the number of species classified as threatened in South Africa. We conclude with recommendations to improve coastal forest conservation and restoration in South Africa.

METHODS

Study area

Lawes (1990), Eeley *et al.* (1999) and Lawes *et al.* (2007) reviewed the climatic history, palaeoclimatic change and biogeographic forces that explain the distribution of coastal and Afromontane forests in KwaZulu-Natal (KZN). Despite discrepancies in the classification of coastal forest types (see Moll & White, 1978; Lubke *et al.*, 1997; Midgley *et al.*, 1997; Mucina & Rutherford, 2006), we opted to recognize coastal forests as comprising lowland forests, dune forests and swamp forests. We included swamp forests in our analysis because of their close proximity to lowland and dune forests, with which they also share a number of forest-dependent species (Von Maltitz *et al.*, 2003; Mucina & Rutherford, 2006).

Historical records and published reports suggest that coastal forests were once more widespread than what they are today. Archaeological records indicate that agricultural activities have been widespread in the region from the late Iron Age (1300s). These probably intensified as the region experienced an influx of people as well as political and social unrest (Feely, 1980; Sundnes, 2013). Forest clearing for agriculture, iron smelting and stock farming may also have caused an increase in grass-fuelled fires that promoted the spread of grassy ecosystems by carving holes in existing

forest fragments (Acocks, 1953; Bond *et al.*, 2003; Bond & Keeley, 2005). Subsistence farming, cattle grazing, unregulated burning, commercial logging, agricultural plantations and urban developments, all which accelerated since Europeans arrived in the region contributed to further forest losses (Fourcade, 1889; Bews, 1920; Feely, 1980; Avis, 1992; Thompson, 2002; Mucina & Rutherford, 2006). By 2010, these forests comprised 3087 patches (range 0.002–80 km²) that collectively accounted for 663 km² (Ezemvelo KZN Wildlife, Conservation Planning, 2009) of the 16300 km² flat coastal plain (altitude 0–450 m) along the east coast of KZN (Mucina & Rutherford, 2006). These fragments are embedded within a matrix of mixed habitat and land use types that range from natural grasslands and woodlands to agricultural plantations and human settlements.

Habitat suitability modelling

Environmental data

We assembled digital maps of 10 environmental variables (Schulze, 2006) relating to four principal traits associated with coastal forest distribution: temperature (maximum daily temperature in winter), precipitation (daily rainfall in winter, humidity, plant available water), geology (soil type, geology, soil clay content) and topography (aspect, elevation, slope) (Mucina & Rutherford, 2006). The maps were 200 × 200 m raster (grid cell) layers for KZN. A digital map (LandSAT, 2010) that covered the distribution of coastal forest was converted to a 200 × 200 m raster format for analysis. Grid cells that contained forest were coded separately for lowland, dune and swamp forests. Each coded grid cell represented a single observation of forest presence. Grid cells that comprised both forest and non-forest were coded as forest. Where more than one forest type occurred within a grid cell, the grid cell was coded for the forest type that made up the largest proportion of the cell. For our models, we assumed that there had been no significant change in climate since the end of the 18th century when the development of Iron Age commercial centres caused the number of settlements in KZN to increase rapidly and the first Europeans began to settle along the coast (Holmgren & Öberg, 2006).

Modelling algorithm and evaluation

We used MaxEnt version 3.3.2 (<http://www.cs.princeton.edu/~schapire/maxent>) to construct separate models for each forest type (see Phillips *et al.*, 2006 and Elith *et al.*, 2010). We used a presence-only modelling approach because we could not classify the absence of forests with certainty. In our study area, absence of forest could be due either to unsuitable environmental conditions or anthropogenically driven causes. We relied on recommended default values for the convergence threshold (10^{-5}) and maximum number of iterations (1000) (Phillips & Dudík, 2008). The programme automatically selected suitable regularization values to reduce

over-fitting. A jackknifing procedure was used to examine the importance of each variable, by comparing models with a particular variable absent or present.

We evaluated modelling performance based on the area under the curve (AUC) (Fielding & Bell, 1997). The value of an AUC index varies between 0 (performance worse than random) and 1 (perfect discrimination), with 0.5 being indistinguishable from random. Consequently, model performance can be ranked as fair (0.7–0.8), good (0.8–0.9) and excellent (0.9–1.0) (Phillips *et al.*, 2006). We used a cross-validation procedure to evaluate the performance of our models by modelling each forest type 10 times and splitting the data in each partition between calibrations (70% training data) and evaluation (30% test data) for all three data sets. The AUC, average AUC and standard deviation of the AUC were calculated for all 10 models per forest type.

