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## The effect of the spatial scale of recruitment on tree diversity in Afromontane forest fragments

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### ABSTRACT

In fragmented landscapes, tree recruitment is critical for forest persistence. We examined the effects of disturbance and environmental factors, isolation distance, and forest area on the spatial scale (grain) of regeneration of tree species in Afromontane forest fragments in South Africa. A species' grain is defined by whether it typically regenerates within its own canopy shadow (fine-grained) or over a larger spatial scale (coarse-grained). Species richness did not differ between small and large forest fragments but there were proportionately more coarse-grained species and fewer fine-grained species in small than in large fragments. While coarse-grained species richness increased with decreasing disturbance and increasing fragment isolation, fine-grained species richness increased with increasing fragment area. Fine-grained species are vulnerable to area-dependent fragmentation pressures. Although they regenerate in their canopy shadow, fine-grained species do not dominate disturbed fragments as expected. While able to survive in small fragments, fine-grained species are potentially dispersal limited and are not good colonisers and depend for their persistence on establishment in large forests. Conversely, because coarse-grained species have effective dispersal mechanisms they can colonise small fragments and are important for the maintenance of tree diversity in fragmented Afromontane forests. Thus, consideration of species grain of regeneration is necessary in conserving Afromontane tree diversity. Fine-grained species are conserved by protecting large forests while coarse-grained species are effectively conserved by maintaining small forest fragments often assumed to be ecologically unviable.

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## 1. Introduction

Increasing anthropogenic fragmentation of forested landscapes has drawn attention towards regeneration dynamics in fragmented forest tree communities (Laurance et al.,

2006; Nascimento et al., 2006). Several studies have demonstrated both area- and isolation-dependent loss of tree species in recently (<100 years) fragmented forests (Holt et al., 1995; Harrington et al., 1997; Benítez-Malvido, 1998; Laurance et al., 1998; Laurance et al., 2000; Benítez-Malvido and

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Martínez-Ramos, 2003; Hill and Curran, 2003). However, analyses of the sensitivity of plant life-history traits to habitat fragmentation and studies of the spatial scale over which tree species regenerate in fragments (i.e., establishment of recruits near or far from parent) are relatively few (Bond, 1994; Ghazoul and McLeish, 2001; Aguilar et al., 2006).

While seed production, seed dispersal and recruitment of forest plants may be affected by fragmentation, conclusions are not straightforward. Some studies have documented reduced seed production (Curran et al., 1999; Ghazoul, 2001) and reduced recruitment (Benítez-Malvido, 1998; Cordeiro and Howe, 2001) in fragments, whereas others have found increased recruitment of successional species, probably due to interactions related to edge effects (Laurance et al., 1998) or alteration of the seed disperser/predator community (Chapman and Onderdonk, 1998; Wright and Duber, 2001), and others have detected no difference in recruitment between the edge and interior of fragments (Lawes et al., 2005). Wright and Duber (2001) suggest that in fragments where human activities disrupt mammalian seed disperser and seed predator communities, increased seedling recruitment and survival near conspecific trees may in time reduce tree diversity. Thus, it is likely that the recruitment response is species- and disturbance-specific, and predictions of fragmentation effects have to account for the regenerative properties of each species (Eriksson and Ehrlén, 2001) within the disturbance context.

Under conditions of natural disturbance forest tree species show differences in their spatial scale and pattern of regeneration (Janzen, 1970; Connell, 1971; Clark and Clark, 1984; Schupp, 1992; Wright et al., 2003) that may affect species persistence in fragmented landscapes, particularly where forest fragments are small (<1 ha). Typically, species that colonise gaps or disturbed areas in forests (gap-dependent species) recruit over large spatial scales and recruits seldom persist in shaded sites beneath adult trees. Shade-tolerant species are the opposite and recruit near to parent trees over smaller spatial scales (Wright et al., 2003). Classification of the spatial scale or grain of regeneration (hereafter referred to as grain) among forest tree species has been slowed by the apparent need for species-by-species analyses of grain from dynamic data obtained from large permanent plots (e.g., Wright et al., 2003). In this study we demonstrate a rapid method of assessing species grain based on static sample plot data that are easily collected and often already available in forestry records.

The concept of grain of regeneration has been used to define the spatial scale of forest dynamics (Everard et al., 1995) and as a way of classifying forests (Everard et al., 1994; Everard et al., 1995; West et al., 2000; Obiri et al., 2002; Lawes and Obiri, 2003). The dynamic processes considered in grain analysis are the spatial scales of tree regeneration and forest disturbance (Everard et al., 1995). Species that regenerate over large areas are categorized as coarse-grained and seldom regenerate within their own canopy shadow. These species are often light-demanding and have relatively few, widely spaced recruits (Everard et al., 1994; Wright et al., 2003). Coarse-grained species are typically early-successional species and their dominance in the forest canopy often indicates past large-scale disturbance (Everard et al., 1994). In contrast, fine-grained species regenerate over small spatial scales, often within their canopy shadow and have large numbers of

recruits in relatively close proximity to mature trees (Lawes and Obiri, 2003; Wright et al., 2003). These species are usually shade-tolerant during recruitment (Lawes et al., 2004) and dominate the canopy in old-growth forests (Everard and van Wyk, 1995; Wright et al., 2003). Typically, there are not many functionally equivalent species at either extreme of the regeneration continuum. Rather, there are few very fine-grained and extremely coarse-grained species. Most species have intermediate light requirements and intermediate to moderately coarse-grained spatial scales of regeneration (Lawes and Obiri, 2003; Wright et al., 2003).

