Journal of Vegetation Science 19: 729-738, 2008
doi: 10.3170/2008-8-18445, published online 16 April 2008
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Tree spacing and area of competitive influence do not scale with tree size in an African rain forest

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Abstract

Questions: Is the area of influence of individual trees determined by tree size? Does competition, inferred from spatial pattern between neighbouring trees, affect adult tree spacing patterns in an tropical forest? At what size-class or stage is competition between neighbours most likely to affect adult tree spacing patterns?
Location: Kibale National Park, western Uganda.
Methods: Relationships between focal tree size and nearest neighbour distance, size, density, and species in a 4-ha permanent plot, using point pattern analyses.
Results: We found non-random patterns of distribution of nearest tree neighbours (stems > 10 cm DBH). Independent of identity, tree density was highest and neighbours were regularly spaced within 3-5m of an individual. Tree densities were lower and relatively constant at distances >5m and neighbours were typically randomly spaced. In general, conspecific patterns conformed to the latter trends. Thus, individual area of influence was small (within a radius of 3-5 m). Rarer species were more clumped than common species. Weak competitive thinning occurred among more densely packed small trees (<20 cm DBH), and rapidly disappeared with increasing tree size and distance from an individual. The clumping and density of individuals was not significantly affected by tree size.
Conclusions: Negative effects of competition among trees are weak, occur within the crown radius of most individuals, and are independent of adult tree size and identity. The density of neighbouring trees (aggregation) did not decline with increasing focal tree size at either the conspecific or the community level and **t**ree diameter (tree size) was not a good estimator of the implied competitive influence of a tree. Mechanisms operating at the recruitment stage may be important determinants of adult tree community diversity and spacing patterns.

Keywords: Aggregation; O-ring analysis; Point pattern analysis; Ripley's K; Thiessen polygon; Neighbourhood effect.

Nomenclature: Hamilton (1991).

Introduction

Evaluation of the patterns and causes of the spatial distribution of trees has dominated rain forest tree ecology for several decades (1970; Connell 1971; Hubbell 1979; Lieberman & Lieberman 1987; Condit et al. 2000; Hubbell et al. 2001). Measures of aggregation or dispersion of individuals of a species can point to mechanisms that maintain the low population densities but high diversity typical of rain forest trees. Although some studies have found rain forest trees to be randomly dispersed, at least with respect to available light conditions in forest (Lieberman & Lieberman 1987; Lieberman et al. 1995; Condit et al. 2000), evidence from several sites suggests that most species, and particularly rare species, are more aggregated than expected by chance alone (Condit et al. 2000). However, aggregation of neighbouring individuals may tend to weaken with increasing tree diameter class across species (Condit et al. 2000; Hubbell et al. 2001), suggesting that large trees competitively inhibit conspecifics over a larger area of influence than smaller trees and that tree spacing patterns are influenced by tree size and species.

To date, the interpretation of tree spatial patterns in forests has been based on the assessment of crowding and conspecific density, neighbour identity and size, and tree growth and survival (Condit et al. 2000; Schwarz et al. 2003; Canham et al. 2004; D'Amato & Puettmann 2004; Uriarte et al. 2004a, b. 2005). For example, at Barro Colorado Island (BCI), Panama, Hubbell et al. (2001) found strongly and consistently negative conspecific density effects and much weaker effects of relative tree size and neighbourhood species richness on focal tree and sapling growth and survival. The reduced survival associated with density of conspecific neighbours was greater in canopy tree species than in shrub species, and greater in gap species than in shade-tolerant species. Conspecific neighbourhood effects were not detectable beyond 10–15m from a tree (Hubbell et al. 2001; Uriarte et al. 2005). Although Uriarte et al. (2005) describe this area of influence (10-15 m radius) among conspecific individuals as extremely local, we argue that this is a surprisingly large area of influence.

Nearest-neighbour distances have been used in point-pattern analyses (Condit et al. 2000; Ripley 2004; Wiegand & Moloney 2004) of tree spacing to define an individual's neighbourhood or circular area of influence on neighbours (Condit et al. 2000; Hubbell et al. 2001). We use point-pattern analyses of static data to examine tree spacing patterns as a function of tree size and species identity. Based on the premise that tree spacing patterns in closed canopy forest reflect differential survival and competition between adult individuals (e.g., Herwitz et al. 2000), we: (1) infer the role of competition in determining adult tree spacing patterns; (2) determine the area of potential competitive influence of a given tree on its neighbours; and (3) discuss whether tree diameter is a good predictor of a tree's area of influence. We examine tree spacing at a finer spatial scale than Hubbell et al. (2001) and Uriarte et al. (2005) and compare their findings to ours from an African old-growth lowland rain forest.

Methods

Study site and sample plot

This study was conducted at Kanyawara field station in the Kibale National Park located in western Uganda. The park (795 km^2; 0˚13' - 0˚41' N and 30˚19' - 30˚32'E) is classified as moist, mid-altitude (920–1590 m) lowland rain forest and receives 1712 mm of rainfall annually (1990-2004) in two rainy seasons (Chapman et al. 2005). The park was a forest reserve until 1993, and certain parts were selectively logged. The study site is located in an unlogged old-growth stand (K-30, near trail grids CC7-9) and there was no evidence of cutting or of large-scale natural disturbance (e.g., fire, drought related mortality, spatially correlated windthrow) of the vegetation in the plot.

