Landscape Ecol (2018) 33:307–322
https://doi.org/10.1007/s10980-017-0604-x

RESEARCH ARTICLE

Matrix transformation alters species-area relationships in fragmented coastal forests

Marc T. Freeman · Pieter I. Olivier · Rudi J. van Aarde

Received: 10 March 2017 / Accepted: 18 December 2017 / Published online: 17 January 2018

Abstract

Context Ecological theory suggests that large habitat fragments should harbour more species than small fragments. However, this may depend on the surrounding matrix. Matrices in fragmented landscapes may either amplify or reduce area effects, which could influence predicted extinctions based on species-area relationships (SARs).

Objective To determine the influence of matrix type on SARs.

Methods We surveyed birds within 59 coastal forest fragments in two matrix types, anthropogenic (South Africa) and natural (Mozambique). We classified species as forest specialists or habitat generalists and fitted species-area models to compare how SAR slopes differed among matrix types. We also calculated nestedness and evenness to determine if these varied among matrix type and used logistic regressions to identify species-specific responses to matrix type.

Results For habitat generalists, SARs were weak within both matrices, while for forest specialists it was strong in the anthropogenic but weak in the natural matrix. In the former, the SAR was similar to those recorded for real islands within archipelagos. Forest specialist assemblages were nested by area within anthropogenic, but not natural matrices. Matrix type did not influence evenness. Area only affected the occurrence of one species when the matrix was natural, compared to 11 species when it was anthropogenic.

Conclusions Forest specialist bird species conformed to island biogeographic predictions of species loss in forest fragments embedded in anthropogenic, but not natural matrices. Extinctions from small forest fragments might be prevented by conserving natural- or restoring anthropogenic matrices, as well as by increasing forest area.

Keywords Birds · Extinction · Forest specialists · Habitat generalists · Island biogeography · Nestedness · Anthropogenic habitats

Introduction

Habitat loss and fragmentation are accompanied by a loss of species (Fahrig 2003; Haddad et al. 2015).

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10980-017-0604-x) contains supplementary material, which is available to authorized users.

M. T. Freeman · P. I. Olivier · R. J. van Aarde (✉)
Conservation Ecology Research Unit, Department of Zoology and Entomology, University of Pretoria, Hatfield 0083, South Africa
e-mail: marc.freeman@zoology.up.ac.za

P. I. Olivier
e-mail: polivier@zoology.up.ac.za

R. J. van Aarde
e-mail: rjvaarde@zoology.up.ac.za

Species losses are usually greatest in the smallest fragments and increase with time (Pardini et al. 2010; Haddad et al. 2015)—however, this may depend on the quality of the surrounding matrix (Öckinger et al. 2012). The matrix is an extensive land cover with different land-use types embedded within it, which may be inhospitable for some, but not all species (Driscoll et al. 2013). For example, matrices made up of human land-use types such as agricultural plantations and urban developments may be inhospitable for habitat specialists, but not habitat generalists. However, matrices, which include natural habitats such as secondary forests or grasslands, may not only represent complementary habitat for generalists, but also for specialists by allowing for dispersal and resource acquisition (Dunning et al. 1992). Consequently different matrices can either amplify or reduce area effects in remaining habitat fragments (Öckinger et al. 2012). If matrices amplify area effects, predictions based on conventional species-area relationships (SARs) may underestimate deterministic species losses (Koh and Ghazoul 2010; Jamoneau et al. 2012). Conversely, if matrices reduce area effects, the influence of fragmentation on biodiversity losses may be overestimated (e.g. Tscharntke et al. 2012).

Matrices that are inhospitable to fragment-dwelling species may amplify SARs. SARs are then likely to conform to island biogeography theory (IBT), i.e. where species richness increases with fragment size, irrespective of the size of the community assemblage (MacArthur and Wilson 1967). This effect is likely to be stronger when dispersal is impaired compared to when it is more frequent (Brooks et al. 1997) and may also be dependent upon the total amount of remaining habitat in a landscape (Fahrig 2003). Some studies suggest SARs may be intensified when the threshold of remaining habitat decrease below one-third of the landscape (e.g. Andrén 1994; Fahrig 2003), but this is not always the case. For example, Pardini et al. (2010) only found strong area effects in landscapes with intermediate amounts of forest cover, but not in forested and deforested landscapes. Area effects may furthermore vary across study locations, taxa and spatial scale (Fahrig 2013). This highlights the complexity involved in applying island theory to anthropogenically modified landscapes (Haila 2002) and why SARs are rare for fragments embedded in terrestrial matrices (Drakare et al. 2006). For instance, Mendenhall et al. (2014) found that bats follow island-biogeographic predictions of species loss when water surrounds habitat fragments, but not where coffee plantations and pastures do. It follows that matrices may also reduce area effects in fragmented landscapes, i.e. small and large fragments will harbour a similar number of species. This could be because an increased in landscape heterogeneity provides for higher resilience and stability of ecological processes (Martensen et al. 2012), species are able to utilise matrices through cross habitat spill-over (Ries et al. 2004), and/or the amount of available habitat increases for some species (Fahrig 2013). If this is the case, SARs are more likely to conform to a landscape complementation (sensu Dunning et al. 1992) and/or countryside biogeography framework (Daily et al. 2001). These frameworks recognises that matrices are not completely inhospitable (as assumed by the island biogeographic model), but could provide resources for many species to increase their abundances and mitigate extinctions of populations and species from habitat fragments (Daily et al. 2001; also see the landscape-moderated insurance hypothesis—Tscharntke et al. 2012).

Because generalist species are able to utilize resources in the surrounding matrix, they are more likely to conform to a landscape complementation and/or countryside biogeography framework (Daily et al. 2001). Indeed, anthropogenic matrices may provide generalist species with a platform from which to invade habitat fragments (Bridgman et al. 2012). A few generalist species may, therefore, replace many specialist species (biotic homogenization) and bring about an increase fragment assemblage evenness (Lôbo et al. 2011; Carrara et al. 2015; Ibarra and Martin 2015). This effect may be particularly evident in small fragments where core habitat is lacking (Mac Nally 2007). When habitat generalists replace specialists, the expected SAR may even be reversed, i.e. small fragments may harbour more generalist species than large fragments (Morante-Filho et al. 2015). Specialist species, on the other hand, may be more likely to conform to an island biogeography framework because the disruption of metapopulation dynamics (Eycott et al. 2010; Prevedello and Vieira 2010), edge effects (Driscoll and Donovan 2003; Ries et al. 2004), and altered resource availability (Gascon et al. 1999; Brotons et al. 2003) may lead to their disappearance from small forest fragments. As a result, specialist assemblages may be nested within fragments embedded within an anthropogenic matrix

(Wethered and Lawes 2005). Nestedness is a type of richness pattern where species present in one site are a subset of species occurring at another more species-rich site (Ulrich et al. 2009). When assemblages are nested, conservation efforts may be better off focusing on large fragments, simply because large fragments will harbour most of the species found in the region (Matthews and Whittaker 2015). This does not, however, imply that smaller fragments do not serve an important role in fragmented landscapes, for example promoting dispersal and the recolonization of species poor fragments (Dunning et al. 1992; Mueller et al. 2014).

In this study, we tested whether matrices amplified or reduced SARs of birds that occur within fragmented coastal forests along the east coast of southern Africa. We defined matrices as any land-use type that was not coastal forest, but in which coastal forest fragments were embedded. We surveyed birds in 29 coastal forest fragments surrounded by anthropogenic matrices (sugarcane, *Eucalyptus* and *Pinus* plantations, urban settlements) and 30 fragments surrounded by natural matrices (grasslands and woodlands). We categorised all species as either forest specialists or habitat generalists and then tested three hypotheses. First, we hypothesised that the SAR for forest specialists would conform to the predictions of IBT in the natural and anthropogenic landscape (Guldemond and van Aarde 2010). However, we expected the slope of the SAR to be steeper when the matrix is anthropogenic, compared to when it is natural because specialist species may not be able to disperse through an anthropogenic matrix (Brooks et al. 1997). Conversely, the SAR for generalist species would fit into a countryside biogeography framework, where large and small fragments harbour a similar number of species. Second, we hypothesised that forest specialist bird assemblages would be more nested than habitat generalists. We also expected nestedness to be greater for anthropogenic than natural matrices because of the loss of specialist species from small fragments. Third, we hypothesised that large fragments would support rarer forest specialist species, which would increase assemblage unevenness. Conversely, as forest fragments become smaller we expected many forest specialist species to be lost and for a few generalist species to dominate the assemblage, bringing about a more evenly distributed assemblage (Sanchez-de-Jesus et al. 2016). Assemblage evenness should therefore decrease with an increase in fragment area and we expected this pattern to be stronger in anthropogenic than natural matrices. Finally, we investigated species-specific responses to matrix transformation.