Forest fragmentation and the attendant habitat disturbance and fragment isolation, clearly has the potential to affect the persistence of tree species in small forest fragments. For example, if seed and seedling predation are reduced in fragments, finer-grained tree species whose recruits often establish at high density may come to dominate (Connell et al., 1984; Webb and Peart, 1999; Wright and Duber, 2001), while disturbances that create gaps may favour coarse-grained tree species that have good colonising abilities (Wright et al., 2003). Several forest fragmentation studies have demonstrated a decline in recruitment and loss of late-successional tree species, and a domination of fragments by early-successional tree species with higher recruitment rates (Harrington et al., 1997; Benítez-Malvido, 1998; Laurance et al., 1998; Sizer and Tanner, 1999; Laurance et al., 2001; Laurance et al., 2006; Nascimento et al., 2006). Based on the latter, we examine the proposition that tree communities of small Afromontane forest fragments are dominated by coarse-grained early-successional species, and that the relative abundance of fine-grained species is correlated with lower levels of disturbance and fragment isolation from large forests. Our main aims were to: (1) determine the grain of regeneration of commonly-encountered tree species in small forest fragments (0.1–2 ha) and in the largest forest fragments in the local landscape; (2) examine the effect of disturbance and environmental factors on the grain of regeneration of tree species in these fragmented forests; and (3) develop tree conservation management strategies for small forests based on knowledge of species grain of regeneration.

## 2. Methods

### 2.1. Study area

The Afromontane or Afrotemperate forests of the Balgovan district (130.5 km<sup>2</sup>, 29.43°S, 30.05°E) occur between 1000 and 1500 m a.s.l. in the KwaZulu-Natal midlands, South Africa, approximately 40 km north-west of the city of Pietermaritzburg. Forests are located on south facing slopes subject to frequent mists and mean annual rainfall is approximately 1600 mm, falling mainly from November through February. The forests are naturally small (range = 0.01–1649 ha;  $\bar{x}$  = 5.28 ha, median = 0.29 ha,  $n$  = 1277 forests; Lawes et al., 2004) due to the Holocene climatic history (Eeley et al., 1999). Although there has been anthropogenic fragmentation of these forests in recent times, the boundaries of the small fragments included in this study have been stable for at least 60 years (Lawes et al., 2004). The forests are embedded in a mixed-agricultural landscape of natural grasslands, pastures,

crops, and tree plantations. We selected forests surrounded by a natural grassland matrix, although for some larger forest fragments a small part (<20%) of their edge was adjacent to pastures or plantation forest. Although forest edges are relatively abrupt, they are enclosed and stable.

Dominant canopy tree species are *Podocarpus falcatus*, *Podocarpus latifolius*, *Celtis africana*, *Calodendrum capense*, *Vepris lanceolata*, and *Kiggelaria africana* with a canopy height of 15–20 m. Important sub-canopy trees include *Clauseria anisata*, *Cassinopsis ilicifolia*, *Diospyros whyteana*, *Eugenia zuluensis*, *Gymnosporia mossambicensis*, *Rothmannia globosa*, and *Xymalos monospora*. Stem density (>5 cm dbh) is  $730 \pm 310 \text{ ind ha}^{-1}$  ( $\bar{x} \pm 1\text{SD}$ ) and  $17.7 \pm 4.3$  species were recorded per 0.1 ha plot ( $n = 52$  plots). There is a fairly well developed herb stratum. The forest margins can be affected by fire in the adjacent grassland, while cattle sometimes trample small fragments and the local community that lives at low population density very seldom harvests pole-sized stems.

## 2.2. Vegetation sampling

The diameter at breast height (dbh), height, and species identity of all tree individuals >5 cm dbh were recorded from 52 rectangular (50 × 20 m; 0.1 ha) sample plots located in five large (45.8–96.8 ha) and 22 small (0.07–2 ha) forest fragments that were within a 1 km radius of the large fragments. Few exotic species were recorded and were not included in the analyses. To achieve sampling saturation, five plots were sampled in each of three large forests (Woodwind, Lythwood, Fort Nottingham) and seven (Maritzdaal) and eight (Dargle) plots in the two largest forests. A single plot was sampled in each of the small forest fragments. In large forests human-disturbed sites were avoided and plots were placed in the interior >50 m from the forest edge. In very small fragments (<0.1 ha) the sample plots were proportionately reduced in area to fit the shape of the fragment. We avoided small forest fragments that had a long history of anthropogenic disturbance.

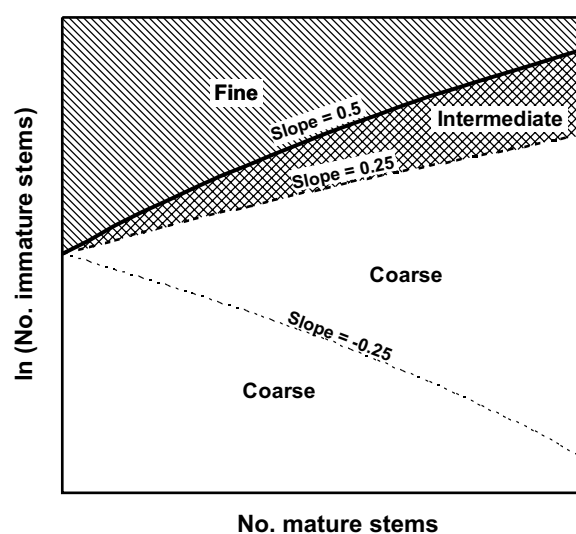
## 2.3. Measurement of disturbance

We scored the level of disturbance in each fragment on a scale of 1–5 (none to severe disturbance) for the categories: fire, trampling by cattle, removal of pole-sized stems, presence of alien invasive plants, accessibility (evidence of walking paths), and damage to the forest margin. Forest fragments in agricultural landscapes are susceptible to increased fire frequency and increased grazing by stock sheltering in the forest (Schelhas and Greenberg, 1996). These scores were summed across the categories of disturbance to give an overall index of disturbance (out of 30) for each fragment. The distance of small forests from the nearest large forest and forest area were calculated from digital maps of the area (Lawes et al., 2004) using ArcView v3.0 (ESRI, 1998). Lastly, the curator of the University of KwaZulu-Natal herbarium (T. Edwards) assigned successional status (i.e., early vs. mid-to-late successional) to tree species independently of knowing the goals of our study. Early-successional species were typically heliophilic pioneers that were good dispersers and common in gaps or at forest edges.