Data were collected from a 200 m × 200 m (4 ha) plot (0˚33.034' N, 30˚22.106' E) during June 2005. Using a Suunto KB-14/360 R compass (accuracy 0.33˚), the external boundaries of both the whole plot and each of the four internal 100 m × 100 m (1 ha) plots were laid out and marked at 10 m intervals. All trees >10 cm DBH (n = 2356) were surveyed along adjacent 100 m × 10 m transects, one hectare at a time. Each tree was identified and labelled with an aluminium tag. The DBH (diameter at a breast height of 1.3 m) and the map (x, y) coordinates were recorded for each tree. The aspect of the plot was SW with slope in the NE to SW plane of 9.5˚ ± 4.9˚ (mean ± 1 S.D.) and in the NW to SE plane of 1.6˚ ± 2.3˚, yielding an error in distance measurements along transects of 0.06-1.23%. Given this small error range, we did not correct tree map coordinate values for slope. Although soil nutrients were not measured, there was no apparent heterogeneity across the plot. The soils are red sandy loams or sandy clays of moderate fertility (Struhsaker 1997). The plot was bounded on two sides by and intersected the permanent grid trail system on one side, and was crosscut at one corner by a narrow elephant trail.

Although 42 tree species were recorded from the site (28-35 species/ha), six abundant species accounted for 81% of all stems on the plot: *Uvariopsis congensis* (31%), *Markhamia lutea* (12%), *Leptonychia mildbraedii* (10%), *Funtumia africana* (10%), *Celtis durandii* (9%), and *Diospyros abyssinica* (9%). Relatively low species richness recorded in this study is commensurate with previous studies at Kibale forest (Chapman et al. 1997). Tree nomenclature follows Hamilton (1991) with appropriate revisions. Canopy height was between 25 and 30 m and mean (± 1 SD) DBH was 23.3 ± 21.1 cm. The understorey was generally sparse comprising mainly woody saplings, with little or no herb layer.

Estimating the area of influence of a focal tree

In the absence of growth and mortality data for the trees in our plot, we used four methods using inter-tree distance and tree size to estimate the influence of neighbours on each other: we (1) estimated the potential area of influence about individuals using Thiessen polygons; (2) computed Ripley's K and Ripley's L-function; (3) conducted O-ring ($O_{(r)}$) analyses and (4) examined the relationship between focal tree size and nearest neighbour distance.

Thiessen polygon area

We used Dirichlet tessellation to create a cell or Theissen (Voronoi) polygon around each individual tree in ArcView 3.3 (ESRI 2002) with the extension Thiessen avx, taking these polygons as estimates of individual areas of influence. This method, based on the distance between neighbouring stems, has been used in plant ecology to estimate individual area of influence (Mithen et al. 1984; Hubbell et al. 1990). However, forest canopy stratification may confound the method by allowing portions of the area directly beneath the crown of larger trees to be allocated to polygons associated with subcanopy trees. This indicates a denser packing of stems than might be effectively experienced by larger trees. Nevertheless, we use Thiessen polygons as a first approximation of the area of influence about an individual and examine whether tree size (DBH) is positively correlated with polygon area.

Individuals at the plot edge were removed before analysis. Adjacent polygon areas were spatially autocorrelated (Moran's $I = 0.081$, $t = 28.7$, $P < 0.001$) so that neighbouring polygons tended to be similar in area, while more distant polygons showed negative, positive, or no spatial autocorrelation. To ensure independence of polygon samples we selected four independent sets of non-adjacent polygons for comparison of the relationship between tree size and its polygon area. These analyses were repeated for each of the six dominant species.

In the absence of measurements of factors directly affecting spatial distribution of trees, we examined the relationship between tree size and distance to the nearest neighbour to approximate the effect of competition among individual trees. To ensure independence of data points we removed all cases of duplicated distances where a focal tree was also nearest neighbour to its own nearest neighbour. These data exhibited unequal variation in their distribution ('envelope effect', *sensu* Thomson et al. 1996) (Levene test for homogeneity of variances, $P < 0.001$). The confounding effect of heteroscedasticity can be statistically controlled for by using quantile regression, which estimates multiple rates of change (slopes) from the minimum to maximum response, providing a more complete picture of the relationships between variables (tree size and nearest neighbour distance) missed by standard regression methods (Cade & Noon 2003). Quantile regressions of nearest neighbour distance on tree size were conducted using the software program Blossom (Cade & Richards 2005).

Ripley's K and the L-function

We used the K function (Ripley 2004), based on the co-occurrences of pairs of points, to analyse point patterns. This function ($K_{(r)}$) is measured as the average number of trees found within a set distance r from each focal tree, divided by the mean intensity (λ) of the pattern. The mean intensity is the number of trees per area, $\lambda = n / A$. To correct for edge effects we weighted each count by the inverse of the proportion of the circle of radius r centred on tree i that fell within the study plot, $w_{ij} = 1 / p_{ij}$. The expectation for K when trees are randomly distributed is λ times the area of the sampled circle, or $\lambda\pi r^2$. It is difficult to interpret $K_{(r)}$ visually but a square root transformation of $K_{(r)}$, called the L-function (Wiegand & Moloney 2004) has expected value of zero when trees are randomly distributed; $L_{(r)} < 0$ indicate regular spacing up to distance r, $L_{(r)} > 0$ indicate clumping or aggregation up to distance r.