To aid model validation and interpretation, it is necessary to distinguish 'suitable' areas from 'unsuitable' areas by setting a decision threshold above which model output is considered to be an accurate prediction of presence (Pearson *et al.*, 2004). This is important because when the logistic model output is converted to only forest presence and forest absence, the choice of threshold determines the amount of area classified as suitable for forest occurrence. We evaluated five optimal threshold criteria that have been found to produce accurate predictions when compared with other threshold criteria (Liu *et al.*, 2005; Jiménez-Valverde & Lobo, 2007; Bean *et al.*, 2012): (1) sensitivity-specificity equality, where positive observations are just as likely to be wrong as negative observations, (2) sensitivity-specificity sum maximization, where the mean error rate for positive observations and the error rate for negative observations is minimized, (3) lowest presence threshold, which is the lowest value associated with any of the observed presence records and (4) observed presence equals predicted presence, where the predicted presence is equal to the observed presence. We also evaluated the 10th and 20th percentile training presence threshold where the suitability threshold selects the value above which 90% and 80% of training locations are correctly classified. We then conducted a sensitivity analysis on threshold selection by calculating the amount of forest cover predicted based on each threshold value that we evaluated. We opted to underestimate rather than overestimate forest distribution because of the uncertainty associated with a modelling approach (Pearson *et al.*, 2006). We therefore selected the threshold that minimized the predicted area of forest cover for each forest type. Subsequent analyses were based on this estimate of forest cover. Optimal thresholds were calculated using R software (R Development Core Team, 2012) along with the Presence–Absence Model Evaluation package (Freeman, 2007).

Spatial structure of coastal forests

We calculated the fragmentation parameters: (1) number of fragments, (2) mean fragment size and (3) average nearest

neighbour distance (ANND) for modelled and present-day coastal forest distributions. Modelled fragment parameters were then compared with present-day fragments using Mann–Whitney U tests. All calculations were made in Geospatial Modelling Environment (Beyer, 2011) in combination with ArcGIS 10 (ESRI, 2011) and R (R Development Core Team, 2012).

Extinction debts

Field surveys

We conducted bird surveys using point counts (Bibby *et al.*, 2000) within 11 randomly selected coastal forest fragments that ranged in size from 0.29 to 80 km². Survey sites were stratified by forest type and forest area resulting in two swamp, three lowland and six dune forest fragments. The number of survey points per fragment ranged from 3 to 9 for fragments < 5 km², 9 to 18 for fragments between 5 and 20 km² and 27 to 54 for fragments > 20 km². In total 293, point counts were conducted between November 2011 and March 2012.

Point counts were conducted between 04:00 h and 10:00 h by the same three observers. Each observer surveyed 4–5 points per day. Observers were trained in and had prior experience of local bird identification. Point counts were at least 180 m apart and were located using handheld GPSs. An observer allowed for a 2-min period for birds that may have been disturbed upon arrival at the survey point to resettle and thereafter recorded birds for 10 min. All birds seen or heard within a 60-m radius were recorded, but those that flew above the forest canopy were excluded. Point counts were also not surveyed during rain or windy conditions.

SAR model evaluation

We fitted a power function (Arrhenius, 1921) to our survey data of birds that occurred within coastal forest fragments of varying sizes. As our focus was on the effect of forest loss, we only included forest-dependent species in our model evaluations. We then evaluated the model fit against seven other functions that have been proposed to model SARs (Guilhaumon *et al.*, 2010; Triantis *et al.*, 2012). SAR models were fitted in arithmetic space employing nonlinear regressions by minimizing the residual sum of squares (RSS) using the unconstrained Nelder–Mead optimization algorithm (Dennis & Schnabel, 1983). Assuming normality of the observations, this approach produces optimal maximum likelihood estimates of model parameters (Rao, 1973). Model fit was evaluated in two ways. First, we statistically evaluated normality and homoscedasticity of residuals. A model is considered not to be valid for a given data set if Pearson's product-moment correlation coefficient between residuals and/or Shapiro's normality tests on residuals were significant at the 5% level (Guilhaumon *et al.*, 2010). Second, we used the information-theoretic framework for model selection proposed by

Burnham & Anderson (2002). We compared the fit of the SAR models using the small-sample corrected Akaike's information criterion (AIC_c), a modification of the AIC that contains a bias correction term for small sample size. The model with the lowest AIC_c value was considered to fit the data best (Burnham & Anderson, 2002). For each model, we obtained a model selection profile and an adequate fit profile, and we used these to evaluate how the different species–area functions compared to the power function when fitted to our data. We also calculated z (the slope of the SAR) and c (a constant) for all of the fitted SAR functions. Analyses were carried out using the 'mmSAR' package (Guilhaumon *et al.*, 2010) in R (R Development Core Team, 2012).

