Multi-scale sampling boosts inferences from beta diversity patterns in coastal forests, South Africa

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ABSTRACT

Aim We used a hierarchical fractal-based sampling design to test how sampling scale influences i) beta diversity and ii) inferences on the modelled contribution of niche- versus dispersal-based assembly processes in structuring tree and bird assemblages.

Location Coastal forest fragments, South Africa

Methods We surveyed 103 tree and 267 bird points within eight forest fragments and partitioned beta diversity (β_{sor}) into its turnover (β_{sim}) and nestedness (β_{nes}) components. We evaluated how sampling at fine, intermediate and coarse scales influenced beta diversity components and compared how tree and bird beta diversity respond to sampling grain variation. We then explored the relative contributions of niche- and dispersal based assembly processes in explaining spatial turnover as a function of sampling grain and/or study taxon by using multiple regression modelling on distance matrices and variance partitioning.

Results Beta diversity (β_{sor}) of trees and birds was mainly explained by spatial turnover (β_{sim}) at all sampling scales. For both taxonomic groups, β_{sor} and β_{sim} decreased as sampling scale increased. Beta diversity differed among trees and birds at fine, but not at coarse sampling scales. Dispersal-based assembly processes were the best predictors of community assembly at fine scales, whereas niche-based assembly processes were the best predictors at coarse scales. Most of the variation in tree community composition was, however, explained at fine scales (by dispersal-based assembly processes), while most of the variation in bird community composition was explained at coarse scales (by niche-based assembly processes).

Main conclusions Our study shows that inferences from beta diversity are scale dependent. By matching the grain of the data with the grain at which predictor variables and associated processes are likely to operate, multi-scale sampling approaches can improve biodiversity conservation and should be part of incentives directed at ecological sensible conservation plans.

Keywords: conservation; dispersal-based assembly; dispersal limitation; fractal sampling; fragmentation; nestedness; niche-based assembly; Sørensen's dissimilarity; sampling scale; spatial turnover;

INTRODUCTION

Studies on the variation in species composition among sites (beta diversity) allow inferences on the processes which generate and maintain diversity (Anderson *et al.,* 2011). Estimates of beta diversity, however, are influenced by both spatial grain (the size of the sampling unit) and spatial extent (the total area encompassed) (e.g. Mac Nally *et al.,* 2004; Barton *et al.,* 2013). Processes inferred from beta diversity estimates might therefore in many instances also be a function of the scale at which studies were conducted.

Inferred processes are often derived from the deconstruction of beta diversity estimates into nestedness and spatial turnover components (e.g. Baselga, 2010). Nestedness reflects differences in the number of species that occur among sites; species present in one site are a subset of the species occurring at another more species-rich site (Ulrich *et al.,* 2009). Spatial turnover instead involves the replacement of species present at one site by different species at another site (Gaston & Blackburn, 2000). The correlation between spatial turnover and environmental or geographic distance are often used to infer the relative contributions of niche- and dispersal based community assembly processes in structuring communities (e.g. Nekola & White, 1999; Tuomisto *et al.,* 2003). Whether community composition is controlled by niche- or dispersal-based assembly processes continue to fuel contemporary debates in ecology (see Chase & Meyers, 2011 and references therein), yet one may expect that because estimates of spatial turnover are influenced by spatial scale, inferences on the relative contribution of niche- and dispersal-based assembly processes may also be a function of scale (e.g. Freestone & Inouye, 2006). Indeed Weiher *et al.,* (2011) noted that the scaling of community assembly deserves increased research attention; however such studies remain rare.

Assembly processes inferred from beta diversity estimates may not only be a function of spatial scale, but also of the life-history traits of the study organism (Barton *et al.,* 2013). For instance, dispersal-based assembly processes, such as dispersal limitation, may play a greater role in shaping community assembly in taxa that are poor dispersers, compared to taxa that are more mobile (Weiher *et al.,* 2011). Furthermore, species traits associated with different trophic levels may also determine the relative contribution of community assembly processes. For instance, niche-based assembly processes may play a greater role in shaping the community composition of birds than plants (e.g. Driscoll & Lindenmayer, 2009; Özkan *et al.,* 2013). Unravelling the relative contribution of assembly processes in shaping community composition is not only important from a theoretical perspective, but also from a practical one because if these processes vary across taxa and spatial scales, conservation efforts that focus on maintaining them will also have to differ. For

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instance, communities that are assembled by mostly niche-based processes may be more susceptible to habitat loss and may thus benefit from site-scale conservation initiatives. Conversely, communities that are driven by dispersal-based assembly processes may benefit more from a coarser landscape perspective to conservation.

Most previous studies on the influence of spatial scale on beta diversity and assembly processes consider these factors as separate entities and in isolation (e.g. Mac Nally *et al.,* 2004), and focused either on single taxa (e.g. Kristiansen *et al.,* 2013) or more than one taxa within the same taxonomic group (e.g. Josefson & Göke, 2013) (but see Gossner *et al.,* 2013). These limitations may be due to the limits associated with simultaneously sampling at different scales and across taxonomic groups. To address the limitations imposed by scale Marsh & Ewers (2013) proposed a sampling design based on fractal geometry which explicitly addresses questions about beta diversity and spatial scale. Such a design provides the opportunity to aggregate data on different ecological groups at different spatial grains and could enable investigators to match the grain of the data with the grain at which predictor variables and associated processes are likely to operate (Ewers *et al.,* 2011).