Monte Carlo simulations randomizing coordinates of each stem were used to construct 95% confidence envelopes and test the fit of the observed data against the null model (complete spatial randomness) (Bailey & Gatrell 1995). K or L are cumulative distributions and confound effects at a particular distance with those at shorter distances (Condit et al. 2000; Wiegand & Moloney 2004). This is an appropriate property if the process in question (e.g., the negative effect of competition) operates up to a certain distance between neighbours. We take the distance at which $\hat{L}_{(r)}$ (the estimated L-function) no longer differs from zero as the radius of the circle defining the potential area of influence of individuals in the study area. Analyses were conducted using the method and algorithms in the software Programita (Wiegand & Moloney 2004).

The O-ring statistic

Although closely related to the K-function, the O-ring statistic, $O_{(r)}$ (Wiegand & Moloney 2004) detects aggregation or dispersion *at*, as opposed to *up to*, a given distance r, and is a probability density function rather than a cumulative distribution. $O_{(r)}$ is synonymous with the relative neighbourhood density index (Ω) that has been used to describe spatial distribution of tropical tree species (Condit et al. 2000). Because $O_{(r)}$ refers to an annulus, unlike the cumulative K statistic, it does not confound effects at larger distances with effects at shorter distances. Thus, the O-ring statistic is a more accurate estimate of aggregation of individuals at particular distances from a focal point or tree than Ripley's K.

As for the K-function, significance of observed values of $O_{(r)}$ is determined by comparison against Monte Carlo envelopes derived from multiple simulations of a spatially randomized null model (Wiegand & Moloney 2004). In a perfectly random distribution $O_{(r)} = \lambda$ for all distances r. Aggregation of neighbours at distance r is indicated when $O_{(r)} > \lambda$. $O_{(r)} < \lambda$ at short distances indicates regularity (Wiegand & Moloney 2004). For comparison between species, $O_{(r)}$ can be standardized to give the Ω (relative neighbourhood density) index, by dividing it by the mean density of a given species across the whole plot (Condit et al. 2000), in which case a random distribution yields $\Omega = 1$ for all distances, aggregation at distance r yields $\Omega > 1$ and at short distances $\Omega < 1$ indicates regularity or hyperdispersion (Condit et al. 2000).

Loosmore & Ford (2006) are critical of using simulation envelopes to estimate the range of distances over which an observed pattern deviates from the hypothesized model, because the Monte Carlo simulated patterns involve simultaneous inference and the type I error rate may be greatly underestimated. This is particularly problematic when using the cumulative *K* statistic, but is not a concern when using the *O*-ring method in Programita (pers. comm. T. Wiegand). To deal with potential underestimation of type I error rate we used a goodness-of-fit (GoF) test implemented in Programita (November 2006).

Using the *O*-ring method and the Ω index we examined whether conspecific individuals were aggregated relative to a null model (spatially random distribution). We also conducted a bivariate *O*-ring analysis ($g12_{(r)}$) using the toroidal shift null model in Programita (Wiegand & Moloney 2004) to evaluate whether other species were aggregated around individuals of the most abundant 18 species. In addition, because large trees (≥ 20 cm DBH) may influence the pattern of distribution of small trees (< 20 cm DBH) within their area of influence (by competitive thinning), we conducted a bivariate *O*-ring analysis for these two size classes using both the toroidal shift and the antecedent condition null model options in Programita (Wiegand & Moloney 2004). This tests whether the patterns of distribution of small and large trees were generated by independent processes. The antecedent condition model tests whether one pattern (small trees) is influenced by a second pattern (large trees), assessing whether there are more (or less) small trees in the neighbourhood of large trees than expected under a random distribution of small trees (Wiegand & Moloney 2004).

In addition to examining spatial patterns that may reflect competitive thinning, we tested whether aggregation of individuals weakened with increasing focal tree size. We did this in two ways. First, we regressed the number of individuals within a 5-m radius of all focal individuals against the $\log_{10}$-transformed DBH size-class range. Stem counts up to a radius of 5 m were conducted because the negative effects of competition among individuals appeared to decay to background levels at this distance (see Results section). Because circles about focal individuals overlapped, these variables for all individuals were not independent. Accordingly, we selected only individuals whose circles did not overlap and estimated the regression intercept and slope from this reduced dataset. Second, we tested the hypothesis by calculating univariate *O*-ring values ($g11_{(r)}$) for the size classes separately and comparing to expectations derived from a random labelling null model (Wiegand & Moloney 2004). This analysis examines whether the univariate spacing pattern of a given size class differs from the univariate structure of the entire population. Values of $g11_{(r)}$ within the 95% confidence envelopes indicate that the spatial structure of the given size class does not differ significantly from the overall structure of the tree population. Values of $g11_{(r)}$ above the 95% C.L. indicate that a size class is more aggregated than the overall tree population at the indicated spatial scale; values of $g11_{(r)}$ below the 95% C.L. indicated lower aggregation (approaching a more regular pattern) for the size class at that scale (pers. comm. T. Wiegand).

