

Spatial patterns of trees from different development stages in mixed temperate forest in the Hyrcanian region of Iran

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Abstract

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Mixed beech (*Fagus orientalis* Lipsky) forests are very important to the Hyrcanian region of Iran because of their high degree of naturalness and as a source of wood production. Determination of tree spatial patterns over development stages is a first step in understanding underlying processes driving regeneration and forest dynamics. Spatial patterns of trees from three development stages (initial, optimal and decay) of an untouched mixed beech forest were quantified within three 1-ha plots. To prepare the stem maps, we measured each tree with a DBH larger than 7.5 cm using the azimuth-distance method. Spatial patterns were then analysed using Ripley's *K*-function. Results indicated that the number of trees decreased from the initial stage to the decay stage, with tree spatial patterns being aggregated, slightly aggregated and highly randomized for initial, optimal and decay stages, respectively. Differences in spatial patterns among the development stages are not unexpected considering that such unmanaged forests are driven by gap dynamics which results in interactions between gap filling individuals.

Keywords: close-to-nature silviculture; gap dynamics; mixed beech forests; Ripley's *K*-function

The Hyrcanian vegetation zone is part of the most ancient forests of the world (MARVIE MOHADJER 2011) and forms a green belt covering the slopes of the Alborz mountain range and the southern coasts of the Caspian Sea. These forests are similar to broadleaved forests of central Europe, but are richer in terms of species diversity (MARVIE MOHADJER 2011). Oriental beech (*Fagus orientalis* Lipsky) has an important role in the succession dynamics of these forests and is considered to be one of the main late-successional species in the forests

of northern Iran (Delfan Abazari et al. 2004). Mixed beech forests are among the most important natural ecosystems with the highest commercial value and characterized by irregular uneven-aged stand structures (Habashi et al. 2007). Analogous to natural European beech (*Fagus sylvatica* Linnaeus) forests which are generally characterized by three major development stages, i.e. the decay, initial and optimal (Leibundgut 1993; Korpel 1995), oriental beech forests are subject to a wind disturbance regime that produces a mosaic of

patches characterized by these three stages occurring adjacent to each other in space or developing in a cycle over time (SAGHEB-TALEBI et al. 2003; DELFAN ABAZARI et al. 2004). The initial stage is characterized by rapid young tree growth that leads to a gradual canopy closure, subsequent high mortality in dense regeneration due to light competition. Although the stand structure at the early initial stage is still uneven-aged and multilayered, at the late initial stage, the stand structure gradually shifts to almost a single story as the remaining over-story trees die (KORPEL 1995; EMBORG et al. 2000). Later, the optimal stage is built by a single-layered dense canopy with small dead standing trees and little regeneration. The stand dynamics of this stage is very similar to that of managed even-aged stands (KORPEL 1995; EMBORG et al. 2000). In the decay stage, stem density and stand volume decrease as a result of mortality of older trees, which creates gaps that promote tree seedling establishment and development (KORPEL 1995; EMBORG et al. 2000).

Determining the spatial pattern of trees in each of these development stages may help to describe the dynamics of these forests by providing information on changes in between plant-plant interactions from one development stage to the other (DIMOV et al. 2005). Furthermore, better understanding of tree spatial patterns over a time gradient provides guidance for managers practicing close-to-nature silviculture intended to conserve or restore naturally established stand structures while preventing unplanned removals (ABDOLLAHPOUR, ASSADI ATUI 2005). Generally, there are three main tree spatial patterns in natural communities: (i) clumped or aggregated, (ii) regular or uniform, (iii) random (WONG, LEE 2005). A specific tree spatial pattern may result from various underlying mechanisms such as seed dispersal, inter- and intra-specific competition, ecosystem disturbances, herbivory or site heterogeneity (WIEGAND, MOLONEY 2004). Random spatial patterns between individuals are produced by nonselective behavioural patterns and site homogeneity, but may also appear temporarily when clumped patterns shift to regular patterns because of density-dependent mortality (REYBURN 2011).

Spatial point pattern analysis can be useful in surveying tree species and their associates, determining the effectiveness of silvicultural interventions, selecting an appropriate forest inventory method, marking trees for a partial cutting treatment, improving the understanding of natural processes and is consequently an important tool in environmental planning and protection (MALTEZ-MOURO et al. 2007; WIEGAND et al. 2007).

