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Acorn dispersal and its consequences for forest stand regeneration and expansion.

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ABSTRACT

Seed dispersal generates the initial template of plant regeneration and has cascading effects on all subsequent plant demographic processes. In animal-dispersed plants, the behaviour of the dispersal agents can profoundly impact plant reproductive success and the resulting spatial and genetic structure of populations. Several decades of ecological research on seed dispersal have unravelled the great complexity of plant-disperser interactions. However, further progress towards a better understanding of the specific role of seed dispersers for plant regeneration is hampered by the difficulties involved in unequivocally linking the post-dispersal fate of seeds with their origin.

The overall goal of this doctoral thesis is to investigate drivers of oak acorn dispersal by scatter-hoarding animals and its implications for early oak regeneration and the resulting reproductive success of individual trees. The study was carried out in a small, naturally regenerating and actively expanding mixed Pedunculate oak-Pyrenean oak (*Quercus robur and Q. pyrenaica*) forest stand, representative of a scattered but widespread vegetation type in the Landes de Gascogne region (SW France). A recently germinated seedling cohort was extensively sampled and genotyped using microsatellite (SSR) and single nucleotide polymorphism (SNP) markers. All individuals were mapped and tagged and their performance was assessed until an age of 3 years. The mother trees of the monitored seedlings were identified by means of Bayesian parentage analyses and their phenotype was assessed by field and laboratory measures.

The thesis document is divided in three main chapters, each corresponding to an independent study. The first chapter explore which characteristics of fruiting oak trees influence their attractiveness towards acorn-harvesting animals. The analysis showed that acorn dispersers selected individual trees was guided by local acorn abundance, whereas traits such as the oak species, acorn size or form played a negligible role. The second chapter address oak maternal reproductive success, its determinants and evolution through the early recruitment process. The study reveals that a few highly fertile trees dominated the reproduction in the stand. However,

differential recruitment success tended to reduce their initial advantage, they suffered disproportionately from the satiation of their dispersers, resulting in higher acorn dispersal failure and seedling mortality. Their reproductive dominance hence should rapidly decline as more trees start to reproduce along the expansion process of the forest stand. The third chapter investigates consequences of the dispersal process on seedling performance, complementing the previous chapters by a whole-cohort perspective on recruitment patterns. The study indicates that seedling fates depended basically on the environment at their establishment sites. Among-habitat differences in recruit arrival and performance provide interesting insights into the putative effectiveness of the two major types of acorn dispersers, jays and rodents. Strikingly, seedling genetic diversity varied neither across different subcohorts (e.g. local vs immigrant origin, dispersal to different habitats) nor through the three-year monitoring period in spite of an extensive mortality (ca. 70%).

Overall, this thesis helps elucidate precise ecological processes that act during a very short stage of the oak life cycle: seed dispersal and early recruitment. It provides an unprecedented perspective upon the interaction between fruiting oaks and their scatter-hoarding dispersers and upon its implications for spatial and genetic patterns of oak regeneration. Its one-cohort snapshot character implies that the reported results must be interpreted with caution, yet different lines of evidence suggest that they might indeed be representative and relevant for the dynamics of oak regeneration in the region of this study. If this were true then we must conclude that the foraging behaviour of acorn-hoarding animals can indeed have a measurable long-term impact on the population structures of naturally regenerating oak forests.

GENERAL INTRODUCTION

Seed dispersal links the end of the reproductive cycle of adult plants with the establishment of their offspring and generates the initial template of plant regeneration. Because it has cascading effects on all subsequent plant demographic processes (e.g. seed predation, germination, seedling survival and growth), it is widely accepted to have a profound influence on vegetation structure and the demographic cycle of plants (Harper 1977; Howe & Smallwood 1982; Wang & Smith 2002; Howe & Miriti 2004). Patterns and dynamics of seed dispersal influence a wide range of ecological processes ranging from the colonization of new habitats to the maintenance of diversity, with implications for succession, regeneration and conservation. A vast number of studies have assessed patterns of plant recruitment over the last decades with the purpose to accurately predict regeneration outcomes (Figure 1) (Nathan & Muller-Landau 2000; Schupp *et al.* 2010; Robledo-Arnuncio *et al.* 2014). Besides the interest from a point of view of ecological theory (Levin *et al.* 2003; Levine & Murrell 2003), research in dispersal ecology provides key information for the management and conservation of plant populations and communities (Clark *et al.* 1999; Wright *et al.* 2007; McConkey *et al.* 2012; Corlett & Westcott 2013).

Seed dispersal by vertebrates: a complex plant-animal interaction

Plants use a great diversity of vehicles to mobilize their seeds and disperse them to suitable sites for plant establishment (Willson & Traveset 2000; Vander Wall *et al.* 2002). Many species rely on abiotic vectors, such as wind or water, or on biotic vectors that transport seeds inadvertently (e.g. within vertebrate guts or attached to the outer surface) or intentionally (i.e. seed-storing corvids, rodents or ants). Seed dispersal by vertebrates is considered a key innovation in angiosperm evolution (Tiffney 2004) and is widely distributed in both gymnosperms (Herrera 1989) and angiosperms (Tiffney & Mazer 1995). In turn, most major groups of vertebrates count with species that regularly consume fruits and disperse their seeds, including fishes, frogs, tortoises, lizards and iguanids, besides the two most concerned groups birds and mammals (Stiles 2000). Some of these animals are more effective seed dispersers than others and they can provide different benefits in addition to the mere movement of the propagule (e.g. seed scarification, hiding from predators etc., Stiles 2000; Vander Wall *et al.* 2005; Vander Wall & Beck 2012). Overall, the activity and behaviour of animal seed dispersers can strongly influence the fitness of reproducing plants and their offspring and leave measurable imprints in the spatial, demographic and genetic structure of plant populations (Jordano & Godoy 2002; Schupp *et al.* 2010; Hamrick & Trapnell 2011). Their loss can consequently create severe problems for plant regeneration and conservation (Guimarães *et al.* 2008; McKonkey *et al.* 2012).

Two major types of vertebrate-mediated seed dispersal can be distinguished, each associated with a distinct guild of animals: frugivory and scatter-hoarding (Howe & Smallwood 1982; Jordano 2000; Vander Wall & Beck 2012). In frugivory, animals ingest fleshy fruits and then defecate or regurgitate their seeds across the landscape. This dispersal mode can usually rely on relatively diverse disperser guilds and is especially effective at distributing large numbers of (usually small) seeds across the landscape. However, many of these seeds fail to establish because they are delivered to unsuitable sites (Schupp *et al.* 2010). In contrast, scatter-hoarding animals transport seeds in the mouth, bill or oesophagus and bury them in small, spatially scattered caches for later consumption. Scatter-hoarding hence only turns into effective seed dispersal when seeds are not recovered and destroyed by the hoarder but can produce plants. This occurs when hoarders fail to recover their caches, for example because they forget their location, cache more seeds than they need, are forced out of their territory or perish, or retrieve the cotyledons after the seedling is established (Vander Wall 1990; 2010).

Because the specific behaviour of caching seeds in soil and the ability to recover them for later consumption involves specific adaptations (e.g. pouches in which to carry seeds, strong bills, spatial memory, territorial behaviour), scatter-hoarding has evolved in relatively few terrestrial vertebrates including several groups of rodents (e.g., tree squirrels, chipmunks, mice, kangaroo rats, spiny rats, some cavimorph rodents), many corvids (e.g., jays, rooks, nutcrackers), some other birds (e.g. woodpeckers, nuthatches) and a couple of species of marsupials (Vander Wall 1990; Dennis 2003; Murphy *et al.* 2005). In accordance with this rather narrow guild, the evolutionary diversity of seeds and nuts that are regularly dispersed by scatter-hoarders remains comparatively limited, even though the syndrome is exhibited by some prominent groups of trees (e.g. pines, Fagaceae, palms) as well as by a few forbs and grasses (Longland *et al.* 2001; Borchert 2004).

Scatter-hoarded seeds and nuts are among the most nutritious foods available that typically contain relatively little water but high contents of lipids and proteins (Vander Wall 2001a). Food hoarding animals can only consume a few at a time, whereas their inclination to cache them is much more difficult to quench (Vander Wall 2010). As a consequence, hoarders commonly store far more seeds than they could possibly eat during a future period of food scarcity. For instance, jays can regularly cache 5,000 or more acorns over a single fruiting season, often recovering fewer than half of them (DeGange *et al.* 1989). On the other hand, the delivery of a large number of seeds to conditions that favour germination and seedling establishment is one of the unique aspects of scatter-hoarding seed dispersers (Vander Wall & Beck 2012). For instance, jays are well known to cache acorns preferably in habitats that provide little shelter to rodent seed predators (Bossema 1979; Mosandl & Kleinert 1998; Gómez 2003). Moreover, most scatter-hoarders store only one or a few food items per cache, thrusting them into the substrate, positioning them in a way that they cannot be seen, and covering them with materials from the surrounding area. Such a behaviour considerably difficults their identification by seed predators (Stapanian & Smith 1978; Vander Wall 1992; den Ouden *et al.* 2005). In the case of acorns, it also protects them from dehydration and the resulting loss of germination capacity (Gosling 1989).

Scatter-hoarders and the regeneration of European oak forests

Forests are the natural vegetation across much of Europe (Ellenberg 1988). Many of the most widespread and dominant European forest tree species rely on scatter-hoarders for the dispersal of their seeds. The phenomenon concerns principally the Fagaceae with oaks (*Quercus*), beech (*Fagus*), walnuts (*Juglans*), chestnuts (*Aesculus* and *Castanea*) and hazelnuts (*Corylus*), as well as some species of pines (notably stone pine *Pinus pinea* and Swiss pine *P. cembra*) (Vander Wall 1990; Pesendorfer *et al.* 2016). Across Europe, around 650,000 km^2 are covered by broadleaf, mixed and sclerophyllous dry forests harbouring oak, beech and related species (Iremonger *et al.* 1997). Oak forests are particularly widespread in France where they cover 54,000 km^2 (52% of all hardwood forests) with 700 million m^3 of standing stock (Derrière *et al.* 2013). Oaks are important foundation species (Ellison *et al.* 2005) that probably maintain more associated organisms depending on them than any other plant species in Europe (Southwood 1961; Brändle & Brandl 2008). Efficient natural regeneration of these forests is critical for their conservation as it helps sustain biodiversity, improves resistance to a wide array of natural and anthropogenic disturbances and considerably facilitates management and silviculture.

The natural regeneration of European oak forests is maintained by a small guild of acorn-dispersing animals. Eurasian Jays (*Garrulus glandarius*) are the principal dispersers over large distances (Bossema 1979; Gȯmez 2003; Pons & Pausas 2008; Pesendorfer *et al.* 2016). Acorns are also regularly moved and cached by different rodents such as wood mice (*Apodemus* spp.) or red squirrels (*Sciurus vulgaris*) (e.g. Crawley & Long 1995; den Ouden *et al.* 2005; Muñoz & Bonal 2007; Gȯmez *et al.* 2008; Perea *et al.* 2011) and even by dung beetles (*Thorectes lusitanicus*) (Perez-Ramos *et al.* 2013). Finally, a series of further vertebrates, such as wild boars (*Sus scrofa*), deer (*Cervus* spp.) or wood pigeons (*Columba palumbus*), regularly consume acorns, although they typically destroy them and effective dispersal events are likely to occur only very rarely and accidentally (Mellanby 1968; Groot Bruinderink et al. 1994; Crawley & Long 1995; Gȯmez *et al.* 2008).

Jays and rodents differ in their scatter-hoarding behaviour, and these differences have been shown to generate different patterns of acorn dispersal (den Ouden *et al.* 2005). Their behaviour can exert a direct and potentially strong influence on the establishment chances of acorns and thereby on the fitness of reproducing oak trees. This can happen during different stages of the acorn foraging and dispersal process. Adopting the framework of Schurr *et al.* (2008), we can distinguish 'source effects' and 'path effects' in the behavioural sequence of acorn dispersers. Source effects determine how the source plant's character and local environment influence the probability of an acorn to be dispersed, whereas path effects determine the dispersal process itself and the environment at the site of delivery.

Various source effects have been shown to affect the behaviour of acorn-dispersing animals. For instance, individual tree crop size can increase the per capita acorn dispersal rate (Pesendorfer & Koenig 2016a). Morán-Lȯpez *et al.* (2015) showed that oak tree selection by foraging jays in oak forests and adjacent savannahlike 'dehesas' was mediated by the size and the spatial location of fruiting trees. Jays tended to prefer trees located in or nearby the forest. Within the forest, crop size was a major driver of tree selection whereas outside the forest, the distance to other oaks was the predominant trigger of acorn removal. On the other hand, numerous experimental studies have investigated the influence of acorn characteristics on disperser choice and shown that both jays and rodents clearly differentiate between acorns of different oak species, size, shape and chemical composition (e.g. Bossema 1979; Muñoz & Bonal 2008; Pons & Pausas 2007a, 2007b; Myczko *et al.* 2014; Shimada *et al.* 2015). Field studies have reported that dispersers inspect acorns and avoid those with obvious damage caused by insects (Bossema 1979; Darley-Hill & Johnson 1981; Crawley & Long 1995; Fleck & Woolfenden 1997; Hubbard & McPherson 1997; den Ouden 2005; Pons & Pausas 2007b). This avoidance of damaged seeds by scatter-hoarding birds should contribute to enhance their quality as seed dispersers.

Different path effects have equally been addressed. Thus, the abundance of local acorn crops can influence distances of acorn dispersal either positively (Pesendorfer *et al.* 2016b) or negatively (Moore *et al.* 2007). The size of transported acorns has also been shown to positively affect dispersal distances (Moore et al 2007; Gómez *et al.* 2008; Wang & Chen 2009), although acorns that are too heavy may fail altogether to be dispersed (Muñoz & Bonal 2008). Most importantly, the vegetation structure usually triggers both dispersal distances and the sites of acorn delivery. Jays usually transport them over several metres to kilometres (Gómez 2003; Pons & Pausas 2007c). They tend to avoid enclosed conditions and cache acorns in open areas or at the interface between two distinct habitats (Bossema 1979; Kollmann & Schill 1996; Gómez 2003). In contrast, the activity of rodent dispersers strongly depends on the small-scale vegetation structure as these usually seek the protection of vegetation cover. Rodents move by far most acorns over short distances (a few metres), although dispersal distances up to 70 m have been reported (den Ouden *et al.* 2005; Gómez *et al.* 2008). Rodents can change their caching behaviour depending on the risk of predation (Vander Wall 2001b) or the presence of ungulates (Muñoz & Bonal 2007), with potentially significant consequences for the resulting establishment success of recruiting oak seedlings (Smit *et al.* 2008).

On the difficulty of linking drivers and consequences of acorn dispersal

Both source effects and path effects involved in acorn dispersal need to be addressed to thoroughly understand the role of scatter-hoarding acorn dispersers for oak regeneration. This has to date not been attempted, however. The difficulty with obtaining the required empirical data may go a long way in explaining this gap. One of the major gaps in seed dispersal research consists in the fact that extremely few studies have been able to unequivocally link the origin of dispersed seeds with their post-dispersal fate (Figure1) (but see Wenny 2000 for a fleshy-fruited species). This empirical gap has hampered attempts to quantify how the behaviour of seed dispersers influences the reproductive success of fruiting plants (Schupp *et al.* 2010).

Molecular ecological approaches can help overcome this limitation (García & Grivet 2011). Hypervariable molecular markers such as nuclear microsatellites (SSR) or single nucleotide polymorphisms (SNP) are now readily available for ecological studies. Parentage analyses based on genetic markers allow to infer the source plants of dispersed seeds or seedlings and thus to quantify their reproductive success. Early parentage analyses were still burdened with the constraint that they did not allow to distinguish between the mother tree and the father tree of dispersed seeds or seedlings. However, this constraint has now been overcome by different research approaches. Some use specific seed tissues of maternal inheritence (Godoy & Jordano 2001). Others rely on modelling approaches that allow to infer the most likely mother tree based on different sources of information besides the genotype (Burczyk *et al.* 2006; Oddou-Muratorio & Klein 2008; Moran & Clark 2011).

Applying these approaches now enables us to identify the origin of dispersed acorns (and thus to assess source effects of dispersal success) with relative ease. Fully understanding the role of acorn dispersers for oak recruitment still requires the assessment of path effects. This can be achieved through the environmental characterization of the sites where acorns arrive and the fate of recruiting oak seedlings as a function of these environments. Ultimately, establishing this link enables us for the first time to systematically estimate the realized reproductive success of fruiting trees as a function of acorn dispersal processes and the resulting establishment success of the offspring.

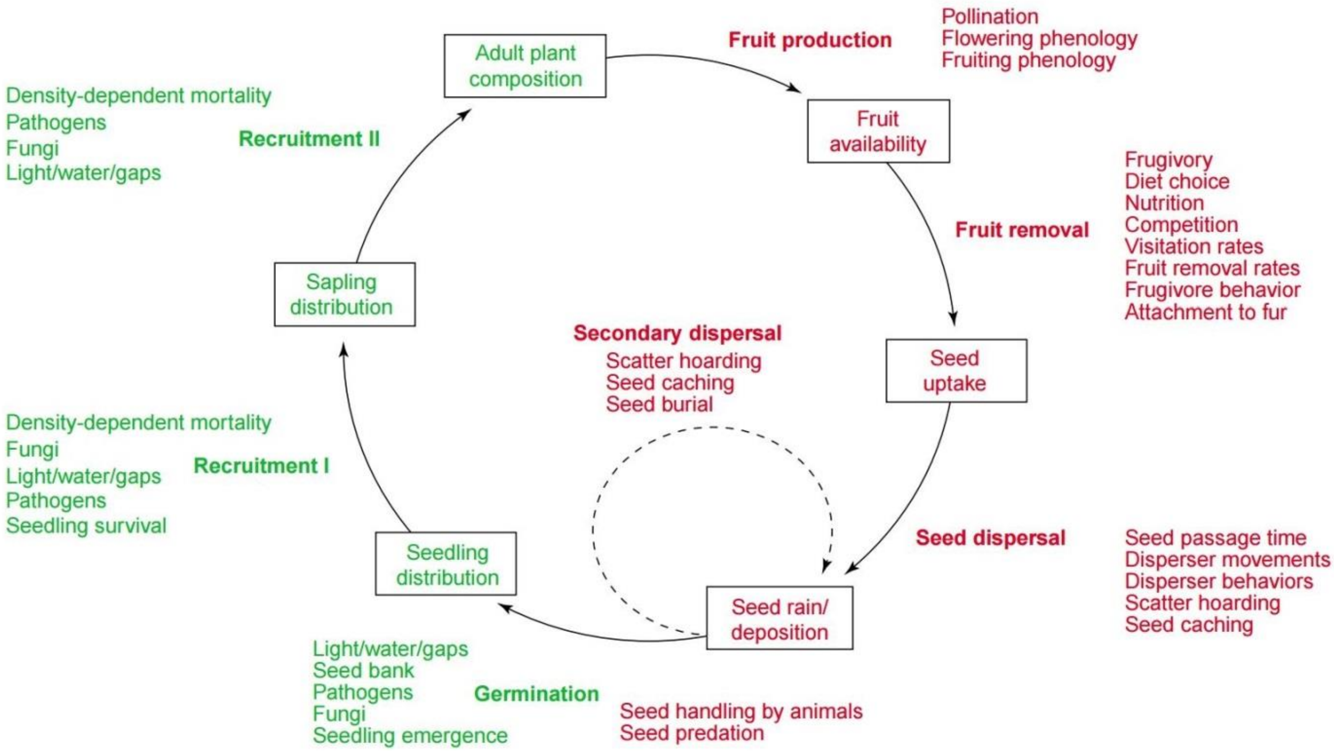

Figure 1. The two main approaches used to investigate animal-mediated seed dispersal and its consequences: (1) Working forwards entails trying to follow the seed dispersal process in the direction that it happens in nature (in the direction of the arrows). These studies tend to focus on patterns and processes on the right side (given in red), and many of them are classified as 'seed dispersal studies'. A major hurdle has been the difficulty of following the dispersers from parent plants to where they deposit seeds to track the fates of those seeds. (2) Working backwards examines the consequences of the seed dispersal process – seed, seedling, sapling, and adult plant distribution – and tries to deduce the influence of seed dispersal in determining those patterns. These studies focus on patterns and processes on the left side (given in green), and many of them are studies of plant demography. Processes (given in bold) generate the patterns (given in boxes) that can be measured. From Wang & Smith 2002.

