

**The Response of Bird Feeding Guilds to Forest Fragmentation Reveals Conservation Strategies for a Critically Endangered African Eco-region**

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## **Abstract**

South African coastal forests form part of two critically endangered eco-regions and harbour an extinction debt. Remaining fragments are small, isolated, and embedded within a range of human land-use types. In this study we ask: how should we invest conservation resources if we want to restore this landscape and prevent predicted extinctions? To answer this question we use path analyses to determine the direct and indirect effects of forest area, forest connectivity, and matrix land-use types on species richness within five bird feeding guilds. We found that forest connectivity had a significant direct effect on insectivores – fragments that were more connected had more species of insectivores than those that were isolated. Moreover, forest area had a significant indirect effect on insectivores that was mediated through tree species richness. Larger fragments had more species of trees, which led to more species of insectivores. Fragment area, connectivity, matrix land-use type, and tree species richness had no significant effects on the species richness of frugivores, nectarivores, granivores or generalist feeders. To conserve insectivores in coastal forests, conservation efforts should focus on maximizing fragment connectivity across the landscape, but also protect the tree community within fragments from degradation. This can be achieved by including matrix habitats that adjoin forest fragments within forest conservation and restoration plans. Natural matrix habitats can increase connectivity, provide supplementary resources, buffer fragments from degradation, and could play an important role in safeguarding diversity and preventing extinctions in this threatened human-modified landscape.

**Keywords:** area; connectivity; extinction debt; direct effects; indirect effects; insectivores; path analyses; South Africa.

COASTAL FORESTS IN SOUTH AFRICA ARE IN TROUBLE. They form part of two critically endangered eco-regions, the Maputaland Coastal Forest Mosaic and the KwaZulu-Cape Coastal Forest Mosaic (Burgess *et al.* 2004), and have been plagued by anthropogenic disturbances that likely started with the arrival of Iron Age farmers in the early 1300's (Feely 1980, Bond *et al.* 2003). Since then subsistence farming, cattle grazing, unregulated burning, commercial logging, agricultural plantations, urban developments, and dune mining all contributed to an estimated forest loss of 82 percent (Olivier *et al.* 2013). Remaining forest fragments now cover only about 620km<sup>2</sup> and are smaller, further apart and more 'hemmed in' by human land-use types than what was the case in the past (Olivier *et al.* 2013, van Aarde *et al.* 2014, Jewitt *et al.* 2015). Moreover, the extent of forest loss means that these forests likely harbour an extinction debt (Olivier *et al.* 2013).

Forest loss reduces the area of habitat and the size of fragments. It also decreases habitat connectivity and expose fragment edges to novel matrix habitats (Fahrig 2003, Ewers *et al.* 2010). To restore the coastal forest landscape and prevent predicted extinctions, conservation resources could be invested into (1) increasing forest area, (2) increasing forest connectivity, (3) decreasing the amount of forest exposed to high contrast edges and/or (4) maintaining natural matrix habitats among forest fragments. However, given the budgetary and logistical constraints commonly associated with conservation resources (Bradshaw *et al.* 2009), it is unlikely that all of these measures will be realised. It thus makes sense to prioritise goals to ensure conservation efficiency. This can be done by determining how species respond to each of these so-called 'fragmentation parameters' (*i.e.* area, connectivity, edges and matrix habitats) and then investing resources to restore the specific parameter to which target species are likely to respond.

Species persistence in fragmented habitats partly depends on local extinction and colonization (Hanski & Ovaskainen 2000), whereas the probability of extinction and

colonization depend on the life-history traits (Öckinger *et al.* 2010). Because fragmentation alters the quality, quantity and distribution of food resources in a landscape, specialist species with narrow feeding niches may be less likely to utilize resources in the habitats that surround fragments than generalist species with broad feeding niches (Lees and Peres 2008, Vetter *et al.* 2011, Newbold *et al.* 2012). Species that occupy specialist feeding guilds may therefore be less likely to likely to maintain metapopulation dynamics within fragmented landscapes (Schnell *et al.* 2013), making them particularly susceptible to habitat fragmentation and land-use change. For example, insectivorous and frugivorous birds are sensitive to habitat fragmentation, whereas granivores and nectarivores are generally not (Bregman *et al.* 2014, Peter *et al.* 2015). Diet may therefore be an important factor that could be used to predict the sensitivity of species to fragmentation (*e.g.* Gray *et al.* 2007, Arriaga-Weiss *et al.* 2008).

Due to differences in diet, species could differ in their sensitivity to different aspects of fragmentation. For instance, large-bodied frugivores, such as hornbills, can easily move across transformed habitats while foraging (Neuschulz *et al.* 2012, Chasar *et al.* 2014). A loss of forest area may thus have little effect on these species because they can disperse among forest fragments (*e.g.* Lenz *et al.* 2011, Mueller *et al.* 2014). Focusing conservation resources on many small forest fragments that enhance landscape connectivity may therefore benefit such species. Conversely, many forest insectivores move widely within habitat fragments, but not among fragments, even if distances that separate fragments are small (*e.g.* Laurance *et al.* 2004; van Houtan *et al.* 2007). A decrease in fragment area, but not reduced connectivity, therefore may decrease insectivore diversity (Ferraz *et al.* 2007). It follows that for forest dwelling insectivores conservation resources should be invested into maintaining large forest fragments. However, the effects of fragmentation are not always negative (Tschardtke *et al.* 2012). The colonization of disturbance-adapted species may compensate for the disappearance of disturbance sensitive species (Morante-Filho *et al.* 2015). For instance, the

creation of forest edges and novel matrix habitats may provide a range of different and/or supplementary resources that may boost the diversity of generalist feeders (*e.g.* Neuschulz *et al.* 2012). Forest edges may also lead to the proliferation of flowering plants that attract nectarivores (Vetter *et al.* 2011), while granivores have been shown to thrive in small habitat fragments embedded within agricultural matrices (Donoso *et al.* 2004). If this is the case, the influence of forest fragmentation as a driver of landscape wide biodiversity losses may be overestimated (Tscharntke *et al.* 2012).