Methods

Study areas

We studied forest birds within two fragmented landscapes located in South Africa (32°5′32.151″E, 28°43′44.871″S) and Mozambique (32°50′8.133″E, 26°29′31.008″S) (Fig. 1). Both landscapes formed part of the critically endangered Maputaland Coastal Forest Mosaic (Burgess et al. 2004), the Maputaland Centre of Plant Endemism (Van Wyk and Smith 2001) and the Maputaland-Pondoland-Albany biodiversity hotspot (Küper et al. 2004). Historically, natural grasslands and woodlands adjoined these forests. However, in many areas sugarcane and Eucalyptus plantations, mines, and rural and urban settlements have replaced these habitats. This is specifically true for coastal forests in KwaZulu-Natal, South Africa, where 1.2% of the natural landscape has been transformed per annum since 1994 (Jewitt et al. 2015). However, this has not been the case in the Maputo province of southern Mozambique. Here coastal forests are embedded within a matrix of grasslands, woodlands, and low-density rural settlements. Vegetation types were defined as woodlands when trees dominated the vegetation, but not to the extent that the canopies were continuous or overlapping (less than 50% canopy cover) (Lawes et al. 2004). These two contrasting landscape types provided us with a valuable opportunity to assess the influence of matrices on SARs because we could take into account habitat type (coastal forests) within the different matrices (human land-use types in South Africa and natural grasslands and woodlands in Mozambique). We surveyed 29 (range 0.02–30.40 km^2) and 30 (range 0.05–74.30 km^2) forest fragments in South Africa and Mozambique respectively.

Data collection

Bird communities were surveyed in forest fragments embedded within both matrix types using point counts

(Bibby et al. 2000). Both surveys were conducted during the breeding season (Dec, Jan, Feb) during the 2007/2008 and 2014/2015 summer survey seasons. We surveyed 220 points within 30 fragments in the natural landscape and 227 points within 29 fragments in the anthropogenic landscape. Each survey point was visited only once during the study. Both landscapes included dune, swamp, and coastal lowland forests. Thirteen sand forest fragments were surveyed within the natural landscape, but we did not survey any sand forest fragments in the anthropogenic landscape. One scarp forest fragment was surveyed in the anthropogenic landscape. Despite discrepancies in the classification of these different forest types, we opted to recognize coastal forests as comprising these five forest types because they share more than 90% of forest bird species (Von Maltitz et al. 2003; Lawes et al. 2007).

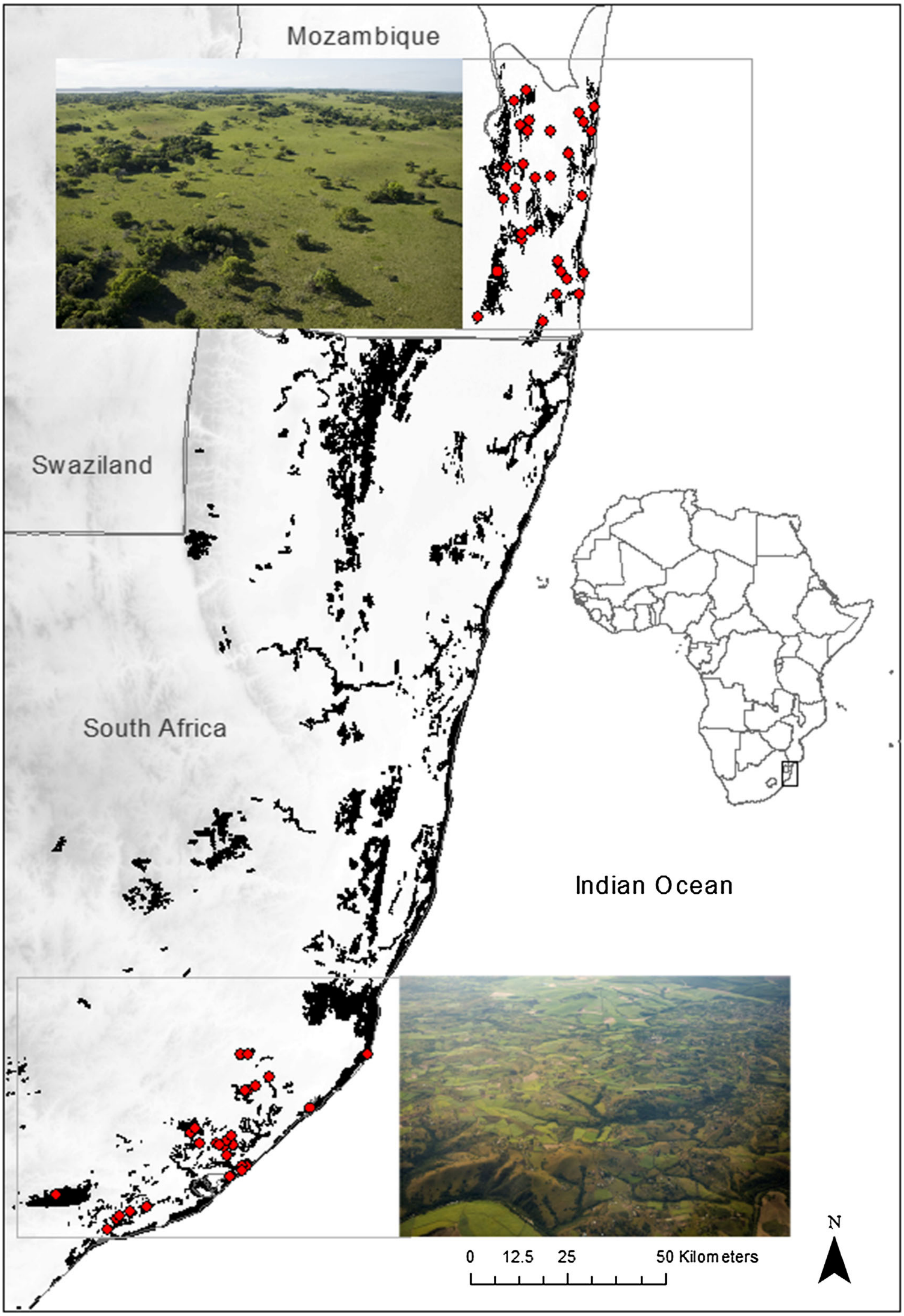
Point counts took place between ~ 05:00 and 09:00 h to avoid high midday ambient temperatures that may reduce bird activity. All observers (seven in total) had prior knowledge or were trained to identify coastal forest birds based on calls and appearance. Observers were randomly assigned to forest fragments. More than half (60%) of the survey points in both landscapes were surveyed by the same two observers. Each forest fragment was randomly assigned survey points, which were located using a GPS (Garmin Map 62). The number of survey points per forest fragment ranged from 3 to 6 for fragments < 5 km^2, 6–15 for fragments between 5 and 20 km^2 and 15–36 for fragments > 20 km^2. Sampling effort varied with fragment size, in an attempt to ensure that the sufficient coverage of bird assemblages within each fragment was achieved. Upon arrival at the survey point, observers waited for two minutes to allow birds that might have been disturbed to acclimatise to their presence. The observer then recorded bird species that were judged to be heard or seen, within an approximate 60 m radius for 10 min. Surveys were abandoned on windy and rainy days. Species flying above the canopy were not recorded.

All species recorded during our surveys were categorised as either forest specialist or habitat generalist species based on Hockey et al. (2005) and the South African Bird Atlasing Project (www.sabap2.adu.org.za) (see Table S1 in Appendix S1). We classified forest specialist species as those that live and reproduce only in forest habitats (also see Lawes et al. 2007). Habitat generalists were classified as those species that occur within more than one habitat type based on (Hockey et al. 2005). Consequently, edge species were also classified as habitat generalists because they could utilize more than one habitat type.

