

**MERGED TREES IN SECOND-GROWTH, FIRE-ORIGIN FORESTS IN
 PATAGONIA, CHILE: POSITIVE SPATIAL ASSOCIATION PATTERNS
 AND THEIR ECOLOGICAL IMPLICATIONS¹**

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- *Premise of the Study:* Negative density-dependent processes have been thought to be the primary cause of shifting spatial patterns of tree populations through time. The existence of adult tree clusters might challenge this classical prediction. Here, we document the prevalence of merged stems (clustering of mature trees leading to stem fusion) in second-growth forests of *Nothofagus pumilio* and hypothesize that it is nonrandom but predictable in space.
- *Methods:* We stem-mapped nine sites in second-growth edge and interior forests of fire origin and in mature forests of *N. pumilio* (>3500 trees) in central Patagonia, Chile. The spatial structure of stand-level and individual-level features was estimated with spatial analyses (pair-correlation function and nearest-neighbor distances).
- *Key Results:* Multistemmed trees were merged clusters of separate individuals. Merged trees were predominantly found at the edge of the second-growth forests. We found strong clustering (≤ 5 m) at forest edge sites and none at interior sites. Nearest-neighbor distance distributions were unimodal for unmerged trees and monotonically decreasing for merged trees; interstem distances were much smaller at the edge sites than at the interior sites.
- *Conclusions:* The occurrence of merged trees at the forest edge, and the resulting high spatial aggregation of stems, is consistent with the hypothesis that establishment was probably aggregated. The spatial pattern found at the forest edge changes the standard spatial pattern sequence through time in temperate forests, altering traditional forest-stand-dynamics models.

Key words: competition; forest stand dynamics; multistemmed trees; neighborhood analysis; *Nothofagus pumilio*; pair-correlation function; Reserva Coyhaique; spatial patterns.

The dynamics of plant populations are the expression of numerous processes, such as competition for resources, and generally exhibit a predictable time-sequence of spatial patterns (Kenkel, 1988; Silvertown and Charlesworth, 2001). These spatial patterns, in turn, give us insight into the responsible processes (McIntire and Fajardo, 2009). Density-dependent mortality of temperate tree species (i.e., self-thinning) mediated through competition for resources (e.g., light) leads to changes in the original aggregated distribution of regeneration toward regularity in adults and randomness in mature trees at larger scales (e.g., Antonovics and Levin, 1980; Kenkel, 1988; Szwagrzyk and Czerwczak, 1993; Diggle, 2003; Fajardo and Alaback, 2005). This time-sequence of spatial patterns is the spatial manifestation of the population-dynamics concept of negative density-dependence (Yoda et al., 1963), but within a generation. Higher densities can increase mortality through greater competition for resources (self-thinning), which is ultimately responsible for both the shift of individual spatial patterns, from clustering to regularity and randomness, and the negative relationship between

individual size and density (Silvertown and Charlesworth, 2001). Self-thinning should, then, remove individuals that are nearby neighbors (Fajardo and McIntire, 2007), resulting in a decrease in aggregation with size-class (Kenkel, 1988; Moer, 1997; Getzin et al., 2008). All the theoretical concepts described above depend on a stable, invariable environment, which seldom is the case (Hewitt et al., 2007; Murrell, 2009). In this respect, we know of no study that has investigated the role of abiotic heterogeneity (e.g., resource variation, presence of stress) in determining how the pattern of aggregation changes in plants.

Multistem growth architecture (i.e., a single stem at ground level and multiple vertical stems partway up the bole) occurs in tree populations and is typically the result of simultaneous growth of several shoots that originated from a single root system, a phenomenon known as “sprouting” (Bond and Midgley, 2001; Bellingham and Sparrow, 2009). Alternatively, in many species several distinct individuals contribute to the formation of a multiple-individual entity. For example, in members of the subgenus *Strobos* in the genus *Pinus* (e.g., *Pinus albicaulis* and *P. flexilis*), multistemmed groups of individuals are common (Linhart and Tomback, 1985; Carsey and Tomback, 1994). In these examples, the proximate mechanism resulting in multistemmed individuals was multiseeded caches made by Clark’s nutcracker (*Nucifraga columbiana* Wilson). The knowledge of this proximate mechanism, however, does not obviate the need for a more general mechanism to explain merging within the contexts of stand dynamics and density-dependent mortality—that is, why does one individual not win and all the others die?

