

Spatial pattern of *Quercus* regeneration limitation and *Acer rubrum* invasion in a Piedmont forest

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Abstract. Across eastern North America, there is a temporal trend from open *Quercus* forests to closed forests with increased *Acer rubrum* in the understory. We used a series of Ripley's $K(d)$ analyses to examine changes in the spatial pattern of *Quercus* and *Acer rubrum* stems greater than 2.5 cm DBH over 45 yr in a 2-ha mapped stand. Specifically, we asked whether changes over time were consistent with the hypothesis that *Quercus* is being competitively replaced by *Acer rubrum*. Both *Acer rubrum* and *Quercus* stems are spatially clumped, but have become less clumped over time. Stem mortality from Hurricane Fran (1996) was more clumped in all strata of the forest, at all spatial scales, than expected if damage had occurred to stems at random. *Acer rubrum* ingrowth occurred more often near established trees (all species) in the midstory, whereas *Quercus* ingrowth occurred less often near established trees in the midstory. The specific hypothesis that stems of *Acer rubrum* in the midstory of the forest are associated with a lack of *Quercus* regeneration was strongly supported. This effect occurred at all spatial scales tested, including scales larger than that at which direct competition for light can occur. Edaphic gradients in the plot are correlated with many of the observed trends at large spatial scales, and our results suggest that the presence of such gradients can generate complex spatial patterns over time.

Keywords: Competition; Duke Forest; K -function; Oak decline; Self-thinning; Succession.

Nomenclature: Kartesz & Meacham (1999).

Abbreviations: DBH = Diameter at breast height; CSR = Complete spatial randomness.

Introduction

In deciduous forests of the eastern United States, *Quercus* populations seem to be in decline (Clark 1993; Abrams 1992). Several causal factors have been implicated (Lorimer 1993), such as disease (e.g. Donaubauer 1998; Bruhn et al. 2000), seed predation (Marquis et al. 1976; Sork 1984), and drought (e.g. Dwyer et al. 1995; Jenkins & Pallardy 1995), although in many cases oaks are better adapted to deal with drought than other taxa (Abrams 1996). Some attribute *Quercus* decline to a failure of *Quercus* seedlings and saplings to survive in competition with more shade-tolerant species (e.g. Lorimer 1984, 1994) that were previously held in check by low-intensity surface fires, but which have increased under anthropogenic fire suppression (e.g. Abrams 1992; Lorimer 1985). Consistent with this model, shade-tolerant species such as *Acer rubrum* and *A. saccharum* have increased dramatically following fire suppression (Christensen 1977; Orwig & Abrams 1984). Other factors contribute to increases in *Acer rubrum* populations as well (Abrams 1998), and in some instances, *Quercus* decline is not strongly correlated with *A. rubrum* density at a landscape scale (McDonald et al. 2002). However, direct competition between *A. rubrum* and *Quercus* occurs at the much smaller scale of interactions between stems, and in this study we analyse within-stand patterns of *Quercus* and *A. rubrum* stems for evidence of competitive interactions.

The spatial pattern observed in forests is of interest for its own sake, as it mediates the processes of competition and establishment (Levin 1992). Furthermore, we can sometimes draw inferences about what processes are operating from the pattern observed (Watt 1942, but see Cale et al. 1989). One of the most commonly observed spatial patterns in forests is the tendency for understory stems to be clumped and for canopy stems to be more uniformly distributed (e.g. Moer 1997). Although the decline in density between the understory and overstory of the forest can often be explained by

simple 'self-thinning' laws (Yoda et al. 1963, but see Weller 1987), the change in spatial pattern between the two strata suggests some form of spatially heterogeneous, density-dependent competition (Kenkel 1988). Many studies of mature and old-growth forests have found that establishment occurs preferentially in canopy gaps, leading to characteristic spatial clumping of new stems at the scale of a gap (e.g. Leemans 1991; Moer 1993; Busing 1996). Over time, stems that are crowded by other stems are more likely to die, and the remaining stems are more regularly dispersed (Kenkel 1988; Moer 1993; Busing 1996; He & Duncan 2000). Many other factors may obscure the trend from a clumped understory distribution to a more regular overstory distribution, including patterns of seed dispersal (Fowler 1986), windthrow events (Ida 2000), and surface fire (Miller & Urban 1999). More generally, environmental heterogeneity (Antonovics & Levin 1980) and changes over time in species composition (Busing 1996) can change spatial patterns in forests in important ways. As many of these factors are of interest to ecologists in and of themselves, the spatial pattern observed in a forest at a moment in time can also be seen as the integration of factors causing uniformity in species distributions (e.g. density-dependent competition) and factors that cause clumping in species distributions (e.g., windthrow events or environmental heterogeneity).

We examine spatial patterns, across 45 years of remeasurement, in a mapped stand in the North Carolina Piedmont. Several of the factors listed above are present, which could obscure a trend towards a more uniform stem distribution resulting from density-dependent thinning. Hurricane Fran caused extensive, spatially heterogeneous damage to forests in the area in 1996 (Pasch & Avila 1999), which we predict will increase clumping of species distributions, particularly in the canopy of the forest. Historically, variation in low-intensity surface fires could also have caused clumping of species distributions (Cooper 1961; White 1985). There is high fine-scale variation in soil characteristics in the area (Palmer 1991; Reed et al. 1993), which might generate clumping at the scales over which soil characteristics vary. Furthermore, while *Quercus* dominates the canopy of the plot, *A. rubrum* saplings and other shade-tolerant species are abundant in the understory; since shade-tolerant species may be less affected by density-dependent competition, they could remain more clumped as stems mature into the canopy. This leads us to predict that forests, on average, get more spatially clumped over time as shade-tolerant species become more abundant.

We address the following specific questions about spatial pattern as related to *Quercus* regeneration and competition with *A. rubrum*:

- How do the spatial patterns of *Quercus* and *A. rubrum* change during the transition from a forest with an open understory to a forest with a high density of *A. rubrum* stems in the understory?
- Do significant disturbance events such as hurricanes increase the degree of clumping in species distributions?
- Is the establishment of new *Quercus* and *A. rubrum* stems limited by the locations of established stems regardless of species, and if so at what scales is this important?
- Is the establishment of *Quercus* stems limited by established *A. rubrum*, and if so at what scales is this competitive interaction important?