Finally, we examined the area of influence of small versus large focal trees by counting the number of stems and/or their combined basal area in circles of increasing diameter about a focal tree. If smaller focal trees have a smaller area of influence than large focal trees, then one should initially find more stems (and a greater basal area) within the area of circles of the same size about small focal trees than about larger focal trees. The number of stems and basal area should accumulate more steeply for small focal stems (< 20 cm DBH) than large (30 cm < DBH < 200 cm) ones.

Results

The potential area of influence, as measured by Thiessen polygons was independent of tree size in OLS regression (Fig. 1) and this result was confirmed by quantile regression. Mean polygon area was constant at 14.09 m^2 across all tree sizes ($F_{1,\,615} = 0.19$, $P = 0.66$, Area = 14.09 - 0.53[$\log_{10}$ DBH Focal tree]). In independent analyses for the six dominant species polygon area was independent of tree size and the slope of the relationship between polygon area and tree size did not differ from zero in any case ($P > 0.2$; Table 1). Neither the DBH nor the basal area of stems was spatially autocorrelated ($P > 0.05$) and stems of similar sizes did not appear to be clumped in their distribution. Thus, the spatial autocorrelation in polygon area (see Methods) is likely independent of focal stem size.

The maximum distance between nearest neighbours over all species was 6.75 m and the mean was 2.32 m (SD = 1.06, n= 1518). Nearest neighbour distance decreased slightly with increasing tree size (Δ = 0.75 m across the range of tree sizes; $F_{1,\,1517} = 4.09$, $P = 0.04$, NN dist. = 2.38 - 0.00272 [DBH Focal tree]), but the number of stems > 10 cm DBH within 5 m of a focal tree did not change significantly with increasing focal tree size (slope = – 0.005, t = – 1.25, $F_{1.517} = 1.57$, $P = 0.21$; mean = 4.69, SD = 1.99). Overall, the values of $g11_{(r)}$ were within the 95% confidence envelopes and individuals were not less aggregated with increasing size of a focal tree. However, at close distances (< 2 m) from the focal individual, smaller trees (< 20 cm DBH) were slightly more regularly spaced than the overall population structure. These findings suggest weak competitive thinning among the more densely packed smaller trees, but this effect quickly faded with increasing tree size and distance from the focal individual. Although the number of stems

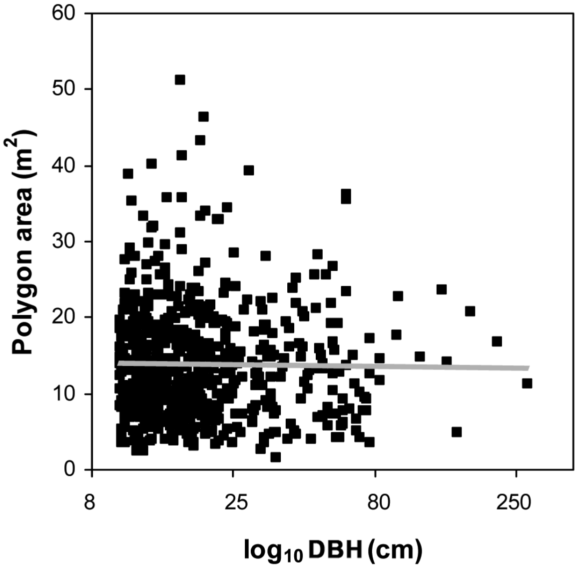

Fig. 1. The relationship between the potential area of influence (Theissen polygon area) of a focal tree and the size (DBH) of the focal tree, indicating a constant potential area of influence (14.09 m^2; regression line) across the range of tree sizes.

(and the basal area) did accumulate more steeply for small than large trees in circles of increasing diameter about a focal tree, the difference in slope between small and large stems was small relative to the variation involved (Fig. 2), again suggesting little or no influence of tree size on tree spacing and aggregation.

When considering all trees in the stand, trees > 10 cm DBH displayed non-random patterns of distribution with respect to one another at small spatial scales. Ripley's L showed regular spacing of individuals up to a distance of 4 m (GoF test, $P = 0.016$), and aggregation of stems at distances > 8 m (GoF test, $P = 0.033$; Fig. 3). The more conservative and less spatially confounded O-ring analysis revealed a non-random pattern with regular spacing at distances of 1-3 m (GoF test, $P = 0.016$), but random spacing at greater distances with a constant neighbourhood density $O_{(r)}$ that was only slightly above the overall intensity λ (Fig. 4).