Determining the effects of different fragmentation parameters on diversity is complicated for at least three reasons. First, habitat loss is to some extent mediated by the changing spatial arrangement of habitat (Didham *et al.* 2012). Colinearity between fragmentation parameters may therefore arise, which could hamper effect estimation using standard statistical techniques such as multiple regressions (Smith *et al.* 2009, Dormann *et al.* 2013, Ruffel *et al.* 2015). Second, habitat loss may indirectly influence ecological systems by driving changes in habitat fragmentation (Didham *et al.* 2012). In other words, indirect effects associated with habitat loss could influence estimates of the direct effects of habitat fragmentation on diversity. Third, the effect of habitat fragmentation on diversity may be mediated by other local factors not measured in fragmentation studies that typically only focus on landscape parameters. For example, Brudvig *et al.* (2015) found that the effects of different fragmentation parameters (*e.g.* connectivity, shape, and distance to edge) on plant-animal interactions were mediated through herbivory, pollination and seed predation. In such scenarios, the direct effect of one variable also represents the indirect effect of another (see Ruffel *et al.* 2015). Therefore, to unravel the specific mechanistic pathways through which fragmentation affect ecological systems requires a statistical approach that can specifically measure and account for indirect effects (Didham *et al.* 2012, Ruffel *et al.* 2015).

In this study, we use path analyses (Shipley 2000) to determine the direct and indirect effects of different fragmentation parameters (area, connectivity, and matrix land-use types) on species richness within different bird feeding guilds. Path analyses allow researchers to empirically test whether collinear metrics are causally related, and account for indirect effects that such causal relationships imply (Ruffel *et al.* 2015). We surveyed birds within and adjacent to sub-tropical coastal forest fragments in South Africa and placed bird species within five feeding guilds (frugivores, generalist feeders, granivores, insectivores, and nectarivores). We developed a path model for each feeding guild based on the basic tenets of island biogeography theory (*i.e.* species richness will decline with a decrease in area and connectivity; MacArthur & Wilson (1967)), but which also allowed for the possible influence of matrix land-use types that adjoin forest fragments. We also included the possible effects of biotic (tree species richness) and abiotic environmental variables (rainfall, elevation, humidity, plant available water). We then ask: where would the investment of conservation resources be most effective if we want to restore the landscape and prevent predicted extinctions? In other words, should we invest conservation resources into increasing forest area, connectivity or restoring natural matrix habitats? We aim to answer this question by testing two hypotheses. First, we hypothesise that different guilds will be influenced differently by different fragmentation parameters. We expect that forest fragment area and fragment connectivity will significantly influence frugivores and insectivores, but not species richness of granivores, nectarivores or generalist feeders. Rather, the matrix land-use type that adjoins forest fragments will have a significant influence on species richness within these groups (Vetter *et al.* 2011, Newbold *et al.* 2012, Bregman *et al.* 2014). Second, we hypothesise that given the amount of forest loss in the area, most threatened species will be restricted to guilds that are affected by forest area and connectivity.

## METHODS

**STUDY REGION.**-Coastal forests in South Africa represent the southernmost end of East African Tropical Coastal Forest which extends from tropical central Africa along the east African coast (Burgess and Clarke 2000) (Fig. 1). In addition to forming part of two critically endangered eco-regions (see Burgess *et al.* 2004), they also occur within the Maputaland-Pondoland-Albany biodiversity hotspot (Küper *et al.* 2004) and the Maputaland Centre of Plant Endemism (van Wyk and Smith 2000). These regions support high levels of floristic endemism as well as a number of narrowly endemic species, including relict species (Burgess *et al.* 2004). In this study, we opted to recognize coastal forests as comprising lowland forests, dune forests and swamp forests (see Olivier *et al.* 2013). We did this because of discrepancies in the classification of coastal forest types (*e.g.* Moll & White, 1978, Lubke *et al.* 1997, Midgley *et al.* 1997, Mucina & Rutherford, 2006) and because these different forest types share many bird and tree species (Von Maltitz *et al.* 2003, Olivier & van Aarde, 2014).

Our survey sites were located within and adjacent to nine of these fragments (range of fragment sizes = 2.1 – 87.3 km<sup>2</sup>) situated along approximately 300 km of coastline between the Tugela river mouth in the south (S -29.2268°; E 32.8578°) and Lake Kosi in the north (S -27.0019°; E 32.8578°) (Fig. 1 and Table 1). Survey sites were located at random positions within forest fragments and surveys were conducted during the summers (November to February) of 2011 and 2012.

