

# Dispersal, host genotype and environment shape the spatial dynamics of a parasite in the wild

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**Abstract.** Dispersal, environment and genetic variation may all play a role in shaping host-parasite dynamics. Yet, in natural systems, their relative importance remains unresolved. Here, we do so for the epidemiology of a specialist parasite (*Erysiphe alphitoides*) on the pedunculate oak (*Quercus robur*). For this purpose, we combine evidence from a multi-year field survey and two dispersal experiments, all conducted at the landscape scale. Patterns detected in the field survey suggest that the parasite is structured as a metapopulation, with trees in denser oak stands characterized by higher parasite occupancy, higher colonization rates and lower extinction rates. The dispersal experiments revealed a major impact of the environment and of host genotype on the presence and abundance of the parasite, with a weaker but detectable imprint of dispersal limitation. Overall, our findings emphasize that dispersal, host genotype and the environment jointly shape the spatial dynamics of a parasite in the wild.

**Key words:** colonization; disease dynamics; dispersal; epidemiology; *Erysiphe alphitoides*; host-parasite interaction; landscape scale; metapopulation; pedunculate oak; powdery mildew; *Quercus robur*; spatial dynamics.

## INTRODUCTION

Theoretical and experimental studies have convincingly demonstrated that dispersal, host genotype and the environment may jointly shape the ecology and evolution of host-parasite interactions (Burdon 1987, Combes 2001, Schmid-Hempel 2011). Nonetheless, the majority of the experimental studies have been restricted to a small spatial scale (Jessup et al. 2004, Gómez and Buckley 2011, Tack et al. 2014), whereas the persistence of many species may depend on landscape-level processes (Hanski 1999). As a second limitation, many studies have focused on laboratory (Boots and Meador 2007, Vogwill et al. 2009) or agricultural and forestry systems (McNew 1960, Mullett et al. 2016, Farber et al. 2017), and few studies are available from natural systems. Third, while dispersal is a central life-history trait (Kokko and López-Sepulcre 2006), we lack direct assessments of the dispersal and colonization ability of wild parasites (Zheng et al. 2015, Becheler et al. 2016). Overall, we are simply short of empirical data on the relative importance of dispersal, genotype and the environment in shaping the spatial dynamics of host-parasite interactions in natural systems.

Parasites frequently live within heterogeneous fragmented landscapes, with long-term persistence based on a balance between the extinction and (re-)colonization

of local habitat patches (Parratt et al. 2016). In such landscapes, the ability of hosts and parasites to disperse plays a major role for their ecology and evolution, as indicated by theory (Thrall and Burdon 1999, Gandon 2002), microcosm studies (Boots and Meador 2007, Fellous et al. 2012) and meta-analyses (Greischar and Koskella 2007, Hoeksema and Forde 2008). Dispersal can be seen as a multi-step process, with the three phases of departure, movement and settlement (Clobert et al. 2012, Tack et al. 2014). Importantly, spatial and temporal variation within the environment may affect each stage of the dispersal process (Clobert et al. 2012, Tack et al. 2014).

During the movement phase, differences in the dispersal environment (i.e., the matrix) may affect the speed and direction of movement, as well as the survival of dispersing propagules. Survival of propagules in the air may, for example, be affected by abiotic factors like UV radiation and relative humidity, whereas movement direction and speed will differ between habitat types such as open fields and forests. The dispersal kernel may also be indirectly rather than directly related to the colonization process, as the environment at the destination (i.e., patch quality) may play a major role in successful establishment (i.e., colonization). Here, abiotic factors like humidity, shade and temperature (Schnathorst 1965, Duniway 1979, Jarosz and Burdon 1988) and biotic factors like the genotype and phenotype of the host and parasite (Edelaar and Bolnick 2012, Tack et al. 2014) may strongly affect the probability of colonization. Notably, in contrast to plant studies on seed dispersal

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kernels, field surveys (Jousimo et al. 2014, Ericson et al. 2017) and experimental studies (Thrall et al. 2003, Johnson and Haddad 2011) on pathogens have generally focused on successful colonization rather than propagule movement per se (but see e.g. Tack et al. 2014). Like the colonization process, the environment, host genotype and dispersal may all affect the extinction process: for example, host genotype (Jousimo et al. 2014) and local environmental conditions such as humidity and temperature (Burdon and Jarosz 1991, Tack et al. 2015) may affect the persistence of local parasite populations, whereas colonization may rescue a local population from extinction (Brown and Kodric-Brown 1977). Ultimately, dispersal, genotype and the environment may jointly affect the colonization and extinction processes, and thereby shape the prevalence and distribution of the parasite within the metapopulation.

Here, we explore the impact of dispersal, plant genetic variation and the environment on the spatial dynamics of the powdery mildew *Erysiphe alphitoides* on the pedunculate oak *Quercus robur*. More specifically, we conducted a multi-year field survey to explore the impact of the spatial connectivity of host trees on the spatial dynamics of the tree's parasite. We then use two single-source dispersal experiments to disentangle the relative importance of dispersal limitation as compared to plant genotype and the environment, where the environment refers to the habitat type where the trees are located: an oak stand, a forest or an open field. In the first dispersal experiment, we assess the relative importance of parasite dispersal and habitat type. In the second dispersal experiment, we pinpoint the relative importance of parasite dispersal, host genotype and early-season exposure on host colonization by parasites.

## MATERIALS AND METHODS

### Study system

The pedunculate oak *Quercus robur* is the only oak species in Finland, where it reaches its northern limit. Here, it mainly grows in the coastal zone and in the southwestern archipelago (Ferris et al. 1998). The distribution of individual oak trees is frequently sparse, with both clumped stands and isolated trees scattered across the landscape. Other characteristic trees in the landscape are silver birch (*Betula pendula*), downy birch (*Betula pubescens*), Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*).

