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Associational resistance to both insect and pathogen damage in mixed forests is modulated by tree neighbour identity and drought

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Abstract

1. Tree health declines can be caused by interactions between pests and pathogens and many studies have shown a reduction in their damage in mixed species forests compared to monocultures. Yet few authors have considered tree diversity effects on both groups simultaneously. Moreover, it is unclear whether diversity effects on tree pests and pathogens are robust to changes in abiotic conditions, such as drought.
2. We addressed tree diversity effects on foliar insect herbivory, oak powdery mildew and their interaction under contrasting water regimes in a large-scale tree diversity experiment in SW France. Using an irrigation treatment that alleviated drought conditions, we were able to experimentally assess the effects of tree diversity under contrasting abiotic environments. We surveyed plots along a richness gradient from one to four tree species, in which a focal study species of oak (*Quercus robur*) was mixed with other oak species (*Q. pyrenaica* and *Q. ilex*) and a taller, broadleaved species (*Betula pendula*).
3. Increasing tree species richness lowered leaf miner abundance, leaf chewer damage and oak powdery mildew infection, consistent with a protective effect of resource dilution. However, richness effects on leaf miners were stronger in irrigated compared to non-irrigated blocks, indicating that environmental conditions can modulate diversity effects. Separate from the effect of tree species richness, the presence of birch in a plot increased damage by leaf choppers and powdery mildew, but lowered leaf miner damage, suggesting additional tree neighbour identity effects potentially linked to modulation of microclimate. We found a negative association between leaf miner abundance and oak powdery mildew, consistent with antagonism between oak damage agents.
4. *Synthesis*. Overall, our study illustrates the importance of considering both tree diversity and composition (neighbour identity) in designing forests more resistant to pest and pathogen damage.

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KEYWORDS

biodiversity, *Erysiphe alphitoides*, mixed forest, multi-trophic interactions, oak powdery mildew, plant apparency, plant vigour, *Quercus robur*

1 | INTRODUCTION

The importance of biodiversity for ecosystem functioning and services is being increasingly recognized globally (Cardinale et al., 2012; Isbell et al., 2017; van der Plas et al., 2016). In spite of this, most new forests are still planted as monocultures rather than mixed species forests (Nichols, Bristow, & Vanclay, 2006; Paquette et al., 2018). Over recent decades, much evidence has accumulated to suggest that mixed species forests can have higher levels of productivity (Chamagne et al., 2016; Jactel et al., 2018), stability to environmental changes (Morin, Fahse, de Mazancourt, Scherer-Lorenzen, & Bugmann, 2014; van der Plas et al., 2016) and resistance to abiotic and biotic disturbances (Jactel et al., 2017). Planting mixed species forests is often reported as reducing forest insect damage compared to monocultures, which has been supported by meta-analyses of evidence from planted and natural forests, and biodiversity-ecosystem functioning experiments (Castagnéyrol, Jactel, Vacher, Brockerhoff, & Koricheva, 2014; Jactel & Brockerhoff, 2007). The trend towards lower damage to hosts in more diverse ecosystems is termed associational resistance, as opposed to associational susceptibility (Barbosa et al., 2009). The impact of mixed forests on pathogens has been less extensively studied, but several papers report cases of associational resistance (Hantsch et al., 2014; Pautasso, Holdenrieder, & Stenlid, 2005). However, previous studies showed mixed forests do not always show associational resistance to pests and pathogens (Kambach, Kühn, Castagnéyrol, & Bruelheide, 2016; Schuldt et al., 2010), suggesting that associational effects may be context dependent, for instance, on abiotic conditions (Jactel, Poeydebat, van Halder, & Castagnéyrol, 2019).

There are at least three proposed mechanisms hypothesized to underpin reduced damage in mixed forests that can apply to both insect pests and pathogens. Firstly, when total tree density is approximately constant, increasing tree diversity will reduce susceptible host density. This thereby reduces the availability of breeding substrate for a pest or pathogen, meaning it is less likely to build up to population epidemic levels—the dilution effect (Civitello et al., 2015). Secondly, associational resistance in mixed stands may be driven by a reduction in herbivore ability to locate and reach its resource in the presence of non-host neighbour trees. Reduced physical apparency of a focal host when surrounded by taller heterospecific neighbours has been shown to reduce insect herbivory (Castagnéyrol, Giffard, Péré, & Jactel, 2013; Damien et al., 2016). Plant apparency may also be reduced through interference with chemical cues used by insects to locate hosts. For instance, Jactel, Birgersson, Andersson, and Schlyter (2011) found that the release of non-host volatile organic compounds impacted the ability of the

pine processionary moth to find its host in mixed species stands. Thirdly, and leading from the second hypothesis, tree diversity, and the particular species composition of mixed forests, can lead to alterations to microclimatic conditions (Ehbrecht, Schall, Ammer, & Seidel, 2017) with knock-on effects on pests and pathogens. In particular, differences in tree height between species can lead to alterations in canopy closure between plots differing in tree diversity (Muiruri & Koricheva, 2017). Alterations to the abiotic environment (such as changes to light availability, temperature and humidity) can all have direct impacts on pests and pathogens' survival or performance (Dillon & Meentemeyer, 2019; Jactel, Koricheva, & Castagnéyrol, 2019; Stoepler & Lill, 2013), as well as indirect effects via changes to tree leaf traits, such as secondary metabolites (Castagnéyrol, Jactel, & Moreira, 2018; Forey et al., 2016; Walter et al., 2012).