Methods

Study site

The study site is located in the Duke Forest, Orange County, NC, USA (Bormann 1950, 1953). This forest has been extensively studied, and information on the physical environment of the area can be found in Ashe (1897), Billings (1938), Oosting (1942), Keever (1950), and Peet & Christensen (1980). Temperatures range from a mean daily maximum of 10.1 °C in January to 31.5 °C in July. Mean annual precipitation is 1052 mm, with slightly more precipitation in summer than autumn or winter (NC Climate Office 2001). The study plot is located on a dry upland site with Appling sandy loam the predominant substrate (Anon. 1971, 1975). The area experienced some selective cutting before 1930, but has subsequently been undisturbed.

The 140 m × 140 m study plot was established in 1949 (Bormann 1950, 1953), and has been sampled at irregular intervals since (1974, 1982, 1989, 1993, 1997). During the 1949 and 1974 surveys, diameter at breast height (DBH) and species of each stem > 2.5 cm DBH were recorded, whereas in subsequent surveys all stems > 1 cm DBH were recorded. For consistency, data from latter surveys were censored to include only stems > 2.5 cm DBH. The spatial location of each stem was recorded using various techniques to within 0.5 m (Bormann 1953; Christensen 1977; Christensen & Peet 1981). The canopy of the plot is dominated by *Quercus alba*, with several other *Quercus* species present (*Q. falcata*, *Q. rubra*, *Q. stellata*, *Q. velutina*). The midstory of the forest is generally dominated by *Oxydendron arboreum* and *Cornus florida* with some *A. rubrum*. The majority of stems in the understory are *A. rubrum* or *C. florida* (Christensen 1977). More information about changes in species composition over time in the Duke Forest can be found in Peet & Christensen (1980) and McDonald et al. (2002).

Statistical methods

We used a series of Ripley's $K(d)$ analyses to describe the spatial patterns in our plots. Ripley's K -function is based on the empirical distribution of point-to-point distances (Ripley 1976, 1981):

$$K(d) = \lambda^{-1}E(d) \quad (1)$$

where $E(d)$ is the expected number of points (e.g. trees) within a distance d from any point. If there is only one class of points (e.g. one species of tree) considered in the analysis, then $E(d)$ is simply estimated from the empirical distribution of point-to-point distances between points in that class, and the analysis is referred to as univariate. If there are two classes of points (e.g. two species of trees) considered in the analysis, then $E(d)$ is the empirical distribution of point-to-point distances between points in one class and points in the other class, and the analysis is referred to as bivariate. In either case, $E(d)$ is estimated by calculating all the point-to-point distances in a stand and then partitioning them among a finite number of discrete classes. The number of point-to-point distances in each bin is then the estimate of $E(d)$ for that distance class. In the univariate case, the mean intensity is estimated as the average density of points within the total sampled area, whereas in the bivariate case the estimation is slightly more complex (Cressie 1993). Because edge effects can distort Ripley's $K(d)$, we apply the correction suggested by Cressie (1993, following Diggle 1983).

If points were distributed spatially at random, then the expected value of $K(d)$ is πd^2 . To ease interpretation, we perform the transformation:

$$L(d) = \sqrt{\frac{K(d)}{\pi}} - d \quad (2)$$

which scales the test statistic such that the expectation under spatial randomness is zero for all values of d (after Besag 1977). With this transformation, positive values of $L(d)$ suggest contagion (or in the bivariate case, attraction), whereas negative values suggest uniformity (or in the bivariate case, repulsion). We perform significance tests of various hypotheses using specific randomization and permutation tests described below.

Univariate analyses

To determine how the clustering of *Quercus* and *A. rubrum* stems has changed over time, we first conducted a series of univariate Ripley's $K(d)$ analyses. All *Quercus* species were lumped together to increase sample size –

this lumping is defensible ecologically because the upland *Quercus* species in the plot are similar in shade tolerance and drought tolerance (Ferrill 1953; Bourdeau 1954; Burns & Honkala 1990). All stems of a particular taxon (*A. rubrum* or *Quercus*) present during a particular census were subdivided into three strata, based upon size: understory (2.5 - 5 cm DBH), midstory (5 - 20 cm DBH), and overstory (> 20 cm DBH). These breaks, although somewhat arbitrary, approximate strata discernable in the plot. Univariate $K(d)$ analyses were then calculated for a particular taxon in a given stratum, to reveal general trends in spatial pattern among strata of the forest and over time.

Differences in $K(d)$ values between strata and over time were assessed graphically. To test whether particular patterns (for each taxon-stratum-census combination) departed from complete spatial randomness (CSR), we took random values for (x, y) coordinates of each point (within the bounds of the study area) 100 times, and then recalculated the $K(d)$ statistic for each set of random coordinates. Approximate 90% confidence limits under CSR can be found by saving the 5th and 95th largest $K(d)$ values from the randomized data. Although the number of randomizations here is lower than with many other applications, the confidence intervals obtained are stable (Manly 1997), since each randomization involved drawing many random numbers (two for each stem whose location is randomized).

After Hurricane Fran in 1996, trees were given condition codes that recorded whether a tree had died during the hurricane, usually from being uprooted. To determine whether this hurricane damage had any spatial pattern, we conducted a univariate $K(d)$ analysis of trees that died of hurricane damage. We wished to know whether, given the location of stems in the plot, the spatial clustering of the set of stems that were damaged was significantly different from that which might be expected if stems were damaged randomly. Following the method of Kenkel (1988), we drew 100 random sets, each of the same size as the number of stems actually damaged, randomly from the pool of stems that were present in 1998. For each one of these sets, the actual locations of the selected stems were used to conduct a univariate $K(d)$ analysis; thus, the spatial location of stems was held constant, and only which stems died was varied. Approximate 90% confidence limits under this null hypothesis, that trees that die were a random draw of live stems, can be found by saving the 5th and 95th largest $K(d)$ values from the randomized sets. Although this analysis is somewhat simplistic in that hurricane damage was likely anisotropic, it should suffice to reveal the general scales of hurricane damage.