Central Patagonia, Chile, was previously covered by massive forests of *Nothofagus pumilio* (Poeppig et Endlicher) Krasser (southern beech, Nothofagaceae) (Marticorena and Rodríguez,

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2003). In an attempt to open the land for livestock, pioneers of this region 60–80 yr ago initiated catastrophic fires that burned down a large portion of these woodlands (2.8 million ha), reducing their original area by half (Otero, 2006). In some cases, these forests regenerated in marginal fringes that were exposed to strong wind. Casual observations of some of these forests showed the presence of multistemmed mature individuals that appeared to be more common at the forest edges. The potential dominant occurrence of multistemmed trees of *N. pumilio* mostly at the outer edge of second-growth forests of fire origin would suggest that negative density-dependence may act differently according to the location in the forest (e.g., intraspecific competition being more important in some areas than in others). The implication of this is that self-thinning—the result of negative conspecific interactions—should also vary depending on where trees are located in the gradient of abiotic influence (Getzin et al., 2006; Murrell, 2009). We know that populations and communities living in environments characterized by increased resource availability or a high degree of abiotic stress, such as ecotones, may show different size–density relationships (Deng et al., 2006). But, first, it is not certain how often merged trees occur at the forest edge and whether their occurrence is less common in other circumstances (e.g., closed forest). To infer the exact location of merged trees would help in building hypotheses about whether they are actually the consequence of positive interactions or just negative or neutral interactions. Second, it is unknown whether density dependence in heterogeneous environments fits the more traditional stand-dynamics models described for temperate forests (Oliver, 1980). We know already that during the stem-exclusion phase (*sensu* Oliver, 1980), the negative density-dependence process acts with distance, making initial clustering disappear with time. It is pertinent, then, to ask how spatial patterns of merged trees fit spatial patterns expected to emerge in the stem-exclusion phase.

We examined the purported multiple origin, spatial occurrence, and spatial characteristics of multistemmed trees, as well as the consequences for density dependence in forest stand dynamics, with four specific objectives. First, we tested for a multiple origin of multistemmed trees using stem dissection through the root collar. Second, we examined whether merged stems of *N. pumilio* occur more often in edges than in interior forest. Third, we assessed and tested the relative importance of location and merging as drivers of growth to distinguish edge effects from positive density-dependence. Fourth, we tested whether stem spatial patterns differ from standard expectations of forest-stand dynamics when merged trees are present by comparing the patterns of clustering and distributions of merged trees with those of nearby single-stem trees of the same age (standard expectations) and with trees of much older mature forests (alternative expectations).

MATERIALS AND METHODS

Study site, tree species, and field sampling—The research was conducted in the Reserva Coyhaique (45°52'S, 72°00'W; 800 m above sea level, on average), Coyhaique province, Patagonia, Chile. This region belongs to the supratemperate belt, with humid climatic conditions (Amigo and Ramírez, 1998). The annual precipitation is ~1350 mm, most of which falls as snow from May to October (Informe Meteorológico de Chile, Dirección General de Aguas, 2008). The soil is derived from aeolian volcanic-ash deposits. The aspect, in general, is south, with a slope of 10–20%, and the stands are located ~500 m below the upper tree line. In this particular reserve area, a large-scale human-induced fire in 1950 burned some 600 ha of old-growth *N. pumilio* forest (CONAF, personal communication). A fire boundary was then created, where seeds from the unaf-

ected old-growth forest of *N. pumilio* germinated. Thus, a fringe of regeneration was formed that led, within decades, to a second-growth forest. This sequence of fire followed by formation of a second-growth *N. pumilio* forest is pervasive in this region.

Forests of *N. pumilio* in Patagonia are mostly monospecific and represent a transition between the temperate rainforest of western Patagonia and the steppe formations of eastern Patagonia (Fajardo and de Graaf, 2004). *Nothofagus pumilio* is a deciduous, monoecious, semi-shade-intolerant species (Donoso, 1993; Martínez Pastur et al., 2007) that exhibits mast seeding at intervals of 3–8 yr (Mascareño, 1987). Its lighter seeds are dispersed widely, principally by wind. The species has thin-barked stems that make it very susceptible to being killed by severe fires (Fajardo and González, 2009). Unlike most other South American species in the genus, *N. pumilio* does not appear to resprout (Donoso, 1993). Cattle and guanaco (*Lama guanicoe*) commonly browse regeneration of *N. pumilio* (Cavieres and Fajardo, 2005); however, this is not a problem in Reserva Coyhaique, where cattle have been fenced off for decades, and the presence of guanaco in this part of Patagonia is nil.