Previous studies of the impacts of tree diversity on pest organisms have mostly considered either insect herbivores or fungal pathogens in isolation rather than both groups simultaneously on the same trees (for instance, on oak: Castagnéyrol et al., 2013; Hantsch et al., 2014; Moore, Warrington, & Whittaker, 1991). Yet, fungi and insects can have reciprocal interactions on each other's performance through multiple biological mechanisms (Fernandez-Conradi, Jactel, Robin, Tack, & Castagnéyrol, 2018; Tack, Gripenberg, & Roslin, 2012). This reduces our ability to understand if the same mechanisms of associational effects apply to both pests and pathogens, and if multi-trophic interactions alter the outcome of associational effects. Initial damage by primary pests or pathogens may lead to opportunistic colonization of a stressed tree by secondary pests or pathogens, for instance by altering leaf chemical defences or phenology (Adams et al., 2013; Marçais & Bréda, 2006). For example, it has been reported that high leaf insect defoliation on pedunculate oak *Quercus robur* early in the season can induce changes to oak phenology by promoting the growth of second flush shoots ('lammas shoots') that are infected by oak powdery mildew, a specialist biotrophic (developing on living host tissue) pathogen (Delatour, 1983; Glazebrook, 2005; Marçais & Desprez-Loustau, 2014). Sequential attack by insect herbivores and pathogens on the same host plant may trigger different plant defence signalling pathways, leading to cross-talk between pathways and antagonistic or facilitative interactions between attackers (Erb, Meldau, & Howe, 2012; Pieterse, Van der Does, Zamioudis, Leon-Reyes, & Van Wees, 2012). For instance, a meta-analysis showed that herbivores inducing the jasmonic acid defence signalling pathway (such as leaf miners and chewers) reduced subsequent damage by herbivores inducing the salicylic acid defence pathway, the pathway also used by biotrophic pathogens (Moreira, Abdala-Roberts, & Castagnéyrol, 2018). Dependent on the study system, any effect of tree diversity on insects may therefore have indirect effects on

pathogens, and *vice versa*. Unravelling the complex interactions between insect pests and fungal pathogens will shed light on the still poorly understood mechanisms underpinning the effects of tree diversity on resistance to biotic hazards (Castagneyrol et al., 2017; Schuldt et al., 2017).

The environmental context in which biotic interactions are embedded has recently been shown to influence the effects of tree diversity on pests and pathogens. For example, Castagneyrol, Jactel, et al. (2018) found that leaf insect herbivory on birch increased with tree species richness, but only under drought conditions. Drought stress can have strong plant-mediated effects on both insects and pathogens (Desprez-Loustau, Marçais, Nageleisen, Piou, & Vannini, 2006; Jactel et al., 2012). The Plant Stress Hypothesis predicts an increase in insect damage under conditions of plant water stress, for instance, due to changes to leaf defensive chemistry or C:N ratio (Walter et al., 2012; White, 1974). Similarly, for pathogens, the 'predisposition concept' (Schoenweiss, 1986) argues that water stress can predispose plants to infection by opportunistic plant pathogens. There is also emerging evidence that drought impacts on forests are altered by tree diversity (Grossiord, 2019). Drought could modulate diversity effects on insects and pathogens, for instance, if water stress impacts tree growth, in turn impacting associational effects. So-called 'neighbour modulated' or 'bottom-up' impacts of drought on diversity effects, where neighbours modify plant responses to drought, have been shown in several studies, although the mechanisms at play are still elusive (Castagneyrol, Moreira, & Jactel, 2018; Forrester, Theiveyanathan, Collopy, & Marcar, 2010; Grossiord, Granier, Gessler, Jucker, & Bonal, 2014).

In this study we used a tree diversity experiment in SW France to investigate how different components of tree diversity (species richness, host dilution, tree apparency) altered insect herbivore and fungal pathogen damage. We further asked whether tree diversity effects on a specialist fungal pathogen (oak powdery mildew) were influenced by tree diversity effects on insect herbivory. Finally, we asked whether independent and interactive effects of tree diversity on insect herbivore and pathogen damage were altered under drought (ambient drought conditions vs. irrigation treatment). We tested the following hypotheses on focal oak hosts (*Quercus robur* L.):

1. increasing species richness and/or increasing resource dilution reduces damage by both oak insect herbivores and oak powdery mildew;
2. reducing plant apparency as a result of mixing oak with a much taller broadleaved species (birch) lowers mildew and herbivore damage more than predicted just from increasing tree species richness (impacts of neighbour identity as well as diversity);
3. more vigorously growing oaks (taller, with longer shoots) receive more damage by insect herbivores and higher mildew infection;
4. oak powdery mildew infection is positively associated with insect herbivore damage (i.e. a positive interaction between plant antagonists).
5. drought stress increases damage by insect herbivores (leaf chewers and leaf miners) and oak powdery mildew compared to irrigation conditions;
6. drought stress could alter the strength and direction of tree diversity effects on both insect herbivory and powdery mildew infection.

By considering both the abiotic context of tree diversity effects, and the potential for multi-trophic interactions, our work extends our current understanding of the mechanisms of tree diversity effects on insects and pathogens.

2 | MATERIALS AND METHODS

2.1 | Study system

Quercus robur is a widespread broadleaved tree species throughout the Western Palearctic harbouring a diverse insect herbivore community (Brandle & Brandl, 2001; Eaton, Caudullo, Oliveira, & de Rigo, 2016). In SW France, the main defoliating insects are leaf miners, chewers and skeletonizers, along with oak powdery mildew (*Erysiphe* sp.), a specialist foliar pathogen that is also the most common foliar pathogen on oaks in Europe (Marçais & Desprez-Loustau, 2014). It is caused by multiple cryptic species of ascomycete fungi of the genus *Erysiphe* with different phenological niches: *E. quercicola* infects oak buds and leaves, while *E. alphitoides* infects only leaves (Desprez-Loustau et al., 2018; Mougou, Dutech, & Desprez-Loustau, 2008). However, in the absence of molecular identification of mildew species, we use the term 'oak powdery mildew' to describe the pathogen.

