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RESEARCH PAPER

Recruitment of a genotyped *Quercus robur* L. seedling cohort in an expanding oak forest stand: diversity, dispersal, and performance across habitats

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Abstract

· ***Key message*** **Few studies have linked the origin of dispersed tree seeds with their post-dispersal fate. We show that habitat-dependent mortality in a pedunculate oak (*Quercus robur* L.) seedling cohort reshapes the effective fecundity of individual mother trees but has little effect on the cohort's genetic diversity.**

· ***Context*** Initial tree recruitment plays a key role in forest regeneration, yet little is known on how patterns of recruit mortality feed back on the fecundity of reproducing trees.

· ***Aims*** To investigate how among-habitat variation in seedling arrival and survival alters initial patterns of genetic diversity and maternal reproductive success.

· ***Methods*** We genotyped a pedunculate oak seedling cohort ($n = 809$) and monitored it over 3 years. The mother trees of 81% of the seedlings were identified through parentage analysis. Seedlings were assigned to one of three habitats (broadleaved forest, pine plantation, or open area).

· ***Results*** Broadleaved forest received most seedlings (≈ 65%) but their survival was reduced by a third compared with pine plantations or open areas. Thus, mother trees dispersing many descendants to broadleaved forest suffered a disproportionate reduction of their reproductive success. Genetic diversity did not vary among habitats, nor over the monitoring period.

· ***Conclusion*** The quality of seed dispersal, in terms of delivery sites, can considerably influence the reproductive success of individual mother trees without affecting the overall genetic diversity of the recruits.

Keywords Genetic diversity · *Quercus robur* L. · Reproductive success · Seed dispersal · Seedling · Recruitment

1 Introduction

Seed dispersal creates the initial template for 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 (Jordano and Godoy 2002; Wang and Smith 2002). A vast number of studies have assessed patterns of seed dispersal and early plant recruitment over the last decades with the purpose to accurately predict regeneration dynamics, a key information for the management and conservation of forest tree populations and associated communities (Clark et al. 1999; Schupp et al. 2010; Robledo-Arnuncio et al. 2014). Despite the wealth of empirical evidence accumulated, we are still far away from a proper understanding of how spatio-temporal patterns of seed dispersal and seedling recruitment in a heterogeneous environment translate into the dynamics and genetics of plant populations, especially in long-lived species such as trees.

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This article is part of the topical collection on *Establishment of second-growth forests in human landscapes: ecological mechanisms and genetic consequences*

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One major research gap consists in the fact that extremely few studies have achieved to link the source tree of dispersed seeds with their post-dispersal fate (Schupp et al. 2010; Côrtes and Uriarte 2013). Demographic field studies typically monitor recruiting plants and perform experiments to infer the causes of their establishment success or failure, but they are only very rarely able to track their sources (but see Wenny 2000; Gerzabek et al. 2017b). In turn, molecular ecological studies typically infer the parents of dispersed recruits but usually lack detailed demographic information for the genotyped descendants (Dick et al. 2008; García and Grivet 2011; but see Steele et al. 2007; Gerzabek et al. 2017b). The scarcity of empirical studies that tightly integrate demographic and molecular research approaches strongly constrains our understanding of how the fertility and ultimately the fitness of reproducing trees are affected by the recruitment success of their offspring. It also hampers detailed insights into the ecological drivers that shape the genetic structure and diversity of entire plant cohorts throughout the recruitment process. Since the pioneer study of Augspurger (1983), only few studies addressed these issues (e.g. Gonzalez-Martinez et al. 2006; Jacquemyn et al. 2007; Hampe et al. 2010; Oddou-Muratorio et al. 2011; Moran and Clark 2012; Bontemps et al. 2013). Bontemps et al. (2013) showed that density-dependent mortality could shift the effective dispersal distance between young and old seedlings cohorts of European beech (*Fagus sylvatica* L.). Moran and Clark (2012) observed a strongly skewed distribution of maternal reproductive success in both seeds and seedlings. This variance in individual reproductive success could however be reduced during seedling establishment, because of a trade-off between maternal reproductive success and seed-to-seedling survival as well as subsequent seedling growth rate in red oaks. By comparing genetic differentiation among multiple beech seedling cohorts, Oddou-Muratorio et al. (2011) showed temporal stability in the genetic structure of seedlings derived from successive seed rains and found no genetic differentiation between dead and alive seedlings. Hampe et al. (2010) also observed a similar spatial genetic structure between adults and animal-dispersed seedlings in pedunculate oak (*Quercus robur* L.), suggesting temporal stability of the underlying ecological processes.

