Efficient mitigation of founder effects during the establishment of a leading-edge oak population

Arndt Hampe1,2, Marie-Hele`ne Pemonge3 and Remy J. Petit1,2

1INRA, UMR 1202 BIOGECO, 69, Route d’Arcachon, F-33610 Cestas, France
2Univ. Bordeaux, UMR 1202 BIOGECO, Av. des Facultes, F-33405 Talence, France
3Univ. Bordeaux, UMR 5199 PACEA, Av. des Facultes, F-33405 Talence, France

Numerous plant species are shifting their range polewards in response to ongoing climate change. Range shifts typically involve the repeated establishment and growth of leading-edge populations well ahead of the main species range. How these populations recover from founder events and associated diversity loss remains poorly understood. To help fill this gap, we exhaustively investigated a newly established population of holm oak (Quercus ilex) growing more than 30 km ahead of the nearest larger stands. Pedigree reconstructions showed that plants belong to two non-overlapping generations and that the whole population originates from only two founder trees. The four first-generation trees that have reached maturity showed disparate mating patterns despite being full-sibs. Long-distance pollen immigration was notable despite the strong isolation of the stand: 6 per cent gene flow events in acorns collected on the trees (n = 255), and as much as 27 per cent among their established offspring (n = 33). Our results show that isolated leading-edge populations of wind-pollinated forest trees can rapidly restore their genetic diversity through the interacting effects of efficient long-distance pollen flow and purging of inbred individuals during recruitment. They imply that range expansions of these species are primarily constrained by initial propagule arrival rather than by subsequent gene flow.

1. Introduction

Modern climate change is driving the expansion of numerous plant and animal populations worldwide towards higher elevations and latitudes [1]. Climate envelope models predict extensive redistributions of many species, but it is unclear whether they will be able to colonize new territories in pace with a rapidly changing climate. Such uncertainty is particularly worrying in long-lived sessile organisms such as forest trees [2,3]. Assessing the capacity of trees to respond to modern climate change is crucial, because they play a prominent role in many ecosystems and provide vital habitat for a great diversity of other organisms. However, direct empirical evidence for contemporaneous poleward range expansions of forest trees following a changing climate remains scant and the corresponding evolutionary processes poorly understood [4].

Those populations that form the leading edge of an expanding species range are predicted to experience profound evolutionary changes [5–7]. In many organisms, including trees, range expansions are typically promoted by rare events of long-distance dispersal that enable small pioneer populations to establish far ahead of the continuous range and to fill the empty area with their progeny [5,8]. The associated successive founder events represent a spatial analogue of genetic drift, reducing genetic diversity and increasing differentiation of populations near the leading edge [9]. This intense drift can result in allele surfing (i.e. the increase in frequency of formerly rare alleles) [6]. On the other hand, leading-edge populations are disproportionately susceptible to Allee effects; that is, a lower per capita growth rate at low densities, caused in particular by reduced mating opportunities and inbreeding [10]. Allee effects...
can significantly delay or even impede the establishment of leading-edge populations unless there is some gene immigration from other parts of the range. Hence, the performance and evolution of such populations should ultimately depend on the interplay between gene immigration and local reproductive success [3].

These evolutionary mechanisms have been well established in theory and through simulations, yet empirical evidence for their role during the initial establishment of leading-edge populations remains scant (but see [11] for a bird, [12] for insects and [13] for a mammal). Hence, we are lacking a sound understanding of the processes that accompany the establishment of tree populations at the leading edge. In particular, it remains unclear how such populations recover from the strong loss of genetic diversity experienced during the founder event. Levels of diversity can have important consequences for plant fecundity, mating patterns and offspring performance, which in turn exert a strong influence on population growth, and ultimately on the capacity for rapid range expansion [14,15].