Objectives and structure of the thesis

The overall goal of the present doctoral thesis was to investigate drivers and consequences of acorn dispersal by scatter-hoarding animals on natural patterns of early oak regeneration and the resulting reproductive success of trees within a small, naturally regenerating oak forest stand. The thesis is divided in three main chapters that follow the chronological sequence of events. The first chapter focuses on the question which cues guide acorn dispersers in their choice of fruiting oak trees, the second chapter investigates how this choice affects maternal tree reproductive success and its evolution during the seedling recruitment process, and the third chapter closes the dispersal loop (Wang & Smith 2002) by examining consequences of acorn dispersal for seedling recruitment and genetic diversity at the stand level.

Chapter 1. It is widely accepted that seed dispersal significantly increases the establishment probability of resulting recruits (Schupp *et al.* 2010). Therefore, differences in dispersal success among trees may have important and long lasting consequences for population dynamics. The aim of the first chapter was to identify the drivers that guide the selection of individual oak trees by acorn-foraging dispersers. The study revealed that dispersal success was exclusively driven by spatial patterns of acorn abundance. The behaviour of acorn dispersers resembles closely that known from frugivores of fleshy fruits, and it should favour the relevance of large, prolific trees for the dynamics and genetic composition of naturally regenerating oak stands.

Chapter 2. Tree populations almost invariably show highly skewed distributions of seed production, but how this reproductive skew evolves during plant recruitment remains understudied. Even small differences in individual reproductive success can generate large differences in the genetic composition of the resulting population, especially during demographic expansions. This chapter assessed how the reproductive success of individual oak trees is modified through the dispersal and early recruitment process. It showed that differential recruitment success tended to reduce the initial advantage of the most fecund trees, suggesting that reproductive inequality might rapidly decline as more trees start to reproduce during the expansion of the investigated forest stand.

Chapter 3. Early seedling recruitment is broadly assumed to be a major bottleneck in the plant life cycle that is characterized by a distinct peak of mortality. As dispersed seedlings experience different environmental pressures that can greatly influence their probability of survival with consequences for the regeneration dynamic, the third chapter investigates how dispersal-mediated differences in habitat of establishment influences genetic diversity, recruitment patterns and performance of a seedling cohort. Our findings suggest high habitat-related variability in seedling performance. The observed high early recruit mortality had however limited consequences for the genetic diversity of the recruiting cohort.

The study system and research approaches used

The Landes de Gascogne, located South-West France, is covered by almost one million ha of maritime pine (*Pinus pinaster Ait.*) plantations with intense stand management and rotation periods ranging from 40 to 50 years. This sylvicultural scheme translates into a mosaic-like landscape structure of uneven aged parcels interspersed by clear-cuts, fire breaks and roads. Deciduous trees, represent a small minority in this landscape that typically grow scattered in little stands (typically <5 ha) or along roads. The most common species are pedunculate oak (*Quercus robur*) and Pyrenean oak (*Q. pyrenaica*), together with silver birch (*Betula pendula*), different willows (*Salix* spp.) and a limited number of other taxa. Such oak stands are largely exempt from forest management. Ecological studies have shown their beneficial effects for the biodiversity and health of the surrounding pine plantations (Barbaro *et al.* 2007, Jactel *et al.* 2009). Resulting changes in sylvicultural management hence have helped promote oak regeneration as many oaks growing up within pine plantations are not any longer removed when these are cut. On the other hand, forest areas in the Landes de Gascogne areas are currently expanding due to the abandonment of rural landscapes (Forest Europe 2015). The surface cover of deciduous forests in the region thus rose from 8 to 15% through the last decade (Mora *et al.* 2012).

This particular context offers a unique opportunity to study acorn dispersal and its consequences for natural oak regeneration. First, the relatively small size and spatial isolation of oak stands allow a comprehensive sample of the entire adult population. Second, the strong dominance of pine plantations in the surrounding landscape matrix induces acorn dispersers to concentrate their activity at small spatial scales. Third, the landscape management creates notably distinct and spatially separated habitats that allow clearly identifying and classifying the environments at sites of acorn delivery and seedling recruitment.

This thesis investigates a representative mixed Pedunculate oak-Pyrenean oak stand located ca. 50 km SW of Bordeaux (France). This forest stand had been the object of previous ecological and genetic work on oak acorn dispersal and regeneration conducted from 2006 to 2008 (see Hampe *et al.* 2010). The thesis could benefit from and further advance upon this previous work. In particular, I could use the field data as well as some genetic data available for both adult oaks and seedlings. I myself completed the available SSR data (whose power was insufficient for performing effective parentage analyses) with a new dataset based on SNP markers. I also performed all numerical analyses contained in this thesis, and my work contributed to the development of the parentage analysis MEMMseedlings (see Gerzabek *et al.* 2017; Oddou-Muratorio *et al.*, submitted manuscript). Finally, I also designed, executed and analysed a further combined field and molecular study that investigated the effect of acorn dispersal to different habitats on the mycorrhization and fungal diversity of recruiting oak seedlings. This study could unfortunately not enter the thesis document because of time constraints but will instead be published in a future, independent research article.

Chapter 1:

Drivers of individual oak tree selection by acorn dispersing animals inferred from a genotyped seedling cohort

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ABSTRACT

Seed-dispersing animals can strongly influence plant reproductive success and resulting population structures. Few studies have disentangled different drivers of disperser foraging behaviour in natural settings and their actual relevance for plant fitness. Here we adopt a novel approach to investigate the drivers of individual trees' dispersal success in a mixed Pedunculate oak-Pyrenean oak (*Quercus robur* and *Q. pyrenaica*) forest stand. We genotyped a recently germinated seedling cohort (n = 825) and performed Bayesian parentage analyses to infer the acorn dispersal success of each oak tree in the stand. We then modelled this estimate as a function of six tree characteristics. The absolute number of dispersed seedlings was exclusively predicted by crop size and the proportion of dispersed seedlings by the number of fruiting oaks in the neighbourhood. Neither the oak species nor tree height, acorn size or shape played any role. Our findings contrast with results from experimental studies and suggest that acorn dispersers (mostly Eurasian jays, *Garrulus glandarius*), despite being scatter-hoarders, behave much like avian dispersers of fleshy-fruited species when selecting trees to forage on. Their behaviour should favour the dominance of large, prolific trees for the dynamics and genetic composition of naturally regenerating oak stands.

INTRODUCTION

Seed dispersal by vertebrates is considered a key innovation in angiosperm evolution (Tiffney 2004). Effective seed dispersal is critical for the successful establishment of new individuals and the resulting dynamics of plant populations and communities (Schupp *et al.* 2010). Seed-dispersing animals hence can exert a direct and potentially strong influence on the fitness of reproducing plants through their choice of the individuals they forage on. Their activity leaves measurable imprints in the genetic structure and diversity of plant populations (García & Grivet 2011; Hamrick & Trapnel 2011) and can drive rapid microevolutionary changes (Galetti *et al.* 2013). A better understanding of the cues that guide foraging seed dispersers in their choice of fruiting plants hence can provide valuable insights into the role of plant-disperser interactions for the reproduction and resulting demo-genetic structure of plant populations. Yet few studies have achieved to disentangle and compare different drivers of seed disperser behaviour under natural conditions. Moreover, short-term observations or experiments tell little about the actual relevance of disperser behaviour for plant reproductive success.

Seed dispersers rely on a complex system of decision cues and spatial memory for selecting the plants they forage on (Corlett 2011). Decision cues can be used hierarchically or sequentially, and their role can vary depending on the animal's spatial scale of perception or nutritional status. Scatter-hoarding species that collect and store seeds for later consumption tend to behave differently than species that seek fleshy fruits to eat them immediately (Vander Wall & Beck 2012). Most studies on disperser foraging decisions have focused on cues related with either fruit abundance or fruit traits. Fruit crop size usually is a consistent predictor for the amount of seeds removed from individual plants (Carlo & Morales 2008; Prasad & Sukumar 2010). The abundance of fruits in the neighbourhood (conspecific or heterospecific) can also influence rates of seed removal, either positively through an increased attraction of dispersers (Morales *et al.* 2012) or negatively owing to their satiation (Hampe 2008; Saracco *et al.* 2005). On the other hand, diverse morphological, physical and chemical fruit traits have experimentally been shown to influence fruit choice, highlighting the capacity of frugivores to differentiate even subtle signals (Corlett 2011). Fruit traits can also influence disperser foraging behaviour under natural conditions, although their actual relevance varies greatly across systems (Jordano 2000; Vander Wall 2010).

Despite these advances, our understanding of disperser behaviour and its consequences for plant recruitment remains fragmentary. Studies on scatter-hoarders have largely focused on fruit characteristics but rarely on the identity of the source plant (Vander Wall 2010; Pesendorfer *et al.* 2016) (but see Wästljung 1989; Morán-López *et al.* 2015), while studies of other frugivores have focused much on fruit abundance and less on individual-level variation in fruit traits (but see e.g. Sallabanks 1993; García *et al.* 2001). Most importantly, virtually no studies have to date linked frugivore behaviour with the fitness of the fruiting plant due to the difficulty of tracking animal-mediated seed dispersal events and resulting plant establishment (Schupp *et al.* 2010). Molecular ecological approaches can help overcome this limitation (García & Grivet 2011). Parentage analyses based on genetic markers allow to infer the source plants of dispersed seeds or seedlings and thus to quantify the reproductive success of all adults in terms of the number of descendants they have achieved to disseminate and establish across the population. This fitness measure can then be related with characteristics of the fruiting plant and its environment.

Here, we combine field and molecular ecological research approaches to assess drivers of individual oak tree selection by acorn-dispersing animals in a mixed Pedunculate oak-Pyrenean oak (*Quercus robur* and *Q. pyrenaica*) forest stand. Acorn dispersal is primarily performed by the Eurasian jay (*Garrulus glandarius*) in our study area (Gerzabek *et al.* 2017). Jays are major dispersers of oak acorns across much of temperate Eurasia (Pesendorfer *et al.* 2016). They are very efficient scatter-hoarders that can harvest, disperse and store thousands of acorns within a single fruiting season (Kollmann & Schill 1996; den Ouden *et al.* 2005). Their foraging behaviour hence can have direct and significant implications for the relative contribution of individual oak trees to plant recruitment at forest stand level. Eurasian jays have been shown to favour large and slim acorns and to differentiate among oak species in choice experiments (Bossema 1979; Pons & Pausas 2007; Myczko *et al.* 2014). But it remains little known whether their foraging decisions under natural conditions are primarily guided by acorn traits, local acorn abundance, or other drivers (Pesendorfer *et al.* 2016, Morán-López *et al.* 2015).

We genotyped a cohort of recently germinated oak seedlings and performed parentage analyses to quantify the effective dispersal success - estimated through the absolute number or the proportion of seedlings emerging away from the mother tree - of each adult oak growing within the forest stand. This estimate was then related with several tree features to simultaneously test how these influenced the choice of individual oak trees by foraging jays. Specifically, we addressed the following research questions: 1) How many seedlings does each tree of the forest stand contribute to the genotyped cohort? 2) Can trees' dispersal success be predicted from their species identity, height, crop size, acorn size or shape, or oak abundance in their neighbourhood? 3) What is the relative importance of these predictors for explaining acorn dispersal success?

MATERIALS AND METHODS

Study system

The study was performed in the Forêt de Nezer (44°34' N, 1°00' W) ca. 50 km SW of Bordeaux, SW France. The area is covered by extensive plantations of maritime pine (*Pinus pinaster* Ait.) interspersed with small stands of broadleaf forests dominated by Pedunculate oak (*Quercus robur* L.) and, to a lesser extent, Pyrenean oak (*Q.pyrenaica* Willd.). Such stands are largely exempt from forest management. Most acorn dispersal in the area is performed by the common jay (*Garrulus glandarius L.*), although some dispersal by rodents (wood mice, *Apodemus sylvaticus* L., bank voles, *Myodes glareolus* Schreiber, and eventually European squirrels, *Sciurus europaeus* L.) should also take place. We selected an mixed oak forest stand with ca. 280 adult Pedunculate and Pyrenean oaks (90% *Q. robur*, 10% *Q. pyrenaica*) for this study. A detailed description of the stand can be found in (Hampe *et al.* 2010). Importantly, several jays were regularly present in the area and different lines of evidence - field observations, the spatial locations and microhabitats of sampled seedlings (Gerzabek *et al.* 2017) and complementary experiments on acorn predation and dispersal on the ground (A. Hampe, unpublished data) - suggest that only a very limited proportion of the seedlings we sampled would have been dispersed and cached by other animals than jays.

Field sampling and laboratory analyses

In early spring 2006, we delimited a study plot of 6 ha enclosing the oak forest stand and surveyed all adult trees within this area and an adjacent belt of 100 m width. Trees were identified as adults based on their size and on fruit set observations. Each tree was individually tagged and mapped, its diameter at breast height (dbh) was measured, and several buds were collected and stored at -80° C for later DNA isolation. We subsequently measured six further variables for a subset of 79 arbitrarily chosen trees: (i) The oak species (*Q. robur* or *Q. pyrenaica*) was determined in the field based on leaf morphology. (ii) Tree height was measured with an ultrasound vortex. (iii) Acorn crop size during the 2005 fruiting episode was quantified by counting the number of empty acorn cups in four 50x50 cm squares randomly placed beneath the canopy in early 2006 and multiplying the census mean with the dbh of the target tree (which served as a proxy for the canopy size). Moreover, we collected 50 acorns from each tree in September 2006 to determine (iv) acorn size (by measuring their weight to the nearest 0.1 mg) and (v) acorn shape (by measuring length and width to the nearest 0.1 mm and calculating their ratio). (vi) We quantified the abundance of adult oaks in the neighbourhood by summing the number of trees within a radius of 10 meters around the focal tree.

During late April and early May 2006, we performed a comprehensive survey of newly emerged oak seedlings (i.e., those stemming from the 2005 fruiting episode) in our 6 ha study plot. We sampled all seedlings emerging more than 2 m away from any adult oaks, searching every part of the study plot at least twice and up to six times. Furthermore, we sampled 20% of all seedlings emerging beneath adult oaks (i.e., up to 2 m beyond the canopy projection to account for potential short-distance dispersal of acorns by wind or bouncing off of branches). These 20% were sampled using a strict randomisation protocol (see Hampe *et al.* 2010 for details). We estimate that the resulting data set (n = 825 individuals) includes 25-30 % of the overall seedling cohort within the study plot. All sampled seedlings were individually tagged and mapped, and one leaf was collected and stored at -80°C until DNA isolation.

Trees and seedlings were genotyped using eight nuclear microsatellite (SSR) markers (QrZAG11, QrZAG96, QrZAG112, QpZAG110, QrZAG5b, QrZAG7, QrZAG20, and

QrZAG87) as described in detail in (Hampe *et al.* 2010). In addition, we genotyped all individuals at 39 SNP loci as described in (Gerzabek *et al.* 2017). We obtained readily usable data for 33 SNPs that we merged with the SSR data to obtain individual multilocus genotypes.

Data analyses

Our analysis proceeded in two steps. First, we quantified the fecundity and acorn dispersal success of individual trees. Then we assessed how dispersal success was affected by a series of tree-related parameters.

Quantifying individual dispersal success - We performed a parentage analysis using a Bayesian approach as implemented in the software MEMMseedlings (Gerzabek *et al.* 2017; Oddou-Muratorio *et al.* submitted). Unlike many other parentage assignment procedures (but see Moran & Clark 2012), our approach jointly considers genotypes, spatial locations and tree mating parameters to infer parentage and allowed us to distinguish between the mother and the father tree of a given seedling - a highly relevant information for our study purpose. We adapted MEMMseedlings to use a two-step procedure (explained in detail in Gerzabek *et al.* 2017) where the first step consisted in the estimation of all fecundity and dispersal parameters (Oddou-Muratorio *et al.* submitted). The second step consisted in computing the posterior probability of each tree within the stand to be the mother of a given sampled seedling and the posterior probability that this seedling originates from seed migration. Based on these probabilities, we then assigned each sampled seedling categorically to its most likely mother tree (that is, either the tree with the highest posterior probability or a non-sampled mother-tree from outside the stand if the posterior probability of immigration exceeded those of the local mother trees).

Our parentage analysis served two purposes: First, it enabled us to identify the mother trees of our seedlings and to estimate the maternal reproductive success of each tree within the stand by summing up the number of seedlings assigned to this individual. Second, it allowed us to infer categorically whether a given seedling had been dispersed away from its source tree or not (we consider that an animal is always the vector in the former case). We considered that any seedling growing beneath its assigned mother tree stemmed from an acorn that had directly fallen from the mother tree to the ground without being handled by an animal seed disperser. These acorns were classified as “non-dispersed” and the remaining acorns (i.e., those growing either away from any adult oak or beneath an oak that was not assigned as their mother tree) as “dispersed”. The sum of dispersed acorns was used as a proxy for individual trees’ “absolute” dispersal success and the proportion between the dispersed acorns and the overall number of acorns mothered by a given tree was used as an estimate of its “relative” dispersal success.