Seed dispersal and early recruitment are strongly influenced by the landscape context, i.e. the spatial distribution and heterogeneity of habitats in the neighbourhood of dispersing plants. Dispersal vectors tend to move seeds nonrandomly, generating highly heterogeneous landscape-scale patterns of seed abundance and leaving seeds in habitats of variable suitability (Jordano and Godoy 2002; Gómez 2003; Morán-López et al. 2015). The seedling stage is the most vulnerable stage of the plant life cycle and characterized by extensive mortality (Petit and 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 are typically distributed very unequally across the landscape, and they are often not identical with the most suited sites for seed arrival (Schupp and Fuentes 1995; Clark et al. 1999). As a consequence, different habitats can receive different subsets of the overall offspring pool, and these subsets can further change considerably during the early recruitment process owing to differential recruit survival. 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 across habitats of a cohort of animal-dispersed pedunculate oak seedlings evolve 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 (see Gerzabek et al. 2017b), while the demographic data informed us about patterns of post-dispersal survival and growth. In a previous study (Gerzabek et al. 2017b), we had characterized the heterogeneity in reproductive success and demonstrated that reproductive inequality tends to decrease through the recruitment process. Here, we focus on the impact of variation in habitat suitability on the change in genetic structure and diversity of the seedlings cohort during recruitment. Each seedling was assigned to one of three habitats (broadleaved forest, pine plantation, or open area). Based on the combined genetic and demographic evidence and the information upon the habitat of establishment, we addressed the following research questions: (i) Do genetic diversity, parental contributions, and spatial distributions differ among the habitats where seedlings are recruited? (ii) Does seedling performance differ across habitats? (iii) Does differential seedling mortality alter 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 and Burczyk 2010; Oddou-Muratorio et al. 2011; Millerón et al. 2013; Vranckx et al. 2014), we chose to explicitly identify recruits actively dispersed away from their mother trees and to focus primarily on them, because offspring recruiting beneath the mother plant is typically assumed to suffer virtually ineludible mortality and hence to be irrelevant for regeneration (Howe and Miriti 2004; Schupp et al. 2010).

2 Material and methods

2.1 Study system

The study was performed in SW France (44° 34′ N, 1° 00′ W), in an area covered by extensive plantations of maritime pine

(*Pinus pinaster* Ait.) interspersed with small stands of broadleaved forests dominated by pedunculate oak (*Quercus robur* L.). Oak stands are largely exempt from sylvicultural treatments. Many are actively expanding, favoured by a recent change in the regional forest 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* Schreber; and European squirrels, *Sciurus europaeus* L., being present in the area) (Hampe et al. 2010). We selected an isolated mixed oak forest stand with ca. 280 adult pedunculate and Pyrenean oaks (90% *Q. robur*, 10% *Q. pyrenaica* Willd.) for this study (see Fig. 3 in Annex). Detailed descriptions of the study system can be found in Hampe et al. (2010) and Gerzabek et al. (2017b).

2.2 Field sampling and laboratory analyses

In early spring 2006, we delimited a study plot of ca. 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 ($n = 254$). Each tree was individually tagged, mapped, and genotyped.

During late April and early May 2006, we performed a comprehensive survey of newly emerged pedunculate oak seedlings. We sampled all seedlings emerging more than 2 m away from the crown projection of any adult oaks. Furthermore, we sampled 20% of all seedlings emerging beneath adult oaks (including the surrounding 2 m radius). We estimate that the resulting sample ($n = 809$ individuals) includes 25–30% of the overall seedling cohort recruiting this year within the study plot. Importantly, the performed 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, mapped, and genotyped. Each seedling was assigned to one of three major habitat types: (i) broadleaved forest (including silver birch [*Betula pendula* Roth.] and willows [*Salix* spp.] besides the two oak species), (ii) pine plantations, and (iii) open areas without a tree layer. We used hemispherical photography to assess differences in understory-level light availability among habitats. Hemispherical photographs were taken above a randomly selected subsample of 212 seedlings scattered across the study plot and images were analysed with HemiView® version 2.1 (Delta-T Devices, Burwell, Cambridge, UK) to compute the global site factor (GSF), a commonly used estimate of light availability that quantifies the proportion of direct and diffuse solar radiation at a given site relative to that in the open.

Seedlings were monitored twice per year from emergence until September 2008 (that is at an age of 3 years). Their status (living or dead) was recorded, and their height and number of leaves was measured. Here, we only compare data from the first and the last census.

Trees and seedlings were genotyped using eight nuclear microsatellite (SSR) markers as described in detail in Hampe et al. (2010) and at 39 SNP loci as described in Gerzabek et al. (2017a, b) (for details see Dryad data repository: https://doi.org/10.5061/dryad.3j33t). We obtained readily usable data for 33 SNPs that we merged with the SSR data to obtain individual tree and seedling multilocus genotypes.