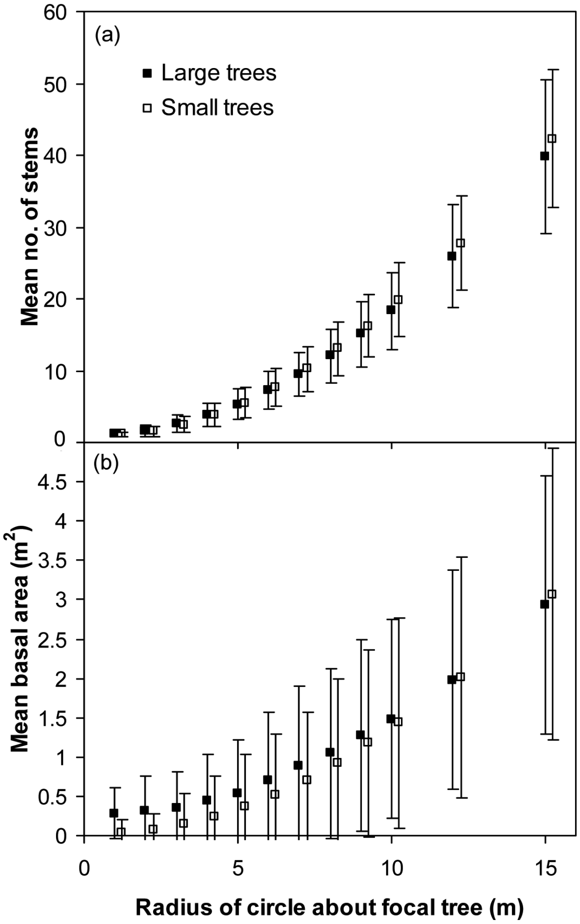

Fig. 2. Comparison of (**a**) cumulative counts of stems and (**b**) cumulative basal area about small (< 20 cm DBH) and large (30 cm < DBH < 200 cm) focal trees for circles of increasing radius about a focal tree. Error bars are 1 SD.

Table 1. Thiessen polygon area for each of the six dominant species in the plot and their level of aggregation based on the $O_{(r)}$ index. The area is calculated based on conspecific stems only. In each instance, the polygon area was invariant with increasing stem size based on the linear regression slope coefficient.

Species	No. stems	Polygon area (m^2) mean ± 1SE	*t*-value	*P*	Aggregation
Uvariopsis congensis	714	56.7 ± 16.2	–0.47	0.63	Moderate
Markhamia lutea	284	118.5 ± 24.9	0.15	0.87	Slight
Leptonychia mildbraedii	242	126.0 ± 65.5	–0.35	0.72	Moderate
Funtumia africana	241	106.4 ± 27.4	1.26	0.21	Slight
Celtis durandii	219	145.2 ± 31.9	0.99	0.32	Random
Diospyros abyssinica	216	147.9 ± 31.5	1.17	0.24	Random

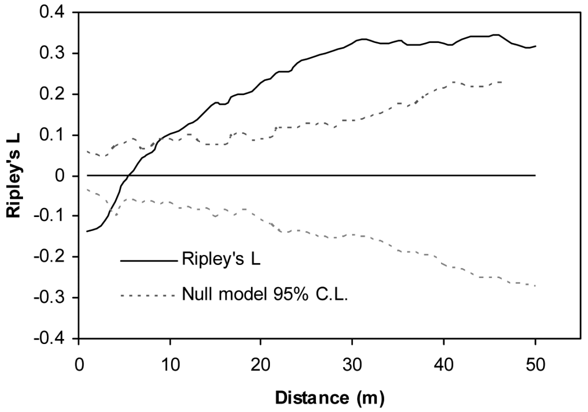

Fig. 3. The univariate Ripley's *L*-function with confidence envelopes showing a generally non-random pattern of distribution of all trees within the study area. Up to short distances from focal individuals, trees appear to be regularly spaced, while at longer distances the *L*-function suggested aggregation of stems. Confidence envelopes are the highest and lowest $L_{(r)}$ of 99 randomizations of the pattern over the study area.

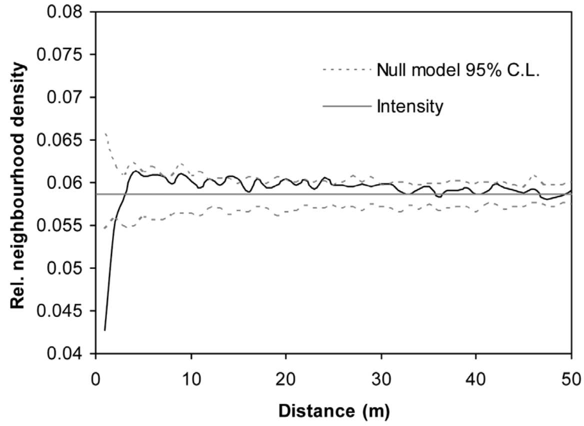

Fig. 4. The univariate O-ring statistic, giving the local neighbourhood density of the pattern for all trees at increasing distances from the focal tree. Confidence envelopes are constructed in the same way as in Fig. 3. The intensity (λ) of the pattern in the study area is given for comparison and interpretation of the statistic (see Methods). A regular pattern of distribution of stems occurs at short distances, but in contrast to the *L*-function (Fig. 3), stems are only weakly aggregated, if at all, at longer distances from the focal tree.

