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Title

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.

Keywords

Coppicing; European Beech; Spatial Genetic Structure; Genetic Diversity; Traditional Management; Gene flow

Abbreviations

Abbreviations for study site names: Germany High Forest (GH), Germany Coppice (GC), France High Forest (FH), France Coppice (FC), Italy High Forest (IH), and Italy Coppice (IC).

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; Fuller and Warren, 1993; Peterken, 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 10km 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.

2.3 Sample collection and microsatellite analysis

To account for short distance classes and hence allow the detection of fine-scale SGS, trees were sampled on a grid (approximately 150m x150m in size) with points at every ~10m. An additional 20 trees were sampled along a 100m transect extending out of the grid to extend the spatial range covered (not implemented in IH site as it was not possible due to topographic restrictions) (see S1

for diagram of sampling design). Sample size ranged from 100 to 170 samples (see Table 1). Geographic coordinates were recorded for each tree sampled using a GARMIN 62s handheld GPS. As beech typically produces shoots originating from the stool, instead of roots in response to coppicing (Coppini and Hermanin, 2007), individuals can be easily distinguished and the sampling of clones avoided and confirmed from genetic data.

Genomic DNA was obtained from leaf or cambium samples (Colpaert *et al.*, 2005). Samples were dried in silica gel and DNA was isolated using BIOLINE Isolate Plant Kit and QIAGEN 96 Plant Kit according to the manufacturer's instructions. A total of 812 individuals (Table 1) were genotyped at 13 polymorphic SSRs (fs1-03, fs1-15, fs3-04, fs4-46, fcm5 (Pastorelli *et al.*, 2003), mfc7 (Tanaka *et al.*, 1999), mfs11 (Vornam *et al.*, 2004), sfc0007-2, sfc0018, sfc0036,sfc1143, sfc1061, sfc1063 (Asuka *et al.*, 2004)) in three multiplexes designed for this study; FSNplex1, FSNplex2, and FSNplex3. Multiplex PCR was carried out using 10ng of template DNA and the QIAGEN Type-it Microsatellite PCR Kit with the following combinations for primer mixes. FSNplex1 consisted of primers fs3-04, sfc1143, mfc7, and fs4-46 at concentrations of 1µM, 3µM, 1µM, and 2µM respectively. FSNplex2 consisted of primers sfc0007-2, fs1-15, sfc1063, sfc1061, fcm5 at a concentration of 0.5µM, 1µM, 2µM, 0.5µM, and 3µM respectively. FSNplex3 consisted of primers sfc0036, sfc0018, fs1-03, mfs11 at a concentration of 3µM, 1µM, 1µM, and 2µM. Annealing temperature for each multiplex was 60°C, 58°C, and 60°C respectively. The total PCR reaction volume was 10µl. Fragment analysis was performed using an ABI 3730 DNA Analyzer (Applied Biosystems).

The presence of genotyping errors and null alleles were checked using MICRO-CHECKER (Van Oosterhout *et al.*, 2004). Repeated sampling of null genotypes and significant deviations from Hardy-Weinberg equilibrium suggested that there was a significant proportion of null alleles in fs4-46 and fcm5 in more than half of the stands in this study. Analyses presented exclude fs4-46 and fcm5 and use a total of 11 loci. However, similar results in genetic diversity estimates and SGS were obtained

when performing analysis on all 13 loci (data not shown). Pairs of loci were checked for gametic disequilibrium. Analysis was performed using FSTAT 2.9.3.2 (Goudet, 1995), with significant associations identified by randomly associating genotypes at pairs of loci 1100 times and using a 5% nominal level after Bonferonni correction.

