



Extensive sib-mating in a refugial population of beech (*Fagus sylvatica*) growing along a lowland river



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ABSTRACT

Many temperate and boreal tree species have small and scattered populations near the low-latitude margins of their range that have persisted over extended periods of time in microrefugia. It remains poorly understood how patterns of mating and gene flow influence key components for their long-term persistence such as effective population size or genetic diversity. Yet such information is critical for designing effective protection measures and informing programs for the conservation of forest genetic resources.

Here we investigate the mating system and pollen dispersal of a long-term refugial population of beech (*Fagus sylvatica*), a major European forest tree. This population stretches over ca. 7 km along the ravines of a small lowland river in SW France. We exhaustively mapped the adult population ($n = 932$ trees) and collected seed families ($n = 450$ seeds) from 30 mother trees spread across the stand. All individuals were genotyped at 113 SNP markers and submitted to paternity analyses. We estimated various mating parameters and tested whether among-individual variation was related with the ecological neighbourhood of the mother tree.

A unique father could be identified for all seeds analysed. We detected neither pollen immigration nor selfing events. Instead, we observed extensive mating between neighbouring trees that resulted in a very steep decline of the pollen dispersal kernel and a low effective number of fathers (median $N_{ep} = 7.9$). In turn, male fecundity was tightly related with the distance between mates. The adult population showed an exceptionally strong and far-reaching spatial genetic structure indicating that neighbouring trees are most often sibs. The predominant mating between these neighbours suggests that patterns of reproduction and pollen flow are not constrained by cross-compatibility issues. Instead, dense conspecific neighbourhoods even tend to bar long-distance pollen flow by saturating the stigmas of mother trees through pollen swamping. The observed patterns are a direct consequence of the refugial habitat that imposes the population's linear distribution and whose dense vegetation represents a further obstacle to pollen dispersal. The elevated capacity of sib-mating might be a microevolutionary consequence of the population's long-term persistence in isolation. The resulting spatial genetic structure and the critical role of tree density in assuring an effective reproduction have important consequences for the design of forest genetic resources programs as well as for the conservation management of refugial and other riparian tree populations.

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1. Introduction

The long-term survival of populations in climate refugia during the Quaternary cold stages has been critical for the present-day composition of the world's temperate and high-latitude tree floras (Gavin et al., 2014). Today, the remainders of these populations often form outposts near species' low-latitude range limit that persist in particularly favourable habitats, commonly called

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microrefugia (Dobrowski, 2011). These stands are important conservation targets and highly informative natural laboratories for investigating how tree populations can persist within a hostile greater environment (Hampe and Petit, 2005; Woolbright et al., 2014). Refugial populations are often so isolated that local extinctions cannot easily be buffered by regional meta-population dynamics. Their performance and viability therefore depend strongly on their inherent population characteristics in addition to the constraints imposed by their environment (Hampe and Jump, 2011). While the latter has attracted the interest of a rapidly growing research activity (Dobrowski, 2011; Keppel et al., 2012), the intrinsic dynamics of refugial populations and their role for

population persistence still remain poorly understood. Thus, we virtually ignore how patterns of mating and pollen flow influence key components for long-term population persistence such as effective population size, genetic diversity and its spatial structure. Yet such information is critical for designing effective protection or restoration measures as well as for informing programs for the conservation of forest genetic resources (Lefèvre et al., 2013; Fady et al., 2016).

Refugial tree populations are often small owing to the constraints of their environment, and their effective size is likely to be even smaller due to the extensive inequality in fecundity that is typical of trees (Oddou-Muratorio et al., 2005). In such a context, the mating system and spatial patterns of gene flow play a crucial role for long-term population viability and evolution. A wealth of studies on small and isolated plant populations has documented that these tend to show reduced allelic richness, gene diversity, heterozygosity, and individual fitness (Leimu et al., 2006; Aguilar et al., 2008; Eckert et al., 2008). Yet tree populations are comparatively little affected by anthropogenic landscape fragmentation (Kramer et al., 2008; but see Jump and Peñuelas, 2006). Trees share life history characteristics that render them particularly resistant to the erosion of genetic diversity, including a long life span, great fecundity, widespread self-incompatibility, and a great propensity for long-distance gene dispersal (Petit and Hampe, 2006; Kremer et al., 2012). These characteristics might help refugial tree populations with maintaining their viability over extended periods of time in spite of their confinement (Leonardi et al., 2012; Moracho et al., 2016).