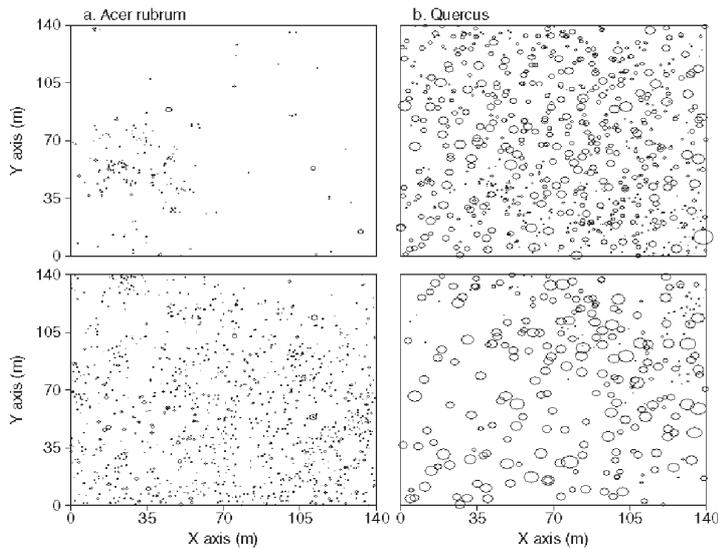


Fig. 1. Locations of (a) *Acer rubrum* and (b) *Quercus* stems in 1949 and 1997 (c, d). Coordinates shown are internal coordinates of the plot. Diameters are scaled at $10\times$ the scale of the map to allow the range of sizes of stems to be seen more easily, so stems with similar coordinates may appear to overlap.

Bivariate analyses

We tested the degree to which ingrowth (i.e. stems that had reached 2.5 cm DBH since the previous plot census) was clustered in gaps in the forest by conducting a series of bivariate Ripley's $K(d)$ analyses. For each plot census after the first one, distributions of *A. rubrum* or *Quercus* ingrowth stems were compared with distributions of all species in all strata using a bivariate $K(d)$ analysis. The relevant statistical question for ingrowth is whether the location of ingrowth was random, given the location of older stems. We tested the null hypothesis that the location of ingrowth was random with respect to older stems, by randomly drawing new (x, y) coordinates for each stem of ingrowth $100\times$ while holding the location of previously established stems constant. In this, new coordinates were constrained only by the bounds of the study site. Confidence limits were calculated as in the univariate case from the distribution of randomized $K(d)$ values.

Finally, we tested the hypothesis that established *A. rubrum* stems in the understory and midstory of a forest inhibit *Quercus* regeneration (Abrams 1991; Lorimer 1985). For each plot census after the first one, a bivariate $K(d)$ analysis was conducted comparing *Quercus* ingrowth to established *A. rubrum* stems in a particular stratum (understory or midstory). Significance was assessed as with the previous bivariate test, by randomizing the location of *Quercus* ingrowth while keeping *A. rubrum* stems fixed.

Results

To facilitate interpretation of our spatial results, we provide a map of *Acer rubrum* and *Quercus* stems in 1949 and 1997 (Fig. 1). In this orientation, the upper right portion of the plot is uphill, has shallower, rockier soils, and is presumably more xeric, compared to the downhill areas (lower left) of the plot.

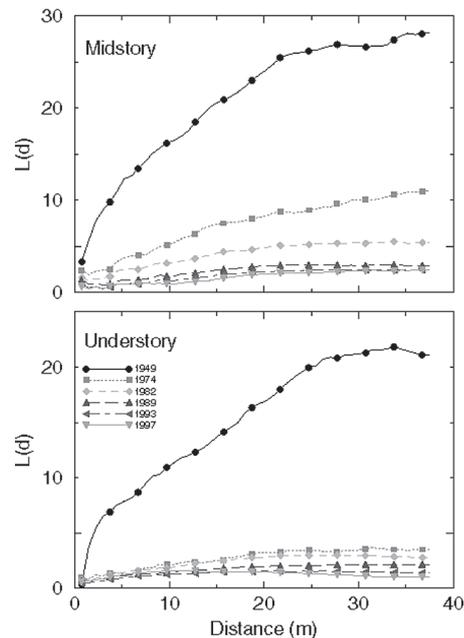


Fig. 2. Transformed Ripley's $K(d)$ for *Acer rubrum* stems over time in the midstory (5 - 20 cm DBH) and understory (< 5 cm DBH). There are insufficient *Acer rubrum* stems in the overstory (> 20 cm DBH) to assess spatial patterns. Both strata displayed are more clumped at all spatial scales tested ($P < 0.05$) than would be expected from a random distribution of stems, with the exception of distances < 5 m in 1997.

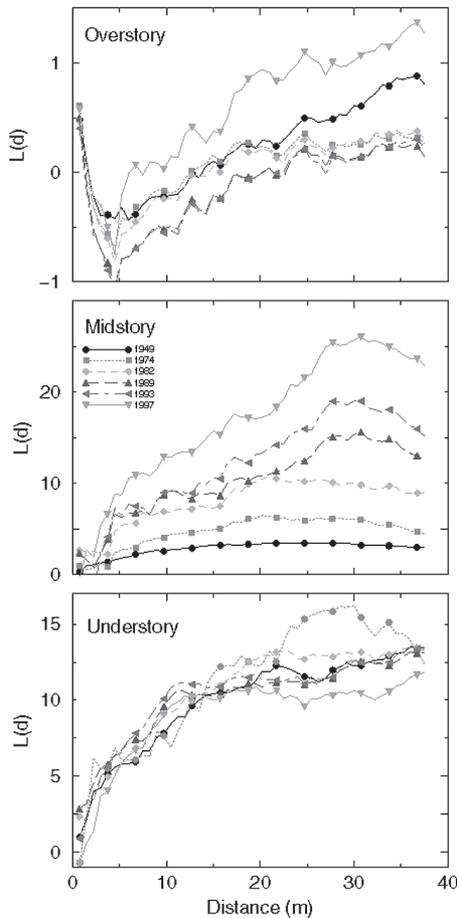


Fig. 3. Transformed Ripley's $K(d)$ for *Quercus* stems over time in the overstory (> 20 cm DBH), midstory (5 - 20 cm DBH) and understory (< 5 cm DBH). Understory and midstory strata are significantly more clumped at all spatial scales tested ($P < 0.05$) than would be expected from a random distribution of stems, except for distances < 1m in 1997. Overstory *Quercus* are regularly distributed for some years, particularly at 1.5 - 5 m; see text for more detailed explanation.