Ripley's *K*-function is effective to describe tree spatial patterns at different scales (KIANI et al. 2011) and has often been used in the Hyrcanian forests (AKHAVAN et al. 2010, 2012; SAGHEB-TALEBI 2014; AMANZADEH et al. 2015) and elsewhere (WANG et al. 2003; ROZAS et al. 2009; ZENNER, PECK 2009; LEE et al. 2012; POZNANOVIC et al. 2014) within the last decade. In the Guilan province of Iran, POURBABAEI et al. (2004) characterized a random spatial pattern of maple (*Acer platanoides* Linnaeus) that was associated with its seed production. HABASHI et al. (2007) found different spatial patterns between species composing mixed Hyrcanian beech (*F. orientalis*) forest while AKHAVAN et al. (2010) observed different spatial patterns between development stages of Hyrcanian beech stands. KARAMI et al. (2012) concluded that both random and clumped patterns characterized the seedling spatial arrangement in regeneration patches of natural beech forests of Iran. Finally, SAGHEB-TALEBI (2014) found different tree spatial patterns in initial, optimal and decay stages of four old-growth oriental beech stands that were explained by climate driven differences in tree density and beech tree abundance.

In Hyrcanian forests, no studies on tree spatial patterns have been carried out in different development stages of unmanaged mixed beech forests. In this study, we analysed tree spatial patterns of species within different development stages to address these questions. The results obtained from this study may be useful to establish comparisons with pure stands of oriental beech and in developing silvicultural programs of natural processes.

MATERIAL AND METHODS

Study area. The study site is located in the Hyrcanian forest of the Sistan district in northern Iran (longitudes 49°49'4"E to 49°53'15"E, latitudes 36°55'10"N to 36°58'16"N) (Fig. 1). The study area covers 59 ha with an elevation range between 350 and 750 m a.s.l., average annual temperature of 14°C and average annual precipitation of 1,273 mm. Precipitation is distributed evenly throughout the year, preventing drought periods. Soils are acidic brown or forest brown with textures varying from clay to clay-loam, mostly with granular structure and low permeability rate. The study area consists of a naturally mixed deciduous forest dominated by beech (*F. orientalis*) and with a lower proportion of hornbeam (*Carpinus betulus* Linnaeus) along with minor presence of Persian maple (*Acer velutinum* Boissier), coliseum maple (*Acer cappadocicum* Gleditsch),

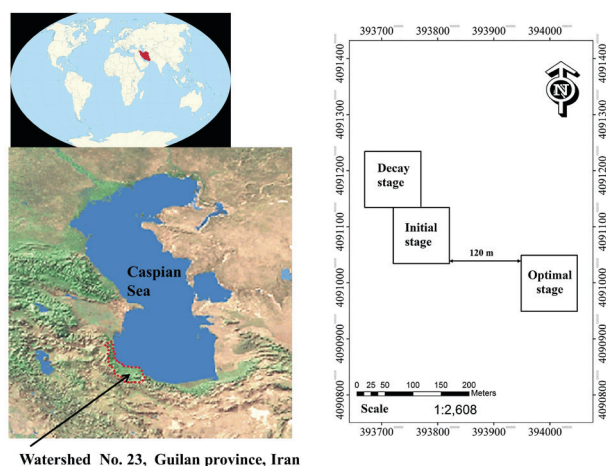


Fig. 1. Geographic map of the study area and spatial position of the three 1-ha plots in reference to one another

Caucasian alder (*Alnus subcordata* C.A. von Meyer), wych elm (*Ulmus glabra* Hudson), persimmon (*Diospyros lotus* Linnaeus), ironwood (*Parrotia persica* (de Candolle) C.A. von Meyer) and lime (*Tilia begonifolia* Steven). Because the study area is exposed to events of periodic wind disturbances, it is composed of a mosaic of small forest patches, each corresponding to a specific development stage, but forming an uneven-aged forest on the whole. The study area has developed with minimal human disturbance and without silvicultural interventions during the last decades. Hence, this forest represents an untouched and unmanaged natural forest typical of ancient native forests to this region.

Data collection. We first conducted a forest survey in the study area to locate forest patches corresponding to different development stages. To determine the development stage of each forest patch, we used the same criteria as those of previous studies: the number and volume of stems, dead

