Functional diversity mediates contrasting direct and indirect effects of fragmentation on below- and above-ground carbon stocks of coastal dune forests

Victor Rolo[1,2*], Pieter I. Olivier[1], Marion Pfeifer[3] and Rudolph J. van Aarde[1]

[1]Conservation Ecology Research Unit, University of Pretoria, Hatfield, 0028, Pretoria, South Africa
[2]Present address: Forest Research Group, INDEHESA, University of Extremadura, Plasencia, 10600, Spain.
[3]School of Biology, Newcastle University, Newcastle NE17RU, UK

*Corresponding author: victorroloromero@gmail.com

Running head: Carbon storage in fragmented coastal dune forest

Abstract

Changes in structure and functioning of tree communities in response to forest fragmentation may alter tropical forest's capacity to store carbon and regulate climate. However, evidence for indirect effects of forest fragmentation on above - and belowground carbon pools through changes in forest biodiversity is scarce. Here we focus on understanding the relative importance of taxonomic and functional diversity and tree cover to explain above- and below-ground carbon stocks in coastal dune forest fragments. We surveyed tree species composition and structure in six coastal forest patches varying in size from 215 to 13350 ha, in Kwa-Zulu Natal, South Africa. For each fragment, we estimated carbon stocks of two pools, aboveground biomass (AGC) and soil organic carbon (SOC). We used structural equation models to test if and to what extent the effects of forest fragmentation on AGC and SOC were mediated by tree cover and taxonomic and functional diversity. Our results showed that forest fragmentation directly reduced AGC, but increased SOC. In contrast, forest fragmentation indirectly, through decreasing functional diversity, increased AGC, but decreased SOC. Small patches therefore had few tree species that were functional similar and had high AGC, but low SOC, which led to a negative relationship between species richness and AGC. Tree cover was not affected by fragmentation, and had a direct positive effect on AGC but not on SOC. Our results suggest that forest fragmentation simultaneously affect multiple processes which directly and indirectly affects carbon stocks of different pools. Fragmentation may trigger a process of biotic homogenization, in which a few species are positively related with carbon storage above-, but not below-ground.

Keywords: biodiversity homogenization; carbon sequestration; fragmented landscapes; functional traits; piecewise structural equation models

1. Introduction

Deforestation, forest fragmentation and degradation threaten biodiversity and affect ecological functions (Barlow et al., 2016; Haddad et al., 2015; Lewis et al., 2015). Following habitat loss and fragmentation, species richness generally decreases, while assemblages become less even and more structurally homogenous (Collins et al., 2017). Such changes in biological diversity often reduce ecological functions (Isbell et al., 2011; Liang et al., 2016). For example, the loss of biodiversity has a strong negative effect on above ground carbon storage, not only in simple temperate systems, but also in structurally diverse and complex tropical forests (Poorter et al., 2015). However, other components of the carbon cycle, such as soil carbon stocks, may increase following fragmentation (Barros and Fearnside, 2016). Higher rates of tree mortality, as well as changes in vegetation structure, composition, and function could boost decomposition of organic matter, thereby transferring carbon to the soil compartment and increasing soil carbon stocks (Laurance et al., 2011). Such increases in soil carbon following fragmentation could offset above-ground carbon losses - however if, and how this happens remains unclear.

The majority of studies investigating fragmentation impacts on forest carbon stocks have focussed on carbon stored aboveground in living trees. The soil organic carbon stock, which has been estimated to contribute between 36-60 % of total carbon stocks in the tropics (Dixon et al., 1994; FAO, 2010; Malhi et al., 1999), has remained understudied in comparison. In particular, linkages between soil carbon stocks and tree functional diversity remain an important knowledge gap, even though plant species diversity has been directly linked to soil carbon (Lange et al., 2015). Plant traits, such as whole plant structure or the partitioning of biomass among plant organs, control carbon inputs into soil through primary productivity and belowground carbon allocation, while other traits, such as growth rate, control carbon loss from soil through respiration and volatilization of organic compounds (De Deyn et al., 2008). This dependencies suggests that changes in the functional composition of tree communities after

fragmentation can simultaneously mediate above- and below-ground carbon stocks.

Tree communities along forest edges often resemble disturbed communities with low functional diversity (Laurance et al. 2011). In these systems, pioneer tree species and lianas benefit from the creation of more open canopies whilst mature trees, typical of closed forest canopies, suffer greater mortalities due to unfavourable micro-climatic conditions (Laurance et al. 2011). Such compositional changes in the tree community can boost soil carbon because of increased litter inputs and decomposition rates (e.g. Barros and Fearnside 2016; but see Laurance et al. 2011). Conversely, such changes can reduce the above-ground component of carbon storage (Magnago et al., 2017). Pioneers are typically soft-wooded species that share traits that maximize growth rates at the expense of survival. Along forest edges, these species may form homogenous communities with a reduced trait space (Rolo et al., 2016) and decreased above-ground carbon storage potential (Magnago et al. 2017). Moreover, because mature trees store the vast majority of carbon in tropical forests (Bastin et al., 2015), their disappearance along forest edges can reduce above-ground carbon storage. Forest fragmentation, through its impacts on functional composition, may thus lead to the decoupling of above- and below-ground carbon storage potential of tree species communities – however, this idea remains largely untested.

In this study, we investigate the effects of fragmentation on above- and below-ground carbon stocks in sub-tropical coastal forests in South Africa. This system, a centre of plant endemism (Wyk and Wyk, 2013), have suffered an extensive reduction in area during the last decades (Olivier et al., 2013). We were particularly interested in the relative importance of functional composition, forest structure and environmental attributes as drivers of carbon stocks in forest fragments. This assessment often requires the inference of the relative importance of direct and indirect effects that link the multiple processes underlying carbon storage. The relative importance of different mechanisms underlying ecosystem processes can

be inferred using piecewise structural equation models (SEM; Lefcheck, 2016). We used SEMs to answer three questions: 1) How does fragmentation affect forest structure, taxonomic and functional diversity? 2) How does changes in structure, taxonomic and functional diversity affect above- and below-ground carbon stocks? and 3) What is the role of functional diversity in above- and below-ground carbon storage? We expect that fragmentation will decrease taxonomic and functional diversity and that this decrease will reduce the ability of coastal forests to store carbon above- but not below-ground.

2. Material and Methods

2.1. Study area

Coastal dune forests in South Africa covers approximately 160 km^2 and represent the southernmost tip of the East African Tropical Coastal Forest ecoregion, which extends northward to the southern Somalian coast (Burgess and Clarke, 2000). Dune forests here form part of the Indian Ocean Coastal Belt Forests, which also include other forests such as coastal lowland, riparian sand and swamp forests. Although these different forest types share a number of species, they also differ from dune forests and each other in species composition, recruitment and regeneration patterns and evolutionary history (van Aarde et al., 2014). Dune forests established on porous and leached sand deposits left by a regressing Indian Ocean during the end of the last glacial period 8000 to 10000 years ago and are disturbance prone, both through natural and human causes (Eeley et al., 1999; Nzunda et al., 2007). In South Africa, coastal dune forests form part of a biodiversity hotspot (Küper et al., 2004) as well as two critically endangered eco-regions (Burgess et al., 2004), and harbour several species of conservation concern (van Aarde et al., 2014). These include plants (e.g. *Ceropegia arenaria*, *Pristimera delagoensis*, *Warburgia salutaris*), mammals (e.g. Samango monkey *Cercopethicus mitis erythrarchus* and forest shrew *Myosorex sclateri*), birds (e.g. spotted ground thrush (*Zoothera*

4

guttata) and amphibians (e.g. Pickersgill's reed frog (*Hyperolius pickersgilli*)). They may also harbour an extinction debt incurred from recent forest losses (Olivier et al., 2013).