**BIRD AND TREE SURVEYS.**-Our bird survey comprised of 293-point counts within coastal forest fragments and 357-point counts in the adjacent matrix. Counts were conducted between 0500 h and 0900 h by the same two observers. Each observer surveyed 4 to 9 points per day depending on habitat type. Observers were trained in, and had prior experience of local bird identification. Points were at least 178m apart and were located using handheld

GPSs. An observer allowed for a 2min period for birds that may have been disturbed upon arrival at the survey point to resettle and thereafter recorded birds for 10min. For each encounter, estimated distances from the observer to the bird were recorded by a digital rangefinder (Nikon Laser 550As). Only birds seen or judged to be calling within a 60m radius based on the rangefinder distances, were recorded. We excluded birds that flew above the canopy in forest fragments and birds that did not settle within a 60m radius in the various matrix land-use types. Surveys did not take place during rainy or windy days. We evaluated sampling effort for each fragment by generating species accumulation curves using the software program EstimateS (Colwell 2006). Survey effort ranged from 15 points in the smallest fragment to 42 in the largest. Trees were recorded in 70, 16m x 16m plots. The number of survey points per fragment ranged from 4 to 6 for fragments < 5km<sup>2</sup>, 6 to 9 for fragments between 5 and 20km<sup>2</sup> and 9 to 13 for fragments > 20km<sup>2</sup>. Every tree taller than 30cm was identified and measured. Species richness was then calculated for each fragment

All bird species recorded within forest fragments during our surveys were assigned to feeding guilds based on the information in Hockey *et al.* (2005). The feeding guilds were insectivores (n=35 species), generalist feeders (n=13), frugivores (n=11 species), granivores (n=7 species), and nectarivores (n=7 species). (Table S1). We then calculated species richness of each guild for each fragment. Carnivores were not included in our analysis as we recorded too few individuals to run meaningful models. We used the conservation assessment published on South African birds (Taylor *et al.* 2015) to identify threatened coastal forest species. South Africa directly follows the International Union for the Conservation of Nature (IUCN) categories when assigning conservation statuses to bird species (Taylor *et al.* 2015).

**MODEL VARIABLES: ENVIRONMENTAL FACTORS.**-A habitat suitability modelling exercise showed that median rainfall in winter, minimum relative humidity in winter, annual mean plant available water and elevation explained 90 percent of the probability of coastal



forest occurrence (for details on the methodology see Olivier *et al.* 2013). We therefore assembled digital maps of these four variables (Schulze 2006), and used these as predictors of bird and tree species richness in our models. Maps were 200m x 200m raster (grid cell) layers and covered the distribution of coastal forests in the study area. We extracted the mean raster value of each variable for each fragment in ArcGIS 10 (Environmental Systems Research Institute, Redlands, California, [www.esri.com](http://www.esri.com)). A principal components analysis (PCA) was then used to reduce these potentially correlated variables into orthogonal principal components. The first two components accounted for 99 percent of environmental variation and were retained for analysis. Principal component axis one (PCA1) represented elevation, while median rainfall in winter, humidity and plant available water were represented by principal component axis two (PCA2).

The latitudinal position of each fragment was also included as a model variable. This was done for two reasons. First, Mantel tests suggests spatial autocorrelation in community composition across fragments (trees: Mantel  $r = 0.46$ ;  $P = 0.02$ ; birds: Mantel  $r = 0.77$ ;  $P = 0.001$ ). By including latitude as a model variable, we accounted for the possible effects of spatial autocorrelation that violates the assumption of independently distributed errors in regression models and inflate Type I errors (see Legendre 1993). Second, forest fragments were distributed linearly along the coastline (Fig. 1). We therefore wanted to account for the possible indirect effects of a latitudinal gradient on guild diversity that are mediated through tree diversity and other environmental variables (elevation, rainfall, humidity, plant available water). For instance, in a review of global patterns and predictors of bird species responses to forest fragmentation, Bregman *et al.* (2014) found severe fragmentation effects in tropical, but not in temperate regions.

MODEL VARIABLES: FRAGMENTATION PARAMETERS.-Fragment area was calculated from a digital map (LandSAT 2010) of the distribution of coastal forests in South

Africa. We used the ‘mean proximity index’ calculated in the software program Fragstats 4.2 as an index of fragment connectivity (McGarigal & Ene 2013). This index considers the size and proximity of all fragments whose edges are within a specified search radius from the focal fragment. The index is then computed as the sum of each fragment size divided by the square of its edge-to-edge distance to the focal fragment of all fragments whose edges are within the specified search radius (1000m in this study). The index equals zero if a fragment has no neighbours and increases as the neighbourhood is increasingly occupied by fragments of the same type.

To determine the influence of adjacent matrix land-use types on guild species richness within forest fragments, we calculated the Sørensen’s dissimilarity index ( $\beta_{\text{SOR}}$ ) between the matrix bird community and the adjacent forest bird community using the vegan package (Oksanen *et al.* 2013) in R version 2.15.1 (R Development Core Team 2012). For example, we calculated the dissimilarity among forest and matrix insectivores for each matrix type that surrounded each forest fragment. We did this for each feeding guild and each forest fragment. Dissimilarity values therefore differed among feeding guilds. Guild dissimilarities were then converted into dummy variables where  $\beta_{\text{SOR}} = 0.8 - 1.0$  was five,  $\beta_{\text{SOR}} = 0.6 - 0.79$  was four,  $\beta_{\text{SOR}} = 0.4 - 0.59$  was three,  $\beta_{\text{SOR}} = 0.2 - 0.49$  was two and  $\beta_{\text{SOR}} = 0 - 0.19$  was one. We reasoned that high levels of dissimilarity would indicate high contrast matrices, while low levels of dissimilarity will indicate low contrast matrices for each feeding guild. These dummy variables were then included as predictors in our models.