The oak tree is attacked by the powdery mildew *Erysiphe alphitoides*, which is a specialist and obligate fungal parasite. In Finland, its host range is restricted to *Quercus robur* (Braun and Cook 2012, Tack et al. 2012a). The parasite overwinters in the form of sexual structures (i.e., chasmothecia) which are formed on the leaves in autumn. In spring, the chasmothecia release the ascospores, which are the source of the first infections in spring. The parasite is known to overwinter as mycelium in buds in parts

of its range (Woodward et al. 1929, Kerling 1966), which results in the emergence of heavily infected “flag” shoots from infected buds in spring. However, such flag shoots have never been observed on oak trees in our field site, or on the experimental trees used in this or previous studies (A. J. M. Tack, unpublished; Roslin et al. 2007). We have not found any surviving chasmothecia on the small shoots or twigs of seedlings in the field or on the experimental trees (see below), even though chasmothecia may survive in cracks or hollows of older branches and tree trunks. The chasmothecia may also survive in the leaf litter or the soil. During the summer, the powdery mildew produces asexual spores (i.e., conidia).

### Colonization and extinction dynamics in the field

To characterize the spatial dynamics of the plant parasite, we surveyed the presence of *E. alphitoides* on 196 small trees (1–3 m) growing on the island of Wattkast in southwestern Finland (Fig. 1B). For each tree, we annually recorded the presence/absence of powdery mildew, and hence also occupancy, colonization and extinction rates. Roughly half of these trees were surveyed annually from 2003 to 2006 ( $n = 97$ ), while the other trees were surveyed for less than the full survey period (see Table 1 for the number of trees surveyed in each year).

We further calculated the spatial connectivity of each of the surveyed oak trees. For this, we took advantage of the fact that the GPS location and diameter of all oak trees over half a meter in height have been mapped in the study area ( $n = 1868$  trees; Fig. 1B; Gripenberg and Roslin 2005). Based on these data, we calculated the spatial connectivity index of each tree  $i$  (Hanski 1999, Tack et al. 2010):

$$S_i = \sum_{j \neq i} N_j e^{-\alpha d_{ij}},$$

where  $j$  ranges over all trees on the island,  $N_j$  is the number of leaves on each tree, and  $d_{ij}$  is the distance in meters between the focal tree  $i$  and tree  $j$ . Following Tack et al. (2010), the parameter  $\alpha$  was set to 1/250 m and  $N_j$  was estimated using the formula  $\log(\text{Number of Leaves}) = 0.92 + 2.55 \times \log(\text{Girth at Breast Height in cm})$  (Gripenberg et al. 2008).

### Dispersal experiment I: the impact of distance and habitat type on mildew colonization

To investigate the importance of the environment and distance from the infection source on mildew colonization and abundance, we distributed a set of 70 small potted trees (henceforth referred to as “mobile trees”) at different distances around an isolated oak stand. The use of such “mobile” or “sentinel” trees allowed us to place uninfected targets for parasite dispersal at regular distances from a single oak stand of  $c. 100 \times 50$  m. The oak stand (henceforth “the source stand”) that we