Here, we report on the genetic composition of an exhaustively sampled small pioneer population of holm oak (Quercus ilex L.) that has established and reproduces more than 30 km ahead of the species’s nearest larger stands. Holm oak reaches the northern distribution limit of its natural range in southwestern and western France (figure 1a), and projections indicate that the range and local abundance of the species could strongly increase during the coming decades (figure 1b). The capacity of leading-edge populations to recover from founder events could thus have important impacts on population structure, diversity and ultimately expansion success of the species in the region. Our study enabled us to reconstruct the first three generations of the investigated holm oak population, to quantify changes in allele frequencies across generations, and to assess patterns of mating and gene flow at the seed and at the recruit stage. Specifically, we attempted to (i) determine within-population mating patterns and the contribution of reproductive individuals to the pool of established offspring, (ii) quantify the frequency of inbreeding and pollen-mediated gene immigration, as well as their connections, and (iii) evaluate implications for the subsequent evolution of this expanding pioneer population.

2. Material and methods

(a) Study organism

Holm oak is one of the most widespread and abundant trees of the Mediterranean Basin, and a keystone species of many forest ecosystems in the area. This evergreen species is considered to have expanded from Iberia into southern France after the last ice age [17]. It is common along the Mediterranean coast and more sparsely distributed along the Atlantic coast (figure 1a). Today, it is increasingly planted in parks and gardens of southern and central France, as well as in Britain, where it has been listed as a potential invader [18]. Projections based on bioclimatic envelope modelling indicate that the species should encounter suitable climatic conditions for establishment throughout the southern half of France by 2100 (figure 1b).

Holm oak is largely self-incompatible and pollinated by wind. Pollen has been shown to remain viable for more than a month [19]. Holm oak acorns are regularly dispersed by different vertebrates. In particular, the Eurasian jay (Garrulus glandarius) can regularly transport them up to several kilometres [20].

(b) Study area and field sampling

The study was conducted in 2004 and 2005 in Cestas, some 25 km southwest of Bordeaux in southwestern France (44°45' N 0°38' W; figure 1a). Only four reproductive trees grow at the site, which is located about 32 km away from the nearest larger, natural holm oak populations growing along the Atlantic coast. An extensive survey was conducted to locate potential parent trees in the surroundings of the study population. All tree-bearing areas within a radius of 5 km around the study site were searched during the winter months (i.e. when the evergreen holm oak trees are most conspicuous) without spotting a single adult-size individual. Searching an area of roughly 2 ha around the four reproductive trees, we located, tagged and mapped all established recruits. Although we do not know under which circumstances the first holm oak individuals arrived at our study site, the spatial distribution of the existing plants (figure 2) and the characteristics of their growing sites suggest that their offspring have established by natural means. In addition, a total of 255 ripe acorns were collected from the two trees that
reproduced in 2003 (T1 and T4, hereafter). Acorns were weighed and germinated in an incubator, and leaf tissue was used for DNA isolation.

(c) Molecular analyses
All established plants were genotyped at 13 nuclear microsatellites (simple-sequence repeat, SSR): Msq4, Msq13, Qp9, Qp15, Qp36, Qp46, Qp104, Qr4, Qr7, Qr11, Qr20, Qr96 and Qr112 [21–23]. All loci except Qp104 were also used for genotyping acorns. The DNeasy Plant Mini Kit (Qiagen) was used for DNA isolation from fresh buds or leaves. Loci were amplified individually according to the study of Barreneche et al. [24]. PCR products were visualized on a Li-Cor model 4000L automatic DNA sequencer. Gel scoring was performed manually by two of the authors (M.-H.P. and R.J.P.). All SSRs were amplified twice and sometimes up to four times to confirm scorings. We checked for Mendelian segregation of the markers whenever at least one of the two parent trees studied was a heterozygote, to detect weak or null alleles as well as linkage between loci.

All field and genotypic data are available in the electronic supplementary material, appendix S1.

(d) Parentage analysis by genotype exclusion
For the established plants, we used simple rules of inheritance to manually assign all genotypes to either of two groups: (i) those that could have been derived by at least one of the four adult trees and (ii) those that could not be offspring of any of these four trees. For the latter, we checked for sib relationships using simple expectations such as the four allele rule (i.e. no more than four alleles can segregate within a full-sib family).

