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

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ABSTRACT

Aim We used a hierarchical fractal-based sampling design to test how sampling grain influences (1) beta diversity of and (2) inferences from 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 plots 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 responded 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 The β_{sor} of trees and birds was mainly explained by 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. However, most of the variation in tree community composition was 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 help improve planning for biodiversity conservation and should be part of initiatives aimed at ecological conservation plans.

Keywords

Conservation, dispersal-based assembly, dispersal limitation, fractal sampling, fragmentation, nestedness, niche-based assembly, sampling scale, Sørensen dissimilarity, spatial turnover.

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INTRODUCTION

Studies of the variation in species composition among sites (beta diversity) allow inferences about the processes that generate and maintain diversity (Anderson *et al.*, 2011). However, estimates of beta diversity 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 the 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, in contrast, 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 geographical distance is 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 continues to fuel contemporary debates in ecology (see Chase & Myers, 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 poorer dispersers compared with 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 example, 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 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-scale perspective to conservation.

Most studies so far on the influence of spatial scale on beta diversity and assembly processes have considered these factors as separate entities and in isolation (e.g. Mac Nally *et al.*, 2004) and have 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 because of the constraints associated with simultaneously sampling at different scales and across taxonomic groups. To address the limi-

tations imposed by scale, Marsh & Ewers (2013) proposed a sampling design based on fractal geometry that 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 used fractal sampling to assess how beta diversity and associated contributions of niche- and dispersal-based assembly processes vary across multiple sampling scales and taxa within a fragmented, subtropical coastal forest along the east coast of South Africa. Unravelling the processes that drive community assembly is of particular importance for conservation here, as these forests form part of two critically endangered ecoregions (Burgess *et al.*, 2004) and may also harbour an unpaid extinction debt (Olivier *et al.*, 2013).

We defined changes in sampling scale as changes in sampling grain. We sampled tree and bird communities that occurred within the coastal forests, and built 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 beta diversity will decrease as sampling scale increases (i.e. plot size increases) for both taxonomic groups (H_1). We focused on tree and bird communities because they represent two taxa with distinctly different dispersal strategies, and they 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 hypothesized that tree beta diversity will be significantly higher than bird beta diversity at all sampling scales (H_2). Lastly, we hypothesized 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 (H_3). 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.

MATERIALS AND METHODS

Study region

In addition to forming part of two critically endangered ecoregions, the Maputaland Coastal Forest Mosaic and the KwaZulu–Cape Coastal Forest Mosaic, the east coast forests of South Africa 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). These coastal 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 (8000–10,000 BP) (Eeley *et al.*, 1999). Niche-based assembly processes play important roles in structuring coastal forest 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 hinterland habitats or distant coastal areas, most notably, in the study area, the tropical coastal forests to the north and the temperate forests to the south (van Aarde *et al.*, 2014). Dispersal-based assembly processes may therefore also be of relevance in structuring coastal forest communities. We therefore considered these dunes to be 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 km²) situated along approximately 300 km of coastline between the Tugela river mouth in the south (−29.2268° S, 32.8578° E) and Lake Kosi in the north (−27.0019° S, 32.8578° E; Fig. 1). These fragments were embedded in a matrix of either sugarcane or agroforestry plantations, rural homesteads and urban settlements. Some fragments were also adjoined by natural grasslands and woodlands. Survey sites were positioned randomly within the 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, intermediate-coarse, 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 sizes $n = 103$ and $n = 267$, respectively). These plots/points were then arranged as equilateral triangles with sides of 564 m for trees and 178 m for birds. These first-order fractals represented the intermediate sampling scale for trees and birds ($n = 20$ and $n = 55$, respectively). Each tree plot was placed in the middle of a first-order bird fractal. The sampling design therefore also allowed us to have a second-order bird fractal that comprised nine survey points. We defined this sampling scale as intermediate-coarse ($n = 16$; Fig. 1) and was only applicable to birds, not to trees. Second-order fractals were at least 564 m apart. The sum of tree plots and bird survey points within a forest fragment represented our coarsest sampling scale ($n = 8$). Within the forest fragments we also surveyed extra points in order to achieve sampling saturation at 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 ESTIMATE S 8 (Colwell, 2006).

