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Point pattern analysis of crown-to-crown interactions in mountain forests

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Abstract

Pattern analysis of tree stems in forests stands is commonly used to assess the type and intensity of tree-to-tree interactions. Crowns are directly involved in competition for light, and plastically react by growing asymmetrically. We tested the hypothesis that the spatial pattern of crown centers is different than that of stem bases, and specifically more regular due to optimal foraging. We also postulated that shift to regularity in crown spatial pattern was directly related to individual crown asymmetry and the intensity of competition in the stand. We computed point pattern statistics in four long-term forest monitoring plots, established in Scots pine forests of the Alps, and the intensity of spatial association of crown centroids versus stem locations. Crown asymmetry was significantly correlated to competitive status. Crowns were more regularly distributed than stems in mature stands, but not so in a young stand where competition was at a lower intensity. At the stand level, the shift towards regularity was related to relative density and mean crown asymmetry. We propose that studies of competition in mature forests routinely analyze spatial pattern of crowns in addition to that of stems, in order to collect stronger evidence of competitive processes.

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1. Introduction

A large body of ecological research has been based upon the relationship between pattern and process [1]. The spatial arrangement of trees in a mature forest results from the interplay between establishment, competition-related mortality and disturbance-related mortality [2]. When tested against a Poisson null hypothesis, univariate point pattern of tree stems can exhibit higher-than-random aggregation, e.g., as a

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result of facilitation between seedlings or patch disturbance [3], or segregation (over-dispersion), usually interpreted as a result of competition for light [4]. Indices of spatial statistics such as Ripley's K [5] test the validity of the null hypothesis on multiple distances within a stand, providing information on the spatial extent associated to maximum signal strength.

Point pattern analysis in forests is routinely carried out using stem locations. These stay unchanged from the establishment phase to the onset of competition-induced mortality (self-thinning). In forest ecosystems, light is a critical resource, and often distributed heterogeneously. Competition directly involves tree crowns as light-capturing organs. Crown centers have therefore been considered more important than stems for defining the representative positions of trees [6].

The acknowledgment of such processes prompted us to formulate the following hypotheses: (1) in mature stands, individual crown asymmetry is a consequence of competitive stress; (2) crowns are more regularly distributed than stems, due to optimal foraging of available light and growing space [7]; (3) the difference in spatial pattern of stems and crowns is higher in stands with a higher mean crown asymmetry, and hence, in stands experiencing more intense competition.

2. Methods

We established four 70x70m research plots in mature, even-aged forests dominated by Scots pine (*Pinus sylvestris* L.). This species was chosen due to its wide distribution in the European Alps, light-demanding life traits, and high crown plasticity [8]. Selected stands are located in Nothwestern Italy, at elevations ranging from 985 to 1116 m a.s.l. (Table 1).

Plot	UTM (datum: WGS84)	Elevation (m)	Mean slope	Aspect	Age (years)
Challand	5062482 N 402270 E	1116	40%	W	90
Morgex	5069859 N 344753 E	1091	77%	S	90
Toceno	5110964 N 458567 E	1050	80%	W	110
Saint Denis	5068071 N 387870 E	985	62%	SW	40

Table 1. Overview of permanent sample plots used in this study. Age from forest management plans.

All living tree stems with a diameter at breast height (dbh) >2.5 cm were mapped with a spatial resolution of 10 cm. For each tree, we recorded species, dbh, total height, and crown projections relative to the stem base in four orthogonal directions (to the nearest 0.1 m). We drew crown polygons by fitting bidimensional splines to the four crown projection endpoints in a computer-aided design (CAD) system (AutoCAD, Autodesk Inc., Sausalito, CA). We exported the polygons to ArcGIS 9.3 (ESRI Inc., Redlands, CA), and computed the x,y coordinates of polygon centroids relative to the plot origin. Crowns of multi-stem hardwoods were merged into one.

For each tree we computed the direction and length of the displacement vector connecting stem base to crown centroid. Since branch elongation is proportional to tree size, we computed an index of relative crown asymmetry by taking the ratio of absolute displacement to tree dbh. In order to test hypothesis (1), we scrutinized Pearson's product moment correlation between asymmetry and height-to-diameter (H/D) ratio, an indicator of tree competitive status [9]. The intensity of competition in each stand was computed by means of percent Stand Density Index (SDI), an age-free, site-independent measure of stand density

[10, 11]. We computed relative density as the ratio of actual to maximum SDI for monospecific Scots pine stands in the Alps [12].

For each site, we characterized the spatial distribution of both stems and crown centroids by means of Ripley's L(t) function [13]. The L value expresses the expected number of events in circular plots with radius t around each event. The null spatial model used in this study is the complete spatial randomness model (CSR), or Poisson process [14]. The empirical L(t) function was estimated for t <25 m, in steps of 0.5 m, and using a rectangular edge correction [15]. We produced 99 Monte Carlo simulations to compare observed L(t) with the one expected under CSR (95% confidence envelop). Positive values of L(t) indicate regularity, while negative ones signify clumping [13]. Point pattern analyses were performed using the software Programita [16].

In order to test hypothesis (3), we assessed the shift in point pattern by computing the difference between L(t) computed on crowns and stem bases. The mean difference was computed for t <10m, in order to filter out the undesired cumulative effects inherent in Ripley's metric [16], and then related to mean crown asymmetry and SDI of each site.