Extinction debts

We used the SAR to estimate extinction debts rather than the endemics area relationship (EAR) (He & Hubbell, 2011) because we were modelling a community-level process of relaxation in remnant habitat, rather than a sampling process within continuous habitat (also see Wearn *et al.*, 2012). The SAR integrates the effects of increased isolation and density compensation in smaller habitat patches. Therefore a species may be committed to extinction before its entire habitat has been lost, while the EAR requires every individual of a species to lose its habitat for extinction to occur. As we also only focused on species that are dependent on forest habitat, we opted to use the SAR and not the countryside SAR proposed by Pereira & Daily (2006) that takes into account the ability of species to persist in human-modified habitats.

The SAR presents a modelling framework that can be used to predict the number of species to go extinct after habitat loss by using an extension of the power function: $S_n/S_o = (A_n/A_o)^z$, where S_n is the new number of species occurring within the habitat after disturbance, (S_o) the original number of species that occurred within the habitat prior to disturbance, (A_n) the new habitat area after disturbance, (A_o) the original habitat area prior to disturbance and z the slope of the log-log plot of the power-law SAR. We based (A_o) on our modelled estimate of the original extent of coastal forest and (A_n) on the present extent of coastal forests derived from a 2010 LANDSAT image. For (S_o) and z , we only included bird species that are dependent on coastal forests. Forest-dependent species were those that live and reproduce only in forest habitat (see Lawes *et al.*, 2007). There are no records of bird extinctions from these forests, and we therefore assumed that species found here now are similar to those that occurred prior to forest losses. Species lists were compiled from the literature and nomenclature followed Hockey *et al.* (2005). We calculated three estimates of extinction debts by using the lower, mean and upper value of z .

Threatened species and extinction debts

We used conservation assessments published on birds (Barnes, 2000) as a tally of the numbers of coastal forest species likely

to become extinct in South Africa (locally). We used the IUCN Red List of Threatened Species (IUCN, 2012) to count species likely to go extinct globally. These were species classified as critically endangered, endangered, vulnerable or near-threatened within both sets of assessments. As South Africa directly follows the IUCN categories when assigning conservation statuses to bird species (Barnes, 2000), we assumed that the two sets of assessments would be comparable. We then compared estimates of extinction debt for each group with a) the number of species classified as threatened in South Africa (locally) and b) the number of species classified as threatened on the Red List (globally). The IUCN Red List is widely regarded as the most authoritative list of globally threatened species (Rodrigues *et al.*, 2006). However, because the IUCN system is a probabilistic assessment of the likelihood that a species within a particular threat category will go extinct within a particular time frame, it is inevitable that certain species will be listed as at risk yet do not actually go extinct. Furthermore, because the system is precautionary, it is inevitable that there will be some over-listing (see Mace *et al.*, 2008). We attempted to overcome uncertainty associated with the listing process by evaluating the reasons why species were listed as threatened on the Red List as well as in South Africa.

The second part of this analysis distinguished between forest-dependent species that reach their northernmost distribution within coastal forests in KZN (hereafter referred as southern species) and species that reach their southernmost distribution in KZN (hereafter referred as northern species). We used IUCN range maps (IUCN, 2012) to assess the distribution patterns of forest-dependent species that occur within coastal forests. We defined a southern species as a species that had all or most of its range within South Africa. However, we also considered a species 'southern' when it had a South African population that was geographically isolated from populations further north in Africa with no possibility of dispersal between subpopulations. We then

calculated extinction debts by considering southern and northern species separately in the analysis and evaluated their local and global conservation statuses. We also used the Red List to assess if the population was stable, declining, increasing or if the population status was unknown.

RESULTS

Habitat suitability models

Model evaluations

Modelling performance ranked from good to excellent for all three models as indicated by high AUC values that ranged from 0.819 (lowland forest) to 0.953 (swamp forest) (Table 1). The predicted amount of forest cover based on the optimal thresholds evaluated ranged from 3595 km² to 44054 km² which suggest that the models are sensitive to the threshold metric used (see Appendix S1 in Supporting Information). The threshold that yielded the smallest fraction of predicted area was predicted presence = observed presence (Table 2).

Jackknife tests revealed that median winter rainfall, minimum humidity in winter, elevation and plant available water contributed more than 70% to the lowland, dune and swamp forest models. For all three models, aspect was of least importance. Maximum daily temperature in winter contributed significantly to the lowland (23.2%) and swamp forest (13.2%) models, but not at all to the dune forest models.