Pollen is the primary vehicle for gene flow in many trees, especially those pollinated by wind (Petit et al., 2005). Patterns of pollen dispersal are intimately linked with the mating system, which can be characterised by analysing the pollen cloud of seed-producing trees to quantify i) the rate of selfing (s), ii) the extent of correlated paternity among the seeds produced by a mother tree (r_p), and iii) the amount of pollen stemming from outside the population (m) (Ritland, 2002; Gaüzère et al., 2013). Numerous studies have examined among-population variation in the mating system to understand the impact of population size, density or related factors on mating parameters (e.g. in the context of habitat fragmentation; see Aguilar et al., 2008). An increasing number have also analysed how mating parameters differ among individuals within populations owing to fine-scale variation in their abiotic and biotic environment. Such studies commonly report extensive variation (e.g. García et al., 2005; Tamaki et al., 2009; Gaüzère et al., 2013; Sánchez-Robles et al., 2014) driven by the ecological settings surrounding the pollen recipient, or the 'ecological maternal neighbourhood' (García et al., 2005). Only a few studies have however investigated all three mating system components and related pollen dispersal distances at the individual scale and determined their drivers, especially for anemophilous species (but see de Lucas et al., 2008; Gaüzère et al., 2013; Sánchez-Robles et al., 2014).

In refugial tree populations, mating system and patterns of pollen flow may be constrained both by intrinsic population features as well as by habitat constraints. The long-term persistence of refugial populations at roughly stable size can result in marked family structures, which may in turn affect the cross-compatibility of individuals (Vekemans and Hardy, 2004). On the other hand, refugial populations are commonly located near water bodies that mitigate high temperatures and drought, such as lakes, bogs or rivers, and they are often further sheltered by ravines or dense vegetation (Hampe and Jump, 2011). The spatial configuration of such specific habitats often results in populations that have a highly scattered or a linear distribution. This imposes important additional constraints on patterns of pollen flow and further favours the formation of small-scale mating clusters and a rapid disconnection of more

distant individuals (Ghazoul, 2005; Moracho et al., 2016). The long-term persistence of refugial populations suggests that they have been able to cope with such problems, but through which biological mechanisms remains unclear.

Here we assess the mating system and contemporary pollen flow in a long-term refugial population of beech (*Fagus sylvatica* L.), a major forest tree species in Europe. This population grows along a lowland river in SW France, a region whose dry summers relegate beech otherwise to high-elevation forests in the Pyrenees. A singular feature of our target population is that exactly the same place that currently represents an interglacial (or cool-humid) refugium of beech already served as a glacial (or warm-humid) refugium for the species during the Late Quaternary (de Lafontaine et al., 2014). Using this beech stand as an empirically validated model for long-term refugial tree populations, we performed an extensive paternity analysis of freely pollinated seed families produced during a medium masting event in order to: (i) examine the composition of individual pollen clouds and assess levels of selfing, correlated paternity and pollen immigration; (ii) quantify the distances and directionality of effective pollen dispersal; and (iii) address effects of the ecological neighbourhood on patterns of mating. Based on our results, we infer the major ecological processes involved in forming the spatial distribution of genetic diversity in our stand and derive recommendations for the conservation of refugial tree populations and the sampling of forest genetic resources.

2. Materials and methods

2.1. Study species and site

European beech (*Fagus sylvatica* L.) is a late-successional forest tree widely distributed across central and western Europe. The species is monoecious and highly outcrossing with selfing rates usually below 10% (Merzeau et al., 1994; Wang, 2003; Gaüzère et al., 2013). Flowering occurs in April and May, shortly after bud burst. Reported average within-stand pollen dispersal distances typically span a few scores of metres (Piotti et al., 2012: 80–184 m; Gaüzère et al., 2013: 35–63 m). Beech is a masting species whose annual seed production shows strong links with climate (Piovesan and Adams, 2001). Successful recruit establishment appears to occur primarily following mast years (Oddou-Muratorio et al., 2011).

The study was conducted in the Ciron valley (44°23'N, 0°18'W, 60 m a.s.l.), situated some 60 km southeast of Bordeaux, SW France. Beech occurs over approximately 7 km along a karstic canyon formed by the river (Fig. 1). Some scattered individuals grow also outside the ravine, typically in the vicinity of sources. Two further beech populations with 18 and a few hundred adult trees, respectively, are located at 14 and 40 km in ecological settings similar to the Ciron population (Timbal and Ducouso, 2010). Extensive beech forests grow on the northern slopes of the Pyrenees at ca. 150 km.

A recent palaeoecological study identified charcoal fossils of beech at the site of the extant Ciron beech stand and dated the oldest ones at 42 kyr BP (de Lafontaine et al., 2014). This evidence, together with a peculiar genetic composition of the population (de Lafontaine et al., 2013), led the authors to conclude that the extant stand is very likely to represent the remainder of a Quaternary cold stage refugium. On the other hand, the Ciron beech stand was proposed in 2006 by the French Ministry of Agriculture to serve as a conservation genetic unit for the species and is one of four French beech populations included in an ongoing national program for assisted migration.

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