## 2.4. Data analyses

Although several methods have been used to determine the grain of regeneration of tree species, all have used a form of comparison of the ratio of immature to mature individuals of a species in the forest (Everard et al., 1994, 1995; West et al., 2000; Lawes and Obiri, 2003). The shape of size-class stem density distributions has commonly been used to determine species grain. Coarse-grained species have J-shaped, unimodal or bell-shaped size-class frequency distributions, all representing relatively few individuals in the immature stratum compared to the mature tree or canopy stratum. Fine-grained species show an inverse J-shaped frequency distribution, representing many immature individuals relative to mature individuals. In our case, a species' grain of regeneration was estimated from comparisons of stem ratios of immature to mature individuals over the spatial scale of sample plots. Sample plots were relatively large (0.1 ha) to better capture the spatial scale of regeneration.

The statistical estimation of species grain was based on a conceptual model (Fig. 1) of the relationship between the number of immature (dependent variable; y-axis) and mature (independent variable; x-axis) stems of a species over the sample plots. We predicted that for fine-grained species, given that the number of recruits is usually considerably in excess of mature stems, the number of immature stems would increase exponentially ( $y = e^x$ ) as the number of mature stems increased (Fig. 1). In contrast, because recruits of coarse-grained species are typically found at some distance from parent or adult trees, the possibility of encountering many recruits in the near absence of adults exists. Conversely, where there are many adults of a coarse-grained species there are likely to be few recruits. The relationship between immature and mature stems is more complicated for coarse-grained species than fine-grained ones, but can be described by  $y = e^{-x}$ , where the coefficient may be zero or



**Fig. 1** – A conceptual model of the spatial scale or grain of regeneration in tree species. The number of immature stems are plotted against the number of mature stems. In fine-grained species, immature individuals are well represented over a small area.

negative. In this way, the slope of the exponential relationship between immature ( $y$ ) and mature ( $x$ ) stems can be used to interpret the strength of the grain of regeneration for a species.

The exponential relationship between immature and mature stems was modeled in GENSTAT 8.1 (Lawes Agricultural Trust 2005) using a generalized linear model (GLM) based on a Poisson distribution and with a  $\log_e$  (ln) link function. The model took the form

$$\ln y = a + bx + cS \cdot LS$$

where  $y$  is the number of immature stems,  $x$  the number of mature stems,  $S$  is species identity,  $LS$  is forest fragment size (large or small), and  $a$ ,  $b$ , and  $c$  are the associated regression coefficients. This model is essentially an analysis of covariance and the coefficient value for  $c$  gives the slope of the relationship between immature and mature stems for a species and fragment size. Plot identity was included in the full model as a check that no plot departed too much from the expected. To avoid statistical problems with pseudoreplication, data were blocked by forest identity, thus data from plots in each large forest were combined.

To estimate the grain of regeneration, the slope coefficient ( $c$ ) was interpreted as follows: fine-grained  $c > 0.5$ ; coarse-grained  $c \leq 0.25$  and intermediate-grained  $0.25 > c \leq 0.5$ ; the critical alpha value for fine- and intermediate-grained slopes was  $\leq 0.15$  (Fig. 1). A slope coefficient  $> 0$  indicates that the number of immature stems increases with increasing number of mature stems, characteristic of a fine-grained regeneration pattern. A slope  $\leq 0$  indicates that the number of immature stems remains constant or decreases with an increasing number of mature stems, indicative of an increasingly coarse-grained pattern of regeneration. Because we were only interested in whether species are fine- or coarse-grained, we restricted the intermediate category by the above criteria. The model was tested on a hypothetical data set for which species grain was known and against a separate data set gathered during this study comprising five species for which the spatial scale of regeneration was measured by distance of immature trees from a focal adult in ten circular plots. In both cases species grain was accurately predicted by the model slope.

Determining tree size at the onset of maturity is important for defining immature stems in the above model. Because this is variable among species (Wright et al., 2005) we classified species into three categories according to whether they reached reproductive size as understorey trees ( $< 5$  m), at mid-canopy height ( $< 10$  m), or above mid-canopy height ( $\geq 10$  m). Categories were determined from a modal height size class frequency distribution of mature stems by species. For each category we assigned an upper dbh limit to immature stems: understorey trees – dbh  $\leq 10$  cm, mid-canopy trees – dbh  $\leq 15$  cm, and canopy trees = dbh  $\leq 20$  cm. Numbers of immature and mature stems for each species included in the model were estimated according to the above criteria.

We further examined the effect of disturbance and environmental factors (i.e., fragment size and distance from the nearest large fragment) on the numbers of coarse- and fine-grained species in a fragment using multiple regression (GLM with normal distribution of errors and the identity link function) to evaluate seven candidate models. We fitted the

main disturbance effect (combined index) in addition to fragment area and distance to the nearest large fragment, on coarse- and fine-grained species richness of a fragment. Fragment area and distance were  $\log_{10}$  transformed. The main effects were added to the models in their order of expected importance and effect on species richness. Akaike's information criterion adjusted for small samples ( $AIC_c$ ) was used to select the most parsimonious model (Anderson et al., 2000). The model with the smallest AIC value (and a difference of at least two AIC units from other models) was accepted as the best fit to the data. For models that differed by  $< 2$  in AIC value the model with the fewest parameters was favoured (Anderson et al., 1994). We also calculated the Akaike weight ( $w_i$ ) for each model as the approximate probability that model  $i$  is the Kullback–Leibler best model in the set of models considered (Anderson et al., 2000). In addition, we estimated the relative importance of the predictor variables by the method of summing the Akaike weights ( $w_i$ ) across all models in the set of all possible models in which the variable occurred (Burnham and Anderson, 2002). The larger the  $w_i$  (range = 0–1), the more important a variable is relative to the other variables.