Model output

Coastal lowland forest was predicted to be the most widespread (2900 km²), followed by swamp (1220 km²) and dune forest (555 km²) (Figs 1 & 2). These values suggest that potential areas for 85% of lowland, 94% of swamp and 70% of dune forest are not made up by these forests. Coastal

Table 1 AUC scores for lowland, dune and swamp forests for all model runs. Models were calibrated using training data (70% of occurrence points, randomly selected), and AUC values were calculated from test data (30% of occurrence points, randomly selected)

	Lowland forest		Dune forest		Swamp forest	
	Training AUC	Test AUC	Training AUC	Test AUC	Training AUC	Test AUC
Full model	0.819	0.818	0.901	0.900	0.953	0.951
Cross-validation models						
1	0.790	0.791	0.882	0.877	0.953	0.951
2	0.790	0.789	0.882	0.876	0.953	0.953
3	0.790	0.799	0.882	0.886	0.953	0.952
4	0.790	0.789	0.882	0.885	0.953	0.954
5	0.790	0.796	0.882	0.886	0.953	0.949
6	0.790	0.785	0.882	0.879	0.953	0.951
7	0.790	0.787	0.882	0.875	0.953	0.950
8	0.791	0.790	0.882	0.885	0.953	0.952
9	0.791	0.779	0.882	0.880	0.953	0.950
10	0.790	0.792	0.881	0.886	0.953	0.950
Mean	0.790	0.789	0.882	0.881	0.953	0.951
Standard deviation	0.0004	0.006	0.0003	0.005	0	0.002

Table 2 Thresholds of occurrence evaluated for each of the forests models. The thresholds that minimized the predicted area of forest cover were used in all the subsequent analyses and are highlighted in bold

Threshold criteria	Lowland forest	Dune forest	Swamp forest	Predicted forest area (km ²)	Estimate of forest loss (%)
Sensitivity-specificity equality	0.498	0.517	0.446	5013	86.7
Sensitivity-specificity maximization	0.337	0.301	0.235	13094	94.9
Lowest presence threshold	0.001	0.005	0.007	44054	98.5
Predicted prevalence equals observed prevalence	0.508	0.533	0.514	3595	81.5
Percentiles					
10th percentile	0.447	0.499	0.452	8236	91.9
20th percentile	0.491	0.528	0.482	5128	87.1

forests therefore occupied 663 km² (18%) out of a possible 3595 km² that had suitable environmental conditions for forest occurrence (Table 3).

Our results suggest that lowland, dune and swamp forest have always been naturally fragmented (Table 3 & Fig. 2) as indicated by similar size class distributions of modelled and current forest fragments (Fig. 3). However, lowland, dune and swamp forest may have lost as much as 23%, 53% and 75% of fragments, respectively. Current fragment sizes were also significantly smaller than modelled fragment sizes and indicate forest loss rather than increased fragmentation ($P < 0.0001$, Mann–Whitney U tests).

Extinction debts

Field surveys

Our survey resulted in 2018 records of 65 bird species found within 11 coastal forest fragments that ranged in size from 0.29 km² to 80 km². Of these 65 species, 28 were categorized as forest-dependent. Species accumulation curves suggest sampling saturation despite few records in the smallest forest patches.

Model evaluation and estimates of z

The power model was considered the single ‘best’ model for our data set, as judged by the lowest AIC_c value, followed by

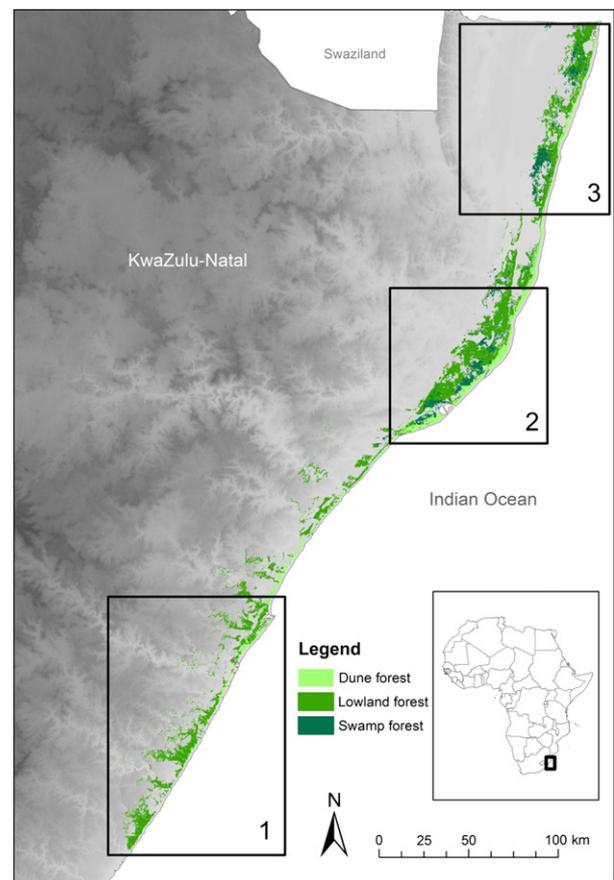


Figure 1 Map of KZN indicating where coastal forests (lowland, dune and swamp forest) are predicted to occur by the three forest models. Different shades of green represent different forest types. Black squares are linked to Fig. 2 which illustrates how modelled coastal forest distributions differ from present-day coastal forest distributions within selected areas.

the Lomolino, Weibull and exponential models (Table 4). The non-significance of both the normality and homoscedasticity tests also suggest our assumption that coastal forest bird diversity follows the relationship $S = cA^z$ was met. A mean z -value of 0.23 (95% CI: 0.16–0.30) was calculated by fitting the power model to the bird diversity data (Fig. 4).