We sampled second-growth forest stands at the immediate outer edge and in the interior forest. We defined the forest edge as the first 50 m from the treeless area (prairie) inside the forest. We also sampled the mature forest, which is the likely seed source of the second-growth forest. The mature forest is adjacent to the second-growth forest and located ~500 m north of the outer edge (i.e., forest–prairie ecotone). Structural information on this mature forest can be found elsewhere (Fajardo and de Graaf, 2004). At each location we established plots of varied size (from 420 m² at the edge to 1536 m² at the mature forest; Table 1) and stem-mapped all trees >0.5 m tall. We estimated the coordinates of each tree stem center at breast height (1.35 m, DBH) by using a handheld laser range finder (Impulse; Laser Technology, Centennial, Colorado, USA) equipped with a digital compass, which measures the distance and azimuth to the center of each tree to the nearest 1 cm. The field measurements were converted to coordinates using trigonometric functions. For each tree, we recorded live or dead condition and diameter at breast height. The condition of being “dead” can encompass decades in this area, where wood decomposes slowly because of low temperatures. We also classified each stem mapped as being merged with other stems or not merged (single). For each mapped tree stem at the edge and interior second-growth forest sites, one core was taken ~30 cm above the ground (in total, 987 trees were cored). In the laboratory, the cores were air dried, mounted into specially constructed grooved boards, and sanded with successively finer grades of sandpaper to reveal annual rings (Stokes and Smiley, 1996). The rings were counted to determine tree age using a stereomicroscope mounted on a dendrochronometer with a Velmex sliding stage and Accurite measurement system. Cross-dating accuracy was checked using COFECHA v6.06P (Holmes, 2001).

Hypotheses and analyses—To test for multiple origins of the multistemmed trees, we selected 10 representative individuals and cut them in 3-cm-wide slices through the root collar. If the piths converged to a single location, the multistemmed cluster was deemed a cluster of vegetative sprouts of the same genetic individual. If the piths did not converge, we concluded that the cluster had multiple genetic origins. Furthermore, we had three pieces of supplemental evidence from outside the present study that supported the multiple-genetic-origins hypothesis for multistemmed trees: (1) sprouting is not known to occur in *N. pumilio* (Donoso, 1993), excepting some observations of potential vegetative multiplicity made in krummholz individuals at the altitudinal treeline (Barrera et al., 2000); (2) in our widespread observational surveys of *N. pumilio* forest, we have seen examples of all stages of the purported merging process, from dense clusters of independent saplings, to just touching, to beginning stages of fusion, to the multistemmed trees with a “clover” cross section (all individuals in our study); and (3) in an unpublished genetic study in which we genotyped foliage from purported individuals in multistem clusters, we found multiple genetic origins (E. J. B. McIntire and A. Fajardo, unpublished data). Because our sample of 10 individuals is only a small subset of our cored trees, all 10 samples had to be found to have unambiguous multiple origins to proceed with the remaining objectives of the present study.

For our second objective, we provide descriptive summary statistics showing the frequency and location of merging, stand density (number of stems ha⁻¹), tree age and basal area (BA; m² ha⁻¹), as well as basic site descriptors. We used mixed-effects model analysis to compare these descriptive statistics (i.e., stand density, age, and basal area) between locations with fixed effect as location (edge or interior) and with a random effect of site acting on the intercept ($n = 2$ for interior and $n = 4$ for edges). In each location, a relative importance value (RIV) was calculated for merged trees as an average of the relative density

TABLE 1. Stem density (trees ha⁻¹), basal area (BA, m² ha⁻¹), and relative importance values (RIV) for total (stand level) and merged trees >50 cm in height by site in second-growth (E = edge, I = interior) stands and mature (M) forests of *Nothofagus pumilio*.

Plot	Plot size	Status	Stands		Merged trees				RIV
			Density	BA	Density	RD	BA	RBA	
E1	700	Alive	1243	36.27	914	73.53	21.29	58.70	66.12
		Dead	529	2.26	243	45.94	1.21	53.61	49.77
E2	1000	Alive	1310	31.77	1240	94.66	29.35	92.38	93.52
		Dead	210	0.96	210	100	0.68	70.83	85.42
E3	800	Alive	1638	33.73	575	35.10	16.18	47.97	41.54
		Dead	488	2.66	163	33.40	1.31	49.19	41.30
E4	420	Alive	3190	48.33	1167	36.58	22.10	45.73	41.16
		Dead	1071	3.26	0	0	0	0	0
I1	1000	Alive	1160	31.45	377	32.50	11.71	37.23	34.87
		Dead	1260	6.62	131	10.40	0.90	13.60	12.00
I2	1220	Alive	4074	46.63	0	0	0	0	0
		Dead	697	2.49	0	0	0	0	0
M1	1536	Alive	2695	74.38	0	0	0	0	0
		Dead	618	2.27	0	0	0	0	0
M2	1536	Alive	573	72.92	0	0	0	0	0
		Dead	78	1.73	0	0	0	0	0
M3	1536	Alive	1491	71.88	0	0	0	0	0
		Dead	202	8.54	0	0	0	0	0