wood volume, proportion of dead wood volume by diameter class, proportion of volume by diameter class, presence of canopy gaps and number of tree layers (Table 1) (DELFAN ABAZARI et al. 2004; SAGHEB-TALEBI et al. 2005; ESLAMI, SAGHEB-TALEBI 2007; MATAJI, SAGHEB-TALEBI 2007; AKHAVAN et al. 2012; SAGHEB-TALEBI 2014). Then, three forest patches were randomly selected to establish 1-ha (100 m × 100 m) sample plots during the summer of 2015 in each of three development stages (initial, optimal and decay). Previous studies have confirmed the appropriateness of the 1-ha plot size to conduct the structure studies of oriental beech stands in Iran (SAGHEB-TALEBI, SCHÜTZ 2002; ESLAMI, SAGHEB-TALEBI 2007). All plots were established in mixed beech stands with the same local climate, elevation, soils, aspect and slope. These plots had eastern aspect with an average slope of about 24°. In each plot, we recorded the species height and diameter of all trees with DBH larger than 7.5 cm along with their spatial coordinates using slope-corrected distances and azimuths from a reference point (i.e., the southwest corner of each plot). Distances and azimuths were transformed to Cartesian coordinates, and all measured trees were assigned to one of the four diameter classes: small (DBH ≤ 32.5 cm), medium (32.5 cm < DBH ≤ 52.5 cm), large (52.5 cm < DBH ≤ 72.5 cm), and extra-large (DBH > 72.5 cm) (AKHAVAN et al. 2012; ZENNER et al. 2015).

Furthermore, the vertical structure of trees was analysed using the IUFRO classification scheme (MARVIE MOHADJER 2011). This scheme categorizes a vertical structure of vegetation into upper, middle and lower story.

Statistical analysis. We used univariate Ripley's *K*-function to analyse the spatial pattern of trees in

Table 1. Criteria for identifying the three development stages

	Development stage		
	initial	optimal	decay
Age	young	middle-aged	old
No. of canopy strata	more than 2	usually 1 to 2	more than 2
No. of trees/area unit	high	medium	low
Proportion of trees in canopy strata	greatest in lower and middle strata	greatest in upper stratum	greatest in middle and upper strata
Proportion of trees in diameter classes	greatest amount in small and medium sizes	greatest amount in medium and large sizes	greatest amount in large and extra-large sizes
Stand volume	medium	high	low
Dead wood volume	medium	low	high
Proportion of dead wood volume in timber size	usually greatest amount in large and extra-large sizes	usually greatest amount in small and medium sizes	usually greatest amount in extra-large sizes
Gap	present	usually absent	present

each of the three development stages. This function considers the distance between all pairs of points (trees) in a two-dimensional space by using the number of points available in a circle of radius r centred on each tree. The univariate estimator of the K -function for a certain point pattern is calculated as Eq. 1:

$$K_r = \frac{\bar{n}_{(r)}}{\rho} \quad (1)$$

where:

$\bar{n}_{(r)}$ – mean number of neighbours within a distance r from a subject tree,

ρ – stand density.

To facilitate the interpretation of results, we used the linearized L -function presented by BESAG (1977). The L -function modifies the shape of the K -function, stabilizes its variance (CRESSIE 1993) and is calculated as Eq. 2:

$$L_r = \sqrt{\frac{K_r}{\pi}} - r \quad (2)$$

Values of $L_r = 0$ indicate a random spatial pattern while values smaller and larger than 0 correspond to regular and aggregated spatial patterns, respectively. We applied Ripley's isotropic correction formula for edge correction (RIPLEY 1988). To test the statistical significance of the deviation of L_r values from zero under the null hypothesis of complete spatial randomness, we used the Monte Carlo simulation method. We computed the 95% confidence interval of L_r with 99 random permutations. In this study, the range of distances used to calculate the L -function ranged between 0 and 50 m. The maximum value of $r = 50$ m is equal to one half of the side of each 1-ha (100 m × 100 m) plot (SALAS et al. 2006; ZHANG et al. 2009). The software package used for the geostatistical analysis was GS⁺ (Version 5.1, 2000) and all statistical analyses and simulations were conducted using the Programita for point pattern analysis (WIEGAND 2006).

RESULTS

We measured the diameter and determined the Cartesian coordinates of 857 trees in the three sample plots. The initial stage had the highest frequency of shorter trees whereas the decay stage was mostly composed of mature trees, and the optimal stage showed a bell-shaped, skewed distribution of tree frequency (Fig. 2).

Mean tree DBH increased from initial to decay stages, while the number of trees followed the op-

Table 2. Species characteristics of each development stage (based on 1-ha area)

	Development stage															
	initial						optimal						decay			
	beech	hornbeam	others	total	beech	hornbeam	others	total	beech	hornbeam	others	total	beech	hornbeam	others	total
No. of stems	217	127	30	374	175	132	2	309	91	57	26	174				
Frequency (%)	58	34	8	100	56.6	42.7	0.7	100	52.3	32.7	14.9	100				
Mean DBH (cm)	20	28	34	23.8	31	27.5	30	30.4	40	36	36	38				
DBH CV (%)	68	51	71	66	57	45	–	54	72	41	48	61				
Mean height (m)	14	18	20.5	15.9	23.7	22.1	23	23	27	27.5	31	27.6				
Basal area (m ²)	15.04	14.61	4.25	33.9	19.3	9.4	0.18	28.9	17	7	3.25	27.25				
No. of snags	2	1	1	4	1	6	–	7	4	5	–	9				
No. of snags > 60 cm DBH	–	–	–	–	1	1	–	2	2	–	–	2				