In this study, we use fractal sampling to assess how beta diversity and associated contributions of niche- and dispersal-based assembly processes change across multiple sampling scales and taxa within a fragmented, sub-tropical coastal forest along the east coast of South Africa. For our study we defined changes in sampling scale as changes in sampling grain. Unravelling the processes that drive community assembly is of particular importance for conservation here as these forests form part of two critically endangered eco-regions (Burgess *et al.,* 2004), and may also harbour an unpaid extinction debt (Olivier *et al.,* 2013). We sampled tree and bird communities that occur within coastal forests and build on previous findings that metrics of beta diversity may be influenced by spatial grain and extent (e.g. Mac Nally *et al.,* 2004; Martiny *et al.,* 2011; Steinbauer *et al.,* 2012) to hypothesize that (H1) beta diversity will decrease as sampling scale increase for both

taxonomic groups. We focused on tree and bird communities because they represent two taxa with distinctly different dispersal strategies, and furthermore also occupy different trophic levels. Because assemblages of less mobile species are expected to differ more between sites than those of more mobile species (Kessler *et al.,* 2009) we hypothesize that (H2) tree beta diversity will be significantly higher than bird beta diversity across sampling scales. Lastly we hypothesize (H3) that the relative contribution of niche- and dispersal-based assembly processes in shaping community assembly will differ as a function of sampling scale and study taxon. Dispersal-based processes will play a greater role in tree community assembly, while niche-based assembly processes will play a greater role in bird community assembly. We conclude that multi-scale management approaches will be necessary to maintain coastal forest diversity.

MATERIALS AND METHODS

Study region

In addition to forming part of two critically endangered eco-regions, the Maputaland Coastal Forest Mosaic and the KwaZulu-Cape Coastal Forest Mosaic, coastal forests are also situated within the Maputaland-Pondoland-Albany biodiversity hotspot (Küper *et al.,* 2004) as well as the Maputaland Centre of Plant Endemism (van Wyk & Smith, 2000). In South Africa, these forests are limited in extent and occur mainly on calcareous sand dunes formed by deposits left by the regression of the Indian Ocean during the last glacial period (8000 – 10000 BP) (Eeley *et al.,* 1999). Here niche-based assembly processes play important roles in structuring communities (e.g. Griffiths & Lawes, 2006; Tsvuura *et al.,* 2012). However, coastal forests may also be a meeting ground for species that are typical of hinterlands habitats or distant coastal areas, most notably the tropical coastal forests to the north and the temperate forests to the south of the study area (van Aarde *et al.,* 2013). Dispersal-based assembly processes may therefore also be of relevance in structuring coastal forest

communities. We therefore consider these dunes as an appropriate testing ground to quantify the influence of sampling scale on inferred assembly processes.

Our survey sites were located within and adjacent to eight coastal forests fragments (range = 2.1 – 87.3 km^2) situated along approximately 300 kilometres 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). These fragments were embedded in a matrix of either sugarcane or agroforestry plantations, rural homesteads and urban settlements. Some fragments also were adjoined by natural grasslands and woodlands. Survey sites were positioned randomly within forest fragments and surveys were conducted during the summers (November-March) of 2011, 2012 and 2013.