Predictors of individual dispersal success - We constructed generalised linear models to assess the relative effect of different tree features on the absolute and the relative dispersal success of individual trees. Models included the following predictor variables: tree species, tree height, crop size, acorn size, acorn shape, and adult oak abundance in the neighbourhood. Crop size and adult oak abundance were log transformed to reach a better fit. We considered no interaction terms in the final model after preliminary tests. Our models assumed quasi-Poisson (absolute dispersal success) and binomial (relative dispersal success) errors.

Finally, we assessed direct relationships between tree crop size and absolute dispersal success using an analysis of density dependence. For this purpose, we performed a linear regression with our crop size index as predictor and the number of successfully dispersed seedlings as response variable (both log-transformed). All but the parentage analysis were performed in R version 3.3.0 (R Development Core Team).

RESULTS

We could assign a total of 678 seedlings (82% of the overall sample) to a local mother tree and classify 307 of them as non-dispersed and 371 as dispersed. A total of 115 trees (39% of the local adult population) mothered at least one seedling and 87 (30%) at least one successfully dispersed seedling. The distribution of seedling production was highly skewed (Fig. 1), although the trend was weaker among the dispersed seedlings (Kolmogorov-Smirnov: $D = 0.24$, $P = 0.002$).

The subset of 79 trees that we had characterized in the field produced 468 seedlings, of which 237 had been dispersed. A total of 47 trees mothered at least one seedling and 38 at least one successfully dispersed seedling.

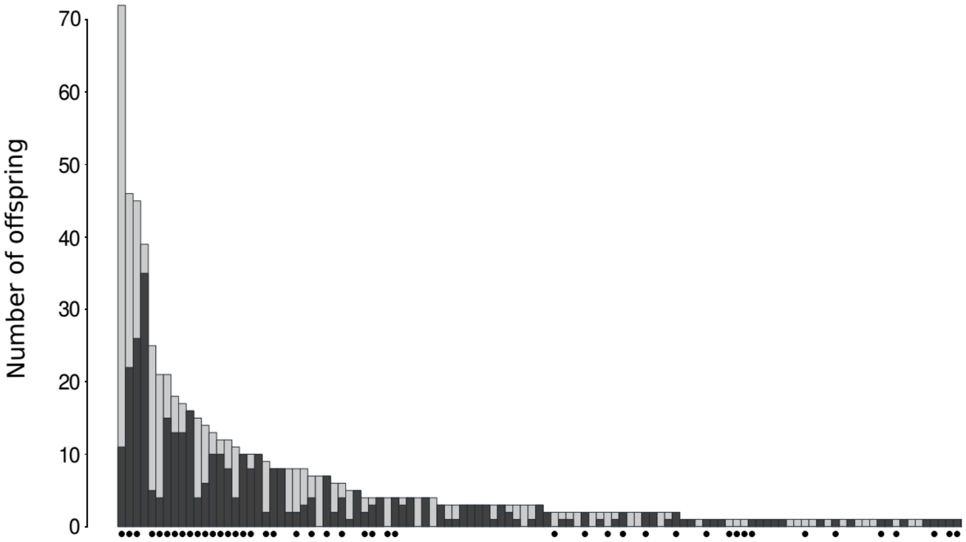

Figure 1. Seedling production by individual *Quercus robur* mother trees. Each column corresponds to a reproducing tree. Dark grey bars indicate those seedlings that were actually dispersed away from the mother tree and light grey bars those that failed to be dispersed. Black circles beneath columns indicate trees for which trait data (see Table 1) were gathered.

Predictors of individual seed dispersal success – Most traits measured showed large variation (Table 1; note that this variation is not representative for the entire forest stand as the sampled trees were not randomly chosen). The generalised linear model on absolute dispersal success revealed a marked positive effect of crop size (slope = 0.78), whereas relative dispersal success was exclusively predicted by, and negatively related (slope = -1.26) with, the number of fruiting oak trees within the neighbourhood of the focal tree. (Table 2). Neither the oak species nor tree height or the acorn traits size and shape exerted any noteworthy effect on dispersal success (either absolute or relative). Finally, the regression between our crop size index and absolute dispersal success generated a slope of 0.30 ($F = 29.7$, $P < 0.001$, $R^2 = 0.28$), significantly smaller than 1 ($t = -12.52$, df = 77, $P < 0.001$).

Variable	Mean ± SD	Range
Crop size index	553 ± 695	0 - 3194
Tree height (m)	15.3 ± 3.7	9.2 - 25.0
Acorn weight(mg)	3962.3 ± 1075.8	1822.5 - 7374.3
Acorn shape (ratio length:width)	1.7 ± 0.2	1.2 - 2.3
Number of adult oaks within 10m	2.8 ± 2.3	0 - 8

Table 1. Individual variation in different traits measured at 79 *Quercus robur* trees from the target forest stand. Note that trees were arbitrarily chosen and values hence are not representative for the entire stand.

	Absolute dispersal success			Relative dispersal success		
Variable	*F*	d.f.	*P*	χ^2	d.f.	*P*
Species	1.43	1	0.23	1.24	1	0.27
Tree height	0.21	1	0.64	0.38	1	0.54
Crop Size	25.87	1	**<<0.001**	0.23	1	0.63
Acorn size	1.27	1	0.26	0.77	1	0.38
Acorn shape	0.66	1	0.42	0.95	1	0.33
Number of adult oaks	1.13	1	0.29	48.72	1	**<<0.001**

Table 2. Effects of the oak species, tree height, crop size, acorn size and shape, and the number of adult oaks in a radius of 10 meters around the target tree on the absolute number (= absolute dispersal success) and the proportion (= relative dispersal success) of effectively dispersed offspring according to generalised linear models (type II ANOVA, Wald χ^2 test).

DISCUSSION

Dispersal success of individual trees

A large part of the seedling cohort stemmed from only a handful of mother trees while many trees did not at all contribute to the seedling pool. Strong inequality in individual fecundity is a widespread phenomenon in tree populations (Moran & Clark 2012) and can persist into the stage of dispersed and established recruits (Schnabel *et al.* 1998; Sezen *et al.* 2007; Hampe *et al.* 2013). Our systematic distinction of dispersed and non-dispersed offspring enabled us however to detect that the skew in tree fecundity was weaker among the dispersed descendants than among the overall cohort. The most likely explanation for this difference is that trees with large crop sizes have a lower proportion of their acorns dispersed as a consequence of disperser satiation (Hampe 2008). The existence of such an effect is confirmed by the analysis of density dependence, and it is little surprising: Even highly efficient scatter-hoarders such as Eurasian jays (Pesendorfer *et al.* 2016; Kollman & Schill 1996; Bossema 1979) should be overwhelmed by a stand-scale crop that is likely to sum hundreds of thousands of acorns. Our result is at odds with the hypothesis of Vander Wall & Beck (2012) that scatter-hoarding seed dispersers should rarely be satiated when foraging (but rather when recovering the cached seeds). The relatively marked satiation effect that we observed (regression slope between crop size and dispersal success = 0.30) implies that acorn dispersers are a limited resource in our system for which fruiting trees have to compete. Under such circumstances, tree traits that influence disperser behaviour can directly affect dispersal success and resulting mother tree fitness (Gerzabek *et al.* 2017).

Tree-related predictors of dispersal success

Both absolute and relative dispersal success were exclusively driven by patterns of acorn abundance, although in different ways. The most fecund trees achieved to effectively disperse the greatest absolute amount of descendants. This finding fully supports the predator dispersal hypothesis (Vander Wall 2010; Pesendorfer *et al.* 2016), which poses that larger seed crops result in fitness benefits from increased seed dispersal by seed-hoarding animals. When we accounted for the effect of tree fecundity by calculating relative instead of absolute dispersal success, we found that this measure was negatively related with the abundance of adult oaks in the neighbourhood of the target tree. Although we could not quantify the crop sizes of all these trees, the number of adult oaks is likely to represent a reasonably suitable proxy for the local abundance of acorns. In line with our detection of a satiation effect, this finding indicates that trees are competing for dispersers with their direct neighbours (corresponding to the spatial scale addressed by our 10m radius).

On the contrary, neither the oak species nor acorn size or shape had any measurable influence on dispersal success. This finding is particularly noteworthy because to date most quantitative studies of drivers assumed to influence the behaviour of acorn dispersers have primarily focused on the oak species, morphological and/or chemical features of the acorns (e.g. Bossema 1979; Pons & Pausas 2007; Scarlett & Smith 1991; Wang & Chen 2009; Shimada 2015). These traits have often been shown to influence the choice of scatter-hoarders under experimental conditions. However, their actual relevance for effective acorn dispersal success in natural settings is questioned by the results of our multi-factor study, which confirm instead the role of more rarely investigated drivers such as the crop size or the spatial distribution of fruiting trees (Morán-López *et al.* 2015; Pesendorfer & Koenig 2016; see also Pesendorfer *et al.* 2016).

Taken together, our results suggest that the selection of trees by acorn dispersers relies primarily on visual choice based on acorn abundance and not on features that can only be properly perceived from within the tree (such as acorn traits) and would have to be memorised until subsequent foraging visits. In this sense, acorn dispersers behaved much like many avian frugivores of fleshy-fruited species (Vander Wall & Beck 2012; Carlo & Morales 2008; Prasad & Sukumar 2010; Saracco *et al.* 2005; Blendinger *et al.* 2008). Our research approach prevented us from assessing whether acorn dispersers, once settled within (or beneath) a given tree, tended to select certain acorn phenotypes over others. Such hierarchical selection behaviour is also known from frugivores of fleshy-fruited species (Corlett 2011; Sallabanks 1993). However, acorn choice within the same tree should be of relatively minor relevance for its dispersal success and resulting fitness.

Consequences for oak regeneration

Foraging decisions of seed dispersers are particularly important for plant species that depend on a small suite of vectors for their dispersal. This is the case with the European oaks, for which the Eurasian jay is widely acknowledged to be the major effective seed disperser (Pesendorfer *et al.* 2016; Bossema 1979; Gómez 2003). The species' relevance stems not only from the quantity of acorns it can mobilise and the average distance of dispersal events but also from its tendency to increase the survival chances of dispersed acorns by hiding them within the ground, often in microhabitats that are favourable for seedling establishment (Kollman & Schill 1996; den Ouden *et al.* 2005; Bossema 1979; Gómez 2003). Different lines of evidence suggest that jays are likely to be responsible for most effective acorn dispersal in our study stand. Our findings that they i) base their foraging decisions on tree crop size and ii) are satiated by the stand-scale acorn crop implies that the foraging behaviour of jays tends to favour the dominance of large, prolific trees in the recruitment and resulting genetic composition of naturally regenerating oak forests. A previous study performed in our oak stand revealed that the spatial genetic structure of the adult tree population strikingly resembles that of the dispersed seedling cohort (Hampe *et al.* 2010). This similarity was explained by the fact that most younger adults and most dispersed seedlings probably stem from the same few large founder trees. It nicely underlines that jay foraging behaviour may have a measurable long-term impact on the population structure of naturally regenerating oak forests.

DATA ACCESSIBILITY

Both the genotypic data and the field data underlying this study have been deposited in Dryad (doi:10.5061/dryad.3j33t).

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Chapter 2:

Temporal change and determinants of maternal reproductive success in an expanding oak forest stand

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ABSTRACT

1. Global change is generating widespread local-scale expansions of tree populations. During demographic expansions, even small differences in individual reproductive success can generate large differences in the genetic composition of the resulting population. Colonising tree populations almost invariably show highly skewed distributions of seed production, but the evolution of this reproductive skew during plant recruitment remains understudied.

2. We examine how recruit mortality modifies initial patterns of acorn dispersal and maternal reproductive success in a recently established, expanding Pedunculate oak (*Quercus robur*) forest stand and test different predictors of successful recruit establishment.

3. We mapped and genotyped a cohort of seedlings (n = 809) emerging within and around the stand (n = 254 adult trees), identified their habitats and monitored their fate until an age of 3 years. Their mother trees were inferred by Bayesian parentage analysis and the number of assigned descendants was used as a proxy for tree maternal fertility. We examined temporal trends in tree fertility and patterns of dispersal, and tested effects of seed number-quality tradeoffs, dispersal failure, dispersal distance and habitat of propagule arrival on the probability of seedling establishment.

4. We observed marked inequality in maternal reproductive success at the time of seedling emergence. A positive relationship between tree fertility and the proportion of non-dispersed seedlings pointed to disperser satiation. An overall seedling mortality of 69% generated considerable reshuffling in the fertility ranking of individual trees. Non-dispersal more than doubled seedling mortality. The establishment success of actually dispersed seedlings was independent of mother fertility and dispersal distance but strongly related with the habitat of arrival. Recruit survival was markedly higher in pine plantations or non-forested areas than in broadleaved forest.

5. *Synthesis.* A few highly fertile trees dominated reproduction in the stand. Differential recruitment success tended to reduce their initial advantage, however, suggesting that reproductive inequality might rapidly decline as more trees start to

reproduce along the expansion process. Our results also suggest that field estimates of size or seed production are unlikely to provide reliable estimates of lifetime reproductive success in trees.

INTRODUCTION

The establishment and expansion of secondary forests is a widespread phenomenon in many regions worldwide as a consequence of rural abandonment, changing land use and management, and the arrival of invasive tree species (Rudel *et al.* 2005; Sezen *et al.* 2007; Rundel *et al.* 2014). In forests, local-scale colonisations and increases in tree species abundance are pervasive as transient or persistent changes in environmental conditions favour the recruitment of some species to the detriment of others (Carnicer *et al.* 2014, Chisholm *et al.* 2014). Such non-equilibrium succession dynamics are likely to be further exacerbated by ongoing and impending climate change (Hampe 2011; Svenning & Sandel 2013). Efficient management of the regeneration of degraded forests or the establishment of new forests requires a sound understanding of the ecological and micro-evolutionary processes involved in tree recruitment (Rey Benayas *et al.* 2008). In a context of demographic expansion, even small differences in recruitment success can generate large differences in the relative contribution of reproducing individuals to the pool of recruiting offspring and the resulting genetic composition of the forest stand (Excoffier *et al.* 2009). Expanding tree populations are known to be characterized by strongly skewed distributions of offspring production (e.g. Schnabel *et al.* 1998; Sezen *et al.* 2007; Hampe *et al.* 2013). But the progression of this reproductive skew during plant recruitment and its underlying biological mechanisms remain understudied.

Any natural plant and animal population experiences, to a greater or lesser extent, inequality in reproductive success (Clutton-Brock 1988; Snyder & Ellner 2016). Trees are especially prone to it owing to their life history that combines a long lifetime and a successively increasing, potentially prodigious fertility with extensive mortality at early life stages (Petit & Hampe 2006). As a result, the effective size of tree populations typically is considerably smaller than their census size. This situation is exacerbated during the foundation and expansion of new populations, where recruitment often is dominated by few large founder trees that fill the surroundings with their offspring (Schnabel *et al.* 1998; Sezen *et al.* 2007; Hampe *et al.* 2013). This process can lead to strong founder effects, kinship structures, and genetic drift (Petit *et al.* 2004).

Inferences about life-time reproductive success can be strongly affected by the demographic stage at which it is measured. In trees, seed production is often used as a proxy for overall reproductive success (Moran & Clark 2012). However, seed production is not necessarily a good proxy because mortality at the seed stage and the seed-seedling transition typically is very high. The only study that has to our knowledge assessed tree reproductive success at different life stages (Moran & Clark 2012) reported lower reproductive skew in established seedlings than in seeds but did not identify underlying processes.

At least four non-exclusive mechanisms can contribute to reduce reproductive inequality through the recruitment process: (i) Highly fertile individuals can be more susceptible to seed dispersal failure, especially in biotically dispersed species that are susceptible to disperser satiation (Hampe 2008). (ii) Recruits from highly fertile individuals can experience lower fitness owing to a number-quality trade-off in seed production (Venable 1992). (iii) Higher offspring abundance around fertile individuals can result in higher density-dependent or distance-dependent mortality (Venable 1992). (iv) Highly fertile individuals can disperse a disproportionately high proportion of offspring to sites that are little suitable for recruit establishment (Schurr *et al.* 2008). The first two effects cause recruit survival to vary as a function of the mother tree's character ('source effects' *sensu* Schurr *et al.* 2008), whereas the latter two effects depend on the environments that recruits encounter following dispersal ('path effects' *sensu* Schurr *et al.* 2008). Their relevance for recruitment and the resulting evolution of tree reproductive inequality remains untested. The difficulty with acquiring the extensive combined pedigree and dispersal data required to calculate the relative offspring production of individual trees may go a long way in explaining this gap.

Here we examine how early recruit mortality modifies initial patterns of acorn dispersal and maternal reproductive success in an expanding Pedunculate oak (*Quercus robur*) stand and test different predictors of recruit survival. For this aim, we monitored the fate of a naturally recruiting, genotyped seedling cohort until an age of 3 years. The survey initiated with a single cohort of recently germinated seedlings to avoid the typically high mortality at the seed-seedling transition (often >90%; Moran & Clark 2012) while avoiding confounding effects that might arise from mixing seedlings that stem from different reproductive events. With this dataset, we calculated the maternal reproductive success of each adult tree in the forest stand and addressed the following questions: (1) What is the distribution of maternal reproductive success among trees at the time of seedling emergence? (2) How do patterns of reproductive success change through the recruitment process? (3) Which determinants are most influential for recruit establishment? Specifically, we model seedling survival as a function of two source effects (seed dispersal success and seed number-quality trade-offs) and two path effects (dispersal distance and habitat of arrival).

MATERIAL AND METHODS

Study system

The study was performed in the Forêt de Nezer (44°34' N, 1°00' W) ca. 50 km SW of Bordeaux, SW France. The area is covered by extensive plantations of maritime pine (*Pinus pinaster* Ait.) interspersed with small stands of broadleaved forests dominated by Pedunculate oak (*Quercus robur* L.) or, more rarely, Pyrenean oak (*Q. pyrenaica* Willd.). Such stands are largely exempt from forest management. Many are actively expanding, favoured by a recent change in silvicultural management that tends to conserve oaks recruiting within adjacent pine plantations as a means of biological pest management (Dulaurent *et al.* 2012). Most acorn dispersal in the area is performed by the common jay (*Garrulus glandarius* L.), although some dispersal by rodents (wood mice, *Apodemus sylvaticus* L., bank voles, *Myodes glareolus* Schreiber, and European squirrels, *Sciurus europaeus* L.) should also take place (Hampe *et al.* 2010). We selected a mixed oak forest stand with ca. 280 adult Pedunculate and Pyrenean oaks (90% *Q. robur*, 10% *Q. pyrenaica*) for this study (see Fig. 1). The spatial and age structure of the stand clearly indicated that it currently is undergoing an expansion. The nearest oak forest stand (smaller than the investigated one) is approximately 1 km away.