PATH ANALYSES.-We first used Pearson correlations to explore correlations among variables. We then used path analysis (Shipley 2000, Grace 2006) to examine the relationship between feeding guild diversity, fragmentation parameters, and biotic and abiotic environmental variables. Path analysis allow the partitioning of the correlations between predictor and response variables into direct and indirect effects and thus enable the evaluation

of hypothesized causal relationships in data sets with more than one dependent variable (Grace 2006). We developed five *a priori* theoretical models based on the hypothesis that forest fragment area, fragment connectivity, and matrix habitat composition would directly influence the diversity within bird feeding guilds. Moreover, because we expected local habitat conditions to directly affect feeding guilds, we included tree species diversity as a covariate in our models. Tree species richness may be influenced by abiotic environmental variables such as elevation, rainfall, humidity and plant available water (represented in our models by PCA1 and PCA2) and, similar to birds by fragment area and connectivity. By including these variables in our models, we accounted for the possible indirect effects of area and connectivity on guild richness that may have been mediated through tree species richness. We made one model for each guild that included all the hypothesised potential links between variables (Fig. 2). The structures of these five *a priori* models remained the same except for guild species richness, which was substituted in each model. For example, in the first model insectivore species richness was the response variable, in the second model frugivore species richness was the response variable and so on.

Models were then fitted using piecewise SEM (Lefcheck 2015). In piecewise SEM, the path diagram comprises a set of linear equations that are evaluated individually. This approach is particularly relevant to our study because it allows the fitting of smaller data sets, since there only need to be enough degrees of freedom to fit any given component of the model. Moreover, it also allows for the inclusion of site as a random effect in our models. This is important because the nested structure of our data (i.e. many sampling points in large fragments compared to few sampling points in small fragments) may bias results. To evaluate model fit we used Fisher's *C* statistic and its associated P-value. This procedure is based on Shipley's test of directed separation and tests the assumption that there are no missing relationships among unconnected variables (Shipley 2000). The hypothesized relationships

are considered to be consistent with the data when there is weak support for the sum of the conditional independence claims ( $P > 0.05$ ) (see Lefcheck (2015) for a more detailed description of the model evaluation procedure).

All variables in our models were observed variables. Fragment areas were log transformed to conform to normality. Variables were then scaled to have a mean of zero and a standard deviation of one by transforming them to a z score (Kline 2005). Path analyses were carried out in R version 2.15.1 (R Development Core Team 2012) using the LAVAAN (Rosseel 2012) and PIECEWISESEM (Lefcheck 2015) packages.

## RESULTS

We identified 74 bird species from 2584 records and 293-point counts within old growth coastal forest fragments. Surveys in the adjacent matrix habitats yielded twice as many (121) bird species from 1694 records and 357-point counts. For trees we collected 22 542 records of 195 tree species from 113 survey plots. The average number of tree species per plot was 27.6 (range = 12 to 50), and the average number of bird species per plot was 8.5 (range = 1 to 17) and 2.0 (range = 0 to 7) in forest and matrix habitats respectively.

For all five feeding guilds, most species were recorded in both forests and matrix land use types (Table S2). Insectivores had the highest proportion of species recorded only in forests (10 out of 35), while generalist feeders had the lowest (1 out of 13) (Table S3).

**GUILD SPECIFIC RESPONSES TO FRAGMENTATION.**-All the final path models had a satisfactory fit ( $P > 0.05$ , range of Fisher's  $C = 16.96 - 26.28$ ) (Table 2) – however, we only recorded significant path effects for insectivores. Fragment connectivity (path weight = 0.85,  $P=0.01$ ) and tree species richness (path weight = 0.42,  $P=0.02$ ) had significant direct effects

on insectivore species richness. Forest fragment area also had a significant indirect effect on insectivore species richness that was mediated through tree species richness (path weight = 0.26,  $P = 0.02$ ). The model for insectivores also explained nearly double the variation than what was the case for any of the other feeding guilds ( $R^2=0.93$ ).

The low amount of variation explained for frugivores ( $R^2=0.21$ ), nectarivores ( $R^2=0.30$ ), generalist feeders ( $R^2=0.38$ ) and granivores ( $R^2=0.51$ ) may reflect on the lack of statistical significant path effects in these models. Similar to what we recorded for insectivores, fragment connectivity had the strongest direct effect on species richness of frugivores (path weight = 1.10,  $P = 0.30$ ), generalist feeders (path weight = 1.38,  $P = 0.12$ ) and granivores (path weight = 1.28,  $P = 0.10$ ). Although these pathways were not statistically significant, they were stronger than those recorded for area, matrix habitat types and tree species richness (Fig. 2 and Table 3). Fragmentation parameters also did not have any significant indirect effects on species richness within these guilds (Table 3).

**SPECIES OF CONSERVATION CONCERN.**-Threatened species were evenly distributed among feeding guilds. Insectivores had two locally threatened species (2 out of 35). These were the endangered spotted ground-thrush (*Geokichla guttata*) and the vulnerable African broadbill (*Smithornis capensis*). Frugivorous (1 out of 11; Eastern bronze-naped pigeon (*Columba delegorguei*)), nectarivorous (1 out of 7; Neergaard's sunbird (*Nectarinia neergardi*)) and granivorous (1 out of 7; lemon-breasted canary (*Crithagra citrinipectus*)) guilds each included one threatened species. None of the 13 generalist feeders were threatened (see Table S3).