Sampling design

A fractal-based sampling design provides a clearly defined structure for aggregating data on ecological phenomena that vary over different spatial scales (Ewers *et al.,* 2011; Marsh & Ewers, 2013). We therefore used a fractal sampling procedure to develop a sampling hierarchy that consisted of three sampling grains for trees (fine, intermediate, and coarse) and four sampling grains for birds (fine, intermediate, mid-intermediate, and coarse). Each sampling grain comprised a number of aggregated sampling units. Survey plots and points represented the finest sampling scale for trees and birds respectively (sample size: n=103 and n=267). These plots/points were then arranged as equilateral triangles with sides 564m sides for trees and 178m for birds. These first-order fractals represented the intermediate sampling scale for trees and birds respectively (n=20 and n=55). Each tree plot was placed in the middle of a first-order bird fractal. The sampling design therefore allowed us to also have a second-order bird fractal that comprised nine survey points. We defined this sampling scale as mid-intermediate (Fig. 1) (n=16). This sampling scale was only applicable to birds and not trees. Second-order fractals were at least 564m apart. The sum of tree plots and bird survey points within a forest fragment represented our coarsest sampling scale (n=8). Within forest fragments we also surveyed extra points so as to achieve sampling saturation at coarse
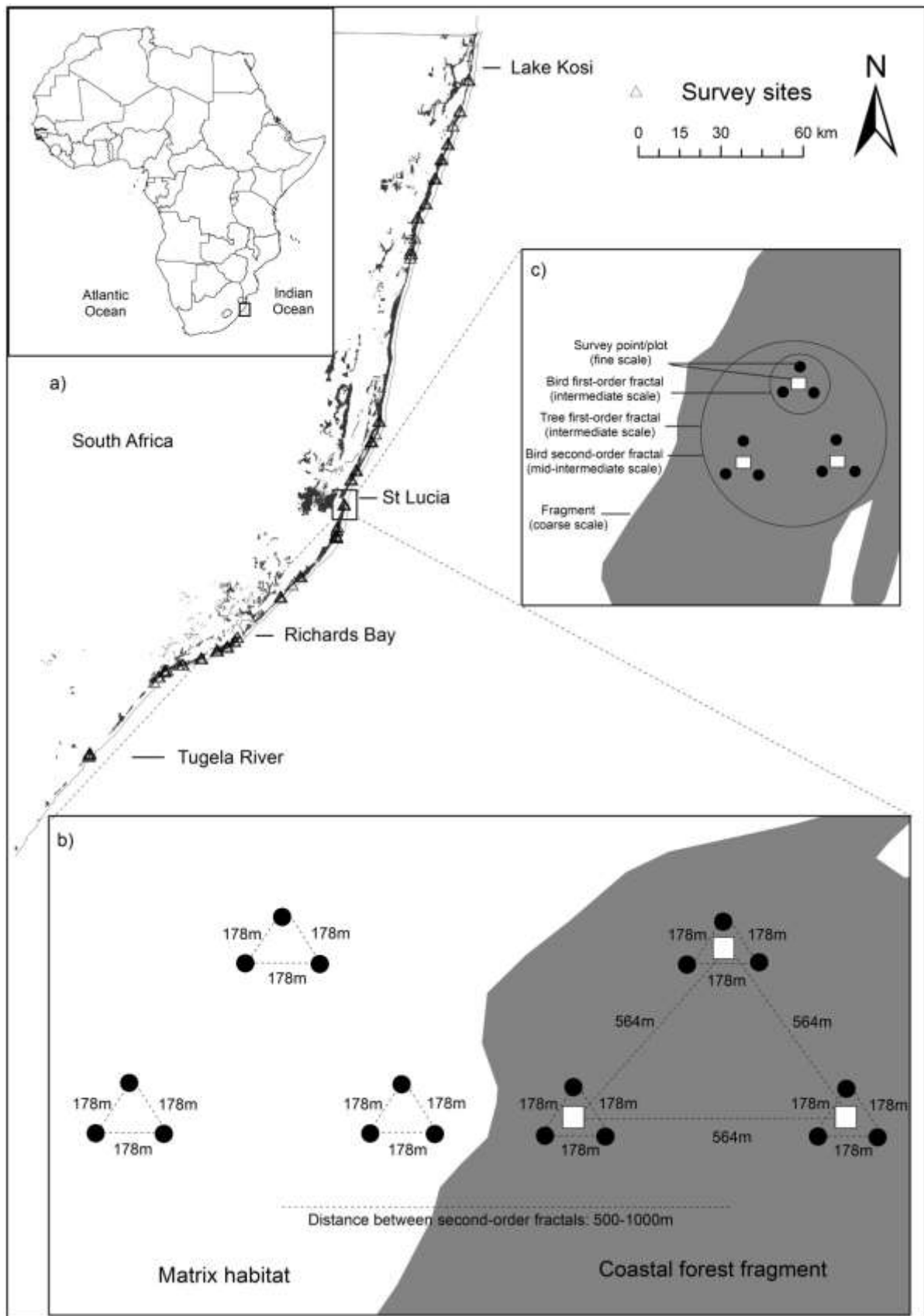
Figure 1. a) The study area along the north-east coast of South Africa. Black triangles represent survey sites that were located within eight coastal forest fragments along approximately 300km of coastline. b) A schematic representation of our sampling design. Black circles represent bird survey points which were located on the vertices of equilateral triangles with sides of length 178m. White squares represent tree survey plots that were located on the vertices of equilateral triangles with sides of length 564. Each tree plot was also located in the centre of a first-order bird fractal, which allowed us to also have a second-order bird fractal that comprised nine survey points. Each second-order fractal was paired with another second order fractal placed in the matrix habitat directly adjacent to the focal forest fragment. These two second order fractals (forest and matrix fractal) were located on the same longitude and were a minimum of 500m and a maximum of 1000m apart respectively. Only bird points were surveyed in the adjacent matrix habitats and were included as a covariate in our models. c) A schematic representation of our sampling hierarchy. Black dots represent bird survey points and white squares tree survey plots. Each sampling grain comprised a number of aggregated sampling units. We defined three sampling grains for trees (fine, intermediate, and coarse) and four sampling grains for birds (fine, intermediate, mid-intermediate, and coarse).

sampling scales. Bird survey points were always added as equilateral triangles around a single tree survey point. We evaluated sampling effort for each fragment by generating species accumulation curves using the software program EstimateS version 8 (Colwell, 2006).

To access whether the adjacent matrix habitat influenced bird community composition within forest fragments, we paired each second-order forest fractal with another second-order fractal placed in the matrix habitat directly adjacent to the focal forest fragment. By doing so we were able to include matrix species composition as a covariate in our models. These second-order matrix fractals comprised nine bird survey points and were located in agricultural plantations, rural settlements, woodlands and grasslands. The forest and matrix second-order fractals were positioned on the same longitude and were a minimum of 500m and a maximum of 1000m apart respectively (Fig. 1).

Tree censuses and bird surveys

Trees were recorded in 103 16m x 16m plots while birds were surveyed using point counts (Bibby *et al.,* 2000). We surveyed 267 and 162 bird points within forest and matrix habitats. The number of survey points per fragment ranged from 12 to 48 for birds and 4 to 18 for trees. For birds we also conducted point counts in adjacent matrix habitats: sugarcane and agroforestry plantations, rural subsistence areas, grasslands and woodlands. Point counts were conducted between 04.00 h and 09.00 h by the same two observers. Each observer surveyed 4-9 points per day depending on habitat type. To reduce potential observer bias, observers 'shared' fractal points, in other words, a first or second order fractal were never surveyed by only one observer. We allowed for a two minute period for birds that may have been disturbed on arrival at the survey point to resettle and thereafter recorded birds for 10 minutes. For each encounter, estimated distances from the observer to the bird were recorded by a digital rangefinder (Nikon Laser 550As, Tokyo, Japan). All birds seen and heard were recorded, but we excluded largely aerial species such as swifts and swallows and birds that flew above the forest canopy. Point counts were not surveyed during rain or windy conditions.

For trees, every individual tree ≥30cm tall, diameter at breast height (d.b.h.) was measured and the individual was identified to species level. Surveyors were trained in, and had prior experience of, local tree and bird identification.