2.4 Genetic diversity and spatial genetic structure

We obtained general multilocus estimates of genetic diversity within stands on SPAGeDi 1.4b (Hardy and Vekemans, 2002). We used ADZE 1.0 to obtain mean private allelic richness (A_P) (Szpiech *et al.*, 2008). Because of the definition of private alleles, i.e. unique to a single population, analysis was performed within sites to compare differences between treatments. The minimum number of gene copies used for allelic richness and private allelic richness was 198. We tested differences in allelic richness (A_R), unbiased gene diversity (H_S), and the inbreeding coefficient (F_{IS}) among groups of coppiced stands and high forest stands using FSTAT 2.9.3.2 (Goudet, 1995). Groups are compared, by calculating the average of the desired estimator (x) over all samples and loci for each group to obtain an observed statistic (OS_x). OS_x is obtained from the difference between the estimators of the two groups, $OS_x = x1 - x2$. 10000 permutations were performed between the groups to obtain a randomised dataset from which the statistic S_x can be calculated. P-values for the tests are interpreted as the proportion of randomised datasets with $S_x > OS_x$.

Analysis of fine-scale SGS was performed in SPAGeDi 1.4b (Hardy and Vekemans, 2002). Pairwise comparisons between individuals within each stand were used to compute a codominant estimator of the kinship coefficient (F_{ij}) as reported by Loiselle *et al.* (1995). The kinship coefficient can be described as $F_{ij} = (Q_{ij} - Q_m)/(1 - Q_m)$, where Q_{ij} is the probability of identity by state for random genes coming from two individuals i and j, and Q_m is the average probability of identity by state for gene copies coming from a reference population of random individuals (Hardy and Vekemans, 2002). SPAGeDi 1.4b performs a Mantel test to test for statistically significant structuring within a stand.

The observed regression slope, b_F, of F_{ij} on the natural logarithm of the distance, $ln(r_{ij})$, was compared to the expected estimate after permuting locations among individuals 10000 times, also used to attain upper and lower 95% confidence intervals. Standard errors and mean multilocus F_{ij} estimates within each distance class, $F_{(d)}$, were obtained through jackknifing over loci following Sokal and Rohlf (1995). Analyses were performed using 17 even distance classes of 10m, ranging from 0 to 170m.

To allow comparisons in the intensity of SGS between stands we used the *Sp* statistic, as proposed by Vekemans & Hardy (2004), Piotti *et al.* (2013). The *Sp* statistic quantifies SGS by the ratio $-b_F/(1 - F_{(1)})$, where b_F is the regression slope of F_{ij} on the natural logarithm of the distance, r, between individuals i and j, $ln(r_{ij})$, and $F_{(1)}$ is the mean F_{ij} belonging to the individuals of the first distance class (0-10m) which includes all pairs of neighbours. The variability of the *Sp* statistic is expressed in the standard error of b_F, which is calculated by jackknifing over loci (Hardy *et al.*, 2006).

Summary forest inventory data were recorded in two 20m x 20m plots of each site (see Table 2). Data from both plots were combined to give a summary in Table 2. The diameter at breast height (DBH) for all species of adult trees (i.e. height > 140cm) was recorded. All saplings, defined as trees between 10cm and 140cm in height, were counted. A chi squared test for independence was used to determine the differences between paired stands in the proportions of multi-stemmed vs. single stemmed trees. Differences in the largest stem DBH between paired stands were tested using Welch's t-test.

3 Results

Across the 11 loci investigated here, the maximum number of alleles ranged from 6 to 40 per locus, with a multilocus average of 17.91 in all populations combined. All pairs of microsatellite loci were in gametic equilibrium considering a 5% nominal level after Bonferroni correction. Multilocus estimates

of allelic richness, A_R, were high, ranging from 9.58 to 14.34, with little difference in allelic richness between paired stands. For unbiased gene diversity, H_S, multilocus estimates ranged from 0.695 to 0.788. Positive F_{IS} values indicated a significant departure from Hardy-Weinberg genotypic proportions in three stands GC, IH, and IC presenting an excess of homozygotes (see Table 3). Permutation tests on genetic estimators revealed no significant differences in A_R, H_S, and F_{IS} when stands of coppice and stands of high forest were analysed as groups; A_R: High Forest 11.38, Coppice 11.40 (P = 1.00), H_S: High Forest 0.72, Coppice 0.74 (P = 0.50), and F_{IS}: High Forest 0.024, Coppice 0.043 (P = 0.47). No consistent pattern in private allelic richness, A_P, was found between coppice and high forest stands (see Table 3).