Univariate analyses

Understory and midstory *A. rubrum* stems are significantly ($P < 0.05$) more clumped at all spatial scales than would be expected if stems were distributed according to CSR, although the degree of clumping has decreased over time (Fig. 2). *A. rubrum* stems in the overstory are too few to extract information about spatial pattern. Note that after 1974 *A. rubrum* in the midstory has been more clumped than *A. rubrum* in the understory. Furthermore, there is a clear trend towards lower values of $L(d)$ over time, and hence a less clumped distribution, in both strata and at all scales. The statistical significance of this trend is difficult to fully assess without a more complicated randomization. In both the midstory and the understory, for all distance classes the value of $L(d)$ is ordered $L_{1949} >$

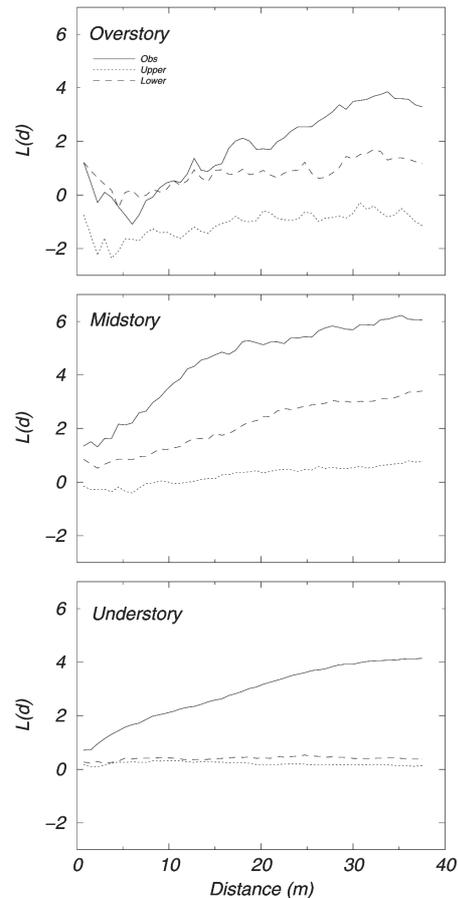


Fig. 4. Transformed Ripley's $K(d)$ for stems of all species damaged or killed by Hurricane Fran in 1996. The upper and lower confidence limits are the 95% confidence limits for predicted pattern if the probability of hurricane damage was the same for all stems regardless of location. The observed pattern is significantly more clumped at most point-to-point distances except for distances < 10 m for overstory trees.

$L_{1974} > L_{1982} > L_{1989} > L_{1993} > L_{1997}$, which is highly unlikely to occur by chance (for one point, Kendall's $\tau = -1$, $P = 0.0048$; Sokal & Rohlf 1981). However, the magnitude of the change in $L(d)$ over particular time periods is difficult to interpret, as the intervals between censuses vary in length. In addition, values of $L(d)$ at larger spatial scales are known with less precision than the values of $L(d)$ at smaller spatial scales, simply because there are fewer pairs of points in larger distance classes than in smaller distance classes.

Trends in spatial patterns in *Quercus* stems differ from those of *A. rubrum* (Fig. 3). As with *A. rubrum*, both understory and midstory *Quercus* stems are significantly more clumped ($P < 0.05$) at almost all spatial scales than one would expect under CSR. However, midstory *Quercus* stems are actually becoming more

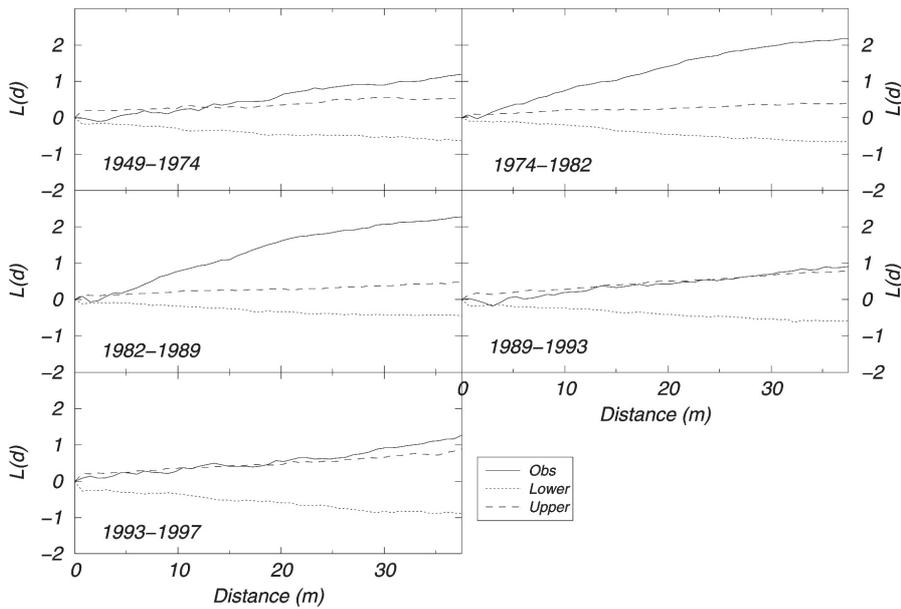


Fig. 5. Transformed bivariate Ripley's $K(d)$ showing the spatial relationships between *Acer rubrum* ingrowth and stems of all species present in the midstory. The upper and lower confidence limits are the 95% confidence limits of the spatial pattern that would be expected if ingrowth were distributed randomly with respect to the fixed set of stems in the midstory. Observed values of $L(d)$ for distances > 5-10 m are generally greater than predicted, implying that there is more *Acer rubrum* ingrowth at these distances from midstory stems than would occur by chance alone.