For acorn genotypes, a paternity search was conducted manually by simple exclusion using the four reproductive trees as candidates. When two or more loci resulted in seedling genotypes that were clearly incompatible with any of the four candidate fathers, we considered that the acorn had been sired by a tree from outside the stand. If there was only one mismatch, we re-amplified the corresponding locus at least once to confirm that this mismatch was not due to a scoring error. All manual assignments were subsequently checked and corroborated with the software GIMLET [25]. Finally, diversity estimates for the two generations detected (see below) were obtained with FSTAT v. 2.9.3. [26]. The loci Qp36 and Qp46 were excluded from this last analysis as they contained null alleles.

3. Results
(a) Established plants
We identified a total of 65 individuals (including the four reproductive trees) within the surveyed area. Four groups of saplings had identical genotypes. As saplings from each group grew close to each other, we concluded that they represent different ramets of the same genet and excluded all but the largest ramet from subsequent analyses. A total of 58 unique genotypes (i.e. four reproductive trees and 54 recruits) were therefore available for further studies.

We could distinguish two generations of plants and infer a third one by reconstructing the relationships among the unique multi-locus genotypes of all individuals (figure 2a; see also pedigree reconstruction in electronic supplementary material, figure S2). All except two individuals could be unequivocally assigned to their respective generation from their multi-locus genotypes. The combined genotypic and plant size data for the two remaining plants allowed us also to infer their respective generations also with high confidence.

First, we identified a total of 33 recruits as offspring of either one or two of the four reproductive trees (figure 2b). Both parents could be identified for 24 of these recruits.
gene diversity were sired by immigrant pollen, generating an F1 generation study population; (ii) these mated either with each other or two now absent ‘ghost’ trees were the founders of the consistent solution that comforted our hypothesis.

We were able to reconstruct the multi-locus genotypes of the two hypothesized for the putative half-sibs; table 1). Nine recruits had at least two (and up to seven) alleles not present in the adult population and hence inferred to result from pollen immigration. The remaining 21 recruits had genotypes indicating that they could be half-sibs of this family. We consequently hypothesized that two unknown parental trees had produced this family group by receiving immigrant pollen from outside the population (for the putative half-sibs; table 1). We were able to reconstruct the multi-locus genotypes of the two hypothesized trees from these 25 individuals (i.e. the four reproductive trees plus the 21 other recruits), finding a unique and fully consistent solution that comforted our hypothesis.

Based on our inferences, we concluded therefore that: (i) two now absent ‘ghost’ trees were the founders of the study population; (ii) these mated either with each other or were sired by immigrant pollen, generating an F1 generation of 22 full-sibs (including the four reproductive trees) and three half-sibs; and (iii) the four reproductive trees of the F1 generation produced an F2 generation of 33 established recruits by either mating with each other (24 individuals) or receiving immigrant pollen from outside the population (for the putative half-sibs; table 1). We were able to reconstruct the multi-locus genotypes of the two hypothesized trees from these 25 individuals (i.e. the four reproductive trees plus the 21 other recruits), finding a unique and fully consistent solution that comforted our hypothesis.

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Diversity estimates of the generations F1 and F2 are shown in table 1. Both generations showed similar levels of moderate gene diversity \( H_E \) and marked heterozygote excess \( F_{IS} \). Interestingly, the F2 generation contained a higher number of immigrant alleles and showed a higher allelic richness than the F1 generation (paired \( t \)-test: \( t = 2.37, d.f. = 9, p = 0.04 \)).

### Table 1. Diversity estimates for the F1 and F2 generations identified among the established plants. The number and percentage of immigrant genotypes refer to individuals with alleles not found in the local parent trees (and hence assumed to originate from pollen immigration). The number of foreign alleles refers to unknown parental trees had produced this family group by receiving immigrant pollen from outside the population (for the putative half-sibs; table 1).