and the relative basal area (BA). Relative importance values of merged trees were calculated as (relative density of merged trees + relative basal area of merged trees)/2 (Orwig et al., 2001).

For our third objective, assessing changes in growth and thereby assessing the identification and importance of primary drivers of competition, we compared DBH among sites and merged status in two ways. First, to test whether being in the edge per se or being merged drives growth, we used mixed-effects regression on log(DBH) with two fixed effects, site type (edge or interior) and merged status (merged or single), with a random effect of site acting on the intercept ($n = 2$ for interior and $n = 4$ for edges). Second, we compared DBH distributions for both merged and single trees. In mature forests, because of the semi-shade-intolerance of *N. pumilio*, regeneration is occurring principally in canopy gaps, and the size-class distribution is a classically negative exponential (Fajardo and de Graaf, 2004). We predicted that stand density is at its maximum in the second-growth forest, so that there is little or no regeneration (these forests are monospecific); the DBH size-class distribution will be unimodal (e.g., normal) if the suppressed trees die rapidly (stem-exclusion stage; sensu Oliver, 1980), whereas, if the suppressed trees persist, the DBH distributions will be best represented by a monotonically negative trend (e.g., negative exponential distribution). We fitted the empirical distributions to exponential and normal distributions (Ricci, 2005) and compared relative fit using Akaike's information criterion for small samples (AIC_c) (Burnham and Anderson, 2002).

For our fourth objective, we used nearest-neighbor (NN) distances (Diggle, 2003) and the pair-correlation function (Wiegand and Moloney, 2004) to quantify the small-scale spatial-correlation structure of patterns. We compare these patterns between merged trees and single trees for contrasts at the individual level and between edge sites and interior sites for contrasts at the stand level. In each case, we assume that single trees and interior stands represent the standard stand-dynamics trajectory for expected spatial patterns.

First, using spatial patterns tied to a priori mechanisms (McIntire and Fajardo, 2009), we compared NN distance distributions between merged and single trees (individual-level) and between edge and interior sites (stand-level) and fit our empirical distributions with functions characterizing plant-interaction processes. We hypothesized that positive tree-tree interactions would be best represented by a monotonically decreasing distribution—that is, the most common nearest-neighbor occurrence is very close (an exponential or log-normal function). By contrast, if competition has been the main process shaping tree

population, the NN distance distribution will be best fitted by a unimodal distribution with the mode (a gamma function with shape parameter >1) occurring at some larger distance from the tree (i.e., fewer trees are located relatively near each other). We also fit the data to a Weibull function, as an alternative unimodal distribution with slightly different shapes than a gamma function. As part of the exploration, generation, and testing of multiple a priori spatial hypotheses (McIntire and Fajardo, 2009), we were unable to conceive of another mechanism whereby the closest neighbors consistently survive within the standard stem-exclusion model of stand development. As in the previous analysis, we fitted the empirical distributions with the above functions and compared relative fit using Akaike's information criterion (AIC_c) for small sample sizes (Burnham and Anderson, 2002).

Finally, to determine whether spatial patterns at the stand level differ from standard expectations for temperate forests, we used second-order spatial-point-pattern analyses based on the univariate pair-correlation function, $g(r)$, which is a normalized distance-dependent neighborhood density function applicable to completely mapped point patterns (Stoyan and Stoyan, 1994; Wiegand and Moloney, 2004). For homogeneous patterns the pair-correlation function can be interpreted as the expected density of points (i.e., trees) at distance r from an arbitrary point, divided by the intensity λ of the pattern (Stoyan and Stoyan, 1994). Values of $g(r)$ that are >1 indicate that interpoint distances around r are more frequent, which indicates aggregation, and values of $g(r)$ that are <1 indicate that they are less frequent than they would be under complete spatial randomness (CSR), which indicates regularity. To reveal significant second-order effects in the univariate pattern (i.e., uniformity, aggregation), we compared the observed pattern with the 99% Monte Carlo simulation envelope (Stoyan and Stoyan, 1994). In a CSR situation, any point of the pattern has an equal probability of occurring at any position in the study area, and the position of the point is independent of the position of any other point (Wiegand and Moloney, 2004). Finally, we used a goodness-of-fit (GOF) test (Diggle, 2003), along with the simulation-envelope method for inference, to avoid Type I error (Loosmore and Ford, 2006). This GOF test summarizes the scale-dependent information contained in the pair-correlation function into a single test statistic that represents the total squared deviation between the observed pattern and the theoretical result across the distances of interest. Second-order spatial-point-pattern analyses were done with Programita software (Wiegand and Moloney, 2004).