Fig. 1 The two landscapes included in our study. In South ▶ Africa, coastal forest fragments were embedded within a matrix of human land-use types that included sugarcane, Pine, and Eucalyptus plantations, as well as rural and urban settlements. In Mozambique, most fragments were located within the Maputo Elephant Reserve and were embedded within a natural matrix of woodlands and grasslands. Photographs courtesy of Rudi van Aarde

Data analyses

We assessed sampling saturation for each of the 59 surveyed forest fragments using sample based accumulation curves calculated in EstimateS 8.2.0 (Gotelli and Colwell 2001; Colwell 2013). The program uses abundance based data as an input and then calculates rarefied estimated species richness as Choa1 values for each forest fragment (Colwell 2013). Chao1 is the most commonly used index for estimating species richness and is based on the frequency of an individual's occurrence within a sample (Chao 1984). By extrapolating from the recorded observations, estimated species richness (Chao1) within each of the surveyed forest fragments at both landscapes was obtained. These values were then used to fit the respective species-area models. We also calculated the coverage based estimate values for each forest fragment using the iNEXT package in the R programming environment. Coverage based estimates provide a measure of sample completeness, giving the proportion of the total number of individuals in an assemblage that belong to the species represented in the actual sample (Chao and Jost 2012). This ensured that species richness for all forest fragments was comparable as the set of communities in each forest fragments was based on samples of equal completeness (Gotelli and Colwell 2001; Chao and Jost 2012). We tested for spatial autocorrelation in each landscape using Mantel tests based on the Bray–Curtis dissimilarity among fragments. Bird assemblages were not spatially auto-correlated in the anthropogenic (Mantel $r = 0.07$; $P = 0.25$) or natural landscape (Mantel $r = -0.06$; $P = 0.91$).


Mozambique
Swaziland
South Africa
Indian Ocean
0
12.5
25
50 Kilometers
N

Species-area relationships

Numerous functions, which vary in complexity, have been proposed for modelling SARs (Dengler 2009; Triantis et al. 2012). The most widely used of these is the power model $S = cA^z$ where S is species richness, A is area of fragment, and c and z are constants (Arrhenius 1921; Preston 1962). The power model is particular useful when modelling SARs because the z value, which represent the slope of the SAR, provides information on the spatial arrangement of habitat fragments (Preston 1962). Low z values that range from 0.12 to 0.18 suggest continuous habitats (Johnson et al. 1968; Brooks et al. 1997) where populations in small habitat fragments are "rescued" from local extinction by the constant immigration of species from surrounding areas (Rosenzweig 1995). Real island systems in archipelagos typically display a z value which ranges between 0.25 and 0.35 (Johnson et al. 1968). Conversely, high z values that range from 0.7 to 0.9 suggest fragmented systems with no immigration between fragments (Brooks et al. 1997).

The power model, however, may not always provide the best fit for SARs. To evaluate SARs we fitted eight species-area models to forest specialists and habitat generalist's species richness for forest fragments embedded in the anthropogenic and natural matrices respectively. These models included the power, exponential, negative exponential, monod, rational functional, logist, Lomolino and the cumulative Weibull model (see Triantis et al. 2012) for descriptions of the analytical formulae for each model). Species-area models were fitted using the mmSAR package (Guilhaumon et al. 2010) in the R programming environment (R Development Core Team 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 and Schnabel 1983). Assuming normality of the observations, this approach produces optimal maximum likelihood estimates of model parameters (Rao 1973). We evaluated model fit by statistically evaluating 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 and/or Shapiro's normality tests on residuals were significant at the 5% level (Guilhaumon et al. 2010). We also used the information theoretic framework for model selection proposed by Burnham and Anderson (2002). We compared the fit of the SAR models using the small-sample corrected Akaike's information criterion (AICc), a modification of the AIC that contains a bias correction term for small sample size. The model with the lowest AICc value was considered to fit the data best (Burnham and Anderson 2002). Models with ΔAICc values < 2 of the best model were considered to have similar support (Burnham and Anderson 2002). We also calculated z (the slope of the SAR) and c (a constant) for all of the fitted SAR functions.

Evenness and dominance

We used Pielou's J value (Pielou 1967) to calculate evenness of species assemblages within each forest fragment embedded in both matrix types. The J value ranges from zero to one—a higher J value reflects less variation between species abundances within a community (i.e. more even), while a lower J value reflects higher variation (i.e. less even). We may, therefore, expect that assemblages dominated by a few generalist species will have a higher J value than those with similar numbers of specialists and generalists. We tested if there was a significant difference in the J values (mean J value ± SE) calculated for the anthropogenic and natural matrices using a Mann–Whitney test (non-parametric, two-tailed). We then used general linear regressions to evaluate the relationship between evenness and forest fragment area to test if these relationships differed among the natural and anthropogenic landscape. Evenness was calculated with the VEGAN package (Oksanen et al. 2013) in the R programming environment (R Development Core Team 2012).

Nestedness

We calculated nestedness for forest specialist and habitat generalist assemblages within both matrix types using the nestedness metric based on overlap and decreasing fill (NODF) (Almeida-Neto et al. 2008). The NODF is considered to be the most appropriate metric for measuring nestedness (Ulrich and Almeida-Neto 2012). A score between 0 and 100 is obtained when using NODF, with 100 being completely nested and 0 not nested. The metric calculates nestedness independently for (i) sites (numerical matrix rows), (ii) species occurrences (numerical matrix columns) and (iii) the entire numerical matrix combined ("max matrix") (Matthews and Whittaker 2015). We followed a procedure similar to that of Matthews and Whittaker (2015), by which NODF values were calculated using presence-absence matrices in the VEGAN R package (Oksanen et al. 2013). Three nestedness values were obtained, namely global NODF (nestedness of entire matrix), maximal NODF (maximum nestedness for rows), and nestedness by area (area NODF). Global nestedness indicates the nestedness for the entire matrix (i.e. nestedness for the entire landscape), while maximal NODF indicates the highest nestedness value recorded within the presence-absence matrix (i.e. the fragment with the highest level of nestedness in the landscape). Nestedness by area indicates the effect that fragment area has on estimates of nestedness.

The global NODF value for the entire presence-absence matrix was calculated initially, and row orders were not held constant. The maximal NODF amongst rows were then calculated, followed by the area NODF value during which rows were held constant and arranged in descending order of area (largest forest fragment as the top row) (Matthews and Whittaker 2015). Using a standard Spearman's correlation test, we were able to determine if the maximal NODF and area NODF values were significantly correlated. A strong correlation suggests that the patterns of nestedness observed in the study were driven by area (e.g. Wang et al. 2010). Therefore, the NODF metric allowed for inferences as to whether the transformation of the matrix leads to a more nested bird community amongst forest fragments, and whether area drives nestedness.

Species presence and forest fragment area

To determine the relationships between the occurrence of each species and the size of forest fragments in each matrix type we used binomial logistic regressions. We used presence-absence data to model the relationship between species occurrence and fragment area for each forest specialist and generalist bird species recorded more than once within each matrix type (17 forest specialist and 33 habitat generalist species—100 models that included each species for both matrix types). This was done for two reasons. First, we wanted to determine if forest specialist species in anthropogenic matrices were more likely to occur in large forest fragments, while forest specialists in natural matrices would not be affected by forest fragment size. Second, we wanted to identify which species were sensitive to fragment area. For each model (i.e. species), we obtained a *P* value, which indicated whether the presence of a species was significantly influenced by forest fragment area. *P* values > 0.05 indicate no or little effect of area on a bird species, while *P* values < 0.05 indicate a strong effect of fragment area.

Results

We identified 123 bird species among 5 527 records in 59 forest fragments. Surveys in the anthropogenic landscape yielded 99 species from 3 200 bird records, of which 33 were forest specialist and 66 habitat generalist species. Coverage based estimates suggested that in the natural landscape sampling coverage amongst forest fragments ranged from 67 to 98% with a mean value of 88%. While in the anthropogenic matrix sampling coverage ranged from 60 to 95% with a mean value of 82%. The natural landscape yielded 89 species from 2 327 records, of which 27 were forest specialist and 62 habitat generalist species. Sixty-five out of 123 species were recorded in both landscapes. However, the overlap in the distributional ranges suggests that 111 out of 123 species occurred within both landscapes (Hockey et al. 2005). Forest specialist composition between landscapes was similar with 24 out of 36 species recorded in both landscapes. Thirty of 36 forest specialists occurred at both landscapes (Hockey et al. 2005). Only about half (41 out of 87) of habitat generalists were recorded at both landscapes. Yet, based on distributional ranges, 81 out of 87 recorded habitat generalist species occurred within both landscapes (Hockey et al. 2005).