We modeled the likelihood of occupancy of the forest sizes by a typical coarse-grained (*C. africana*) and a typical fine-grained (*D. whyteana*) species using binomial logistic regression. Lastly, because the number of trees from a regeneration category varied among plots, we used individual rarefaction to compare species richness of early succession and grain category between large and small forests. Rarefaction analyses were conducted in the software BioDiversity Pro (McAleece, 1997).

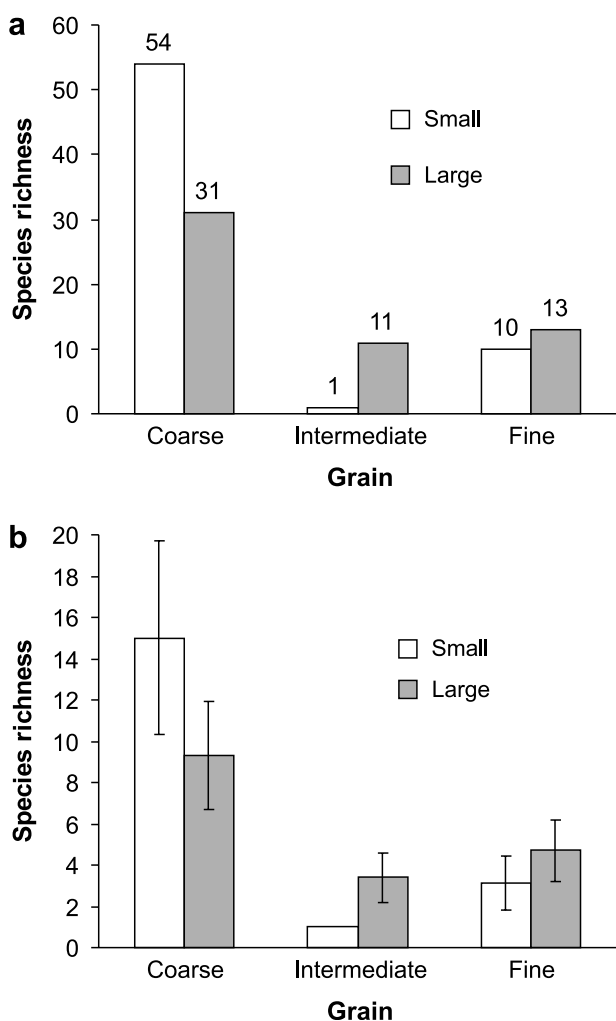
### 3. Results

#### 3.1. Species richness

Species richness did not differ between large ( $17.3 \pm 4.2$  species per plot,  $n = 30$  plots) and small ( $18.2 \pm 4.6$ ,  $n = 22$ ;  $t = -0.69$ ,  $df = 50$ ,  $p = 0.5$ ; two-sample t-test) forests and was not affected by tree density as confirmed by rarefaction analysis ( $t = -1.02$ ,  $df = 50$ ,  $p = 0.31$ ). However, combined tree diversity was greater in small (65 species) than large forest fragments (55 species) because of sampling 22 small and only five large forests, even though more plots were sampled in large ( $n = 30$  plots) than small forests ( $n = 22$ ). Overall, 67 species were recorded (3806 stems), of which 29 were identified as early-successional species (Appendix A; T. Edwards, pers. comm., University of KwaZulu-Natal herbarium). Based on GLM estimates of overall species grain, 41 species were identified as coarse-grained, 12 as intermediate in grain, and 14 as fine-grained. As expected, there was a greater diversity of early-successional species in small (28 species) than large (20 species) forests, although there was no difference in the number of early-successional species in plots from small ( $7.1 \pm 2.1$ ) and large ( $6.4 \pm 1.7$ ;  $t = -1.45$ ,  $df = 50$ ,  $p = 0.15$ ; two-sample t-test) forests. GLM estimates of species grain demonstrated that of the 29 species categorized as early-successional species most were coarse-grained ( $n = 24$  species) with relatively few recruits in the advanced regeneration near to adult individuals, and only a few species were intermediate ( $n = 2$ ) or fine-grained ( $n = 3$ ).

### 3.2. Grain or spatial scale of regeneration

Estimates of grain using GLM varied among species and within species between large and small forest fragments. Some species were intermediate-grained ( $n = 10$ ) or fine-grained ( $n = 6$ ) in large fragments but coarse-grained in small fragments. This indicates a degree of plasticity in the spatial scale of regeneration within species, with the direction of intraspecific change from finer- to coarser-grain in larger to small for-



**Fig. 2** – The number of species in three grain categories for small and large Afrotropical forest fragments. (a) Total species richness across all plots. (b) Mean species richness  $\pm$  1SD across all plots.

ests, respectively. This also demonstrates that some finer-grained species are capable of regenerating over larger spatial scales. There were two instances of coarse-grained species in larger fragments (*Eugenia natalitia* and *Allophylus dregeanus*) displaying fine-grain in small fragments. In both cases, these were understorey species, shade-tolerant, and not early-successional species. Although there was no difference in the number of early-successional species in plots from small and large forest fragments (see above), there were proportionately more coarse-grained species in small than large fragments (Fig. 2a), and by plot in small ( $15.1 \pm 4.7$  species per plot) than large fragments ( $9.3 \pm 2.6$ ;  $t = -5.64$ ,  $df = 50$ ,  $p < 0.001$ ; Fig. 2b). The latter difference persisted even when we controlled for stem density in the plots ( $t = -2.71$ ,  $df = 50$ ,  $p = 0.009$ ). These results demonstrate that species with, or at least capable of, larger spatial scales of regeneration are better able to colonise small fragments. Coarse-grained species have the potential to establish in small forest fragments. Indeed, several early-successional and coarse-grained species were recorded only in small fragments (12 species in total).

