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Fine-scale spatial patterns in oak sprouting and mortality in a newly restored coppice

Martin Svátek *, Radim Matula

Department of Forest Botany, Dendrology and Geobiocoenology, Faculty of Forestry and Wood Technology, Mendel University in Brno, Zemědělská 3, 613 00 Brno, Czech Republic

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ABSTRACT

Sprouting is a common life history strategy in tree communities and is crucial for coppice management of woodlands. Recently, there has been increasing interest in coppice restoration throughout Europe and several studies have explored the sprouting ability of tree stumps in the restored stands. Though the spatial distribution of trees has been previously found to affect ecological processes in many ecosystems, no study has so far considered the importance of spatial interactions during the process of coppice restoration. The present study attempts to fill this gap by analyzing fine-scale spatial patterns in sprouting and mortality in a newly restored oak coppice with different densities of residual timber trees. Univariate and bivariate point pattern analyses were used to quantify the observed spatial patterns. While no significant spatial associations were found between residual trees and dead (post-harvest non-sprouting) stumps, our mortality analysis revealed clear non-random interactions between stumps themselves. Negative distance- and density-dependent effects in post-harvest stump mortality were observed at short scales; stumps with more neighboring stumps at a close distance were significantly more likely to die after harvest. Our study demonstrated that non-random effects in mortality are not limited only to generative reproduction of trees but play also an important role in vegetative regeneration of one of the main European broadleaved tree species.

1. Introduction

For many centuries, European forests have been managed by coppicing (Rackham, 2003; Honnay, 2004; Szabó, 2005), relying on the ability of broadleaved trees to regenerate themselves from stumps cut on a short rotation (Buckley, 1992). However, beginning in the second half of the 19th century, socio-economic changes and a declining market for coppice products have subsequently led to the abandonment of this traditional form of woodland management throughout Europe (Buckley, 1992; Peterken, 1993). Large areas of former coppice have been converted to high forest, especially in Central and Northwestern Europe (Hédl et al., 2010), or have, through neglect, become stored (Buckley, 1992). Recent years have seen increased interest in coppice restoration in Europe, which has been triggered by either nature conservation (Peterken, 1993; Benes et al., 2006; Spitzer et al., 2008) or economic reasons such as the increasing use of biomass as a renewable energy source (Hall, 2002; Scholz and Ellerbrock, 2002; Jansen and Kuiper, 2004; Frater and Read, 2005; Nestorovski et al., 2009).

The potential candidates for both economic- and conservation-motivated coppice restoration in Central Europe are often oak-dominated stands that were last cut many decades ago (Matula et al., 2012; Pyttel et al., 2013). However, there is considerable uncertainty as to whether such stands have retained their ability to resprout and which factors may affect resprouting (Pyttel et al., 2013). Because of the lack of information on the resprouting ability of aged oak stands, several recent studies have explored their post-harvest sprouting ability in relation to several variables, such as stump parameters (Matula et al., 2012; Šplíchalová et al., 2012), density of residual trees (Matula et al., 2012), harvesting method and browsing intensity (Pyttel et al., 2013). Nevertheless, to our knowledge, no study has so far investigated the role of spatial interactions in stump sprouting and mortality during the process of coppice restoration. Nonetheless, the spatial pattern of the plants is widely considered to be a crucial aspect of vegetation (Legendre and Fortin, 1989; Fortin and Dale, 2005; Stoll and Bergius, 2005) and has been proven to have profound effects on interactions between plants (Dale, 2000). Spatial patterning of individuals within a population is closely linked to the ecological processes shaping the population (Stoll and Bergius, 2005). Thus, tree spatial pattern analysis may not only characterize the spatial distribution of individual trees within a stand but also help to

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* Corresponding author. Tel.: +420 545134058.
E-mail address: msvatek@centrum.cz (M. Svátek).

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understand the underlying ecological processes producing the pattern (Dale, 2000; Wiegand and Moloney, 2004, 2013). Fine-scale spatial analysis using second-order statistics, such as the pair correlation function (Stoyan and Penttinen, 2000; Illian et al., 2008), has been increasingly applied in ecology to identify the type of underlying pattern present and to precisely detect the spatial scale at which the ecological process is operating (Wiegand and Moloney, 2013).

Processes such as competition between neighboring trees and mortality resulting from their small-scale spatial arrangement are crucial for recruitment of trees within a forest. While there have been numerous fine-scale spatial analyses on the recruitment of tree seedlings in European old-growth forests (e.g., Nagel et al., 2006; Szewczyk and Szwagrzyk, 2010; Petritan et al., 2014), studies on spatial patterns of vegetative regeneration of main European tree species are largely missing. Previous studies on oak sprouting have not considered the effects of spatial patterns and have often yielded inconsistent and contradictory results about which factors may affect the sprouting ability of oak (Pyttel et al., 2013). Therefore, the examination of spatial patterns in a newly restored coppice could contribute to a better understanding of the ecological mechanisms involved during the early phase of oak vegetative regeneration and thus potentially increase the success of future coppice restoration projects.