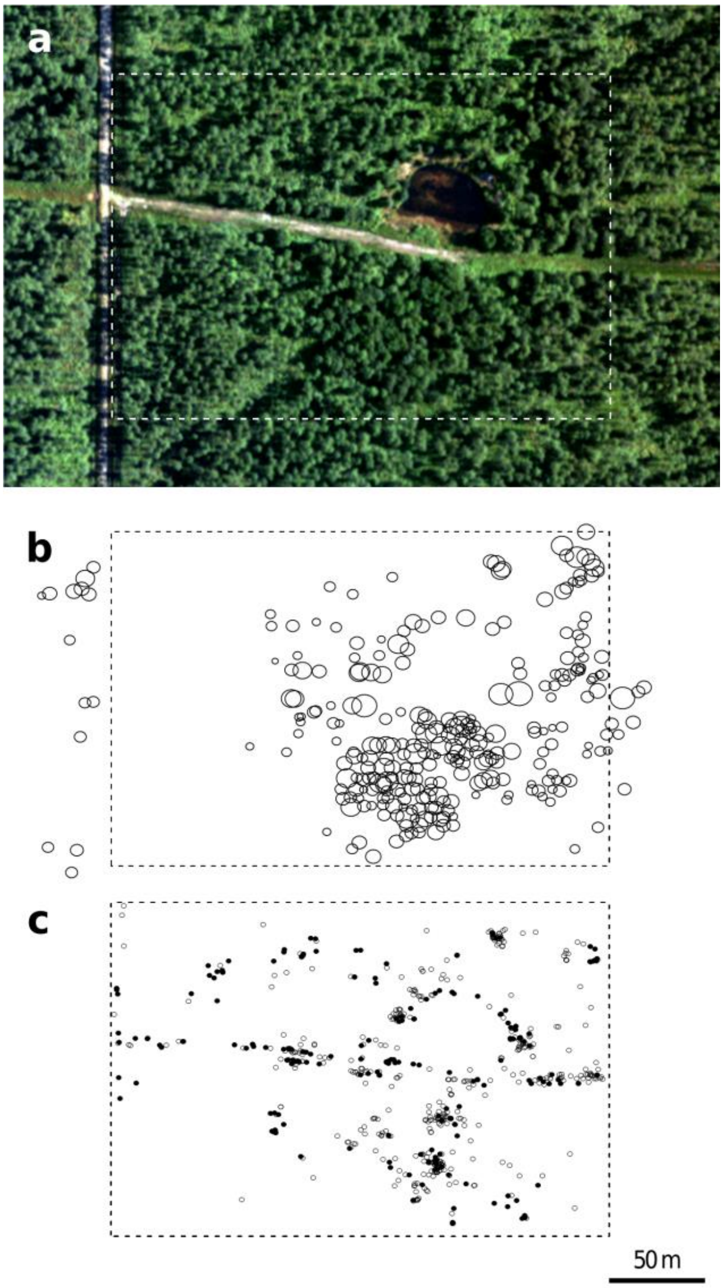

Figure 1. Aerial photograph of the study area (a), locations of adult oak trees with circle sizes proportional to their diameter at breast height (b), and locations of seedlings sampled with filled circles indicating individuals that survived through the study period and empty circles indicating non-surviving individuals (c). The broken line shows the limits of the seedling sample plot. Straight lines without tree cover in the aerial photograph are forest aisles that serve as firebreaks and routes for vehicles, whereas the dark treeless area in the upper right part of the sampling plot is a small pond.

Field sampling and laboratory analyses

In early spring 2006, we delimited a study plot of 6 ha enclosing the oak forest stand and surveyed all adult Pedunculate oak trees within this area and an adjacent belt of 100 m width (*n* = 254). Trees were identified as adults based on their size and on fruit set observations performed during two ripening seasons. Each tree was individually tagged and mapped to the nearest 0.1 m using laser telemetry and several buds were collected and stored at -80° C for later DNA isolation.

During late April and early May 2006, we performed a comprehensive survey of newly emerged Pedunculate oak seedlings (i.e., those stemming from the 2005 fruiting episode) in our 6 ha study plot. We sampled all seedlings emerging more than 2 m away from the crown projection of any adult oaks, searching every part of the study plot at least twice and up to six times. Furthermore, we sampled 20% of all seedlings emerging beneath adult oaks (i.e., up to 2 m beyond the canopy projection to account for potential short-distance dispersal of acorns by wind or bouncing off of branches). These 20% were sampled using a strict randomization protocol (see Hampe *et al.* 2010). We estimate that the resulting sample (*n* = 809 individuals, see Fig. 1) includes 25-30 % of the overall seedling cohort within the study plot. Importantly, our hierarchical sampling design is unbiased concerning the present study because each oak tree canopy area was sampled with the same intensity. All sampled seedlings were individually tagged and mapped, and one leaf was collected and stored at -80°C until DNA isolation. All seedlings were assigned to one of three major habitat types: (i) broadleaved forest (including silver birch [*Betula pendula*] and willows [*Salix* spp.] besides the two oak species), (ii) pine plantations and (iii) open areas without a tree layer. Seedlings were monitored twice a year until September 2008 and their status (living or dead) was recorded. The present study will only refer to the initial and the last survey. Some seedlings could not be unequivocally identified through the last survey and were therefore removed from all further analyses.

Survey	n_{total}	n_D	Broadleaved forest	Pine plantation	Open area	Median dispersal distance (m)
Emergence	644	359	365[a]	53	226	9.2
3 years	202	153	67[b]	30	105	18.1

[a] 274 individuals located beneath the mother tree and 91 dispersed away

[b] 48 individuals located beneath the mother tree and 19 dispersed away

Table 1. Sample sizes underlying this study. Only those seedlings for which we could successfully identify the mother tree are shown. Columns indicate the overall number (n_{total}), the number of of successfully dispersed individuals (n_D), and the number of of individuals emerging in a given habitat, as well as the median dispersal distance for the sampled *Quercus robur* seedling cohort.

Trees and seedlings were genotyped using eight nuclear microsatellite (SSR) markers (QrZAG11, QrZAG96, QrZAG112, QpZAG110, QrZAG5b, QrZAG7, QrZAG20, and QrZAG87) following the protocol of Lepais *et al.* (2006); the analysis has been described in detail in Hampe *et al.* (2010). In addition, we genotyped all individuals at 39 SNP loci (for details see Dryad data repository: doi:10.5061/dryad.3j33t). The loci were combined into a multiplex and sequenced on an iPLEX Gold genotyping kit (Sequenom) at the Genomic and Sequencing Facility of Bordeaux (France) following the procedure described in Chancerel *et al.* (2013). We obtained readily usable data for 33 SNPs that we merged with the SSR data to obtain individual tree and seedling multilocus genotypes for the parentage analysis. The overall set of markers provided an exclusion power of 0.9998 for single parents and of 0.99997 for parent pairs.

Parentage analysis

Seedlings were categorically assigned to their mother tree based on their multilocus genotypes and geographical coordinates using the Bayesian approach MEMMseedlings (Oddou-Muratorio *et al.*, ms under review). Unlike many other parentage assignment procedures (but see Moran & Clark 2012), our approach jointly considers genotypes and distances to infer parentage and allows us to distinguish between the mother and the father tree of a given seedling, which is highly relevant information for our study purpose. MEMMseedlings is one of the recently developed full-probability mating models based on naturally established seedlings (see also Burczyk *et al.* 2006; Goto *et al.* 2006; Oddou-Muratorio & Klein 2008; Moran & Clark 2011). Briefly, these approaches rely on a spatially explicit mating model where each seedling can generally originate either (i) from a mother tree located outside the study site (implying seed immigration) or (ii) from a mother tree located within the study site . The latter case includes three possible origins of the fertilizing pollen: (i) pollen immigration, (ii) selfing, or (iii) pollination by a male tree located within the study site.

Originally, the principal purpose of full-probability mating models is to estimate patterns of male and female fecundities together with the pollen and seed dispersal kernels and mating system parameters (see Appendix S1 in Supporting Information). In this context, the approach bypasses parentage assignation and focuses instead on the fractional contribution of all adults, either as female or as male parent, to each seedling. For instance, the probability π_{Sij} of each sampled female tree j to contribute to the seedling pool at the spatial location of seedling i is typically modelled as:

$$\pi_{S\,ij} = \frac{F_{Fj}\theta_s\left(d_{ij}\right)}{\sum\limits_{l:mother} F_{Fl}\theta_s\left(d_{il}\right)} \quad (1)$$

where F_{Fj} and F_{Fl} are the female fecundities of mother j and l, respectively; d_{ij} and d_{il} are the distances between seedling i and mother j and l, respectively; and θ_s is the seed dispersal kernel. In hermaphroditic species such as oaks, each focal reproductive individual l is considered as a male with male fertility F_{Ml} and a female with female fertility F_{Fl}. When considering a couple of parents, the closest one is not automatically assumed to be the mother, but the prior distributions are usually chosen to indicate that seed dispersal is likely to be more limited than pollen dispersal.

Here, we used a two-step procedure where the first step corresponded to the original purpose of MEMMseedlings (i.e., estimating all fertility and dispersal parameters). We accounted for genotyping errors at this stage by assuming an error rate of 0.001 for SNP and 0.02 for SSR loci and allowing up to two mismatches between parent and offspring genotypes (see Appendix S1 for details). The second step consisted in categorical parentage assignment based on the posterior probability π'_{ij} of each tree j within the stand to be the mother of a given particular seedling i with genotype g_i, and the posterior probability $P_{mig,i}$ that this seedling i originates from seed migration. For this aim, we exploited the Monte Carlo Markov Chain (MCMC) that provides the posterior distribution for the dispersal parameters in MEMMseedlings. At each step t of the chain, we computed a posterior probability for each event:

$$\pi'^{(t)}{}_{Sij} = \left(1-m_S^{(t)}\right)\frac{F^{(t)}{}_{Fj}\theta^{(t)}{}_s\left(d_{ij}\right)}{\sum\limits_{l:mother} F^{(t)}{}_{Fl}\theta^{(t)}{}_s\left(d_{il}\right)}\left[m_P^{(t)}T_2\left(g_i \middle| g_j, BAF\right) + (1-m_P^{(t)})\sum_{k:father}\frac{F^{(t)}{}_{Mk}\theta^{(t)}{}_p\left(d_{jk}\right)}{\sum\limits_{f:father} F^{(t)}{}_{Mf}\theta^{(t)}{}_p\left(d_{jf}\right)}T_3\left(g_i \middle| g_j, g_k\right)\right] \Big/ L\left(g_i \middle| param^{(t)}\right),$$

$$P^{(t)}{}_{mig,i} = m_S^{(t)}T_4\left(g_i \middle| BAF\right) \Big/ L\left(g_i \middle| param^{(t)}\right)$$

where exponent *(t)* indicates that at each time step t, the current values of the chain are used for the parameters and fecundities. $F_{Mk}{}^{(t)}$ and $F_{Mf}{}^{(t)}$ are the male fecundities of father k and f, respectively; d_{jk} and d_{jf} are the distances between mother j and father k and f, respectively; and $\theta_p{}^{(t)}$ is the pollen dispersal kernel. T_2, T_3 and T_4 are the Mendelian transition probabilities computed from the genotypes and $L(g_i|param)$ is the probability of observing a seedlings with genotype g_i given the model and its parameters (see eq. 1 in Appendix S1). Finally, the posterior probabilities π'_{sij} and P_{mig} were computed at the end of the chain by averaging the intermediate values obtained all along the chain:

$$\pi'_{Sij} = \frac{1}{\tau}\sum_{t=1\ldots\tau}\pi'^{(t)}{}_{Sij} \quad \text{and} \quad P_{mig} = \frac{1}{\tau}\sum_{t=1\ldots\tau}P^{(t)}{}_{mig}$$

where τ is the number of steps of the chain. We ran 10 MCMC chains of 10,500 steps each, with the 500 first MCMC steps as burn-in. The posterior probabilities $\{\pi'_{sij}\}$ and $\{P_{mig,i}\}$ were averaged across the 10 MCMC chains, and this information was then used to assign each sampled seedling categorically to its most likely mother tree, *i.e.* either the individual with the highest π'_{Sij}, or a non-sampled mother-tree if $P_{mig,i} > \pi'_{Sij}$.

Results of the parentage analysis were combined with the mapping data and specific notes taken in the field to infer whether a given seedling had emerged beneath the canopy of its mother tree or whether it had actually been transported away from the tree by some biotic dispersal agent. In the following, we will refer to the first case as 'failed' and to the second as 'successful' dispersal.

Statistical analyses

Maternal reproductive success - To assess the inequality of maternal reproductive output, we summed all seedlings assigned to a given mother tree and used this measure as a proxy for its fecundity. We then assessed the fit of the resulting frequency distribution to the Poisson and negative binomial distributions using a χ^2 test, and to the lognormal distribution using the Anderson-Darling normality test for log-transformed values. The empirical distributions from the first survey (seedling emergence) and the second survey (age 3 years) were compared with a two-samples Kolmogorov-Smirnov test.

We also assessed to what extent seedling mortality changed the ranking of individual mother trees within the overall distribution of seedling production. For this purpose, we first calculated Kendall's τ between individual tree ranks in the first and in the second survey. Then we tested whether trees' tendency to climb up or fall back in the fertility ranking was related with their dispersal success. We performed this test by grouping trees with dispersal success above the stand average *versus* those with dispersal success below average and comparing their respective tendency in the fertility ranking with a χ^2 test.

Dispersal - We plotted the empirical distribution of effective seed dispersal distances for seedlings at emergence and at age 3 years based on the observed distance between successfully assigned seedlings and their inferred mother trees. For this aim, we fitted a nonparametric smoothing spline to the empirical distance distribution and to bootstrapped estimates (n = 100 randomisations). Note that the distribution only integrates local dispersal as immigration events are not considered. We compared the two dispersal distance distributions with a Kolmogorov-Smirnov test for discrete samples to assess possible mortality related changes in patterns of effective dispersal.

Determinants of seedling survival – We first assessed relationships between tree fertility and offspring survival by an analysis of density dependence. For this purpose, we fitted a generalized linear model with binomial errors and a logit link function with the number of seedlings per mother tree at the time of emergence as predictor and the number of seedlings at age 3 as response variable. Relationships of the form Y *vs.* X+Y (here: surviving *vs.* total seedling number) are commonly subject to spurious correlations and tend to produce inflated *r*-values. Therefore we calculated significance levels from bootstrapped estimates after 10,000 resamplings, as suggested by Brett (2004). A second analysis explored whether the fertility of mother trees was related with their success in dispersing acorns away from their canopy. This was done using an analysis of density dependence as described above with the total number of seedlings of a given mother tree as predictor variable and the number of successfully dispersed seedlings as response variable.

Finally, we fitted two generalised linear mixed models with individual seedling survival as a binomially distributed response variable to assess the joint relevance of different source and path effects for the probability of seedling establishment. The first model included all seedlings and considered the effect of dispersal success (coded as a binary variable with the classes successful *vs.* failed dispersal). The second model included only the actually dispersed seedlings and considered the following predictor variables: (1) mother tree fertility (to test for the existence of seed number-quality trade-offs); (2) dispersal distance (to assess density or distance-dependence of mortality) and; (3) habitat of arrival (to examine the role of propagule dispersal to suitable establishment sites). All variables were treated as fixed factors. We also included an interaction term for the two path effects (2 and 3). Tree identity entered both models as an error term. We used a type II ANOVA approach (Wald χ^2 test) to ensure that significance testing was unaffected by the order in which variables entered the model. This and all other analyses were performed in R version 3.3.0 (R Development Core Team 2016) using the packages fitdistrplus, bootstrap, and lme4.

RESULTS

We could identify the mother tree for 653 of our 809 seedlings (81%). We removed 9 seedlings that could not unequivocally be identified during the second survey and retained a total of 644 individuals for the subsequent analyses (Table 1). A total of 359 (56% of the retained seedlings) emerged away from the canopy of their mother trees. A total of 202 seedlings (31%) survived until the second field survey. This sample was extensive enough to robustly estimate the frequency distributions of individual tree seedling production and the associated (stand-level) seedling dispersal curves.

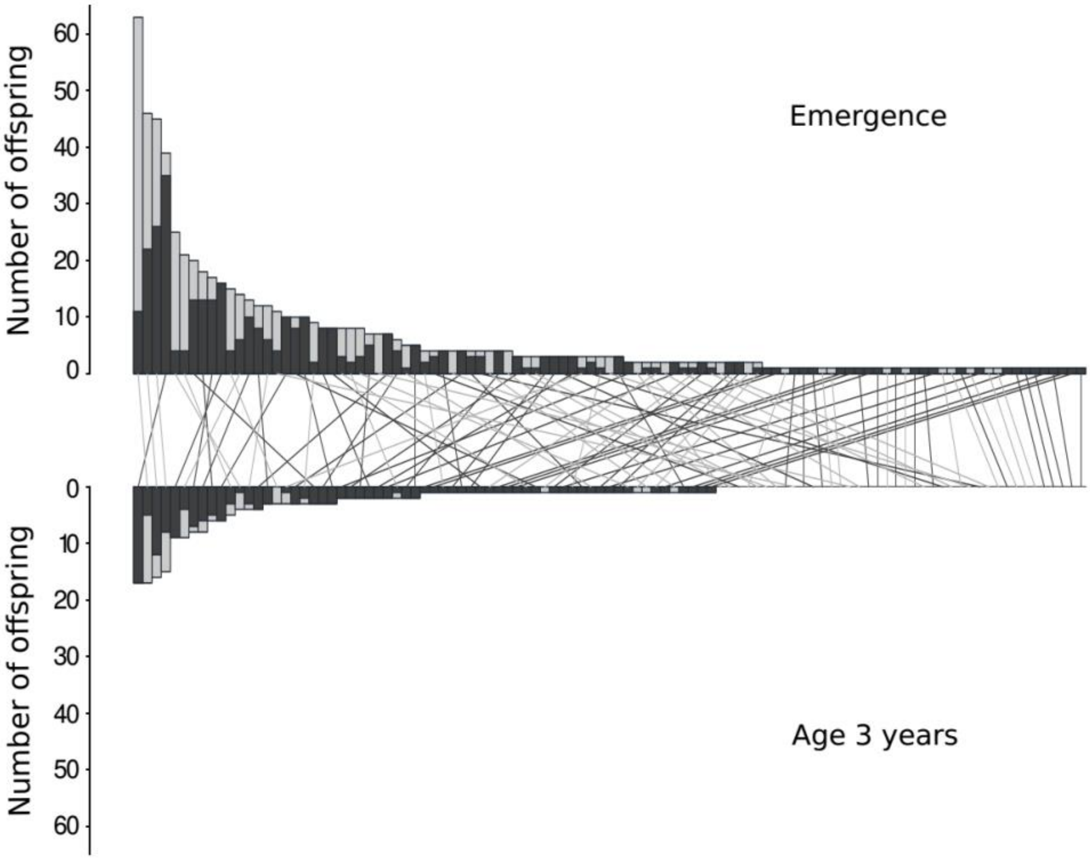

Figure 2. Seedling production by individual *Quercus robur* mother trees at the moment of seedling emergence (above) and at age 3 years (below). Each column corresponds to a reproducing tree. Black bars indicate seedlings that have been dispersed away from the tree and greay bars those that have failed to be dispersed and emerged beneath its canopy. Lines between the two histograms connect the same mother tree, showing shifts in its ranking of fecundity. Black lines indicate trees with seedling dispersal success above stand average and grey lines those with dispersal success below average.