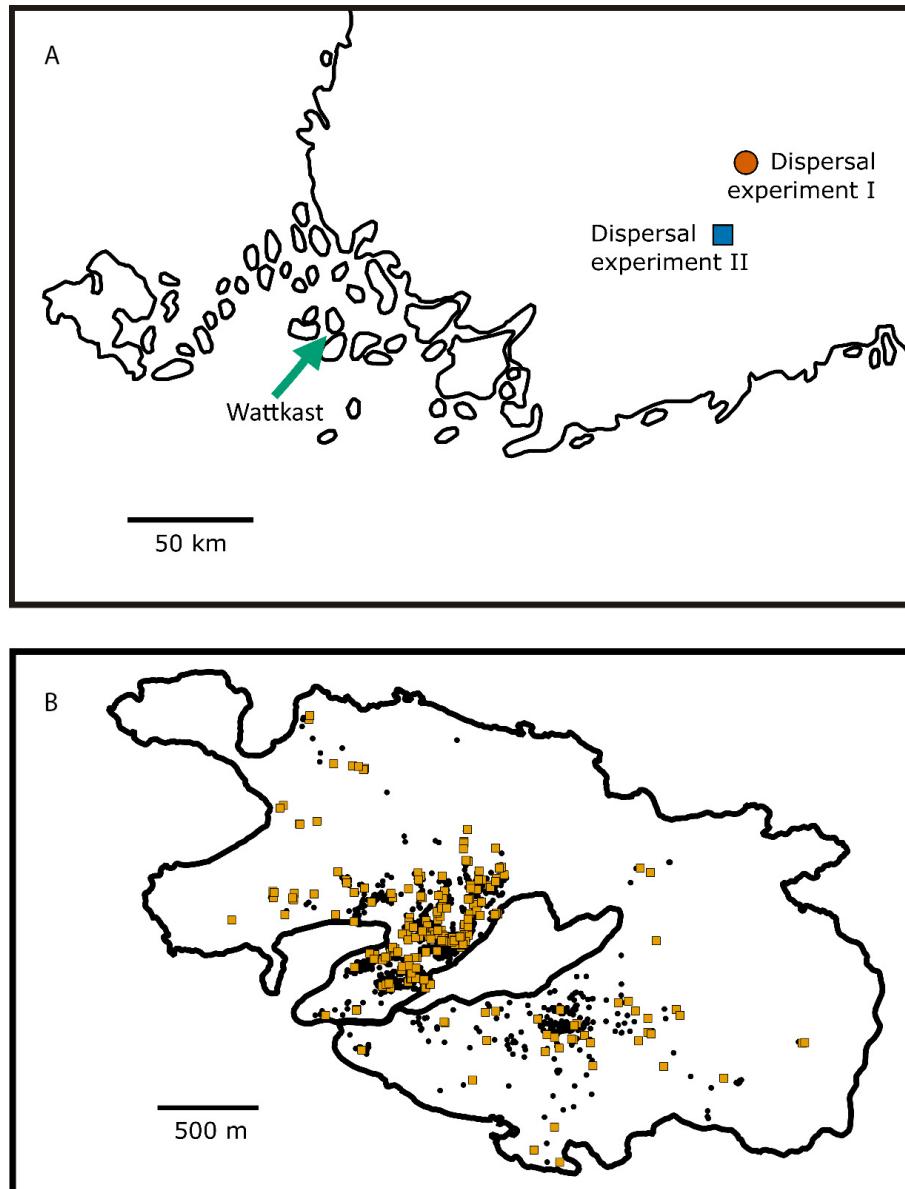


FIG. 1. Location of dispersal experiments and surveyed trees. (A) The location of the two dispersal experiments (orange circle and blue square) and the location of the island of Wattkast in SW Finland (bluish-green arrow). (B) The island of Wattkast with the location of the surveyed trees (orange squares) and of all 1868 oak trees occurring on the island (black circles).

selected for this experiment grows at the range margin of oak in south-central Finland ( $60^{\circ}52'29''$  N  $24^{\circ}33'15''$  E; Fig. 1A), and is set in a mixed landscape, with forest (without oak trees) on its northern side but an abrupt change to an open field on its southern edge. The mobile trees were *c.* 1 m in height and were moved into place before bud break in spring 2006. Twelve trees were located within the source stand. The other trees were located at 37.5 m ( $n = 13$ ), 75 m ( $n = 13$ ), 150 m ( $n = 16$ ) and 300 meter ( $n = 16$ ), with all distances represented both in the open field ( $n = 25$ ) and in the closed forest ( $n = 33$ ). Differences among these two habitat types

involve differences in (at least) shade, humidity and temperature. Such variation may affect propagule movement and survival, as well as plant leaf traits and resistance (Jarosz and Burdon 1988, Laine 2008). Trees were randomly assigned to one of the fixed distance categories, after which they were placed individually in the matrix at a randomly selected angle from the oak stand. As there were no other oak trees in the surrounding area, and since oak powdery mildew is an obligate specialist parasite on oak, we may safely assume that any infections on the experimental trees originated from the source stand. To avoid any possibility of re-infection of trees from

TABLE 1. Spatial dynamics of the powdery mildew *Erysiphe althitoides* on small trees (1–3 m height) on the island of Wattkast. Shown are the occupancy (i.e., prevalence), colonization rate and extinction rate, as well as the impact of spatial connectivity on these three metapopulation descriptors. Significant values are highlighted in bold, with the direction of the effect given between brackets (for quantitative estimates, see Appendix S1: Fig. S1).

Year	Occupancy <sup>1</sup>	Impact of spatial connectivity on occupancy	Colonization rate <sup>2</sup>	Impact of spatial connectivity on colonization rate	Extinction rate <sup>3</sup>	Impact of spatial connectivity on extinction rate
2003	0.75 ( <i>n</i> = 111)	$X^2_1 = 0.02$ ; $P < 0.90$		–		–
2004	0.70 ( <i>n</i> = 161)	<b><math>X^2_1 = 11.53</math>;</b> <b><math>P &lt; 0.001 (+)</math></b>	0.46 ( <i>n</i> = 28)	$X^2_1 = 2.44$ ; $P = 0.12$	0.24 ( <i>n</i> = 80)	<b><math>X^2_1 = 6.92</math>;</b> <b><math>P = 0.009 (-)</math></b>
2005	0.90 ( <i>n</i> = 182)	$X^2_1 = 3.55$ ; $P = 0.06 (+)$	0.77 ( <i>n</i> = 47)	$X^2_1 = 0.16$ ; $P = 0.69$	0.05 ( <i>n</i> = 108)	$X^2_1 = 0.36$ ; $P = 0.55$
2006	0.92 ( <i>n</i> = 177)	<b><math>X^2_1 = 15.35</math>;</b> <b><math>P &lt; 0.001 (+)</math></b>	0.71 ( <i>n</i> = 17)	<b><math>X^2_1 = 6.53</math>;</b> <b><math>P = 0.01 (+)</math></b>	0.06 ( <i>n</i> = 157)	<b><math>X^2_1 = 9.00</math>;</b> <b><math>P = 0.003 (-)</math></b>

<sup>1</sup>The fraction of trees infected by powdery mildew, with the total number of trees surveyed in each year given in brackets.

<sup>2</sup>The colonization rate is calculated as the fraction of trees infected in year *t* that were not infected in year *t*–1. Shown in brackets are the number of trees used in the analysis.

<sup>3</sup>The extinction rate is calculated as the fraction of uninfected trees in year *t* that were infected in year *t*–1. Shown in brackets are the number of trees used in the analysis.

chasmothecia in the soil, we replanted all trees into 50 liter pots before the start of the experiment. To assess the colonization of the trees by powdery mildew, each tree was surveyed for the presence and abundance of mildew during (15–23 July) and at the end of (28–30 August) the growing season. Abundance was scored on an ordinal scale: 0 = no mildew; 1 = small amounts of mildew, detectable only on close inspection; 2 = clearly visible infections, but only on a fraction of the leaves; 3 = the majority of the leaves are infected, but with some parts of the tree remaining without mildew; and 4 = the whole tree is infected. One tree died early in the season, and one tree disappeared between the two survey dates.