Fourteen fine-grained species (21%) occurred in these forests. Of these, 13 were recorded from large and 10 from small forest fragments. There were significantly fewer fine-grained species in plots in small ( $3.0 \pm 1.3$  species per plot) than large fragments ( $4.7 \pm 1.5$ ;  $t = 4.22$ ,  $df = 50$ ,  $p < 0.0001$ ; Fig. 2b), even when we controlled for stem density in the plots ( $t = 5.72$ ,  $df = 50$ ,  $p < 0.0001$ ).

### 3.3. Environmental effects

The forests differed in their type and level of disturbance ( $\chi^2 = 69.8$ ,  $df = 20$ ,  $p < 0.001$ ). More forest fragments than expected were moderately affected by alien invasive plants, accessibility (evidence of walking paths), and damage to the forest margin, while most fragments (>80%) were not affected by fire, trampling, and cutting of stems. Disturbance reached severe levels in <5% of forest fragments only, and was mainly represented by numerous trails or paths cross-cutting the fragment, suggesting frequent visits by cattle. Thus, the combined disturbance index mainly reflects the frequency of visits by cattle with the concomitant damage to the forest margin, opening up of the interior of fragments and trafficking and establishment of invasive plants into fragments.

The most parsimonious model for the fit to coarse-grained species richness in a forest fragment included parameters for disturbance to a fragment and fragment isolation from a large forest (Model 3; Table 1). The number of coarse-grained species increased with decreasing disturbance to a fragment

**Table 1** – Coarse-grained species in small and large Afrotropical forest fragments

Model number	Model structure	Rank	K	Residual deviance	AIC <sub>c</sub>	$\Delta$ AIC <sub>c</sub>	Akaike weights
1	Disturbance + area + distance	5	4	16.38	26.20	2.21	0.326
2	Disturbance + area	4	3	19.07	26.11	2.13	0.227
3	Disturbance + distance	1	3	16.94	23.98	0.00	0.659
4	Area + distance	6	3	19.59	26.63	2.65	0.175
5	Area	7	2	22.96	27.46	3.48	0.057
6	Distance	3	2	21.28	25.78	1.80	0.134
7	Disturbance	2	2	20.82	25.32	1.34	0.168

Area and isolation distance are  $\log_{10}$  transformed. K is the number of parameters in the model.

**Table 2 – Fine-grained species in small and large Afrotropical forest fragments**

Model number	Model structure	Rank	K	Residual deviance	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	Akaike weights
1	Disturbance + Area + Distance	6	4	39.27	49.09	3.89	0.059
2	Disturbance + Area	2	3	39.43	46.47	1.27	0.218
3	Disturbance + Distance	5	3	41.69	48.73	3.53	0.070
4	Area + Distance	3	3	40.41	47.45	2.25	0.133
5	Area	1	2	40.70	45.20	0.00	0.412
6	Distance	4	2	44.02	48.52	3.32	0.078
7	Disturbance	7	2	46.00	50.50	5.30	0.029

Area and distance are log<sub>10</sub> transformed. K is the number of parameters in the model.

and increasing isolation of a fragment from a potential source of propagules (coarse-grained species richness =  $20.54 - 0.723[\log_{10}\text{Disturbance}] + 0.971[\log_{10}\text{Distance}]$ ,  $F_{2,24} = 5.06$ ,  $p = 0.01$ ). Although the number of coarse-grained species per plot differed significantly between large and small forests overall, at the level of the forest fragment there was no significant species-area effect (slope coefficient =  $-0.929$ ,  $t = -0.98$ ,  $df = 25$ ,  $p = 0.34$ ) even though coarse-grained species richness tended to decline with increasing fragment area. The effect of disturbance and distance on the number of coarse-grained (potentially early-successional) species in fragments was stronger than the effect of area, in that the sum of the normalized Akaike weights ( $w_i$ ) for the models including these variables were 0.72 and 0.66, respectively, while the area effect was comparatively weak (0.37).

The effects of disturbance, fragment isolation (distance) and area, on fine-grained species richness in a forest were tested (Table 2; Akaike model weights, range = 0.06–0.41;  $0.023 < p < 0.139$ ). The most parsimonious model included only area (Model 5; Table 2; fine-grained species richness =  $3.37 + 0.62[\log_{10}\text{Area}]$ ,  $F_{1,25} = 5.9$ ,  $p = 0.023$ ) and fine-grained species richness increased significantly with increasing fragment area. Although fine-grained species richness decreased

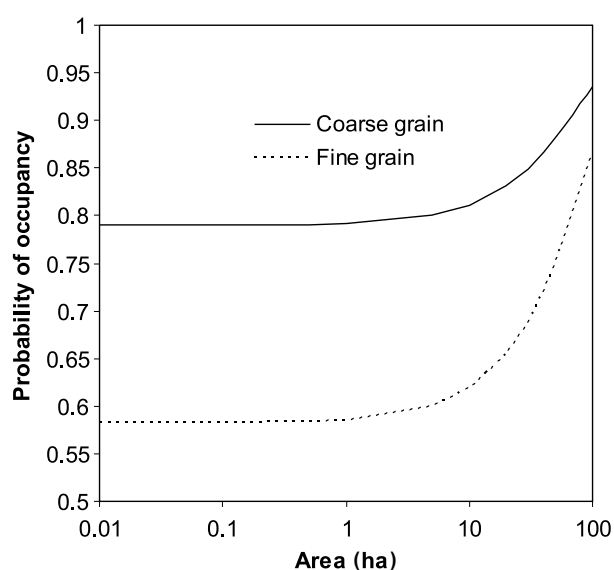
with increasing isolation and disturbance, neither was significant ( $p > 0.1$ ). The  $w_i$  for the effect of area, isolation and disturbance were 0.822, 0.341, and 0.376, respectively, indicating the relatively weak influence of all variables, except forest area, on fine-grained species richness in a fragment.