2.3 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. 2018) as explained in detail in Gerzabek et al. (2017b). Briefly, this method estimates the probability π'_{Sij} of each tree j within the stand to be the mother of a given particular seedling i with genotype g_i, by accounting both for (i) compatibility between genotypes g_i and g_j and (ii) distance d_{ij} through the seed dispersal kernel and the spatial locations of parents and seedlings. We accounted for genotyping errors 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. In hermaphroditic species like oak, the probability of each parent to contribute as the father or the mother of each given seedlings is accounted for. The probability P_{mig} that each seedling originated from seed migration is also estimated, and maternity is granted to the mother tree j with the highest π'_{Sij} value if $\pi'_{ij} > P_{\mathrm{mig}}$.

We used the results of the parentage assignment together with the spatial location of seedlings and trees to infer, for each analysed seedling, whether it had emerged beneath the canopy of its mother tree or whether it had 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) 'animal' dispersal. Finally, we summed all animal-dispersed seedlings assigned to a given mother tree and used this measure as a proxy for its effective fecundity. Our reasoning assumes that acorns not dispersed away from the mother tree and cashed by an animal disperser are irrelevant for forest regeneration owing to their high mortality from density-responsive seed and seedling enemies, as predicted by the Janzen-Connell model and commonly documented in forests (Howe and Miriti 2004; Gómez et al. 2008; Schupp et al. 2010).

2.4 Statistical analyses

Creation of cohort subsets Several analyses compared different groups of seedlings. For these comparative analyses, we divided the overall seedling cohort in subsets based on three different criteria: (i) the origin of seedlings according to the parentage assignment ('local' vs 'immigrants'); (ii) the dispersal status ('successful dispersal' vs 'failed dispersal'); and (iii) the habitat of arrival ('broadleaved forest' vs 'pine plantation' vs 'open area'). In addition, a 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), the inbreeding coefficient (F_{IS}) per locus, and allelic richness (A_r) using FSTAT version 2.9.3 (Goudet 2001). Differences of F_{IS} from zero and among-group variation of A_r were tested by computing 95% confidence intervals by means of 5000 bootstraps within populations. Genetic differentiation among groups was investigated by computing the fixation indices F_{ST} (estimator θ; Weir and Cockerham 1984) and D (Jost 2008) and their 95% confidence intervals (5000 bootstraps) for pairwise comparisons of the groups. Because we did not aim to compare genetic differentiation among all possible pairs of groups, we limited our comparisons to (1) trends through time for a given group ('emergence' vs 'age 3 years' for 'immigrants') and (2) comparisons of groups for a given time (e.g. 'local' vs 'immigrants' at 'age 3 years').

Habitat cover and distribution In order to characterize the cover and the spatial distribution of the three habitat types, we created 100 random coordinates within the limits of the plot and assessed the habitat type at each of these points (see Electronic Supplementary Material S1). Then, we computed the distance matrix between every adult tree and every random point. Both the habitat cover and distance between the random points belonging to a given habitat and the seed sources were

Table 1 Sample sizes and genetic diversity of different subsets of a genotyped *Quercus robur* seedling cohort, classified according to the origin (i.e. the mother tree), 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 $n_{\text{Seedlings}}$ 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) and allelic richness (A_r) for 8 SSRs

Seedling subset	Survey	$n_{\text{Seedlings}}$	n_{Trees}	H_E		F_{IS}		A_r [a]		
				SNP (± sd)	SSR (± sd)	SNP (± sd)	SSR (± sd)	Mean	Lower 95% CI	Upper 95% CI
All	Emergence	798	-[b]	0.43 ± 0.11	0.78 ± 0.14	0.01 ± 0.05	0.01 ± 0.02	9.47	8.38	10.75
	3 years	250	-[b]	0.41 ± 0.11	0.76 ± 0.13	0.01 ± 0.08	0.01 ± 0.02	9.36	8.25	10.63
Seedling origin										
Local	Emergence	656	110	0.43 ± 0.11	0.76 ± 0.17	0.01 ± 0.06	0.01 ± 0.03	9.34	8.13	10.50
	3 years	204	65	0.43 ± 0.12	0.74 ± 0.16	0.01 ± 0.07	0.00 ± 0.03	9.08	7.88	10.25
Immigrant	Emergence	142	-[b]	0.42 ± 0.11	0.78 ± 0.13	0.03 ± 0.10	0.04* ± 0.04	9.68	8.50	10.88
	3 years	46	-[b]	0.42 ± 0.11	0.78 ± 0.13	0.03 ± 0.17	0.04* ± 0.02	9.64	8.38	10.75
Dispersal status (only local seedlings)										
Animal dispersed	Emergence	368	87	0.41 ± 0.12	0.78 ± 0.14	0.02 ± 0.07	0.00 ± 0.04	9.42	8.25	10.75
	3 years	156	60	0.40 ± 0.13	0.77 ± 0.13	0.01 ± 0.08	0.00 ± 0.04	9.1	8.00	10.25
Non-dispersed	Emergence	288	60	0.42 ± 0.11	0.78 ± 0.13	0.00 ± 0.09	0.01 ± 0.03	9.05	8.00	10.13
	3 years	48	18	0.42 ± 0.11	0.77 ± 0.14	0.00 ± 0.16	0.00 ± 0.08	8.3	7.38	9.38
Habitat of establishment (only local, animal-dispersed seedlings)										
Broadleaved forest	Emergence	99[c]	48	0.42 ± 0.11	0.78 ± 0.13	0.08* ± 0.12	− 0.01 ± 0.08	9.37	8.13	10.75
	3 years	21[c]	16	0.43 ± 0.11	0.78 ± 0.14	0.10* ± 0.21	0.03 ± 0.08	7.66	6.63	8.50
Open area	Emergence	216	63	0.42 ± 0.11	0.79 ± 0.14	0.00 ± 0.08	0.02 ± 0.04	9.2	7.88	10.50
	3 years	105	43	0.42 ± 0.11	0.78 ± 0.14	− 0.01 ± 0.11	0.00 ± 0.04	8.96	7.75	10.13
Pine plantation	Emergence	53	32	0.42 ± 0.11	0.78 ± 0.13	− 0.02 ± 0.17	− 0.05* ± 0.04	8.57	7.50	9.50
	3 years	30	21	0.42 ± 0.11	0.76 ± 0.14	− 0.03 ± 0.17	− 0.04* ± 0.07	8.13	7.13	9.00