To determine 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 500 m and a maximum of 1000 m apart, respectively (Fig. 1).

Tree censuses and bird surveys

Trees were recorded in 103 16 m × 16 m 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 from 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 four to nine 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 was never surveyed by only one observer. We allowed a 2-min period for birds that may have been disturbed on arrival at the survey point to resettle, and thereafter recorded birds for 10 min. For each encounter, estimated distances from the observer to the bird were recorded with a digital rangefinder (Nikon Laser 550As; Nikon, 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 rainy or windy conditions. For every individual tree ≥ 30 cm 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 an ongoing debate (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

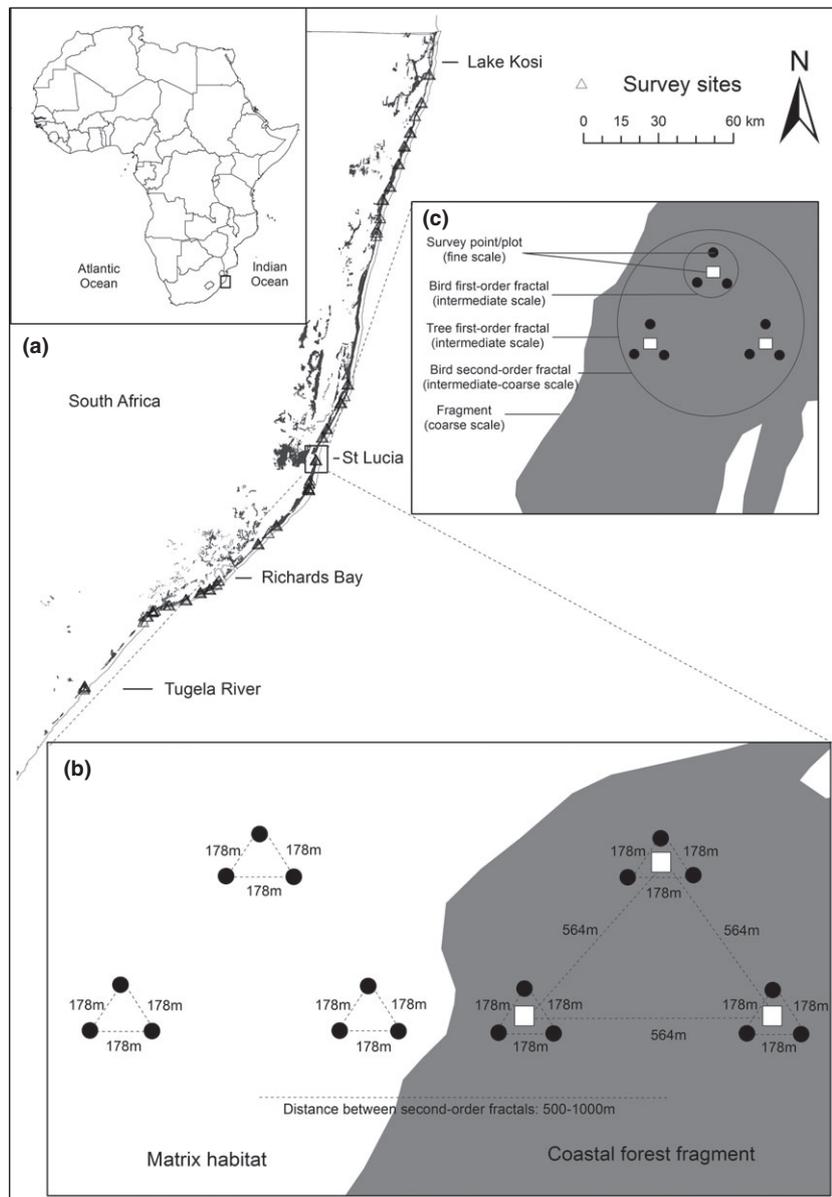


Figure 1 (a) The study area along the north-east coast of South Africa. Triangles represent survey sites that were located within eight coastal forest fragments along approximately 300 km of coastline. (b) A schematic representation of the sampling design. Black circles represent bird survey points that were located on the vertices of equilateral triangles with sides of length 178 m. White squares represent tree survey plots that were located on the vertices of equilateral triangles with sides of length 564 m. Each tree plot was also located in the centre of a first-order bird fractal, which allowed for 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 500 m and a maximum of 1000 m apart. Only bird points were surveyed in the adjacent matrix habitats, and were included as a covariate in the models. (c) A schematic representation of the sampling hierarchy. Black dots represent bird survey points and white squares represent tree survey plots. Each sampling grain comprised a number of aggregated sampling units. There were three defined sampling grains for trees (fine, intermediate and coarse) and four defined sampling grains for birds (fine, intermediate, intermediate-coarse and coarse).

pairwise dissimilarities and evaluated how sampling scale influenced the slopes of the distance decay curves for β_{SOP} , β_{sim} and β_{nes} . Following Baselga (2010), subscripts in small capitals refer to multiple-site dissimilarities and subscripts in lower case refer to pairwise dissimilarities.

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 geographical 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 coordinates 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 coordinates of the centroids to construct a dissimilarity matrix. To account for the inherent dependence of the dissimilarity values, the 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, CA, USA; <http://www.graphpad.com/>). We used the same procedure to see whether the intercepts and slope of the distance decay relationship for β_{sov} , β_{sim} and β_{nes} varied with sampling scale and among taxa. All other analyses were performed in R (R Core Team, 2012) using the packages 'betapart' 1.1 (Baselga & Orme, 2012) and 'vegan' 1.8-5 (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 median rainfall in winter, minimum relative humidity in winter, annual mean plant-available water and elevation explained 90% of the probability of coastal forest occurrence (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. The maps comprised 200 m \times 200 m 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 (ESRI, Redlands, CA, USA). 