We surveyed six coastal dune forest fragments (size range 215 – 13349 ha) along 300 km of coastline that stretched from Lake Kosi in the north (27°01´S, 32°51´E), to the mouth of the Tugela river in the south (29°14´S, 31°28´E). A mix of human (e.g. sugarcane, Eucalyptus and Pine plantations, rural settlements) and natural (grasslands and woodlands) land uses adjoin these forests in the west, while the Indian Ocean adjoins the forests in the east (Fig. 1). The climate of the area is subtropical with average annual rainfall ~ 1200 mm (Richards Bay weather station). The soils belongs to the Namib Soil Formation and are composed of regic sand with a thick layer of litter on an orthic A horizon (Rooyen et al., 2013).
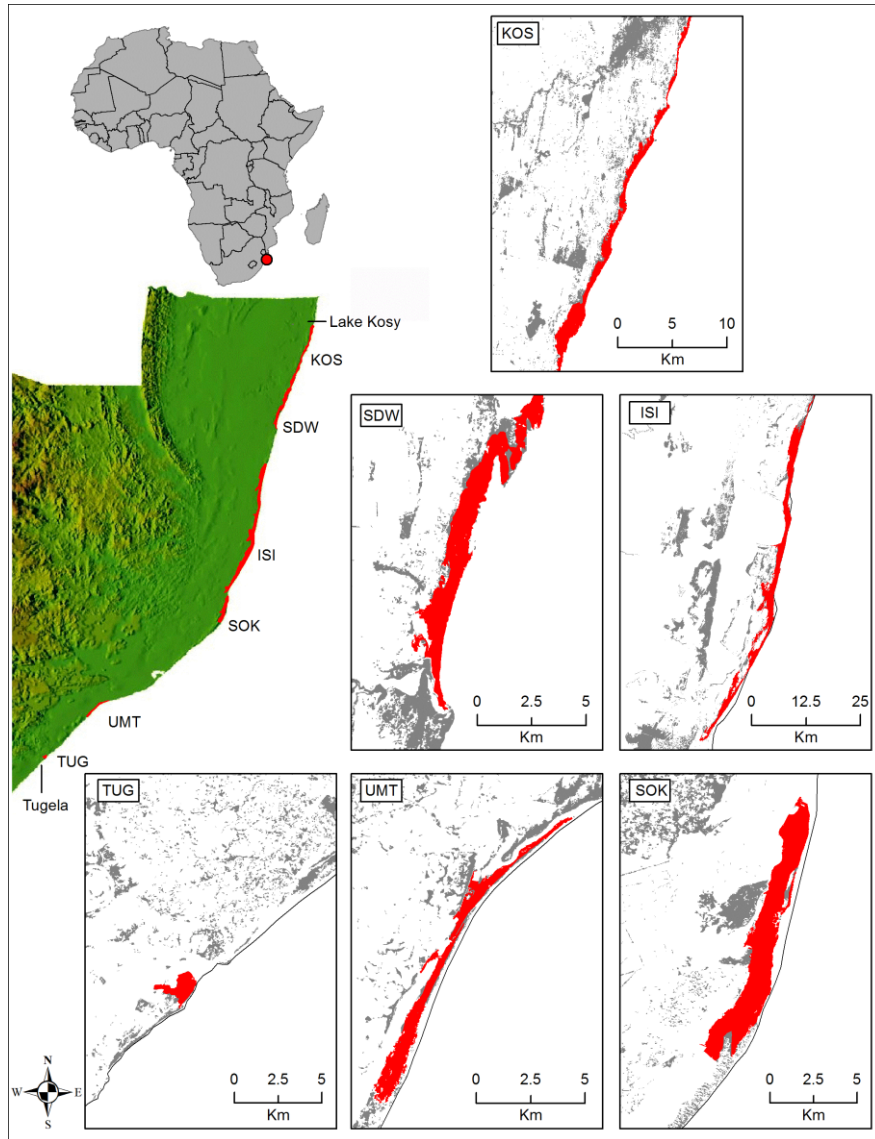
Figure 1. Coastal dune forest fragments delineations. Red colours depict forest fragments included in this study from Lake Kosi in the north, to the mouth of the Tugela river in the south. Insets depict studied fragments (red) and surrounding forest fragments (grey) in detail. Names of fragments follow the notation of Table 1.

2.2. Data collection

To quantify tree species composition, we surveyed trees in 49 plots of 16 m x 16 m distributed randomly across the six forest fragments between August and October of 2012. Plots were distributed based on the fractal sampling design of (Marsh and Ewers, 2013). Each fractal comprised three plots, of which the first plot were located at the forest edge, the second plot in the forest interior and the last plot located at the 'ocean-forest edge'. Plots were at least

6

560m apart. This design allowed us to sample across the gradient of different conditions typically found in coastal dune forests. The number of plots per fragment ranged from four in the smallest- to 12 in the largest fragment (TUG = 4; UMT = 6, SOK = 9; ISI = 12; SDW = 6; KOS = 12). We recorded and identified all woody individuals taller than 30 cm in each plot and measured the diameter at breast height (DBH) of all individuals higher than 1.7 m. For individuals with DBH higher than one cm we recorded if they had more than one stem originating at the base (multi-stemming) and its maximum height, recorded as a categorical factor in steps of two meters. Height values were always estimated by the same surveyor. Estimations were validated by measuring actual tree height with a clinometer (Suunto Height Meter PM-5/1520) in a selection of individuals across size classes (CERU unpublished results).

In June 2015, we revisited each plot to quantify forest canopy structure. We acquired 12 to 13 hemispherical photographs per plot using a standardised sampling design (Pfeifer et al., 2012). Images were taken with a Canon 6D camera (Canon Inc. Tokyo, Japan) mounted on a 1m tripod (Benro, KB1, USA) and fitted with a Canon 8-14mm lens (Canon Inc. Tokyo, Japan). We pre-processed hemispherical images (blue band extraction and thresholding to create binary images showing vegetation and non-vegetation) using an in-house developed Matlab-based algorithm and subsequently derived canopy structure attributes, including tree cover, using the freeware canopy image analysis software CAN-EYE v 6.3.8 (Weiss & Baret, 2010). We also took four soil cores per plot, one in each quarter of the plot. Soil cores were aggregated for each plot prior to analyses. The depth of soil cores was ~30 cm deep, the minimum soil depth proposed by (Penman et al., 2003) to report soil organic carbon in mineral forest soil. We took additional soil samples of known volume to calculate soil bulk density.

2.3. Aboveground and soil carbon stocks

Above-ground biomass (AGB) was derived for each tree with DBH > 5 cm using an improved pan-tropical allometric equation (Chave et al., 2014).We used the allometric equation that included DBH, wood density and height.

$$AGB \text{ (kg)} = 0.0673 \cdot (\rho \cdot D^2 \cdot H)^{0.976}$$

Where ρ is wood density (g cm^{-3}), D is DBH (cm) and H is height (m). We used height values estimated in the field. Wood density values were collated from the literature (see below). We applied a factor of 0.47 (Martin and Thomas, 2011) to convert tree biomass into aboveground carbon (AGC). We summed across trees to obtain aboveground carbon stocks (Mg C ha^{-1}) per plot.

We oven-dried soil samples at 65 °C for 48 h and separated large roots (> 2 mm) manually. Then we sieved samples through a 2-mm mesh, and, ground on a mortar if necessary, to pass through a 250-μm mesh. We determined the organic carbon content by means of the Walkley-Black wet chemical oxidation method (Nelson and Sommers, 1982) and computed soil organic carbon stock using the following equation:

$$SOC \text{ (Mg C ha}^{-1}) = \text{soil depth (cm)} \cdot \text{bulk density (g/cm3)} \cdot \text{carbon content (decimal)} \cdot 100$$

2.4. Landscape metrics

To characterize the landscape context of each sampling point, we calculated a series of landscape metrics that have been commonly used as surrogates of landscape fragmentation (Schindler et al., 2013). We measured the total amount of forest area, the total amount of edge and the edge density in a buffer of 1 km surrounding each sampling point. The scale at which landscape metrics are computed can influence inferences that do not necessarily reflect the "true scale of effect" (sensu Jackson and Fahrig, 2015). However, previous studies in the region have shown that landscape properties in a buffer of 1 km are a good predictor of tree species

richness (Olivier and van Aarde, 2017).

2.5. Topographic Wetness Index

The Topographic Wetness Index (TWI) has been shown to be a good predictor of tree species occurrence (e.g. Quercus spp. Petroselli et al., 2013) and could be especially important in dune forests given the variable topography underlying the distribution of these forests and the limited differences in climate across the study landscape (Mucina et al., 2006). We computed TWI based on a digital elevation model at 30 m resolution from ASTER GDEM. This index quantifies the capacity of an area to accumulate water. Low values are typical of steep areas and indicate low water accumulation capacity, whereas high values are typically from flat areas that are prone to accumulate water. TWI was calculated for each pixel as:

$$TWI = \ln(As/\beta)$$

where As is the drainage area (m^2) and β is the slope in radians (Beven and Kirkby, 1979).