RESULTS

Multitemmed trees—As hypothesized, all 10 purported multitemmed individual trees for which we did cross-section slices through the root collar were merged clusters of separate individuals (i.e., they were found to have multiple origins). Between two and six piths were clearly identified within each of these cross sections, and old bark was generally encapsulated within the wood.

Site demography—*Nothofagus pumilio* was the only dominant species in both second-growth and mature forests: a total of 3898 trees were surveyed. The two types of second-growth stands (e.g., edges and interiors) showed that they very likely originated at the same time and with similar traits (means \pm SE): neither tree age (44.2 ± 2.4 and 45.8 ± 3.7 yr, respectively; $z_{1,4} = 1.11$, $P = 0.27$), stem density (edge: 1845 ± 527 , interior: 2617 ± 2060 stems ha^{-1} ; $F_{1,4} = 0.47$, $P = 0.53$) nor basal area (edge: 37.53 ± 4.29 $\text{m}^2 \text{m}^{-2}$, interior: 39.04 ± 10.73 $\text{m}^2 \text{m}^{-2}$; $F_{1,4} = 0.04$, $P = 0.85$) differed significantly between forest edge and forest interior sites (“stand” section of Table 1).

Merging occurrence—Consistent with casual observations, we found merged trees, composed of two to six merged stems, predominantly at the edge of the second-growth forest of fire origin. At the edge locations we found significantly ($F_{1,8} = 31.32$, $P < 0.01$) more merged trees per hectare (1873 ± 379) than in interior and mature stands (88 ± 88). Relative importance values (RIV based on relative density and relative basal area) of merged trees were always above 40% in the edge forests, peaking at 93% in forest E2 (Table 1). Only in one interior forest were some merged trees found with an RIV value of 19%. Not a single merged tree was found in forest I2 and the mature forests. In general, the mean DBH was 12% and significantly larger in merged stems than in single stems (back-transformed to 14.7 cm and 13.1 cm, respectively: $F_{1,1129} = 7.74$, $P = 0.01$) but did not differ by site type ($F_{1,4} = 0.33$, $P = 0.59$). When we

compared the frequency distributions of size-classes (DBH) with theoretical models, we found that both growth forms were best fitted by a normal distribution (lowest AIC values for merged: $\text{AIC}_{\text{Normal}} = 2123.2$, $\text{AIC}_{\text{Exponential}} = 2496.7$; for single trees: $\text{AIC}_{\text{Normal}} = 5930.1$, $\text{AIC}_{\text{Exponential}} = 6439.6$; Fig. 1).

The second-growth forests had different spatial patterns according to location; in the edge stands, individual stems were clumped at distances of <0.5 m ($P < 0.01$ GOF; Fig. 2A–D), whereas for the interior forests a random distribution of individuals was characteristic at all distances ($P > 0.05$ GOF; Fig. 2E–F). Clustering at short scales (≤ 5 m) was also found for saplings and regeneration in the mature forest ($P < 0.01$ GOF; Fig. 2G–I). Thus, clustering of mature trees declined from edge to interior forest, and clustering at edges was similar to that in the regeneration and sapling layers in the mature forest, in direct contrast to the normal stem-exclusion phase of stand-dynamics models.

Nearest-neighbor distances for each tree taken at its base differed depending on whether the tree was part of a multi- or single-stemmed tree. At the stand level, NN distance distributions were best fitted by a log-normal model for all the edge stands and by a unimodal gamma distribution for interior stands (Table 2), which means that interstem distances were much smaller among trees in the edge stands than in the interior stands because of the pervasive presence of merged-stem trees. Complementarily, and also at the stand level, when multitemmed trees were treated as if they were separate stems, we found that NN distances were shorter than those of multitemmed trees treated as single stems (i.e., one “super tree”; Fig. 3).