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 1 (PCA1) represented elevation and accounted for 89%, 74% and 88% of environmental variance at fine, intermediate and coarse scales, respectively. Principal component axis 2 (PCA2) represented median rainfall in winter, minimum relative humidity in winter and mean annual plant-available water, and accounted for 8%, 21% and 11% of environmental variation at fine, intermediate and coarse scales, respectively. 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 might explain dissimilarity in species composition: (1) tree species composition and (2) the density of individual trees per sampling plot. We also included matrix bird species composition as a covariate in our model, to determine whether 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 geographical distances among sampling points (fine, intermediate and coarse scales) as a model variable. The variation explained by the geographical 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 pairwise 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 with 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 geographical distance (representing dispersal-based community assembly) as well as PCA1 and PCA2 (representing niche-based community assembly). For birds, our predictor variables were geographical distance (representing dispersal-based community assembly), turnover in tree species composition ($\beta_{\text{sim-tree}}$), tree stem densities (representing niche-based community assembly), and turnover in matrix bird species composition ($\beta_{\text{sim-matrix birds}}$). 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 (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 include 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: 12–50, SD = 7.7) and the average number of bird species per plot was 8.5 (range: 1–17, SD = 3.1). The bird species richness of forest points was four times higher than for points surveyed in the adjacent matrix, which had an average of 2.0 (range: 0–7, 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).

Beta diversity

The β_{sor} of trees and birds in coastal forests was mainly explained by β_{sim} , with a small explanatory contribution from β_{nes} (Table 1). This pattern held at all sampling scales for both multi-site and pairwise dissimilarity measures (Tables 1 & 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 compared with 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 compared with 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 were 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 each 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 ($R^2 = 0.45$). However, explanatory powers decreased as sampling scale increased

Table 1 Comparison of multi-site dissimilarity values for overall dissimilarity (β_{SOR}), dissimilarity resulting from nestedness (β_{NES}) and turnover (β_{SIM}) for trees and birds in coastal forest fragments, South Africa, at four sampling scales. Tree beta diversity values at intermediate-coarse scales are not shown because the sampling design did not allow investigation at this scale for trees.