*$P < 0.05$

[a] Allelic richness based on 8 SSRs with a minimum sample size of 21 seedlings

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

[c] Those effectives include only the sampled and genotyped seedlings among the ~ 500 estimated

used as a ‘null model’ for comparison with the observed animal-dispersed seedling cohort (Table 3). We performed a one-way ANOVA to test for differences in GSF among habitats.

Inequalities in maternal contributions We used the method developed by Smouse and Robledo-Arnuncio (2005) and adapted by Grivet et al. (2005) to characterize differences between habitats in terms of contributing mother trees (Table 4). For this purpose, we computed two different metrics for each habitat, (1) the number of seedlings per mother tree, and (2) the effective number of seed donors defined as $N_{\mathrm{em}} = (1/r_{\mathrm{gg}})$ were r_{gg} is the unbiased estimator of the probability of maternal identity (PMI; i.e. the probability of identical mother trees drawn from two random seedlings from the same habitat; see Grivet et al. 2005 for further details).

Dispersal distance We plotted the empirical distribution of seedling dispersal distances based on the observed distances between successfully assigned seedlings and their inferred mother trees. Note that the distribution only integrates local dispersal because dispersal distances could not be inferred for immigrant seedlings. 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 two-sample Kolmogorov-Smirnov test for discrete samples.

Seedling performance across habitats 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 a growth index.

High mortality rates forced us to pool seedlings of local and of putatively immigrant origin for the following analyses in order to increase their robustness. 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 qualitative predictors. Then, we fitted a linear model with the habitat of establishment and seedling origin as qualitative explanatory variables and seedling growth as a dependent quantitative 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). We investigated the effect of ground-level light availability on seedling survival and growth using GSF as a dependent variable in two separate models to explain (1) survival by means of a logistic regression and (2) growth index in a simple linear regression.

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 a proportion of animal-dispersed seedlings towards broadleaved forest above the stand average versus those with a proportion of animal-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 3.6.2 (R Core Team 2019) using the packages hierfstat, adegenet, diveRsity, ade4, car, and lme4.

3 Results

Composition of the seedling cohort We could identify the mother tree for 656 out of 809 sampled seedlings (81%). The remaining 142 seedlings (22%) were assumed to stem from a mother tree outside the stand (Table 1). A total of 250 seedlings (31%) survived until the second field survey. We detected 510 (64%) seedlings that emerged away from the canopy of their mother trees as a consequence of successful animal mediated acorn dispersal, 368 could be assigned to a local mother tree. A total of 202 of these animal-dispersed seedlings (40%) survived until an age of 3 years.