2.6. Functional traits of tree species

We compiled data on four functional traits (specific leaf area, wood density, maximum plant height and resprouting ability) shown to be related to aboveground biomass and nutrient cycling (Finegan et al., 2015; Lavorel et al., 2007). These functional traits belongs to different components of the economic spectrum of plants and life history strategies (Díaz et al., 2016). Specific leave area (SLA, cm^2/ g) is associated with the leaf economic spectrum and relates to the plant's ability to acquire and use nutrients (Wright et al., 2004). It ranges from "exploitative" plants with fast nutrient acquisition and turnover (high SLA), to "conservative" plants with thicker leaves and slower growth (Wright et al., 2004). Wood density (WD) is part of the stem economic spectrum and co-varies with other hydraulic traits. High values of wood density indicate low growth rates, high stress tolerance to shade, wind, drought and herbivores (Chave

9

et al., 2009; Wright et al., 2010). Maximum plant height (H_{max}) belongs to one major dimension of the global economic spectrum of plants, tree size, (Díaz et al., 2016; Gleason et al., 2017) and is related to resource availability, especially light, and competitive environments, with high values indicating competitive advantages through prior access to light (Westoby et al., 2002). Resprouting ability (RA) is related to the capacity of an individual to resprout after a disturbance. Resprouting species are frequent in coastal dune forest because of chronic low-severity disturbances (Nzunda et al., 2007) which could be worsened by the presence of edges. Resprouting species have different patterns of biomass allocation among organs (Nzunda et al., 2008) which can potentially affect primary productivity and carbon stocks (Lavorel and Garnier, 2002). These traits have been related to net primary productivity, standing biomass, and carbon stocks (Lavorel et al., 2007; Lavorel and Garnier, 2002). RA was computed as the frequency of multi-stemmed individuals of a given species (Nzunda et al., 2007). H_{max} values were collected from (Germishuizen et al., 2003). SLA, WD trait data (83 %) were gathered from Rolo et al. (2016), who also sampled coastal dune forest, including one fragment surveyed in this study. WD values not included in Rolo *et al.* (2016) (6%) were extracted from a global wood density database (Zanne et al., 2009). When a given species was not present in Zanne *et al.* (2009), we took the mean of the genus. Aggregated trait values from regional databases could be poor indicators of functional diversity at finer spatial scales (i.e. community level). We assume that this effect was not a major drawback in our analysis as we mostly focused on the linkages between functional diversity and ecosystem functions (Cordlandwehr et al., 2013). The rest of the missing values of SLA (9%) and WD (3%) were estimated by means of dissimilarity imputation (Taugourdeau et al., 2014). This method uses the functional proximity between species to calculate new data and has been shown to be a robust option for computing functional diversity indices in data sets that have a maximum of 30% missing values (Taugourdeau et al. 2014).

2.7. Community weighted mean trait value and functional dispersion

For each trait, we calculated community-level weighted mean values (CWM) to describe the dominant trait value per plot. This metric was calculated as:

$$CWM = \sum_{i=1}^{n} p_i \, trait_i$$

where p_i and $trait_i$ are the relative abundance and the trait value for species i, respectively, and n is the total number of species. This index estimates the most probable attribute that a species drawn at random from a community would display (Swenson, 2014). Additionally, to describe the distribution of the trait space at the plot level, we computed functional dispersion values (FD; Laliberté and Legendre, 2010). This metric is the mean distance in multi-dimensional space of individual species to the centroid of all species present and describes if a community shows convergent or divergent trait values. We computed both functional diversity indices weighing abundance by the number of individuals. All functional trait values were centered and scaled (z-score).

2.8. Rarefied species richness and functional diversity

To compare the number of species among patches that differed in sampling effort due to their different areas, we computed rarefied species richness based on Hill numbers (Chao et al., 2014). Similarly, to control for the variation of individuals and species richness among patches, we rarefied functional dispersion following Whitfeld et al. (2014). We created rarefied assemblages with 5, 20, 35, 50, 65, 80, 100, 140, 180, 225 individuals, and generated 50 random assemblages using rarefaction in the 'vegan' package in R (Oksanen et al., 2016). For each iteration, we permuted the randomly generated assemblage another 50 times, keeping species richness constant. This generated a null model from which we calculated a standardized effect

size using the following equation:

$$SES = \frac{(Observed-Null)}{SD\ (Null)}$$

Where Observed is the functional dispersion value of each rarefied assemblage and Null is the functional dispersion value of the null distribution of the rarefied assemblage. We then calculated the average SES values of the 50 rarefied assemblages per level of rarefaction and computed 95 % confidence intervals by bootstrapping (Smith and van Belle, 1984). By calculating SES values, we can directly compare if the functional dispersion of a given community is different than expected by chance (Swenson 2014). Thus, an SES value that is significantly lower than zero indicates a lower than average expected value in a random community (trait value convergence, i.e. environmental filtering), or vice versa. We considered that SES values are significant when their 95 % CIs did not include zero.

2.9. Structural Equation Models (SEMs)

We used SEMs to test for the direct and indirect effects of landscape metrics, TWI, taxonomic and functional diversity, and forest structure on AGC and SOC (Fig. 2). We repeated this procedure in a series of SEMs that were structurally the same but included different functional diversity indices (SES FD or CWM of SLA, WD, H_{max} and RA). We constructed separate models for AGC and SOC. Our conceptual model is based on previous studies that have reported direct and indirect effects of biodiversity, landscape and abiotic metrics on forest carbon pools (Andivia et al., 2016; Magnago et al., 2017; Poorter et al., 2015). We used piecewiseSEM to test the validity of our conceptual model (Lefcheck, 2016). PiecewiseSEM allows fitting (generalized) linear mixed models and can account for hierarchy in the data by incorporating random effects to test a single conceptual model. The overall fit of the models was assessed using Shipley's test of d-separation which is accepted when χ^2-test of Fisher's C statistic is higher than a significance level ($p < 0.05$). Accepted models were then compared

using the second-order Akaike's information criterion (AICc) for small sample size. We fitted the component models of the piecewiseSEM as linear models including patch as a random effect. To reduce the dimensionality of the landscape metrics and avoid collinearity, we run a principal component analysis and kept the first component as a surrogate of landscape metrics (Fig. A1). The first component explained 57 % of the variance and was positively related to edge density (r = 0.46) and negatively related to total amount of forest area and total amount of edges (r = -0.75 and r = -0.46, respectively). We report the standardize path coefficient of each significant link to allow comparisons across variables of varying units. Standardize path coefficients can be interpreted as the expected change in the response variable (e.g. AGC) as a function of the change in the predictor (e.g. fragmentation), in standard deviation units (Grace, 2006). We also report the conditional R^2 values of response variables (i.e. variance explained by fixed and random effects). All statistical analysis were performed using R version 3.2.5 (R Core Team, 2016).
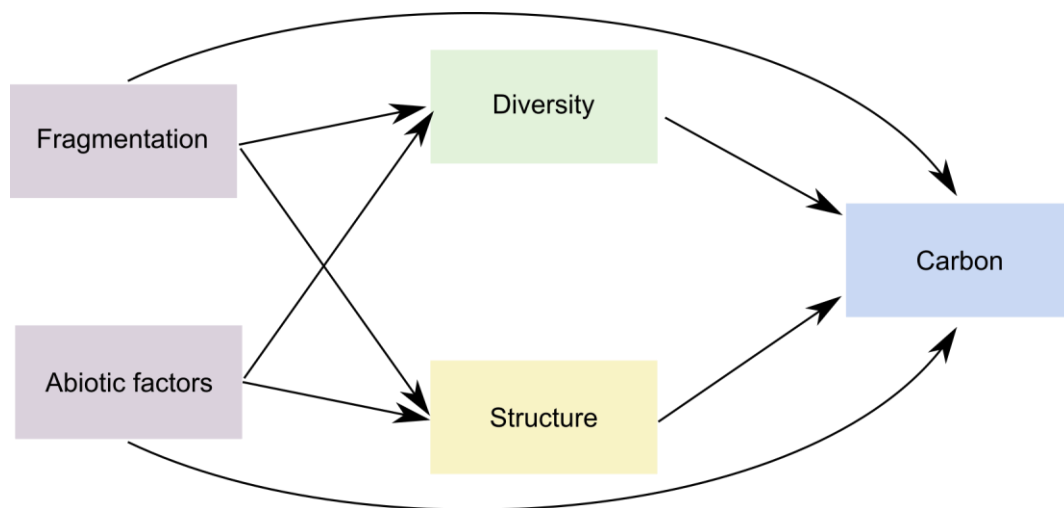

Figure 2. Conceptual model depicting how fragmentation and environmental attributes relates to taxonomic and functional diversity and forest structure, and how all of them relates to carbon stocks. To test the conceptual model, we used the total amount of forest area, the total amount of edge and the edge density as surrogates of forest fragmentation (landscape), topographic wetness index (abiotic factors), species richness and functional dispersion or community weighted means (diversity), tree cover (forest structure) and above- and below-

ground carbon stocks (carbon). See methods for details.