Data analyses

Beta diversity

The most appropriate way to decompose beta diversity is currently debated (see Podani & Schmera, 2011; Baselga, 2012; Carvalho *et al.,* 2013) and beyond the scope of our analyses. We disentangled the relative contributions of nestedness and spatial turnover to overall beta diversity at each sampling scale by partitioning total diversity (Sørensen dissimilarity, β_{sor}) into contributions by turnover (Simpson dissimilarity, β_{sim}; Lennon *et al.,* 2001) and nestedness-driven dissimilarity (β_{nes}) following Baselga (2010). This approach relies on the fact that Sørensen and Simpson dissimilarities are equal in the absence of nestedness, so their difference is a measure of the nestedness component of beta diversity (Baselga, 2010).

First, we calculated multiple-site dissimilarities (Baselga, 2013) for trees and birds and evaluated how sampling scale influenced β_{SOR}, β_{SIM} and β_{NES}. Second, we calculated pair-wise dissimilarities and evaluated how sampling scale influenced the slopes of the distance decay curves for β_{sor}, β_{sim} and β_{nes}. This method is equivalent to the distance-decay of similarity proposed by Nekola & White (1999) where rates of distance decay are estimated through regression of compositional dissimilarities against geographical distance. We measured geographic distances as the minimum straight line distance between sampling units at each sampling scale using the Haversine formula which takes into account the spherical shape of the earth when calculating the distance between two points (Sinnott, 1984). Euclidean distances between first- and second-order fractals were calculated from the longitudinal and latitudinal co-ordinates in the centre of each equilateral triangle. For forest fragments, we first calculated the centroid of each fragment and then

used the straight line distances between the longitudinal and latitudinal co-ordinates of the

centroids to construct a dissimilarity matrix. To account for the inherent dependence of the

dissimilarity values, significance of the Pearson correlations was computed by means of Mantel

permutation tests (999 permutations). To test for differences in intercepts and slopes we compared

the linear and quadratic terms of the regression lines between β_{sim} and β_{nes} using an analysis of

covariance (ANCOVA) (Zar, 1984) in the software program Graphpad Prism 5.00 (GraphPad Software,

San Diego California USA, www.graphpad.com). We used the same procedure to compare if the

intercepts and slope of the distance decay relationship for β_{sor}, β_{sim} and β_{nes} varied with sampling

scale and among taxa. All other analyses were performed in R (R Development Core Team, 2012)

using the packages betapart (Baselga & Orme, 2012) and vegan (Oksanen *et al.,* 2007).

Niche- versus dispersal-based assembly processes

A habitat suitability modelling exercise that also included variables such as soil type, clay content,

aspect, slope and temperature showed that daily rainfall in winter, humidity, plant available water

and elevation explained 90% of the probability of coastal forest occurrence (see Olivier *et al.,* 2013).

We assembled digital maps of these four variables (Schulze, 2006), and used these as predictors of

tree species community assembly in further analyses. Maps comprised of 200m x 200m raster (grid

cell) layers and covered the distributional range of coastal forests in the study area. We extracted

the raster value of each variable at each sampling scale in ArcGIS 10 (Environmental Systems

Research Institute, Redlands, California, www.esri.com). Where sampling scales overlapped with

more than one grid cell (e.g. intermediate and coarse scales) we calculated the mean value of the

overlapping grid cells. We used a principal components analysis (PCA) to reduce potentially

correlated variables into orthogonal principal components. The first two components accounted for

97%, 95% and 99% of environmental variation for fine, intermediate, and coarse sampling scales

respectively and were retained for analysis. Principal component axis one (PCA1) represented

elevation, while daily rainfall in winter, humidity and plant available water were represented by

principal component axis two (PCA2). We then constructed Euclidean dissimilarity matrices of each

principal component axis at fine, intermediate and coarse sampling scales.

For birds we considered three sampling scales in our models: fine scale (first-order fractal),

intermediate scale (second-order fractal) and coarse scale (forest fragment). This was because each

tree plot was associated with a first-order bird fractal at the finest sampling scale. We focused on

two environmental variables that may explain dissimilarity in species composition: i) tree species

composition and ii) the density of individual trees per sampling plot. We also included matrix bird

species composition as a covariate in our model to determine if differences in the bird community

that inhabit the adjacent matrix influence the community composition of birds within forest

fragments. We calculated the mean density of tree stems in each tree survey plot and constructed a

Euclidean distance matrix for fine, intermediate and coarse sampling scales.

For both trees and birds we included geographic distances among sampling points (fine,

intermediate and coarse scales) as a model variable. The variation explained by the geographic

distance between sites was taken as evidence of dispersal-based community assembly.

Modelling approach and variation partitioning

We used multiple regressions on distance matrices (MRM) (Lichstein, 2007) to examine how niche

and dispersal assembly processes explained the variability in community composition at different

sampling scales. Each explanatory matrix contained distances or dissimilarities between all pair-wise

combinations of *n* environmental or spatial factors. Each model used all the combinations of

explanatory variables at each sampling scale. Tests of statistical significance were then performed by

999 random permutations (Legendre *et al.,* 1994). The response variables in our models were the

dissimilarity matrices of species turnover (β_{sim}) for birds and trees. For trees our predictor variables

were geographic distance (representing dispersal-based community assembly) as well as PCA1 and

PCA2 (representing niche-based community assembly). For birds our predictor variables were

geographic distance (representing dispersal-based community assembly), turnover in tree species composition ($\beta_{sim-tree}$), tree stem densities (representing niche-based community assembly), and turnover in matrix bird species composition ($\beta_{sim-matrix\ birds}$). We interpreted variance fractions on the assumption that a relatively large R^2 value provides evidence that the processes modelled by the corresponding explanatory variables are important in shaping community structure, whereas a relatively small R^2 value provides evidence that they are not (see Tuomisto *et al.,* 2012).

