

RESEARCH ARTICLE

Spring phenology and pathogen infection affect multigenerational plant attackers throughout the growing season

Álvaro Gaytán^{1,2}  | Karl Gotthard^{2,3}  | Ayco J. M. Tack^{1,2} 

¹Department of Ecology, Environment and Plant Sciences, Stockholm University, Stockholm, Sweden

²Bolin Center for Climate Research, Stockholm University, Stockholm, Sweden

³Department of Zoology, Stockholm University, Stockholm, Sweden

Correspondence

Álvaro Gaytán

Email: alvarogaytan@live.com

Funding information

Bolin Centre for Climate Research; Svenska Forskningsrådet Formas, Grant/Award Number: 2015-03993 and 2021-03784

Handling Editor: Elisa Thébault

Abstract

1. Climate change has been shown to advance spring phenology, increase the number of insect generations per year (multivoltinism) and increase pathogen infection levels.
2. However, we lack insights into the effects of plant spring phenology and the biotic environment on the preference and performance of multivoltine herbivores and whether such effects extend into the later part of the growing season.
3. To this aim, we used a multifactorial growth chamber experiment to examine the influence of spring phenology on plant pathogen infection, and how the independent and interactive effects of spring phenology and plant pathogen infection affect the preference and performance of multigenerational attackers (the leaf miner *Tischeria ekebladella* and the aphid *Tuberculatus annulatus*) on the pedunculate oak in the early, mid and late parts of the plant growing season.
4. Pathogen infection was highest on late phenology plants, irrespective of whether inoculations were conducted in the early, mid or late season. The leaf miner consistently preferred to oviposit on middle and late phenology plants, as well as healthy plants, during all parts of the growing season, whereas we detected an interactive effect between spring phenology and pathogen infection on the performance of the leaf miner. Aphids preferred healthy, late phenology plants during the early season, healthy plants during the mid season, and middle phenology plants during the late season, whereas aphid performance was consistently higher on healthy plants during all parts of the growing season.
5. Our findings highlight that the impact of spring phenology on pathogen infection and the preference and performance of insect herbivores is not restricted to the early season, but that its imprint is still present – and sometimes equally strong – during the peak and end of the growing season. Plant pathogens generally negatively affected herbivore preference and performance, and modulated the effects of spring phenology. We conclude that spring phenology and pathogen infection are two important factors shaping the preference and performance of

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial](https://creativecommons.org/licenses/by-nc/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

© 2022 The Authors. *Journal of Animal Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.

multigenerational plant attackers, which is particularly relevant given the current advance in spring phenology, pathogen outbreaks and increase in voltinism with climate change.

KEYWORDS

pathogen, performance, preference, *Quercus robur*, spring phenology, voltinism

1 | INTRODUCTION

Plant-based food webs consist of a large diversity of insects and microbes, each with a distinct phenology and life-history (Mattson, 2012; Price, 1997; Real & Brown, 2012). Climate change has already advanced spring phenology of many of these plants, insects and microorganisms, which has resulted in changes in plant-based species interactions (Bellemin-Noël et al., 2021; Lehmann et al., 2020; Menzel et al., 2006; Nanninga et al., 2017; Schwartzberg et al., 2014) and increased pest and disease outbreaks (Ahanger et al., 2013; Isaev et al., 2018). Beyond shifts in phenology, climate change has also increased the number of generations of a large number of herbivore species (Gaytán et al., 2022a). For example, many insect species that used to be univoltine (i.e. they had a single generation per growing season) have now become multivoltine, and are now present within the community at several, sometimes distinct, periods of the growing season (Altermatt, 2010). These climate-induced changes in spring phenology, disease dynamics and the number of herbivore generations may have profound consequences for the ecology and evolution of food webs. Despite this, we lack insights into the impact of spring phenology on the preference and performance of multi-generational insects across the growing season, as well as how these interactions may be modified by the presence of other species within the food web.

Plants with different spring phenology commonly co-exist within populations and landscapes, and such differences in spring phenology of plants can have pronounced effects on the preference and performance of insect herbivores (Despland, 2018; Posledovich et al., 2015; Tack et al., 2010; Toftegaard et al., 2019). However, the sign and strength of this effect is highly variable, with some studies reporting positive (Coyle et al., 2010; Ekholm et al., 2020), negative (Fowler & Lawton, 1984; Niemelä, 1983) or no effects (Chen & Poland, 2009; Scheirs et al., 2002) of earlier spring phenology on herbivore preference and performance. Most studies on the effect of spring phenology have focused on herbivores feeding in the early season, and we lack insights into the effect of spring phenology during the summer and autumn. The few studies that reported on the impact of spring phenology on the preference and performance of the same species of plant-feeding insects during different parts of the growing season show mixed results (Chen & Poland, 2009; Coyle et al., 2010; Fowler & Lawton, 1984; Niemelä, 1983; Scheirs et al., 2002). Two studies found a consistent preference for, or a better performance on, early or late phenology plants during all parts of the growing season (Coyle et al., 2010; Niemelä, 1983), one study

reported a preference for early phenology plants during the early season and for late phenology plants during the late season (Fowler & Lawton, 1984), and two studies found no impact of spring phenology on herbivore preference and performance during any part of the growing season (Table 1). Although each generation of a multivoltine herbivore may be confronted with the same set of plants, they will be faced with a different plant-trait landscape, and we do not know whether different herbivore generations will have the same preference for and performance on certain plant individuals. For example, if herbivores prefer particular plant individuals because of specific trait combinations, changes in those traits throughout the growing season might explain seasonal shifts in insect preference and performance. Although the effect of plant-level variation in spring phenology is often assumed to leave a weaker imprint on plant traits and biotic interactions during the middle and late parts of the growing season, we still lack quantitative data on this.