3. Results

3.1. Biodiversity and landscape metrics

Landscape metrics differed among the six forest fragments (Table 1). The two southern fragments (TUG and UMT) were small, had high edge:area ratios, high edge density, and were surrounded by a number of small fragments, which added up to low total amounts of forest cover in the landscape. Three other fragments were medium sized, with intermediate values of edge:area ratios and edge densities. Forest cover around these three fragments was ~ 20 %. The sixth and largest forest fragment, located within the iSimangaliso Wetland Park (i.e. ISI), was surrounded by ~ 20% forest cover, and was nearly three times the size of the second largest fragment, and had the lowest edge: area ratio and edge density.

Table 1. Patch size and edge area ratio of each forest fragment. The rest of landscape metrics were computed in a buffer of 10 km around each forest fragment.

Patch name	Patch Size (ha)	Edge:Area (m/ha)	Forest %	Number Patches/ha	Mean Patch size (ha ± SE)	Edge density (m/ha)
ISI	13349	13.90	0.18	2.50	7.35 ± 5.5	18.31
KOT	4530	22.42	0.21	7.37	2.82 ± 2.1	35.10
SOK	2614	14.48	0.20	7.44	2.68 ± 1.5	30.79
SDW	1705	23.32	0.19	5.45	3.54 ± 2.3	25.90
UMT	769	42.16	0.13	7.91	1.62 ± 0.6	31.96
TUG	215	33.92	0.09	9.54	0.96 ± 0.4	32.79

Fragment-level species richness varied with landscape metrics (Fig. 3). When controlling for the number of individuals, forest fragments clustered in two distinctive groups, with the lowest values of species richness in the two small southern fragments, and the highest values in the largest. The remaining forest fragment had intermediate species richness values (Fig. 3). The smallest forest fragment had a significantly lower functional dispersion values than expected by chance (Fig. 3). Despite the differences in number of species, functional

dispersion values of the large fragments was lower than expected by chance or did not differ from a random community, suggesting that standardized effect size values of functional dispersion and species richness patterns were decoupled across forest fragments. For example, the second largest forest fragment (SDW) featured low standardized effect size values of functional dispersion (similar to the second smallest fragment UMT) but high species richness (similar to the smallest fragment ISI). Only the third largest forest fragment (SOK) had a functional dispersion values wider than expected by chance (Fig. 3).
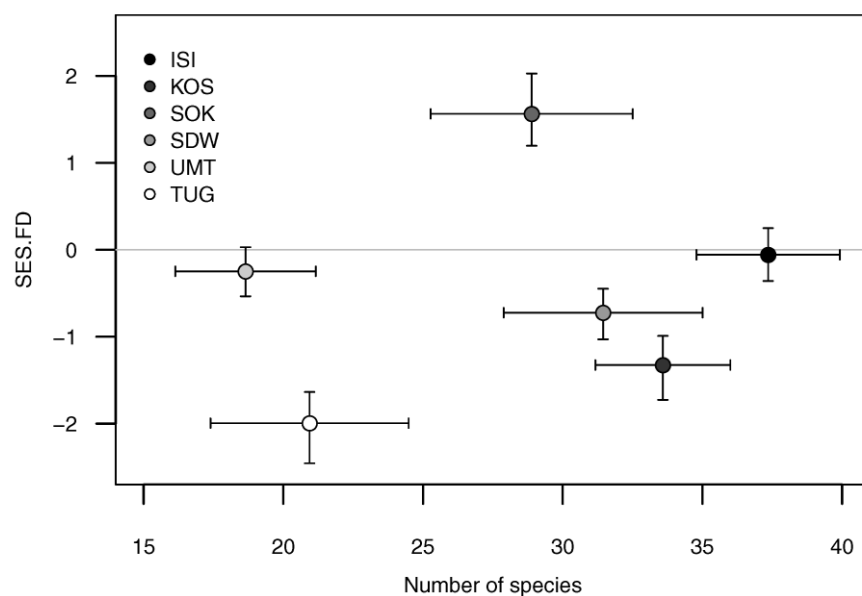

Figure 3. Rarefied species richness and functional diversity ± 95 % confidence intervals among remnant forest fragments across a gradient of fragmentation, from small (TUG) to large (ISI) fragments. See Table 1 for differences in landscape metrics among forest fragments. Functional diversity represents the standardize effect size of functional dispersion (SES FD) as compared to a random community. Values are compared among fragment at a similar number of individuals.

3.2. Determinants of forest carbon stocks

SEMs explained 81 % of the variation in AGC ($C_{12} = 14.3$, $p = 0.284$) and 39 % of the variation in SOC ($C_8 = 31.3$, $p = 0.913$) (Fig. 4). The lack of significance indicates that the models fit the data well, particularly for SOC. Tree cover directly increased AGC (0.35 SD, p

< 0.001), but had no significant effect on SOC. Topography (TWI) was negatively related to tree cover (-0.33 SD, p = 0.008; R^2=0.28), and SOC (-0.31 SD, p = 0.021), and indirectly affected AGC (-0.13 SD).

Edges had a direct negative effect on AGC (-0.17, p < 0.001), but a direct positive effect on SOC (0.31, p = 0.048). Edges also had contrasting indirect effects on AGC and SOC mediated by standardized effect size values of functional dispersion. Edges had a positive indirect effect on AGC (0.11 SD), but a negative indirect effect on SOC (0.08 SD). When summing the direct and indirect effects, the total effect of edge on AGC was negative, i.e. edges decreased AGC, while the total effect of edge on SOC was positive, i.e. edges increased SOC.
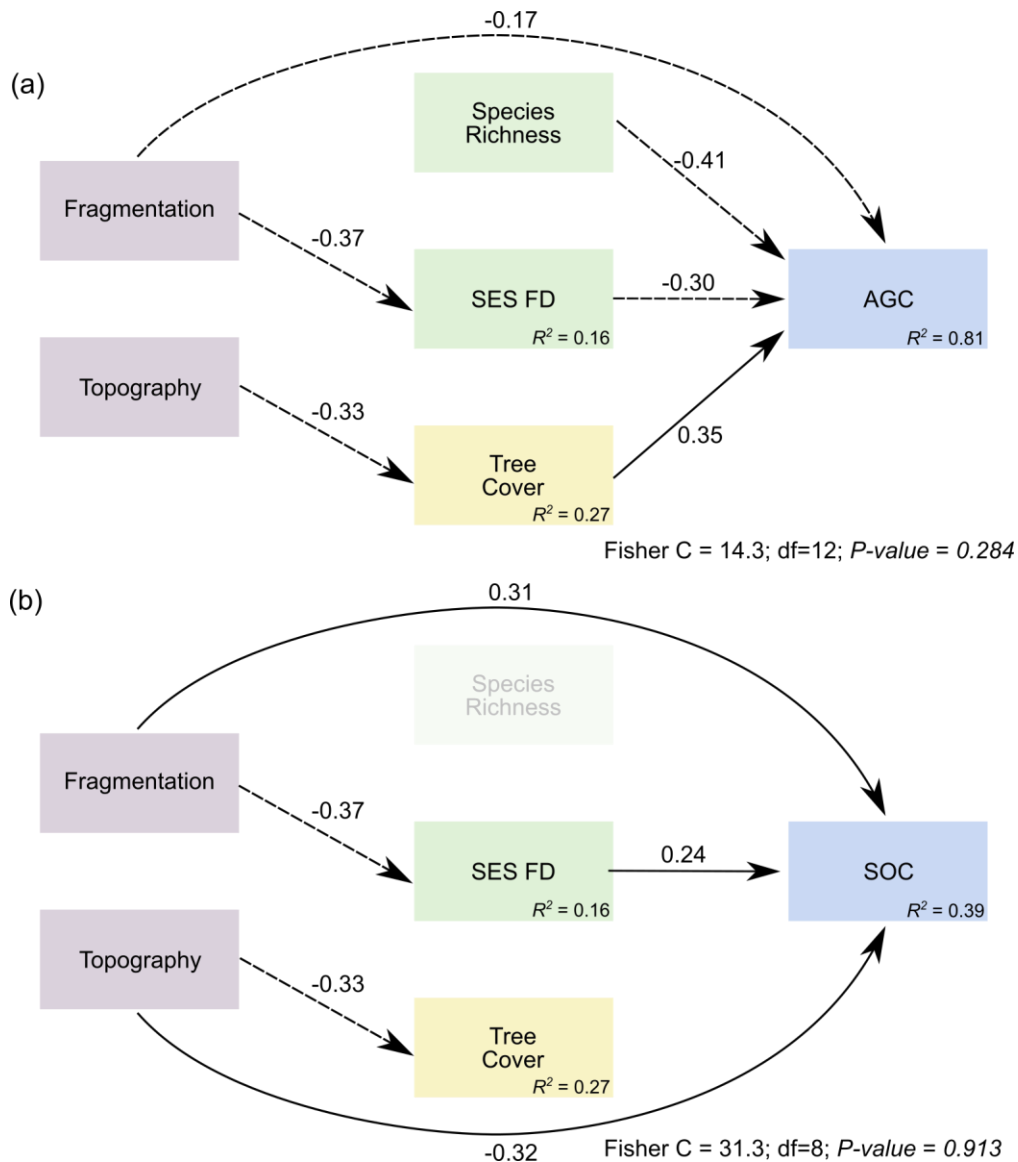
Figure 4. Final parsimonious SEM depicting direct and indirect links, through biodiversity and forest structure, between forest fragmentation and local environment and a) above-ground (AGC) and b) soil (SOC) carbon stocks. Only significant paths are depicted. Broken paths depict negative and solid positive links among variables. Topography depicts terrain wetness index and fragmentation depict the first component of a principal component analysis of landscape metrics as a surrogate of forest fragmentation.