The likelihood of occupancy of small forests was much greater for a typical coarse-grained species (*C. africana*) than a typical fine-grained (*D. whyteana*) species, and although their likelihood of occupancy increased and converged at large forest sizes, it remained higher for the coarse-grained species (Fig. 3).

## 4. Discussion

### 4.1. The grain of regeneration

The concept of the grain or spatial scale of regeneration is well established in the literature dealing with the regeneration continuum among forest trees (Connell et al., 1984; Everard et al., 1995; Condit et al., 1998; Wright et al., 2003). In general, coarse-grained species regenerate over large spatial scales and were more common (62%,  $n = 41$ ) than fine-grained species in small Afrotropical forest fragments. This may be because fine-grained species were narrowly categorized, while coarse-grained species ranged from moderately to very coarse-grained. However, a more likely explanation is that greater seedling survival further from adult trees (Janzen, 1970; but see Condit et al., 1992; Connell, 1971; Chapman and Chapman, 1995) selects for long-distance dispersal of propagules (escape hypothesis; Howe and Smallwood, 1982), causing most species to be coarse-grained (Wright et al., 2003) and more likely to be present in isolated fragments (Harrington et al., 1997; Benítez-Malvido, 1998; Laurance et al., 1998; Sizer and Tanner, 1999; Laurance et al., 2001; Laurance et al., 2006; Nascimento et al., 2006; Holmgren and Poorter, 2007). Coarse grain is most prevalent in early-successional species, including invasive pioneer and understorey species that regenerate in dense stands (e.g., *C. anisata*) similar to *Cecropia* spp. or *Vismia* spp. at forest edges and in fragments in the Amazon (Laurance et al., 1998; Nascimento et al., 2006), but that seldom recruit in their crown shadow, and in light-tolerant, gap-filling species (very coarse-grained; e.g., *C. africana*). Fast-growing early-successional species (pioneers) are coarse-grained because they have fewer juveniles than slower growing species, even when population growth is equal (Condit et al., 1998). Thus, coarse grain occurs over a regeneration continuum and although it may be represented by high adult stem densities in pioneer species, it is also associated with late-successional species (Wright et al., 2003).



**Fig. 3 – The influence of forest area on the probability of occupancy for a typical coarse-grained (*Celtis africana*) and fine-grained (*Diospyros whyteana*) species. Model fits were excellent in both cases ( $p < 0.001$ ).**

#### 4.2. Forest fragmentation and species grain

It is unlikely contemporary Afromontane tree communities owe their diversity and community structure (more coarse-grained than fine-grained species) to recent fragmentation effects, as forests in the region have always been fragmented (Eeley et al., 1999) and fragment areas have remained stable for the last 60–100 years (Lawes et al., 2004). Having evolved in a fragmented landscape Afromontane forest species appear to be more resilient than most to contemporary fragmentation effects (Balmford, 1996; Lawes et al., 2005; Lawes et al., 2007), potentially resulting in the prevalence of coarse-grained tree species in these forests (Lawes et al., 2005).

In our study, coarse-grained species comprised mostly (24 of 41 species) fast-growing, early-successional species that were light-tolerant and able to colonise disturbed sites (Clark, 1990; Laurance et al., 2006; Holmgren and Poorter, 2007). While an advantage in an ancient fragmented habitat, a coarse-grain of regeneration predisposes species to cope with contemporary fragmentation effects. Fragmentation favours species with dispersal mechanisms that ensure their seeds reach isolated sites (Clark, 1990; Laurance et al., 1998) causing coarse-grain species dominance in small fragments. The arrival of these successional species may also exclude fine-grained species with time (Laurance et al., 2006). For example, small forest fragments in Ghana contained a higher proportion of early-successional, light-demanding species (Hill and Curran, 2001; Hill and Curran, 2003; Hill and Curran, 2005). Small fragments also have elevated levels of disturbance compared to large forests (Laurance et al., 2000) with more opportunities for coarse-grained species to establish. The small forest fragments at our study site were moderately disturbed and only a few (<5%) severely so, creating conditions for coarse-grained species establishment. Counter to expectation, the richness of early-successional and coarse-grained species declined as disturbance levels in fragments increased, probably because severely disturbed fragments contained fewer species overall.

Unlike coarse-grained species, fine-grained species are potentially dispersal limited and, although able to survive in small fragments, they are poor colonisers and persist best in large forests where they can compete more effectively for shaded sites. Fine-grained species are most vulnerable to contemporary fragmentation pressures, as evidenced by their species-area response. Furthermore, it is usual for fine-grained species, which typically have high persistence, but low colonisation rates, to maintain area-dependent extinction debts for prolonged periods (Vellend et al., 2006). Thus, with time fine-grained species should slowly disappear from very small forest fragments, as indeed is happening in this study. Similar trends are found in Amazonian forest fragments where successional trees increased in smaller and older fragments (Laurance et al., 2006), while old-growth forest trees declined in older fragments (Laurance et al., 1998).

#### 4.3. Conservation management

The conservation of habitat fragments is often predicated on maintaining maximum species diversity, with the assumption that higher diversity is best. However, this study demonstrates that the type of species in a fragment is also

important. The conservation of longer-lived, late-successional and fine-grained species is more important in this fragmented forest landscape than the conservation of coarse-grained and early-successional species that already cope well with fragmentation effects. Lower overall tree diversity in relatively undisturbed large forests, but higher diversity of fine-grained species, and an overall fine-grained pattern of regeneration, indicates that these larger forests are converging on a mature/old growth state (Everard and van Wyk, 1995). Preventing further fragmentation of large forests is vital for ensuring that fine-grained shade-tolerant species are not lost from the system (Hill and Curran, 2001).

Wright and Duber (2001) cautioned that increased seedling recruitment near conspecifics by fine-grained (shade-tolerant) species may reduce tree diversity in forests, particularly in forest fragments where natural seed and seedling predation rates and dispersal distances are reduced. However, even though our Afromontane forest fragments were disturbed and sufficient time had passed for species reaction and relaxation following fragmentation to occur, these fragments were dominated by coarse-grained species. This is probably because important forest processes are not disrupted in these small fragments, increasing their conservation value (Kotze and Lawes, 2007). For example, even in the smallest fragments where seedling predation rates were likely to be most reduced, seed predation levels did not differ significantly from large fragments (Kotze and Lawes, 2007).