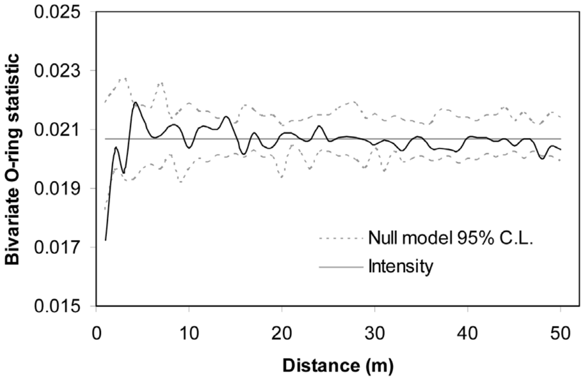

Fig. 5. Test of the independence of the patterns of distribution of small and large trees in the study plot. Note that the O-ring statistic falls within the confidence envelopes for the independence null model – toroidal shift null model (see Wiegand & Moloney 2004).

Regular spacing at small distances may have been an artefact of the small cell size (ca. 1 m^2) used in the analyses. However, this regularity is likely real at small distances as it persists over several values of *r*. Assuming that regular spacing is indicative of the competitive effect of individuals on each other, the influence of individual trees appears to be local, extending no more than 3-5 m from a focal individual.

Bivariate *O*-ring analysis indicated that in general, patterns of distribution of small and large trees were not generated by two independent processes, except perhaps for those small individuals (< 20 cm DBH) in very close proximity to one another (Fig. 5). Overall, based on the antecedent condition null model, the pattern of distribution of small (< 20 cm DBH) trees was not influenced by the pattern of distribution of large (≥ 20 cm DBH) trees.

At the species level, four of the six dominant species had a slightly (*M. lutea*, *F. africana*) or moderately aggregated (*U. congensis*, *L. mildbraedii*) conspecific spacing pattern at short distances (5 m), and their neighbourhood density indices were above the overall intensity and just outside the 95% confidence envelopes of the Monte-Carlo tests for random distribution. Two of the dominant species (*C. durandii*, *D. abyssinica*) appeared to be randomly distributed with $O_{(r)}$ values well within the confidence limits of the Monte-Carlo tests over all distances. We compared the degree of clumping (Ω) of conspecific individuals among the 18 species, including the six dominant species (Fig. 6), for which there were sufficient individuals. This relative neighbourhood density index (Ω) declined with distance for all species. Although all 18 species had relative neighbourhood densities for distances of 1 to 10 m ($\Omega_{1\text{-}10}$) > 1, only six of the 18 species were

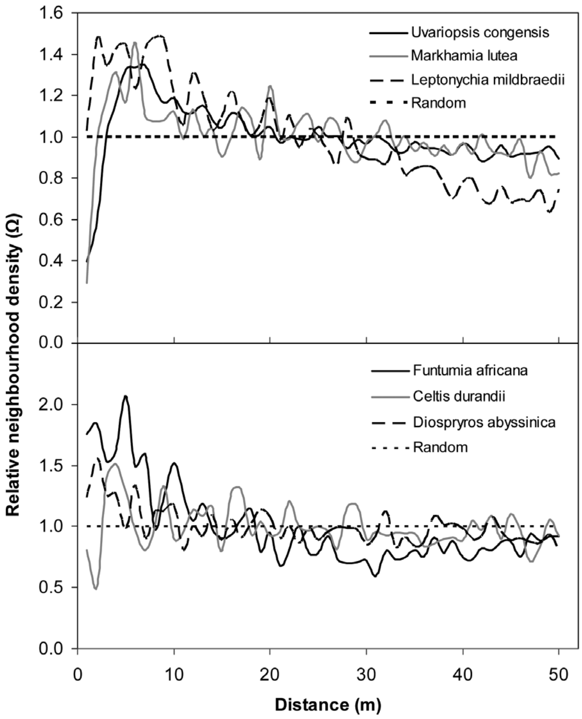

Fig. 6. Relative neighbourhood density (Ω_x as defined in the text) as a function of distance for the six dominant species in the sample.

significantly aggregated at $\Omega_{1\text{-}10}$, and only five of these six species at $\Omega_{>10}$ (App. 1). Among these 18 species the degree of clumping correlated negatively with species overall density (Spearman's rank correlation, $\varrho = -0.578$, $P < 0.01$); rarer species were more clumped than were common species.

Lastly, we examined the neighbourhood density index ($g12_{(r)}$) for the most abundant 18 species. For seven species the spacing pattern of individuals of other species in their immediate neighbourhood ($g12_{(1\text{-}5)}$) was less aggregated (a more regular distribution) than the overall spatial structure of the tree population and at distances > 5 m was no more or less aggregated than the overall pattern. Three of these seven species were significantly less aggregated than expected and were among the six most abundant species (*U. congensis*, *L. mildbraedii*, *F. africana*). For the other 11 species, the spacing patterns of individuals of other species at all neighbourhood distances conformed to the overall spacing pattern (randomly spaced neighbours) for the tree population.