Edges also had a direct negative effect on standardized effect size values of functional dispersion (-0.37, p = 0.011, R^2 = 0.17) – i.e. edges led to the narrowing of the functional trait space. However, functional dispersion had contrasting effects on carbon storage by negatively affecting AGC, while positively affecting SOC. A wide trait space was related to lower AGC,

but higher SOC and vice versa. This finding was confirmed by the direct negative effect of species richness on AGC (-0.41, p < 0.001) – where species richness was high, AGC was low. Species richness had, however, no effect on SOC.

Explorations of the effect of edges on community-level weighted mean values differed from the effect on functional dispersion, only community-level weighted mean values of specific leaf area showed a similar response (Fig 5). Particularly, edges reduced community-level weighted mean values of specific leaf area, but they increased community-level weighted mean values of resprouting ability. For the rest of the metrics, edges did not affect community-level weighted mean values of wood density and maximum height.
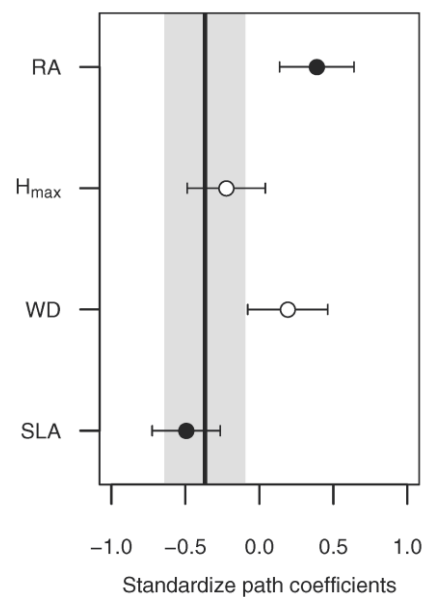

Figure 5. Standardize regression coefficients derived from SEMs ± 95 % confidence intervals (1.96SE) of the effect of fragmentation on CWM of specific leaf area (SLA), wood density (WD), maximum height (H_{max}) and resprouting ability (RA). Filled points depict a significant effect of fragmentation ($p < 0.05$). The vertical line represents the coefficient of standardize effect size of functional dispersion (SES FD) as included in the final SEMs and ± 95 % confidence intervals (shaded rectangle).

4. Discussion

We show that the effect of fragmentation on tropical forests' capacity to store carbon

is dependent on the carbon pool considered and partly mediated by functional diversity. Forest fragmentation directly reduced AGC but increased SOC. Conversely, indirect effects of fragmentation on carbon storage showed that tree communities exposed to strong edge effects had a reduced trait space with high levels of AGC but low levels of SOC. These contrasting findings suggest that forest fragmentation simultaneously affects multiple properties of forests (e.g. structure, function and composition), and consequently ecosystem function. It also highlights the difficulty of simultaneously assessing the consequences of diversity loss on different carbon pools.

An increase in tree mortality and the subsequent proliferation of pioneer species in edge-affected vegetation may explain observed differences between direct and indirect effects of fragmentation on carbon stocks. The mortality of large trees is greater near forest edges than in forest interiors (Laurance et al., 2000), which should disproportionally reduce AGC stores at edges. This would explain the direct negative relationship between edge effects and AGC. However, at the same time, pioneers may benefit from the altered abiotic conditions and the demise of large trees that open gaps in the canopy in edge-affected vegetation (Magnago et al., 2017). A likely increase in pioneers is further corroborated by the changes in community-level weighted mean values in edge affected communities. The reduction in community-level weighted mean values of specific leaf area and the increased in resprouting ability indicates that species with high growth rates and resistant to disturbance are common in edge affected tree communities (Nzunda et al., 2007; Poorter and Bongers, 2006). In this communities a positive relationship between a reduced trait space and above-ground carbon would be likely. In other words, the filtering effect induced by edges will promote the establishment of communities with few species where above-ground carbon is determined by fast growing strategies. However, at the patch level, the low carbon residence times of fast growing species can negatively affect whole-forest carbon storage in the biomass (Galbraith *et al.,* 2013;

Schnitzer *et al.,* 2014). These findings supports the idea of a 'retrogressive effect' of fragmentation (Ewers et al., 2017), where structurally and biologically complex forests are reduced to a homogeneous and simplified state, as in early successional stages (Pütz et al., 2011). Such a scenario would resemble a situation where the relationship between species richness and productivity is likely to be negative (Mouquet et al., 2002).

Our findings suggest that fragmentation promotes the transfer of carbon from the above- to the below-ground compartment. The increase of soil organic carbon in small, edge affected patches could be explained by the high litter inputs and decomposition rates at forest edges (Barros & Fearnside 2016). Decomposition rates can also be accelerated due to the presence of pioneers with soft wood, thinner stems, and fast demographic rates, transferring carbon rapidly from the necromass to the soil compartment (Nascimento and Laurance, 2004). Given that the stability of carbon stocks after a disturbance is higher in the mineral soil than in the biomass (Kauffman et al., 2009), the transfer of carbon from the above- to the below-ground compartment might be seen as a positive effect of landscape fragmentation. However, only a small fraction of the dead biomass is ultimately transferred to the mineral soil (Rice et al., 2004). Moreover, the accumulation of dead biomass increases respiration rates, which result in net carbon losses (Rice *et al.* 2004). Indeed, (Brinck et al., 2017) estimate that forest edges could be responsible for an additional 10.3 Gt of carbon emissions per year.

Similar to the indirect effect of fragmentation on above-ground carbon, the indirect effect of fragmentation on soil organic carbon had an opposite direction than its direct effect. This suggests that edge-affected communities with a reduced trait space had more carbon stored in the above-ground biomass than in the soil. A reduction in soil organic carbon may be caused by a decrease in litter inputs or decomposition rates or an increased respiration. Yet, the multiple contrasting effects of fragmentation we recorded on the different carbon pools suggests that local communities could exhibit a continuum of responses to fragmentation and

specifically forest edges. The direct effect of fragmentation could be regarded as a first response where mortality is the main driver of changes in species composition and ecosystem functions. The indirect effects will become apparent when pioneers replaced forest specialists and are now the dominant group in the community. Change in abiotic conditions can be the underlying driver of both processes that could be operating simultaneously. Indeed, the lower support for models including community-level weighted mean values indicates that the most abundant species still does not dominate ecosystem functions. Carbon stocks may rather be influenced by the combined effect of environmental filtering and the presence of relict individuals resistant to changes in the biophysical environment.

The minor effects of environmental and structural variables on carbon stocks indicate that, in coastal forests, changes in species composition following fragmentation is the main driver of changes in ecosystem functions. In agreement with previous studies, we observed that tree cover was an important predictor of above-ground carbon (Bohn and Huth, 2017; Poorter et al., 2015). However, its relative effect was similar to that of species richness and functional diversity. Moreover, it was not related to soil organic carbon that was directly affected by topography. These results suggest that the effect of structure was controlled to a higher extent by the physical configuration of the local environment than by the presence of edges.

Environmental policies that aim to promote carbon storage while preserving biodiversity, such as the REDD+, are based on results drawn from non-degraded forests where positive relationship between biodiversity and carbon storage are common (e.g. Liang et al., 2016; Poorter et al., 2015). However, our study shows that, for coastal dune forest, landscape fragmentation may have led to the opposite pattern, where few species increase carbon storage and promoted a trade-off between different compartments of the carbon cycle. This likely happened because fragmentation triggered the biotic homogenization of coastal forest tree communities. Niche complementarity has been suggested as a key property underpinning

positive biodiversity-ecosystem function relationships (Isbell et al., 2011). However, if fragmentation leads to the dissapearance of large trees, coupled with the development of even cohorts of functionally similar pioneers, then negative biodiversity-ecosystem function relationships are likely to emerge. Given that human pressure is increasing on forests worldwide, this may have important consequences for management efforts based on win-win situations between biodiversity conservation and carbon storage.

