

**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; Moeur, 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 *Strobis* 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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