Species-area relationships

The power model yielded the best-fit model for the relationship between forest specialist and generalist's estimated species richness (mean Chao1) and forest area in natural and anthropogenic matrices (Fig. 2). AICc values for the power model were the lowest amongst the eight models or were within ΔAICc values < 2 of the best model (Table 1).

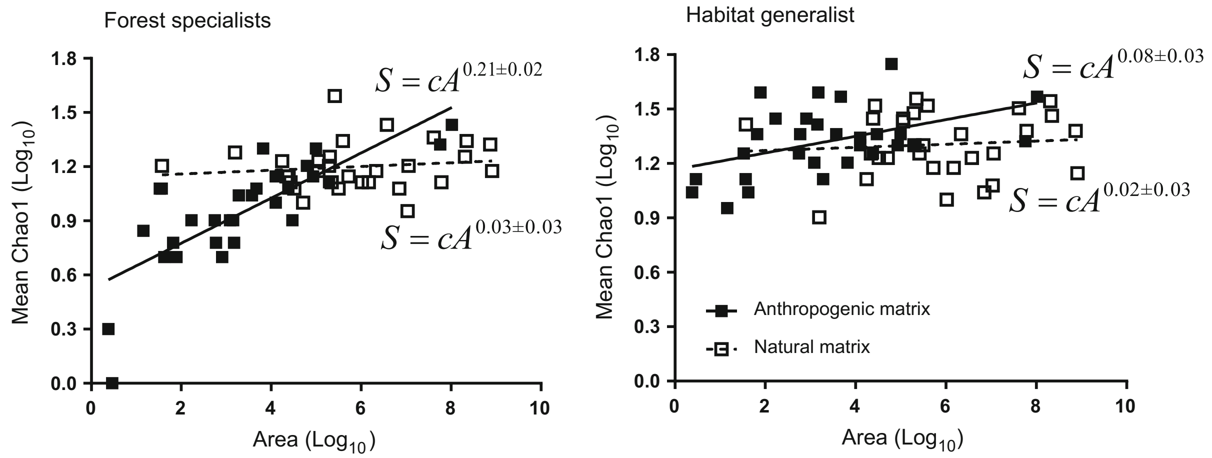


Fig. 2 Species-area relationships for habitat generalists and forest specialists within both matrix types. The power model provided the best fit for forest specialist and generalist species in natural and anthropogenic matrices

Table 1 ΔAICc and Akaike weight (ωAICc) values for the eight different SAR models calculated for forest specialists and habitat generalist assemblages in both landscapes

Model	Function		Anthropogenic matrix				Natural Matrix			
	K		Forest specialist		Habitat generalist		Forest specialist		Habitat generalist	
			ΔAICc	ωAICc	ΔAICc	ωAICc	ΔAICc	ωAICc	ΔAICc	ωAICc
Power	$S = cA^Z$	2	0	0.74	1.23	0.16	0	0.22	0	0.16
Exponential	$S = c + zlog(A)$	2	5.41	0.05	1.17	0.17	0.02	0.22	0.01	0.16
Negative exponential	$S = d(1 - \exp(-zA))$	2	19.84	0.00	0.00	0.30	0.47	0.17	0.19	0.15
Monod	$S = d/(1 + cA^{-1})$	2	13.74	0.00	2.18	0.10	0.46	0.18	0.04	0.16
Rational	$S = (c + zA)/(1 + dA)$	3	5.98	0.04	2.87	0.07	3.13	0.05	0.18	0.15
Logistic	$S = D/(1 + \exp(-zA + f))$	3	9.93	0.01	3.94	0.04	2.57	0.06	2.34	0.05
Lomolino	$S = d/1 + (z^{\log(f/A)})$	3	4.39	0.08	2.84	0.07	3.16	0.05	0.23	0.14
Weibull	$S = d/(1 - \exp(-zA^f))$	3	4.44	0.08	2.67	0.08	2.68	0.06	2.69	0.04

Mean Chao1 were used as estimates of species richness per forest fragment. K refers to the number of parameters associated with each function. Minimum AICc values recorded in the anthropogenic landscape for forest specialists and habitats generalists were 73.02 (Power model) and 135.78 (Negative exponential model) respectively. While minimum AICc values recorded in the natural landscape for forest specialists and habitats generalists were 111.55 (Power model) and 130.81 (Power model) respectively

Evaluations of the z values for the four different models suggest that the relationship between Chao1 estimated species richness and area was strongest for forest specialists in anthropogenic matrices ($z = 0.21 \pm 0.02$). Forest specialist species in natural matrices did not show a strong relationship between species richness and area ($z = 0.02 \pm 0.03$). Generalist species showed a weak relationship between species richness and area in anthropogenic ($z = 0.07 \pm 0.04$) and natural matrices ($z = 0.02 \pm 0.04$) (Fig. 2).

Linear regressions based on log transformed area data indicated that the relationship between forest specialists and area differed significantly ($P < 0.001$) between the anthropogenic (slope $= 0.13 \pm 0.02$, $F = 38.97$, dfn $= 1$, $P < 0.001$) and natural habitat (slope $= 0.01 \pm 0.01$, $F = 0.51$, dfn $= 1$, $P = 0.47$). Conversely, the relationship between habitat generalists and habitat area at the anthropogenic (slope = 0.04 ± 0.02, F = 7.05, dfn = 1, P = 0.01) and natural habitat (slope = 0.01 ± 0.02, F = 0.51, dfn = 1, P = 0.48) was not significantly different (P = 0.12).

Evenness and dominance

Bird assemblages within forest fragments were significantly less even when the matrix was anthropogenic (Mean J value = 0.92 ± 0.004) compared to when it was natural (Mean J value = 0.95 ± 0.0032) (Mann–Whitney Test, P < 0.001). Linear regressions indicated that evenness of bird assemblages decreased with forest fragment area in both landscape types. Although this effect was stronger in the anthropogenic (slope = − 0.02 ± 0.002, F = 16.51, P < 0.001) than the natural (slope = − 0.01 ± 0.001, F = 6.34, P = 0.018) landscape the slopes were not significantly different (F = 1.927, dfn = 1, P = 0.17) (Fig. 3).

Nestedness

The global NODF for species assemblages was similar between landscapes, with the natural matrix returning a global NODF of 54.65 and the natural matrix a global NODF of 47.68. Global NODF values for forest specialist species in both natural (global NODF = 70.05) and anthropogenic (global NODF = 73.21) matrices were also similar. Both these values for forest specialists were higher than habitat generalist species with global NODF values of 48.21 and 43.90 in anthropogenic and natural matrices respectively.

Maximal NODF values for forest specialist species in both anthropogenic and natural matrices were also similar, with values of 77.57 and 72.34 respectively. The difference in nestedness between matrices was only evident in the area NODF values; forest specialist species in the anthropogenic matrix had an area NODF of 67.66, while forest specialists in the natural matrix had an area NODF of 45.53.

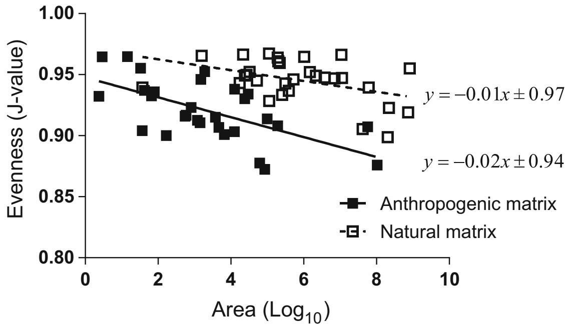


Fig. 3 Linnear regressions fitted to Pielou's evenness index that was calculated for each forest fragment in both matrix types

For both forest specialists and habitat generalists in anthropogenic landscape the Maximal NODF and area NODF values were strongly correlated (all Spearman rho > 0.7, P < 0.01). Forest specialist and generalist species in the natural matrix returned significant Spearman's correlations < 0.5 (see Table 2).