Acknowledgements

References

Andivia, E., Rolo, V., Jonard, M., Formánek, P., Ponette, Q., 2016. Tree species identity mediates mechanisms of top soil carbon sequestration in a Norway spruce and European beech mixed forest. Ann. For. Sci. 73, 437–447. doi:10.1007/s13595-015-0536-z

Barlow, J., Lennox, G.D., Ferreira, J., Berenguer, E., Lees, A.C., Nally, R.M., Thomson, J.R., Ferraz, S.F. de B., Louzada, J., Oliveira, V.H.F., Parry, L., Ribeiro de Castro Solar, R., Vieira, I.C.G., Aragão, L.E.O.C., Begotti, R.A., Braga, R.F., Cardoso, T.M., Jr, R.C. de O., Souza Jr, C.M., Moura, N.G., Nunes, S.S., Siqueira, J.V., Pardini, R., Silveira, J.M., Vaz-de-Mello, F.Z., Veiga, R.C.S., Venturieri, A., Gardner, T.A., 2016. Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. Nature 535, 144–147. doi:10.1038/nature18326

Barros, H.S., Fearnside, P.M., 2016. Soil carbon stock changes due to edge effects in central Amazon forest fragments. For. Ecol. Manag. 379, 30–36. doi:10.1016/j.foreco.2016.08.002

Bastin, J.-F., Barbier, N., Réjou-Méchain, M., Fayolle, A., Gourlet-Fleury, S., Maniatis, D., de Haulleville, T., Baya, F., Beeckman, H., Beina, D., Couteron, P., Chuyong, G., Dauby, G., Doucet, J.-L., Droissart, V., Dufrêne, M., Ewango, C., Gillet, J.F., Gonmadje, C.H., Hart, T., Kavali, T., Kenfack, D., Libalah, M., Malhi, Y., Makana, J.-R., Pélissier, R., Ploton, P., Serckx, A., Sonké, B., Stevart, T., Thomas, D.W., De

Cannière, C., Bogaert, J., 2015. Seeing Central African forests through their largest trees. Sci. Rep. 5, 13156. doi:10.1038/srep13156

Beven, K.J., Kirkby, M.J., 1979. A physically based, variable contributing area model of basin hydrology. Hydrol. Sci. Bull. 24, 43–69. doi:10.1080/02626667909491834

Bohn, F.J., Huth, A., 2017. The importance of forest structure to biodiversity–productivity relationships. R. Soc. Open Sci. 4, 160521. doi:10.1098/rsos.160521

Brinck, K., Fischer, R., Groeneveld, J., Lehmann, S., Paula, M.D.D., Pütz, S., Sexton, J.O., Song, D., Huth, A., 2017. High resolution analysis of tropical forest fragmentation and its impact on the global carbon cycle. Nat. Commun. 8, 14855. doi:10.1038/ncomms14855

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

Burgess, N.D., Clarke, G.P., 2000. Coastal Forests of Eastern Africa. IUCN The World Conservation Union, Cambridge, UK.

Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K., Ellison, A.M., 2014. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecol. Monogr. 84, 45–67. doi:10.1890/13-0133.1

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G., Zanne, A.E., 2009. Towards a worldwide wood economics spectrum. Ecol. Lett. 12, 351–366. doi:10.1111/j.1461-0248.2009.01285.x

Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M.S., Delitti, W.B.C., Duque, A., Eid, T., Fearnside, P.M., Goodman, R.C., Henry, M., Martínez-Yrízar, A., Mugasha, W.A., Muller-Landau, H.C., Mencuccini, M., Nelson, B.W., Ngomanda, A., Nogueira, E.M., Ortiz-Malavassi, E., Pélissier, R., Ploton, P., Ryan, C.M., Saldarriaga, J.G., Vieilledent, G., 2014. Improved allometric models to estimate the aboveground biomass of tropical trees. Glob. Change Biol. 20, 3177–3190. doi:10.1111/gcb.12629

Collins, C.D., Banks-Leite, C., Brudvig, L.A., Foster, B.L., Cook, W.M., Damschen, E.I., Andrade, A., Austin, M., Camargo, J.L., Driscoll, D.A., Holt, R.D., Laurance, W.F., Nicholls, A.O., Orrock, J.L., 2017. Fragmentation affects plant community composition over time. Ecography 40, 119–130. doi:10.1111/ecog.02607

Cordlandwehr, V., Meredith, R.L., Ozinga, W.A., Bekker, R.M., van Groenendael, J.M., Bakker, J.P., 2013. Do plant traits retrieved from a database accurately predict on-site measurements? J. Ecol. 101, 662–670. doi:10.1111/1365-2745.12091

De Deyn, G.B., Cornelissen, J.H.C., Bardgett, R.D., 2008. Plant functional traits and soil carbon sequestration in contrasting biomes. Ecol. Lett. 11, 516–531. doi:10.1111/j.1461-0248.2008.01164.x

Díaz, S., Kattge, J., Cornelissen, J.H.C., Wright, I.J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Colin Prentice, I., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P.B., Moles, A.T., Dickie, J., Gillison, A.N., Zanne, A.E., Chave, J., Joseph Wright, S., Sheremet'ev, S.N., Jactel, H., Baraloto, C., Cerabolini, B., Pierce, S., Shipley, B., Kirkup, D., Casanoves, F., Joswig, J.S., Günther, A., Falczuk, V., Rüger, N., Mahecha, M.D., Gorné, L.D., 2016. The global spectrum of plant form and function. Nature 529, 167–171. doi:10.1038/nature16489

Dixon, R.K., Solomon, A.M., Brown, S., Houghton, R.A., Trexier, M.C., Wisniewski, J., 1994. Carbon Pools and Flux of Global Forest Ecosystems. Science 263, 185–190. doi:10.1126/science.263.5144.185

Eeley, H.A.C., Lawes, M.J., Piper, S.E., 1999. The influence of climate change on the distribution of indigenous forest in KwaZulu-Natal, South Africa. J. Biogeogr. 26, 595–617. doi:10.1046/j.1365-2699.1999.00307.x

Ewers, R.M., Andrade, A., Laurance, S.G., Camargo, J.L., Lovejoy, T.E., Laurance, W.F., 2017. Predicted trajectories of tree community change in Amazonian rainforest fragments. Ecography 40, 26–35. doi:10.1111/ecog.02585

FAO, 2010. Global Forest Resources Assessment. Main Report. Rome.

Finegan, B., Peña-Claros, M., de Oliveira, A., Ascarrunz, N., Bret-Harte, M.S., Carreño-Rocabado, G., Casanoves, F., Díaz, S., Eguiguren Velepucha, P., Fernandez, F., Licona, J.C., Lorenzo, L., Salgado Negret, B., Vaz, M., Poorter, L., 2015. Does functional trait diversity predict above-ground biomass and productivity of tropical forests? Testing three alternative hypotheses. J. Ecol. 103, 191–201. doi:10.1111/1365-2745.12346

Germishuizen, G., Meyer, N., others, 2003. Plants of southern Africa: an annotated checklist. National Botanical Institute Pretoria.

Gleason, S.M., Stephens, A.E.A., Tozer, W.C., Blackman, C.J., Butler, D.W., Chang, Y., Cook, A.M., Cooke, J., Laws, C.A., Rosell, J.A., Stuart, S.A., Westoby, M., 2017. Shoot growth of woody trees and shrubs is predicted by maximum plant height and associated traits. Funct. Ecol. In press. doi:10.1111/1365-2435.12972

Grace, J.B., 2006. Structural Equation Modeling and Natural Systems. Cambridge University Press.

Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers, R.M., Foster, B.L., Jenkins, C.N., King, A.J., Laurance, W.F., Levey, D.J., Margules, C.R., Melbourne, B.A., Nicholls, A.O., Orrock, J.L., Song, D.-X., Townshend, J.R., 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Sci. Adv. 1, e1500052. doi:10.1126/sciadv.1500052

Isbell, F., Calcagno, V., Hector, A., Connolly, J., Harpole, W.S., Reich, P.B., Scherer-Lorenzen, M., Schmid, B., Tilman, D., van Ruijven, J., Weigelt, A., Wilsey, B.J., Zavaleta, E.S., Loreau, M., 2011. High plant diversity is needed to maintain ecosystem services. Nature 477, 199–202. doi:10.1038/nature10282

Jackson, H.B., Fahrig, L., 2015. Are ecologists conducting research at the optimal scale? Glob. Ecol. Biogeogr. 24, 52–63. doi:10.1111/geb.12233

Kauffman, J.B., Hughes, R.F., Heider, C., 2009. Carbon pool and biomass dynamics associated with deforestation, land use, and agricultural abandonment in the neotropics. Ecol. Appl. 19, 1211–1222. doi:10.1890/08-1696.1

Küper, W., Sommer, J.H., Lovett, J.C., Mutke, J., Linder, H.P., Beentje, H.J., Rompaey, R.S.A.R.V., Chatelain, C., Sosef, M., Barthlott, W., 2004. Africa's Hotspots of Biodiversity Redefined. Ann. Mo. Bot. Gard. 91, 525–535.