In SW France, we observed that insect herbivore and oak powdery mildew damage were temporally and spatially separated on trees, due to oaks exhibiting indeterminate growth with multiple bud flushes occurring over the growing season. Most insect herbivore damage occurred on primary shoots from the first bud burst in late spring (April–May), with oak leaf quality then declining sharply over time for insects (Feeny, 1970; Tikkanen & Julkunen-Tiitto, 2003). Oak powdery mildew infection occurred on 'lammass' shoots resulting from subsequent bud bursts in mid-summer (July–August), as mildew ascospores are released from overwintering chasmothecia from June onwards (Marçais, Kavkova, & Desprez-Loustau, 2009). Oak powdery mildew infection success also declines rapidly with leaf age (Ayres & Edwards, 1982). Mildew infection success is therefore highest on young leaves produced from lammass shoots, with July generally being the peak period for mildew infection (Marçais & Desprez-Loustau, 2014; M.-L. Desprez-Loustau, pers. comm.).

2.2 | Experimental design

Data collection took place at a large tree diversity experiment in SW France planted in 2008, ORPHEE (44°44'00"N, 00°46'00"W). The ORPHEE

experiment follows a randomized blocked design (see Figure S1). Eight blocks covering 12 ha were established using five native tree species: three oak species (*Quercus robur*, *Quercus pyrenaica*, *Quercus ilex*) one other broadleaved tree species, silver birch *Betula pendula* and one conifer species, maritime pine *Pinus pinaster*. The experiment consists of eight blocks of 32 treatments each, in a fully factorial design for tree species richness spanning a gradient from monocultures to five species mixtures with all possible combinations. Each treatment combination is replicated once per block, plus an additional replication of the five species mixture giving a total of 32 treatment plots randomly distributed within each block. Each plot consists of 10 rows of 10 trees planted at 2-m spacing (100 trees per plot). Tree species were planted according to a systematic alternate pattern, so that each tree of a given species is surrounded by at least one tree of all other tree species present in a given composition. In addition, from 2015 an annual irrigation treatment has been applied at the block level from May–October to half of the blocks (irrigation + rainfall vs. rainfall only). Irrigation consists of sprinkling the equivalent of 3 mm precipitation per night and per experimental plot from a 2.30 m pole at the centre of each plot. This treatment is designed to alleviate the severe summer drought that is typical of the climate in this region. The irrigation treatment was previously shown to significantly increase the water content of plants and soil, and to increase summer predawn water potential (Castagneyrol et al., 2017; Castagneyrol, Jactel, et al., 2018) so will not be further described here.

We selected plots to survey along a tree diversity gradient, including all mixtures with the focal host *Q. robur* except those with pine, in order to focus on broadleaved species only. This spanned from *Q. robur* monoculture, three 2-species mixes with *Q. robur*, three 3-species mixes with *Q. robur* and the 4-species mix of the three oak species and birch, for a total of eight treatments. We chose these treatments in order to span a gradient of oak apparency, with apparency defined as the height of focal oaks relative to the mean height of surrounding trees (Castagneyrol et al., 2013). Birches are faster growing than oaks, thus at ORPHEE at the time of observation, birches were significantly taller than all three oak species (Figure S2; File S2). The apparency of focal oaks was therefore primarily driven by the proportion of birch in a plot, which we also corroborated by comparing canopy closure between treatments with and without birch (Figure S2; File S2). This allowed us to compare plots identical in tree species richness but differing in oak apparency. We surveyed blocks 1–6 (three irrigated, three non-irrigated blocks). Within each plot we randomly selected four *Q. robur* trees for damage assessment. We focused on *Q. robur* as it is an important species economically in Europe (Eaton et al., 2016), and is the most frequently studied of the three oak species planted, for example in relation to tree diversity, insect herbivory and oak powdery mildew, enabling better comparison with previous studies.

2.3 | Data collection

We recorded insect herbivory on primary shoots, and powdery mildew infection on lammas shoots, with the shoot types being easily

differentiated by a ring scar separating bud flushes. At the time of the survey, *Q. robur* was the only susceptible species to oak powdery mildew. No mildew was observed on *Q. ilex*, since evergreen oaks are known to be resistant to mildew (Marçais & Desprez-Loustau, 2014). No mildew was observed on *Q. pyrenaica* during the survey period, likely due to the later date of bud flush of this species (Marçais & Desprez-Loustau, 2014). Lammas shoots had not yet been produced on *Q. pyrenaica* when spores of oak mildew were released. For insect herbivores, we assessed damage by leaf chewers, skeletonizers and miners. Leaf galls were found to be very rare in the experiment at the time of surveying. Most leaf chewing and skeletonizing species present at ORPHEE have been found to be generalist species feeding on both oak and birch, while the leaf mining species present are specialists feeding on a narrow range of hosts within Fagaceae (Castagneyrol et al., 2013; Giffard, Jactel, Corcket, & Barbaro, 2012). Therefore, while *Q. robur* and birch may overlap in terms of leaf chewing and skeletonizing species, leaf miners are likely to feed only on the oak species present at ORPHEE.