Species presence and forest fragment area

Eleven of the 17 forest specialist species in forest fragments in the anthropogenic matrix were influenced by forest fragment size (*P* value < 0.05) (see Fig. S3 in Appendix S3).In contrast, only 1 out of 17 forest specialists (Narina Trogon, *Apaloderma narina*) was significantly influenced by forest fragment size when the matrix was natural (see Table 3). In forest fragments in the anthropogenic matrix, only 3 out of 33 habitat generalists were affected by forest fragment size. In the natural matrix, only 1 out of 33 habitat generalist species was affected by forest fragment area (see Table 3 for reported *P* values for each species).

Discussion

Large forest fragments should harbour more species than small forest fragments (MacArthur and Wilson 1967). The reduction and division of extensive forests into smaller fragments should therefore result in local extinctions (Haddad et al. 2015; but also see Laurance 2008). However, our results suggest that this effect was stronger when human land-use types surround forest fragments than when grasslands or woodlands do. When the matrix was natural, small and large forest fragments harboured a similar number of forest specialist species. Forest area did not affect the number of habitat generalist species when the matrix was anthropogenic or natural. A landscape complementation or countryside biogeography framework would therefore be applicable to generalist species in both matrix types, but only to forest specialist species when natural matrices surround forest fragments. However, where human land-use types surround

Table 2 Nestedness values calculated by using the nestedness metric based on overlap and decreasing fill—a metric that can quantify nestedness for the whole numerical matrix and for rows and columns separately (Almeida-Neto et al. 2008)

	Natural matrix			Anthropogenic matrix		
	All species	Forest specialist	Habitat generalist	All species	Forest specialist	Habitat generalist
Global NODF	54.65	70.05	48.21	47.68	73.21	43.90
Maximal NODF	68.14	72.34	63.43	63.77	77.57	59.53
Area NODF	41.65	45.53	37.93	55.1	67.66	45.23
Spearman's (rho)	0.32	0.41	0.29	0.88	0.86	0.74
P value (Spearman's)	0.084	0.024	0.012	< 0.01	< 0.01	< 0.01

We calculated three nestedness values for habitat generalists and forest specialists within each matrix type: (i) global nestedness, (ii) maximal nestedness and (iii) area nestedness. We also include the Spearman's correlation between area NODF and maximal NODF along with its associated *P* value

forests fragments, forest specialist species conform to island biogeographic predictions of species loss.

The power model performed slightly better than most SAR models and was therefore selected to assess SAR for forest specialist and habitat generalist species in both natural and anthropogenic landscape. This selection was also based on Triantis et al. (2012) who found that the power model ranked first for 465 island data sets, while Dengler (2009) also suggests that the power function should be used to describe and compare any type of SAR. The power model performs well when predicting species richness over a ten-fold increase in area, and may be one of the reasons why it was the best fit for all four of our datasets (Dengler 2009). However, it is necessary to exercise caution when assigning an ecological interpretation to the parameters of the power model (Triantis et al. 2012). For instance, the sampling scheme, spatial scale, taxa and habitat type may influence the slope of the SAR (z value) (Drakare et al. 2006). In our study, these variables were kept constant among landscapes and study fragments. The SAR slopes were thus comparable—specialist species in anthropogenic matrices had a high value of z (0.21), compared to the low z value of specialists in natural matrices (0.03) and generalists in natural (0.02), and anthropogenic matrices (0.08).

Why do forest specialist species disappear from small forest fragments when the matrix is anthropogenic? Anthropogenic effects on landscapes may homogenize landscape patterns, introduce novel patches and dynamics, and alter patch dynamics (Urban et al. 1987). The heterogeneous, tree-grass matrix typical of the coastal plains of southern Africa may provide forest specialists species with stepping stones that allow them to recolonize isolated forest fragments (Mueller et al. 2014). However, the transformation of the matrix into homogeneous agricultural fields may remove these stepping-stones, and could therefore disrupt dispersal and metapopulation dynamics (Mueller et al. 2014). Following local extinctions, small fragments cannot be recolonized, leading to the absence of forest specialists from small forest fragments. Moreover, natural matrices such as grasslands and woodlands may provide supplementary resources to forest specialist species (Dunning et al. 1992). For example, Trumpeter Hornbills (*Bycanistes bucinator*) nest in large forest fragments but frequently visit fruiting trees in the matrix (Lenz et al. 2011). It may therefore be a mistake to regard natural grasslands and woodlands that surround forest fragments as matrices, as these land-use types may provide additional habitat to forest specialist species. The third reason, and one we consider most likely is that matrix transformation alters patch dynamics by influencing tree community composition and structure within forest fragments (Laurance et al. 2006; Botzat et al. 2015). Forests with a high diversity of trees provide for a higher variety of birds (Tews et al. 2004). However, the replacement of natural matrices with human land-use types may lead to the occurrence of more light-tolerant tree species within forest fragments (see Botzat et al. 2015). The increase of light tolerant, early successional trees, as well as invasive plant species, may correlate with a decline of shade tolerant trees and a simplification of forest structure. The absence of

Table 3 The relationships between the occurrence of each species and the size of forest fragments in each matrix type

Forest specialist species	Anthropogenic matrix				Natural matrix			
	Estimate	SE	*z*	*P* value	Estimate	SE	*z*	*P* value
Notopholia corruscus	0.496	0.530	0.937	0.349	− 0.123	0.520	− 0.236	0.813
Trochocercus cyanomelas	2.619	1.114	2.351	**0.0187**	0.928	0.599	1.549	0.122
Erythropygia signata	1.835	0.900	2.037	**0.0416**	− 0.145	0.638	− 0.228	0.82
Ploceus bicolor	3.571	1.319	2.706	**0.0068**	1.451	0.776	1.869	0.062
Nicator gularis	1.867	0.849	2.198	**0.028**	0.205	0.516	1.821	0.069
Ceuthmochares australis	3.318	1.504	2.206	**0.0274**	1.334	0.757	0.397	0.692
Camaroptera brachyura	2.96E−08	5.12E+04	0	1	− 2.54E−09	5.48E+04	1.763	0.078
Cyanomitra veroxii	0.5295	0.5318	0.996	0.32	0.838	0.573	0	1
Tauraco livingstonii	1.368	0.673	2.033	**0.042**	1.368	0.673	1.463	0.144
Apaloderma narina	1.724	0.824	2.092	**0.0364**	0.477	0.540	2.033	**0.042**
Cyanomitra olivacea	3.980	1.449	1.625	0.104	1.161	0.638	0.883	0.377
Indicator variegatus	1.3813	0.3432	1.858	0.063	0.937	0.916	1.571	0.116
Dicrurus ludwigii	2.148	0.677	2.45	**0.0143**	1.410	0.898	1.022	0.307
Bycanistes bucinator	2.352	0.263	2.213	**0.0269**	0.397	0.566	1.33	0.183
Chlorocichla flaviventris	3.214	1.557	2.064	**0.039**	0.607	0.703	0.701	0.484
Pogoniulus bilineatus	0.605	0.303	0.002	0.998	2.394	1.632	0.864	0.388
Turtur tympanistria	2.893	1.245	2.324	**0.0201**	0.819	0.616	1.467	0.142
Habitat generalist species								
Treron calvus	0.726	0.653	1.113	0.266	0.232	1.026	0.226	0.821
Terpsiphone viridis	0.595	0.604	0.986	0.324	0.210	1.025	0.205	0.838
Muscicapa caerulescens	0.118	0.760	0.155	0.877	− 0.912	0.884	− 1.031	0.303
Erythropygia quadrivirgata	− 0.222	1.375	− 0.161	0.872	0.719	0.618	1.164	0.244
Dryoscopus cubla	1.991	0.977	2.038	**0.0416**	5.017	2.366	0.001	0.999
Tchagra senegalus	0.813	0.619	1.314	0.189	1.244	0.858	1.45	0.147
Oriolus larvatus	0.232	0.542	0.429	0.668	− 0.578	0.700	− 0.825	0.41
Merops persicus	− 1.647	1.91	− 0.862	0.389	0.348	1.033	0.337	0.736
Halcyon albiventris	0.662	0.607	1.091	0.276	0.172	0.529	0.325	0.745
Centropus burchellii	− 0.437	0.500	− 0.872	0.383	0.211	0.512	0.412	0.68
Zosterops capensis	0.414	0.553	0.748	0.454	− 0.802	1.028	− 0.78	0.435
Hedydipna collaris	3.017	1.366	2.209	0.027	1.236	0.639	1.934	0.053
Pycnonotus tricolor	1.647	1.91	0.862	0.862	0.766	0.649	1.18	0.238
Chrysococcyx caprius	0.886	0.586	1.511	0.131	0.807	0.652	1.236	0.216
Turtur chalcospilos	0.208	0.5429	0.383	0.702	0.391	0.585	0.669	0.503
Dicrurus adsimilis	0.080	0.619	0.129	0.897	0.756	0.681	1.111	0.267
Campethera abingoni	2.423	0.988	2.453	**0.0141**	0.522	0.538	0.969	0.332
Chlorophoneus viridis	0.151	0.507	0.297	0.766	1.105	0.621	1.779	0.075
Bostrychia hagedash	2.96E−08	5.12E+04	0.759	0.448	0.082	0.513	0.159	0.874
Chrysococcyx klaas	0.851	0.569	1.495	0.135	1.718	1.067	1.611	0.107
Indicator minor	− 0.163	0.973	− 0.167	0.867	1.117	1.554	0.719	0.472
Cinnyris bifasciatus	0.334	0.603	0.554	0.58	1.414	0.678	2.087	**0.0369**
Cossypha natalensis	1.443	1.73	0.918	0.359	2.148	1.194	1.799	0.072
Cuculus solitarius	0.322	0.875	0.368	0.713	0.673	0.561	1.2	0.23
Streptopelia semitorquata	− 0.040	0.487	− 0.082	0.935	− 0.749	0.680	− 1.102	0.271