Discussion

These data provide evidence for non-random patterns of distribution of nearest tree neighbours (≥10 cm DBH) in Kibale forest. Individuals appear to be regularly spaced at short distances (≤ 5 m) and only slightly aggregated or mostly randomly spaced at greater distances. Several separate analyses confirmed that the overall area of influence of individuals was small (tessellation estimate = 14.09 m^2) and highly local, extending no more than 3-5 m for all neighbours, including conspecifics (point-pattern analysis). It should be noted that the tessellation estimate is likely an underestimate as trees of all sizes that were within the canopy shadow of larger trees, including understorey trees, were used to define the same polygon boundaries. The point-pattern analyses suggest a two to five times larger area of influence than the mean tessellation estimate. Nevertheless, the negative effects of competition among individuals appear to occur over only small distances, and within the crown radius of most individuals (Hubbell et al. 1990). These findings contrast with other studies of rain forest trees where conspecific neighbourhood effects were no longer detected beyond 10-15 m from a focal tree using distance intervals of 2.5 m (Hubbell et al. 1990; 2001; Uriarte et al. 2005) and beyond 4-6 m of understorey tree species (Condit et al. 1994). The larger area of influence of individual trees detected in some studies may be because neighbourhood patterns were analysed using a relatively large and fixed radius to begin with so that the most 'local' patterns detectable implied larger neighbourhoods than suggested here (Condit et al. 1994). Interestingly, when even wider neighbourhoods than a 10 m radius were considered (Condit et al. 2000), there was an increased area of influence in a few species, but for the most part, conspecific neighbourhood effects (recruitment, mortality) were strongest at very local scales (< 4 m) (Condit et al. 1994). Another possibility is that lower tree species diversity at Kibale compared to Central American forests may result in less diffuse competition effects, stronger conspecific competition, and consequently a narrowing of the area of influence about individuals at Kibale. That the potential conspecific area of influence was invariant with increasing focal tree size in our study further suggests that tree spacing mechanisms are likely weak in their direct effects at distances > 5 m.

Heterospecific tree spacing mechanisms limit the overall density of a forest and are implicated in determining tree biomass (Midgley et al. 2002). Thus, studies of heterospecific spacing patterns among forest trees are important for understanding how tree biomass accumulates and varies in forests (Enquist & Niklas 2001; Niklas et al. 2003). Of course, spacing or neighbourhood patterns are caused by dynamic processes, which we do not explicitly measure. Nevertheless, our static data do suggest the influence of various mechanisms. For example, density-dependent competition for resources may influence seedling and sapling survival and ultimately community-wide tree spacing patterns and neighbourhood effects (Hubbell et al. 2001; Wright 2002; Coomes et al. 2003; Uriarte et al. 2005). Regular spacing of pole-size (10 - 20 cm DBH) individuals may imply competitive thinning in the sapling size class and we found evidence for weak competitive thinning among closely spaced smaller trees (< 20 cm DBH). Competition and mechanisms of establishment in the small-stem phase may influence neighbourhood patterns. Wright (2002) and Porter (2005) suggest that competition among heterospecific seedlings is relatively rare in tropical forests, but Hubbell et al. (2001) found that competitive thinning and crowding were important drivers of sapling survival regardless of the identity of neighbours. However, this density-dependent effect weakened or disappeared as saplings recruited into the pole and larger size classes (Uriarte et al. 2004b). While our study suggests that the small stem phase has been partly shaped by competitive thinning, the aggregation or clumping of individuals did not decline with increasing focal tree size, at either the conspecific or community level. Our results lead us to agree with Coomes et al. (2003) that distribution of large stems (>10 cm DBH) is shaped more by exogenous disturbance events than by inter- or intra-specific competition. Thus, to explain high point diversity in tropical forests, our data suggest that distribution patterns of tree species and the attendant processes should be examined first at a small spatial scale and be focussed on the mechanisms of establishment of seedlings and the fate of saplings (Clark & Clark 2006).

In their meta-analysis of tree census plots on two continents, Condit et al. (2000) found that for most species (90%) the conspecific trees (DBH ≥ 10 cm) were aggregated within circular neighbourhoods of 10 m radius, which is roughly twice the maximum distance at which competitive effects appear to be operating in our study. About half of the species (47%) were significantly aggregated and aggregation intensity also weakened with increasing tree size and individuals of rare species were significantly more aggregated than individuals from common species (Condit et al. 2000). We cannot easily compare our results to Condit et al. (2000) because of the relatively small size of our plot (4 ha vs. 25-52 ha) and the lower tree diversity at Kibale, but more importantly because their circular neighbourhoods were measured in tens of metres and thus at a scale too coarse to detect the local effects suggested by our study. Nevertheless, our results for the Condit et al. (2000) relative neighbourhood density index (Ω) showed some points of congruence: (1) all 18 species that could be tested in our study displayed $\Omega_{1\text{-}10} > 1$, but only six species (33%) were more aggregated than expected at this scale; (2) species were randomly distributed at larger spatial scales ($r > 10$ m) (App. 1); and (3) rarer species were more aggregated than common species at Kibale. It has been suggested that greater aggregation of rare species is a consequence of poor dispersal (Condit et al. 2000), but necessary life-history data to assess this possibility are lacking for the Kibale forest (pers. comm. A. Zanne).