As insect herbivory begins soon after primary bud flush in early spring, while powdery mildew infection begins later in the season, on lammas growth, we assumed that insect herbivory influenced powdery mildew infestation rather than the other way around. On each tree, we haphazardly chose eight shoots at a range of heights and angles around the tree, with both primary and lammas growth. Per primary shoot we haphazardly selected five leaves and recorded the number of mines per leaf, which was then summed at tree level (over 40 leaves). We classified damage by leaf chewers and leaf skeletonizers taken together into seven percentage classes per leaf: 0 (0%); 1 (1%–5%); 2 (6%–15%); 3 (16%–25%); 4 (26%–50%); 5 (51%–75%); 6 (more than 76%), as chewing damage was far more abundant than skeletonization, and some species act as both chewers and skeletonizers during different larval stages (B. Castagneyrol, pers. obs.) We refer to this group hereafter as ‘chewers’. Five leaves were haphazardly chosen on each lammas shoot, and percentage cover by mildew mycelium classified into five classes: 0 (0%); 1 (1%–25%); 2 (26%–50%); 3 (51%–75%); 4 (76%–100%), after previous authors (Bert, Lasnier, Capdevielle, Dugravot, & Desprez-Loustau, 2016; Field, Schönrogge, Barsoum, Hector, & Gibbs, 2019). Percentage damage by chewers and mildew was then averaged at the tree level (40 leaves) using the median point of each damage class. We also measured the length of each primary and lammas shoot (mm), as well as tree height (cm), to use as additional covariates.

2.4 | Statistical analysis

All analyses were completed in R version 3.5.1 (R Core Team, 2018). We analysed miner abundance, chewer damage and mildew infection at tree level using GLMMs (using `LME4` package in R, `glmer()` function), as our design was blocked with trees nested within plots within blocks. Since irrigation was applied at the whole block level, the ORPHEE experiment is akin to a split-plot design, with the block being the experimental unit for irrigation (see Figure S1). In addition to the tree level analysis, we performed the same analysis at shoot level (over five

leaves), to compare the results from identical models at different ecological levels. Results were almost identical between the sets of models, but residual checking plots showed that tree level models performed better in terms of model assumptions. Thus for the sake of clarity, we report tree level models only here, and results of shoot level models can be found in Supporting Information (Table S1). The following starting model equation was used (R syntax, variables in bold are fixed effects, * indicates interaction terms, (1|X) denotes random effects):

$$Y \sim \log(\text{Shoot Length}) + \text{Tree Height} + \text{Irrigation} \\ * (\text{Resource Dilution} + \text{Richness} + \text{Birch}) + (1|\text{Plot}) + (1|\text{Block}).$$

To analyse data at tree level, we averaged shoot length over the eight primary (herbivores) or lammas (mildew) shoots sampled, and log transformed to improve normality. Models of mildew included both primary and lammas shoot length, models of herbivory included only primary shoot length. No continuous variables were sufficiently strongly correlated to prevent inclusion in the same model (Figure S3). To assess the potential for a direct effect of herbivory on mildew, we included miner abundance and chewer damage at the tree level as explanatory terms in models of mildew. For miners, we fitted a negative binomial GLMM with log link, as initial GLMMs

fitted using the Poisson distribution were overdispersed (using the `glmer.nb()` function in R, from the `LME4` package). All other models were gaussian GLMMs with identity link.

We achieved minimal adequate models using backward selection of nonsignificant terms, starting with interactions. Tree species richness and resource dilution were highly correlated (Figure S4) and minimal adequate models included whichever of the two composition variables was most significant following model selection (Table 1). We chose to test the effects of both variables, as they carried different information despite being correlated. Resource dilution refers only to the focal host, *Q. robur*, while tree species richness (tree diversity) included the effects of adding other tree species. In other words, resource dilution was an estimate of focal host density and thus the hypothesized resources available to build up pest and pathogen populations, at least for leaf miners and mildew. Tree species richness, on the other hand, described the barriers to host colonization by dispersing propagules as a result of adding more non-host trees. We estimated model fit by calculating marginal (fixed effects only, R^2_m) and conditional (fixed and random effects, R^2_c) R^2 for each model, as in Nakagawa and Schielzeth (2013). We used residual checking plots to check whether model assumptions were met.

TABLE 1 Results of generalized linear mixed effect models testing the effects of plot composition and tree traits on oak powdery mildew and insect herbivory at shoot and tree level. Given are estimates, standard errors, likelihood ratio test results (χ^2 value, df and p value) and effect direction (+ indicating a positive effect of a variable, – indicating a negative effect of a variable), for minimal adequate models. Estimates for leaf miner and leaf chewer models are on the log scale. Note that for models with interaction effects, likelihood ratio tests cannot be calculated on the main effect without removing all interaction terms from the model, so are not reported here. R^2 values for each model are given in the final column, (R^2_m) = marginal R^2 including fixed effects only; (R^2_c) = conditional R^2 including both fixed and random effects

	Estimate	SE	χ^2	df	p	Direction	R^2_m (R^2_c)
Leaf miner abundance (N = 190)							0.12 (0.15)
Intercept	1.01	0.34					
Richness	0.084	0.096		1			
Presence of birch	-0.26	0.16		1			
Irrigation	0.58	0.30		1			
Log (primary shoot length)	0.29	0.073	15.92	1	<0.001	+	
Richness:irrigation	-0.35	0.14	7.28	1	0.0070	-	
Presence of birch:irrigation	0.46	0.23	4.25	1	0.039	+	
Leaf chewer damage (N = 190)							0.12 (0.15)
Intercept	2.87	0.15					
Resource dilution	-0.51	0.21	5.64	1	0.018	-	
Presence of birch	0.20	0.093	4.57	1	0.032	+	
Irrigation	-0.34	0.16	4.46	1	0.035	-	
Oak powdery mildew (N = 187)							0.12 (0.28)
Intercept	47.26	9.31					
Richness	-4.62	1.79	6.60	1	0.010	-	
Presence of birch	6.40	3.04	4.51	1	0.034	+	
Leaf miner abundance	-0.62	0.22	8.00	1	0.0047	-	
Log(lammas shoot length)	4.31	2.26	3.79	1	0.051	+	
Log(primary shoot length)	-9.52	2.41	15.45	1	<0.001	-	