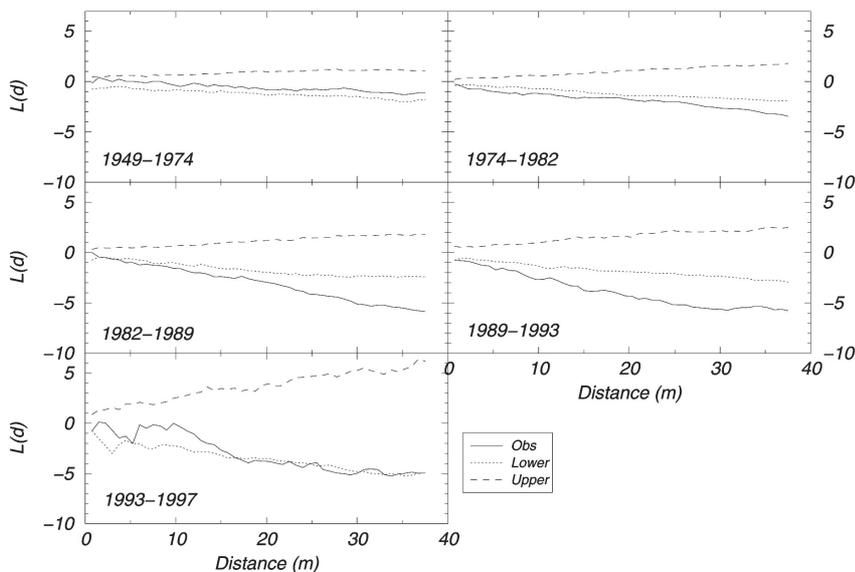


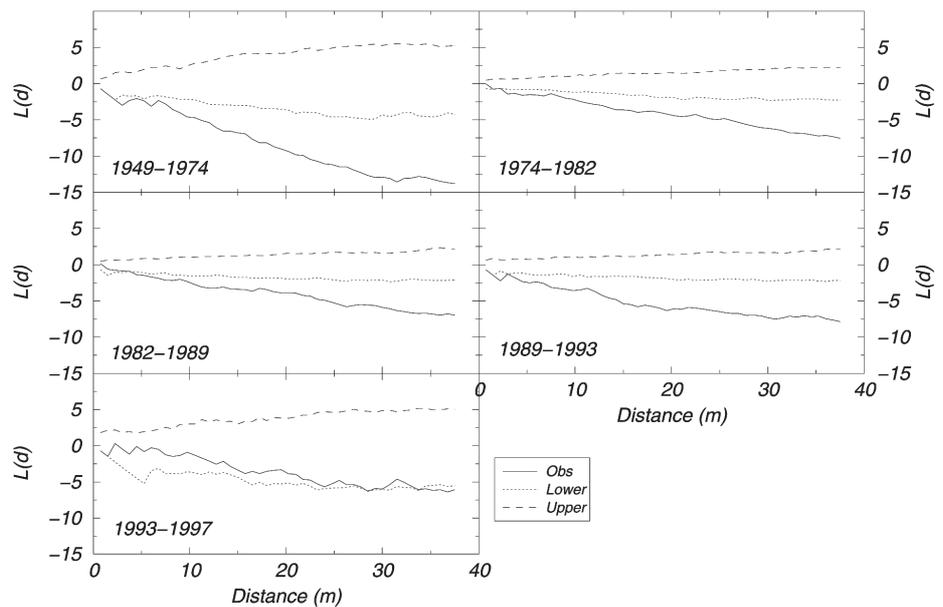
Fig. 6. Transformed bivariate Ripley's $K(d)$ showing the spatial relationships between *Quercus* ingrowth and stems of all species present in the midstory. The upper and lower confidence limits are the 95% confidence limits of the spatial pattern that would be expected if ingrowth were distributed randomly with respect to the fixed set of species in the midstory. From 1974 to 1993, the observed value of $L(d)$ at all point-to-point distances is less than would be expected under this null hypothesis, which implies that there are less *Quercus* ingrowth at these distances from midstory stems than would occur by chance alone.

clumped over time, with values of $L(d)$ ordered for most distance classes such that $L_{1949} < L_{1974} < L_{1982} < L_{1989} < L_{1993} < L_{1997}$ (for one point ordered as above, Kendall's coefficient of rank correlation, $\tau = -1$, $P = 0.0048$). *Quercus* understory stems have no apparent trend in spatial pattern over time, in contrast to *A. rubrum*. *Quercus* stems in the overstory are more regularly distributed than would be expected under CSR at point-to-point distances between 1.5 and 5 to 10 m, depending on the year sampled. There is a slight tendency for overstory *Quercus* to become less clumped in their distribution from 1949 to 1993.

The spatial pattern for *Quercus* in 1997 is more clumped than in 1993 at all spatial scales > 5 m, probably due to damage from Hurricane Fran. Hurricane

damage and mortality appears to have occurred in contagious fashion in all three strata of the forest (Fig. 4). The observed $L(d)$ of hurricane-affected stems is more clumped than one would expect if the set of hurricane-affected stems were drawn randomly from the set of total stems possible in 1997. The single exception to this trend is at point-to-point distances less than 10 m in the overstory, where the hurricane-affected stems were no more clumped than expected under the above null hypothesis. This may simply be because the overstory has fewer stems than the midstory or understory, and therefore the confidence intervals of the null hypothesis are less tight. However, it may also reflect a real trend, seen in all three strata, for hurricane-affected stems to be most clumped at large scales, generally > 30 m.

Fig. 7. Transformed bivariate Ripley's $K(d)$ showing the spatial pattern between *Quercus* ingrowth and *Acer rubrum* stems in the midstory. The null hypothesis tested is that ingrowth is randomly distributed with respect to the fixed set of species in the midstory. For all intervals except the last (1993-1997), the observed value of $L(d)$ at all point-to-point distances is less than would be expected under this null hypothesis, which implies that there is less *Quercus* ingrowth at these distances from *Acer rubrum* stems in the midstory than would occur by chance alone.



Bivariate analysis

A. rubrum ingrowth occurs more frequently near midstory stems than would be expected under random establishment (Fig. 5). For most point-to-point distances > 5 m, the observed bivariate $L(d)$ is significantly ($P < 0.05$) greater than that expected under the null hypothesis that ingrowth established randomly with respect to midstory stems. This effect appears strongest in ingrowth that established in the intervals from 1974 to 1982 and from 1982 to 1989. Similar results were obtained for the bivariate $L(d)$ between *A. rubrum* ingrowth and previously established understory stems. However, at all spatial scales *A. rubrum* ingrowth was significantly ($P < 0.05$) less likely to occur near overstory trees than expected if ingrowth established randomly with respect to overstory stems.