We found differences in the fine-scale spatial genetic structure between paired high forest and coppice stands. SGS_{MAX}, defined by Jump *et al.* (2012) as the greatest distance at which the mean kinship coefficient within a given distance class, $F_{(d)}$, becomes significant to $P < 0.05$, revealed significant structuring in coppices that consistently extended 10-20m further than in its high forest counterpart (see Figure 1 and Table 3). This relationship between the extent of SGS and management was not reflected in the maximum intensity of SGS (Piotti *et al.*, 2013), or by the *Sp* statistic, which showed little difference within sites (See Table 3). Notably, spatial genetic structuring extended up to a maximum distance of 60m in the coppice stand of the French site, FC. This stand also exhibited the strongest kinship coefficient in the first distance class, $F_{(1)}$, as well as *Sp* statistic (see Table 3). $F_{(1)}$ for IH was not statistically significant partly because of the reduced number of pairs of neighbours (N = 61) within that distance class which also contributed to the large standard errors. The remaining stands had a minimum number of 89 pairs for each distance class, with the exception of FH where N = 60 in the first distance class.

Descriptive data obtained from the forest inventory plots revealed a high proportion of multi-stemmed trees in coppice stands, with a significantly higher proportion of multi-stemmed trees in

the coppice plots when compared to their high forest counterpart (Germany X^2 (2, N = 51) = 18.37, P>0.001; France X^2 (2, N = 428) = 19.65, P>0.001; Italy X^2 (2, N = 114) = 9.49, P>0.01) (see Table 2). A significantly higher largest stem DBH ($t_{(361)}$ = 2.99, P>0.01) was found in FC compared to FH. However, no significant differences were found between the stands in the German site ($t_{(44)}$ = 0.78, P=0.44) and the Italian site ($t_{(43)}$ = 1.41, P=0.17) (see Table 2). Higher densities of adult trees and saplings were found in the high forest stands than in the coppice stands (see Table 2).

4 Discussion

There were no statistically significant differences in genetic diversity between coppice and high forest stands. However, consistent differences in the spatial structuring of genetic diversity were found between paired stands. An increase of 10-20m in SGS_{MAX} was found in coppice stands when compared to their paired high forest stand. Beech coppices experience a reduction in sexual reproduction which is evident by the lower sapling densities found in the coppice stands. The increase in SGS_{MAX} might be the reflection of extended seed shadows that can result from rare establishment events, which occur over the long generation times experienced in coppices. As management removes trees from the breeding population through the cutting of stems, the dispersal of pollen and seed, two vectors that shape genetic structure, become less frequent in coppices. The long generation times coupled with rare establishment events in coppice stands, differ from the more frequent establishment of seedlings under high competition pressures in unmanaged populations that can lead to the break-down of spatial genetic structure (Loveless and Hamrick, 1984).

The *Sp* statistic ranged from 0.0032 to 0.0114, which is within the range for that found in the literature for beech (Jump and Peñuelas, 2007; Chybicki *et al.*, 2009; Jump *et al.*, 2012; Piotti *et al.*, 2013) and is typical for other outcrossing, gravity dispersed, and wind pollinated trees (Vekemans and Hardy, 2004). Extensive spatial genetic structure was found in the French coppice site (SGS_{MAX} =

60m, *Sp* = 0.0114) with an SGS_{MAX} that exceeded the generally accepted maximum of 30-40m for European beech in the literature, when obtained from SSR markers (Vornam *et al.*, 2004; Chybicki *et al.*, 2009; Oddou-Muratorio *et al.*, 2010; Piotti *et al.*, 2013). The remaining stands in our study display clustering of related individuals up to a typical distance of 40m found with SSR markers. Jump *et al.* (2007) compare differences in SGS_{MAX} using varying numbers of SSR markers (N_{MAX} = 6) and samples (N_{MAX} = 200) and caution against using less than 6 SSR markers to detect SGS. The greater number of SSR markers used in this study (*N* = 11) could have contributed to the finding of an SGS_{MAX} of 60m in the French coppice stand. However, as the SGS_{MAX} of the remaining sites did not extend over the commonly reported SGS_{MAX} of 40m, it could be argued that this unusually high value for the French coppice stand is a reflection of site characteristics as opposed to the power of our markers.