The colonisation ability of coarse-grained species has the fortuitous consequence that high tree species diversity is maintained in this fragmented Afromontane forest landscape. Area effects *per se* were not significant on coarse-grained or successional tree diversity, probably because of their high colonising potential. Similar trends have been found in recent Amazonian forest fragments (see above; Laurance et al., 2006; Holmgren and Poorter, 2007). In fact, several coarse-grained species appeared to persist only in small Afromontane fragments and greater overall tree diversity was captured in the combined sample of small forests than large forests, emphasising the value of small forests to the maintenance and recovery of tree diversity in this fragmented landscape (Lawes et al., 2005). Thus, no special conservation action is necessary to conserve coarse-grained species in this system, other than to maintain the existing small fragments in the landscape that are often assumed to be ecologically unviable (Kotze and Lawes, 2007). Finally, consideration of species grain of regeneration is clearly necessary to conserve Afromontane tree diversity, in addition to the disturbance type, area, and isolation of forest fragments.

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**Appendix A. Summary of data: ESS = early successional species; LC = understorey species, MC = mid-canopy species, UC = upper-canopy species; C = coarse-grained, F = fine-grained, I = intermediate grain (as defined in this study); Large/Small/Combined = forest size categories**

Species	Successional status	Stratum	Grain			Density (mean) all stems (ind./0.1 ha)			Density (mean) immature stems (ind./0.1 ha)			Density (mean) mature stems (ind./0.1 ha)		
			Large	Small	Combined	Large	Small	Combined	Large	Small	Combined	Large	Small	Combined
<i>Allophylus africanus</i>		MC	C	C	C	2.0	2.3	2.2	0.7	1.5	1.2	1.3	2.4	2.0
<i>Allophylus dregeanus</i>		LC	C	F	C	1.0	6.0	3.5	1.0	6.0	3.5	0.0	0.0	0.0
<i>Apodytes dimidiata</i>		MC	C	C	C	2.4	2.8	2.6	0.9	2.4	1.7	1.6	1.2	1.4
<i>Bersama tysoniana</i>		MC	C	C	C	1.0	2.3	2.0	1.0	1.3	1.3	0.0	1.7	1.3
<i>Buddleja salviifolia</i>	ESS	MC	I	I	I	2.0	2.0	2.0		4.0	4.0		4.0	4.0
<i>Burchellia bubalina</i>	ESS	LC	C	C	C		2.0	2.0		1.5	1.5		0.5	0.5
<i>Calpurnia aurea</i>	ESS	LC	I	C	I	1.8	2.0	1.9	1.5	1.6	1.6	0.3	1.5	0.7
<i>Calodendrum capense</i>	ESS	UC	C	C	C	3.3	1.9	2.9	0.2	0.5	0.3	3.1	1.8	2.8
<i>Canthium ciliatum</i>	ESS	LC	I	C	I	1.8	2.0	1.9	1.6	2.3	1.9	0.2	0.5	0.4
<i>Canthium kuntzeanum</i>	ESS	LC	F	C	F	2.3	2.0	2.1	2.0	2.3	2.1	0.3	0.7	0.4
<i>Canthium mundianum</i>		LC	F	C	F	5.8	2.0	4.1	3.3	2.0	2.7	2.5	1.0	1.9
<i>Carissa bispinosa</i>		LC	I	C	I	1.6	2.0	1.6	1.6	2.0	1.6	0.0	0.0	0.0
<i>Cassinopsis ilicifolia</i>	ESS	LC	C	C	C	1.0	4.0	2.9	0.7	3.0	2.1	0.3	2.8	1.9
<i>Cassine papillosa</i>		MC	I	C	I	2.3	1.5	2.0	1.6	2.0	1.7	0.7	0.5	0.6
<i>Celtis africana</i>		UC	C	C	C	4.7	4.1	4.5	0.9	3.6	2.0	3.8	2.9	3.5
<i>Chionanthus peglerae</i>		MC	F	F	F	3.7	7.0	4.1	2.8	7.0	3.4	0.8	0.0	0.7
<i>Clausena anisata</i>	ESS	LC	C	C	C	2.7	6.4	4.4	1.3	5.3	3.1	1.4	4.2	2.6
<i>Clerodendrum glabrum</i>	ESS	MC	I	C	I	2.2	1.7	2.0	1.6	0.7	1.3	0.6	1.0	0.8
<i>Combretum kraussii</i>	ESS	MC	I	C	I	4.0	4.0	4.0	2.0	2.0	2.0	2.0	2.0	2.0
<i>Cryptocarya woodii</i>		MC	F	F	F	5.7	4.7	5.3	3.5	6.4	4.6	2.2	1.5	1.9
<i>Cussonia sphaerocephala</i>		MC	C	C	C	2.8	2.7	2.7	0.6	1.8	1.1	2.1	1.5	1.9
<i>Dais cotinifolia</i>		MC	C	C	C	1.0	2.7	1.8	0.3	0.9	0.6	0.7	2.9	1.8
<i>Diospyros whyteana</i>		LC	F	F	F	8.6	6.8	7.9	6.8	6.2	6.6	1.8	1.0	1.5
<i>Dombeya tiliacea</i>		LC	C	C	C	1.6	3.9	2.8	0.7	5.1	3.1	0.9	1.0	0.9
<i>Douyalis rhamnoides</i>	ESS	LC	C	C	C		1.0	1.0		1.3	1.3		0.0	0.0
<i>Drypetes gerrardii</i>		LC	C	C	C		1.0	1.0		1.0	1.0		0.0	0.0
<i>Ekebergia capensis</i>		UC	C	C	C	1.0	2.7	1.8	0.0	1.0	0.5	1.0	2.0	1.5
<i>Euclea crispa</i>		MC	C	C	C	2.5	7.5	5.8	1.5	6.4	4.8	1.0	3.1	2.4
<i>Eugenia natalitia</i>		LC	C	F	C	1.0	5.0	4.6	0.0	5.0	4.4	1.0	2.3	2.1
<i>Eugenia zuluensis</i>		LC	F	C	F	15.3	2.7	11.5	12.0	2.0	9.0	3.3	1.5	2.7
<i>Ficus craterostoma</i>		MC	C	C	C	1.8	1.0	1.6	0.5	0.0	0.4	1.3	5.0	2.0
<i>Grewia occidentalis</i>	ESS	LC	C	C	C	1.0	1.8	1.7	0.0	3.1	2.6	1.0	0.3	0.4
<i>Gymnosporia grandifolia</i>	ESS	MC	I	C	I	4.0	5.2	4.7	2.0	4.9	3.7	2.0	2.7	2.4
<i>Gymnosporia heterophylla</i>	ESS	LC	C	C	C		2.0	2.0		0.0	0.0		3.3	3.3
<i>Gymnosporia mossambicensis</i>	ESS	LC	F	F	F	3.0	4.2	3.4	2.7	4.5	3.3	0.3	1.2	0.6
<i>Halleria lucida</i>	ESS	MC	C	C	C	2.8	3.8	3.2	1.1	1.4	1.2	1.7	3.9	2.6
<i>Heteromorpha arborecens</i>	ESS	UC	C	C	C	1.0	5.0	3.0	1.0	7.0	4.0	0.0	0.0	0.0
<i>Heteromorpha trifoliata</i>	ESS	UC	C	C	C		1.5	1.5		2.0	2.0		0.0	0.0
<i>Hyperacanthus amoenus</i>		LC	C	C	C	1.5	2.0	1.7	0.3	1.5	0.7	1.3	0.5	1.0
<i>Kiggelaria africana</i>		UC	C	C	C	2.0	1.6	1.8	0.3	0.8	0.5	1.7	1.4	1.6
<i>Maytenus peduncularis</i>		LC	C	C	C	1.3	2.0	1.4	0.4	1.0	0.5	0.9	2.2	1.1
<i>Maytenus undata</i>		MC	C	C	C	1.0	4.0	3.0	0.0	3.8	2.6	1.0	0.5	0.7
<i>Pavetta lanceolata</i>	ESS	LC	C	C	C	1.3	2.2	1.7	0.1	0.7	0.4	1.1	1.7	1.4
<i>Peddiea africana</i>		LC	C	C	C	1.0		1.0	1.0		1.0	0.0		0.0
<i>Pittosporum viridiflorum</i>		MC	C	C	C		3.0	3.0		5.0	5.0		0.8	0.8