In contrast to *A. rubrum*, *Quercus* ingrowth was negatively associated with midstory stems (Fig. 6). From 1974-1993, for all point-to-point distances, the observed bivariate $L(d)$ was significantly ($P < 0.05$) less than that expected if ingrowth established randomly with respect to midstory stems. However, ingrowth from the first interval, from 1949 to 1974, and the last interval (from 1993-1997) show this trend only weakly, if at all. Furthermore, the results obtained from the bivariate $L(d)$ between *Quercus* ingrowth and either of the other two strata, the understory or overstory, show no significant patterns. However, the small quantity of *Quercus* ingrowth may limit the power to test these interactions.

The relationship between midstory *A. rubrum* stems and *Quercus* ingrowth is shown explicitly in Fig. 7. Excepting ingrowth during the last interval, at all spatial scales the observed $L(d)$ is less than that expected under

the null hypothesis that *Quercus* establish randomly without respect to *A. rubrum* stems in the midstory. This result is consistent with the relationship between *Quercus* ingrowth and all midstory stems (Fig. 6). However, the trend is strongest for ingrowth that appeared in the interval between 1949 and 1974. *Quercus* ingrowth in the last interval (1993 to 1997) displays the same general trend towards 'repulsion' (i.e. an $L(d)$ less than that expected by chance) in that the observed $L(d)$ is less than the mean value of $L(d)$ expected under the null hypothesis for all spatial scales, but is not significant at the 0.05 level.

Discussion

Our evidence supports the general view that spatially heterogeneous, density-dependent competition is important in determining differences in the degree of dispersion between strata in forests (Kenkel 1988). Generally, the stems in the canopy of the forest are less clumped than those in the strata below it. However, after 1974 *A. rubrum* stems in the midstory are more clumped than *A. rubrum* stems in the understory (Fig. 2), which is puzzling if we expect density-dependent competition to be the main factor controlling the survival and maturation of a stem from the understory into the overstory. It is possible that the spatial clumping of *A. rubrum* observed in the midstory reflects differential survival of understory stems in sites that larger *A. rubrum* stems already occupy. This would occur, for example, if certain microsites were edaphically better for *A. rubrum*. Another possibility is that the spatial clumping of midstory *A. rubrum* is indicative of previous distur-

bance events, such as Hurricane Hazel in 1954 (Christensen 1977), which may have altered the spatial distribution of *A. rubrum* in this cohort. Finally, the spatial clumping of midstory *A. rubrum* could be taken as evidence of seed dispersal limitation in this cohort, while younger cohorts have had relatively less seed dispersal limitation, due to the rapid increase in *A. rubrum* populations in this stand and throughout eastern forests (Abrams 1998).

There are also recognizable changes in spatial pattern over time. Clumping has decreased in most strata, confirming Christensen's (1977) observations in an earlier study of the same stand. For these two species the trend over time towards a less-clumped distribution through self-thinning processes, which we expected to play out between strata of the forest, also seems to play out over time. This unexpected result may reflect a response to competitive interactions during the dramatic expansion of *A. rubrum*. This transition is consistent with theories that predict that tree distribution will become more uniform over successional time as processes of species replacement occur (e.g. Laessle 1965), particularly if *Quercus* dominance is viewed as a mid-successional stage in forest development (e.g. Bornkamm 1975). Hurricane Fran also had a major impact on spatial patterns (Fig. 4), further emphasizing the dynamic nature of these patterns. Although hurricane damage seems to be clumped (i.e., spatially heterogeneous) at all scales, it appears to have had its greatest effect on the spatial pattern of canopy *Quercus* (Fig. 3), perhaps because the smaller number of stems in the canopy makes the empirical value of $L(d)$ more susceptible to change than in the more dense midstory and understory. Overall, Hurricane Fran greatly increased the amount of clumping in species distributions in all strata, counteracting the general trend of competition to increase uniformity in species distributions over time.

Different factors appear to control the establishment of *A. rubrum* and *Quercus*. *A. rubrum* ingrowth appears to be less abundant near canopy trees, but more abundant near midstory (Fig. 5) and understory stems. This tendency for *A. rubrum* ingrowth to establish near understory trees seems at odds with the general trend towards less clumping of understory *A. rubrum* over time, but may reflect the fact that favourable soil conditions for *A. rubrum* establishment are more likely to occur where other (slightly older) *A. rubrum* stems occur. Additionally, while it is plausible that light limitation might limit *A. rubrum* ingrowth near canopy trees, the observed effect occurs at spatial scales somewhat coarser (up to 30 m or more) than would be expected for light competition. Edaphic gradients across the site may cause these larger-scale

establishment limitations. For instance, there appear to be fewer *A. rubrum* stems on the uphill portion of the plot, which may reflect the transition from more mesic conditions downhill to more xeric conditions uphill (Bormann 1953; Christensen 1977).

In contrast to *A. rubrum*, *Quercus* establishment seems to be most limited by midstory trees (Fig. 6), and we find no statistically significant effects of either the overstory or understory on spatial patterns of *Quercus* establishment. *Quercus* ingrowth is less abundant near midstory stems than would be expected if ingrowth established at random, and this effect occurs at a range of spatial scales. When we specifically test the hypothesis that *A. rubrum* midstory and understory trees limit *Quercus* ingrowth, we find strong support (Fig. 7). This provides evidence, from at least this one site, in support of the hypothesis that competition in the understory of the forest could be important in limiting *Quercus* regeneration (e.g. Lorimer 1985; Abrams 1992). However, *Quercus* ingrowth is negatively associated with *A. rubrum* in midstory and understory at almost all spatial scales, and so some factor in addition to competition for light, which we could expect to be limited to small spatial scales (Shugart & West 1979; Leemans 1990), may be operating. For example, *A. rubrum* may be expanding its distribution upslope. *Quercus* ingrowth may be more abundant uphill, where fewer *A. rubrum* stems have reached yet, and where, consequently, there is less competition for light. This would mean that there would be fewer *Quercus* ingrowth stems than expected by chance alone over a large range of point-to-point distances from established *A. rubrum* stems, which is the pattern we see in Fig. 7. Thus the past distributions of *A. rubrum* and *Quercus* stems play an important role in structuring competitive interactions for light currently.