3 | RESULTS

3.1 | Insect herbivory

3.1.1 | Leaf miners

The mean number of mines per tree was 8.60 ($SE = 0.41$). The effects of tree species richness and birch presence on miners were contingent on irrigation, with significant interactions between these variables and

irrigation (Table 1). Increasing tree species richness was associated with lower mine abundance, but only in irrigated blocks (Figure 1a). Overall, birch presence lowered mine abundance (Figure 1b). There were also differences in the effect of irrigation when birch was present or absent, with lower mine abundance in drought compared to irrigated conditions, but only in the presence of birch (Figure 1b). None of the other composition variables or their interactions with irrigation were significant predictors (Table 1). Primary shoot length had a highly significant positive effect on the number of mines (Table 1).

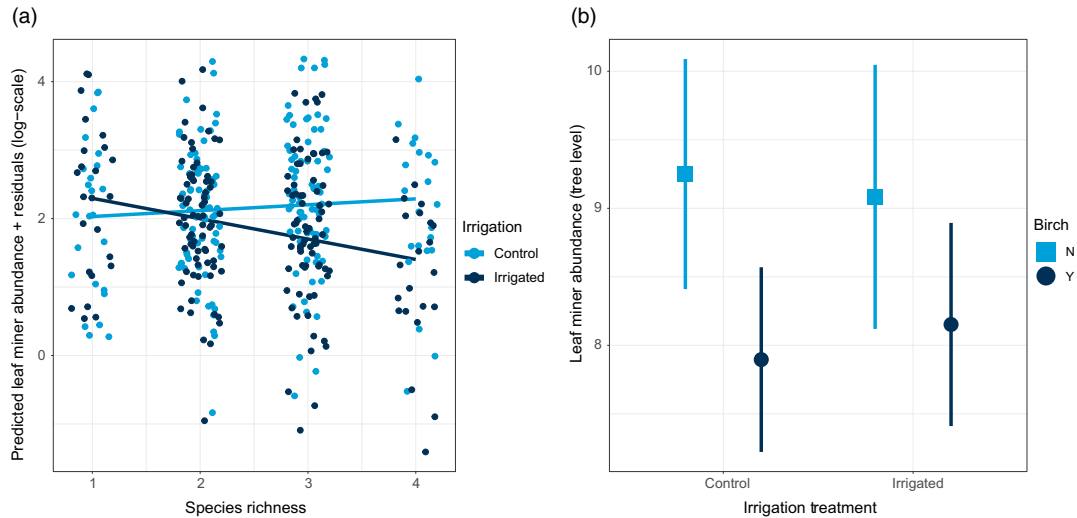


FIGURE 1 The effect of tree species richness and irrigation (a) and irrigation and birch presence (b) on leaf miner abundance. (a) Partial residual plot with the regression lines showing the strength of the relationship between tree species richness and leaf miner abundance when all other variables are held constant in the model. Model predictions are generated using observed values of miner abundance while holding all other continuous variables in the model constant at a mean value, and random effects set to zero. Points plotted are model predictions to which residuals from the minimal adequate model are added. (b) Points show mean of raw data (tree level), error bars are ± 1 standard error of the mean

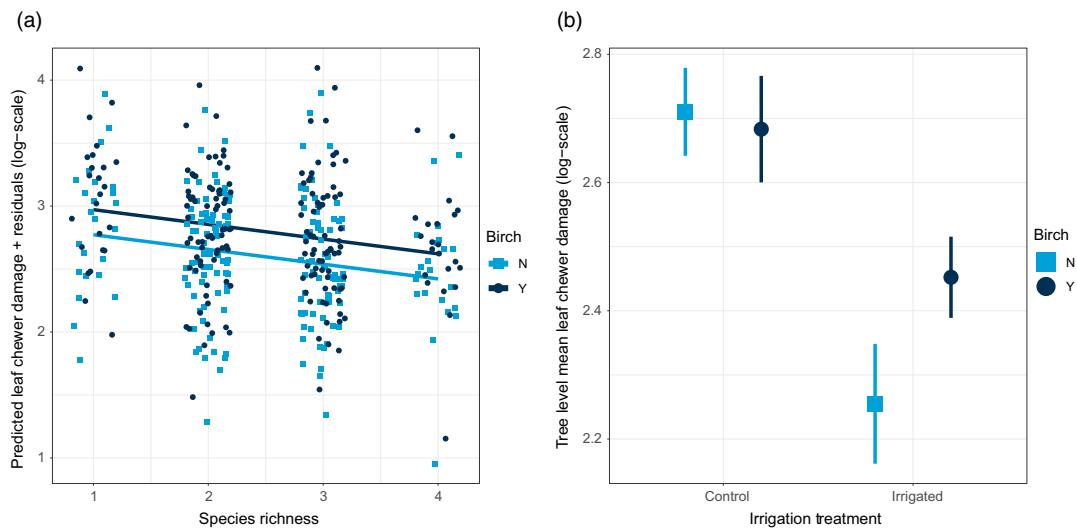


FIGURE 2 The effect of tree species richness and birch presence (a) and the effect of irrigation and birch presence (b) on leaf chewer damage. (a) Partial residual plot with the regression lines showing the strength of the relationship between species richness and leaf chewer damage when all other variables are held constant in the model. Model predictions are generated using observed values of chewer damage while holding all other continuous variables in the model constant at a mean value, and random effects set to zero. Points plotted are model predictions to which residuals from the minimal adequate model are added. (b) Points show mean of raw data (tree level), error bars are ± 1 standard error of the mean