Finally, tree diameter alone appears to be a poor measure of effective tree size and influence on tree neighbours in this rain forest. There are several reasons why this may be so. For instance, competition among individuals for resources and position on the forest floor may be resolved before trees reach 10 cm DBH size. If tree spacing patterns are determined by competition at all, then the most influential competition is likely over small spatial scales (<1 m) among seeds, seedlings and young saplings (Condit et al. 1994; Capers et al. 2005) or between large trees and these small stems (Coomes & Grubb 2000). This may also explain why the density and level of clumping of mature trees did not scale with adult tree size (Coomes et al. 2003) as well as the regularity in distribution of close neighbours. Furthermore, stratification of tree crowns may facilitate stem packing (Herwitz et al. 2000), in a way that is independent of stem diameter. Also, large but senescing individuals may require proportionally fewer resources than younger trees resulting in greater stem aggregation than expected (‘additive basal area’ phenomenon, Lawes et al. 2006). If so, the area of influence about a tree cannot be defined by Theissen polygons, which take no account of the overlap in crown areas or tree height, and is best judged from the relative distribution and aggregation of stems using point-pattern analyses.

For all the above reasons, Theissen polygons provide a conservative and confounded estimate of the area of influence of a tree in stratified rain forest, and we avoid deriving conclusions based on polygon analysis and prefer measures of aggregation. In addition, spatial patterns that are independent of tree size may be caused more by density-dependent mortality effects other than direct competition for resources in relation to tree size. Disease and herbivory/predation are well known density-dependent mortality effects (Janzen 1970; Connell 1971; Connell et al. 1984) that affect mainly seeds or young seedlings in tropical forests (Janzen 1970; Connell 1971; Connell et al. 1984; Harms et al. 2000, 2004) and have been implicated in regulating population density of some species (Condit et al. 1992; Wills et al. 1997; Wills & Condit 1999). Density-dependent seedling recruitment has also been found at Kibale (Chapman & Chapman 1996) and supports our argument that establishment of seedlings and the fate of saplings are the likely primary determinants of tree-spacing patterns.

In conclusion, the static distributions described here suggest that the effect of competition among mature trees on spacing patterns is weak and independent of adult tree size. Distributions suggest that individual trees had local areas of influence and conspecific and heterospecific neighbourhood effects were not easily detectable beyond 5 m from a focal tree, and even then competitive thinning appeared to affect only small stems (10 - 20 cm DBH). Given the implied effects of thinning on small stems in this study, and the importance of density-dependent effects on seedling and sapling growth and survival in other studies (Capers et al. 2005; Uriarte et al. 2005; Clark & Clark 2006), we conclude that competition at the seedlings and saplings stages is likely a fundamental driver (cf. Poorter 2005) of the spatial pattern of tropical forest trees.

Acknowledgements. Funding for this research was provided by the University of KwaZulu-Natal research office to MJL and by the Wildlife Conservation Society and Natural Science and Engineering Research Council (NSERC) Canada to CAC. Permission to conduct this research was given by the National Council for Science and Technology, and the Uganda Wildlife Authority. We are grateful to Tusiime Laurence and 'King' Solomon for their assistance in the field, Rick Condit for comments on drafts of the manuscript, Amy Zanne for comments on the dispersal ecology of rare species, and Thorsten Wiegand for his guidance in the use of Programita to conduct point-pattern analyses.

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Received 21 February 2007;
Accepted 30 November 2007;
Co-ordinating Editor: K.D. Woods.

For App. 1, see below (online version)
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App. 1. Relative neighbourhood density (Ω) values, after the method of Condit et al. (2000), for the six most dominant species in the plot at Kibale National Park, western Uganda..

Scale (m)	SPECIES					
	Uvariopsis congensis	*Markhamia lutea*	*Leptonychia mildbraedii*	*Funtumia africana*	*Celtis durandii*	*Diospyros abyssinica*
1	0.59	0.29	1.03	1.76	0.81	1.24
2	1.00	0.98	1.47	1.84	0.51	1.56
3	1.16	1.18	1.34	1.54	1.39	1.26
4	1.33	1.31	1.42	1.61	1.51	1.27
5	1.33	1.17	1.44	2.06	1.29	0.98
6	1.34	1.46	1.23	1.50	0.97	1.33
7	1.24	1.10	1.43	1.59	0.80	0.90
8	1.16	1.07	1.48	0.98	0.99	1.12
9	1.19	1.08	1.48	1.24	1.33	1.13
10	1.12	1.12	1.20	1.52	0.90	1.17
11	1.12	0.99	1.06	1.26	0.96	0.80
12	1.15	1.13	1.30	1.05	1.14	1.00
13	1.08	1.01	1.20	1.19	1.09	0.92
14	1.04	1.04	1.03	0.98	1.16	1.10
15	1.11	0.90	1.09	0.90	0.80	0.88
16	1.09	1.00	1.22	0.93	1.29	1.05
17	1.00	1.14	1.09	1.05	1.31	0.91
18	1.01	1.09	1.01	1.14	0.93	1.02
19	1.05	0.90	1.06	0.79	1.04	1.14
20	0.97	1.25	1.19	0.95	0.93	1.08

App. 1. Internet supplement to: Lawes, M.J. et al. 2008.
Tree spacing and area of competitive influence do not scale with tree size in an African rainforest
Journal of Vegetation Science 19: 729-738; doi: 10.3170/2008-8-18445

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