Laliberté, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology 91, 299–305. doi:10.1890/08-2244.1

Lange, M., Eisenhauer, N., Sierra, C.A., Bessler, H., Engels, C., Griffiths, R.I., Mellado-Vázquez, P.G., Malik, A.A., Roy, J., Scheu, S., Steinbeiss, S., Thomson, B.C., Trumbore, S.E., Gleixner, G., 2015. Plant diversity increases soil microbial activity and soil carbon storage. Nat. Commun. 6, ncomms7707. doi:10.1038/ncomms7707

Laurance, W.F., Camargo, J.L.C., Luizão, R.C.C., Laurance, S.G., Pimm, S.L., Bruna, E.M., Stouffer, P.C., Bruce Williamson, G., Benítez-Malvido, J., Vasconcelos, H.L., Van Houtan, K.S., Zartman, C.E., Boyle, S.A., Didham, R.K., Andrade, A., Lovejoy, T.E., 2011. The fate of Amazonian forest fragments: A 32-year investigation. Biol. Conserv. 144, 56–67. doi:10.1016/j.biocon.2010.09.021

Laurance, W.F., Delamônica, P., Laurance, S.G., Vasconcelos, H.L., Lovejoy, T.E., 2000. Conservation: Rainforest fragmentation kills big trees. Nature 404, 836–836. doi:10.1038/35009032

Lavorel, S., Díaz, S., Cornelissen, J.H.C., Garnier, E., Harrison, S.P., McIntyre, S., Pausas, J.G., Pérez-Harguindeguy, N., Roumet, C., Urcelay, C., 2007. Plant Functional Types: Are We Getting Any Closer to the Holy Grail?, in: Canadell, J.G., Pataki, D.E., Pitelka, L.F. (Eds.), Terrestrial Ecosystems in a Changing World, Global Change — The IGBP Series. Springer Berlin Heidelberg, pp. 149–164.

Lavorel, S., Garnier, E., 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Funct. Ecol. 16, 545–556. doi:10.1046/j.1365-2435.2002.00664.x

Lefcheck, J.S., 2016. piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. Methods Ecol. Evol. 7, 573–579. doi:10.1111/2041-210X.12512

Lewis, S.L., Edwards, D.P., Galbraith, D., 2015. Increasing human dominance of tropical forests. Science 349, 827–832. doi:10.1126/science.aaa9932

Liang, J., Crowther, T.W., Picard, N., Wiser, S., Zhou, M., Alberti, G., Schulze, E.-D., McGuire, A.D., Bozzato, F., Pretzsch, H., de-Miguel, S., Paquette, A., Hérault, B., Scherer-Lorenzen, M., Barrett, C.B., Glick, H.B., Hengeveld, G.M., Nabuurs, G.-J., Pfautsch, S., Viana, H., Vibrans, A.C., Ammer, C., Schall, P., Verbyla, D., Tchebakova, N., Fischer, M., Watson, J.V., Chen, H.Y.H., Lei, X., Schelhaas, M.-J., Lu, H., Gianelle, D., Parfenova, E.I., Salas, C., Lee, E., Lee, B., Kim, H.S., Bruelheide, H., Coomes, D.A., Piotto, D., Sunderland, T., Schmid, B., Gourlet-Fleury, S., Sonké, B., Tavani, R., Zhu, J., Brandl, S., Vayreda, J., Kitahara, F., Searle, E.B., Neldner, V.J., Ngugi, M.R., Baraloto, C., Frizzera, L., Bałazy, R., Oleksyn, J., Zawiła-Niedźwiecki, T., Bouriaud, O., Bussotti, F., Finér, L., Jaroszewicz, B., Jucker, T., Valladares, F., Jagodzinski, A.M., Peri, P.L., Gonmadje, C., Marthy, W., O'Brien, T., Martin, E.H., Marshall, A.R., Rovero, F., Bitariho, R., Niklaus, P.A., Alvarez-Loayza, P., Chamuya, N., Valencia, R., Mortier, F., Wortel, V., Engone-Obiang, N.L., Ferreira, L.V., Odeke, D.E., Vasquez, R.M., Lewis, S.L., Reich, P.B., 2016. Positive biodiversity-productivity relationship predominant in global forests. Science 354, aaf8957. doi:10.1126/science.aaf8957

Magnago, L.F.S., Magrach, A., Barlow, J., Schaefer, C.E.G.R., Laurance, W.F., Martins, S.V., Edwards, D.P., 2017. Do fragment size and edge effects predict carbon stocks in trees and lianas in tropical forests? Funct. Ecol. 31, 542–552. doi:10.1111/1365-2435.12752

Malhi, Y., Baldocchi, D.D., Jarvis, P.G., 1999. The carbon balance of tropical, temperate and boreal forests. Plant Cell Environ. 22, 715–740. doi:10.1046/j.1365-3040.1999.00453.x

Marsh, C.J., Ewers, R.M., 2013. A fractal-based sampling design for ecological surveys quantifying β-diversity. Methods Ecol. Evol. 4, 63–72. doi:10.1111/j.2041-210x.2012.00256.x

Martin, A.R., Thomas, S.C., 2011. A Reassessment of Carbon Content in Tropical Trees. PLoS ONE 6, e23533. doi:10.1371/journal.pone.0023533

Mouquet, N., Moore, J.L., Loreau, M., 2002. Plant species richness and community productivity: why the mechanism that promotes coexistence matters. Ecol. Lett. 5, 56–65. doi:10.1046/j.1461-0248.2002.00281.x

Mucina, L., Geldenhuys, C.J., Rutherford, M.C., 2006. Afrotemperate, subtropical and azonal forests. Veg. South Afr. Lesotho Swazil. Strelitzia 19, 584–614.

Nascimento, H.E.M., Laurance, W.F., 2004. Biomass Dynamics in Amazonian Forest Fragments. Ecol. Appl. 14, 127–138. doi:10.1890/01-6003

Nelson, D.W., Sommers, L.E., 1982. Total Carbon, Organic Carbon, and Organic Matter. Methods Soil Anal. Part 2 Chem. Microbiol. Prop. agronomymonogra, 539–579. doi:10.2134/agronmonogr9.2.2ed.c29

Nzunda, E.F., Griffiths, M.E., Lawes, M.J., 2008. Sprouting by remobilization of above-ground resources ensures persistence after disturbance of coastal dune forest trees. Funct. Ecol. 22, 577–582. doi:10.1111/j.1365-2435.2008.01405.x

Nzunda, E.F., Griffiths, M.E., Lawes, M.J., 2007. Multi-stemmed trees in subtropical coastal dune forest: Survival strategy in response to chronic disturbance. J. Veg. Sci. 18, 693–700. doi:10.1111/j.1654-1103.2007.tb02583.x

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2016. vegan: Community Ecology Package. R package version 2.3-5.

Olivier, P.I., van Aarde, R.J., 2017. The response of bird feeding guilds to forest fragmentation reveals conservation strategies for a critically endangered African eco-region. Biotropica 49, 268–278. doi:10.1111/btp.12402

Olivier, P.I., van Aarde, R.J., Lombard, A.T., 2013. The use of habitat suitability models and species–area relationships to predict extinction debts in coastal forests, South Africa. Divers. Distrib. 19, 1353–1365. doi:10.1111/ddi.12099

Penman, J., Gytarsky, M., Hiraishi, T., Krug, T., Kurger, D., Pipatti, R., Buendia, L., Miwa, K., Ngara, T., Tanabe, K., 2003. Good practice guidance for land use, land-use change and forestry. IPCC National Greenhouse Gas Inventories Programme and Institute for Global Environmental Strategies, Kanagawa, Japan.

Petroselli, A., Vessella, F., Cavagnuolo, L., Piovesan, G., Schirone, B., 2013. Ecological behavior of Quercus suber and Quercus ilex inferred by topographic wetness index (TWI) - Springer. Trees 27, 1201–1215.