Previous studies have found limited differences in genetic diversity between coppice and unmanaged stands (Aravanopoulos *et al.*, 2001; Mattioni *et al.*, 2008; Dostálek *et al.*, 2011). However, some report trends found in coppices that are absent in natural stands, such as an increased level of linkage disequilibrium (Mattioni *et al.*, 2008) and a higher fixation index (Cottrell *et al.*, 2003). Increases in clonal diversity has been reported by Valbuena-Carabaña et al. (2008). Genotypic diversity was maintained by coppice management as it promoted the persistence of small clonal assemblages owing to the high shoot competition in coppices, which limited the spatial spread of clones. A two-fold increase in the spatial extent of clones was reported in nearby open oak woodland managed as high forest. The effect of coppicing on genetic diversity will be largely influenced by the primary regeneration strategy of the managed species. Valbuena-Carabaña et al. (2008) investigated Pyrenean oak (*Q. pyrenaica*) - a highly clonal tree that naturally spreads through root-suckers. Therefore it is likely that the impact of coppicing on clonal diversity is reduced in species, such as beech, which primarily regenerates naturally and does not produce root-suckers (Coppini and Hermanin, 2007). Clonal plant populations can have a similar level of genetic diversity

to that found in outcrossing species (Hamrick and Godt, 1996). The maintenance of genetic diversity in clonal populations is promoted by their longevity (Booy *et al.*, 2000). Since coppice populations display similar traits to clonal populations, genetic diversity could be maintained though similar mechanisms, as genotypes and their alleles persist in the population for longer, therefore increasing their potential to spread through infrequent events of natural regeneration. Cottrell *et al.* (2003) examined the genetic diversity in mixed forest of pedunculate oak (*Quercus robur*) and sessile oak (*Q. petraea*), both species with similar pollen and seed dispersal mechanisms to beech. The site had been coppiced for at least 300 years and little difference was found in the spatial structuring of genetic diversity when comparing the site to an unmanaged native forest. However, the coppiced site had higher levels of genetic diversity as well as a significant heterozygote deficit. The authors hypothesise that the significant heterozygote deficit was thought to be a remnant of past population dynamics. The site occurred at the range edge where heterozygote deficits are likely to occur due to the mixing of populations from different refugia causing a Wahlund effect which has persisted as genetic variation has become fixed in time through management.

Historic coppice management can alter the structuring of genetic diversity but have no effect on the amount of genetic diversity within an area (Paffetti *et al.*, 2012; Piotti *et al.*, 2013). In contrast to our study, Paffetti *et al.*(2012) and Piotti *et al.* (2013) found a decrease in structuring in stands that have historically been under coppice management. However, it should be noted that the coppice stand examined in both studies had been converted to shelterwood systems by regeneration felling. Work by Rajendra *et al.* (2014) comparing unmanaged beech stands to stands under various management systems in Germany found similar results to Paffetti *et al.*(2012) and Piotti *et al.* (2013). , although it is not clear if coppiced stands were included in this study. The reduction in the maximum extent of SGS (SGS_{MAX}) in managed stands was attributed to the removal of trees, through practices such as thinning, leading to the break-down of familial structures that would otherwise arise through the mating of adjacent, related individuals and the ineffective dispersal of beech mast. Although trees

are removed from the reproductive cohort in coppices, they are not physically removed from the population, thereby preserving the familial structures that have developed prior to management. Such familial structuring can thus be extended when rare establishment events occur, leading to a consequent increase in SGS extent. In contrast, re-establishing thinning and logging in order to convert coppices to other management systems, such as the conversion to shelterwood in Paffetti *et al.*(2012) and Piotti *et al.* (2013), could rapidly reduce the extent of SGS by breaking up established family structures. Spatial genetic structure in beech stands is, therefore, likely to be particularly sensitive to the management type in practice.

