



Coppice management of forests impacts spatial genetic structure but not genetic diversity in European beech (*Fagus sylvatica* L.)



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ABSTRACT

Coppice management of forests was historically common in Europe. Actively managed coppice persists through vegetative regeneration prolonging the lifespan of trees and reducing flowering, seed production, and establishment. As coppicing alters the primary regeneration pathway within a stand, it is expected to alter the level and structuring of genetic diversity within populations. The study species, European beech (*Fagus sylvatica* L.), has historically experienced widespread coppicing throughout the range of the species. Genetic material was obtained from paired coppiced and high forest stands, in each of three study sites across Europe located in Germany, France, and Italy. Trees were genotyped at 11 microsatellite loci. Estimates of genetic diversity were found to be equally high as those found in natural forests. Significant spatial genetic structure of coppice stands extended 10–20 m further than their paired high forest indicating that local-scale patterns of geneflow have been significantly altered by generations of forest management in the coppice stands. Understanding the implications of such changes for the structure and level of diversity within traditionally managed populations can assist with management planning for conservation and resource use into the future.

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1. Introduction

Much of Europe's forest has been subject to human intervention for millennia, with approximately 70% of all forests in Europe being classed as semi-natural (FOREST EUROPE and UN/ECE-FAO, 2011). Prolonged management has shaped their distributions and changed the pattern of genetic diversity within and amongst populations (Bradshaw, 2004; Schaberg et al., 2008; Piotti et al., 2013; Sjölund and Jump, 2013). Maintaining genetic diversity can retain the adaptive potential of a population in response to environmental change (Jump et al., 2009). Furthermore, levels of genetic diversity in dominant species can profoundly influence ecosystem functioning (Christensen et al., 1996; Peterson et al., 1998; Booy et al., 2000; Reusch et al., 2005; Whitham et al., 2010). This effect is particularly relevant to many European forests which are often comprised of a few dominant tree species (EEA, 2007). Therefore the adaptive management of Europe's semi-natural forests is

dependent on understanding how prolonged management has shaped forest genetic resources (Lefèvre, 2004).

Traditional coppice management was historically common in Europe and was sustained by the demand for shoots and poles which were used for fuelwood, animal fodder, crafts, and building materials (Read, 2000). Coppice products were derived by cutting the main stem of a tree at ground level leaving a stump, called a stool, which subsequently produces a re-growth of shoots that are harvested at different intervals (Evans, 1992; Harmer and Howe, 2003). At least 25 million ha of forested areas in Europe (excluding the Russian Federation) have been managed as coppice in the past (UN/ECE-FAO, 2000), with only 2.9 million ha remaining under active coppice regeneration in 2011 (EUROPE and UN/ECE-FAO, 2011).

Continued coppice management often increases the longevity of the tree allowing it to persist as long as vegetative regeneration is exploited (Blake, 1980). One of the oldest coppice stools found was a European Ash (*Fraxinus excelsior* L.) and was thought to be thousands of years old, much older than their unmanaged counterparts, which have a typical lifespan of ~200 years (Rackham, 1986). The resulting microhabitat complexity supports a wide range of species and creates cultural landscapes that are recognised for their heritage and ecological value (Rackham, 1980; Peterken, 1992,

Abbreviations: GH, Germany high forest; GC, Germany coppice; FH, France high forest; FC, France coppice; IH, Italy high forest; IC, Italy coppice.

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1993; Fuller and Warren, 1993; Harmer and Howe, 2003). Traditional coppice practices suffered a decline during the nineteenth century primarily due to socio-economic changes. The ecological value and persistence of many previously coppiced forests has declined owing to cessation of management or the conversion of coppice to high forest for timber production (Bacilieri et al., 1994; Panaïotis et al., 1997; Watkins and Kirby, 1998; Harmer and Howe, 2003; Nocentini, 2009).

Forest management practices, such as coppicing, which alter the primary regeneration pathway within a stand, are expected to have significant effects on the structuring of genetic diversity within populations (Loveless and Hamrick, 1984; Heuertz et al., 2003; Vekemans and Hardy, 2004). Appropriate management of forest genetic resources requires an understanding of the spatial structuring of genetic diversity within populations. Significant structuring within a population can influence local breeding and evolution (Smouse and Peakall, 1999). Gene flow, genetic drift, and selection are the main processes that shape spatial genetic structure (SGS) (Loveless and Hamrick, 1984). In plant populations, the effects of gene flow on SGS are largely driven by pollen and seed dispersal (Sokal et al., 1989), but can also be influenced by clonal propagation depending on the regeneration pathway, i.e. natural vs. vegetative regeneration (Sjölund and Jump, 2013). Coppicing limits the effective population size by reducing flowering and encouraging clonal expansion that can restrict gene flow. Such changes influence the structuring of genetic diversity within a population. It is therefore necessary to assess whether coppicing, a management practice which was historically widespread and long-standing, has altered the genetic diversity and structure of these semi-natural forests.