*Dispersal experiment II: the impact of distance, plant genotype and early-season exposure on mildew colonization*

To investigate how distance from the infection source, plant genotype and early-season exposure may affect the presence and abundance of powdery mildew, we distributed 186 grafted oak trees around another isolated oak stand (*c.* 520 m<sup>2</sup>) in southern Finland (60°36′57.7″ N 24°25′42.0″ E; Fig. 1A) in spring 2016. The grafted trees were produced by grafting of twigs from 12 large mother trees (one twig to each root stock, with all foliage of the root stock pruned after successful grafting). Henceforth, we will refer to grafts from each of the different mother trees as “*Plant genotypes*”. Each grafted tree was *c.* 1.2 m in height, and grown in a 50 liter pot. To investigate the impact of the early-season exposure, we divided the oak trees in two subsets: (1) oaks from set one (S<sub>1</sub>; *n* = 128 trees) were distributed into the matrix on 12 May, and (2) oaks from set two (S<sub>2</sub>; *n* = 58 trees) were initially located within the main oak stand and thereby exposed to a conducive environment with a high spore load, and were subsequently moved into the matrix between 29 June and 2 July. The majority of the trees (*n* = 137 trees) were

assigned a random location within 300 m from the source stand. To study long-distance dispersal, we placed 49 trees further away in the matrix in each of the four cardinal directions: 800 m to the North (*n* = 13), 940 m to the East (*n* = 12), 1,160 m to the South (*n* = 12) and 1,770 m to the West (*n* = 12) of the source stand, with distances varying according to logistic constraints. Beyond the source stand, there were a few scattered trees in the surrounding area, but preliminary simple and multiple regression analyses indicated that these did not influence parasite colonization. Hence, we assume that the majority of the infections on the experimental trees originated from the central oak stand. To assess the colonization of the oak trees by *E. althitoides*, we recorded the presence of mildew at the tree level, as well as on each of ten randomly selected leaves per tree. The survey was conducted between 10 and 13 September.

*Analyses*

*Colonization and extinction dynamics in the field.*—To investigate the impact of spatial connectivity on the metapopulation dynamics of the powdery mildew, we fitted a separate generalized linear model to each of three key descriptors of metapopulation dynamics: incidence, extinction and colonization (Hanski 1999). Each variable was modelled as a function of spatial connectivity, assuming a binomial distribution and a logit-link. We used the function *glm* in R 3.3.2 (R Core Team 2016) to fit the model, and assessed significance using the function ANOVA in the package *car* (Fox and Weisberg 2011).

*Dispersal experiment I: the impact of distance and habitat type on mildew colonization.*—Since the design of Experiment 1 was not fully balanced (with only zero-distances represented in the “*Oak stand*”), we used a two-step approach to explore the impact of habitat type and distance from the infection source on the colonization of trees

by the oak powdery mildew. First, we modelled the presence and abundance of mildew as a function of “*Habitat type*” (Oak stand, Forest and Field). Next, we tested for signs of dispersal limitation by modelling the presence and abundance of mildew as a function of the continuous variable “*Distance from source*” (0, 37.5, 75, 150 and 300 m), separately for each habitat type. Individual models were run for mildew presence and abundance at two points in time: during and at the end of the growing season. To model the presence of infection (0/1), we used the function *glm*. Models on mildew abundance (an ordinal response variable) were implemented using function *brm* in the package *brms* v. 1.1.0 (Bürkner in press), which provides a Bayesian implementation of the cumulative model; to evaluate significance, we used the function *hypothesis* (adopting a two-sided test with parameter alpha set to 0.05).

*Dispersal experiment II: the impact of distance, plant genotype and early-season exposure on mildew colonization.*—To explore the impact of distance from the infection source, plant genotype and early-life exposure on colonization by powdery mildew, we modelled the presence of mildew at two hierarchical scales (i.e., the leaf and tree level) as a function of the continuous variable “*Distance*”, “*Plant genotype*” (i.e., the grafted trees, as produced from  $n = 12$  mother trees) and “*Early-season exposure*” (reflecting whether the oak trees were placed in the oak stand or in the matrix during the early season). We used two response variables: the presence of infection at the tree level (0/1), and the proportion of infected leaves at the tree level. The former we modelled assuming a binary distribution and a logit link, the latter using a quasibinomial distribution, thus accounting for observed overdispersion (Pearson’s  $X^2$  divided by the residual degrees of freedom = 5). To fit the models, we used the function *glm*.

## RESULTS

### *Colonization and extinction dynamics in the field*

The field survey revealed patterns indicative of metapopulation dynamics, including frequent colonizations and extinctions of mildew populations on individual trees (Table 1). The occupancy patterns and spatial dynamics of the powdery mildew were strongly affected by the spatial location of the oak trees: mildew prevalence was higher in dense oak stands in two out of 4 yr, colonization rate was higher in areas with higher spatial connectivity in one out of three years, and extinction rate was lower in dense oak stands in two out of 3 yr (Table 1, Appendix S1: Fig. S1). Occupancy, colonization rate and extinction rate varied considerably among years (Table 1).