Threatened species and extinction debt

We identified 45 forest-dependent bird species that may occur within coastal forests. Using the extent of forest loss calculated from our models, coastal forests in KZN are predicted to have an extinction debt of 14.4 (95% z : 10.6–17.9) bird species (Fig. 5). The number of predicted extinctions closely matched the number of locally threatened species (11), but not the number of globally threatened species (5). In addition, 12.2 (95% z : 9.0–15.1) northern bird species were predicted to go extinct compared to the eight that were classified as threatened locally. However, none of these species was globally threatened. Conversely, 2.3 (95% z : 1.7–2.8) southern species were predicted to go extinct, but three species (Spotted Ground

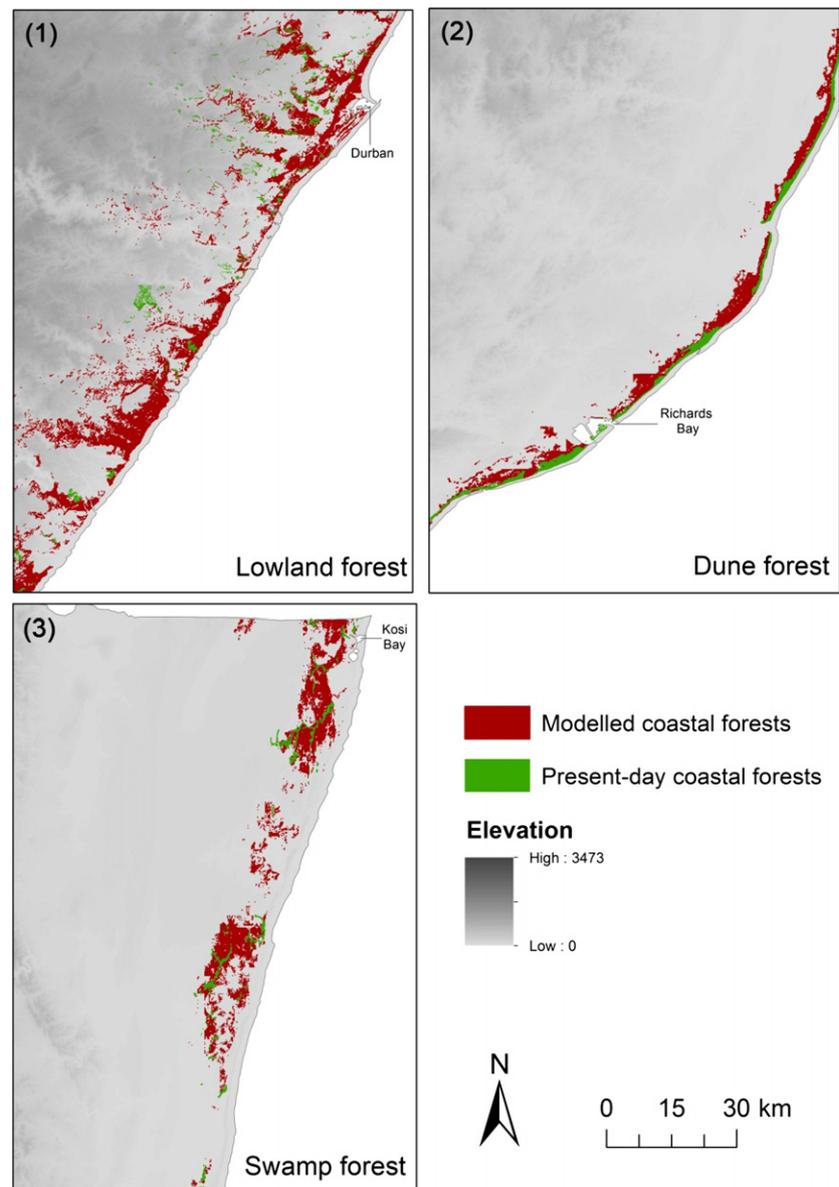


Figure 2 Maps showing the modelled and current distributions of coastal forests for selected areas in KZN. Each forest model is shown independently from other forest models. Red indicates areas that are predicted to be suitable for forest occurrence while shades of green indicate present-day forest occurrence.