To determine the relative contribution of each predictor variable in explaining model variation we used hierarchical partitioning. This method assesses the independent, joint and total contribution of each predictor variable by averaging a measure of goodness-of-fit (R^2 in multiple linear regressions) over all possible models that included the predictor variable (Chevan & Sutherland, 1991). The estimated relative importance of each variable is then represented by the size of its pure effect. To determine the likelihood that the independent contributions of each predictor variable were significant and not a chance event, we performed a randomization test and assessed *z* scores at the 95% level. All analyses were conducted in R using packages ecodist (Goslee & Urban, 2007) and hier.part (Walsh & Mac Nally, 2007).

RESULTS

Our surveys of coastal forests returned 20 548 records of 189 tree species in 103 survey plots. We identified 74 bird species among 2584 records at 267 sampling points. Within the adjacent matrix habitats we identified 121 bird species from 1694 records and 162 sampling points. The average number of tree species per plot was 26.6 (range = 12 to 50; SD=7.7), and the average number of bird species per plot was 8.5 (range = 1 to 17; SD=3.1). Bird species richness of forest points was four times higher than points surveyed in the adjacent matrix that had an average of 2.0 (range = 0 to 7; SD=1.2) species per survey point. The number of bird species recorded within forest fragments ranged from 28 to 40 (SD=5.9), while the number of tree species ranged from 45 to 94 (SD=19.0).

Table 1. Comparison of multi-site dissimilarity values for β_{SOR}(overall dissimilarity), β_{NES} (dissimilarity resulting from nestedness), and β_{SIM} (turnover) for trees and birds at four sampling scales. We do not show tree beta diversity values at mid-intermediate scales because our sampling design did not allow us to investigate this scale for trees.

	Among points/plots (fine scale)		Among first-order fractals (intermediate scale)		Among-second order fractals (mid-intermediate scale)		Among fragments (coarse scale)	
	Birds	Trees	Birds	Trees	Birds	Trees	Birds	Trees
β_{SOR}	0.99	0.97	0.95	0.85	0.78	-	0.63	0.71
β_{SNE}	0.01	0.01	0.02	0.05	0.05	-	0.07	0.12
β_{SIM}	0.98	0.96	0.93	0.80	0.73	-	0.56	0.59

Beta diversity

Beta diversity (β_{sor}) of trees and birds in coastal forests was mainly explained by spatial turnover (β_{sim}), with a small explanatory contribution from nestedness (β_{nes}) (Table 1). This pattern held at all sampling scales for both multi-site and pairwise dissimilarity measures (Table 1 and Table 2).

The absolute values of β_{SOR} and β_{SIM} decreased with increasing sampling scale for both trees and birds (Table 1). The intercepts of the distance decay relationship of β_{sor} for trees and birds were significantly higher at the finest than the coarsest sampling scale (Trees: $P<0.04$; Birds: $P<0.0001$) (Table 2). We recorded the same trend (i.e. intercepts of the distance decay relationship were significantly higher at the finest than the coarsest sampling scale) in trees for both β_{sim} ($P=0.001$) and β_{nes} ($P=0.0004$). However, for birds this trend held only for β_{sim} ($P<0.0001$) and not for β_{nes} ($P<0.98$).

The slopes and intercepts of the distance decay relationships of β_{sor} and β_{sim} among trees and birds was not significantly different at coarse and intermediate sampling scales (first-order fractal β_{sor} $P=0.72$; first-order fractal β_{sim} $P=0.12$; fragment scale β_{sor} $P=0.87$; fragment scale β_{sim} $P=0.26$). However, the slopes of β_{sor} and β_{sim} of trees and birds differed significantly at the finest sampling scale (β_{sor} $P<0.0001$; β_{sim} $P<0.0001$). The slopes and intercepts of β_{sim} and β_{nes} differed significantly at every sampling scale for birds ($P<0.0001$), but only at fine and coarse scales for trees ($P<0.0001$).

Dissimilarity as a function of niche- and/or dispersal-based assembly processes

MRM models explained most of the variability in tree community dissimilarity at fine scales ($R^2=0.45$). Explanatory powers decreased, however, as sampling scale increased from intermediate ($R^2=0.40$) to coarse scales ($R^2=0.30$). Conversely, for birds, MRM models explained half of the variability in community dissimilarity at coarse scales ($R^2=0.50$), but little thereof at fine scales ($R^2=0.15$).

Table 2. Results from ordinary least-sqaure regression of β_{sor} (overall dissimilarity), β_{nes} (dissimilarity resulting from nestedness) and β_{sim} (turnover) as a function of geographic distance (distance-decay of similarity (Nekola & White (1999)) for trees and birds between pairs of survey sites at four sampling scales. Our sampling design allowed us to only investigate tree beta diversity three sampling scales: fine, intermediate and coarse. Regression models were applied separately for β_{sor}, β_{nes} and β_{sim} at each sampling scale. A Mantel test was applied to assess the significance of the Pearson correlation coefficient (r): *P<0.05.

		Among points/plots (fine scale)		Among first-order fractals (intermediate scale)		Among-second order fractals (mid-intermediate scale)		Among fragments (coarse scale)	
		Birds	Trees	Birds	Trees	Birds	Trees	Birds	Trees
B_{sor}	Intercept	0.61	0.56	0.40	0.46	0.27	-	0.25	0.40
	Slope	0.0004	0.001	0.001	0.001	0.001	-	0.001	0.001
	Mantel r	0.16	0.48	0.41	0.40	0.62	-	0.77	0.46
	P	0.001	0.001	0.001	0.001	0.001	-	0.001	0.02
B_{nes}	Intercept	0.11	0.07	0.08	0.07	0.06	-	0.05	0.07
	Slope	-0.00003	-0.00003	-0.00002	0.0002	-0.00003	-	0.0001	0.0004
	Mantel r	-0.02	-0.03	-0.02	0.19	-0.10	-	0.14	0.33
	P	0.816	0.73	0.76	0.03	0.75	-	0.20	0.06
B_{sim}	Intercept	0.5	0.49	0.32	0.39	0.21	-	0.20	0.33
	Slope	0.0004	0.001	0.001	0.001	0.0008	-	0.0001	0.0003
	Mantel r	0.13	0.44	0.37	0.36	0.61	-	0.58	0.19
	P	0.001	0.001	0.001	0.001	0.001	-	0.004	0.16