<table>
<thead>
<tr>
<th>generation</th>
<th>( n )</th>
<th>no. immigrant genotypes (%)</th>
<th>no. foreign alleles</th>
<th>( R_S )</th>
<th>( H_E )</th>
<th>( F_{IS} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>F1</td>
<td>25</td>
<td>3 (12%)</td>
<td></td>
<td>16</td>
<td>3.7</td>
<td>0.44</td>
</tr>
<tr>
<td>F2</td>
<td>33</td>
<td>9 (27%)</td>
<td></td>
<td>33</td>
<td>4.2</td>
<td>0.44</td>
</tr>
</tbody>
</table>

***p < 0.001.

### Table 2. Pollen donors assigned for acorns collected on the two major reproductive trees T1 and T4. Immigrant refers to acorns with at least two loci containing alleles not present in the adult population and hence inferred to stem from pollen immigration. Numbers in parentheses denote percentages.

<table>
<thead>
<tr>
<th>mother tree</th>
<th>T1</th>
<th>T2</th>
<th>T3</th>
<th>T4</th>
<th>immigrant</th>
<th>total</th>
</tr>
</thead>
<tbody>
<tr>
<td>T1</td>
<td>1 (0.7)</td>
<td>5 (3.7)</td>
<td>62 (45.9)</td>
<td>58 (43.0)</td>
<td>9 (6.7)</td>
<td>135</td>
</tr>
<tr>
<td>T4</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>113 (94.2)</td>
<td>7 (5.8)</td>
<td>120</td>
</tr>
</tbody>
</table>

Nine recruits had at least two (and up to seven) alleles not found in any of the four reproductive trees, pointing to pollen immigration events (table 1). Among the 33 recruits, no less than 28 (85%) were offspring of tree T1. Trees T2 and T3 had 12–13 and 8–9 offspring, respectively (one recruit could be offspring of either of these trees). One offspring of T2 stemmed from a selfing event (and died shortly after the study). Tree T4 had only six offspring.

The remaining 21 recruits had genotypes indicating that they could not have been sired by any of the four reproductive trees. Instead, we could infer a single full-sib family that encompasses the four reproductive trees as well as 18 of these 21 recruits (figure 2a). The three remaining recruits had genotypes suggesting that they could be half-sibs of this family. We consequently hypothesized that two unknown parental trees had produced this family group by either mating with each other (for the full-sib family) or receiving immigrant pollen from outside the population (for the putative half-sibs; table 1). We were able to reconstruct the multi-locus genotypes of the two hypothesized trees from these 25 individuals (i.e. the four reproductive trees plus the 21 other recruits), finding a unique and fully consistent solution that comforted our hypothesis.

Based on our inferences, we concluded therefore that: (i) two now absent ‘ghost’ trees were the founders of the study population; (ii) these mated either with each other or were sired by immigrant pollen, generating an F1 generation of 22 full-sibs (including the four reproductive trees) and three half-sibs; and (iii) the four reproductive trees of the F1 generation produced an F2 generation of 33 established recruits by either mating with each other (24 individuals) or receiving immigrant pollen (nine individuals). In line with these conclusions, first-generation plants were on average larger than those belonging to the second generation (mean ± s.d.: 67.4 ± 139.0 mm versus 5.6 ± 5.1 mm; t-test: \( t = 2.56, d.f. = 56, p = 0.01 \); see also figure 2a).

Diversity estimates of the generations F1 and F2 are shown in table 1. Both generations showed similar levels of moderate gene diversity \( H_E \) and marked heterozygote excess \( F_{IS} \). Interestingly, the F2 generation contained a higher number of immigrant alleles and showed a higher allelic richness than the F1 generation (paired \( t \)-test: \( t = 2.37, d.f. = 9, p = 0.04 \)).

### (b) Acorns

The reproductive trees were homozygous at three loci (Qr7, Qr112 and Msq4), whereas Mendelian segregation could be assessed at the nine remaining loci on at least one tree. Null alleles were identified for loci Qp36 and Qp46 (see above).