## DISCUSSION

Where would the investment of conservation resources be most effective if we want to restore the coastal forest landscape and prevent predicted extinctions? Fragments that were connected harboured significantly more insectivorous bird species than those that were not. More connected fragments also had more species of frugivores, granivores and generalist feeders. Given that threatened bird species were evenly distributed among feeding guilds, increasing forest fragment connectivity may be the most effective conservation strategy to protect coastal forest birds.

Forest fragments typically harbour small populations where the maintenance of metapopulation dynamics relies on species ability to disperse among fragments (Schnell *et al.* 2013). When connectivity among coastal forest fragments decrease, colonization-extinction dynamics may be disrupted, which could lead to the disappearance of insectivores from fragments where they would otherwise be present (e.g. Lens *et al.* (2002) but also see Powell *et al.* (2015) and references therein). To therefore maintain metapopulation dynamics and protect coastal forest insectivores, it makes sense to conserve connectivity among fragments. However, just focusing conservation efforts on fragment connectivity may oversimplify a more complex issue. Our models also suggest that fragment area had an indirect effect on insectivore richness that was mediated through tree species richness. Larger fragments had more tree species, which significantly influenced species richness of insectivores. More species of trees may mean more species of insects (Basset *et al.* 2012), which could allow more species of insectivores to co-exist. Furthermore, a species rich tree community may indicate greater structural complexity within fragments (Tews *et al.* 2004). Consequently, more species of insectivores could co-occur in greater numbers because there are more opportunities to exploit (Stratford and Stouffer 2013). However, when fragments become smaller and more isolated, rare and shade-tolerant tree species may disappear while a few disturbance-adapted species may thrive (Arroyo-Rodríguez *et al.* 2013). Such compositional

changes may lead to changes in resource availability and vegetation structure. For example, canopy cover may decrease, while mid-story vegetation and leaf litter depth increase (*e.g.* Stratford & Stouffer 2015). As a result, resources are reduced, which could lead to the decline of insectivores in coastal forest fragments. It follows that only focusing on connectivity may not be sufficient to protect insectivore diversity, because even if insectivores are able to disperse among well-connected fragments they may not find suitable habitats.

To conserve insectivores in coastal forests, conservation efforts should focus on maximizing fragment connectivity across the landscape, but also protect the tree community within fragments from degradation. To achieve this goal, the matrix land-use types that adjoin forest fragments should be part of forest conservation plans. The reason for this is threefold. First, coastal forests are naturally fragmented shaped by thousands of years of climate change and fire (Bond *et al.* 2003, Olivier *et al.* 2013). The conservation of natural matrix land-use types could allow for retractions or expansions of forest margins in response to changes in fire, rainfall, or climate and, in doing so, facilitate connectivity and metapopulation dynamics within a heterogeneous landscape (Hanski and Ovaskainen 2000). This seem to be the case in southern Mozambique where Guldemond & van Aarde (2010) found no evidence for area or isolation effects in bird communities when natural matrix land-use types (*e.g.* grasslands and woodlands) surrounded coastal forests. Second, natural matrix habitats may provide alternative or supplementary resources for species that occur here, which may enhance fragment connectivity (*e.g.* Kennedy *et al.* 2010). Third, intact matrix land-use types may protect forest fragments from edge effects, invasions, and microclimatic fluxes (Kupfer *et al.* 2006). For instance, Bozat *et al.* (2015) found that human activities associated with matrix modification have altered abiotic factors within coastal scarp forest fragments. Light tolerant species therefore are favoured, which could influence forest composition, structure, and regeneration.

The importance of matrix land-use types in forest conservation plans is highlighted by our finding that 87 percent (33 out of 38 species) of nectarivores, frugivores, granivores and generalist feeders, were recorded in both matrix and forest habitats. This apparent multi-habitat occupancy may also explain the lack of significant fragmentation effects on these guilds. For example, many species that occur here may rely on more than one habitat type for food or nesting resources and may therefore not experience the landscape as fragmented (*e.g.* Neuschulz *et al.* 2012). This may be particularly important for generalist feeders that exploit a wide range of resources, and granivores that flourish in open and agricultural habitats between fragments (Donoso *et al.* 2004, Newbold *et al.* 2012). Nectarivores, on the other hand, may benefit from the increased abundance of light-demanding tree species as well as flowering plants that flourish in gaps and edges (Stouffer and Bierregaard 1995, Vetter *et al.* 2011). The reason why the fragmentation parameters included in our model did not explain frugivore richness is more difficult to understand, but may be related to the patchy distribution of food resources (see Kissling *et al.* 2007). To locate and utilize patchy food resources frugivores need to be highly dispersive and occupy large home ranges (Chasar *et al.* 2014). For instance, in KZN, trumpeter hornbills moved up to 14.5km between forest fragments and spent nearly 50 percent of their time in agricultural areas compared to 30 percent in forests (Lenz *et al.* 2011). It may thus not be fragmentation metrics that these frugivores respond to (*e.g.* forest area), but rather the availability of fruiting trees across the landscape. It therefore follows that selective logging, or the clearing of swamp forest patches dominated by fruiting *Ficus* species, rather than forest fragmentation, may pose a greater threat to frugivores within coastal forests.