	Among points/plots (fine scale)		Among first-order fractals (intermediate scale)		Among second-order fractals (intermediate-coarse scale)		Among fragments (coarse scale)	
	Birds ($n = 267$)		Birds ($n = 55$)		Birds ($n = 16$)		Birds ($n = 8$)	
	Trees ($n = 103$)	Trees ($n = 20$)	Trees ($n = 16$)	Trees ($n = 8$)	Trees	Trees	Trees ($n = 8$)	Trees ($n = 8$)
β_{SOR}	0.99	0.97	0.95	0.85	0.78	0.63	0.71	0.71
β_{NES}	0.01	0.01	0.02	0.05	0.05	0.07	0.12	0.12
β_{SIM}	0.98	0.96	0.93	0.80	0.73	0.56	0.59	0.59

Table 2 Results from ordinary least-square regression of overall dissimilarity (β_{sor}), dissimilarity resulting from nestedness (β_{nes}) and turnover (β_{sim}) as a function of geographical distance (distance decay of similarity; Nekola & White, 1999) for trees and birds in coastal forest fragments, South Africa, between pairs of survey sites at four sampling scales. The sampling design allowed investigation of tree beta diversity at only 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 (intermediate-coarse scale)			Among fragments (coarse scale)	
	Birds		Trees	Birds		Trees	Birds		Trees	Birds	Trees
	Intercept	Slope	Mantel r	Intercept	Slope	Mantel r	Intercept	Slope	Mantel r	Intercept	Slope
β_{sor}	Intercept	0.61	0.56	0.40	0.46	0.27	0.25	0.40	0.25	0.40	0.001
	Slope	0.0004	0.001	0.001	0.001	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	0.77	0.46	0.02
β_{nes}	Intercept	0.11	0.07	0.08	0.07	0.06	0.05	0.07	0.05	0.07	0.0004
	Slope	-0.00003	-0.00003	-0.00002	0.0002	-0.00003	-0.00001	0.0004	-0.00001	0.0004	0.33
	Mantel r	-0.02	-0.03	-0.02	0.19	-0.10	0.14	0.33	0.14	0.33	0.06
β_{sim}	Intercept	0.816	0.73	0.76	0.03	0.75	0.20	0.20	0.20	0.33	0.0003
	Slope	0.5	0.49	0.32	0.39	0.21	0.20	0.20	0.20	0.33	0.0001
	Mantel r	0.13	0.44	0.37	0.36	0.61	0.58	0.19	0.58	0.19	0.16
	P	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.004

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 at fine scales ($R^2 = 0.15$).

There was a significant relationship between tree species turnover and geographical distance at fine ($P < 0.001$) and intermediate ($P = 0.001$), but not at coarse, sampling scales ($P = 0.77$) (Table 3). 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 geographical distance ($P < 0.001$ and $P = 0.004$, respectively). 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 geographical distance consistently decreased as sampling scale increased (80–5%). Conversely, the contribution of PCA1 consistently increased with sampling scale (5–89%). For birds a similar pattern emerged. Geographical 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 the 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

Although 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 should therefore 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 influences beta diversity patterns and affects 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.

Our finding that beta diversity decreased with an increase in sampling grain is consistent with the results of others (e.g. Mac Nally *et al.*, 2004; Martiny *et al.*, 2011) and supports our first hypothesis. This apparent trend may simply be the result of a sampling effect, where the proportion of a community included in a sample increases 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 because of the well-known species–area relationship, where the number of species increases as a function of the focal