CV – coefficient of variation, others – *Acer velutinum* Boissier, *Acer cappadocicum* Gleditsch, *Alnus subcordata* C.A. von Meyer, *Ulmus glabra* Hudson, *Diospyros lotus* Linnaeus, *Parrotia persica* (de Candolle) C.A. von Meyer, *Tilia begoniifolia* Steven

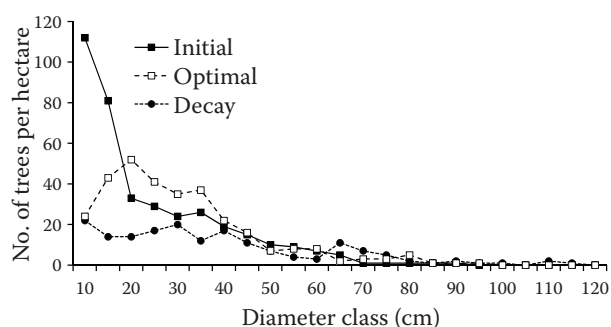


Fig. 2. Stem diameter distribution in each developmental stage

posite trend (Table 2). Accordingly, the initial stage was associated with the largest stem number, the smallest average DBH and the highest coefficient of variation of DBH (Table 2). In the optimal stage, all trees had about the same height and DBH, as indicated by the lowest CV of DBH (Table 2). The decay stage can be recognized by the lowest stem number and basal area (Table 2) and by the greater proportion of trees in large and extra-large DBH classes (Table 3). The stem density of *F. orientalis* was higher than that of *C. betulus* in all development stages (Table 2). Similarly, the DBH of *F. orientalis* was always larger than that of *C. betulus* except in the initial stage, indicating that small diameter trees in this stage were mostly *F. orientalis* (Table 2). *F. orientalis* was less represented in the smallest DBH class of the decay stage compared to other stages, while species other than *F. orientalis* and *C. betulus* were more represented in the decay stage in almost all DBH classes (Table 3). Frequency of *F. orientalis* was higher than that of

C. betulus and other species in lower, middle and upper stories at all development stages except in the initial stage for which the frequency of *C. betulus* was slightly higher than that of *F. orientalis* in the upper storey (Table 4).

Stem maps of the initial stage were drawn to represent tree diameter class and tree species (Figs 3a, b). Trees in the initial stage were mostly clumped from 0 to 28 m, although randomly distributed between 28 and 50 m (Figs 4a–c). This spatial pattern corresponded approximately to that of *F. orientalis* while the spatial distribution of *C. betulus* was ran-

Table 4. Frequency (%) and stem number (*N*) by species for each development stage for each of the following stand storeys

Stage	Species	Stand story					
		lower		middle		upper	
		<i>N</i>	(%)	<i>N</i>	(%)	<i>N</i>	(%)
Initial	beech	103	27.5	65	17.4	49	13
	hornbeam	27	7	41	11	59	16
	others	9	2.5	6	1.6	15	4
	total	139	37	112	30	123	33
Optimal	beech	19	6.1	51	16.5	105	34
	hornbeam	8	2.6	41	13.3	83	26.9
	others	1	0.3	0	0	1	0.3
	total	28	9	92	29.8	189	61.2
Decay	beech	27	15.5	23	13.2	41	23.6
	hornbeam	7	4	20	11.5	30	17.2
	others	5	2.9	5	2.9	16	9.2
	total	39	22.4	48	27.6	87	50

Top heights were 28, 31 and 37.6 m for initial, optimal and decay stages, respectively

Table 3. Frequency (%) and stem number (*N*) by species for each development stage for each of the following diameter classes

Stage	Species	Diameter class								Total	
		small		medium		large		extra-large		<i>N</i>	(%)
		<i>N</i>	(%)	<i>N</i>	(%)	<i>N</i>	(%)	<i>N</i>	(%)		
Initial	beech	177	47.2	29	7.8	11	3	0	0	217	58
	hornbeam	85	23	35	9	6	1.7	1	0.3	127	34
	others	16	4.5	6	1.7	5	1.5	1	0.3	30	8
	total	278	74.3	70	18.7	22	5.9	4	1.1	374	100
Optimal	beech	98	31.7	52	16.9	15	4.9	10	3.2	175	56.7
	hornbeam	96	31	29	9.4	6	2	1	0.3	132	42.7
	others	1	0.3	1	0.3	0	0	0	0	2	0.6
	total	195	63.2	82	26.5	21	6.8	11	3.5	309	100
Decay	beech	47	27	17	9.8	13	7.5	14	8	91	52.3
	hornbeam	30	17.2	19	10.9	7	4	1	0.6	57	32.7
	others	10	5.7	11	6.3	5	2.9	0	0	26	14.9
	total	87	50	47	27	25	14.4	15	8.6	174	100

small – DBH ≤ 32.5 cm, medium – 32.5 cm < DBH ≤ 52.5 cm, large – 52.5 cm < DBH ≤ 72.5 cm, extra-large – DBH > 72.5 cm