DISCUSSION

In the second-growth forests of *N. pumilio*, merging of stems does not happen randomly in space, which suggests a link to characteristics at the forest edges. Given that we found no effect on size of being at the edge (similar DBH and BA), these effects

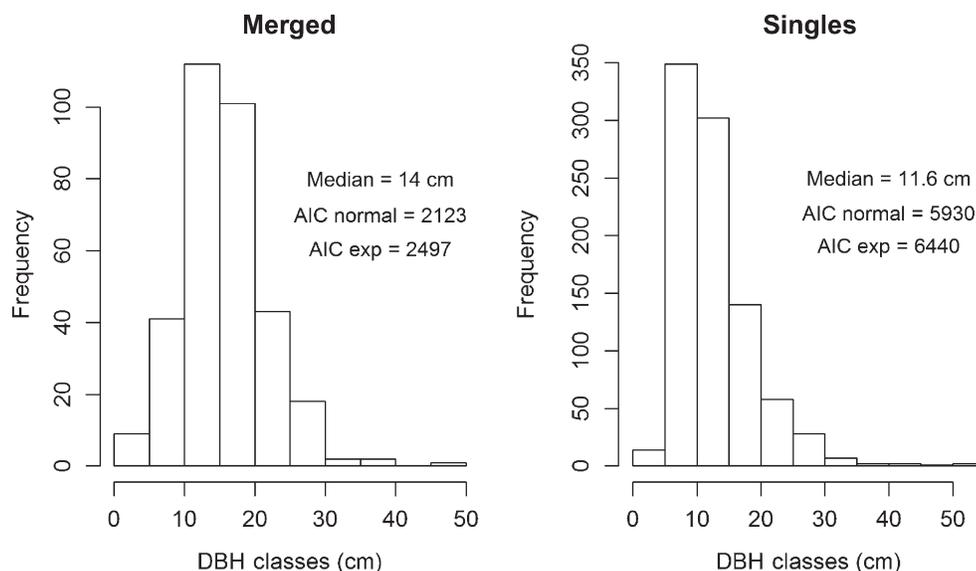


Fig. 1. Tree size distributions for merged (multitemmed) and single trees of second-growth forests (~45 yr) of *Nothofagus pumilio*. Frequency distributions of size-classes (DBH) were compared by fitting with theoretical models (normal and exponential). The frequency distributions did not differ and were best fitted by a normal distribution (see Results).