This study demonstrates the importance of considering the spatial component of genetic diversity and the findings have wide reaching implications as many beech forests in Europe have experienced coppice management in the past. Coppice forests can be as rich in genetic diversity as natural forests. However, consistent differences in the extent of spatial genetic structuring in these populations, while relatively small in their magnitude, indicate 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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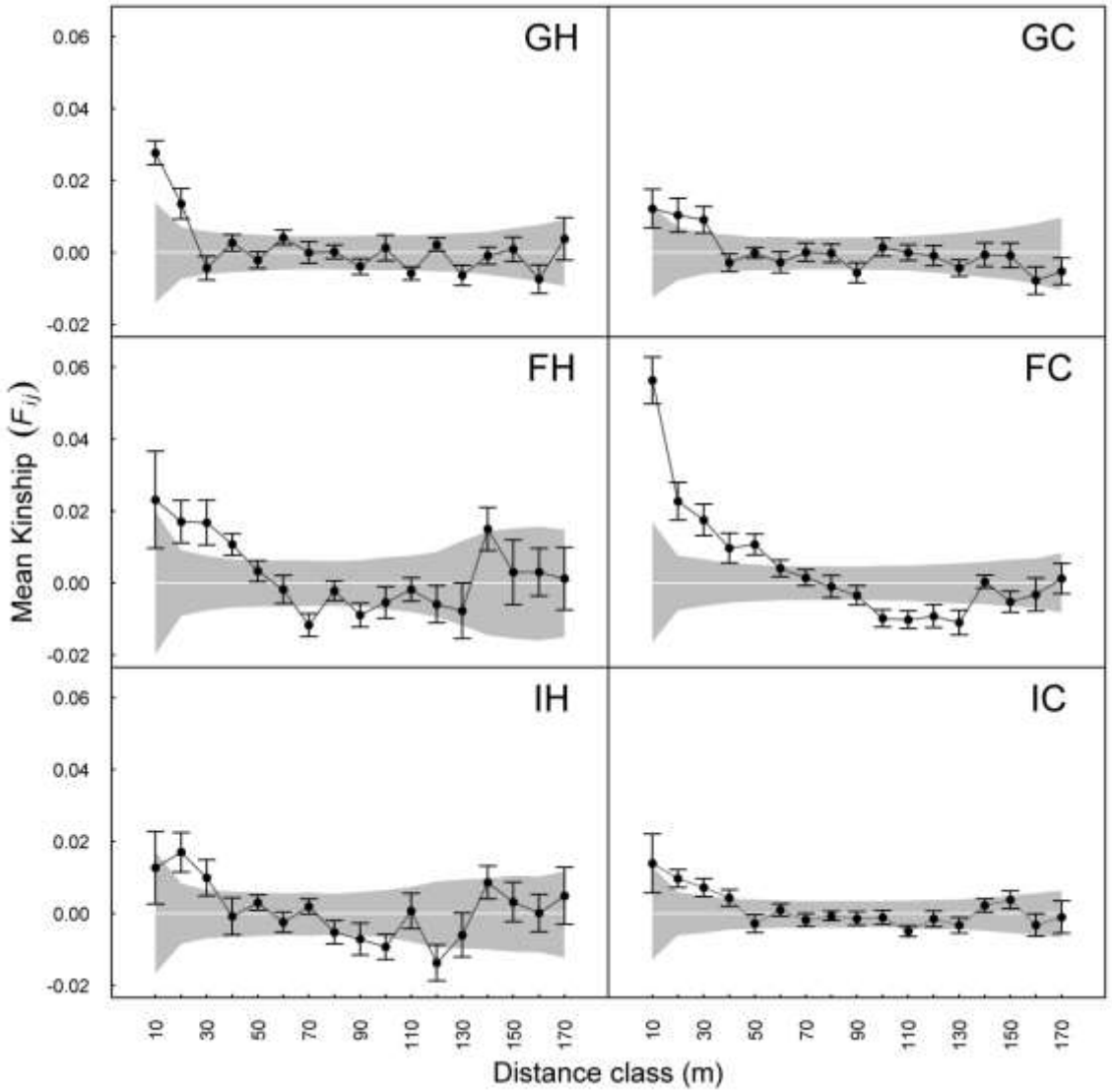
Figures

Figure 1. Spatial autocorrelograms for each stand using the kinship coefficient (F_{ij}) as described in Loiselle *et al.* (1995) and consecutive 10m distance classes. Upper and lower 95% confident intervals derived from 10000 location permutations are indicated by shaded areas. Black bars around mean F_{ij} values represent standard errors obtained through jackknifing over loci following Sokal and Rohlf (1995) to obtain multilocus estimates.