In this study, we analyzed fine-scale spatial patterns in post-harvest stump sprouting and mortality of sessile oak (*Quercus petraea* (Mattuschka) Liebl.) in a restored coppice with different densities of residual timber trees. Specifically, our objectives were the following. First, to determine the impact of logging on an overall tree spatial pattern, we compared the pre-harvest spatial pattern of oak trees with the post-harvest distribution of surviving (sprouting) oak stumps. Second, we expected negative spatial associations between surviving (post-harvest sprouting) stumps and residual trees to occur due to competition. Third, we hypothesized that dead (non-sprouting after harvest) stumps would be more aggregated than expected under random mortality (Kenkel, 1988; He and Duncan, 2000; Yu et al., 2009) and that they would be found preferably in high pre-mortality stump densities due to density-dependent effects (Yu et al., 2009). Distance- and density-dependent tree mortality has been previously found to result from long-term self-thinning (Kenkel, 1988) as well as from one-time stand-scale natural disturbances, such as fire (Yu et al., 2009). However, to our knowledge, there have so far been no studies on anthropogenic disturbances of a similar scale, such as the clearing of a stand, as possible causes of density- and distance-related mortality of tree stumps.

2. Methods

The study area is located at 49°14′43″N, 16°35′59″E in the Training Forest Enterprise Křtiny of Mendel University in Brno, in southeastern Czech Republic, at an elevation of 300 m a.s.l. The average annual air temperature is 8.4 °C. The warmest month is July (average temperature 18.4 °C), and the coldest month is January (−2.1 °C), based on data from 1960 to 2010 obtained from the Brno weather station. The average annual rainfall is 510 mm. The soils are cambisols on granodiorite bedrock.

The study area was an active oak-dominated coppice until the beginning of the 20th century (Kadavý et al., 2011). Since the 1940s, oak coppice shoots have been thinned, and the forest has become a stored even-aged oak coppice that appears nearly identical to a high forest, despite its coppice origin. Such a forest is a typical result of abandonment of oak coppices, and many similar stands can be found throughout Central and Northwestern Europe. In January 2009, the oak-dominated forest in the study area was harvested with the intention to restore a short-rotation coppice system. Prior to this harvest, all of the trees with a diameter at breast height (DBH) ⩾ 7 cm were identified to the species level, and their exact positions to the nearest cm were recorded using Field-Map technology (IFER, Ltd., Jílové u Prahy, Czech Republic; for details of the technology, see Hédl et al., 2009) so that the stumps could be easily located after they were cut. The studied forest had a total basal area (BA) of 27.1 m^2 ha^{-1} with 716 trees/ha with a DBH ⩾ 7 cm and was dominated by sessile oak (*Quercus petraea* (Matt.) Liebl.) (96% of all individuals and 96% of total BA). The only other tree species that represented more than 1% of the measured trees were Scots pine (*Pinus sylvestris* L.) (1.6%) and European hornbeam (*Carpinus betulus* L.) (1.5%). Sixteen square plots of 2500 m^2 each were randomly placed within the restored coppice. The environmental factors such as slope, soils and microclimate within the plots showed no apparent heterogeneity. All plots were located on a flat plain therefore the topographical and microclimatic factors were expected not to differ significantly between the plots. In all of the plots, the trees were cut approximately 5–10 cm above ground level. The season of harvest and the density of residual standing trees (see below) followed the basic management practices that were common in the region in the 19th century, based on the historical management plans of the Training Forest Enterprise.

To study the effects of the spatial distribution and density of residual trees on sprouting, four densities of healthy canopy trees of sessile oak were left uncut, with each density represented in four plots. The four densities used were 0 (i.e., clear-cut), 24 (1.1 m^2 in BA; hereinafter referred to as low density), 35 (1.4 m^2 BA; medium density) and 44 (1.9 m^2 BA; high density) trees per plot. The residual trees averaged 16.7 m in height and 22.3 cm in DBH. The whole stand was fenced because there was significant game pressure in the area. The fence was checked at least once every other week because the game animals had damaged it several times. Two years after the cutting, in winter 2010/2011, every stump in all of the plots was checked to determine whether the stump had produced at least one sprout. In total, we evaluated 2292 oak stumps in the 16 plots, out of which 683 (29.8%) did not sprout. Basic post-harvest structural characteristics of the plots are given in Table 1.

2.1. Spatial analysis

Methods of point pattern analysis (Diggle, 2003; Möller and Waagepetersen, 2007; Illian et al., 2008; Yu et al., 2009; Wiegand and Moloney, 2013) were used to study spatial patterns in the restored coppice. To quantify fine-scale spatial relations between stumps and/or trees within a stand, we calculated the pair correlation function, which is considered to be the most informative second-order summary characteristic (Illian et al., 2008).

The univariate pair correlation function $g(r)$ is based on the expected number of points (i.e., trees or stumps) found at a distance r from an arbitrary point (which is not counted), divided by the intensity λ of the pattern (Ripley, 2004; Wiegand and Moloney, 2004; Illian et al., 2008). To assess the overall tree spatial

Table 1
Mean numbers of residual trees and dead and live oak (*Quercus petraea*) stumps in the four densities of residual trees. Standard deviations are in parentheses. The stump densities did not differ significantly among the four densities of residual trees (ANOVA, $p = 0.230$).

Density of residual trees	Residual trees (ha^{-1})	Dead oak stumps (ha^{-1})	Live oak stumps (ha^{-1})
Low	96	149.0(45.8)	395.0(111.2)
Medium	140	149.0(11.9)	376.0(45.5)
High	176	165.0(77.6)	388.0(79.8)
Clear-cut	0	220.0(67.2)	450.0(62.1)