Table 3 Results of multiple regression modelling on distance matrices (MRM) by sampling scale for trees and birds in coastal forest fragments, South Africa. The response variables in our models were the dissimilarity matrices of species turnover (β_{sim}) for birds and trees. Explanatory variables were categorized as representing either niche- or dispersal-based assembly processes. For trees, the predictor variables were geographical distance, PCA1 and PCA2. PCA1 and PCA2 represented the two axes of a principal components analysis that included four environmental variables: median rainfall in winter, minimum relative humidity in winter, mean annual plant-available water and elevation. For birds, the predictor variables were geographical 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 shown. 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
<i>Dispersal-based assembly</i>												
Geographical distance (km)	–		0.15	< 0.01	–		0.11	0.01	–		0.01	0.77
<i>Niche-based assembly</i>												
PCA1	–		0.001	< 0.01	–		0.001	0.04	–		0.003	0.02
PCA2	–		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
<i>Dispersal-based assembly</i>												
Geographical distance (km)	–		0.08	< 0.01	–		0.08	< 0.01	–		0.12	0.07
<i>Niche-based assembly</i>												
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
<i>Adjacent matrix species</i>												
Matrix species	–		–0.03	0.55	–		0.09	0.41	–		–0.04	0.81

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 each 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 & Drake, 2001). At coarse scales, however, species turnover may be similar among taxa because they respond in the same way to historical factors, as has previously been suggested by Lawes *et al.* (2007) for coastal forest assemblages. Here, geographical 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 suggested 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 may represent 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 probably drive tree community composition within coastal forests because geographical distance explained most of the variation (80%) in the model, with the largest R^2 value (0.45) being for trees. Conversely, the bird community is probably 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 (0.50) being for birds.

Had we only investigated one spatial scale, we may have concluded the opposite. For both taxonomic groups, niche-based assembly processes had the strongest influence on community composition at coarse sampling scales, while dispersal-based assembly processes had the strongest influence at fine sampling scales. This finding has two important implications. First, it supports that much of the ambiguity of niche- versus dispersal-based assembly in structuring communities may be a matter of the spatial scale at which studies are conducted (Chase & Myers, 2011; Weiher *et al.*, 2011). Second, it emphasizes the importance of matching the grain of the data with the grain at which predictors and associated processes are 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