Genetic diversity Gene diversity (H_{E}) and allelic richness (A_{r}) varied very little among the different groups of seedlings that we distinguished and remained virtually constant through the 3-year monitoring period (Table 1). The inbreeding coefficient (F_{IS}) as well as both fixation indices (θ and D) did mostly not differ from zero. At SSR markers, immigrants showed a slight heterozygote deficit and weak albeit statistically significant differentiation from seedlings originating from a local mother tree (Table 2). Low differentiation ($\theta = 0.004$, $D =$

Table 2 Genetic differentiation between pairs of groups and across time. We report the mean as well as the lower and upper 95% confidence interval of two pairwise fixation indices (θ and D) for both types of molecular markers (SSR and SNP)

Seedling subset	SSR						SNP					
	θ			D			θ			D		
	Mean	Lower 95% CI	Upper 95% CI	Mean	Lower 95% CI	Upper 95% CI	Mean	Lower 95% CI	Upper 95% CI	Mean	Lower 95% CI	Upper 95% CI
All emergence vs. All 3 years	0.000	−0.001	0.001	0.000	−0.003	0.002	0.000	−0.002	0.001	0.000	0.000	0.000
Seedling origin												
Local emergence vs. Local 3 years	0.000	−0.002	0.001	0.000	−0.004	0.002	0.000	−0.002	0.002	0.000	0.000	0.000
Immigrant emergence vs. Immigrant 3 years	0.000	−0.008	0.002	0.000	−0.014	0.008	0.000	−0.010	0.002	0.000	−0.001	0.000
Local emergence vs. Immigrant emergence	0.002*	0.000	0.005	0.005	−0.002	0.014	0.001	−0.001	0.004	0.000	0.000	0.001
Local 3 years vs. Immigrant 3 years	0.003	−0.003	0.011	0.003	−0.016	0.030	0.000	−0.008	0.006	0.000	−0.001	0.001
Dispersal status (only Local seedlings)												
Animal dispersed emergence vs. Animal dispersed 3 years	0.000	−0.003	0.001	0.000	−0.006	0.000	0.000	−0.003	0.001	0.000	0.000	0.000
Non-dispersed emergence vs. Non-dispersed 3 years	0.000	−0.006	0.005	0.000	−0.009	0.015	0.002	−0.005	0.010	0.000	−0.001	0.002
Animal dispersed emergence vs. Non-dispersed emergence	0.004*	0.001	0.006	0.008*	0.001	0.016	0.002	0.000	0.004	0.000	0.000	0.001
Animal dispersed 3 years vs. Non-dispersed 3 years	0.005	−0.002	0.015	0.014	−0.008	0.044	0.007	−0.001	0.017	0.000	−0.001	0.003
Habitat of establishment (only Local, Animal-dispersed seedlings)												
Broadleaved forest emergence vs. Broadleaved forest 3 years	0.000	−0.015	0.010	0.000	−0.029	0.028	0.000	−0.017	0.017	0.000	−0.002	0.005
Open area emergence vs. Open area 3 years	0.000	−0.005	0.000	0.000	−0.011	−0.003	0.000	−0.005	0.002	0.000	−0.001	0.000
Pine plantation emergence vs. Pine plantation 3 years	0.000	−0.017	0.001	0.000	−0.053	−0.014	0.000	−0.019	0.002	0.000	−0.009	−0.006
Broadleaved forest emergence vs. Open area emergence	0.003	0.000	0.007	0.004	−0.006	0.017	0.003	−0.001	0.008	0.000	−0.001	0.002
Broadleaved forest emergence vs. Pine plantation emergence	0.005	−0.001	0.013	0.007	−0.013	0.035	0.003	−0.005	0.013	0.000	−0.001	0.003
Open area emergence vs. Pine plantation emergence	0.001	−0.004	0.007	0.000	−0.014	0.022	0.002	−0.004	0.010	0.000	−0.001	0.002
Broadleaved forest 3 years vs. Open area 3 years	0.001	−0.010	0.016	0.000	−0.028	0.044	0.010	−0.007	0.035	0.001	−0.003	0.008
Broadleaved forest 3 years vs. Pine plantation 3 years	0.009	−0.008	0.030	0.006	−0.039	0.069	0.007	−0.013	0.033	0.000	−0.004	0.008
Open area 3 years vs. Pine plantation 3 years	0.003	−0.005	0.014	0.001	−0.023	0.036	0.000	−0.010	0.012	0.000	−0.001	0.003

*$P < 0.05$

0.008) at SSRs markers was also observed between animal-dispersed and non-dispersed seedlings during the first survey. These weak trends in population differentiation were however not consistent across marker types and fixation indices. 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} or genetic differentiation among groups during the 3-year monitoring.

Habitat structure Pine plantation was the most dominant habitat with 50% of random points compared with broadleaved forest (31%) and open areas (19%) (Table 3). It was also the farthest habitat from possible acorn sources (median 159.2 m), while open areas were intermediate (median 131.2) and, unsurprisingly, broadleaved forest was the nearest (median 111.3). All three habitats differed significantly in terms of ground-light availability ($F = 189.96$, df = 2, $P < 0.001$), GSF in pine plantations (0.39) and broadleaved forest (0.17) was reduced by respectively 16 and 38% compared with open areas (0.55).