Table 3 continued

Forest specialist species	Anthropogenic matrix				Natural matrix			
	Estimate	SE	z	P value	Estimate	SE	z	P value
Pogoniulus pusillus	1.067	0.603	1.77	0.077	0.753	0.564	1.335	0.182
Apalis ruddi	1.825	0.7904	2.309	**0.0209**	0.509	0.771	0.66	0.509
Andropadus importunus	1.095	0.770	1.422	0.155	0.287	0.683	0.42	0.675
Laniarius ferrugineus	0.807	0.642	1.256	0.209	0.287	0.604	0.475	0.635
Ploceus ocularis	0.135	0.476	0.283	0.777	− 0.076	0.745	− 0.103	0.918
Cinnyris talatala	0.081	0.918	0.088	0.93	2.805	1.036	2.709	0.007
Stactolaema leucotis	1.146	0.652	1.758	0.079	− 0.063	1.015	− 0.062	0.951
Milvus parasitus	3.214	1.557	2.064	0.133	− 0.684	1.395	− 0.49	0.624
Apalis flavida	3.076	1.178	2.611	0.009	0.779	0.781	0.998	0.318

Bold faced characters indicate statistically significant relationships between species presence and forest fragment size). Estimate indicates the slope coefficient and its standard error (SE). The test statistic for the linear regression is represented by z

large fruiting trees and/or the dominance of pioneers may lead to less specialized and more robust plant-bird networks (e.g. Menke et al. 2012), where forest specialist species decline with increasing matrix modification. Therefore, even if forest specialist bird species are able to disperse through an anthropogenic matrix, they may not find suitable habitats (Stratford and Stouffer 2015).

Species-specific responses to matrix transformation provide support for this idea that specialist species disappear from small forest fragments in anthropogenic matrices. Seven out of 11 bird species whose occupancy was significantly affected by fragment area were insectivores. Olivier and van Aarde (2017) found a direct link between tree species richness and insectivore bird species richness. If tree species richness therefore declines in response to matrix transformation, insectivore richness should also decline (Olivier and van Aarde 2017), possibly because compositional changes in the tree community lead to changes in vegetation structure on which specialised insectivores depend (e.g. Arcilla et al. 2015; Stratford and Stouffer 2015). This may hamper the trophic control of herbivorous insects by insectivorous birds, inhibiting tree growth and fecundity and modifying plant assemblage composition (e.g. Peter et al. 2015; Morante-Filho et al. 2016). The three other bird species that were sensitive to forest area in anthropogenic matrices were frugivorous. In our study area, the disappearance of large fruiting trees from forest fragments in anthropogenic matrices may lead to the local extinction of frugivorous species that depend on the availability of fruiting trees (Lenz et al. 2011).

The selective extinction of vulnerable species may explain why forest specialists were nested by area when the matrix was anthropogenically transformed, but not when it was natural. When specialists disappear, a subset of common, more generalized and disturbance tolerant species may remain (Socolar et al. 2015). When this happens, evenness may increase with a decrease in fragment area because of the loss of rare species. Similar findings were reported for the Lacandona rainforest in Mexico by Sanchez-de-Jesus et al. (2016) who illustrated that the evenness of dung beetle communities increased in small fragments. This suggests that homogenization of coastal forest bird assemblages could be caused by the disappearance of specialists and not because more generalist species invade forest fragments. The reason could be that coastal forests are young (4000-6000 years BP), dynamic, disturbance-prone (Eeley et al. 1999), and fragmented (Olivier et al. 2013). As a result, coastal forest communities are highly resilient (Lawes et al. 2007) and may be more resistant to generalist invasions than their Neotropical counterparts (e.g. Tabarelli et al. 2012). Moreover, bird communities within these forests represent a mixture of species that are typical of subtropical forests, hinterland habitats (e.g. savannahs) and distant coastal areas (van Aarde et al. 2014). The transformation of the matrix might therefore not lead to the invasion of generalists, simply because many species found within these forests are generalists associated with the surrounding matrix.

Although our results are consistent with our expectations, some limitations of our study should be noted. Fragmented habitats have multiple interacting spatial components, which makes it difficult to isolate the main driver of species richness patterns (i.e. habitat amount, habitat area, connectivity, matrix land-use types) (Didham et al. 2012). In our study area, matrix type, forest amount, and levels of connectivity differed between the two landscapes (see Supplementary Material Table S2 and S3). The habitat amount hypothesis (Fahrig 2013) posits that species richness at a sample site should increase with habitat amount in the landscape where it is embedded. The patterns we recorded could therefore be ascribed to differences in forest amount and not matrix type. However, we consider this unlikely and rather argue that grasslands and woodlands represent additional habitat for forest species. Coastal forests are naturally fragmented (Olivier et al. 2013). Bird species here may therefore be buffered from local extinctions associated with forest loss because they have evolved to utilize resources from the ever-changing assortment of grasslands, bushlands, and woodlands that surround forest fragments. We also do not think that fragment connectivity is driving the patterns we observed as forest fragments in the natural matrix were further apart (mean average nearest neighbour = 3340 m) than those in the anthropogenic matrix (mean average nearest neighbour = 442 m). Rather fragments in the natural landscape may have been more connected as a result of a more permeable natural matrix through which forest species could disperse (Daily et al. 2001). Another reason for the patterns we found could be the sample area effect. In a region of continuous habitat, larger sample areas will contain more individuals and, for a given abundance distribution, more species (Fahrig 2013). The occurrence of a SAR is therefore not necessarily related to the delineation of the area as patches, but rather the area sampled (Haila 2002). If this was the case in our study, we would have expected that both specialists and generalists increase with forest area in the anthropogenic landscape. However, only forest specialists, but not generalists increased with area, even though sampling procedures were the same for both groups (e.g. area sampled, the number of survey points). This suggests that specialist species are affected by more than just the sample area effect. We suggest that this is caused by matrix type—natural matrices can be regarded as additional habitat for specialists.