This study focuses on the European beech (*Fagus sylvatica* L.) which forms the dominant forest type over much of Western and Central Europe and extends into the Mediterranean at higher altitudes. Coppice management was historically widespread throughout the range of the species despite the fact that beech rarely reproduces vegetatively under natural conditions and is therefore one of the less responsive species to coppice management (Packham et al., 2012). A variety of systems have been used, including the coppice-with-standards systems, common in the northern and core range of beech and the coppice selection system, which maintains canopy cover and thus is widespread in the drought prone southern range edge (Harmer and Howe, 2003; Coppini and Hermanin, 2007; Nocentini, 2009; Wagner et al., 2010). In addition, trees were sometimes coppiced in silvopastoral systems (Read, 2006; Read et al., 2010). Traditional coppice systems were managed on long rotation cycles that led to a substantial increase in the longevity of individual plants but reduced opportunities for establishment from seed when compared with their high forest counterparts.

Research on the genetic effects of coppicing has been carried out on a few species, (e.g. Beech (Paffetti et al., 2012; Piotti et al., 2012), Pyrenean oak (*Quercus pyrenaica* Willd. (Pyrenean oak) (Valbuena-Carabaña et al., 2008), pedunculate oak (*Q. robur* L.) (Cottrell et al., 2003), sessile oak (*Q. petraea* Matt. Liebl.) (Cottrell et al., 2003; Dostálek et al., 2011), and sweet chestnut (*Castanea sativa* Mill.) (Aravanopoulos et al., 2001; Mattioni et al., 2008)). However, it is difficult to draw general conclusions from these studies due to the lack of paired plots, their limited geographic spread, and the low number of molecular markers used in some studies. Our study differs from previous studies as it employs extensive sampling within paired stands, focusing on the effects of coppice management by comparing those stands with nearby, unmanaged stands in the same forest. In the present work, we were able to determine the effects of promoting vegetative regeneration through traditional coppice management on the amount and structuring of genetic diversity within populations

of European beech using a paired plot design in three regions. We hypothesised that prolonged vegetative reproduction should decrease genetic diversity and increase spatial genetic structure due to the reduced probability of establishment from seed. Such information will be useful for the managers of the large fraction of semi-natural forests that have experienced coppicing in the past. Furthermore, understanding the spatial genetic structure of populations will have consequences for genetic resource management on a spatial scale, for example the collection of seed for gene banks or silviculture.

2. Materials and methods

2.1. Study species

The wind-pollinated European beech is a broadleaved, monoecious tree that is highly outcrossing, with large seeds (beech mast) that are mainly dispersed by animals and gravity (Packham et al., 2012). With a range of roughly 14 million ha, it commonly forms near monospecific stands but is also a major component of many mixed forests. The lifespan of unmanaged beech is typically between 150 and 300 years and rarely exceeds 300 (Packham et al., 2012). Traditional management has been reported to increase the longevity of trees due, in part, to their persistence in a partially juvenile state (Blake, 1980), although coppicing success is variable (Harmer and Howe, 2003). Beech has a shallow root system which makes it particularly vulnerable to wind-throw and drought. All parts of the tree and seedlings are susceptible to frost. Flowering can begin between the age of 40 to 80 years depending on the density of the stand, however coppice management can restrict flowering as stems are not allowed to reach maturity (Blake, 1980).

2.2. Study sites

Three study sites were selected across Europe (Germany, France, and Italy) to attain broad coverage of the species range (see Table 1). In each site, two paired plots were sampled, a coppice and a high forest stand. Paired stands were no further than 10 km apart to maintain comparable colonisation history. High forest stands were defined as having little or no historic or contemporary management and originated from seed primarily through natural regeneration. Coppiced stands were defined as stands with either a history of coppice management which has ceased, or is currently under active coppice management. The primary regeneration pathway is natural in the former and vegetative in the latter. Both stand types originate from native forest with a continuous history. Stand codes are used to refer to stands in this paper, and were derived from the first letter of the country (G = Germany, F = France, I = Italy) and the management history of the stand (H = high forest stand, C = coppice stand).

Sampling was carried out on the original coppiced trees which were the dominant form in the stands and could be easily identified. GC was managed as a simple coppice, after which it was converted to high forest (pers. comm. R. Herrmann). FC is a neglected coppice that occurs in an area of Montagne de Lure which has a history of coppicing dating back at least to the beginning of the 19th century with beech coppice managed on a long rotation coppice system (Simon et al., 2007). IC was managed in the past as a coppice-with-standards system (pers. comm. F. Bottalico), which now experiences low-level harvesting of stems by local residents (pers. obs.). It should be noted that the German high forest was managed as a shelterwood system up until 1988 (pers. comm. R. Herrmann). Although there has been intermittent low intensity harvesting of trees for timber in each of the high forest stands, the three high forest stands differ from the coppice stands in terms of the primary regeneration pathway.

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