Table 3. Results of multiple regression modelling on distance matrices (MRM) by sampling scale for trees and birds. The response variables in our models were the dissimilarity matrices of species turnover (β_{sim}) for birds and trees. Explanatory variables are categorized as either representing niche- or dispersal-based assembly processes. For trees our predictor variables were geographic distance, PCA1 and PCA2. PCA1 and PCA2 represent the two axes of a principal component analysis that included four environmental variables: daily rainfall in winter, humidity, plant available water and elevation. For birds our predictor variables were geographic distance, turnover in tree species composition ($\beta_{sim-tree}$), tree stem densities, and turnover in matrix bird species composition ($\beta_{sim-matrix\ birds}$). Sample size decreased as sampling scale increased from n=103 to n=8 for trees and from n=55 to n=8 for birds. The variation (R^2) explained by each model is reported. The significance of the slopes was evaluated by a permutation test (n=999) *P<0.05.

	Fine scale				Intermediate scale				Coarse scale			
	R^2	Intercept	Slope	P	R^2	Intercept	Slope	P	R^2	Intercept	Slope	P
Trees	0.45	0.31	-	<0.01	0.40	0.19	-	0.01	0.30	0.25	-	0.06
Dispersal-based assembly												
-Geographic distance (km)	-		0.15	<0.01	-		0.11	0.01	-		0.01	0.77
Niche-based assembly												
-PCA 1	-		0.001	<0.01	-		0.001	0.04	-		0.003	0.02
-PCA 2	-		0.001	0.35	-		0.003	0.01	-		-0.001	0.73
Birds	0.15	0.18	-	<0.01	0.27	-0.01	-	0.01	0.50	-0.12	-	0.03
Dispersal-based assembly												
-Geographic distance (km)	-		0.08	<0.01	-		0.08	<0.01	-		0.12	0.07
Niche-based assembly												
-Tree composition	-		0.06	0.25	-		0.16	0.29	-		0.43	0.04
-Tree structure	-		0.04	0.10	-		0.014	0.79	-		-0.11	0.55
Adjacent matrix species												
-Matrix species	-		-0.03	0.55	-		0.09	0.41	-		-0.04	0.81

There was a significant relationship between tree species turnover and geographic distance at fine (P<0.001) and intermediate (P=0.001), but not at coarse sampling scales (P=0.77). At coarse sampling scales PCA1 was the only variable that significantly increased with tree species turnover (P=0.02). A similar pattern emerged for the factors underlying bird community dissimilarity. At fine and intermediate sampling scales, bird species turnover increased with geographic distance (P<0.001 and P=0.004). However, at coarse scales tree species turnover was the only variable that significantly increased with bird species turnover (P=0.04).

The proportion of total variation that was explained by each predictor variable for each model varied with sampling scale (Fig. 2). For trees, the contribution of geographic distance consistently decreased as sampling scale increased (80% to 5%). Conversely, the contribution of PCA1 consistently increased with sampling scale (5% to 89%). For birds a similar pattern emerged. Geographic distance explained nearly 77% of the variation at the finest sampling scale, but only 39% at the coarse sampling scales. For birds, tree species composition explained only 17% of the variation at fine scales, but 49% at coarse scales. Matrix bird species composition and tree stem density never explained more than 18% and 6% of variation, respectively. The individual contributions of all model variables were significantly greater than expected by chance based on z scores at the 95% level.