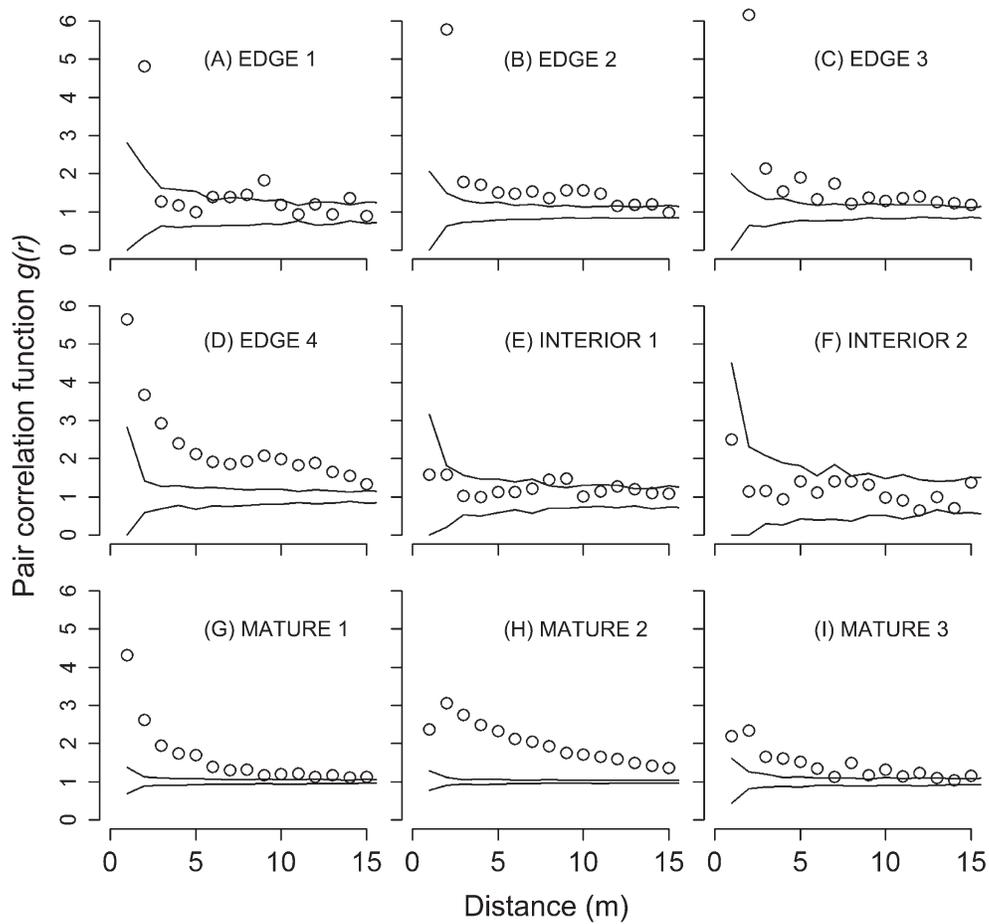


Fig. 2. The univariate pair-correlation function $g(r)$ over distance r (in meters) shows the g function of the data (dots) and the simulation envelopes (solid lines) being the fifth-lowest and fifth-highest $g(r)$ values of the Monte Carlo simulations of the null model (complete spatial randomness, CSR). Dots out of the simulation envelopes represent a deviance from CSR, which can be of clumping (above) or uniformity (below the simulation envelopes). Analyses were done for all the stands located at the edge (A–D), in the inner forest (E–F), and in the mature forests (G–I) of *Nothofagus pumilio*.

are not due to an improved light environment at the edge (the “edge effect”). The most likely explanation is that some characteristics of the forest edge in the past could have triggered the formation of multistemmed trees. In this vein, we have direct

evidence from a companion study (A. Fajardo and E. J. B. McIntire, unpublished data) that original abiotic conditions at the forest edge at the time of establishment probably caused seedlings and saplings of *N. pumilio* to establish in groups by

TABLE 2. Delta Akaike’s information criterion values for small samples (AIC_c) and parameters for the different models fitted to the empirical nearest-neighbor-distance distributions at the stand level of live trees in second-growth forests of *Nothofagus pumilio*. The best model according to AIC_c is rescaled to a value of zero and the others are reported in relation to that model.

	Edge 1	Edge 2	Edge 3	Edge 4	Interior 1	Interior 2
Exponential	17.47	49.68	63.75	57.98	71.59	124.73
Rate	1.51	2.16	2.64	2.15	1.19	1.01
Log-normal	0	0	0	0	11.80	39.11
Mean log	-0.80	-1.12	-1.22	-1.00	-0.41	-0.18
SD log	0.87	0.77	0.65	0.67	0.73	0.65
Gamma	13.36	37.60	30.16	16.08	0	0
Shape	1.43	1.56	2.15	2.31	2.26	3.10
Scale	0.46	0.30	0.18	0.20	0.37	0.32
Weibull	16.36	47.15	45.15	28.70	3.18	2.72
Shape	1.16	1.14	1.36	1.47	1.60	1.84
Scale	0.70	0.49	0.42	0.52	0.94	1.00

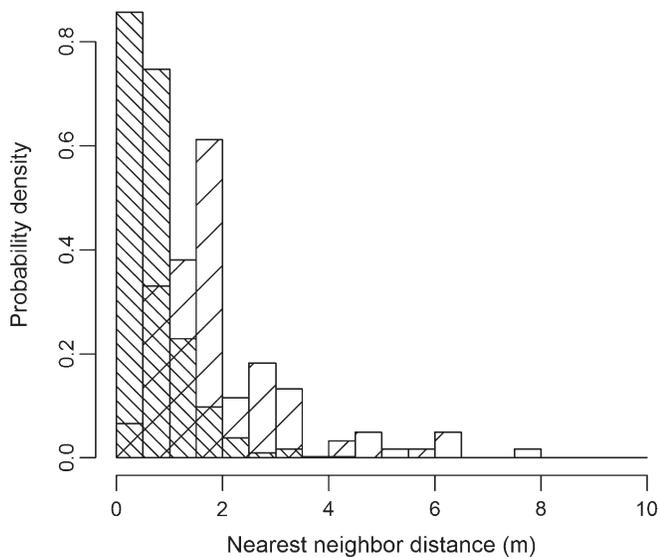


Fig. 3. Nearest-neighbor-distance histogram of live merged trees in second-growth forests of *Nothofagus pumilio*. Columns with narrow dashed style represent all sites when merged stems are treated as if they were separate stems (i.e., larger n), and wide dashed style represents all sites when the merged clusters are treated as single stems (i.e., smaller n). Both edge and interior sites are pooled.

facilitating mutual establishment. Thus, initial abiotic stress may have been the ecological mechanism for the occurrence of merged trees at the edges (i.e., weak self-thinning that maintained initial aggregation led to unusual aggregation of mature trees). Lastly, the increased growth of merged stems implies that positive interactions overcame competitive interactions during the stem-exclusion phase. This merging frees these stems from the standard trajectory of forest-stand dynamics in temperate forests (Oliver, 1980).