### *Dispersal experiment I: the impact of distance and habitat type on mildew colonization*

During the growing season (in July), there was a strong impact of habitat type on mildew colonization:

all twelve trees within the oak stand were infected, and all but two trees in the forest outside of the oak stand were infected, but only a single tree in the open field was infected ( $X^2_2 = 68.87$ ,  $P < 0.001$ ; Fig. 2A). As the trees within the oak stand were all located at distance zero, the high infection level in the oak stand may be due either to a high spore load or to the oak stand providing an environment conducive to infection. A similar pattern was detected for mildew abundance, which was highest on trees in the oak stand, intermediate on trees in the forest outside of the oak stand, and very sparse on the single infected tree in the open field ( $P < 0.05$  for all pair-wise comparisons; Fig. 2B). In the closed forest, we detected an effect of distance from the infection source on mildew abundance ( $P < 0.05$ ; Fig. 2C).

At the end of the growing season (in September), the majority of trees (62 out of 69) were infected by mildew (Fig. 2A). Nonetheless, we found strong variation among habitat types in the presence of infection ( $X^2_2 = 13.60$ ,  $P = 0.001$ ; Fig. 2A): all uninfected trees ( $n = 7$ ) were located in the open field, with five of them at the largest distance from the infection source (300 m). As in July, mildew abundance was highest in the oak stand, intermediate in the closed forest, and lowest in the open field ( $P < 0.05$  for all pair-wise comparisons; Fig. 2B). At the end of the season, there was no relationship between the distance from the infection source and mildew abundance in the forest habitat (Fig. 2C;  $P > 0.05$ ). In contrast, both infection probability and abundance decreased with distance in the open field (both  $P < 0.05$ ; Fig. 2D).

### *Dispersal experiment II: the impact of distance, plant genotype and early-season exposure on mildew colonization*

The colonization of leaves and trees was strongly affected by distance from the source stand, early-season exposure and plant genotype (Fig. 3; Table 2). More specifically, the probability of a tree being infected was higher for trees that were placed in the oak stand during the early season (Fig. 3A; Table 2), varied strongly among plant genotypes (Fig. 3C; Table 2), and decreased with distance from the infection source (Fig. 3E; Table 2). The proportion of leaves infected on a tree showed a similar pattern: the infection probability of leaves was higher on trees that were placed in the oak stand during early leaf development (Fig. 3B; Table 2) and varied among plant genotypes (Fig. 3D; Table 2). However, there was an interaction between the early-season environment and distance (Fig. 3F; Table 2), where leaves on trees placed in the matrix during the early-season showed a trend ( $X^2_1 = 3.42$ ,  $P = 0.06$ ) towards decreased infection level with increasing distance from the oak stand. By contrast, for trees located in the oak stand during the early-season and later moved into the matrix habitat, we found no relationship between distance and infection ( $X^2_1 = 0.89$ ,  $P = 0.35$ ). Plant genotype did not detectably change the impact of the

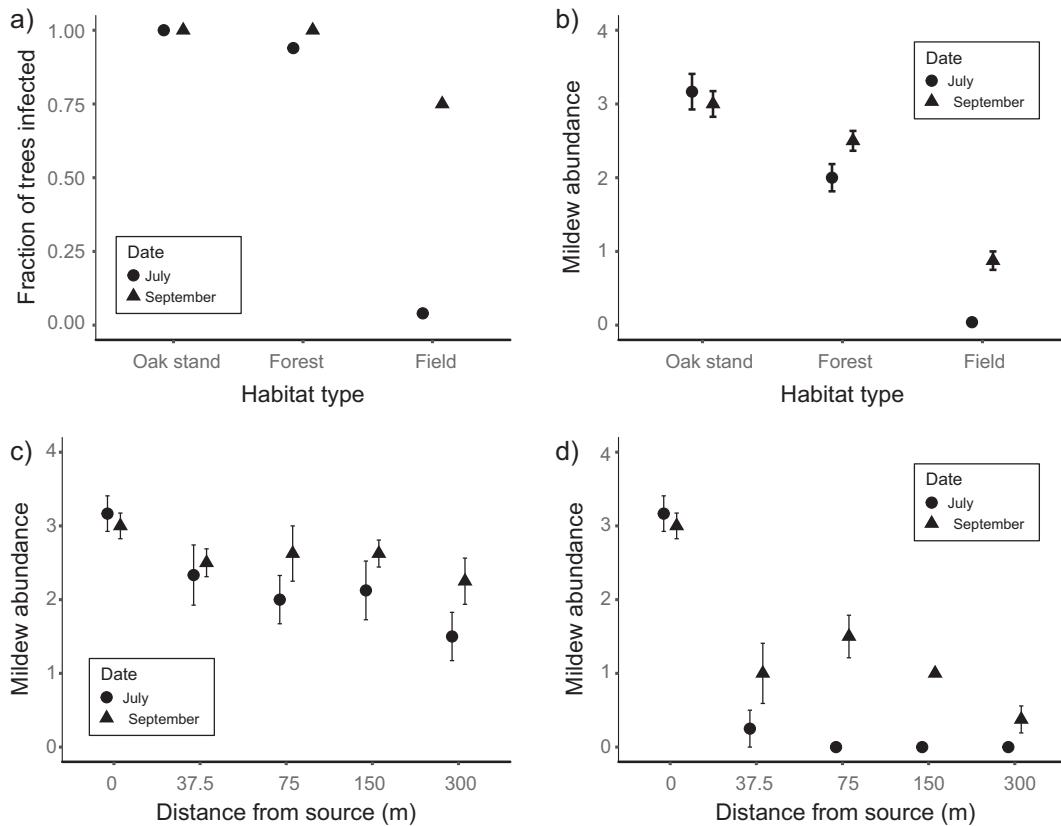


FIG. 2. The impact of habitat type and distance from infection source on the colonization of oak trees (*Quercus robur*) by the powdery mildew *Erysiphe alphitoides*. The upper panels show the impact of habitat type on (a) the fraction of trees infected and (b) mildew abundance. The lower panels illustrate the impact of distance from the infection source on mildew abundance in the (c) forest habitat and (d) open field. Shown are means  $\pm$  SE. Note that there were no oak trees growing in the forest habitat.

early-season environment or distance from the source on mildew presence at either the tree or leaf level (Table 2; no significant interactions involving genotype).