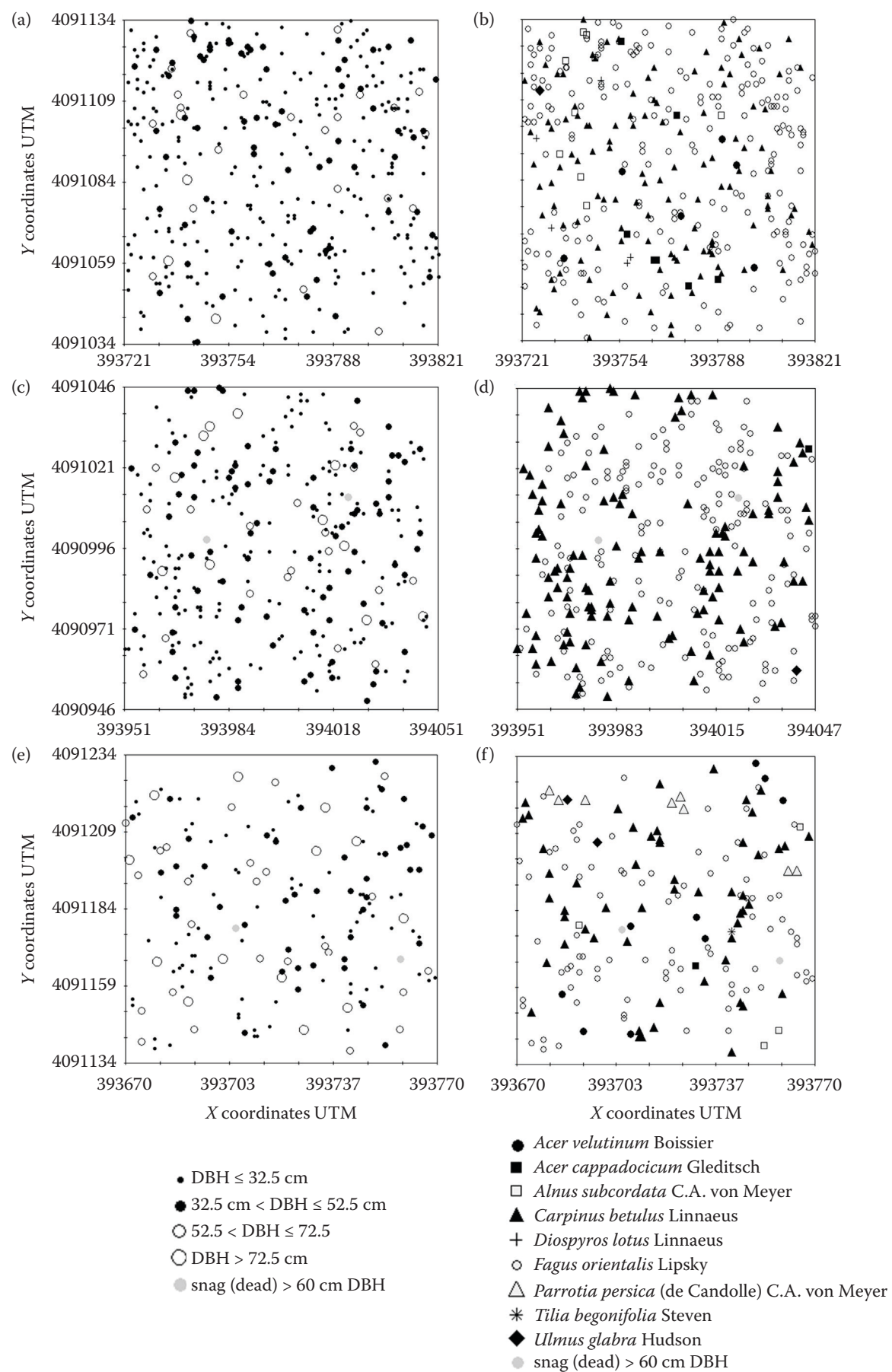


Fig. 3. Spatial patterns of trees in the initial (a, b), optimal (c, d), decay (e, f) stages by tree DBH (a, c, e) and also tree species (b, d, f)

dom between 0 and 28 m and slightly clumped for longer distances (Figs 4b, c).