Spatial interactions between species and multiple habitat types represent a conservation challenge, especially where protected area designation focuses on single habitat types to the exclusion of others. Given the fragmented nature of forests in South Africa, much conservation effort focuses on conserving single forest fragments, whilst ignoring the adjacent matrix (e.g. Berliner 2009). For instance, coastal forests are part of a number of eco-regions to which conservation statuses are assigned (see Burgess et al. 2004). This is problematic because coastal forests form part of a naturally fragmented habitat-matrix landscape mosaic. Therefore, implementing conservation actions at the eco-region scale may not be successful in preventing the bird extinctions we predicted in a previous contribution (Olivier et al. 2013). To prevent local extinctions of forest specialist species, it is important that habitats surrounding coastal forest fragments form part of conservation and restoration plans that focus on these forests. A possible way to accomplish this is to mimic the landscape structure that still exists in southern Mozambique. Here, forest fragments are embedded within a heterogeneous matrix comprised of grasslands, woodlands, and scattered forest trees. In South Africa, this can be achieved within protected areas—the iSimangaliso Wetland Park is a good example of where the matrix surrounding coastal forests fragments are being restored (e.g. Zaloumis and Bond 2011). However, this landscape structure will be difficult to achieve outside protected areas because, in many instances, forest fragments are the only natural habitats remaining in an anthropogenic landscape. We suggest that conservation efforts focus on establishing buffer zones around forests fragments embedded within an anthropogenic matrix. These buffer zones may protect forest fragments from high contrast anthropogenic matrices and prevent the invasion of forest fragments by light tolerant tree species. Making the matrix more heterogeneous may be another way to protect forest specialist bird species in small forest fragments.

Acknowledgements The MOZAL Community Development Trust, BHP Billiton HSC, National Research Foundation, Conservation Ecology Research Unit, Richards Bay Minerals, the Department of Trade and Industry and the University of Pretoria funded the study. Pieter Olivier was supported by an

Innovation post-doctoral grant from the National Research Foundation. We also thank the field assistants who assisted with fieldwork and Thomas Matthews for valuable discussions around nestedness metrics.

Funding Funding was provided by National Research Foundation (Grant No. 8817)

References

Almeida-Neto M, Guimara P, Guimara PR, Ulrich W (2008) A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. Oikos 117:1227–1239

Andrén H (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat—a review. Oikos 71:355–366

Arcilla N, Holbech LH, O'Donnell S (2015) Severe declines of understory birds follow illegal logging in Upper Guinea forests of Ghana, West Africa. Biol Conserv 188:41–49

Arrhenius O (1921) Species and area. J Ecol 9:95–99

Berliner DD (2009) Systematic conservation planning for South Africas forest biome: an assessment of the conservation status of South Africa's forests and recommendations for their conservation. University of Cape Town

Bibby CJ, Burgess ND, Hill DA, Mustoe S (2000) Bird Census Techniques, 2nd edn. Academic Press, London

Botzat A, Fischer L, Farwig N (2015) Regeneration potential in South African forest fragments: extinction debt paid off or hampered by contemporary matrix modification? Plant Ecol 216:535–551

Bridgman LJ, Benitez VV, Graña Grilli M, Mufato N, Acosta D, Laura Guichón M (2012) Short perceptual range and yet successful invasion of a fragmented landscape: The case of the red-bellied tree squirrel (*Callosciurus erythraeus*) in Argentina. Landsc Ecol 27:633–640

Brooks TM, Pimm SL, Collar NJ (1997) Deforestation predicts the number of threatened birds in insular Southeast Asia. Conserv Biol 11:382–394

Brotons L, Mönkkönen M, Martin JL (2003) Are fragments islands? Landscape context and density-area relationships in boreal forest birds. Am Nat 162:343–357

Burgess N, Hales J, Underwood E, Dinerstein E, Olson D, Itoua I, Schipper J, Ricketts T, Newman K, Hales J (2004) Terrestrial ecoregions of Africa and Madagascar: a conservation assessment. Island Press

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, New York

Carrara E, Arroyo-Rodríguez V, Vega-Rivera JH, Schondube JE, de Freitas SM, Fahrig L (2015) Impact of landscape composition and configuration on forest specialist and generalist bird species in the fragmented Lacandona rainforest, Mexico. Biol Conserv 184:117–126

Chao A (1984) Board of the foundation of the scandinavian journal of statistics nonparametric estimation of the number of classes in a population. Scand J Stat 11:265–270

Chao A, Jost L (2012) Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. Ecology 93:2533–2547

Colwell RK (2013) EstimateS: Statistical estimation of species richness and shared species from samples

Daily GC, Ehrlich PR, Sánchez-Azofeifa GA (2001) Countryside biogeography: use of human-dominated habitats by the avifauna of southern Costa Rica. Ecol Appl 11:1–13

Dengler J (2009) Which function describes the species-area relationship best? A review and empirical evaluation. J Biogeogr 36:728–744

Dennis JE, Schnabel RB (1983) Numerical methods for unconstrained optimization and nonlinear equations. classics in applied mathematics, 16. Prentice-Hall, Englewood Cliffs, NJ

Development Core Team R (2012) A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Didham RK, Kapos V, Ewers RM (2012) Rethinking the conceptual foundations of habitat fragmentation research. Oikos 121:161–170

Drakare S, Lennon JJ, Hillebrand H (2006) The imprint of the geographical, evolutionary and ecological context on species-area relationships. Ecol Lett 9:215–227

Driscoll DA, Banks SC, Barton PS, Lindenmayer DB, Smith AL (2013) Conceptual domain of the matrix in fragmented landscapes. Trends Ecol Evol 28:605–613

Driscoll MJL, Donovan TM (2003) Landscape effects moderate edge effects: nesting success of wood thrushes in central Newyork. Conserv Biol 18:1330–1338

Dunning JB, Danielson BJ, Pulliam HR (1992) Ecological processes that affect populations in complex landscapes. Oikos 65:169–175

Eeley HHAC, Lawes MMJ, Piper SES, Forest T (1999) The influence of climate change on the distribution of indigenous forest in KwaZulu-Natal, South Africa. J Biogeogr 26:595–617

Eycott A, Watts K, Brandt G, Buyung-Ali L, Bowler D, Stewart G, Pullin A (2010) Do landscape matrix features affect species movement? Collab Environ Evid 44:0–54

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Rev Lit Arts Am 34:487–515

Fahrig L (2013) Rethinking patch size and isolation effects: the habitat amount hypothesis. J Biogeogr 40:1649–1663

Gascon C, Lovejoy TE, Bierregaard RO, Malcolm JR, Stouffer PC, Vasconcelos HL, Laurance WFL, Zimmerman B, Tocher M, Borges S (1999) Matrix habitat and species richness in tropical forest remnants. Biol Conserv 91:223–229

Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecol Lett 4:379–391

Guilhaumon F, Mouillot D, Gimenez O (2010) mmSAR: an R-package for multimodel species-area relationship inference. Ecography (Cop) 33:420–424

Guldemond RAR, van Aarde RJ (2010) Forest patch size and isolation as drivers of bird species richness in Maputaland, Mozambique. J Biogeogr 37:1884–1893

Haddad NM, Brudvig LA, Clobert J, Davies KF, Gonzalez A, Holt RD, Lovejoy TE, Sexton JO, Austin MP, Collins CD, Cook WM, Damschen EI, Ewers RM, Foster BL, Jenkins

CN, King AJ, Laurance WF, Levey DJ, Margules CR, Melbourne BA, Nicholls AO, Orrock JL, Song D-X, Townshend JR (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. Sci Adv 1:e1500052–e1500052

Haila Y (2002) A conceptual genealogy of fragmentation research: from island biogeography to landscape ecology A. Ecol Appl 12:321–334

Hockey PAR, Dean WRJ, Ryan PG (2005) Roberts birds of Southern Africa VII. The John Voelcker Bird Book Fund, Cape Town

Ibarra JT, Martin K (2015) Biotic homogenization: loss of avian functional richness and habitat specialists in disturbed Andean temperate forests. Biol Conserv 192:418–427

Jamoneau A, Chabrerie O, Closset-Kopp D, Decocq G (2012) Fragmentation alters beta-diversity patterns of habitat specialists within forest metacommunities. Ecography (Cop) 35:124–133

Jewitt D, Goodman PS, Erasmus BFN, O'Connor TG, Witowski ET (2015) Systematic land-cover change in KwaZulu-Natal, South Africa : implications for biodiversity : research article. S Afr J Sci 111:01–09

Johnson P, Mason LG, Raven PH (1968) Ecological parameters and plant species diversity. Am Nat 102:297–306

Koh LP, Ghazoul J (2010) A matrix-calibrated species-area model for predicting biodiversity losses due to land-use change. Conserv Biol 24:994–1001