DISCUSSION

This paper reveals a joint impact of dispersal, host genotype and environment on the dynamics of a parasite in the wild. The field survey of occupancy and turnover patterns demonstrated that the parasite persists as a metapopulation, with frequent extinctions and colonizations. Occupancy and colonization rates were lower, and extinction rate higher, in more isolated trees, indicating some degree of dispersal limitation. This interpretation was supported by our two multi-factorial dispersal experiments, both revealing an imprint of dispersal limitation in parasite dynamics. These experiments also identified a role for host genotype and environment, which each played an equally large, or even larger, role in the spatial dynamics of the parasite than did dispersal. Overall, our findings illustrate how dispersal, environment and host genotype jointly shape the spatial

dynamics of a wild plant parasite on a prominent tree at the landscape scale.

*The role of dispersal and environment in shaping colonization dynamics*

Even though parasites may occasionally or regularly disperse at the global and continental scale (Brown and Hovmöller 2002, Viana et al. 2016), they are likely to be limited by colonization at some spatial scale(s). It is thus of interest to assess the shape of the colonization kernel, the spatial scale at which species are dispersal-limited, and how the abiotic and biotic environment mediates dispersal limitation. Our findings illustrate that, in the forest habitat, there was a significant decrease in mildew abundance with distance during the growing season. However, this pattern was mainly characterized by the very high abundance of mildew on trees growing within the source stand (i.e., at distance zero), whereas there was no significant decrease in colonization pressure over distances ranging from tens of meters to a few hundred meters. This observation suggests that the majority of spores land within