Compared to the initial stage, tree density in the optimal stage was lower, particularly for the smallest diameter class (DBH ≤ 32.5 cm) (Fig. 3c). Also, the tree diameter distribution was more uniform (Fig. 3d), as indicated by the smaller value of the coefficient of variation (Table 2).

When all species were included in the analysis of the optimal stage, L_r values were generally slightly higher than the 95% confidence interval, regardless of the distance between trees (Fig. 4d), indicating a slightly clumped pattern. However, when *F. orientalis* was considered alone, a clear clumped pattern was apparent for distances < 30 m, while *C. betulus* showed a clumped pattern for all distances (Figs 4e, f).

At the decay stage, tree density was significantly lower than those of the two previous stages. In addition, the coefficient of variation of DBH for the decay stage was lower than that of the initial stage but higher than that of the optimal stage (Table 2, Fig. 3e). At this stage, the frequency of *F. orienta-*

lis was lower, but tree numbers of shade-intolerant *A. velutinum*, *A. cappadocicum*, *A. subcordata* and mid-shade-tolerant *U. glabra*, *P. persica* and *T. begoniifolia* species were larger (Fig. 3f).

When all species of the decay stage were considered together, L_r values were within the 95% confidence interval for all distances, which indicates a random spatial distribution (Fig. 4g). In addition, since these L_r values were closer to zero than those of the optimal stage, they may be interpreted as a higher degree of randomness. *F. orientalis* and *C. betulus* showed clumped patterns for distances < 12 m, but random patterns for distances ≥ 12 m (Figs 4h, i). Other species in the decay stage showed a random pattern for distances < 20 m and a regular pattern from 20 to 50 m (Fig. 4j).

DISCUSSION

Since the three development stages were sampled in areas with similar climate, soil and topography, our study shows the basic differences in the