Paternity assignments of the analysed acorns are shown in table 2. Nine (6.7%) out of the 135 acorns collected on tree T1 and seven (5.8%) of the 120 acorns collected on tree T4 contained at least two (and up to nine) loci with alleles not present in any of the four reproductive trees, and were hence inferred to result from pollen immigration. The remaining 126 acorns of tree T1 could be unequivocally assigned to a single father tree: tree T3 in 46% and tree T4 in 43% of the cases. Interestingly, the 113 non-immigrant acorns of tree T4 were interpreted to result exclusively from selfing events. Of these, 106 individuals were in full agreement with this hypothesis across all 12 loci, and seven individuals showed just one mismatch. Mismatches occurred exclusively at loci for which the mother tree was homozygous or had a putative null allele and were interpreted as resulting from artefacts of the amplification process (e.g. three acorns carried a similar PCR product at Msq13 that was not found elsewhere in the population).

The overall frequency of immigrant genotypes in the analysed acorns (6%) did not differ statistically from that observed in the F1 generation of established plants (12%; \( \chi^2 \)-test: \( \chi^2 = 1.18, d.f. = 1, p = 0.28 \)). On the contrary, it was lower than that observed in the F2 generation (27%; \( \chi^2 = 16.3, d.f. = 1, p < 0.001 \)).

The two seed trees produced acorns of different weight (mean ± s.d.: T1, 2.04 ± 0.40 g versus T4, 2.44 ± 0.68 g; \( t \)-test: \( t = 5.68, d.f. = 253, p < 0.001 \), pointing to maternal effects [25]. However, we also found within each seedlot differences in seed weight depending on paternal origin. First, for tree T1, acorns originating from immigrant pollen...
were heavier than acorns sired by local trees (2.28 ± 0.41 g versus 2.02 ± 0.39 g; \( t \)-test: \( t = 2.05, \ d.f. = 133, p = 0.04 \)). Second, for tree T4, acorns originating from immigrant pollen were heavier than those originating from selfing (2.95 ± 0.65 g versus 2.39 ± 0.67 g; \( t \)-test: \( t = 2.53, \ d.f. = 118, p = 0.01 \)).

4. Discussion

While the role of long-distance dispersal events during range expansions has been an object of intense research in the past [5,6,8], empirical evidence for the mechanisms involved in the subsequent establishment of leading-edge populations remains scant (reviewed for plants in [4,27]). Our pedigree reconstruction of a recently founded leading-edge population revealed five phenomena with potentially relevant evolutionary implications: (i) all individuals are closely related; (ii) the four reproductive trees show disparate mating patterns, despite being full-sibs; (iii) one tree strongly dominates the population’s reproduction; (iv) long-distance pollen flow causes a non-negligible amount of gene immigration; and (v) there is a remarkably high fraction of immigrant genotypes in the established recruits of the F2 generation. Overall, our results suggest that the study population should be able to recover high levels of genetic diversity within very few generations, as also found in the case of colonizing Pinus ponderosa populations [4].

(a) Disparate mating behaviour and the reproductive dominance of one tree

All genotyped acorns of tree T4 resulted either from selfing or from siring by immigrant pollen. Regular selfing is very rare in trees, which are highly susceptible to inbreeding depression and depend relatively little on reproductive assurance because of their long lifespan [28,29]. The reduced seed weight of selfed acorns compared with outcrossed ones from the same tree and the quasi-absence of selfed seedlings in the established F2 generation (despite the abundant production of selfed acorns by tree T4) point indeed towards the existence of strong inbreeding depression (which is further confirmed by a very low germination rate of selfed acorns; R. J. Petit 2004, unpublished data). The high selfing rate of tree T4 was probably caused by reduced pollen availability, as self pollen is typically out-competed by outcross pollen [30].

Overall, a small proportion of the potential crosses were observed. For instance, few acorns of tree T1 were sired by tree T2 (3.7%), although both trees are located within a few metres of each other. More strikingly, effective pollen flow between the two largest trees was completely uni-directional (from T4 to T1). A phenological difference in the reproduction of trees T1 and T4 is unlikely to have caused this pattern: while holm oak is protandrous, the delay between male and female flowers on the same branch is only 2–3 days, much less than the temporal variation in flower anthesis that exists across the tree crown [31]. The combination of predominant winds and unequal canopy size (and hence uneven pollen production) could possibly result in such an asymmetric gene flow. In any case, regardless of the mechanism involved, asymmetric mating patterns are a source of departure from panmixia, thereby reducing effective population size.