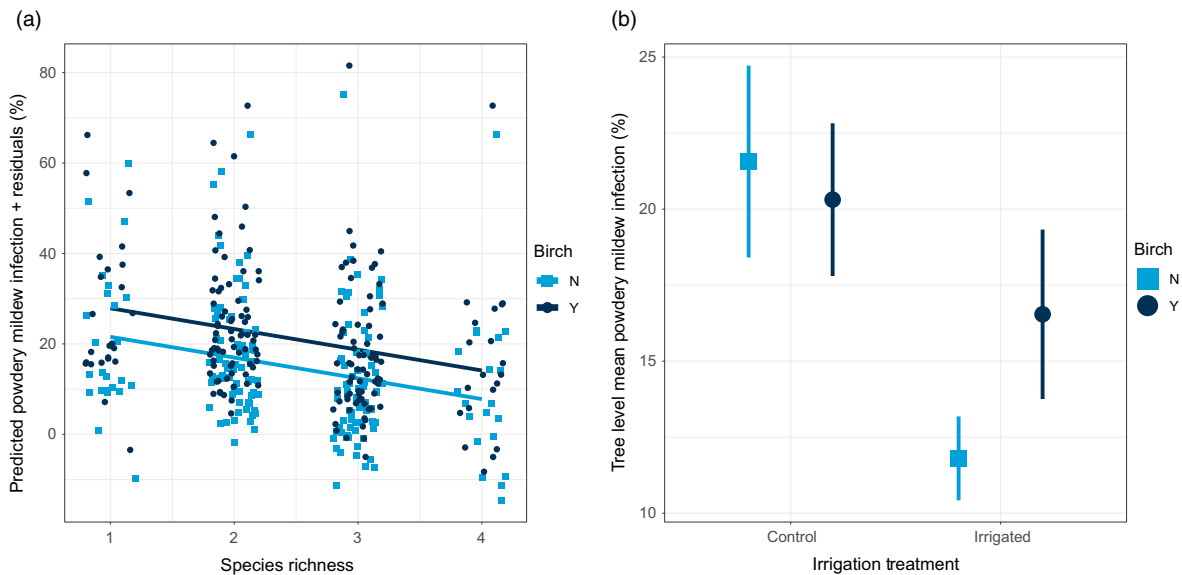


FIGURE 3 The effect of tree species richness and birch presence (a) and the effect of irrigation and birch presence (b) on oak powdery mildew infection. Partial residual plot with the regression lines showing the strength of the relationship between tree species richness and mildew infection when all other variables are held constant in the model. Model predictions are generated using observed values of species richness while holding all other continuous variables in the model constant at a mean value, and random effects set to zero. Points plotted are model predictions to which residuals from the minimal adequate model are added. (b) Points show mean of raw data (tree level), error bars are ± 1 standard error of the mean

3.1.2 | Leaf chewers

Mean chewer damage per tree was 13.54% ($SE = 0.58$). Chewer damage significantly decreased with increased tree species richness (Figure 2a). However, the presence of birch in a plot increased chewer damage (Figure 2a). Chewer damage also decreased with decreasing oak density, i.e. increasing resource dilution (Table 1), but not when included in the same model as richness, likely as the two variables were correlated (Figure S4). Chewer damage was significantly lower in irrigated compared to non-irrigated blocks (Figure 2b; Table 1). None of the interactions between composition variables and irrigation were significant, nor were the other covariates tree height and shoot length (Table 1).

3.2 | Oak powdery mildew

Mean mildew infection per tree was 17.85% ($SE = 1.29$). Increasing tree diversity had a negative effect on oak powdery mildew infection (Table 1; Figure 3a). Including resource dilution of *Q. robur* as a predictor post hoc instead of tree species richness also showed a consistent and significant negative effect on mildew (Table 1). Mildew infection significantly increased in the presence of birch (Figure 3b). Irrigation had no significant effect on mildew infection, either as main or interactive effect.

Longer primary shoots were associated with lower mildew infection, measured on lammas shoots on the same trees (Table 1). Longer lammas shoots were associated with higher mildew infection, but the effect was only marginally significant (Table 1).

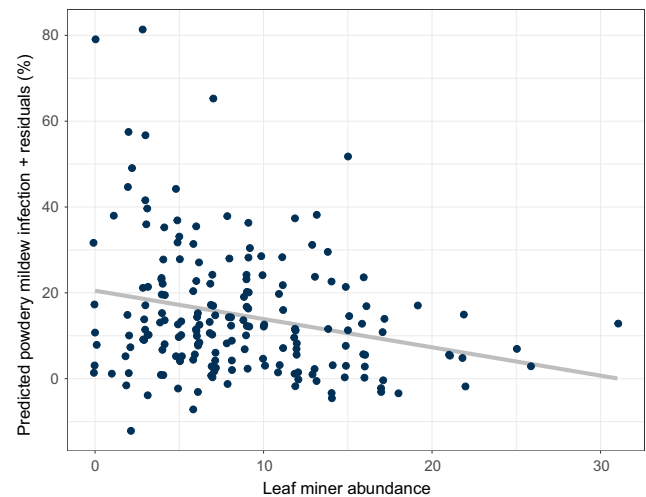


FIGURE 4 The relationship between leaf miner abundance and oak powdery mildew infection. Partial residual plot with the regression line showing the strength of the relationship between miner abundance and mildew infection when all other variables are held constant in the model. Model predictions are generated using observed values of miner abundance while holding all other continuous variables in the model constant at a mean value, and categorical variables constant at a single level. Points plotted are model predictions to which residuals from the minimal adequate model are added

Tree height was not a significant predictor of mildew infection (Table 1).