Maternal reproductive success – A total of 103 trees (41%) mothered at least one seedling at emergence (Fig. 2). Only 63 trees (25%) contributed at least one seedling that survived until an age of 3 years. The distribution of individual seedling production was highly skewed (Fig. 3) but followed none of the tested distributions

(Poisson, negative binomial and lognormal: $P < 0.001$ for all tests). The lognormal distribution came closest to the empirical one except for being less steep at the extremes (Fig. 3). The empirical distributions at the time of seedling emergence and at age 3 years did not differ (Kolmogorov-Smirnov: $D = 0.18$, $P = 0.18$).

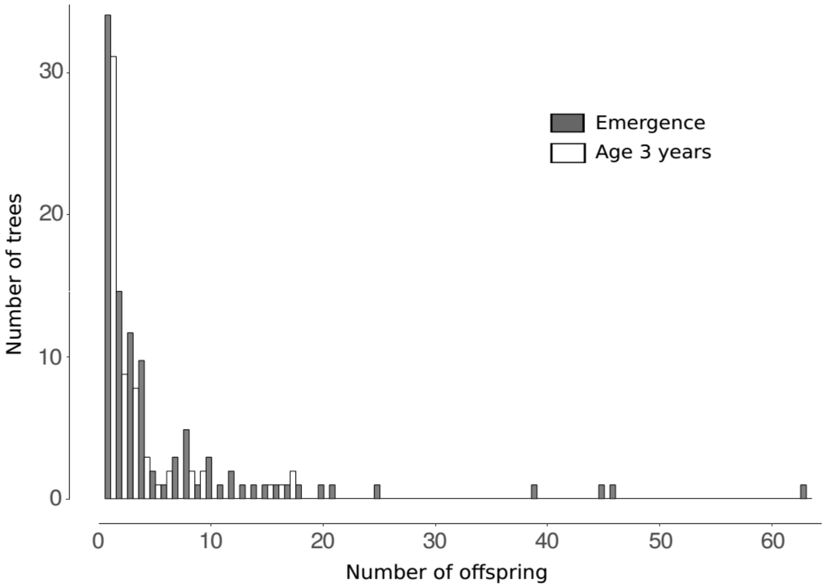

Figure 3. Distribution of seedling production by individual *Quercus robur* mother trees at the time of seedling emergence (empty columns) and at age 3 years (filled columns).

We observed considerable reshuffling in the ranking of individual trees between the original distribution and that observed at the second survey (Fig. 2; Kendall $\tau = 0.61$). Those trees that had successfully dispersed a high proportion of their offspring tended to climb up in the ranking whereas those that had failed to disperse many of their offspring fell back ($\chi^2 = 13.1$, d.f. = 2, $P < 0.01$).

Dispersal - The shape of the dispersal distance distributions at seedling emergence was leptokurtic with the median and the 95th percentile dispersal distances being 8.9 m and 89.9 m, respectively (Fig. 4). At age 3, the median and the 95th percentile dispersal distances were 18.1 m and 114.9 m, respectively (Fig. 4). The principal change through the study period concerned the shortest distance class (i.e., the seedlings resulting from failed dispersal) that lost numerous individuals (Fig. 4). Accordingly, the dispersal distance distributions differed between the original and the final seedling survey when all seedlings were considered (Kolmogorov-Smirnov: D = 0.22, $P < 0.001$) but remained unaltered when the non-dispersed seedlings were discarded (D = 0.10, P = 0.26).

Determinants of seedling survival – Our analysis of density dependence indicated that more fertile trees tended to lose more offspring over the study period: The slope of 0.72 (bootstrapped first and third quartile: 0.68 and 0.75) was significantly smaller than 1 ($P < 0.0001$ according to randomisation with 10,000 resamplings). We also found that more fertile trees suffered higher dispersal failure, as the slope of the corresponding analysis of density dependence was 0.80 (bootstrapped first and third quartile: 0.76 and 0.84), significantly smaller than 1 ($P < 0.0001$ according to randomisation).

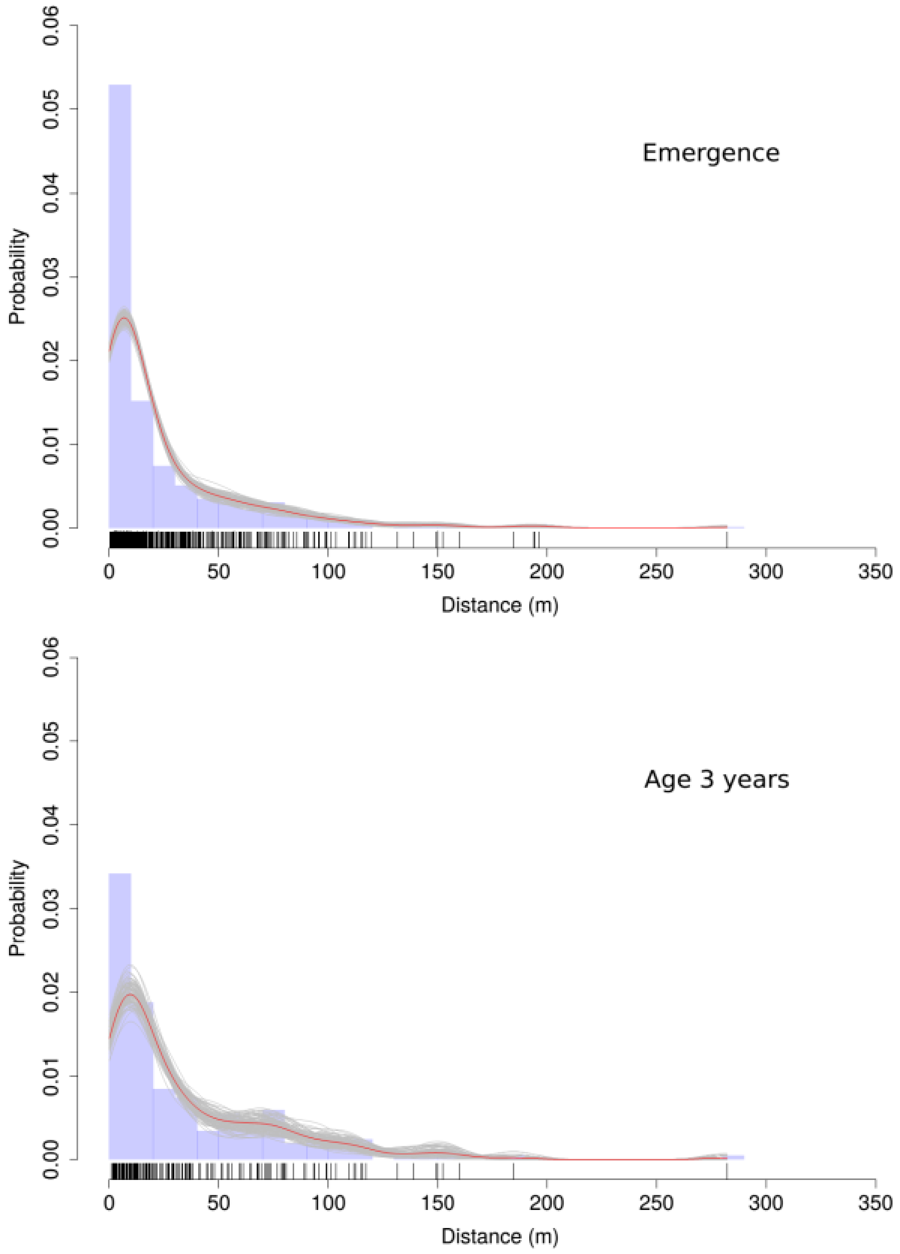

Figure 4. Frequency distributions of *Quercus robur* seedling dispersal distances at the time of seedling emergence (above) and age 3 years (below), estimated via parentage analysis. The line indicates the nonparametric smoothing spline fit to the empirical distance distribution together with bootstrapped estimates (n = 100 randomisations). Individual dispersal events are indicated by vertical lines under the plot.

Seedlings dispersed away from their mother tree had significantly higher survival chances than non-dispersed seedlings (43% vs. 17%; $\chi^2 = 41.7$; d.f. = 1; $P < 0.001$). When considering only dispersed seedlings, we found that their survival was unrelated with mother tree fertility and dispersal distance but clearly related with the habitat of arrival (Table 2). Survival was markedly lower in broadleaved forest than in non-forested areas or pine plantations (proportions for successfully dispersed seedlings: 21%, 48% and 57%, respectively).

Variable	χ^2	d.f.	*P*
Mother tree fecundity	0.47	1	0.49
Dispersal distance	2.13	1	0.14
Habitat of arrival	16.39	2	0.0003
Habitat of arrival : Dispersal distance	5.60	2	0.06

Table 2. Effects of mother tree fecundity, dispersal distance and habitat of arrival on survival of the successfully dispersed *Quercus robur* seedlings according to a generalised linear mixed model (type II ANOVA, Wald χ^2 test). *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ns, $P > 0.05$.

DISCUSSION

Reproductive inequality in a context of demographic expansion

We observed a highly unequal distribution of seedling production with a handful of trees contributing disproportionately many offspring and the majority of trees contributing few or none at all. The skew we observed is, however, considerably weaker than others reported from ongoing tree population expansions. For instance, one of four founder trees in a recently installed leading-edge *Quercus ilex* population mothered or fathered 28 of the 33 established second-generation offspring (Hampe *et al.* 2013). Similarly, two old-growth *Iriartea deltoidea* palms produced 48% of all recruits in a plot undergoing secondary succession while 41 of the remaining 53 parent trees each contributed 1% or less (Sezen *et al.* 2007). And the three most fertile mother trees in two recently established *Gleditsia triacanthos* populations produced 46% and 58%, respectively, of the sampled seedlings (Schnabel *et al.* 1998). The less pronounced skew that we observed is most easily explained by the fact that our study stand is already at a more advanced stage of establishment and hence counts with a considerably larger effective population size. Compared to these results, the distribution of seedling production that we observed resembles rather that reported by Moran & Clark (2012) from two second-growth oak stands, which are already older, larger and show an even less skewed distribution.

Two biological mechanisms could contribute to rapidly levelling out strong initial inequality of reproductive success in colonising tree populations. First, the outcrossing mating system of trees and their susceptibility to inbreeding depression could favour the establishment of immigrants over that of local offspring (Hampe *et al.* 2013). Second, the main dispersers of oak acorns in our area could further contribute to rapidly levelling out an initially strong skew in reproductive output. Jays are known to be highly mobile scatter-hoarders that gather several thousand acorns in a single fruiting season and often carry them over long distances (Pesendorfer *et al.* 2016). Hence they could rapidly enlarge the suite of trees they forage on as more individuals reach maturity through the expansion process. Our failure to assign 19% of the sampled seedlings to a local mother tree actually indicates regular arrival of acorns from trees located outside the study area (see also Gerber *et al.* 2014). Frequent immigration of recruits should help minimize founder effects and genetic drift in our forest stand (Petit *et al.* 2004; see also Moran & Clark 2012).

Trends in reproductive inequality during early recruitment

The initial skew in seedling production did not change through the three-year monitoring period despite an overall seedling mortality of 69%. However, highly fertile trees tended to experience disproportionately high rates of dispersal failure and non-dispersed seedlings showed markedly higher mortality than dispersed ones (83% vs. 57%). This combined evidence indicates that elevated dispersal failure of fertile trees, presumably caused by the satiation of their primary seed dispersers

(Hampe 2008), will homogenise individual reproductive success in the longer term. Finally, the emergence of numerous seedlings beneath their mother trees also indicates that highly fertile trees satiated their acorn predators. This effect might favour the survival of the tree's dispersed seedlings, yet its consequences for the distribution of individual reproductive success is likely to be very minor.

Our comparison of the individual rankings in tree reproductive success (see Fig. 3) revealed a phenomenon that has hitherto received very little attention. We detected considerable (Kendall $\tau = 0.61$) reshuffling that was related with mother trees' success in dispersing their offspring. This observation has potentially important ecological and micro-evolutionary implications: If the probability of acorn dispersal and resulting recruit survival is independent of the mother tree's phenotype then the reshuffling of tree fertility should occur at random. If dispersal success is, however, linked with mother trees' phenotype then the observed reshuffling would directly reflect a process of micro-evolutionary selection that remains completely undetected when only the overall distribution of reproductive success is regarded. Such selection might actually be under way in our system as phenotypic traits such as acorn size and form have been shown to influence the choice of acorn-foraging jays (Bossema 1979; Pons & Pausas 2007; Morán-Lỏpez *et al.* 2015). Moreover, acorn size is known to have direct and significant effects on individual seedling fitness at several stages of early recruitment (Gỏmez 2004). If phenotypic selection is indeed occurring in our study system then its micro-evolutionary effects should be significantly amplified by the forest stand's demographic and spatial expansion (Excoffier *et al.* 2009). In turn, the success of some phenotypes could further increase the long-term growth rate of the oak population, because the average survival rate of cohorts increases with the age of recruits, a phenomenon termed 'cohort selection' (Kendall *et al.* 2011). Note that this cohort selection effect on the population growth rate complements, but is distinct from, possible effects of inequality in fertility itself (Kendall *et al.* 2011).

Ecological drivers of changes in reproductive inequality

As previously outlined, mother tree fertility influenced seedling survival through its effect on disperser satiation and resulting dispersal failure. We also tested the relevance of one further source effect (seed number-quality tradeoffs) and two path effects (distance-dependent and habitat-related seedling performance) on recruit survival. We found that, after discounting the effect of disperser satiation, tree fertility had no more effect on seedling survival. Hence, seed number-quality tradeoffs appear to play no role in our study system. This would be in line with Koenig *et al.* (2009) who found that acorn size of *Quercus lobata* trees was higher in years of large acorn crops. Acorn size typically is a reliable predictor of seedling performance in oaks (Gȯmez 2004 and references therein).

Our failure to detect an effect of dispersal distance on seedling survival indicates that density or distance-dependent mortality similarly plays a negligible role for seedling establishment once individuals have dispersed away from their mother tree. This finding contradicts Venable's (1992) hypothesis that density dependence may lead to diminishing returns in offspring number for increasing levels of seed production. Our result is not really surprising given the low overall density of dispersed seedlings (but see González-Martínez *et al.* 2006). It is, however, likely to be characteristic of expanding plant populations and represents scarce observational evidence in line with the notion that seed dispersal limitation is the overarching constraint for many tree range expansions (Hampe 2011). This study thus supports the importance of incorporating seed dispersal kernels in models of tree population spread and species range dynamics (e.g. Lischke *et al.* 2006; Engler & Guisan 2009; Nathan *et al.* 2011).

On the contrary, we found clear evidence that the movement of recruits away from broadleaved forest into open areas or pine plantations significantly improved their establishment probability. The strength of this effect counteracts eventual intrinsic effects that mother trees might exert on the establishment success of their offspring (as described above). Previous studies have reported that jays tend to store acorns preferentially in habitats where they are likely to persist undamaged until the bird recovers them (e.g. Bossema 1979; Mosandl & Kleinert 1998; Gȯmez 2003; see also Purves *et al.* 2007). Such areas usually contain sparse understory vegetation and hence provide little shelter to acorn predators such as rodents. It has more rarely been systematically documented (but see e.g. Puerta-Piñero *et al.* 2007) that storing acorns in such habitats favours not only the scatter-hoarding jays themselves but also subsequent seedling recruitment. Our finding hence complements current knowledge on the ecological implications of the interaction between oaks and acorn-foraging jays. Overall, jay behaviour should be critical for the chances of recruiting oak plants to become “lucky” individuals (Snyder & Ellner 2016) that can significantly contribute to the future expansion process of their population. The possible long-term effects of acorn dispersal patterns were highlighted by Hampe *et al.* (2010) who showed, for the same oak stand, that the spatial genetic structure of the adult tree population was remarkably similar to that of the successfully dispersed seedling cohort.

Inequality of reproductive success in a context of widespread tree population expansions

Even though insights from our study are constrained by the fact that they rely on a single seedling cohort (Clark *et al.* 2004), our findings have important implications for the ecological and micro-evolutionary dynamics of expanding tree populations. Non-equilibrium vegetation dynamics are now becoming pervasive as a consequence of rapid environmental change (Svenning & Sandel 2013), and tree populations are particularly susceptible to this phenomenon owing to their long generation time (Petit & Hampe 2006; Nathan *et al.* 2011). Clark *et al.* (2001) showed that variation in reproductive success due to stochastic mortality can lower asymptotic spread rates by an order of magnitude relative to estimates based on mean reproductive success. Variation in reproductive success due to skewed fertility is likely to have a similar effect, because most individuals contribute little to the next generation (Moran & Clark 2012). This effect should be exacerbated in small and isolated populations at the leading edge of range expansions (Petit *et al.* 2004; Lesser & Jackson 2013; Hampe *et al.* 2013), eventually leading to micro-evolutionary adaptation for increased investment in seed production (Siemann & Rogers 2001) or seed dispersal ability (Cwynar & MacDonald 1987; Hampe & Bairlein 2000). While such situations may well arise following strong bottlenecks, our study also suggests that the extreme reproductive inequality typical of founder events might rapidly weaken as more individuals start to reproduce. Finally, various lines of evidence indicate that ongoing climate change is profoundly modifying patterns of tree growth, seed production, dispersal and recruitment (Hampe 2011). Although models are beginning to capture the complexity of these processes (Lischke *et al.* 2006; Nathan *et al.* 2011), much remains to be discovered for achieving a better, empirically informed, mechanistic understanding of how future global changes will drive local to continental-scale expansion processes in trees.

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SUPPORTING INFORMATION

Appendix : Detailed description of the parentage analysis with MEMMseedlings.