In general, several mechanisms may generate clumped spatial patterns, including resource heterogeneity (e.g., soil), poor seed dispersal and low growth rates (Murrell, 2009), and vegetative reproduction or facilitation (Purves and Law, 2002; Malkinson et al., 2003). Local seed dispersal and resource heterogeneity among similar-sized neighbors would not be sufficient to generate clumped patterns at the age of our stands (~45 yr old), for they should have already competed. Furthermore, the dominant presence of merged trees at the outer edge of the forest reported here (high RIV values) is inconsistent with low growth rates, because they are the largest trees of the age class, and we were able to reject vegetative reproduction as the cause of this clumped pattern. Thus, it is most likely that the ultimate mechanism for merging is some sort of positive interaction that must have occurred, at least partially, before the present study, enabling the unexpected persistence of most trees in the cluster, considerably reducing their mortality.

A reduction in density-dependent effects has been attributed to a decrease in the intensity of competition due to harsh environmental conditions (e.g., low water availability; Fowler, 1986). Simulation models have given similar results; patterns were largely formed by random mortality and independently of the densities of neighboring vegetation when environmental conditions were limiting (Malkinson and Jeltsch, 2007). Thus, current theories based solely on models of resource competition may not hold in high-stress environments, where facili-

tation plays a more important role in interspecific (Bruno et al., 2003; Callaway, 2007; Maestre et al., 2009) and intraspecific interactions (Chu et al., 2008; Goldenheim et al., 2008). The balance between positive and negative density-dependence in our stands is likely complex, and they are most probably acting in concert (Holmgren et al., 1997). Size distributions for merged and single trees were normal, confirming density dependence; however, for single trees this was more biased toward lower size-classes (median = 11.6), which suggests stronger asymmetric competition than in merged trees (median = 14). Thus, competition may still be strong, but the merged stems appear to individually bypass it, once they have become merged. Thus, competition is probably concentrated among merged trees (larger NN distances between merged trees) and not among stems within multistemmed trees (shorter NN distances). We anticipate that as these edge stands get older, single-stemmed trees will tend to disappear as a result of strong asymmetric competition with larger merged trees. It would be interesting to see whether mature merged trees (older than current trees) will dramatically change the structure of the forest—allowing, for example, an earlier development of regeneration (i.e., understory reinitiation stage; Oliver 1980).

Although vegetative reproduction is absent in *N. pumilio*, multistemmed trees have been reported to occur at treeline, where crooked trees (krummholz) became multistemmed as a consequence of wind and snow pressure (e.g., Barrera et al., 2000). The authors of those studies, however, did not determine unequivocally whether these treeline multistemmed trees were a consequence of merging, vegetative reproduction, or architectural deformation. In western North American mountains, whitebark (*Pinus albicaulis*) and limber pine (*P. flexilis*) exhibit multistemmed trunks of multiple origin that result from seed caches made by Clark's nutcrackers; the seedlings grew in close to one another and eventually merged (Linhart and Tomback, 1985). It is unknown whether the spatial location of those multistemmed trees in the forest was correlated with any abiotic factor or whether the trees mutually benefitted; thus, this example does not provide any framework to incorporate the phenomenon into stand dynamics and density-dependent mortality.

Conclusions—Using a mixture of spatial analyses and observations, we have demonstrated that multistemmed trees had multiple origins and occurred mostly at the forest edge, a pattern consistent with certain evidence that establishment was aggregated and probably aided by positive interactions attributable to a harsh environment. We further hypothesize that this initial aggregation led to weak self-thinning that, with time, did not reduce initial aggregation but maintained it, leading to merging and extremely unusual aggregation of mature trees. Our results suggest a shift in our understanding of forest-stand dynamics following disturbances in locations under restrictive biotic conditions, to include positive interactions as a potential strategy that can readily overcome antagonistic interactions.

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