Table 3 Fragmentation parameters calculated for modelled and present-day coastal forest fragments

Forest type	Area (km ²)		Number of fragments		Mean fragment size (km ²) (SD)		Average Nearest Neighbour (km)	
	Modelled	Present	Modelled	Present	Modelled	Present	Modelled	Present
Lowland	2900	370	3317	2549	0.87 (18.68)	0.17 (1.52)	0.66	0.42
Dune	555	160	411	191	1.34 (9.44)	0.88 (4.89)	0.91	1.57
Swamp	1220	94	1404	347	0.86 (13.98)	0.21 (0.78)	0.70	1.36

Thrush (*Zoothera guttata*), Knysna Woodpecker (*Campethera notata*) and the Bush Blackcap (*Lioptilus nigricapillus*) were classified as threatened – both locally and globally (Fig. 5). Furthermore, five of seven southern bird species were declining compared with 13 of 38 northern species. Only one northern bird species (African Crowned Eagle (*Stephanoaetus*

coronatus)) was classified as threatened on the Red List (globally). Forest loss, degradation and fragmentation were the main reasons for the listing of 10 of 11 locally threatened species. In addition, forest loss and small population sizes were the main reasons for the listing of all five globally threatened species (see Appendix S2 in Supporting Information).

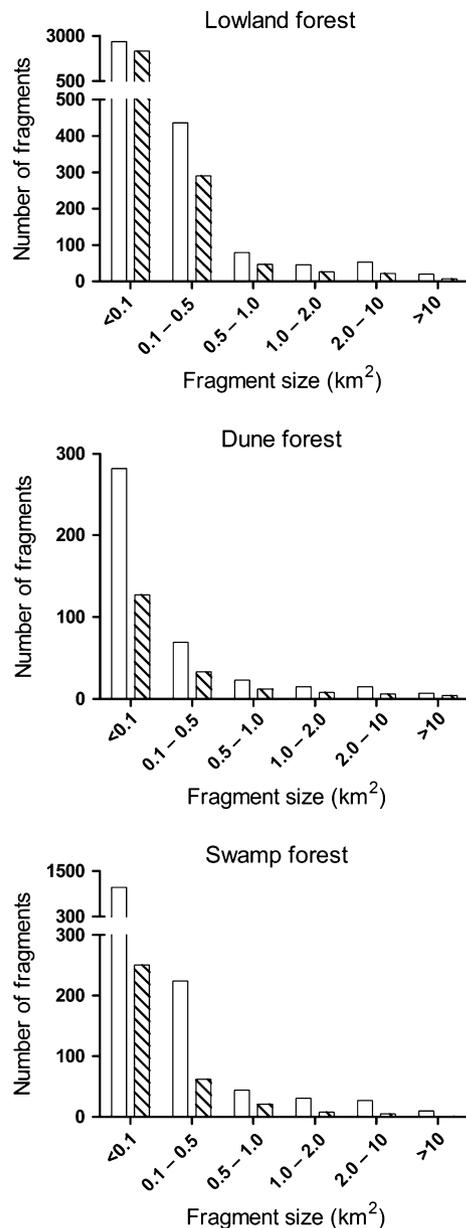


Figure 3 Histograms showing the size distribution of forest fragments for the three different forest types considered in our analysis. Open bars represent the number of modelled fragments while shaded bars represent the number of present-day fragments.

DISCUSSION

One of the goals of conservation scientists is to predict which species are most likely to be threatened with extinction, understand why, and then act to improve the situation (Manne & Pimm, 2001). Our findings suggest that by combining a simple modelling approach with empirical SAR data, scientists can detect extinction debts, determine the driver(s) behind extinction debts, identify species that are threatened with extinctions and develop guidelines to spend limited conservation resources effectively and efficiently.

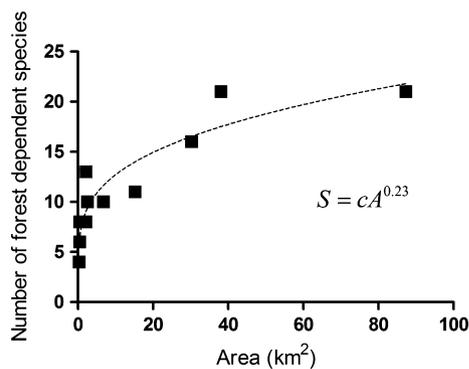
The number of threatened species that occur within coastal forests closely matched the number of species predicted to go extinct. This is nothing new as others have illustrated the same pattern for birds in south-east Asia and birds, mammals and amphibians in the Brazilian Amazon (Brooks *et al.*, 1997; Wearn *et al.*, 2012). However, it is the first time that similar results have been found with the use of a modelled estimate of forest loss. There are, however, potential caveats associated with our approach. First, species distribution modelling are subject to uncertainty which can arise from assumptions associated with a presence–absence modelling framework, conceptual and numerical model formulations, parameter estimates, model evaluation and the potential of adaptation of living systems (Planque *et al.*, 2011; Yackulic *et al.*, 2013). For instance, our results suggest that predicted forest cover differ markedly depending on the threshold criteria selected. We suggest that to calculate extinction debts, researchers should evaluate a range of threshold criteria and settle on the value that is relevant to their study area. Second, extinction debt and locally listed species might be similar, but not casually linked. For our study area, forest loss was the foremost reason for the listing of nearly every locally threatened species. This suggests that the listing of species here is a function of forest loss. This is supported by our observation that none of the species with a range that extended north of KZN were considered threatened globally. We therefore propose that habitat suitability models could be used in conjunction with SAR to detect extinction debts if we assume that extinction debt is driven by habitat loss.