Chapter 3:

Recruitment of a genotyped Pedunculate oak (*Quercus robur*) seedling cohort: diversity, dispersal and performance across habitats

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ABSTRACT

Seed dispersal exerts a strong influence on patterns of recruitment in naturally regenerating plant populations as it determines the sites where plants establish. Very few studies have investigated how seed dispersal influences the dynamics of entire cohorts of recruiting plants, their genetic diversity and parental contributions during the recruitment process. We combined an extensive genotyping of a Pedunculate oak (*Quercus robur*) seedling cohort with a detailed monitoring of the genotyped seedlings that assessed their performance until an age of 3 years as a function of their habitat (broadleaved forest, pine plantations or treeless open areas). The mother trees of seedlings were identified through Bayesian parentage analysis. We found that levels of genetic diversity were remarkably invariable between seedlings with a local mother tree and putative immigrants as well as among the seedlings delivered to different habitats. Disproportionately many seedlings were dispersed to broadleaved forest whereas pine plantations received disproportionately few individuals. In turn, seedlings in pine plantations had travelled over the longest distances and stemmed from the largest relative number of mother trees. Seedling performance was markedly lower in broadleaved forest than in pine plantations or open areas. As a consequence, individual mother trees that had dispersed many of their descendants to broadleaved forest suffered a disproportionately strong reduction of their reproductive success. Notwithstanding, even an elevated seedling mortality (overall 69% during the 3-year monitoring period) did not generate any noteworthy change in the genetic diversity of the overall seedling cohort or its different subgroups. Overall, our results represent the first empirical evidence that the quality of seed dispersal, in terms of seed delivery to favourable establishment sites, can notably influence the reproductive success of individual mother trees. The observed lack of effects of recruit mortality on the cohort's genetic diversity suggests in turn that, in our study context, the establishment success of seedlings probably has a negligible genetic component but is an entirely environment-driven phenomenon.

INTRODUCTION

Seed dispersal creates the initial template of regeneration and is widely accepted to have a profound influence on the spatial, demographic and genetic structure of plant populations because of its cascading effects on subsequent recruitment processes (Harper 1977; Jordano & Godoy 2002; Wang & Smith 2002). A vast number of studies have assessed patterns of seed dispersal and plant recruitment over the last decades with the purpose to accurately predict regeneration outcomes, a key information for the management and conservation of plant populations and communities (Clark *et al.* 1999; Schupp *et al.* 2010; McConkey *et al.* 2012; Robledo-Arnuncio *et al.* 2014). However, despite the wealth of empirical evidence accumulated, we are still far away from a proper understanding of how spatio-temporal patterns of seed dispersal translate into the dynamics and genetics of plant populations, especially in long-lived species such as trees.

One major research gap consists in the fact that extremely few studies have achieved to link the origin of dispersed seeds with their post-dispersal fate. Demographic field studies have monitored recruiting plants and performed experiments to infer the causes of their establishment success or failure, but they have only very rarely been able to track their sources (but see Wenny 2000). In turn, molecular ecological studies have inferred the parents of dispersed recruits but lacked detailed demographic information for the genotyped descendants (but see Gerzabek *et al.* 2017). The scarcity of empirical studies that tightly integrate demographic and molecular research approaches strongly constrains our understanding of how the recruitment success of individual offspring translates into patterns of fertility and ultimately the fitness of reproducing trees. It also hampers detailed insights into the ecological driving forces that shape the genetic structure and diversity of entire plant cohorts through the recruitment process (but see e.g. González-Martínez *et al.* 2006; Jacquemin *et al.* 2007; Hampe *et al.* 2010; Oddou-Muratorio *et al.* 2011; Moran & Clark 2012).

Seed dispersal and early recruitment typically are strongly influenced by the landscape context (Jordano & Godoy 2002). Dispersal vectors tend to move seeds nonrandomly, generating highly heterogeneous landscape-scale patterns of seed abundance (Gómez 2003; Levey *et al.* 2005; Damschen *et al.* 2014). In turn, the seedling stage is the most vulnerable stage of the plant life cycle and characterised by extensive mortality (Petit & Hampe 2006), with early establishment success largely depending on the small-scale environment that surrounds the seedling (Schupp *et al.* 2010). Suitable sites for plant establishment typically are distributed very unequally across the landscape, and they are often not identical with the most suited sites for seed arrival (Schupp & Fuentes 1995). As a consequence, different habitats can receive very different subsets of the overall offspring pool, and these subsets can further change during the early recruitment process. A detailed knowledge of such changes would represent an important step ahead for properly understanding how patterns of seed dispersal translate into the dynamics and genetics of plant populations.

Here, we quantify to which extent the composition, genetic diversity, spatial distribution and paternal contribution to a cohort of dispersed Pedunculate oak (*Quercus robur*) seedlings is transformed during the early recruitment process. For this purpose, we combined an extensive genotyping of the cohort with a detailed monitoring of the genotyped seedlings until an age of 3 years. The genetic data enabled us to infer the source trees of seedlings - or their putative immigration from outside the stand - by means of Bayesian parentage analysis, while the demographic data informed us about patterns of habitat-related post-dispersal survival and growth. Based on the combined genetic and demographic evidence, we addressed the following research questions: i) Do genetic diversity, parental contributions and spatial distributions differ among habitats? ii) Does recruit performance differ across habitats? iii) Does differential seedling mortality transform levels of genetic diversity? iv) Which consequences do observed trends have for the reproductive success of individual mother trees? Contrary to previous studies on similar topics (e.g. Chybicki & Burczyk 2010; Oddou-Muratorio *et al.* 2011; Milleron *et al.* 2013; Vranckx *et al.* 2014), we chose to explicitly identify actually dispersed recruits and to focus primarily on them, because non-dispersed offspring recruiting beneath the mother plant is most often assumed to suffer virtually ineludible mortality and hence to be irrelevant for regeneration (Howe & Miriti 2004).

MATERIAL AND METHODS

Study system

The study was performed in the Forêt de Nezer (44°34' N, 1°00' W) ca. 50 km SW of Bordeaux, SW France. The area is covered by extensive plantations of maritime pine (*Pinus pinaster* Ait.) interspersed with small stands of broadleaved forests dominated by Pedunculate oak (*Quercus robur* L.) or, more rarely, Pyrenean oak (*Q. pyrenaica* Willd.). Such stands are largely exempt from forest management. Many are actively expanding, favoured by a recent change in silvicultural management that tends to conserve oaks recruiting within adjacent pine plantations as a means of biological pest management (Dulaurent *et al.* 2012). Acorn dispersal in the area is performed by the common jay (*Garrulus glandarius* L.) as well as by rodents (with wood mice, *Apodemus sylvaticus* L., bank voles, *Myodes glareolus* Schreiber, and European squirrels, *Sciurus europaeus* L. being present in the area) (Hampe *et al.* 2010). We selected a mixed oak forest stand with ca. 280 adult Pedunculate and Pyrenean oaks (90% *Q. robur*, 10% *Q. pyrenaica*) for this study. The spatial and age structure of the stand clearly indicated that it currently is undergoing an expansion. The nearest oak forest stand (smaller than the investigated one) is approximately 1 km away.

Field sampling and laboratory analyses

In early spring 2006, we delimited a study plot of 6 ha enclosing the oak forest stand and surveyed all adult Pedunculate oak trees within this area and an adjacent belt of 100 m width (n = 254). Trees were identified as adults based on their size and on fruit set observations performed during two ripening seasons. Each tree was individually tagged and mapped to the nearest 0.1 m using laser telemetry and several buds were collected and stored at -80° C for later DNA isolation.

During late April and early May 2006, we performed a comprehensive survey of newly emerged Pedunculate oak seedlings (i.e., those stemming from the 2005 fruiting episode) in our 6 ha study plot. We sampled all seedlings emerging more than 2 m away from the crown projection of any adult oaks, searching every part of the study plot at least twice and up to six times. Furthermore, we sampled 20% of all seedlings emerging beneath adult oaks (i.e., up to 2 m beyond the canopy projection to account for potential short-distance dispersal of acorns by wind or bouncing off of branches). These 20% were sampled using a strict randomization protocol (see Hampe *et al.* 2010). We estimate that the resulting sample (*n* = 809 individuals) includes 25-30 % of the overall seedling cohort within the study plot. Importantly, our hierarchical sampling design is unbiased concerning the present study because all areas situated beneath oak tree canopies were sampled with the same intensity, resulting in a representative sample of seedlings. All seedlings were individually tagged and mapped, and one leaf was collected and stored at -80°C until DNA isolation. Each seedling was assigned to one of three major habitat types: (i) broadleaved forest (including silver birch [*Betula pendula*] and willows [*Salix* spp.] besides the two oak species), (ii) pine plantations and (iii) open areas without a tree layer. Seedlings were monitored twice a year until September 2008, their status (living or dead) was recorded, and their height and number of leaves was measured. This study only considers data from the first survey (that is, at seedling emergence) and the last survey (that is, at an age of 3 years). Some seedlings could not be unequivocally identified through the last survey and were therefore removed from all further analyses.

Trees and seedlings were genotyped using eight nuclear microsatellite (SSR) markers (QrZAG11, QrZAG96, QrZAG112, QpZAG110, QrZAG5b, QrZAG7, QrZAG20, and QrZAG87) following the protocol of Lepais *et al.* (2006); the analysis has been described in detail in Hampe *et al.* (2010). In addition, we genotyped all individuals at 39 SNP loci (for details see Dryad data repository: doi:10.5061/dryad.3j33t). The loci were combined into a multiplex and sequenced on an iPLEX Gold genotyping kit (Sequenom) at the Genomic and Sequencing Facility of Bordeaux (France) following the procedure described in Chancerel *et al.* (2013). We obtained readily usable data for 33 SNPs that we merged with the SSR data to obtain individual tree and seedling multilocus genotypes for the parentage analysis. The overall set of markers provided an exclusion power of 0.9998 for single parents and of 0.99997 for parent pairs.

Parentage analysis

Seedlings were categorically assigned to their mother tree based on their multilocus genotypes and geographical coordinates using the Bayesian approach

MEMMseedlings (Oddou-Muratorio *et al.*, ms under review). Unlike many other parentage assignment procedures (but see Moran & Clark 2011), our approach jointly considers genotypes and distances to infer parentage and allows us to distinguish between the mother and the father tree of a given seedling, which is highly relevant information for our study purpose. MEMMseedlings is a recently developed full-probability mating model based on naturally established seedlings (for similar approaches see Burczyk *et al.* 2006; Goto *et al.* 2006; Oddou-Muratorio & Klein 2008; Moran & Clark 2011). Briefly, it relies on a spatially explicit mating model where each seedling can generally originate either (i) from a mother tree located outside the study site (implying seed immigration) or (ii) from a mother tree located within the study site. The latter case includes three possible origins of the fertilizing pollen: (i) pollen immigration, (ii) selfing, or (iii) pollination by a male tree located within the study site.

Originally, the principal purpose of full-probability mating models is to estimate patterns of male and female fecundities together with the pollen and seed dispersal kernels and mating system parameters. In this context, the approach bypasses parentage assignment and focuses instead on the fractional contribution of all adults, either as female or as male parent, to each seedling. Here, we used a two-step procedure (described in detail by Gerzabek *et al.* 2017) where the first step corresponded to the original purpose of MEMMseedlings (i.e., estimating all fertility and dispersal parameters). We accounted for genotyping errors at this stage by assuming an error rate of 0.001 for SNP and 0.02 for SSR loci and by allowing up to two mismatches between parent and offspring genotypes. The second step consisted in a categorical parentage assignment based on the posterior probability π'_{ij} of each tree *j* within the stand to be the mother of a given particular seedling *i* with genotype g_i, and the posterior probability $P_{mig,i}$ that this seedling *i* originates from seed migration. For this aim, we exploited the Monte Carlo Markov Chain (MCMC) that provides the posterior distribution for the dispersal parameters in MEMMseedlings. The posterior probabilities π'_{sij} and P_{mig} were computed at the end of the chain by averaging the intermediate values obtained all along the chain.

We ran 10 MCMC chains of 10,500 steps each, with the 500 first MCMC steps as burn-in. The posterior probabilities $\{\pi'_{sij}\}$ and $\{P_{mig,i}\}$ were averaged across the 10 MCMC chains, and this information was then used to assign each sampled seedling categorically to its most likely mother tree, *i.e.* either the individual with the highest $\pi\text{'s}_{ij}$, or a non-sampled mother-tree if $P_{\mathrm{mig},i} > \pi\text{'s}_{ij}$.

Results of the parentage analysis were combined with the mapping data and specific notes taken in the field to infer whether a given seedling had emerged beneath the canopy of its mother tree or whether it had actually been transported away from the tree by some biotic dispersal agent. In the following, we will refer to the first case as 'failed' and to the second as 'successful' dispersal. Finally, we summed all seedlings assigned to a given mother tree and used this measure as a proxy for its fecundity.

Statistical analyses

Creation of cohort subsets – Several of our analyses compared different groups of seedlings. For these comparative analyses, we divided the overall seedling cohort in different subsets based on three different criteria: (1) the origin of seedlings according to the parentage assignment ('local' vs 'immigrants'); (2) the dispersal status ('successful dispersal' vs 'failed dispersal'); and (3) the habitat of arrival ('broadleaved forest' vs 'pine plantation' vs 'open area'). In addition, our repeated survey enabled us to compare seedlings at two points in time ('emergence' vs 'age 3 years'). Sample sizes for each of these different subsets are shown in Table 1.

Genetic diversity - For each seedling group, we calculated gene diversity (H_E) and the inbreeding coefficient (F_{IS}) per locus using FSTAT version 2.9.3 (Goudet 2001). Differences of F_{IS} from zero were tested computing confidence intervals by means of 5,000 bootstraps within populations. Differences between different groups were then tested using Wilcoxon matched pairs signed ranks tests, because the nature of the data rendered the use of parametric tests impossible.

Dispersal distance - We plotted the empirical distribution of effective seedling dispersal distances based on the observed distances between successfully assigned seedlings and their inferred mother trees. For this aim, we fitted a nonparametric smoothing spline to the empirical distance distribution and to bootstrapped estimates (n = 100 randomisations). Note that the distribution only integrates local dispersal because immigration events are not considered. We then compared the dispersal distances of seedlings established in different habitats (for the first survey) with a one-way ANOVA. Finally, we tested for possible density or distance-dependent mortality during early seedling recruitment by comparing the dispersal distance distributions to each habitat at seedling emergence and at age 3 years with a Kolmogorov-Smirnov test for discrete samples.

Seedling performance – We used two variables to estimate seedling performance during early recruitment: (1) survival until the second survey, and (2) a composite seedling growth index that integrates the total height and the number of leaves at age 3 years. We constructed this growth index by means of a PCA after checking that both underlying variables were positively correlated (Pearson $r = 0.65$; $t = 24.4$, df = 804, $P < 0.001$). We used the first component of the PCA (which explained 89.2% of the overall variance) as our growth index.

Partly high mortality rates led us to pool seedlings of local and of putatively immigrant origin in order to increase the robustness of the following analyses. Therefore we accounted for possible effects of seedling origin by including this variable as a factor in all models. First, we assessed relationships between the habitat of establishment and seedling survival. For this purpose, we performed a logistic regression fitting a generalized linear model with individual survival as binomially distributed response variable and the habitat of arrival and seedling origin plus their interaction term as predictors. Secondly, we fitted a linear model with the habitat of establishment and seedling origin as explanatory variables and seedling growth as dependent variable. The significance of individual contrasts between habitats was analysed by merging levels of the habitat factor, rerunning the model and comparing the runs (Crawley 2002).

Reproductive success of mother trees - We explored whether the probability of a mother tree to disperse its seedlings to a given habitat influenced its overall reproductive success after 3 years of recruitment. For this purpose, we used a weighted regression assuming a binomial distribution of errors (Crawley 2002). The predictor variable was the proportion between the number of seedlings that each tree dispersed to broadleaved forest and the number that it dispersed to the other two habitats (which were pooled since they showed similar seedling performance; see below for further details). The response variable was the odd-ratio of seedlings that survived until the second survey. We then tested whether this proportion impacts trees' tendency to climb up or fall back in the fertility ranking. We performed this test by grouping trees with proportion of dispersed seedlings towards broadleaved forest above the stand average *versus* those with proportion of dispersed seedlings towards broadleaved forest below average and comparing their respective tendency in the fertility ranking with a χ^2 test. This and all other analyses were performed in R version 3.3.0 (R Development Core Team 2016) using the packages hierfstat, adegenet, ade4 and lme4.

RESULTS

Composition of the seedling cohort - We could identify the mother tree for 644 of our 809 seedlings (81%). The remaining 154 seedlings (19%) were assumed to stem from a mother tree outside the stand. We removed 9 seedlings that could not unequivocally be identified during the second survey and hence retained a total of 798 individuals for subsequent analyses (Table 1). A total of 250 seedlings (31%) survived until the second field survey. We detected 512 (64%) seedlings that emerged away from the canopy of their mother trees as a consequence of successful acorn dispersal. A total of 202 these successfully dispersed seedlings (39%) survived until an age of 3 years.

Genetic diversity – Gene diversity (H_E) varied very little among the different groups of seedlings that we distinguished and remained virtually constant through the 3-year monitoring (Table 1). The inbreeding coefficient (F_{IS}) did mostly not differ from zero. Immigrants showed a slight heterozygote deficit at SSR markers. Seedlings established in broadleaved forest showed a somewhat more pronounced heterozygote deficit at SNPs while those delivered to pine plantations showed a slight heterozygote excess at SSRs. We observed virtually no changes in F_{IS} during the 3-year monitoring.

Seedling subset	**Survey**	$n_{Seedlings}$	n_{Trees}	H_E		F_{IS}	
				SNP (± sd)	**SSR (± sd)**	**SNP (± sd)**	**SSR (± sd)**
All	Emergence	798	-[a]	0.43±0.11	0.78±0.14	0.01±0.05	0.01±0.02
	3 years	250	-[a]	0.41±0.11	0.76±0.13	0.01±0.08	0.01±0.02
Seedling origin							
Local	Emergence	644	104	0.43±0.11	0.76±0.17	0.01±0.06	0.01±0.03
	3 years	202	63	0.43±0.12	0.74±0.16	0.01±0.07	0.00±0.03
Immigrants	Emergence	154	-[a]	0.42±0.11	0.78±0.13	0.03±0.10	**0.04****±0.04
	3 years	48	-[a]	0.42±0.11	0.78±0.13	0.03±0.17	**0.04*****±0.02
Dispersal status (only local seedlings)							
Dispersed	Emergence	362	82	0.41±0.12	0.78±0.14	0.02±0.07	0.00±0.04
	3 years	154	58	0.40±0.13	0.77±0.13	0.01±0.08	0.00±0.04
Not dispersed	Emergence	282	104	0.42±0.11	0.78±0.13	0.00±0.09	0.01±0.03
	3 years	48	18	0.42±0.11	0.77±0.14	0.00±0.16	0.00±0.08
Habitat of establishment (only local, successfully dispersed seedlings)							
Broadleaved forest	Emergence	94	44	0.42±0.11	0.78±0.13	**0.08****±0.12	-0.01±0.08
	3 years	20	15	0.43±0.11	0.78±0.14	**0.10****±0.21	0.03±0.08
Open area	Emergence	215	62	0.42±0.11	0.79±0.14	0.00±0.08	0.02±0.04
	3 years	104	42	0.42±0.11	0.78±0.14	-0.01±0.11	0.00±0.04
Pine plantation	Emergence	53	32	0.42±0.11	0.78±0.13	-0.02±0.17	**-0.05***±0.04
	3 years	30	21	0.42±0.11	0.76±0.14	-0.03±0.17	**-0.04***±0.07

[a] The number of contributing mother trees could not be calculated for those cohort subsets that included non-assigned (and putatively immigrant) seedlings.