Powdery mildew significantly decreased with increasing abundance of leaf mines, measured on primary shoots on the same trees (Figure 4). The amount of leaf chewer damage did not impact mildew

infection (Table 1). One route for the negative association between primary shoot length and mildew could be an indirect effect, via the direct positive effect of primary shoot length on leaf miner abundance (Table 1). However, the fact that both primary shoot length and miner abundance had significant effects on powdery mildew rather suggests the two had independent direct effects (Table 1).

4 | DISCUSSION

In this study of a tree diversity experiment in SW France, increasing tree diversity reduced both oak insect herbivory and powdery mildew infection, while the presence of birch independently increased damage by all groups. In the case of oak leaf miners, tree diversity and neighbour identity effects were context dependent on drought stress. Our results show that tree diversity effects are dependent upon both abiotic context and the identity of species neighbours.

4.1 | Tree diversity promotes associational resistance to both herbivory and pathogen damage

In line with our hypothesis, increasing tree species richness lowered damage by oak insect herbivores and oak powdery mildew, which confirms the general pattern of associational resistance in temperate, mixed species forests and highlights its relevance to both pests and pathogens (Jactel et al., 2017). Earlier studies on oak in the same experiment (Castagneyrol et al., 2013) and elsewhere also found support for associational resistance with increasing tree species richness, for insect herbivores (Alalouni, Brandl, Auge, & Schädler, 2014; Moore et al., 1991; Setiawan, Vanhellefont, Baeten, Dillen, & Verheyen, 2014) and oak powdery mildew (Hantsch et al., 2014). It is likely that associational resistance to both herbivores and mildew was partially driven by increasing host dilution of *Q. robur* as richness increased, the two being conflated in this experiment (Castagneyrol et al., 2013; Figure S4). Indeed, resource dilution was a more significant predictor of leaf chewer damage than tree species richness, although both composition variables were significant predictors of leaf chewers and oak powdery mildew.

4.2 | Tree diversity effects can be dependent on environmental context

We hypothesized that the presence of birch, a taller tree species that is a non-host for oak powdery mildew and has the most separate insect herbivore community, would reduce focal oak apparency and thus lower mildew infection and herbivore damage on *Q. robur*. We found support for this hypothesis for miners, consistent with a previous study (Castagneyrol et al., 2013). However, both chewer damage and mildew infection were greater in the presence of birch (Figures 2 and 3), which could have occurred through both direct and indirect effects. Previous observations suggest that

leaf chewers at ORPHEE are more likely to be generalist herbivore species than leaf miners, with several species feeding on both *Quercus* and *Betula* (Castagneyrol et al., 2013). Thus, the presence of birch could have led to some spill-over onto neighbouring oak hosts, leading to associational susceptibility in the presence of birch (Barbosa et al., 2009). However, White and Whitham (2000) observed that associational susceptibility was only likely to occur when the preferred host was heavily defoliated, which is generally not the case for birches at ORPHEE (Castagneyrol, Jactel, et al., 2018).

A knock-on effect of birch on plot microclimate may therefore provide a stronger explanation for the positive effect of birch on herbivory. Increasing shading by adding birch could have directly modified the microclimate of plots; plots without birch had open canopies and thus high light intensity, as all three oak species were similar in height and had not yet formed closed canopies (Figure S2; File S2). High light has frequently been observed to negatively impact insect herbivores, by promoting a hot, dry microclimate unfavourable for insect development (Stiegel, Entling, & Mantilla-Contreras, 2017; Stoepler & Lill, 2013). However, some studies in temperate environments have also found evidence for increased insect activity in sunny versus shade conditions, in contrast to our finding for leaf chewers (Dudt & Shure, 1994; Mooney, Tiedeken, Muth, & Niesenbaum, 2009). For oak powdery mildew, previous studies reported conflicting results on the impact of light (Giertych & Suszka, 2010; Kelly, 2002). Microclimatic measurements taken from 2016 to 2018 suggested that the presence of birch buffered some climatic variability, which could have led to a more beneficial environment for leaf chewers and powdery mildew (Figure S6). Our finding that irrigation increased miner abundance, but only in plots containing birch, also suggests that the effect of birch could have been mediated by an effect on microclimate, interacting with irrigation.

Differences in insect and mildew damage in the presence of birch could also be explained by indirect effects of birch via changes to host plant traits (Dudt & Shure, 1994; Muiruri et al., 2019; Roberts & Paul, 2006). For instance, Roberts and Paul (2006) found that shading by other trees often increased foliar nutrition and reduced anti-herbivore foliar defences in focal trees, with correlated increases in insect abundance in shaded environments. Future work should prioritize linking changes in tree species composition with differences in microclimatic conditions, through to subsequent modification of plant traits, with implications for pest and pathogen damage.

We found that the effect of tree diversity on leaf miners was contingent on irrigation treatment. Mine abundance decreased with tree species richness, but only under irrigation conditions (Figure 1a). Neighbour-modulated effects on water use by trees have been noted by previous authors, for instance, differences in soil water uptake in mixed stands (Grossiord, 2019) as well as water use efficiency (Forrester, 2015). The interaction between stand composition and drought has in turn been shown to influence structural and chemical plant traits (Forey et al., 2016) and some studies have suggested

further cascading effects on insect herbivores (Castagneyrol, Moreira, et al., 2018; Kambach et al., 2016; Walter et al., 2012). Measurement of plant traits was not the main aim of our study, but future work should focus on measurement of multiple plant traits in differing plot compositions and abiotic contexts, to better disentangle the underlying mechanisms leading to associational effects on plant antagonists (Castagneyrol, Jactel, et al., 2018; Forrester et al., 2010; Grossiord, Gessler, et al., 2014).