Because our models involved multiple comparisons among more than one response variable, it predisposed our results to Type I errors *i.e.* we may falsely conclude a significant effect of a fragmentation parameter on insectivore diversity. However, we suggest that Type I



errors are unlikely to influence our conclusions as the P-values for the few significant pathways were very low ( $P < 0.02$ ) while the rest were non-significant. We furthermore did not include 'forest amount' in our models even though it could influence bird diversity within fragmented landscapes (*e.g.* Martensen *et al.* 2012, Fahrig 2013 but also see Hanski 2015). We excluded forest amount because the fit of all our models were consistently poor when forest amount was included as a co-variate. Moreover, our measure of fragment connectivity considered the size and proximity of all fragments within a 1000m radius from the focal fragment, which resulted in a high correlation between forest amount and fragment connectivity (Pearson's  $r = 0.81$ ).

We assumed that species that display similar realised niches with respect to multiple environmental factors and similar traits would behave similarly in the face of environmental change (*e.g.* forest fragmentation) (Henle *et al.* 2004). However, this does not mean that every species that make up these guilds were influenced in the same way by fragmentation parameters. For instance, forest loss may negatively affect forest-dependent insectivores such as the Blue-mantled Crested Flycatcher (*Trochocercus cyanomelas*), but not forest-associated insectivores such as the African Paradise Flycatcher (*Terpsiphone viridis*). The next step will be to investigate vulnerabilities within insectivores at the sub-guild level to determine the life history characteristics that may drive vulnerability (*e.g.* Pavlacky *et al.* 2015). For instance, insectivores can be grouped into sub-guilds based on foraging tactic (*e.g.* sallying species, arboreal gleaners, or terrestrial species) and/or dispersal ability (*e.g.* home range size) (Powell *et al.* 2015). From studies across the tropics, we know that terrestrial insectivores are the most vulnerable to forest fragmentation (Lens *et al.* 2002, Peh *et al.* 2005, Powell *et al.* 2013, Pavlacky *et al.* 2015, Stratford & Stouffer 2015). Our results suggest that insectivore species with large home ranges, but limited dispersal ability might be particularly sensitive to coastal forest fragmentation - however, based on our current findings, we can only make

some inferences about the identities of these species. In South Africa, bird species are classified as threatened based on the IUCN criteria (Taylor *et al.* 2015), which include declines in population size and distribution as well as reasons for decline such as habitat loss ([www.iucnredlist.org](http://www.iucnredlist.org)). We may therefore expect that threatened insectivore species are most likely at risk of extinction. If this is the case, the African broadbill and the spotted ground-thrush should be of special conservation concern. These insectivorous species are classified as threatened in South Africa and, based on our analysis, sensitive to forest loss. Two endemic insectivores, Rudd's apalis (*Apalis ruddi*) and Woodward's batis (*Batis fratrum*) were until recently also listed as near-threatened (Barnes 2000). These two species may also warrant special conservation concern given their sensitivity to coastal forest fragmentation. To protect these species, the protection of natural habitats to increase connectivity and halt degradation must be a conservation priority in this threatened eco-region.

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## AUTHOR CONTRIBUTIONS

PO and RVA designed the study. PO conducted the fieldwork, analysed the data and wrote the manuscript with inputs from RVA.

## SUPPORTING INFORMATION

Additional Supporting Information may be found with online material:

TABLE S1. Functional traits of bird species recorded in coastal forests.

TABLE S2. The number of species from each guild that were recorded only in coastal forests, only in matrix land-use types, and in both coastal forest and matrix land-use types.

TABLE S3. List of species assigned to each feeding guild.

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## Tables

**Table 1** – Number of bird and tree species, as well as the fragmentation parameters recorded for the nine coastal forest fragments included in our study. Fragment connectivity was calculated as the mean proximity index in Fragstats 4.2 (McGarigal & Ene 2013). Values in brackets indicate the number of individuals recorded for each feeding guild.

Fragment	Latitude	Area (km <sup>2</sup> )	Connectivity	Matrix land-use type	Tree species	Frugivores	Generalist feeders	Granivores	Insectivores	Nectarivores
1	29.2375	2.10	0	Sugarcane	45 (649)	6 (47)	8 (37)	3 (9)	8 (51)	3 (14)
2	28.9599	4.00	0	Plantations	60 (1385)	8 (91)	9 (34)	2 (10)	12 (70)	4 (29)
3	28.9269	6.80	1.5	Rural settlements	58 (1185)	7 (74)	6 (35)	1 (2)	10 (62)	4 (15)
4	28.9780	14.00	0	Rural settlements	40 (1294)	6 (80)	6 (49)	2 (11)	9 (79)	3 (26)
5	28.6467	8.30	1.86	Urban settlements	45 (781)	6 (24)	7 (57)	2 (2)	10 (66)	3 (9)
6	28.4619	30.20	8.18	Plantations	60 (1288)	8 (140)	8 (90)	3 (15)	17 (164)	3 (19)
7	28.2292	87.30	10.74	Grasslands	92 (2016)	8 (169)	10 (98)	4 (25)	19 (216)	3 (26)
8	27.4335	22.30	5.97	Grasslands/ Woodlands	74 (1180)	6 (28)	8 (45)	3 (5)	16 (105)	2 (12)
9	27.1869	20.00	1.97	Grasslands/ Woodlands	94 (2741)	6 (168)	7 (83)	2 (14)	16 (167)	4 (26)

**Table 2** – Model evaluation statistics calculated for each bird feeding guild.

Feeding guild	Fisher's <i>C</i>	P-value	R <sup>2</sup> -value	AIC	AICc
Frugivores	26.28	0.24	0.21	72.28	-1.32
Generalist feeders	16.96	0.85	0.38	60.96	-11.33
Granivores	20.05	0.58	0.51	66.05	-7.55
Insectivores	20.20	0.57	0.93	66.20	-7.40
Nectarivores	25.18	0.29	0.30	71.18	-2.42

**Table 3** – The direct, indirect and total effects of different fragmentation parameters on species richness within bird feeding guilds. The path diagram illustrating only the direct effects is shown in Fig. 2 (\* P<0.05; \*\* P<0.01).