<i>Podocarpus falcatus</i>	UC	C	C	2.3	1.9	1.0	1.8	1.3	0.8	1.3	1.0
<i>Podocarpus latifolius</i>	UC	F	F	12.1	9.0	3.4	15.6	9.5	2.6	3.6	3.1
<i>Prunus africana</i>	UC	C	C	1.0	1.0	0.0	0.0	0.0	1.0	1.3	1.3
<i>Psychrax obovata</i>	LC	C	C	1.0	1.0	0.0	0.0	0.0	0.0	1.0	1.0
<i>Ptaeroxylon obliquum</i>	UC	I	C	3.4	5.3	2.3	1.4	2.0	4.1	3.6	3.9
<i>Rapanea melanophloeos</i>	MC	F	C	1.0	3.2	2.3	0.0	1.5	2.0	2.3	2.1
<i>Rhamnus prinoides</i>	LC	C	C	1.0	1.0	0.9	0.9	0.9	1.3	1.3	1.3
<i>Rhus dentata</i>	LC	F	F	4.0	4.0	4.0	4.0	4.0	0.0	0.0	0.0
<i>Rhus pyroides</i>	LC	C	C	4.5	4.5	2.5	2.5	2.5	2.7	2.7	2.7
<i>Rinorea angustifolia</i>	LC	F	F	8.8	19.2	18.0	6.5	14.5	5.8	2.3	4.7
<i>Rohmannia capensis</i>	LC	I	C	1.0	1.4	1.5	0.4	0.7	1.0	0.6	0.7
<i>Rohmannia globosa</i>	UC	F	C	3.2	3.3	2.6	3.0	2.9	0.8	0.8	0.8
<i>Scolopia flanaganii</i>	MC	C	C	5.0	5.0	4.0	4.0	4.0	1.0	1.0	1.0
<i>Scolopia mundii</i>	UC	C	C	4.9	3.4	1.0	4.5	2.2	1.2	1.2	1.5
<i>Scolopia zeyheri</i>	UC	C	C	2.7	1.9	0.6	1.9	1.1	0.8	1.4	1.1
<i>Trichocladus ellipticus</i>	LC	I	C	6.0	3.5	2.0	3.0	1.5	4.0	2.0	2.1
<i>Trimeria grandifolia</i>	MC	C	C	4.9	3.9	1.5	3.8	2.4	1.7	2.6	2.0
<i>Tricalysia lanceolata</i>	LC	F	C	1.0	6.4	7.0	0.6	4.1	3.8	0.4	2.3
<i>Tricalysia sordieriana</i>	LC	F	F	3.0	3.3	3.0	3.8	3.5	0.8	0.8	0.8
<i>Vepris lanceolata</i>	UC	I	C	3.3	3.0	1.5	3.5	2.4	1.2	2.0	1.6
<i>Xymalos monospora</i>	MC	C	C	1.6	3.9	1.0	1.0	1.0	4.0	0.8	2.9
<i>Zanthoxylum davyi</i>	MC	C	C	3.7	2.6	1.0	3.6	2.0	0.9	1.5	1.1

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