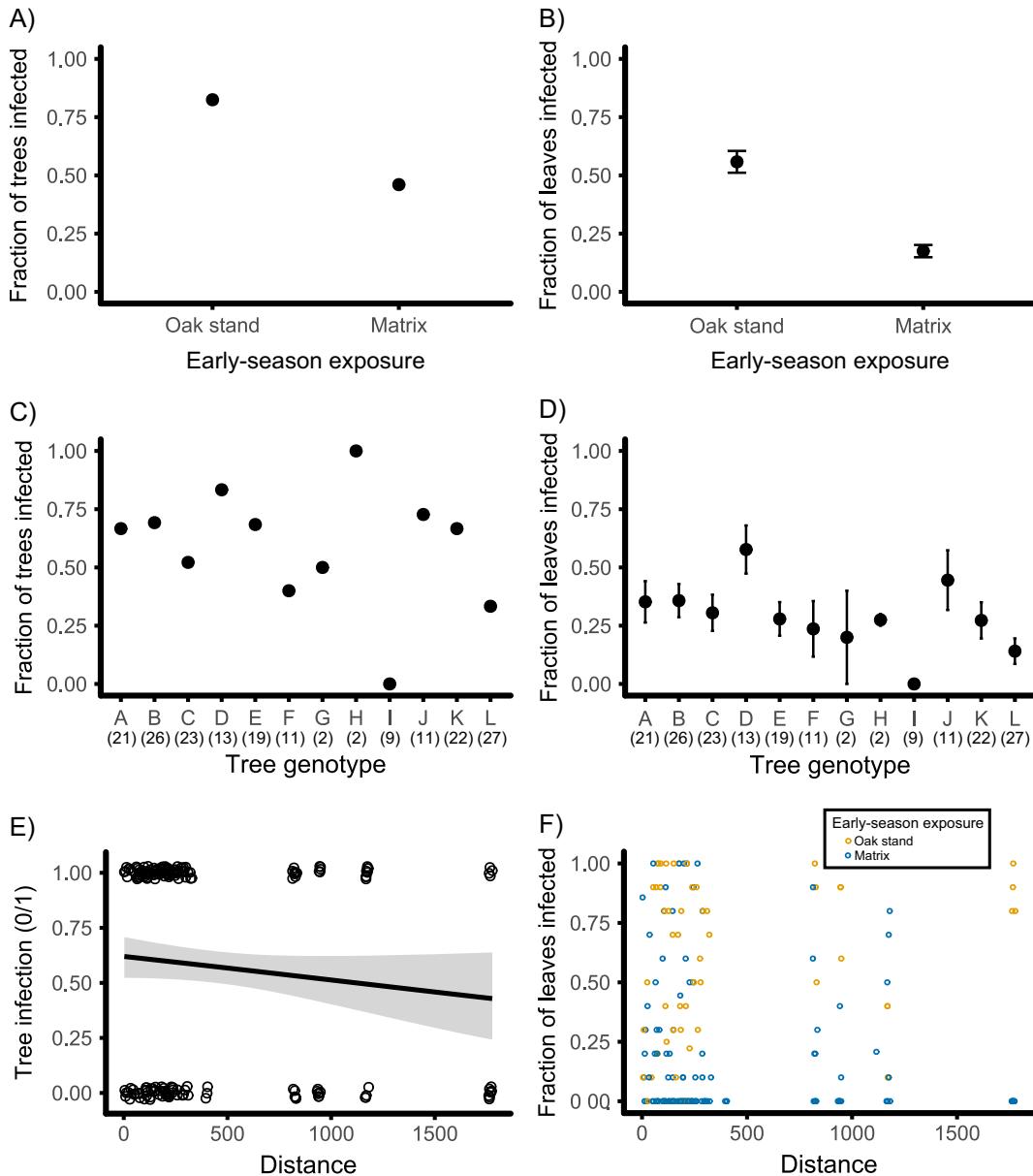


FIG. 3. The impact of early-season exposure, plant genotype and distance from infection source on the colonization of oak trees (*Quercus robur*) by the powdery mildew *Erysiphe alphitoides*. The upper panels show the impact of the early-season exposure (i.e., whether they were placed in the oak stand during the early season or not) on the (A) presence and (B) abundance of powdery mildew. The middle panels show the effect of plant genotype on the (C) presence and (D) abundance of mildew, with the number of replicates per genotype between brackets on the x-axis. The bottom panels show the impact of distance from the infection source on the (E) presence and (F) abundance of powdery mildew. Shown in panels B and D are means  $\pm$  SE; panel E shows the presence/absence of mildew on each of the trees (as represented by the vertically-jittered, open circles), as well as a trend line fitted to the presence/absence data using function *stat\_smooth* in *ggplot2* (assuming a binomial distribution); and panel F shows the fraction of leaves infected (where each open circle is an individual tree).

meters or tens of meters from the infection source, and that the colonization kernel in the forest is relatively flat across distances from tens to hundreds of meters. Alternatively, the environment created by the oak trees in the oak stand may have had a major impact on the probability of infection and pathogen growth. While we regard the former explanation more likely, it will require validation by

future studies. In accordance with both interpretations, trees placed in the oak stand early in the season (and later moved to the matrix) sustained high infection levels.

Patterns compatible with the processes detected in our experiments are also apparent in natural oak forests. Here, heavy mildew infections of small oak trees are most frequently observed on treelets growing under heavily

TABLE 2. The impact of early-season exposure (“environment”), plant genotype and distance from infection source on the colonization of oak trees (*Quercus robur*) by the powdery mildew *Erysiphe alphitoides*. Shown are  $X^2$ -values and associated  $P$ -values from a generalized linear model fitted to the data from dispersal experiment II. Significant values are highlighted in bold.

	Tree infection	Proportion of leaves infected
Distance	$X^2_1 = 5.32$ ; $P = 0.02$	$X^2_1 = 0.658$ ; $P = 0.42$
Genotype	$X^2_{11} = 37.69$ ; $P < 0.001$	$X^2_{11} = 37.43$ ; $P < 0.001$
Environment	$X^2_1 = 27.55$ ; $P < 0.001$	$X^2_1 = 55.52$ ; $P < 0.001$
Distance * Genotype	$X^2_{11} = 9.86$ ; $P = 0.04$	$X^2_{11} = 7.77$ ; $P = 0.73$
Distance * Environment	$X^2_1 = 0.86$ ; $P = 0.35$	$X^2_1 = 4.23$ ; $P = 0.04$
Genotype * Environment	$X^2_9 = 10.99$ ; $P = 0.28$	$X^2_9 = 10.30$ ; $P = 0.33$
Distance * Genotype * Environment	$X^2_8 = 5.59$ ; $P = 0.69$	$X^2_8 = 8.23$ ; $P = 0.41$

infected mature oak trees (A.J.M. Tack, personal observation). Likewise, Farber et al. (2017) demonstrated that in the wheat stripe rust *Puccinia striiformis* f. sp. *tritici*, eighty percent of the new lesions appeared within 0.69 meter from the infection source. In one of the few experimental studies examining parasite dispersal across distances ranging from tens to hundreds of meters, Mullett et al. (2016) showed that the colonization pressure of the pine pathogen *Dothistroma septosporum* was high within the pine stand, but decreased sharply within tens of meters from the infection source. Notably, in the forest habitat we detected no effect of distance from the source on mildew abundance at the end of the growing season, when the majority of trees exhibited high or very high infection levels. A similar pattern was found for the rust fungus *Melampsora larici-populina* along the Durance River valley in the French Alps (Becheler et al. 2016). Here, the pathogen overwinters on larch trees (the host of the sexual parasite generation) growing upstream in the valley, and each year spreads down the valley on the poplar trees (the asexual host). While there is a sharp decline in infection levels across tens of kilometers at the onset of the growing season, this pattern becomes less apparent at the end of the growing season (Becheler et al. 2016). Notably, the earlier arrival of the disease on trees close to the infection source translates into a higher overall disease load across the season (i.e., the area under the disease progress curve; Agrios 2005), with possible implications for tree fitness.

In contrast to the patterns detected in the forest habitat, we resolved a clear signature of dispersal limitation in the field habitat. Here, both mildew presence and abundance consistently decreased with distances from tens to hundreds of meters across the entire season. Interestingly, more than half of the trees situated at the longest distance (300 m) escaped infection, thus further

attesting to the observations that isolated, small oak trees may enter disease-free space.

The higher infection levels observed in the forest habitat as compared to the field habitat may be due to the effect of the environment on different parts of the dispersal process. First, propagule dispersal may differ between habitats (Plantegenest et al. 2007, Clobert et al. 2012), and reduced airflow and higher turbulence in the forest habitat may influence propagule movement and deposition (Aylor 1990, Hussein et al. 2013). Likewise, survival of spores may be higher in the forest habitat, where there is less UV radiation and higher air humidity. Second, the probability of infection, as well as subsequent parasite growth, may differ between the two habitats due to differences in the direct effect of abiotic conditions like humidity, shade and temperature on the infection process (Schnathorst 1965, Duniway 1979, Jarosz and Burdon 1988) – or, equally likely, due to indirect effects of the abiotic environment as mediated by plant traits. For example, oak leaves grown in the sun and shade are readily distinguishable as based on characteristics such as leaf thickness and secondary chemistry (Barber and Marquis 2011, Sevillano et al. 2016). Assessing which abiotic and biotic factors play a role during the movement and settlement stage will be a promising avenue for future research.