Overall, our results demonstrate the dynamic nature of spatial pattern in forests. This appears to result from interactions between factors causing uniformity in species distributions (e.g. density-dependent competition) and factors causing clumping in species distributions (e.g. windthrow events and environmental heterogeneity). Furthermore, our results show that non-stationary point patterns and changes in species composition, conditions that exist in most forests, can lead to complex changes in spatial pattern. The analysis presented here cannot fully resolve how various factors have influenced the interaction between *A. rubrum* and *Quercus*, and more sophisticated spatial analysis techniques are needed to understand the dynamic changes in forest pattern that can occur in a complex, non-equilibrium forest. Specifically, our results suggest that the increase in the *A. rubrum* population and its interaction with *Quercus* regeneration varies spatially with site

characteristics and site history in ways that can cause surprising changes in spatial pattern over time. Future studies of the interaction between *A. rubrum* and *Quercus* should consider variability in environmental conditions and species distributions at a large range of spatial scales.

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References

- Anon. 1971. *Soil survey of Durham County, North Carolina*. United States Department of Agriculture, Washington, DC, US.
- Anon. 1975. *Soil survey of Orange County, North Carolina*. United States Department of Agriculture, Washington, DC, US.
- Abrams, M.D. 1992. Fire and the development of oak forests. *BioScience* 42: 346-353.
- Abrams, M.D. 1996. Distribution, historical development and ecophysiological attributes of oak species in the eastern United States. *Ann. Sci. For.* 53: 487-512.
- Abrams, M.D. 1998. The red maple paradox. *BioScience* 48: 355-364.
- Antonovics, J. & Levin, D.A. 1980. The ecological and genetic consequences of density-dependent regulation in plants. *Annu. Rev. Ecol. Syst.* 11: 411-452.
- Ashe, W.W. 1897. Forests of North Carolina. In: Pinchot, G. & Ashe, W.W. (eds.) *Timber trees and forests of North Carolina*. North Carolina Geological Survey Bull. No. 6, Winston, NC, US.
- Besag, J.E. 1977. Comment on 'Modeling spatial patterns' by B.D. Ripley. *J. R. Stat. Soc. B* 39: 193-195.
- Billings, W.D. 1938. The structure and development of old field shortleaf pine stands and certain associated physical properties of the soil. *Ecol. Monogr.* 8: 436-499.
- Bormann, F. H. 1950. *The statistical efficiency of plot size and shape in forest ecology*. M.A. Thesis. Duke University, Durham, NC, US.
- Bormann, F.H. 1953. The statistical efficiency of sample plot size and shape in forest ecology. *Ecology* 34: 474-487.
- Bornkamm, R. 1975. A vegetation map of the Henry J. Oosting Natural Area, Orange County, North Carolina, with a discussion of the beech-maple climax type in the Piedmont. *Duke Univ. School For. Environ. Stud. Tech. Pap.* 3: 1-19.
- Bourdeau, P. 1954. Oak seedling ecology determining segregation of species in Piedmont Oak-Hickory forests. *Ecol. Monogr.* 24: 297-320.
- Bruhn, J.N., Wetteroff, J.J., Mihail, J.D., Kabrick, J.M. & Pickens, J.B. 2000. Distribution of *Armillaria* species in upland Ozark Mountain forests with respect to site, overstory species composition and oak decline. *For. Pathol.* 30: 43-60.
- Burns, R.M. & Honkala, B.H. (Techn. coord.). 1990. *Silvics of North America*. USDA Forest Service Agricultural Handbook, No. 654. Washington, DC, US.
- Busing, R.T. 1996. Estimation of tree replacement patterns in an Appalachian *Picea-Abies* forest. *J. Veg. Sci.* 7: 685-694.
- Cale, W.G., Henebry, G.M. & Yeakley, J.A. 1989. Inferring process from pattern in natural communities. *BioScience* 39: 600-605.
- Christensen, N.L. 1977. Changes in structure, pattern, and diversity associated with climax forest maturation in Piedmont, North Carolina. *Am. Mid. Nat.* 97: 176-188.
- Christensen, N.L. & Peet, R.K. 1981. Secondary forest succession on the North Carolina piedmont. In: West, D.C., Shugart, H.H. & Botkin, D. (eds.) *Forest succession: Concepts and application*, pp. 230-245. Springer-Verlag, New York, NY.
- Clark, F.B. 1993. An historical perspective of oak regeneration. In: Loftis, D. & McGee, C.E. (eds.) *Oak regeneration: Serious problems, practical recommendations*. USDA Forest Service, Southeastern Forest Experiment Station, Asheville, NC, US.
- Cooper, C.F. 1961. Pattern in Ponderosa pine forests. *Ecology* 42: 493-499.
- Cressie, N.A.C. 1993. *Statistics for spatial data*. Wiley, New York, NY, US.
- Dale, M.R.T. 1999. *Spatial pattern analysis in plant ecology*. Cambridge University Press, Cambridge, UK.
- Diggle, P.J. 1983. *Statistical analysis of spatial point patterns*. Academic Press, New York, NY, US.
- Donaubauer, E. 1998. Die Bedeutung von Krankheitserregern beim gegenwärtigen Eichensterben in Europa – eine Literaturübersicht. *Eur. J. For. Path.* 28: 91-98.
- Dwyer, J.P., Cutter, B.E. & Wetteroff, J.J. 1995. A dendrochronological study of black and scarlet oak decline in the Missouri Ozarks. *For. Ecol. Manage.* 75: 69-75.
- Ferrill, W.K. 1953. Effect of environmental conditions on survival and growth of forest tree seedlings under field conditions in the piedmont region of North Carolina. *Ecology* 34: 667-688.
- Fowler, N.L. 1986. The role of competition in plant communities in arid and semiarid regions. *Annu. Rev. Ecol. Syst.* 17: 89-110.
- He, F.L. & Duncan, R.P. 2000. Density-dependent effects on tree survival in an old-growth Douglas fir forest. *J. Ecol.* 88: 676-688.
- Ida, H. 2000. Treefall gap disturbance in an old-growth beech forest in southwestern Japan by a catastrophic typhoon. *J. Veg. Sci.* 11: 825-832.
- Jenkins, M.A. & Pallardy, S.G. 1995. The influence of drought on red oak group species growth and mortality in the Missouri Ozarks. *Can. J. For. Res.* 25: 1119-1127.
- Kareiva, P. 1990. Population dynamics in spatially complex