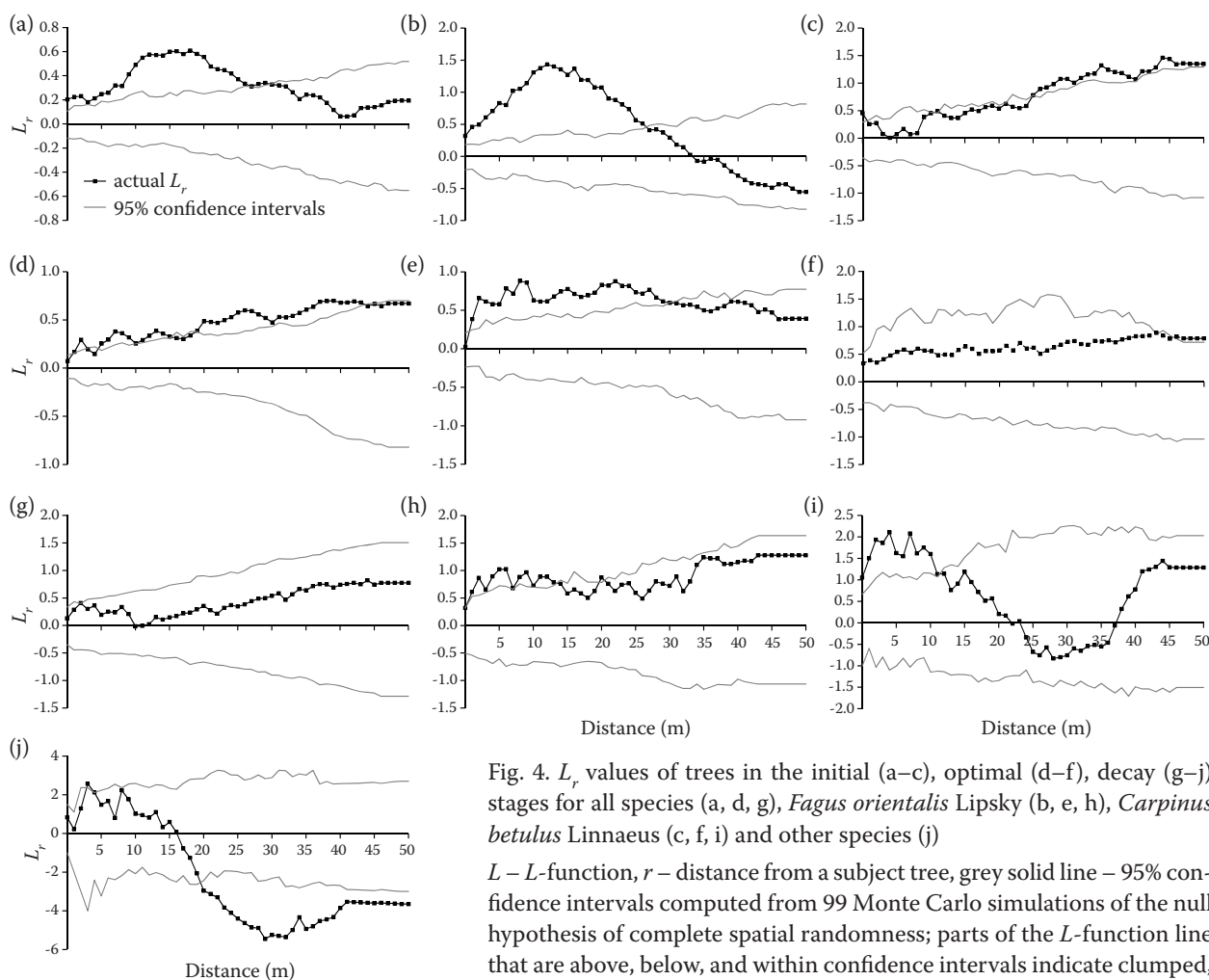


Fig. 4. L_r values of trees in the initial (a–c), optimal (d–f), decay (g–j) stages for all species (a, d, g), *Fagus orientalis* Lipsky (b, e, h), *Carpinus betulus* Linnaeus (c, f, i) and other species (j)

L – L -function, r – distance from a subject tree, grey solid line – 95% confidence intervals computed from 99 Monte Carlo simulations of the null hypothesis of complete spatial randomness; parts of the L -function line that are above, below, and within confidence intervals indicate clumped, regular, and random spatial patterns, respectively

spatial structures of Hyrcanian forests dominated by *F. orientalis* in Northern Iran. The main results of this study indicate that the clumped spatial distribution of trees generally observed at the initial stage of this mixed beech forest becomes increasingly random over time. The following paragraphs explain the reasons for these temporal changes in horizontal structure and discuss the implications for forest management.

The spatial distribution of species using seed regeneration strategies is largely determined by seed dispersal (CALVIÑO-CANCELA 2002). Since the cohort of small trees was dominated by *F. orientalis* at the initial stage, the observed clumped distribution of trees was likely related to the limited seed dispersal of this species caused by its heavy seeds (HABASHI et al. 2007; HASSANI, AMANI 2010; AKHAVAN et al. 2012) and to seedbed conditions. Once established, the shade-tolerant seedlings of this species can survive and develop in the understorey to form clumped distributions at short distances (< 28 m) of parent trees (HOU et al. 2004; HAO et al. 2007). This observation agrees with the results of the study by SAGHEB-TALEBI (2014), who observed a clumped distribution of beech trees in young stands of the Neka region of Iran at scales shorter than 25 m. Over time, however, competition for resources will lead to mortality among individuals within clumps, which will gradually change the spatial distribution of trees from clumped to random (HEGAZY, KABIEL 2007; LAN et al. 2012).

At the initial stage, while a clumped pattern of *F. orientalis* was observed for distances < 28 m, distances > 28 m were characterized by a random pattern. According to SALAS et al. (2006), clumped patterns are common for small trees (DBH \approx 10 cm) located in canopy gaps. In addition, clumped patterns are typically observed in naturally regenerated stands (AKHAVAN et al. 2012), but not in all cases (AMANZADEH et al. 2015). Indeed, as competition decreases with increasing between-tree distance, a random tree distribution gradually appeared at distances larger than 20 m from a subject tree (Fig. 4b). This distance likely corresponds to the average size of the former canopy gaps that were filled by a clumped regeneration stratum of *F. orientalis*. Similar results have been reported by OMIDVAR HOSSEINI et al. (2015), who observed a clumped pattern of the heavy-seeded chestnut-leaved oak (*Quercus castaneifolia* C.A. von Meyer) at short distances in dense stands while the spatial distribution shifted to random as distance increased.

In contrast with *F. orientalis*, the distribution of *C. betulus* trees at the initial stage gave ambiguous

results: neither distinctly random nor clustered patterns for all distances from the subject tree (Fig. 4c). On the one hand, winged seeds of *C. betulus* trees can be easily dispersed (CHAPOLAGH PARIDARI et al. 2012), which promotes the formation of a random tree distribution. On the other hand, the light requirements of this mid-shade-tolerant species suggest that regeneration development should be clumped in canopy gaps where light is more available. Hence, the marginal random-clumped tree distribution of *C. betulus* may result from these two opposing processes as well as the rapid colonization of regeneration niches by *F. orientalis* in this particular sample plot (AMANZADEH 2015).