3. Results

The upper canopy layer was everywhere dominated by Scots pine, accounting for 75% (Saint Denis) to 99% (Toceno) of total basal area (Table 2). Other species were conifers (*Picea abies* (L.) Karst., *Larix decidua* Mill.), downy oak (*Quercus pubescens* Willd.) and sporadically occurring broadleaves.

Challand, Morgex and Toceno were even-aged, mature stands (around 100 years since establishment). Relative density was about 50% in Challand and Morgex, while it approached maximum SDI in Toceno. We also included for comparison a much younger stand in Saint Denis. i.e., one that originated by secondary pine-oak invasion not earlier than 40 years ago. Tree density in Saint Denis was locally high, but large gaps were present where the soil was too shallow to allow tree colonization.

Crown asymmetry was more pronounced in Toceno and Saint Denis (Fig. 1). In 3 out of 4 plots, the highest crown displacement vector was found in the direction of the plot's main slope. In Challand, Morgex and Toceno, crown asymmetry in Scots pine was significantly correlated to H/D ratio (Pearson's R =0.34, 0.18, and 0.40 respectively). A similar pattern was observed for chestnut (*Castanea sativa* Mill.) in Challand (R =0.44) and spruce in Toceno (R =0.64), while in all other cases such correlation was not significant.

Plot	Density [trees ha ⁻¹]	Basal area [m ² ha ⁻¹]	Quadratic mean diameter [cm]	Relative density	Dominant height [m]	Canopy cover
Challand	724	42.3	27.3	56%	17.6	82%
Morgex	824	36.8	23.8	54%	16.7	81%
Toceno	765	70.6	34.3	90%	22.7	78%
Saint Denis	1400	18.0	12.8	34%	7.8	66%

Table 2. Summary data for living trees in the permanent plots. Relative density: ratio of observed to a maximum SDI of 1375 [12], computed by the summation method [11].

Plots with a larger difference between stem and crown L(t) exhibited higher mean crown asymmetry and stand relative density (Table 3), with the latter two variables showing matching trends. Toceno exhibited a lower regularization than expected under crown asymmetry and relative SDI at the site.



Fig. 2. Univariate Ripley's L(t) for tree stems (black) and crown centroids (grey). Positive values indicate clustering, while negative values indicate overdispersion. Empty symbols are not significantly different from CSR.

Table 3. Mean L(t) difference (crowns - stems, t <10 m), mean crown displacement, and relative SDI in the study areas.

Plot	Delta L(t)	Mean crown displacement (cm)	Relative density
Challand	1.02	105.3	0.56
Morgex	0.27	104.6	0.53
Toceno	0.56	391.0	0.80
Saint Denis	-1.75	121.5	0.34

4. Discussion

In stands experiencing intense competition, i.e., where relative density approaches 55-60% [17], high neighborhood densities may be compensated by morphological plasticity, i.e., shifting the crown centers away from the trunks [18, 19].

Hypotheses (1), (2), and (3) were all supported by our results. In the three mature stands, crown displacement in Scots pine exhibited a significant correlation to tree H/D ratio, supporting hypothesis (1). The largest relative displacement was found in Toceno and Saint Denis. In the first case, crown asymmetry was related to the intensity of competition, both of individual trees (significant correlation to H/D ratio for all species) and at the stand scale (highest relative density). Conversely, Saint Denis showed the lowest relative density among the study plots, and no correlation between H/D and relative crown displacement. Asymmetry of crowns may therefore be due to other factors, e.g., slope orientation [20] or direction of most abundant solar radiation [21] that may play a role around canopy gaps. Aspect was significant in our study: in 3 out of 4 plots, the largest displacement was registered along slope orientation.

The spatial pattern of tree stems conformed to expectations, i.e., regular at short distances due to competition-induced mortality at very high relative densities (Toceno). If competition is mainly for light and therefore one-sided, strong local regular patterns of surviving individuals have been shown to develop from initially random or clumped patterns [4, 22].

Despite vertical stratification, the pattern of crowns was more regular than stems at all distances in the three mature stands, in order to maximize light harvesting [23] as postulated by hypothesis (2). In one case, the shape of stem and crown L(t) distributions diverged significantly (i.e., exceeding a 95% confidence envelope) at short distances, while the two curves showed matching trends in all other instances. Regular crown patterns were previously found to prevail in the overstory of temperate forests [6, 24-26], but not tested for significant deviation from stems [7].

Correlation observed between L(t) differences and mean crown displacement (Table 3) suggested that the displacement of crowns tended, at least partly, to make crown distributions more regular. Differences in L(t) towards regularity were related to competition intensity in the stand, assessed by relative SDI (Table 3). In one case, L(t) differences were not as marked as expected under extreme competition and individual crown asymmetry (Toceno). We interpret high crown displacement as the "ghost of competition past", but since competition-induced mortality has already regularized the stem pattern, here crown centroids do not display much additional dispersion in space.

Analysis of spatial pattern of tree crowns has been previously suggested according to several methods [27, 28], but not routinely carried out in ecological research. Studies of competition in mature forests should consistently analyze the spatial pattern of crowns in addition to that of stems, in order to collect stronger evidence competitive processes, even before the onset of mortality. We speculate differences in stem and crown L(t) to decrease when the importance of competition is reduced, and possibly to invert towards a greater clumping if facilitative processes dominate stand dynamics. The difference between L(t) functions could serve as a metric to quantitatively assess the intensity of competition (and possibly facilitation) in a mature forest stand.

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