549 **Tables**

550 **Table 1.** Details of study sites

Country	Site	Stand code[a]	Stand management	N	Latitude Longitude	Elevation (m)
Germany	Spessart	GH	High forest	168	N50.0412 E9.5521	495
		GC	Converted coppice	170	N49.9600 E9.5451	486
France	Mt Lure	FH	High forest	112	N44.1246 E5.8257	1307
		FC	Abandoned coppice	170	N44.1224 E5.8340	1177
Italy	Mt Gelbison	IH	High forest	100	N40.2167 E15.3383	1521
		IC	Abandoned coppice	170	N40.2078 E15.3494	1352

551 [a]Stand codes were derived from the first letter of the country (G = Germany, F = France, I = Italy) and the
552 management history of the stand (H = high forest stand, C = coppice stand).

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554 **Table 2.** Summary of forest inventory plots within each stand

	GH	GC	FH	FC	IH	IC
Proportion of multi-stemmed trees	0.000	0.565***	0.241	0.446***	0.056	0.346**
Mean largest stem DBH [Range] (cm)	32	35	7	9**	28	22
Density adults/ha	35.0	28.6	316.3	218.8	97.5	45.0
Density saplings/ha	85.0	2.5	120.0	93.8	21.3	0.0

555 Significant P-values for differences between the proportion of multi-stemmed trees and the mean largest DBH
556 in high forest and coppice stands (i.e. GH vs. GC; FH vs. FC; and IH vs. IC) are indicated next to the coppice
557 stand values as *P <0.05; **P<0.01; ***P<0.001.

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561 **Table 3.** Summary of multilocus genetic diversity estimators and SGS coefficients

Stand code	Genetic diversity estimators[a]				SGS parameters[b]		
	A_R	A_P	H_S	F_{IS}	$F_{(1)}$	SGS_{MAX} (m)	$Sp \pm$ SE
GH	10.12	1.51	0.695	0.019	0.0277***	20	0.0037 ± 0.0008
GC	10.45	1.94	0.722	0.044***	0.0122*	30	0.0032 ± 0.0014
FH	9.69	1.34	0.704	0.022	0.0231*	40	0.0088 ± 0.0019
FC	9.58	1.28	0.731	0.013	0.0563***	60	0.0114 ± 0.0019
IH	14.34	2.36	0.788	0.034**	0.0127	30	0.0062 ± 0.0018
IC	14.17	1.95	0.780	0.071***	0.0186**	40	0.0040 ± 0.0013

562 [a] Terms for genetic diversity estimators are as follows; A_R, allelic richness (Petit *et al.*, 1998); A_P, private allelic
563 richness (Szpiech *et al.*, 2008); H_S, unbiased gene diversity (Nei, 1978); F_{IS}, inbreeding coefficient (Weir and
564 Cockerham, 1984). The minimum number of gene copies (k) used for rarefication analysis of A_R and A_P is 198.
565 P-values for F_{IS} are obtained after 10000 permutations of gene copies within individuals of each stand.

566 [b] Terms for SGS parameters are as follows; $F_{(1)}$, kinship coefficient for first distance class (i.e. 0-10m); SGS_{MAX},
567 the greatest distance at which the mean kinship coefficient within a given distance class, $F_{(d)}$, becomes
568 significant to $P < 0.05$; $Sp \pm$ SE, Sp statistic ± standard error. Significant P-values are indicated as *P <0.05; **P
569 <0.01; *** P<0.001. 2-sided P-values are presented for F_{IS} with 1-sided P-values presented for $F_{(1)}$ and SGS_{MAX}.

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Supplementary Material

S1 Map of sampling design at the site GH. The boundary of the grid (dashed line) and the transect (arrow) are indicated around the relevant sampled trees (grey circles).