The number of small diameter trees (\leq 32.5 cm) in the optimal stage was about 11% lower than that at the initial stage (Table 3). This indicates that mortality induced by intra- and/or interspecific competition, which mostly affects suppressed trees, was effective at this stage to create a more regular spatial pattern when all species were considered together (Fig. 4d). Such tree spatial patterns were also observed by SAGHEB-TALEBI (2014) in beech stands at the optimal stage from the Kelardasht region of Iran.

The clumped tree distribution of *F. orientalis* observed at the initial stage was still apparent at the optimal stage (Fig. 4e). In addition, the tree spatial pattern of *C. betulus* was clearly clumped at the optimal stage (Fig. 4f) as was also observed by LEE et al. (2012) for *Carpinus cordata* Blume. When all species were considered together, however, the distinct clumping of *F. orientalis* and *C. betulus* was obscured; instead, an only marginally clumped tree pattern emerged (Fig. 4d). It thus seems that the juxtaposition of clumped tree distributions of both *F. orientalis* and *C. betulus*, each at different spatial locations in the stand, produced an overall tendency to randomization in the tree spatial pattern.

In line with the trend observed at the optimal stage, we observed a random spatial distribution of trees at the decay stage when all species were considered together. Tree density was considerably lower at the decay stage than at earlier stages, particularly in the smallest size class (Table 3). Yet, when abundant, these small trees have a large influence on the overall spatial pattern (SAGHEB-TALEBI et al. 2005; AKHAVAN et al. 2012) because they tended to be clumped. As a consequence, the low density of small trees in the decay stage can explain the absence of clumped pattern when all species are considered together. However, when considered individually, the spatial distribution of both *F. orientalis* and *C. betulus* was clumped

at short between-tree distances (< 13 m). Because these clumps are likely composed of regularly spaced individuals as a result of intraspecific competition, tree spatial distribution becomes random when all species are considered at the same time. As for larger trees, they generally tend to be regularly distributed in a forest stand (HE et al. 1997; SAGHEB-TALEBI 2014). Such tree spatial pattern at this stage was also observed by SAGHEB-TALEBI (2014) in beech stands of the Shastkolateh region of Iran. CHENG et al. (2014) found that overmature trees tend to exhibit a random pattern at almost all scales because of stochastic mortality or strong intra- and/or interspecific competition for resources.

As a general rule, clumped tree distributions are the result of regeneration establishment and development that occurred in medium to large gaps as a result of improved light and moisture regimes (AMANZADEH 2015). Over time, intra- and/or interspecific competition, which produces density-dependent mortality, can lead to a less aggregated or even regular tree distribution (HOU et al. 2004). Accordingly, our results show that both beech and hornbeam trees were spatially clustered at all three stages. However, when all species are considered together, the spatial pattern shifts from highly clustered (initial stage) through marginally clustered (optimal stage) to random (decay stage). This result is consistent with the findings of COMMARMOT et al. (2005), who examined the spatial patterns of virgin beech (*F. sylvatica*) trees in stands of various ages in Ukraine. They concluded that old trees tended to be randomly distributed, but trees in the lower storey, and to a lesser degree in the middle storey, tended to be aggregated. Establishment of tree regeneration in gaps created by tree mortality was proposed to explain the formation of these clusters.

Knowledge of tree spatial distributions in unmanaged stands is essential to the 18 effective applications of close-to-nature silvicultural approaches in managed stands. Consequently, implementation of management decisions should be related to the principal characteristics of mixed beech stands at each stage of their development. The primary objectives of these interventions include the improvement of stand structure and composition, with a particular emphasis on regeneration establishment (PARHIZKAR et al. 2011). Uneven-aged mixed forests are generally resistant to natural disturbances while providing sustainable production (ALIJANI et al. 2014); to emulate these stand conditions, implementation of silvicultural treatments may be

an important step in promoting and maintaining a multilayered structure (PARHIZKAR et al. 2011; SAGHEB-TALEBI 2014).

In accordance with our results, we give examples of silvicultural interventions that may be applied at each development stage. At the initial stage, since self-thinning seems to be the principal process among trees in the lower and middle storeys, crop tree thinning could be applied to accelerate this natural process and, alternatively, to promote tree diversity. Because the optimal stage is characterized by a structure resembling that of managed even-aged stands, commercial utilization can be applied to promote the diameter growth of dominant trees and to help establish natural regeneration of shade-tolerant tree species. At the decay stage, protection of tree regeneration seems essential in order to promote it. Moreover, information derived from this study gave us insight into competitive processes for modelling of forest dynamics and could also be useful as a key reference to improve the use of growth models.

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