- environments: theory and data. *Phil. Trans. R. Soc. Lond. B* 330: 175-190.
- Kartesz, J.T. & Meacham, C.A. 1999. *Synthesis of the North American flora*. North Carolina Botanical Garden, University of North Carolina, Chapel Hill, NC, US.
- Keever, C. 1950. Causes of succession on old fields of the Piedmont, North Carolina. *Ecol. Monogr.* 20: 229-250.
- Kenkel, N.C. 1988. Pattern of self-thinning in jack pine: testing the random thinning hypothesis. *Ecology* 69: 1017-1024.
- Laessle, A.M. 1965. Spacing and competition in natural stands of sand pine. *Ecology* 46: 65-72.
- Leemans, R. 1991. Canopy gaps and establishment patterns of spruce (*Picea abies* (L.) Karst.) in two old-growth coniferous forests in central Sweden. *Vegetatio* 93: 157-165.
- Leemans, R., & Prentice, I.C. 1990. Pattern and process and the dynamics of forest structure: a simulation approach. *J. Ecol.* 78: 340-355.
- Legendre, L. & Legendre, P. 1998. *Numerical ecology*. 2nd. English ed. Elsevier, New York, NY, US.
- Levin, S.A. 1992. The problem of pattern and scale in ecology. *Ecology* 73: 1943-1967.
- Lookingbill, T.R. & Zavala, M.A. 2000. Spatial pattern of *Quercus ilex* and *Quercus pubescens* recruitment in *Pinus halepensis* dominated woodlands. *J. Veg. Sci.* 11: 607-612.
- Lorimer, C.G. 1984. Development of the red maple understory in northeastern oak forests. *For. Sci.* 30: 3-22.
- Lorimer, C.G. 1985. The role of fire in the perpetuation of oak forests. In: Johnson, J.E. (ed.) *Challenges in oak management and utilization*. Cooperative Extension Service, University of Wisconsin, Madison, WI, US.
- Lorimer, C.G. 1993. Causes of the oak regeneration problem. In: Loftis, D. & McGee, C.E. (eds.) *Oak regeneration: Serious problems, practical recommendations*. USDA Forest Service, Southeastern Forest Experiment Station, Asheville, NC, US.
- Lorimer, C.G., Chapman, J.W. & Lambert, W.D. 1994. Tall understory vegetation as a factor in the poor development of oak seedlings beneath mature stands. *J. Ecol.* 82: 227-237.
- Manly, B.F.J. 1997. *Randomization, bootstrap and Monte Carlo methods in biology*. 2nd. ed. Chapman and Hall, London, UK.
- Marquis, D.A., Eckert, P.L. & Roach, B.A. 1976. *Acorn weevils, rodents, and deer all contribute to oak regeneration difficulties in Pennsylvania*. USDA Forest Service Northeastern Forest Experiment Station Research Paper NE-356.
- McDonald, R.M., Peet, R.K. & Urban, D.L. 2002. Environmental correlates of oak decline and red maple increase in the North Carolina piedmont. *Castanea* 67: 84-95.
- Miller, C. & Urban, D.L. 1999. Forest pattern, fire, and climatic change in the Sierra Nevada. *Ecosystems* 2: 76-87.
- Moeur, M. 1993. Characterizing spatial patterns of trees using stem-mapped data. *For. Sci.* 39: 756-775.
- Moeur, M. 1997. Spatial models of competition and gap dynamics in old-growth *Tsuga heterophylla*-*Thuja plicata* forests. *For. Ecol. Manage.* 94: 175-186.
- Oosting, H.J. 1942. An ecological analysis of the plant communities of the Piedmont, North Carolina. *Am. Mid. Nat.* 28: 1-126.
- Orwig, D.A. & Abrams, M.D. 1994. Land-use history (1720-1992), composition, and dynamics of oak pine forests within the piedmont and coastal-plain of northern Virginia. *Can. J. For. Res.* 24: 1216-1225.
- Palmer, M.W. 1991. Patterns of species richness among North Carolina hardwood forests: tests of two hypotheses. *J. Veg. Sci.* 2: 361-366.
- Pasch, R.J. & Avila, L.A. 1999. Atlantic hurricane season of 1996. *Month. Weather Rev.* 127: 581-610.
- Peet, R.K. & Christensen, N.L.. 1980. Succession: a population process. *Vegetatio* 43: 131-140.
- Pulliam, H.R. 1988. Sources, sinks, and population regulation. *Am. Nat.* 132: 652-661.
- Reed, R.A., Peet, R.K., Palmer, M.W. & White, P.S. 1993. Scale dependence of vegetation-environmental correlations: A case study of a North Carolina Piedmont woodland. *J. Veg. Sci.* 2: 329-340.
- Ripley, B.D. 1976. The second-order analysis of stationary point processes. *J. Appl. Prob.* 13: 255-266.
- Ripley, B.D. 1981. *Spatial statistics*. Wiley, New York, NY, US.
- Shugart, H.H. & West, D.C. 1979. Size and pattern of simulated forest stands. *For. Sci.* 25: 120-122.
- Sokal, R.R. & Rohlf, F.J. 1981. *Biometry*. W.H. Freeman, New York, NY, US.
- Sork, V.L. 1984. Examination of seed dispersal and survival in red oak, *Quercus rubra* (Fagaceae), using metal-tagged acorns. *Ecology* 65: 1020-1022.
- Watt, A.S. 1947. Pattern and process in the plant community. *J. Ecol.* 35: 1-22.
- Weller, D.E. 1987. A reevaluation of the $-3/2$ power rule of plant self-thinning. *Ecol. Monogr.* 57: 23-43.
- White, A.S. 1985. Presettlement regeneration patterns in a Southwestern Ponderosa Pine stand. *Ecology* 66: 589-594.
- Yoda, K., Kira, T., Ogawa, H. & Hozumi, K. 1963. Intraspecific competition among higher plants. XI. Self-thinning in over-crowded pure stands under cultivated and natural conditions. *J. Biol. Osaka City Univ.* 14: 107-129.

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