DISCUSSION

Even though all aspects of diversity are scale-dependent, they do not respond to changes in scale in the same way (Willis & Whittaker, 2002). Our detection of such responses therefore should be scale dependent, which may influence inferences about the processes that maintain diversity (e.g. Freestone & Inouye, 2006; Martiny *et al.,* 2011). Our assessment suggests that a multi-scale sampling approach can detect how sampling scale influence beta diversity patterns, inferences on community assembly processes, as well as identify the sampling grain at which predictor variables and associated processes are likely to operate for different taxa.
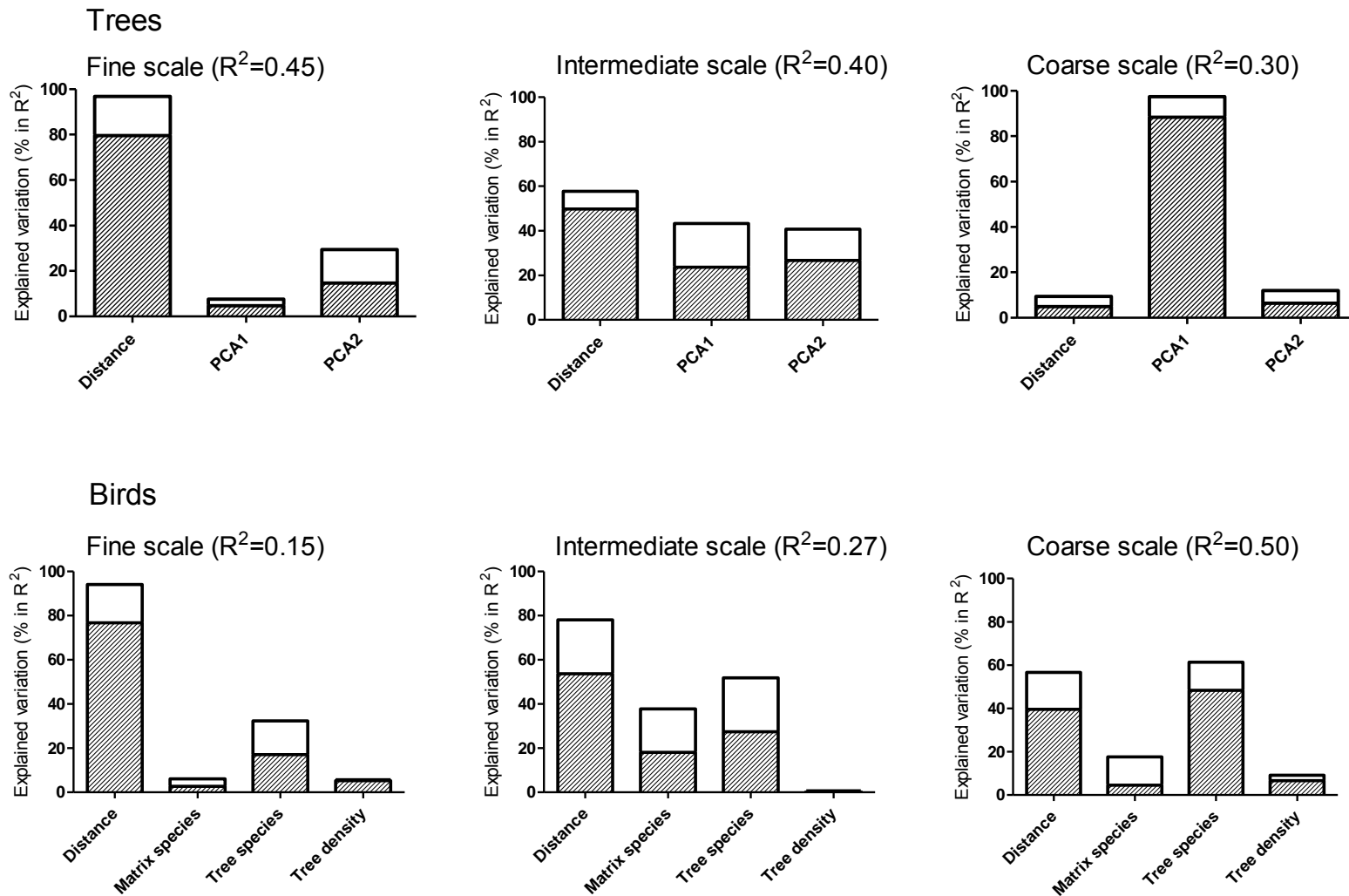
Figure 2. Summary of the results of six separate hierarchical partitions showing the relative contribution of each predictor variable in explaining model variation at fine, intermediate and coarse sampling scales. Predictor variables are categorized as either representing niche- or dispersal-based assembly processes. Dispersal-based assembly is represented by geographic distance (DIST) for birds and trees at each sampling scale. Niche-based assembly is represented by principal component axis one (PCA1) and principal component axis two (PCA2) for trees. PCA1 represented elevation, while daily rainfall in winter, humidity and plant available water were represented by PCA2. For birds niche-based assembly is represented by tree composition (Tree species), matrix habitat species composition (Matrix species) and tree density. Shaded bars correspond to independent effects, and white bars to joint effects. Vertical axes correspond to the proportion of variance explained in each R2 value. The sum of the independent effects equals 100% for each model.

Our finding that beta diversity decreased with an increase in sampling scale is consistent with what have been reported by others (e.g. Mac Nally *et al.,* 2004; Martiny *et al.,* 2011) and support our first hypothesis. This apparent trend may simply be due to a sampling effect where the proportion of a community included in a sample increase with sampling scale because the focal unit size increases. As a result, the similarity of species composition between two sites increases (Mac Nally *et al.,* 2004). This phenomenon may also be due to the well-known species-area relationship where the number of species increases as a function of the focal area (see Schmera & Podani, 2013 and references therein). Community variables from coarse-scaled samples may therefore be more similar than those from fine-scaled samples.

Beta diversity decreased with sampling scale for both taxonomic groups, but the slope of the distance-decay relationship was higher for trees than for birds at every sampling scale. This finding provided support for our second hypothesis - however, contrary to our expectation we only recorded significant differences between the slopes of the distance-decay relationship for tree and bird communities at fine sampling scales. At fine scales, niche structure, biological interactions and environmental characteristics may explain differences in turnover (e.g. McKinney *et al.,* 2001). At coarse scales, however, species turnover may be similar among taxa because they respond in the same way to historical factors as has been implied by Lawes *et al.* (2007) for coastal forest assemblages. Here geographic patterns of speciation, extinction filtering events and, dispersal from areas of origin may have played an important role in shaping forest communities. The similarity between tree and bird beta diversity at coarse scales may also be ascribed to their similar responses to habitat loss and fragmentation. For instance, Arroyo-Rodríguez *et al.,* (2013) found that beta diversity decreased within forest patches in landscapes with high deforestation levels, leading to floristic homogenization. They suggest that this homogenization is a result of the loss of rare species and a gain of disturbance adapted species. This may also be the case for our study and a response to the cumulative large scale habitat loss incurred in recent times (Olivier *et al.,* 2013).

Because species perceive and respond to the world at widely varying spatial scales, we hypothesized that different assembly processes will shape communities with different life-history strategies (Barton *et al.,* 2013). Our results are consistent with this last hypothesis and highlight the importance of sampling at multiple spatial scales. We found that dispersal-based assembly processes likely drives tree community composition within coastal forests because geographic distance explained most of the variation (80%) in the model with the largest R^2 value (R^2=0.45) for trees. Conversely, the bird community is likely driven by niche-based assembly processes because tree species composition explained most of the variation (49%) in the model with the largest R^2 value (R^2=0.50) for birds.