Inequalities in maternal contributions The three types of habitat varied greatly concerning the number of animal-dispersed seedlings they received. Broadleaved forest contained the largest fraction of the overall animal-dispersed seedling cohort ($n \approx 500$, corresponding to 99 identified seedlings from the randomized 20% subsample of the overall cohort in this habitat), open areas an intermediate amount ($n = 216$) and pine plantations the lowest portion ($n = 53$) (Table 1). The overall PMI was low ($0.028 < r_{gg} < 0.039$) (Table 4). Broadleaved forest and pine plantations exhibited similar levels of maternal contribution, whereas markedly fewer effective mother trees contributed to the seedling cohort establishing in open areas (Table 4).

Table 4 Inequalities in maternal contributions towards the three types of habitats described by the number of local animal-dispersed seedlings ($n_{\text{Seedlings}}$), the number of contributing mother trees (n_{Trees}), the number of seedlings per tree ($n_{\text{Seedlings}}/n_{\text{Trees}}$), an estimator of the Probability of maternal identity (r_{gg}) and the effective number of seed donors ($N_{em} = 1/r_{gg}$)

Habitat of establishment	$n_{\text{Seedlings}}$	n_{Trees}	$n_{\text{Seedlings}}/n_{\text{Trees}}$	r_{gg}	N_{em}
Broadleaved forest	99	48	2.06	0.028	35.15
Open area	216	63	3.43	0.039	25.32
Pine plantation	53	32	1.66	0.028	35.33

Dispersal distance The distance distributions of seedlings actively 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).

Seedling performance Both models indicated that seedling performance was related with the habitat of establishment regardless of seedling origin. Survival differed considerably among habitats ($\chi^2 = 55.6$, df = 2, $P < 0.001$) whereas neither origin ($\chi^2 = 1.3$, df = 1, $P = 0.26$) nor the interaction between the two variables ($\chi^2 = 3.4$, df = 2; $P = 0.19$) predicted a significant amount of the observed variation. The survival of dispersed seedlings assigned to a local mother tree declined from 56% in pine plantations through 49% in open areas to 21% 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

Table 3 Habitat and spatial distribution of the observed animal-dispersed seedling cohort compared with expectations based on 100 random points. We report the median and 95% percentile distance of dispersal computed from the distances between all successfully assigned seedlings and their respective mother tree

Habitat type	Observed			Expected		
	n	Median distance (m)	95th percentile (m)	n	Median distance (m)	95th percentile (m)
Broadleaved forest	99 [a] (26%)	15.1	64.6	31 (31.0%)	111.3	223.3
Open area	216 (59%)	25.9	116.0	19 (19.0%)	131.2	279.4
Pine plantation	53 (15%)	59.1	144.1	50 (50.0%)	159.2	281.4

[a] Value corresponds to a fully randomized sample of 20% of the overall seedling cohort recorded in broadleaved forest

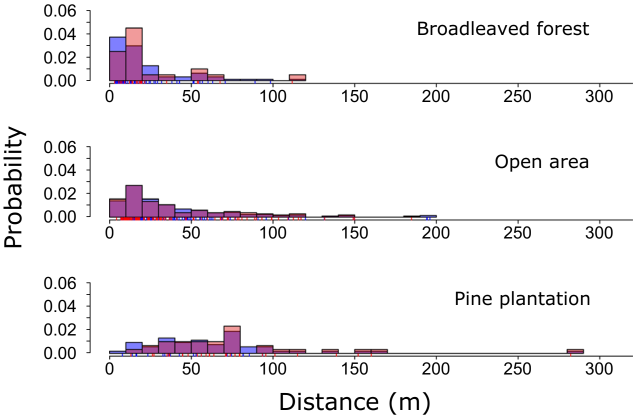

Fig. 1 Frequency distributions of *Quercus robur* seedling dispersal distances to different habitats at the time of seedling emergence (blue columns) and age 3 years (red columns), estimated via Bayesian parentage analysis. Individual dispersal events at the time of emergence (red) and age 3 years (blue) are indicated by vertical lines under the plot

differ between pine plantations and open areas. Moreover, GSF was significantly positively associated with both seedling survival ($\chi^2 = 8.60$, df = 1, $P < 0.01$) and growth ($F = 42.88$, df = 1, $P < 0.001$).

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

4 Discussion

4.1 Genetic diversity, spatial distribution, and parental contributions across habitats

Overall, the different subsets of the seedling cohort showed remarkably similar levels of genetic diversity (total H_E range: SNPs 0.40–0.43, SSRs 0.74–0.79), which was overall slightly lower than reported by other studies on *Q. robur* (e.g. Chybicki and Burczyk 2010: $H_E = 0.83$–0.85 in two stands; Vranckx et al. 2014: $H_E = 0.80$–0.83 in five stands; Elshibli et al. 2015: $H_E = 0.77$–0.84 in three stands, all studies used SSR). The inbreeding coefficient did most often not differ from zero, and the few differences that we observed were not consistent for both types of molecular markers. Hence, we refrain from interpreting them. We observed low but statistically significant genetic differentiation between seedlings assigned to a local mother tree and seedlings originating from immigration (Table 2), most probably because genetic diversity is usually structured in space, and both groups originate (by definition) from slightly different gene pools. Genetic differentiation between the animal-dispersed seedlings and the seedlings established under their mothers' canopy could be driven by the fact that a subsample of adult trees is preferentially selected by disperser agents (Gerzabek et al. 2017b). These results stress the influence of dispersers' foraging behaviour for landscape-scale seed dispersal and ultimately the genetic composition of regenerating tree populations.