Table 1. Sample sizes and genetic diversity of different subsets of a genotyped *Quercus robur* seedling cohort, classified according to the origin, dispersal status and establishment habitat of seedlings, respectively. Data are shown for two surveys performed on the same individuals at seedling emergence and at an age of 3 years. The column $n_{Seedlings}$ indicates the number of seedlings belonging to a given group and n_{Trees} the number of mother trees that have contributed descendants to this group. The following columns indicate the observed values of gene diversity (H_E) and inbreeding coefficient (F_{IS}) for the two types of molecular markers used (SNP and SSR).

Dispersal distance – The distance distributions of seedlings dispersed to broadleaved forest and to open areas were both leptokurtic (Fig. 1). However, median and 95th percentile dispersal distances were much shorter in broadleaved forest than in open areas (15.1 m and 64.6 m vs. 25.9 m and 116.0 m, respectively). The dispersal distance distribution for pine plantations followed a remarkably flat distribution (Fig. 1) with a median of 59.1 m and a 95th percentile of 144.1 m. The dispersal distance distributions did not change between the two surveys (KS test: $D \leq 0.17$, $P \geq 0.74$ for all habitats).

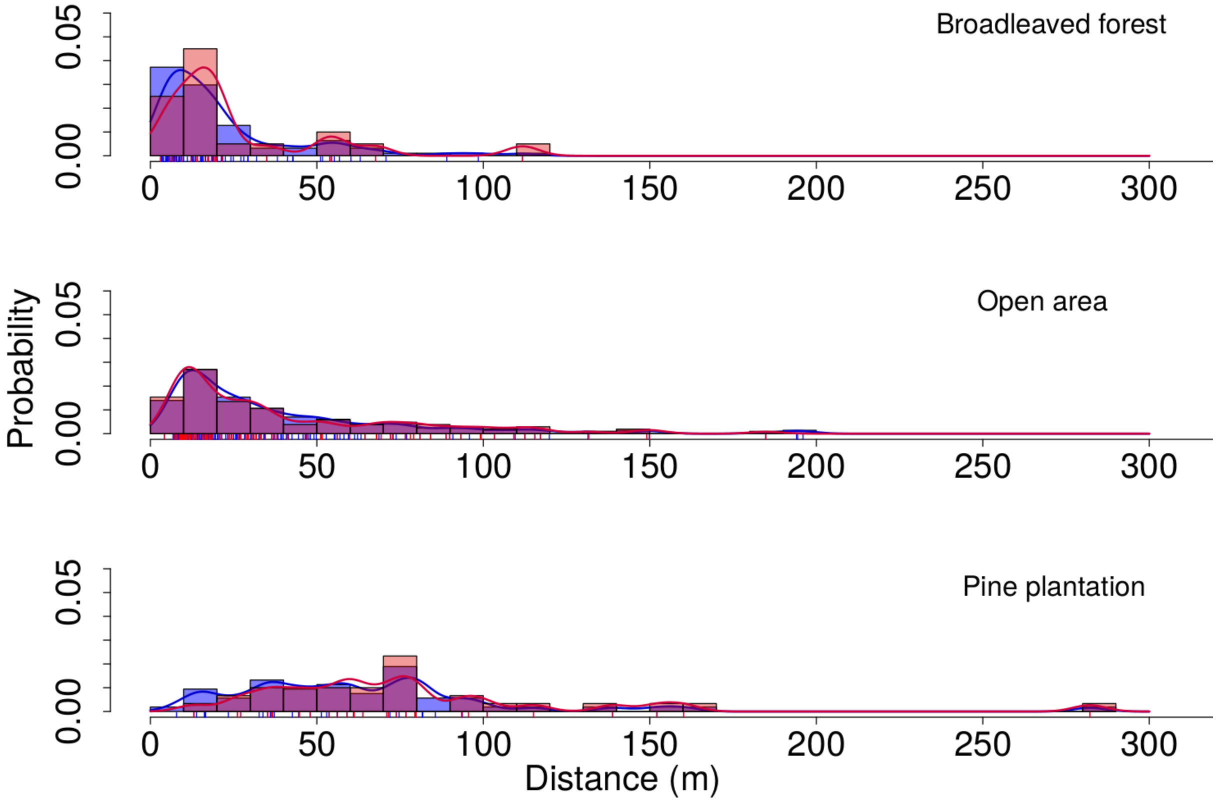

Figure 1. Frequency distributions of *Quercus robur* seedling dispersal distances to different habitats at the time of seedling emergence (blue columns) and age 3 years (red columns), estimated via parentage analysis. The line indicates the nonparametric smoothing spline fit to the empirical distance distribution together with bootstrapped estimates (n = 100 randomisations). Individual dispersal events at the time of emergence (red) and age 3 years (blue) are indicated by vertical lines under the plot.

Seedling performance – Our two models indicated that seedling performance was related with the habitat of establishment regardless of seedlings' origin. Survival differed considerably among habitats (χ^2 = 55.6, df = 2, $P < 0.001$) whereas neither origin (χ^2 = 1.3, df = 1, $P = 0.26$) nor the interaction between the two variables (χ^2 = 3.4, df = 2; $P = 0.19$) predicted a significant amount of the observed variation. Seedling survival over the 3-year monitoring period declined from 60% in pine plantations through 47% in open areas to 17% in broadleaved forest (Table 1). As a consequence, the proportion of seedlings growing in broadleaved forest declined considerably from the first to the second survey (Fig. 2); this trend concerned local seedlings as well as putative immigrants. Seedling growth also was significantly related to the habitat of establishment (F = 7.49, df = 2, $P < 0.001$) but neither to origin (F = 0.91, df = 1, $P = 0.34$) nor to the interaction between the two variables (F = 1.96, df = 2; $P = 0.14$). It was lowest in broadleaved forest while it did not differ between pine plantations and open areas.

Reproductive success of mother trees – Our weighted regression model indicated that those trees with a high proportion of their seedlings dispersed to broadleaved forest tended to suffer disproportionately great losses in reproductive success (χ^2 = 10.87, df = 1, $P < 0.001$). Accordingly, they fell back in the individual ranking of tree fecundity (χ^2 = 12.8, df = 1, $p < 0.001$) (Fig. 2).

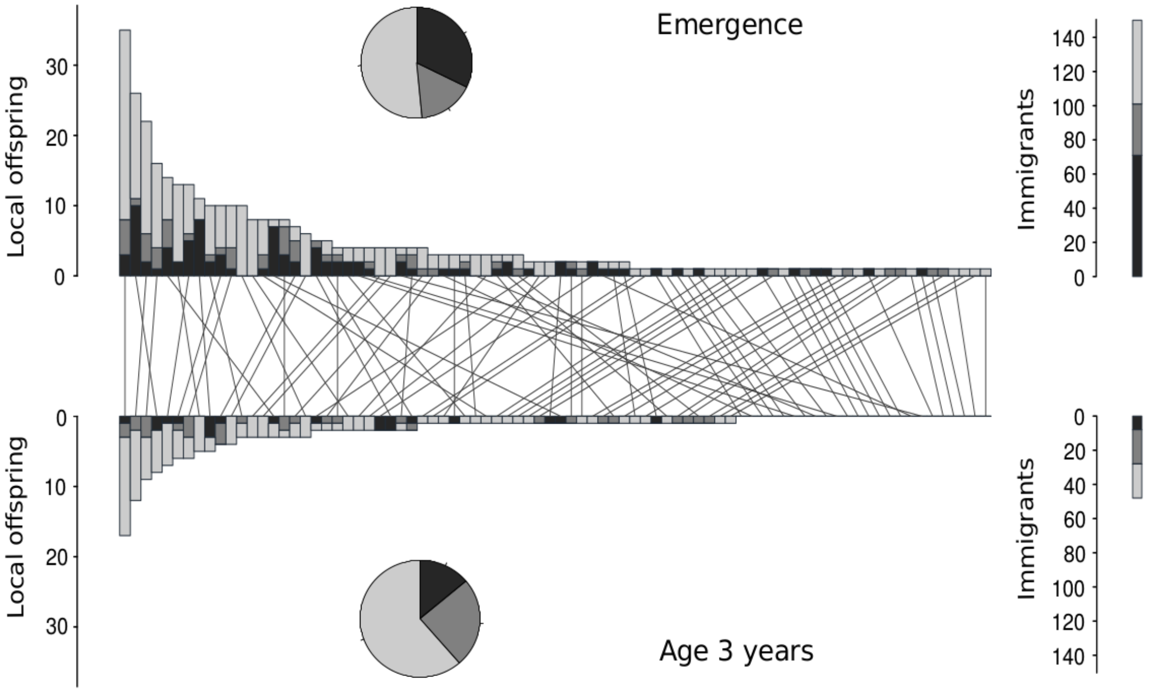

Figure 2. Seedling production by individual *Quercus robur* mother trees at the moment of seedling emergence (above) and at age 3 years (below). Each column corresponds to a reproducing tree. Colours indicate different habitats (black: broadleaved forest, dark grey: pine plantations, light grey: open areas). Lines between the two histograms connect the same mother tree, showing shifts in its fecundity ranking. Inserted circular plots indicate the proportion of local seedlings dispersed to each of the three habitats. Note that this proportion does not directly reflect the total seedling cohort as we sampled only 20% of the seedlings in the broadleaved forest but 100% in the other two habitats. Columns to the right of the graph indicate the absolute number of non-assigned and putatively immigrant seedlings found in each of the three habitats.

DISCUSSION

Genetic diversity, spatial distribution and parental contributions across habitats

Overall, the different subsets of our overall seedling cohort showed remarkably similar levels of genetic diversity. Gene diversity varied very little across seedling groups (total range: SNPs 0.40-0.43, SSR 0.74-0.79) and was slightly lower than reported by other studies on *Q. robur* (e.g. Chybicki & Burczyk 2010: 0.83-0.85 in two stands; Vranckx *et al.* 2014: 0.80-0.83 in five stands; Elshibli *et al.* 2015: 0.77-0.84 in three stands). The inbreeding coefficient diverged rarely did most often not differ from zero, and the few differences that we observed were not consistent for both types of molecular marker types. Hence we refrain from interpreting them.

The three habitats differed greatly in the number of animal-dispersed seedlings they contained and the number of mother trees that contributed to them (Table 1). Pine plantations received the smallest amount of seedlings which stemmed in turn from a relatively high number of mother trees (ratio of seedlings per tree: 1.7). Open areas received about four times more seedlings which stemmed however only from about twice as many mother trees (ratio: 3.4). Finally, our sample of 20% of the seedling cohort occurring in broadleaved forest allows to estimate that the total number of seedlings dispersed to this habitat should more than double that of the seedlings encountered in open areas. The number of contributing mother trees appears to be intermediate between the other two habitats.

Rodents are likely to be responsible for much acorn dispersal within the broadleaved forest because a widespread understorey vegetation of bracken (*Pteridium aquilinum*) reduces the visibility and renders the habitat unattractive for jays. On the contrary, it allows rodents to avoid areas with sparse vegetation or litter (den Ouden *et al.* 2005, Muñoz & Bonal 2007; Gómez *et al.* 2008). The importance of rodent dispersal is further supported by the fact that most seedlings in this habitat emerged within 20 m from the trunk of their mother trees (Fig. 1), which is well in line with distances reported by other studies on acorn dispersal by rodents (e.g. Sork 1984; Iida 1996; Sone & Kohno 1996; den Ouden *et al.* 2005; Gómez *et al.* 2008). The relatively high number of dispersed seedlings that we observed within the broadleaved forest would then point to a noteworthy dispersal activity by rodents in our study system. On the contrary, the seedlings located in open areas or pine plantations had mostly been moved over longer distances. Their location, together with the habitat itself, implies that these individuals had most likely been transported by scatter-hoarding jays. Our distance distribution for these dispersal events is again in line with previous studies on acorn dispersal by jays (Pons & Pausas 2008, Pesendorfer *et al.* 2016b), although others have reported considerably longer average distances (Gómez 2003). It is likely that these depend to a large extent on the specific home-range and space use of scatter-hoarding jays that can considerably vary among case studies (DeGange *et al.* 1989; Grahn 1990; Pesendorfer *et al.* 2016a).

Performance of dispersed seedlings and its cohort-level consequences

Both in terms of mortality and of growth, seedlings dispersed within the broadleaved forest performed markedly worse than those delivered to the other two habitats and their proportion was markedly lower during the second than during the first survey (see Fig. 2). Seedling mortality did not increase the average dispersal distances, indicating that it was not density or distance dependent. This observation is at odds with the widespread notion that the early recruitment stage of many forest trees is characterized by strong density-dependent processes that exert severe selection pressure on recruiting individuals (Petit & Hampe 2006). The low seedling performance in broadleaved forest could instead rather be related with light availability, since a concomitant study using hemispherical photographs (Niort 2007) revealed that seedlings located in broadleaved forest receive on average considerably less light than those growing in the other two habitats (global site factor [mean ± se]: broadleaved forest 0.17 ±0.01, pine plantations 0.39 ±0.03, open areas 0.55 ±0.02).

The observed habitat-related differences in dispersal and in seedling performance, when combined, provide interesting insights into the respective relevance of the two main acorn dispersers for oak recruitment. Rodents probably mobilized a noteworthy number of acorns but moved them only over short distances and deposited them in sites of poor quality for seedling establishment. On the contrary, jays transported acorns farther – both locally and from outside the forest stand - and tended to deliver them to more favourable establishment sites. Both the quantity and the quality of their dispersal service (*sensu* Schupp *et al.* 2010), taken together, should render them far more effective acorn dispersers than rodents, and ultimately far more relevant for oak recruitment and forest stand dynamics (see also Gerzabek *et al.* 2017).

Perhaps the most surprising result of this study was our observation that the relatively high and markedly habitat-specific seedling mortality during the 3-year monitoring (all seedlings: 69%, dispersed seedlings: 57%) had virtually no effect on the genetic diversity of the seedling cohort and its different subgroups. The remarkable stability of gene diversity and the inbreeding coefficient indicates that the establishment success of seedlings appears to be virtually independent of their genotype but instead basically driven by their environment. This comparatively rare evidence represents noteworthy empirical support for the validity of studies that rely on established seedlings for inferring seed dispersal kernels (Moran & Clark 2011; Klein *et al.* 2013; see also González-Martínez *et al.* 2006).

Consequences for the distribution of maternal reproductive success

Because seedling survival is highly habitat dependent, the proportion of seedlings that a mother tree disperses to a particular habitat could have significant consequences for its reproductive success and ultimately fitness. We observed indeed that trees dispersing many of their seedlings within the broadleaved forest tended to fall back in the individual ranking of reproductive success (Fig. 2). A previous study had already shown a similar trend for trees with a high fraction of dispersal failure (Gerzabek *et al.* 2017). The present analysis refines this previous result by documenting, to our knowledge for the first time, that not only the quantity but also the quality of seed dispersal (in terms of the arrival at suitable establishment sites) can directly affect the individual reproductive success of animal-dispersed plants. Ours study thus fully supports the claim of Schupp *et al.* (2010) that a detailed knowledge of plant-seed disperser interactions is indispensible for a sound understanding of their role for natural plant regeneration.

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GENERAL DISCUSSION

A sound knowledge of the ecological mechanisms that underlie plant regeneration is crucial for understanding the dynamics of plant populations (Harper 1977; Schupp & Fuentes 1995; Clark *et al.* 1999; Schupp *et al.* 2010) and a key element for their management and conservation. Seed dispersal links reproducing adults to their descendants and generates the initial spatial template for the new plant generation (Wang & Smith 2002). This thesis attempted to unravel the implications of oak acorn dispersal for early plant recruitment and the resulting reproductive success of fruiting trees within a small, actively expanding oak forest stand. Such a study can of course only provide a very limited snapshot of a system involving long-lived species such as forest trees, that establish very slowly, experience extensive mortality during the recruitment process and, once adult, eventually produce enormous amounts of offspring (Petit & Hampe 2006). However, our study approach that combined parentage analysis (to rebuild the link between reproducing adults and seedlings) with a detailed field monitoring (to assess parameters and patterns relevant to plant fitness) provided a number of novel and interesting insights upon plant-disperser interactions and the role that seed dispersal can play for the population dynamics of forest trees.

Fruiting oak trees: the ‘arena’ for acorn harvesting and dispersal by scatter-hoarders

Why do acorn dispersers forage on some fruiting trees and not on others growing nearby? Chapter 1 addressed this question considering several tree traits that had been investigated separately in previous studies or hypothesized to trigger disperser behaviour. The study returned a clear response (at least for the study stand and year) as patterns of local acorn abundance were the only driver of acorn dispersal rates that I could identify. The trees with the largest acorn crop achieved to effectively disperse the greatest amount of descendants. This finding supports the predator dispersal hypothesis (Vander Wall 2010; Pesendorfer & Koenig 2016), which poses that larger seed crops should result in fitness benefits from increased activity of seed-hoarding animals and resulting dispersal. After taking the effect of crop size into account by calculating relative instead of absolute dispersal success, I found that this measure was negatively related to the local abundance of adult trees. The most likely underlying mechanism for this negative relationship is disperser satiation (Hampe 2008), that is, acorn-harvesting animals were overwhelmed by the stand-scale crop and mobilized a lower proportion of acorns where a greater number was available. As a consequence, more isolated trees tended to be more successful in dispersing the acorns they produced than trees 'hidden' within a large conspecific neighbourhood. The evidence of disperser satiation in the study system is at odds with expectations of Vander Wall & Beck (2012), who argued that scatter-hoarders should be easily satiated when consuming the stored food but not during the harvesting and hoarding process itself. The observation indicates that animal acorn dispersers indeed represent a limited resource in my study system for which individual trees have to compete in order to disperse their offspring.