Finally, 85 per cent of the established plants of the F2 generation were offspring of tree T1. The strong reproductive dominance of tree T1 during the initial stage of population establishment is likely to leave a strong imprint on the future genetic composition and diversity of the study population [32,33]. In addition, most of the corresponding seedlings must have been mothered by this tree, considering that eight of the nine F2 recruits sired by immigrant pollen had been mothered by tree T1. In view of the expectation of strong maternal effects in trees [34], the influence of tree T1 on the next generation is likely to be even stronger than what one might expect from considerations based only on Mendelian inheritance.

(b) Pollen-mediated gene immigration and the rescue of genetic diversity

The above findings suggest that the population should be experiencing strong genetic drift. Along with the strong relatedness detected in the F1 generation and the strong inbreeding depression characteristic of long-lived trees, this should result in severe founder effects. However, our results show that these expected founder effects are in fact alleviated by a non-negligible amount of long-distance pollen inflow. More than six per cent of all genotyped acorns were fathered by immigrant pollen, a notable fraction given that no adult holm oak exists within 5 km around our population and the nearest major stands are more than 30 km away. A rapidly increasing body of evidence indicates that pollen gene flow over many kilometres could indeed be a widespread phenomenon, especially in wind-pollinated tree species [3,35].

The fraction of immigrant genotypes among the established plants of the F2 generation (27%) exceeded by far that observed at the acorn stage (6%). This difference could in principle arise from the increase in local pollen production as trees grow older. This should in turn increase competition for access to ovules, and hence decrease the likelihood of immigration events through time. However, we consider it more likely that the purging of inbred individuals during early plant recruitment has contributed to this result [28]. This interpretation is backed by the facts that (i) inbred seeds were lighter than outbred ones (an indicator for lower fitness [36]), (ii) selfed individuals were virtually absent from the established recruits and (iii) the F1 generation did not contain significantly more immigrant genotypes than the acorn cohort. In fact, the two founder trees are not close relatives, according to our genotype reconstruction, and in-breeding effects in the F1 generation should therefore be negligible, in contrast to what we expect in the F2 generation.

(c) Insights into the evolution of leading-edge populations

Overall, our results, along with those of Lesser & Jackson [4], suggest that leading-edge populations of wind-pollinated trees could restore their genetic diversity within very few generations owing to the combination of efficient long-distance pollen flow and marked inbreeding depression during plant recruitment. Allelic richness is expected to be more immediately affected by this recovery than heterozygosity [15]. The comparison of the F1 and F2 generations supports this prediction (table 2). Various models have recently addressed the evolution of genetic diversity of
leading-edge populations, but few have been confronted with empirical data. Given the marked reproductive dominance of tree T1, our results could in principle be interpreted as a snapshot of an ongoing process of allele surfing [6], although this phenomenon should be partly counteracted by the elevated gene immigration observed. More importantly, our results support the idea that negative demographic consequences of Allee effects can be counter-balanced by their beneficial impacts on gene flow. A good example of this seemingly paradoxical conclusion is the work of Roques et al. [7], which modelled a scenario of expansion with Allee effects (but without long-distance gene flow). Our expectation is that most leading-edge populations of tree species that managed to establish and eventually expand should have benefitted from this rescue effect, in view of their typically high inbreeding depression (that make them prone to Allee effects). To date, the literature on range expansions typically focuses on the negative consequences of Allee effects [4,37]. On the other hand, our study also suggests that mating patterns and kin competition within leading-edge populations could have a great influence on the colonization process itself, two factors that have only recently been incorporated in models of range expansions [38,39].

Finally, our results underpin that, once a few trees have successfully established, long-distance pollen gene flow appears sufficient to rapidly restore the genetic diversity lost during initial establishment [40]. This conclusion supports the widely held but under-investigated idea that range expansions of forest trees are primarily constrained by the initial arrival of viable propagules rather than by subsequent gene flow by pollen [4,8,27].

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