Importantly, the imprint of dispersal limitation found in the field survey, as indicated by an effect of spatial connectivity on occupancy, extinction and colonization, was consistent with the dispersal limitation detected in our two single-source dispersal experiments conducted at the very same scale. This suggests that even for parasites with the potential for long-distance dispersal, dispersal limitation may play an ecologically-relevant role and can, at least in some instances, be inferred from multi-year surveys of metapopulation dynamics. In our multi-year survey, isolated trees proved less likely to be become colonized by mildew, and were characterized by both higher extinction rates and lower occupancy. The lower extinction rate on highly connected oak trees may be ascribed to a “rescue effect”, where the extinction of the mildew population during winter is compensated by efficient re-colonization during the growing season (Brown and Kodric-Brown 1977).

#### *The role of dispersal and plant genotype in shaping parasite epidemiology*

While many studies on parasites have demonstrated the impact of host genotype on infection dynamics in natural (Laine et al. 2011, Busby et al. 2013) and agricultural (Flor 1955) systems, few experiments have simultaneously disentangled the impact of host genotype and dispersal on colonization in a natural setting. Here, we find strong variation among host genotypes in colonization by powdery mildew, independent of the distance between the focal tree and the infection source. Such variation is consistent with patterns detected in a previous study (Roslin et al. 2007), where tree-specific mildew

populations proved locally adapted to their host. Likewise, a recent study by Pohjanmies et al. (2015) across the same landscape documented ample genetic variation among oaks, and found an imprint of the genetic diversity of oaks on the local insect community structure (but see Tack et al. 2010). All three patterns attest to a role for host genotype as a driver of the eco-evolutionary dynamics of mildew across this landscape.

The impact of both plant genotype and dispersal distance on colonization by a powdery mildew was also demonstrated by Tack et al. (2014): while the powdery mildew pathogen *Podosphaera plantaginis* showed limited dispersal across a small spatial scale (i.e., up to 60 cm), some plant genotypes remained uninfected, irrespective of the distance from the infection source. In the current study, we did not detect clear evidence that plant genotypes consistently avoided infection (the only exception was tree genotype I, of which all nine replicates remained uninfected; Fig. 3C, E). This may either suggest that oak trees lack qualitative resistance, or that populations of oak powdery mildew – like the majority of parasite populations (Tack et al. 2012b) – consist of a mixture of strains which differ in their infectivity. Under such a scenario, each oak tree genotype can be attacked by at least one parasite strain (cf. Roslin et al. 2007).

*The role of dispersal, plant genotype and the environment in shaping parasite metapopulation dynamics in the field*

Taken together, our findings illustrate the patterns, and underlying mechanisms, of the persistence of the powdery mildew pathogen within a heterogeneous and fragmented landscape: (1) the field survey indicates that the powdery mildew persists as a metapopulation, with relatively frequent extinction and colonization events, (2) the first dispersal experiment demonstrates how spatial heterogeneity in the environment may strongly impact the colonization process, with large differences in infection prevalence and severity between the forest and field habitat, and (3) the second dispersal experiment indicates that host genotype may be an important component of patch quality. A strong effect of the environment and host genotype on the infection dynamics in the field is matched by several studies that combined field surveys with laboratory inoculations (Carlsson-Granér and Thrall 2002, 2015, Duffy and Sivars-Becker 2007, Jousimo et al. 2014).

In terms of dispersal propensity, our findings illustrate that spore dispersal can, at least in some habitat types and in some years, be a limiting factor. Here, the first dispersal experiment illustrated that, within a single landscape and a single year, the environment can strongly affect the spatial scale of dispersal limitation: while there was no sign of dispersal limitation in the forest habitat across distances up to 300 m at the end of the season, both the prevalence and severity of infection decreased strongly with distance in the field habitat. Interestingly, the field surveys indicated that the role of dispersal was

inconsistent among years, with trees in dense oak stands showing higher levels of occupancy and colonization, and lower extinction, in some years but not in others. In accordance, the nineteen-year study of the rust pathogen *Triphragmium ulmariae* on the wild plant *Filipendula ulmaria* illustrates that the relative impact of environmental factors, and dispersal limitation, varies among years (Smith et al. 2011). In our study, the relatively weak imprint of dispersal across several hundreds of meters in the second dispersal experiment indicates that, at least in some years and in some landscapes, dispersing spores frequently reach distances of a kilometer. Overall, we hope that future studies of the long-term dynamics of oak powdery mildew, as combined with experiments manipulating single or multiple environmental factors, will pinpoint the identity of relevant environmental factors during the different stages of the dispersal process, and provide a predictive understanding of how the identity and relative importance of environmental factors varies among landscapes and among years in shaping the parasite metapopulation dynamics.

#### CONCLUSION

Theory and small-scale experiments have identified the factors that may drive host-parasite dynamics. Here, we provide empirical evidence that dispersal limitation, host genotype and the environment may jointly shape the spatial dynamics of a wild plant parasite at a landscape scale. Importantly, dispersal limitation was only apparent in the field experiments in some environments, and in the multi-year field survey in some years, indicating that the relative importance of different factors will vary in space and time. Overall, we hope that our study will stimulate comparable studies in other host-parasite systems, with the aim to: (1) assess the degree of generality of our findings across study systems, (2) identify the characteristics of the study system, species traits and spatial and environmental variables that underlie differences in the factors that shape parasite dynamics, and (3) offer further integration between theory, small-scale experiments and parasite dynamics in the field.

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