Contrary to what has been shown in experimental studies (e.g. Bossema 1979; Scarlett & Smith 1991; Moore & Swihart 2006; Pons & Pausas 2007a ; Myczko *et al.* 2014; Xianfeng & Zhenyu 2014), I detected no effect of the oak species on effective acorn dispersal. One possible explanation could be insufficient sample size because the study stand harboured only relatively few reproducing *Q.pyrenaica* trees. Moreover, these trees tended to produce smaller crops than *Q. robur* trees, so the variable crop size could account to some extent for eventually existing between-species differences. On the contrary, the lack of any influence of acorn traits such as size or shape cannot be reduced to a simple sampling effect. It also is at odds with results from experimental studies on jays performed in captivity (Bossema 1979; Moore & Swihart 2006; Pons & Pausas 2007a; Bartlow *et al.* 2011), casting doubts on the actual relevance of these studies for jay foraging behaviour in the field. Rodents are also known to differentiate between acorns of different size, both under laboratory conditions and in the field (Gómez 2004; Xiao *et al.* 2005; Moore *et al.* 2007; Pons & Pausas 2007c; Wang & Chen 2009; Perea *et al.* 2011b; Sunyer *et al.* 2014). The fact that their behaviour was not reflected here could be due to a question of scale: Rodents tend to differentiate primarily among the acorns beneath the same mother tree, whereas the study of chapter 1 was not designed to assess within-tree variation but only compared acorn traits among trees (considering one average value per tree).

Overall, the described results suggest that acorn dispersers behaved much like many dispersers of fleshy-fruited plant species (Corlett 2011; Vander Wall & Beck 2012). Their selection of acorns for harvesting and dispersal appeared to be a hierarchical process driven firstly by local acorn abundance. Acorn traits would then only be a secondary cue for acorn selection at a finer spatial scale (i.e., within the tree). Such a hierarchical selection behaviour (see also Sallabanks 1993) with crop size as principal cue should have direct implications for the reproductive success and resulting fitness of fruiting oak trees, especially during an ongoing demographic expansion as was the case in the investigated forest stand.

Acorn harvesting and tree reproductive success

While chapter 1 showed that tree fertility (or seed production) influences disperser behaviour, chapter 2 revealed that disperser behaviour, in turn, influences tree fecundity (or reproductive success). The satiation of acorn dispersers, already inferred from the indirect evidence in chapter 1, was formally confirmed in chapter 2 as trees with larger acorn crops tended indeed to disperse a lower proportion of their descendants. The non-dispersed seedlings suffered a twofold higher mortality than dispersed ones, and those trees that had failed to disperse many of their descendants dropped accordingly in the ranking of individual tree reproductive success. One might have expected that this process would result in an attenuation of the initially very pronounced skew in tree fertility, yet I could not confirm such a trend. A likely explanation is that the three-year monitoring period was too short and the monitored overall seedling mortality of ca. 70% still too low to produce a statistically significant change in the stand-scale distribution of tree reproductive success.

Compared with the clear effect of acorn removal from the tree, the subsequent dispersal process had a more complex impact on the evolution of tree reproductive success. Two major components were considered: the distance of dispersal and the habitat of delivery. Only the latter had a significant effect on seedling survival (see the following section) and caused that trees dispersing many of their seedlings to the least favourable habitat tended to fall back in the fecundity ranking through the three-year monitoring period. Importantly, however, neither dispersal distance nor the habitat of seedling delivery were related with the size, fertility or acorn traits of the fruiting trees. Therefore it appears that the acorn dispersal process and its outcome are independent of the mother tree's phenotype but exclusively guided by extrinsic determinants. In other words, the tree appears to lose any noteworthy influence on the fate of its descendants once they have moved away from its canopy.

Acorn dispersal and it effect on seedling recruitment

The seedling cohort exhibited a leptokurtic distribution of dispersal distances, a typical phenomenon in animal-dispersed plant populations (Nathan & Muller-Landau 2000). The distribution was quite 'fat-tailed' as almost 20% of the genotyed seedlings could not be assigned to a local mother tree and hence are likely to be immigrants that stem from outside the study stand. Jays are well known for their habit to regularly transport acorns over hundreds of metres to a few kilometres (Bossema 1979; Gȯmez 2003), and other studies have reported similar or even higher proportions of seed-mediated immigration into oak stands (e.g. Dow & Ashley 1996; Gerber *et al.* 2014). I also observed significant variation in the absolute amounts and in the average dispersal distances of seedlings dispersed to different habitats. Broadleaved forest harboured the highest number of seedlings which had been transported over relatively short distances, whereas pine plantations contained the smallest number of seedlings which had travelled farthest. This pattern should to a certain extent arise from the spatial distribution of the habitats within the study plot. In addition, it is likely to reflect differences in the disperser guilds that transported acorns to different habitats: As laid out in chapter 3, the combination of habitat characteristics and observed dispersal distances suggests that the seedlings dispersed within the broadleaved forest probably had mostly been transported by rodents, whereas those found in pine plantations or treeless open areas would most likely have been hoarded by jays (Bossema 1979; Gȯmez 2003; den Ouden *et al.* 2005; Muñoz & Bonal 2008). Similar habitat sensitivity has been reported from frugivore guilds of fleshy-fruited plant species (Jordano *et al.* 2007). Unfortunately, it is impossible to empirically test my hypothesis through a molecular marker based identification of the dispersers, as has been elegantly done for frugivores by Varo *et al.* (2014).

The distance of dispersal had no measurable effect on posterior seedling survival, a result that is in line with a previous formal analysis of density dependence (Hampe *et al.* 2010). The lack of either distance or density-dependent seedling mortality in the monitored cohort of actively dispersed seedlings indicates that their relatively low density tends to render Janzen-Connell effects negligible (Hyatt *et al.* 2003; Comita *et al.* 2014). On the contrary, the habitat of acorn delivery exerted a strong effect on seedling performance. As shown in chapters 2 and 3, seedlings dispersed to pine plantations or treeless areas had a markedly higher survival rate (60% and 48% *versus* 17%) and grew considerably better than seedlings dispersed within the broadleaved forest. Evidence from hemispherical photographs taken in the different habitats indicates that the light conditions might go a long way in explaining among-habitat differences in seedling performance (Niort 2007).

Combining the trends described above, one can conclude that the present study system presents an emblematic case of a seed-seedling conflict (Schupp 1995) where the broadleaved forest habitat provides favourable conditions for seed delivery (i.e. proximity to fruiting oaks, shelter for acorn-dispersing rodents) but poor conditions for seedling establishment. On the other hand, if my hypothesis concerning the habitat-dependent acorn dispersal by jays and by rodents is correct, then the reported results also suggest that these two dispersers should play very different roles for oak recruitment (see also den Ouden *et al.* 2005). Even if their importance may be relatively similar in quantitative terms (i.e. concerning the amount of acorns mobilized), they differ considerably in qualitative terms (i.e., concerning the survival chances of dispersed acorns). The fact that jays tend to deliver acorns to more suitable sites for seedling establishment should render them the most effective acorn dispersal vectors (*sensu* Schupp *et al.* 2010) and hence most relevant for oak recruitment and resulting population dynamics.

Consequences for oak regeneration at the cohort level

One of the strengths of this study is that it allowed to scale the dispersal and recruitment fates of known individuals up to the level of an entire seedling cohort, a rarely undertaken exercise (but see Wenny 2000) that can provide a complementary perspective on their consequences for spatial patterns of regeneration. Suitable sites for plant establishment typically are distributed very unequally across the landscape, and they are often not identical with the most suited sites for seed arrival (Schupp & Fuentes 1995; Howe & Miriti 2004; Schupp *et al.* 2010). As a consequence, different habitats can receive very different subsets of the overall offspring pool, and these subsets can further be modified during the early recruitment process, with consequences on spatial pattern of regeneration and genetic population structures. Chapter 3 compared different subsets of the overall seedling cohort and revealed indeed that they partly underwent quite distinct demographic trajectories. In line with the individual-level trends described previously, the seedling group emerging in broadleaved forest lost its initial dominance owing to disproportionately high mortality and the group of non-dispersed seedlings likewise experienced considerably higher losses than the dispersed seedlings. On the contrary, I did not detect any differences in the performance of local and immigrant seedlings, whereas some authors have hypothesized that local recruits might have higher survival chances than long-distance immigrants (e.g. Nathan 2006).

Most strikingly, levels of genetic diversity (measured in terms of gene diversity and the inbreeding coefficient) varied neither among the different groups of seedlings that I distinguished nor through the three-year monitoring period. One might instead have expected several differences. First, levels of diversity could vary between non-dispersed and dispersed seedlings because the former group should include a large proportion of half or full-sibs while this is not necessarily the case with the dispersed seedlings. The fact that both groups show virtually the same levels of diversity suggests however that both non-dispersed and dispersed seedlings probably stemmed to a large extent from the same sources: the handful of large, highly fertile trees that produced the majority of acorns in the stand. Consequently, the group of dispersed seedlings contained almost as many siblings as the non-dispersed group (see Figures 2 and 2 in chapter 2 and 3, respectively). Secondly, levels of genetic diversity could also have varied between local and immigrant seedlings owing to their different origin, with immigrants potentially stemming either from a less or from a more varied sample of mother trees than locals. That both groups showed instead very similar levels of diversity could be interpreted as a sign that the oaks of the study stand and those outside actually belong both to one single, genetically very little differentiated population. This would be in line with observations that extensive gene flow often maintains tree populations tightly connected far beyond apparent barriers in the landscape (Petit & Hampe 2006; Kramer *et al.* 2008; Kremer *et al.* 2012).

Finally, one might have expected that the extensive seedling mortality would modify the genetic diversity of the corresponding cohort subsets. For instance, strong fine-scale spatial genetic structure (SGS) is a widespread phenomenon in tree seedling cohorts that tends to vanish towards older age classes because of the successive disappearance of siblings growing in high density beneath or near their mother (e.g. Chung *et al.* 2003; Jones & Hubbell 2006; Sezen *et al.* 2007; Choo *et al.* 2012). However, to the best of my knowledge only Hampe *et al.* (2010) distinguished between dispersed and non-dispersed seedlings, and this study detected strong autocorrelation in the non-dispersed but not in the dispersed seedling group. The complete absence of recruitment-driven changes in genetic diversity that I observed here underpins that patterns of mortality are not related with seedlings' genotype or pedigree relationships but exclusively depend on the small-scale environment at the place of delivery. The reported evidence casts doubts on the commonly assumed importance of selection during early tree recruitment (Petit & Hampe 2006), at least in situations where this recruitment occurs at moderate or low density. Moreover, my observation represents noteworthy empirical support for the validity of studies that rely on established seedlings for inferring seed dispersal kernels (Moran & Clark 2011; Klein *et al.* 2013; see also González-Martínez *et al.* 2006).

Consequences for forest stand expansion

The investigated oak forest stand is one representative example of a widespread phenomenon in the geographical region where this PhD thesis took place: The extensive pine plantation forests that dominate the Landes de Gascogne in SW France have been vigorously colonized by oaks during the past decades, a process that has been further promoted by recent changes in sylvicultural management (Mora *et al.* 2012). This thesis took a one-cohort snapshot and focused on a fine spatial scale to elucidate precise ecological processes acting during a very short stage of the oak life cycle: seed dispersal and early recruitment. One might therefore argue that its results can hardly be extrapolated to the regional-scale population dynamics of a long-lived forest tree species such as oaks. While there is no doubt that the implications of the reported results must be interpreted with caution, there are some good reasons to believe that they can indeed be of relevance for oak colonization dynamics in the Landes de Gascogne. Firstly, the colonization has occurred without intentional human support and would certainly have been impossible without frequent and effective long-distance acorn dispersal by wild animals (putatively jays). Secondly, a previous study performed in the same oak stand revealed that the spatial genetic structure of the adult tree population strikingly resembles that of a dispersed seedling cohort (Hampe *et al.* 2010). This similarity was explained by the fact that most young adults must, some time ago, have been successfully dispersed descendants of the same few large founder trees that also mothered many of the investigated seedling cohort. If this is true then it would imply that my one cohort study probably represents rather well a key process for the regeneration and expansion (local or regional) of oak stands in the Landes de Gascogne area. And it would nicely underline that the foraging behaviour of acorn-hoarding animals (notably jays) can indeed have a measurable long-term impact on the population structure of naturally regenerating oak forests.

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Appendix

MEMMseedlings

The MEMMseedlings approach relies on a probabilistic mating model which aims to estimate male and female fecundities together with the pollen and seed dispersal kernels in plants, based on naturally established seedlings (see (Burczyk *et al.* 2006; Goto *et al.* 2006; Oddou-Muratorio & Klein 2008; Moran & Clark 2011). It builds on an original mating model developed for maternal progenies collected on mother plants and referred to as the neighborhood model (Adams & Birkes 1991). The MEMMseedlings model used in this study is extensively described in Oddou-Muratorio *et al.* submitted . This appendix describes the main aspects of the model, as well as specific parameters used for this study.

Total probability of a seedling genotype. The core of this model is the equation for the likelihood of observing a seedling genotype g_i at a given position in space:

$$L(g_i) = (1- m_s)\,\Sigma_j\, \pi_{sij}\, [s\, T_1(g_i|\, g_j, g_j) + m_p\, T_2(g_i|g_j,BAF) + (1-s-m_p)\,\Sigma_k\, \pi_{pjk}\, T_3(g_i|g_j,g_k)]$$

$$+m_s\, T_4(g_i|\, BAF) \quad \textbf{(eq.1)}$$

where m_s, m_p and s are respectively seed migration, pollen migration and selfing rate at population level; BAF is the background allelic frequencies outside of the plot; and T represents the Mendelian transition probabilities self-fertilization of a mother-tree with genotype g_j (T1); for fertilization of female j with a pollen with genotype drawn in the allelic frequencies (T2); for mating between the female j and male k, with a genotype g_k, within the neighborhood (T3) (with the sum over k runs over all possible fathers inside the plot); and for mating between an ovule and a pollen with genotypes drawn in the allelic frequencies (T4). Both π_{sij} and π_{pjk} are not true parameters but instead refer to functions of parameters integrating the processes of seed or pollen dispersal and the distribution of female and male fecundities.

Here, the function π_{Pjk}, relates to the probability of each male k to contribute to the pollen pool of female j and is modeled as:

$$\pi_{P\,jk} = \frac{F_{Mk}\theta_p\left(d_{jk}\right)}{\sum\limits_{l:\,father} F_{Ml}\theta_p\left(d_{jl}\right)} \quad \textbf{(eq.2)}$$

where F_{Mk} and F_{Ml} are the male fecundities of father k and l respectively; d_{jk} and d_{jl} are the distances between mother j and father k and l respectively; and θ_p is the pollen dispersal kernel.

The function π_{Sij} relates to the probability of each female j to contribute to the seedling pool at the location of seedling i and is modeled as:

$$\pi_{S\,ij} = \frac{F_{Fj}\theta_s\left(d_{ij}\right)}{\sum\limits_{l:mother} F_{Fl}\theta_s\left(d_{il}\right)} \quad \textbf{(eq.3)}$$

where F_{Fj} and F_{Fl} are the female fecundities of mother j and l respectively; d_{ij} and d_{il} are the distances between seedling i and mother j and l respectively; and θ_s is the seed dispersal kernel.

Pollen and seed dispersal kernels: The pollen dispersal kernel was classically modeled using the exponential power family curve (Klein *et al.* 2006):

$$\theta_p(a_p,b_p;d) = \frac{b}{2\pi a^2\,\Gamma(2/b)}\exp\left(-\left(\tfrac{d}{a}\right)^b\right) \quad \textbf{(eq.4)}$$

with d the distance between the pollen source and the mother-tree, Γ the classical gamma function, a_p the scale parameter linked to the mean pollen dispersal distance:

$$\delta_p = a_p \frac{\Gamma(3/b)}{\Gamma(2/b)} \quad \textbf{(eq.5)}$$

and b_p the shape parameter ($b > 1$: “thin-tailed” kernel; $b < 1$ “fat-tailed” kernel).
The seed dispersal kernel was modeled as a mixture of two exponential power curves in proportion α and $(1-\alpha)$, following Bullock *et al.* (2006) and Nathan *et al.* (2013) (see Gerzabek *et al.* 2017 for details):

$$\theta_s(a_s,b_s,a_{sLDD},b_{sLDD};d) = (1-\alpha)\frac{b}{2\pi {a_s}^2\,\Gamma(2/b_s)}\exp\left(-\left(\tfrac{d}{a_s}\right)^{b_s}\right) + \alpha\frac{b}{2\pi {a_{s,LDD}}^2\,\Gamma(2/b_{s,LDD})}\exp\left(-\left(\tfrac{d}{a_{s,LDD}}\right)^{b_{s,LDD}}\right)$$

(eq.6)

where d is the distance between the mother-tree and the seedlings position; a_s and b_s are the respective scale and shape parameters of the “short-distance” seed dispersal kernel; $a_{s,LDD}$ and $b_{s,LDD}$ are the respective scale and shape parameters of the "long-distance" seed dispersal kernel. The mixture rate between the two seed dispersal functions was modeled as a random variable following a beta distribution of parameter (μ_α ; σ_σ).

Male and female fecundities: We used a model of individual fecundity distribution introduced by Klein *et al.* (2008). Briefly, fecundity of the *k*-th male F_{Mk} is assumed to follow a Gamma distribution with variance $\sigma_M{}^2$ and the mean fixed arbitrarily at 1. Fecundity of the *j*-th female F_{Fj} is assumed to follow a Gamma distribution with variance $\sigma_F{}^2$ and the mean fixed arbitrarily at 1.

Typing error: We distinguished two types of mistyping errors (respectively A and B): in type A (specific for microsatellite), the allele read differs only by one motif repeat from the true allele with a probability P_{err1}, as modeled in Gerard *et al.*(2006)); in type B, the allele read can be any allele observed at this locus with a probability P_{err2} , as modeled in Marshall *et al.* (1998). In this study, we considered a mixture of the two error types for all the 8 microsatellite loci, with $P_{err1} = 0.01$ and $P_{err2}=0.01$. For the 40 SNP, we considered only the second type of error, with $P_{err2}=0.001$. The Mendelian transition probabilities accounting for type A error were computed following the Appendix in Gerard *et al.*(2006) and those accounting for type B error were computed following the Appendix 1 Marshall *et al.* (1998).

Moreover, we considered that a maximum number of possible mismatches was allowed within a parent-offspring trio (Nmis). Results presented in the main manuscript were obtained by fixing Nmis = 2.

Inferential procedures

The model described in equation 1 depends on a large number of parameters: 8 dispersal kernels parameters (a_p, b_p, a_s, b_s, a_{sLDD}, b_{sLDD}, μ_α ; σ_σ), 2 fecundity parameters ($\sigma_M{}^2$ and $\sigma_F{}^2$), 3 mating system parameters (m_s, m_p and s) and also on a large number of latent variables: the individual male and female fecundities F_{Mk}, and F_{Fj} considered as random variables following a Gamma distribution and the individual mixture rate α_i considered as a random variable following a Beta distribution. To estimate them, we used a Bayesian approach that is conceptually similar to that proposed by Klein *et al.* (2008). The Bayesian analysis employed a Monte Carlo Markov chain (MCMC), based on the Metropolis-Hasting algorithm.

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