We observed lower damage by leaf chewers in irrigated compared to non-irrigated blocks (Figure 2). This is consistent with the Plant Stress Hypothesis, which predicts greater defoliation under conditions of drought stress. This can be due to direct effects of the physical environment on the survival or performance of herbivores, and/or effects on leaf traits that impact plant palatability and nutritional quality for insect herbivores (Castagneyrol, Moreira, et al., 2018; Jactel et al., 2012; White, 1974). Microclimatic data indicated that irrigated blocks had lower variability in both summer temperature and humidity, which could have had a positive direct effect on leaf chewers (Figure S6). We did not measure plant traits associated with water availability on study trees, which was a limitation of our study. Despite a trend towards lower oak powdery mildew infection in irrigated blocks, this effect was nonsignificant in our models (Table 1). Again, along with light and humidity, the effect of host water stress on powdery mildews is subject to debate (Marçais & Desprez-Loustau, 2014), and it may be that the effective sample size of 6 (irrigation being applied at the block level) was not large enough in our experiment to disentangle water stress effects on oak powdery mildew.

4.3 | Impacts of shoot length and tree height

We predicted that both tree height and shoot length would be positive predictors of insect herbivory and oak powdery mildew, as has been seen in previous studies (Castagneyrol et al., 2013; Field et al., 2019; Gripenberg, Morriën, Cudmore, Salminen, & Roslin, 2007). We found partial support for this hypothesis, as at both the individual shoot and tree level, leaf mines were more abundant on longer shoots, and individual shoot length positively predicted mildew infection. This supports the Plant Vigour hypothesis, which predicts higher preference and/or performance of insects on more vigorous plant modules (Cornelissen, Wilson Fernandes, & Vasconcellos-Neto, 2008; Price, 1991). However, larger (taller) oaks were not significantly more attacked by leaf miners nor powdery mildew, in contrast to a previous study of both groups on *Q. robur* (Field et al., 2019). Longer shoots may be older shoots, with a longer time period to accumulate damage, but this would not explain why the same relationship was not observed for chewers, despite both miners and chewers being active from early spring. Alternatively, longer shoots could have differed in their defensive chemistry and/or C:N ratio with knock-on benefits on insects and mildew (Hajji, Dreyer, & Marçais, 2009; Hewitt & Ayres, 1976; Lerdau, Litvak, & Monson, 1994).

4.4 | Interaction between insect herbivory and pathogen damage

Contrary to our hypothesis and previous studies, we did not find evidence for a positive association between insect defoliation on primary growth and oak powdery mildew infection on lammas shoot growth (Field et al., 2019; Marçais & Desprez-Loustau, 2014). Leaf chewer damage was the main contributor to leaf defoliation (Figure S7) but was not a significant predictor of oak powdery mildew infection (Table 1). It may be that the level of defoliation we observed on primary growth was not high enough to significantly modify oak phenology, for instance, by promoting lammas shoot growth and therefore resource availability for mildew, one proposed mechanism for the interaction between herbivory and mildew (Delatour, 1983). We instead observed a negative effect of leaf miner abundance on oak powdery mildew (Table 1). The mechanism behind the negative effect of miner abundance on oak powdery mildew has not yet been investigated. However, previous work suggests that mining herbivores and mildew (biotrophic pathogens) induce separate plant defence cascades (jasmonic acid and salicylic acid signalling pathways respectively) that can be antagonistic, which could be tested experimentally in future (Moreira et al., 2018). As miner abundance and mildew infection both decreased with increasing tree species richness (Figures 1 and 3), at higher richness levels, the negative effect of miners on mildew could have been alleviated. However, as mildew infection continued to decline with increasing tree species richness regardless of mine abundance, this provides support for the importance of the dilution effect for this pathogen, as observed elsewhere (Hantsch et al., 2014).

5 | CONCLUSIONS

In addition to providing support for associational resistance in mixed forests to both insect herbivores and a specialist pathogen, we show that the identity of neighbouring species can impact upon associational effects. Adding birch, a fast-growing species that lowered oak apparency, reduced leaf mine abundance. In contrast, adding birch increased leaf chewer damage and powdery mildew infection. This could have resulted from spill-over from neighbouring birch hosts in the case of leaf chewers, and/or modified microclimatic conditions under birch canopy, leading to direct and indirect effects on oak chewers and mildew. Moreover, we found that the effect of tree diversity on leaf miners was contingent on water availability, suggesting bottom-up effects of water relations on tree growth that impacted associational effects. In addition, we found evidence for an antagonistic relationship between miners and mildew. Future work to disentangle the mechanisms underlying associational effects in tree diversity experiments could aim (a) to follow a more holistic approach and consider the response of the whole community of insects and microbes interacting with trees and (b) to characterize microclimatic differences and concurrent modifications to plant traits that are dependent on plot composition. This would provide support for the importance of considering both tree

species diversity and composition elements when designing mixed species plantations.

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AUTHORS' CONTRIBUTIONS

E.F., A.H., B.C. and H.J. conceived the study; all authors contributed to study design; E.F., B.C. and H.J. carried out fieldwork; E.F. analysed the data with input from B.C. and A.H.; E.F. wrote the manuscript. All authors commented on the previous and final versions of the manuscript.

DATA AVAILABILITY STATEMENT

Data from this study are available for download from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.zw3r2285j> (Field et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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