	Area			Connectivity			Matrix land-use types		
	Direct	Indirect	Total	Direct	Indirect	Total	Direct	Indirect	Total
Frugivores	-0.87	0.07	-0.80	1.10	-0.04	1.06	-0.26	-	-
Generalist feeders	-1.03	0.20	-0.83	1.38	-0.03	1.35	0.02	-	-
Granivores	-0.62	0.05	-0.57	1.28	-0.10	1.18	-0.29	-	-
Insectivores	0.07	0.26*	0.33*	0.85**	-0.16*	0.69*	-0.23	-	-
Nectarivores	-0.48	0.35	-0.13	-0.24	-0.21	-0.44	-0.31	-	-



## Figures

**Figure 1** – a) The study area along the north-east coast of South Africa. Triangles represent survey sites that were located within nine coastal forest fragments along approximately 300 km of coastline. Numbered squares show which sites belong to the same fragment and corresponds to the fragment number in Table 1. Despite discrepancies in the classification of coastal forest types, we opted to recognize coastal forests as comprising lowland, dune and swamp forests (see Olivier *et al.* 2013 and references therein). Three close-up panels are shown to illustrate the differences in size, connectivity and matrix land-use types of some of the fragments included in our study: (b) shows a large, connected fragment that are surrounded by a mixture of grasslands and woodlands inside the protected iSimangaliso Wetland Park, (c) shows an intermediate sized fragment that is relatively isolated and surrounded by agroforestry and rural settlements, (d) shows the smallest fragment in our study area, which is also isolated and imbedded within large sugarcane plantations.

**Figure 2** – Path models examining the hypothesised relationships between fragmentation parameters and environmental variables on bird species richness within five feeding guilds in coastal forest fragments. Illustrated are standardized partial regression coefficients showing the strength of effects of variables on each other. Significant pathways are indicated by an asterisk (\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ ) and  $R^2$ -values are given next to the two endogenous variables (tree and bird species richness). The broken arrow in the path model for insectivores illustrate the significant indirect effect of fragment area on insectivore species richness that is mediated through tree species richness. We only show the significant indirect effect – non-significant indirect effects and indirect effects for the other feeding guilds are reported in Table 3.  $n$  denotes the number of bird species within each feeding guild. Abbreviations used in the

models include: CONNECT = connectivity, LAT = latitude, MATRIX = matrix community dissimilarity when compared to the forest community of the adjacent fragment, TREES = tree species richness, PCA1 = principal component axis 1 representing elevation, PCA2 = principal component axis 2 representing median rainfall in winter, minimum relative humidity in winter, and mean annual plant-available water.