Had we only investigated one spatial scale, however, we may have concluded the opposite. For both taxonomic groups, niche-based assembly processes had the stronger influence on community composition at coarse sampling scales, while dispersal-based assembly processes had the stronger influence at fine sampling scales. This finding has two important implications. First, it support the idea that much of the ambiguity on niche- versus dispersal-based assembly in structuring communities may be a matter of the spatial scale at which studies were conducted (Chase & Myers, 2011; Weiher *et al.,* 2011). Second, it emphasises the importance of matching the grain of the data with the grain at which predictors and associated processes is likely to operate before drawing conclusions about the processes that maintain diversity. Our results suggest that processes that drive tree community assembly are likely to operate at finer scales than processes that drive bird community assembly. For instance, based on the variables included in our models, we infer that dispersal limitation likely drive tree community assembly in coastal forests. Dispersal limitation allow for ecological drift that is augmented by stochastic germination of seedlings and random tree deaths (Hubbell, 2001). Along with restricted seed dispersal i.e. when seeds are more likely to fall close to the parent than far from it, these processes create 'patchiness' in community composition (Chave, 2008), therefore giving rise to fine scale heterogeneity in tree community composition. In contrast to tree community assembly, our models suggest that the processes that

drive bird community assembly operate at coarse spatial scales, where the bird community of a forest fragment is a function of that fragment's tree community. This may be because of underlying functional relationships between bird and tree species (e.g. Kissling *et al.,* 2008) or that they respond to similar drivers that influence compositional changes across fragments. These may include habitat fragmentation parameters (e.g. Polyakov *et al.,* 2013), historical factors (Lawes *et al.,* 2007), and/or the temperate-tropical latitudinal gradient that is present in our study area (Bruton & Cooper, 1980). Similar trends in spatial turnover between trees and birds at coarse but not at fine scales might also be due to the influence of tree community variables on birds at coarse scales.

Before concluding we must also consider the potential caveats associated with our approach. The variables included in our models only explained maximally about half of the variability in bird and tree community composition. Variables related to species interactions (e.g. Siefert *et al.,* 2013), historical factors (Svenning *et al.,* 2011), and land-scape effects (Arroyo-Rodríguez *et al.,* 2013) may also explain some of the variability in community composition. Furthermore, small sample sizes at coarse sampling grains and the length of the studied compositional gradient may introduce errors in beta diversity estimates (Crist *et al.,* 2006; Tuomisto *et al.,* 2012; Schmera & Podani, 2013). Our attempt to account for species interactions by including matrix bird species composition in our model did not contribute to the recorded variation in community structure at any sampling scale. Furthermore, because 90% of the probability in coastal forest distribution was explained by the four environmental variables we included in our models, we suggest that these variables are reasonably good proxies for the underlying environmental variability. However, our results suggest that factors driving tree community composition operate at fine spatial scales. Therefore, the scale of our environmental variables may have been too coarse to capture fine-scale environmental variation such as light intensity, soil chemistry and hydrology. It is therefore possible that an unmeasured local environmental variable contributes in part to a local distance effect which may over-emphasise the role of dispersal-based assembly processes in shaping tree communities in coastal forests.

What are the implications of our results for coastal forest conservation? The high level of turnover observed among forest fragments for both tree and bird communities suggests that every fragment contributed to regional diversity and should ideally be incorporated within conservation plans (as has been noted for coastal forests elsewhere (e.g. Guldemond & van Aarde, 2010)). Species turnover here may be a result of the co-occurrence of Afromontane and tropical fauna and floras within coastal forests (Lawes *et al.,* 2007). As conditions become more tropical northwards along the South African coast southern temperate forest species are gradually being replaced with northern tropical forest species. Our results suggest that the conservation of these communities may best be achieved by multi-scale conservation incentives such as site specific case by case approaches to conserve forests as well as landscape approaches that incorporate the role of historical and large-scale processes (e.g. Eeley *et al.,* 1999; Lawes *et al.,* 2007). For instance, our results imply that, in coastal forests, bird community composition depends on the tree community composition. Disturbances that influence tree species composition, such as habitat loss, unsustainable harvesting or the invasion of alien plant species, may therefore also affect the community structure of birds that occur within fragments. However, we also found that the tree community is mostly driven by dispersal-based assembly processes, which conceivably will benefit from large scale conservation initiatives. These may include: stepping stones or corridors to enhance movements and functional connectivity, maintaining natural matrix habitats among forest fragments to facilitate dispersal, and restoration actions to maintain or enhance the coastal forest corridor to enable north-south dispersal along the coastline.

CONCLUSION

We found that beta diversity and inferred assembly processes are a function of sampling scale. We therefore emphasize the importance of studying beta diversity at multiple spatial scales. In doing so, investigators can match the grain of the data with the grain at which predictor variables and associated processes are likely to operate. In this study, sampling only at fine scales may have failed

to detect the importance of the fragment tree community for the fragment bird community. In contrast, had we only considered coarse sampling scales we may have overlooked the likely role played by dispersal limitation in shaping tree community composition. As a consequence, we may have proposed conservation incentives that over-emphasise niche-based assembly processes (e.g. habitat based and at a fine scale) to the detriment of dispersal-based assembly processes (i.e. landscape based and coarse scale) or vice versa. Our results therefore support the idea that conservation strategies will need to focus more explicitly on the requirements of multiple taxa at multiple spatial scales to prevent the loss of species (Barton *et al.,* 2013). To achieve this we propose the use of multi-scale sampling approaches such as fractal sampling to be part of incentives directed at ecological sensible conservation plans.

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