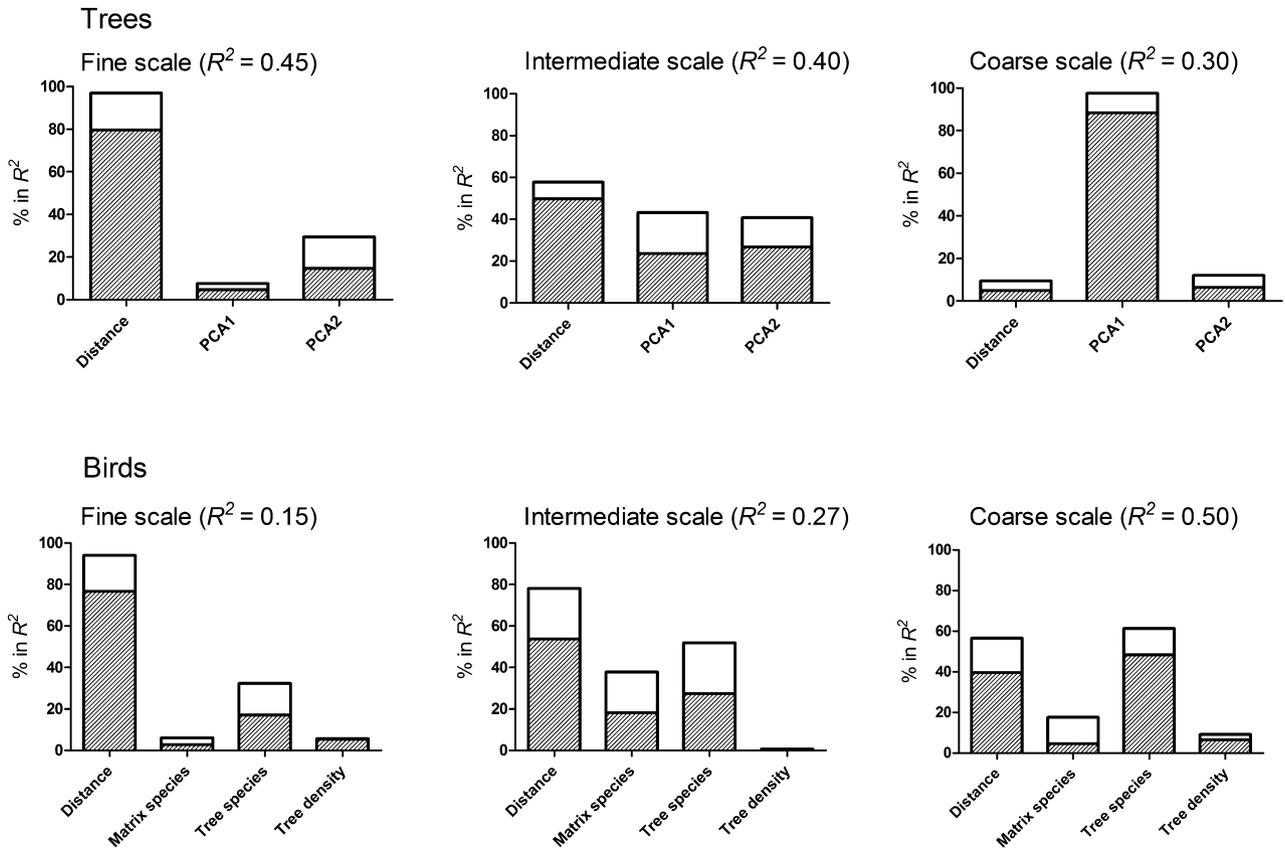


Figure 2 Summary of the results of six separate hierarchical partitions showing the relative contribution of each predictor variable in explaining the model variation at fine, intermediate and coarse sampling scales. The predictor variables were categorized as representing either niche- or dispersal-based assembly processes. The dispersal-based assembly is represented by geographical distance (Distance) for birds and trees at each sampling scale. For trees, the niche-based assembly is represented by principal component axis 1 (PCA1) and principal component axis 2 (PCA2). For birds, the niche-based assembly is represented by matrix habitat species composition (Matrix species), tree composition (Tree species) and tree density (Tree density). Shaded bars indicate independent effects, and white bars joint effects. The vertical axes correspond to the proportion of variance explained in each R^2 value. The sum of the independent effects equals 100% for each model.

that drive bird community assembly. For instance, based on the variables included in our models, we infer that dispersal limitation probably drives tree community assembly in coastal forests. Dispersal limitation allows for ecological drift, which 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 rather 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 the 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 because they respond to similar drivers that influence compositional changes across fragments. These drivers may include habitat fragmentation parameters (e.g. Polyakov *et al.*, 2013), historical factors

(Lawes *et al.*, 2007) and/or the temperate–tropical latitudinal gradient within 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 because of the influence of tree community variables on birds at coarse scales.

Before concluding, we need to consider the potential caveats associated with our approach. The variables included in our models only explained 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 landscape 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 compositional gradient studied may introduce errors in beta diversity estimates (Crist *et al.*, 2003; 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 the four environmental variables we included in our models explained 90% of the probability of coastal forest distribution (Olivier *et al.*, 2013), 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. If so, we may have overemphasized the role of dispersal-based assembly processes in shaping tree communities in these 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 the result of the co-occurrence of Afrotropical 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 be achieved best with multi-scale conservation initiatives, 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 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 could conceivably benefit from large-scale conservation initiatives. These could include stepping stones or corridors to enhance movement and functional connectivity, maintaining natural matrix habitats among forest fragments to facilitate dispersal, and restoration programmes to maintain or enhance the coastal forest corridor to enable north–south dispersal along the coastline.

CONCLUSIONS

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. Based on this study, sampling

only at fine scales could have failed to detect the importance of the fragmented tree community to the fragmented bird community. Conversely, had we only considered coarse sampling scales we could have overlooked the probable role played by dispersal limitation in shaping tree community composition. As a consequence, we could have proposed conservation initiatives that over-emphasized niche-based assembly processes (i.e. habitat based initiatives at a fine scale) to the detriment of dispersal-based assembly processes (i.e. landscape-based initiatives at a coarse scale) or vice versa. Our results therefore support the idea that conservation strategies 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, as part of initiatives directed at ecological conservation plans.

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