Küper W, Henning Sommer J, Lovett JC, Mutke J, Linder HP, Beentje HJ, Rompaey RSARV, Chatelain C, Sosef M, Barthlott W (2004) Africa's hotspots of biodiversity redefined. Ann Missouri Bot Gard 91:525–535

Laurance WF (2008) Theory meets reality: how habitat fragmentation research has transcended island biogeographic theory. Biol Conserv 141:1731–1744

Laurance WF, Nascimento HEM, Laurance SG, Andrade AC, Fearnside PM, Ribeiro JEL, Capretz RL (2006) Rain forest fragmentation and the proliferation of successional trees. Ecology 87:469–482

Lawes MJ, Eeley HAC, Findlay NJ, Forbes D (2007) Resilient forest faunal communities in South Africa: a legacy of palaeoclimatic change and extinction filtering? J Biogeogr 34:1246–1264

Lawes MJ, Eeley HAC, Shackleton BG. (2004) Indigenous forests and woodlands in South Africa: policy, people and practice. University of KwaZulu-Natal Press, KwaZulu-Natal

Lenz J, Fiedler W, Caprano T, Friedrichs W, Gaese BH, Wikelski M, Böhning-Gaese K (2011) Seed-dispersal distributions by trumpeter hornbills in fragmented landscapes. Proc R Soc B Biol Sci 278:2257–2264

Lôbo D, Leão T, Melo FPL, Santos AMM, Tabarelli M (2011) Forest fragmentation drives Atlantic forest of northeastern Brazil to biotic homogenization. Divers Distrib 17:287–296

Mac Nally R (2007) Use of the abundance spectrum and relative-abundance distributions to analyze assemblage change in massively altered landscapes. Am Nat 170:319–330

MacArthur RH, Wilson EO (1967) The theory of island biogeography. Princeton University Press, Princeton

Martensen AC, Ribeiro MC, Banks-leite C, Prado PI, Metzger JP (2012) Associations of forest cover, fragment area, and connectivity with neotropical understory bird species richness and abundance. Conserv Biol 26:1100–1111

Matthews T, Whittaker RJQ (2015) Quantifying and interpreting nestedness in habitat islands: a synthetic analysis of multiple datasets. Divers Distrib 21:392–404

Mendenhall CD, Karp DS, Meyer CFJ, Hadly EA, Daily GC (2014) Predicting biodiversity change and averting collapse in agricultural landscapes. Nature 509:213–217

Menke S, Böhning-gaese K, Schleuning M (2012) Plant–frugivore networks are less specialized and more robust at forest–farmland edges than in the interior of a tropical forest. Oikos 121:1553–1566

Morante-Filho JC, Arroyo-Rodríguez V, Faria D (2015) Patterns and predictors of beta-diversity in the fragmented Brazilian Atlantic forest: a multiscale analysis of forest specialist and generalist birds. J Anim Ecol 85:240–250

Morante-Filho JC, Arroyo-Rodriguez V, Lohbeck M, Tscharntke T, Faria D (2016) Tropical forest loss and its multitrophic effects on insect herbivory. Ecology 97:3315–3325

Mueller T, Lenz J, Caprano T, Fiedler W, Böhning-Gaese K (2014) Large frugivorous birds facilitate functional connectivity of fragmented landscapes. J Appl Ecol 51:684–692

Öckinger E, Lindborg R, Sjödin NE, Bommarco R (2012) Landscape matrix modifies richness of plants and insects in grassland fragments. Ecography (Cop) 35:259–267

Oksanen JF, Blanchet G, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL (2013) Vegan: community ecology package. R package version 2.0-9. R Foundation for Statistical Computing

Olivier PI, van Aarde RJ (2017) The response of bird feeding guilds to forest fragmentation reveals conservation strategies for a critically endangered African eco-region. Biotropica 49:268–278

Olivier PI, Van Aarde RJ, Lombard AT (2013) The use of habitat suitability models and species-area relationships to predict extinction debts in coastal forests, South Africa. Divers Distrib 19:1353–1365

Pardini R, de Bueno AA, Gardner TA, Prado PI, Metzger JP (2010) Beyond the fragmentation threshold hypothesis: regime shifts in biodiversity across fragmented landscapes. PLoS ONE 5(10):e13666

Peter F, Berens DG, Grieve GR, Farwig N (2015) Forest fragmentation drives the loss of insectivorous birds and an associated increase in herbivory. Biotropica 47:626–635

Pielou EC (1967) The measurement of diversity in different types of biological collections. J Theor Biol 15:177

Preston FW (1962) The canonical distribution of commonness and rarity: part I. Ecology 43:185

Prevedello JA, Vieira MV (2010) Does the type of matrix matter? A quantitative review of the evidence. Biodivers Conserv 19:1205–1223

Rao CR (1973) Linear statistical inference and its applications. Wiley, New York

Ries L, Fletcher RJ, Battin J, Sisk TD (2004) Ecological responses to habitat edges: mechanisms, models, and variability explained. Annu Rev Ecol Evol Syst 35:491–522

Rosenzweig ML (1995) Species diversity in space and time. Cambridge University Press, Cambridge

Sanchez-de-Jesus HA, Arroyo-Rodriguez V, Andresen E, Escobar F (2016) Forest loss and matrix composition are the major drivers shaping dung beetle assemblages in a fragmented rainforest. Landscape Ecol 31:843–854

Socolar JB, Gilroy JJ, Kunin WE, Edwards DP (2015) How should beta-diversity inform biodiversity conservation? Trends Ecol Evol 31:67–80

Stratford JA, Stouffer PC (2015) Forest fragmentation alters microhabitat availability for Neotropical terrestrial insectivorous birds. Biol Conserv 188:109–115

Tabarelli M, Peres CA, Melo FPL (2012) The “few winners and many losers” paradigm revisited: emerging prospects for tropical forest biodiversity. Biol Conserv 155:136–140

Tews J, Brose U, Grimm V, Tielborger K, Wichmann MC, Schwager M, Jeltsch F (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. J Biogeogr 31(1):79–92

Triantis KA, Guilhaumon F, Whittaker RJ (2012) The island species-area relationship: biology and statistics. J Biogeogr 39:215–231

Tscharntke T, Tylianakis JM, Rand TA, Didham RK, Fahrig L, Batáry P, Bengtsson J, Clough Y, Crist TO, Dormann CF, Ewers RM, Fründ J, Holt RD, Holzschuh A, Klein AM, Kleijn D, Kremen C, Landis DA, Laurance W, Lindenmayer D, Scherber C, Sodhi N, Steffan-Dewenter I, Thies C, van der Putten WH, Westphal C (2012) Landscape moderation of biodiversity patterns and processes—eight hypotheses. Biol Rev 87:661–685

Ulrich W, Almeida-Neto M (2012) On the meanings of nestedness: back to the basics. Ecography (Cop) 35:865–871

Ulrich W, Almeida-Neto M, Gotelli NJ (2009) A consumer’s guide to nestedness analysis. Oikos 118:3–17

Urban DL, O’Neill RV, Shugart HH (1987) Landscape ecology. Bioscience 37:119–127

van Aarde RJ, Guldemond RAR, Olivier PI (2014) Biodiversity status of coastal dune forests in South Africa. In: Maslo B, Lockwood L (eds) Conservation biology. Cambridge University Press, Cambridge, pp 161–179

Van Wyk AE, Smith GF (2001) Regions of floristic endemism in Southern Africa. Umdaus Press, Pretoria

Von Maltitz G, Mucina L, Geldenhuys CJ, Lawes MJ, Eeley H, Aidie H, Vink D, Fleming G, Bailey C (2003) Classification system for South African indigenous forests: an objective classification for the Department of Water Affairs and Forestry, Environmentek report ENV-PC

Wang Y, Bao Y, Yu M, Xu G, Ding P (2010) Nestedness for different reasons: the distributions of birds, lizards and small mammals on islands of an inundated lake. Divers Distrib 16:862–873

Wethered R, Lawes MJ (2005) Nestedness of bird assemblages in fragmented Afromontane forest: the effect of plantation forestry in the matrix. Biol Conserv 123:125–137

Zaloumis NP, Bond WJ (2011) Grassland restoration after afforestation: no direction home? Austral Ecol 36:357–366