Given the amount of forest loss predicted by our models, why have we not seen species go extinct and can we maintain this status quo? The absence of realized extinctions may be related to the fragmented nature of coastal forests in South Africa. Our z-value of 0.23 for forest-dependent species is similar to 0.25 that has been calculated for islands within an archipelago (Drakare *et al.*, 2006) and which has been widely used as a model for the habitat fragmentation process (Pimm & Askins, 1995; Rosenzweig, 1995). However, because forests here may have been fragmented for a considerable time, shaped by thousands of years of climate change, fire and human activities (Bond *et al.*, 2003), forest-dependent species may have evolved to persist in fragmented habitats where forests are surrounded by an ever changing assortment of grasslands, bush-lands and woodlands (Von Maltitz *et al.*, 1996). Some species may therefore be able to disperse through or utilize resources in the surrounding matrix and be buffered from extinctions associated with forest loss. This has been shown by Pereira & Daily (2006) who illustrated that the number of predicted extinctions derived from the SAR decrease when the areas of the surrounding matrices are incorporated in calculations.

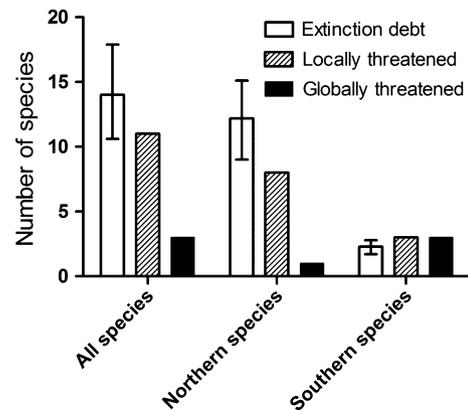
Species occupancy in fragmented landscapes may also be driven by metapopulation processes such as dispersal and colonization (Hanski & Ovaskainen, 2000). Under such conditions, local extinction rates (within fragments) decline

Table 4 Comparison of the performance of eight SAR functions for the number of bird species that occur within coastal forest fragments. Note that c (a constant) and z (the exponent of the SAR) are fitted model parameters

Function	AIC _c	R ²	c (95% CI)	z (95% CI)	Homogeneity of variance	Residuals
Power	22.40	0.85	2.63 (1.20–4.06)	0.23 (0.16–0.30)	−0.09	0.22
Exponential	27.81	0.82	−4.20 (−9.44–1.03)	2.62 (1.79–3.44)	−0.02	0.93
Negative exponential	38.27	0.52	15.75 (11.97–19.52)	0.01 (0.001–0.01)	0.48	0.16
Monod	34.60	0.66	17.26 (13.42–21.09)	135.04 (1.06–269.02)	0.36	0.12
Logistic	25.00	0.83	21.72 (16.41–27.03)	0.0006 (0.0001–0.001)	−0.26	0.16
Rational	32.18	0.83	7.00 (4.39–9.61)	0.009 (−0.02–0.02)	−0.19	0.19
Lomolino	24.39	0.84	41022.63 (28.32–47.56)	1.26 (0.72–1.80)	−0.10	0.20
Weibull	24.39	0.84	3.9e+07 (−3.8e+08–4.6e+08)	6.8e−07 (−6.9e−07–8.3e−07)	−0.01	0.20

**Figure 4** Species–area relationship for forest-dependent bird species that occur within remaining coastal forest fragments. The fit of the power function $S = cA^z$ is shown where z is the exponent of the SAR and c is a constant.

with increasing fragment area and the colonization rate increases with connectivity (Hanski, 1998; Prugh *et al.*, 2008). We speculate that these processes of extinction and recolonizations through constant dispersal may have always maintained species populations within coastal forests in South Africa. This idea is supported by our SAR calculations when we include all the species recorded during our survey. The resultant z -value of 0.16 suggest continuous habitat where immigration constantly ‘rescues’ species populations in smaller areas (Watling & Donnelly, 2006). Extinctions may therefore not have occurred because even with the loss of habitat and increased levels of fragmentation species could still persist by dispersing through the natural matrix and recolonizing empty fragments. However, based on our modelling exercise, coastal forest fragments are now smaller, fewer, further apart and more ‘hemmed in’ by human land uses than what could have been the situation in the past. In addition, matrix habitats are also being transformed at alarming rates and are under no less pressure than forests (CERU unpublished data). The conversion of natural matrix habitats to anthropogenically transformed habitats, together with forest loss may eventually result in the formation of non-equilibrium metapopulations where subpopulation (fragment) extinction rates exceed colonization rates (Hanski & Ovaskainen, 2000). This process may be happening within