The three habitats differed greatly in the number of animal-dispersed seedlings they received and the number of mother

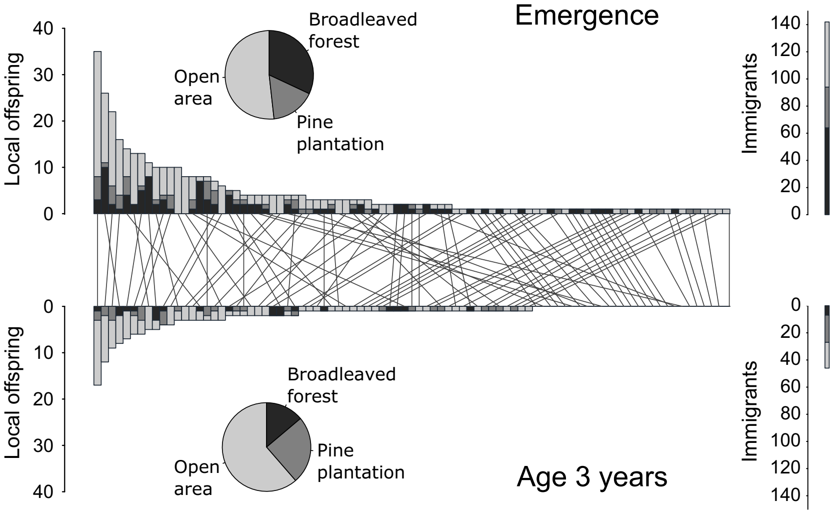

Fig. 2 Production of animal-dispersed seedlings by individual *Quercus robur* mother trees at the moment of seedling emergence (above) and at age 3 years (below). Each column corresponds to a reproducing tree. Colours indicate different habitats (black: broadleaved forest, dark grey: pine plantations, 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 actively 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

trees that contributed to them (Tables 1 and 4). Pine plantations, the most abundant but also the most distant habitat, received the smallest amount of seedlings (7% of the estimated overall seedling cohort) which stemmed however from a relatively high effective number of mother trees ($N_{\mathrm{em}} = 35$). In contrast, open areas received about four times more seedlings (28% of the overall cohort) but these stemmed only from 25 effective mother trees (3.4 seedlings per mother tree). Finally, the sampling of 20% of the total seedling cohort occurring in broadleaved forest enabled us to estimate that the absolute number of seedlings actively dispersed to this habitat more than doubled that of the seedlings encountered in open areas (65% of the overall cohort). The number of effective mother trees contributing to the seed rain in broadleaved forest equalled that for pine plantations, resulting in an intermediate ratio (2.1) of seedlings per mother tree.

Rodents are likely to be responsible for a large proportion of acorn dispersal within the broadleaved forest because a widespread understorey vegetation of bracken (*Pteridium aquilinum* Kuhn) 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; Gómez et al. 2008; Muñoz and Bonal 2011). The importance of rodent dispersal in the broadleaved forest 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; Soné and Kohno 1996; den Ouden et al. 2005; Gómez et al. 2008). 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. The distance distribution for these dispersal events is again in line with previous studies on acorn dispersal by jays (Pons and Pausas 2008; Pesendorfer et al. 2016b), although others based on different study approaches and spatial scales 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). Note also that we could not quantify dispersal distances for the relatively high proportion of immigrant seedlings (most of which were actually found in open areas or pine plantations).

4.2 Performance of animal-dispersed seedlings and its cohort-level consequences

Seedlings actively dispersed within the broadleaved forest performed markedly worse than those delivered to the other two habitats (in terms of both mortality and growth), 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 (Klein et al. 2013). 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 (Augspurger 1983; Petit and Hampe 2006; Bontemps et al. 2013). The high proportion of oak seedlings actively dispersed beyond the canopy of their mother tree (56%) may allow them to escape density-dependent mortality. The low seedling performance in broadleaved forest could instead rather be related with light availability (see also Kunstler et al. 2005; Sevillano et al. 2016). This hypothesis receives substantial support by the analysis of data extracted from hemispherical photographs that shows marked variation in ground-light availability among habitats and its effect on seedling performance. However, we cannot rule out other habitat-related confounding factors such as differences in grazing and pathogen infection that could trigger among-habitat variation in seedling mortality.