Pfeifer, M., Gonsamo, A., Disney, M., Pellikka, P., Marchant, R., 2012. Leaf area index for biomes of the Eastern Arc Mountains: Landsat and SPOT observations along precipitation and altitude gradients. Remote Sens. Environ. 118, 103–115. doi:10.1016/j.rse.2011.11.009

Poorter, L., Bongers, F., 2006. Leaf traits are good predictors of plant performance across 53 rain forest species. Ecology 87, 1733–1743. doi:10.1890/0012-9658(2006)87[1733:LTAGPO]2.0.CO;2

Poorter, L., van der Sande, M.T., Thompson, J., Arets, E.J.M.M., Alarcón, A., Álvarez-Sánchez, J., Ascarrunz, N., Balvanera, P., Barajas-Guzmán, G., Boit, A., Bongers, F., Carvalho, F.A., Casanoves, F., Cornejo-Tenorio, G., Costa, F.R.C., de Castilho, C.V., Duivenvoorden, J.F., Dutrieux, L.P., Enquist, B.J., Fernández-Méndez, F., Finegan, B., Gormley, L.H.L., Healey, J.R., Hoosbeek, M.R., Ibarra-Manríquez, G., Junqueira, A.B., Levis, C., Licona, J.C., Lisboa, L.S., Magnusson, W.E., Martínez-Ramos, M., Martínez-Yrizar, A., Martorano, L.G., Maskell, L.C., Mazzei, L., Meave, J.A., Mora, F., Muñoz, R., Nytch, C., Pansonato, M.P., Parr, T.W., Paz, H., Pérez-García, E.A., Rentería, L.Y., Rodríguez-Velazquez, J., Rozendaal, D.M.A., Ruschel, A.R., Sakschewski, B., Salgado-Negret, B., Schietti, J., Simões, M., Sinclair, F.L., Souza, P.F., Souza, F.C., Stropp, J., ter Steege, H., Swenson, N.G., Thonicke, K., Toledo, M., Uriarte, M., van der Hout, P., Walker, P., Zamora, N., Peña-Claros, M., 2015. Diversity enhances carbon storage in tropical forests. Glob. Ecol. Biogeogr. 24, 1314–1328. doi:10.1111/geb.12364

Pütz, S., Groeneveld, J., Alves, L.F., Metzger, J.P., Huth, A., 2011. Fragmentation drives tropical forest fragments to early successional states: A modelling study for Brazilian Atlantic forests. Ecol. Model. 222, 1986–1997. doi:10.1016/j.ecolmodel.2011.03.038

R Core Team, 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rice, A.H., Pyle, E.H., Saleska, S.R., Hutyra, L., Palace, M., Keller, M., de Camargo, P.B., Portilho, K., Marques, D.F., Wofsy, S.C., 2004. Carbon balance and vegetation dynamics in an old-growth Amazonian forest. Ecol. Appl. 14, 55–71. doi:10.1890/02-6006

Rolo, V., Olivier, P., van Aarde, R., 2016. Seeded pioneer die-offs reduce the functional trait space of new-growth coastal dune forests. For. Ecol. Manag. 377, 26–35. doi:10.1016/j.foreco.2016.06.039

Rooyen, M.W. van, Rooyen, N. van, Stoffberg, G.H., 2013. Carbon sequestration potential of post-mining reforestation activities on the KwaZulu-Natal coast, South Africa. Forestry 86, 211–223. doi:10.1093/forestry/cps070

Schindler, S., von Wehrden, H., Poirazidis, K., Wrbka, T., Kati, V., 2013. Multiscale performance of landscape metrics as indicators of species richness of plants, insects and vertebrates. Ecol. Indic., Linking landscape structure and biodiversity 31, 41–48. doi:10.1016/j.ecolind.2012.04.012

Smith, E.P., van Belle, G., 1984. Nonparametric Estimation of Species Richness. Biometrics 40, 119–129. doi:10.2307/2530750

Swenson, N.G., 2014. Functional and Phylogenetic Ecology in R. Springer, New York.

Taugourdeau, S., Villerd, J., Plantureux, S., Huguenin-Elie, O., Amiaud, B., 2014. Filling the gap in functional trait databases: use of ecological hypotheses to replace missing data. Ecol. Evol. 4, 944–958. doi:10.1002/ece3.989

van Aarde, R., Guldemond, R.A.R., Olivier, P.I., 2014. Biodiversity status of coastal dune forest in South Africa, in: Maslo, B., Lockwood, J.L. (Eds.), Coastal Conservation. Cambridge University Press, Cambridge, UK.

Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A., Wright, I.J., 2002. Plant ecological strategies: Some leading dimensions of variation between species. Annu. Rev. Ecol. Syst. 33, 125–159.

Whitfeld, T.J.S., Lasky, J.R., Damas, K., Sosanika, G., Molem, K., Montgomery, R.A., 2014. Species Richness, Forest Structure, and Functional Diversity During Succession in the New Guinea Lowlands. Biotropica 46, 538–548. doi:10.1111/btp.12136

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H., Diemer, M., others, 2004. The worldwide leaf economics spectrum. Nature 428, 821–827.

Wright, S.J., Kitajima, K., Kraft, N.J.B., Reich, P.B., Wright, I.J., Bunker, D.E., Condit, R., Dalling, J.W., Davies, S.J., Díaz, S., Engelbrecht, B.M.J., Harms, K.E., Hubbell, S.P., Marks, C.O., Ruiz-Jaen, M.C., Salvador, C.M., Zanne, A.E., 2010. Functional traits and the growth–mortality trade-off in tropical trees. Ecology 91, 3664–3674. doi:10.1890/09-2335.1

Wyk, B.V., Wyk, P.V., 2013. Field Guide to Trees of Southern Africa, Second Edition. ed. Struik, Cape Town.

Zanne, A.E., Lopez-Gonzalez, G., Coomes, D.A., Ilic, J., Jansen, S., Lewis, S.L., Miller, R.B., Swenson, N.G., Wiemann, M.C., Chave, J., 2009. Global wood density database. Dryad Identifier Httphdl Handle Net10255dryad 235.
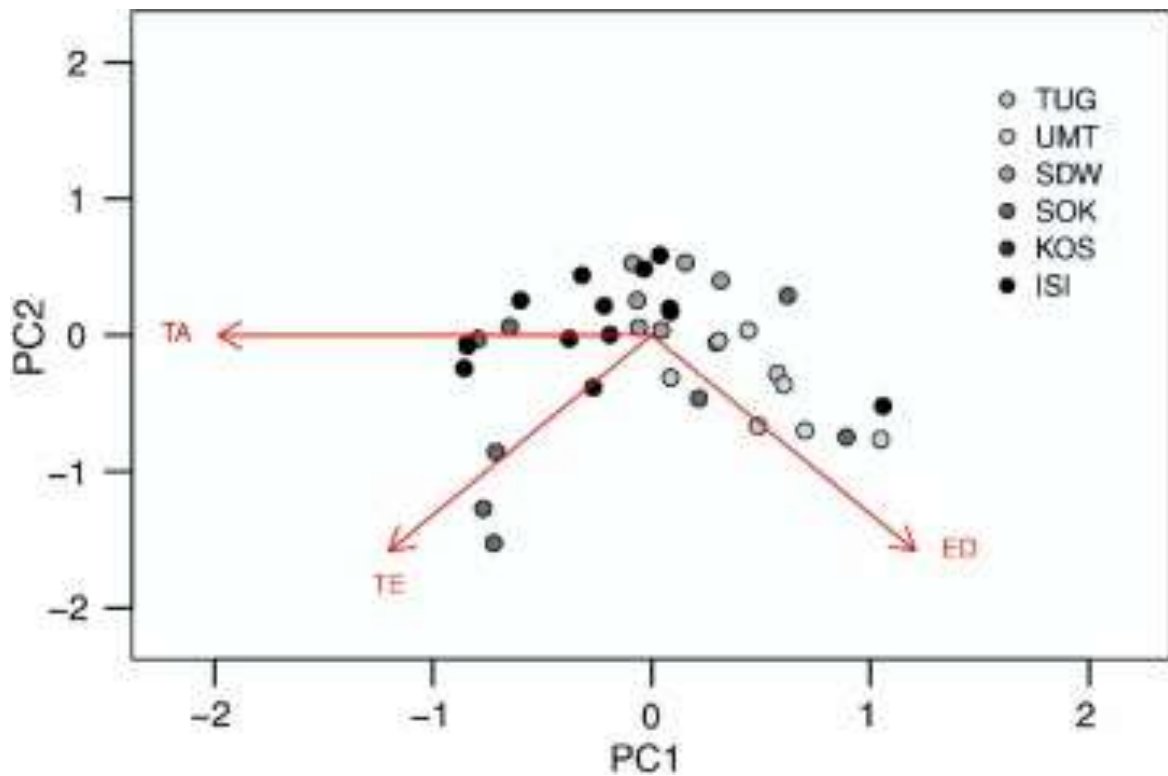
Fig. A1. Ordination of forest patches based on a principal component analysis of the amount of forest (TA), total edge (TE), and edge density (ED) in a buffer of 1 km surrounding each sampling point. The palette of grey depicts patch size, from the smallest (light grey) to the largest (black). Arrows represents the association of each variable with each principal component.