**Figure 5** Comparison between the number of bird species predicted to go extinct based on our modelled estimate of forest loss and the number of locally and globally threatened species. Predictions of extinction debts closely matched the number of species classified as threatened in South Africa (locally), but not the number of species classified as threatened on the Red List (globally). Northern species were mostly locally threatened. For southern species predictions of extinction debts closely matched the number of both locally and globally threatened species.

coastal forest fragments in KZN. For one study site where long-term monitoring data were available, Trimble & van Aarde (2010) recorded that the densities of 57% of species declined in new and old growth dune forests over the last two decades. Without management interventions, non-equilibrium metapopulations will eventually go extinct, locally as well as regionally (Harrison, 1991).

Colonization and extinction may also be driving patch occupancy in other taxa (e.g. Lawes *et al.*, 2000; Olivier *et al.*, 2009). For instance, even though we did not have empirical data to evaluate extinction debts for other taxa, the same pattern observed for birds also held for mammals. Ten out of 13 forest-dependent mammal species were considered locally threatened, but none of these were threatened globally. If we assume that this represents an extinction debt it would mean that the slope of mammal SAR within coastal forests approaches 0.75. Such a high z -value suggests that mammals in these forests occur within small isolated patches that contain very few individuals of each species, with

limited dispersal between patches. The large differences in our z -values for mammals and birds reflect on differences in their susceptibility to forest loss, some of which may be ascribed to differences in life history properties associated with dispersal. In addition, mammals may also be facing high levels of subsistence hunting pressure in disturbed fragments (Hayward, 2009) that result in them being particularly vulnerable to local extinction (e.g. Canale *et al.*, 2012).

How long will it take for threatened forest species to go extinct? The time to extinction depends on variables such as population size, the colonization processes maintaining metapopulations, the magnitude of forest loss, as well as the future rate of deforestation (Wearn *et al.*, 2012; Hylander & Ehrlén, 2013). We have no information on past rates of forest loss or on the bird species that occupy the remaining forest fragments in KZN. We therefore can only speculate on the time it will take for predicted extinctions to be realized. However, we do know from historical records that five bird species have gone locally extinct, purportedly, due to the clearance of coastal forest (Siegfried *et al.*, 1976; Brooke, 1984). Predicting future forest cover under different land use scenarios as well as long-term monitoring of forest fragments therefore may enable us to set timeframes of conservation opportunities to protect species threatened by extinction.

In view of our findings, the good news is that there is still time to carry out conservation actions such as the active management of threatened species, the protection of remaining forests from disturbance and restoration of degraded forests. The bad news, however, is that the existence of extinction debts implies that even with no further habitat loss some species may go extinct locally (see Kuussaari *et al.*, 2009). The prevention of future extinctions may therefore depend on restoring and conserving natural landscapes. This could be achieved by maintaining or enhancing the coastal forest cordon as a migration corridor that may facilitate dispersal from north to south, thereby reducing extinction risk due to the loss of forests in KZN.

Furthermore, geographical isolation, small range sizes and high levels of historical habitat loss render southern species particularly vulnerable to extinction. Targeted habitat restoration efforts may therefore be the best strategy to ensure the persistence of these species, even though the selection of restoration sites remains a challenge (Thompson, 2011). Our analysis gives some indication of where one should target restoration efforts to complement remaining forest fragments, protected areas and other natural habitats in the human-modified landscape mosaic. Fragments that are surrounded by an inhospitable matrix may be linked with other fragments through restoration corridors or stepping stones (e.g. Baum *et al.*, 2004; Kupfer *et al.*, 2006). Conversely fragments that are surrounded by a permeable matrix may benefit more from an increase in area (e.g. Wethered & Lawes, 2003). Given the naturally fragmented nature of these forests, conserving natural habitats that link forest may also be just as important to prevent future extinctions as conserving remaining forest fragments. Knowing where forest occurred in the past and

where they do not occur at present will be crucial for obtaining the best return on efforts to regain some forests and restore important ecological processes to prevent future extinctions.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Maps of KZN indicating the predicted extent and occurrence of coastal forests (lowland, dune, and swamp forest) based on the optimal thresholds evaluated.

Appendix S2 Table of forest-dependent bird species that are categorized as threatened in South Africa with the motives for their listing in South Africa and the IUCN Red List.

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Pieter Olivier is a PhD student with the Conservation Ecology Research Unit at the University of Pretoria. His research focuses on spatial patterns and how biodiversity respond to these at local and regional scales. He is also interested in the causes and consequences of biodiversity loss, biodiversity conservation and ecological restoration.

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