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. 2017b).

Perhaps the most surprising result of this study was that, despite a relatively high and markedly habitat-specific seedling mortality during the 3-year monitoring (all seedlings 69%, animal-dispersed seedlings 57%), we observed virtually no effect on the genetic diversity of the seedling cohort and its different subgroups. The remarkable stability of allelic richness, gene diversity, the inbreeding coefficient, and the two fixation indices further supports that the establishment success of seedlings appears to be virtually independent of density-dependent effects. Positive density-dependence of seedling mortality is a widespread phenomenon in forest trees (Petit and Hampe 2006), and it often triggers decreases of inbreeding and increases of allelic richness and gene diversity because siblings are more likely to grow at high densities and hence are more affected than unrelated individuals. That we could not detect such effects either for the entire cohort or its subsets represents empirical support for the validity of studies that rely on established seedling genotypes for inferring seed dispersal kernels (e.g. MEMMseedlings) and inherently assume that their previous dispersal and establishment success is genotype-independent (Moran and Clark 2011; Klein et al. 2013; see also Gonzalez-Martinez et al. 2006).

4.3 Consequences for the distribution of maternal reproductive success and patterns of within-species diversity

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). Our previous study had already shown a similar trend for trees with a high fraction of dispersal failure (Gerzabek et al. 2017b). Based on the same dataset and parentage assignment procedure, 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. This study thus fully supports the claim of Schupp et al. (2010) that a detailed knowledge of plant-seed disperser interactions is indispensable for a sound understanding of the role played by animal seed dispersers for natural plant regeneration.

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Data availability Both the genotypic data and the field data underlying this study have been deposited in the Dryad repository: https://doi.org/10.5061/dryad.3j33t (Gerzabek et al. 2017a).

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Annex

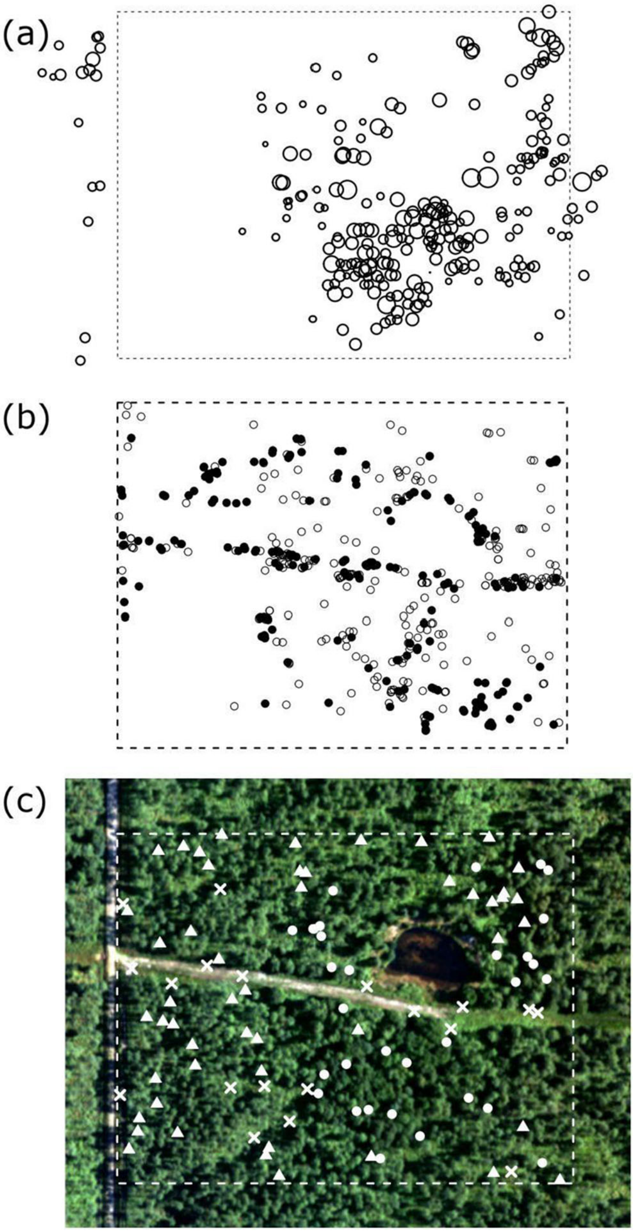

Fig. 3 Locations of adult oak trees with circle sizes proportional to their diameter at breast height (**a**); locations of the animal-dispersed seedlings sampled (filled circle: individual survived the three-year monitoring period, empty circle: individual died) (**b**); aerial photograph of the study area with symbols indicating random points used for the habitat characterization (circle: broadleaved forest, cross: open area, triangle: pine plantation) (**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. See also Fig. 1 in Gerzabek et al. (2017b)

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