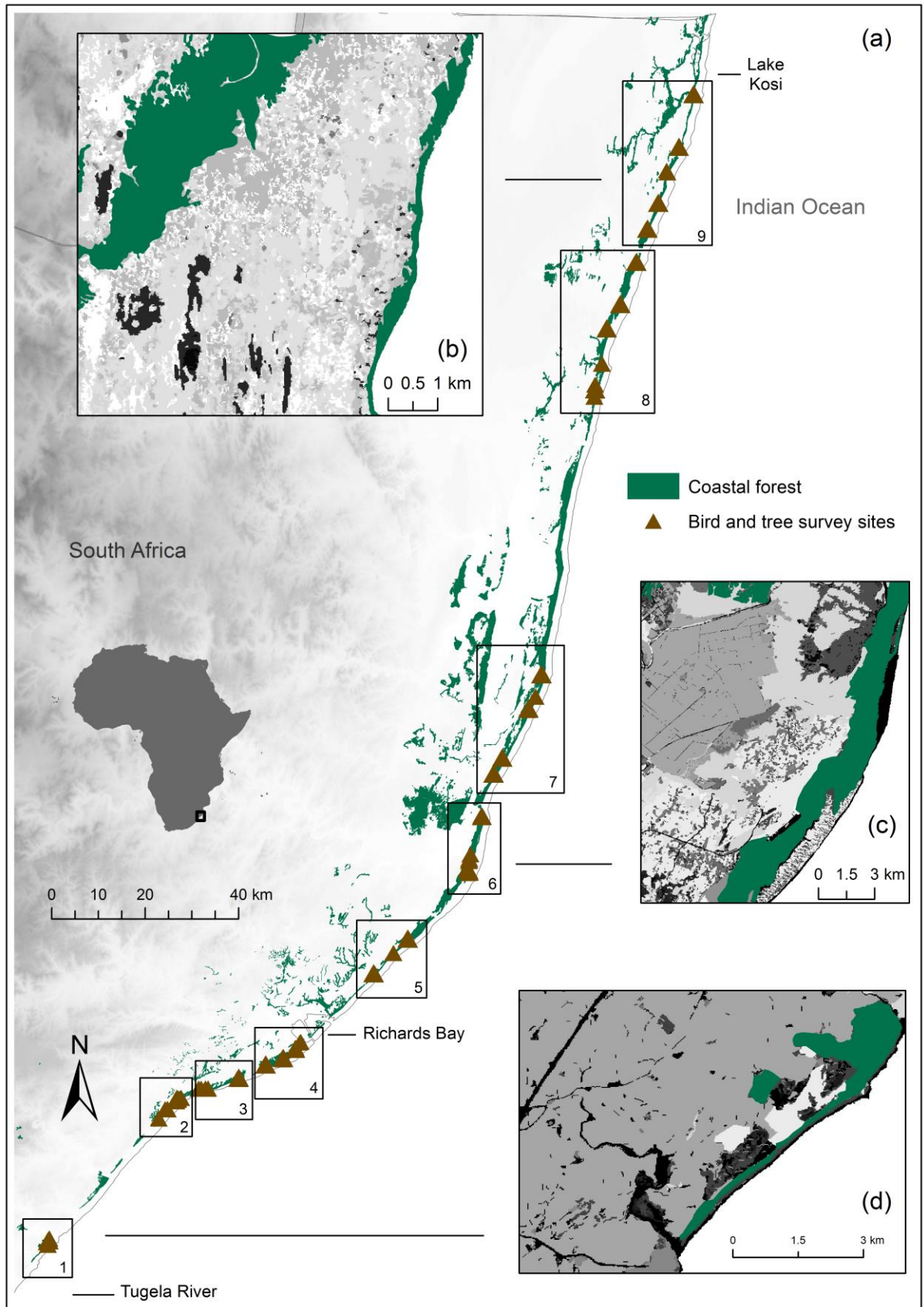


Figure 1.

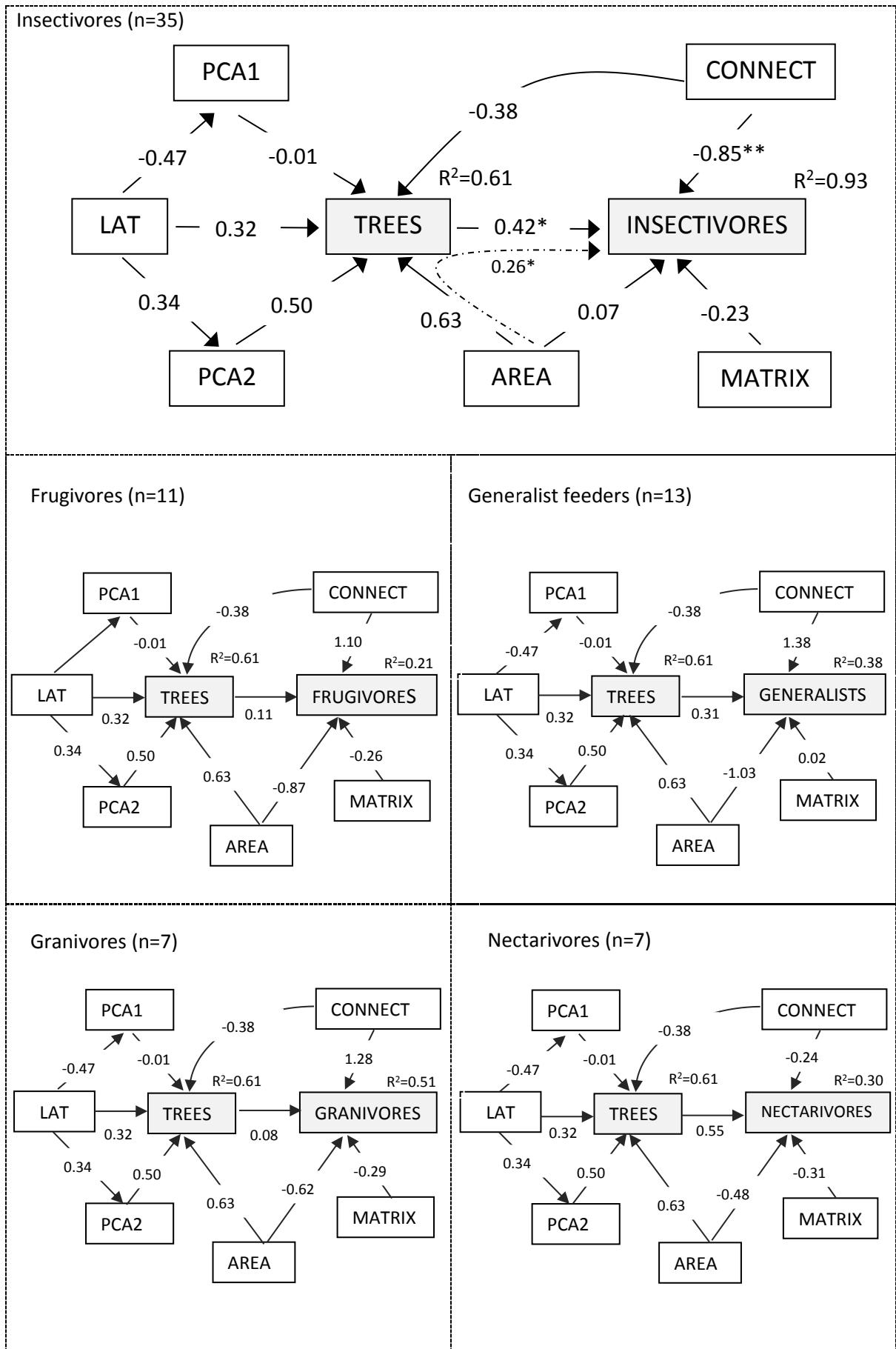


Figure. 2