Spring phenology may also affect other plant attackers, like plant pathogens. Young leaves are commonly more susceptible to fungal pathogens than mature leaves and we can thus expect higher infection levels on late phenology plants when infection takes place in spring, whereas spring phenology may have a weaker or no impact on infection levels when infection takes place during summer or autumn (Jain et al., 2019). Infections of plants by pathogens may strongly affect the preference and performance of herbivores, with plant-feeding insects generally avoiding or performing worse on (heavily) infected plants, which commonly have lower nutritional value (Fernandez-Conradi et al., 2018). Still, only very few studies have assessed the combined effect of spring phenology and biotic factors such as pathogen infection on herbivore preference and performance, especially during multiple parts of the growing season (Table 1; Chen & Poland, 2009). Importantly, spring phenology and pathogen infection may interactively shape the preference and performance of multivoltine herbivores during the different parts of the growing season. For instance, herbivores may prefer plants with a late spring phenology in the absence of pathogen infection, but prefer more resistant early phenology plants when pathogen infection in the population is high.

With global warming, multivoltinism has become more common (Altermatt, 2010; Gaytán et al., 2022a; O'Neill et al., 2012), and at the same time other changes are happening in the plant food web. For example, leaves have started to flush earlier in spring (Menzel et al., 2006; Nanninga et al., 2017), and pathogen infection levels have increased, at least for some pathogen species (Ahanger et al., 2013; Isaev et al., 2018). The climate-induced changes in plant phenology, biotic context and multivoltinism might affect insect

TABLE 1 Overview of studies that report on the impact of spring phenology on the preference and/or performance of one or multiple plant-feeding insects during different parts of the growing season

Study	Preference and/or performance	Herbivore	Host	Experimental manipulation of spring phenology	Experimental manipulation of other factors	Seasons	Key findings
Chen and Poland (2009)	Performance	Chewing insect (<i>Agrillus planipennis</i>)	<i>Fraxinus pennsylvanica</i>	Yes	Light intensity Foliar chemistry	Early and mid	No effect of plant-spring phenology on herbivore performance
Coyle et al. (2010)	Preference and performance	Chewing insect (<i>Phyllobius oblongus</i>)	<i>Acer saccharum</i>	No	No	Early and late	The herbivore preferred late phenology plants during the early and late season, but the pattern was weaker during the late season The herbivore performed better on late phenology plants during all parts of the growing season
Fowler and Lawton (1984)	Preference	Aphids, free feeders, leafhoppers and leaf miners	<i>Betula pendula</i>	Yes	No	Early and mid	Generally, herbivores preferred early phenology plants during the early season and late phenology plants during the late season
Niemelä (1983)	Preference and performance	Free feeders (macrolepidoptera)	<i>Quercus robur</i> <i>Prunus padus</i> <i>Populus</i> spp. <i>Betula</i> spp. <i>Alnus</i> spp.	No	No	Early, mid and late	Specialists preferred late phenology plants during all parts of the growing season Generalists performed better on early phenology plants during all parts of the growing season
Scheits et al. (2002)	Preference and performance	Leaf miner (<i>Chromatomyia miii</i>)	<i>Holcus lanatus</i>	Yes	No	Early, mid and late	No effect of plant-spring phenology on herbivore preference and performance

preference and performance. In this study, we examined the impact of spring phenology on plant pathogen infection, as well as the independent and interactive effects of spring phenology and pathogen infection on the preference and performance of multigenerational herbivores on the pedunculate oak *Quercus robur* during a full growing season. For this, we used a two-step approach. First, we tested the influence of timing of spring germination on infection by oak powdery mildew *Erysiphe alphitoides*. Second, we conducted a multi-factorial experiment to identify the influence of spring phenology and pathogen infection on the preference and performance of a leaf miner (Lepidoptera: *Tischeria ekebladella*) and an aphid (Hemiptera: *Tuberculatus annulatus*). More specifically, we examined the impact of spring phenology on the severity of oak powdery mildew infection during the early, mid and late season, as well as the impact of spring phenology, pathogen infection and their interaction on the preference and performance of multigenerational herbivores during the early, mid and late season. By exploring the impact of spring phenology and pathogen infection on the preference and performance of multiple multigenerational plant attackers during different parts of the season, this study contributes to our understanding of the ecological and evolutionary consequences of climate-induced changes in spring phenology for plant-based food webs.

2 | MATERIALS AND METHODS

2.1 | Study system

The pedunculate oak *Q. robur* (Fagaceae) is distributed widely in Europe, and it reaches the northern part of its distribution in Fennoscandia (Petit et al., 2002). In Sweden, oak budburst generally takes place during late May, while leaf senescence starts between late August and early September (Ekholm et al., 2019). The pedunculate oak harbours a diverse community of generalist and specialist insects belonging to different feeding guilds, including several leaf miners and sap-sucking insects (Southwood, 1961). Among the leaf miners, *T. ekebladella* (Lepidoptera: Tischeriidae) is found in most of Europe, where it is univoltine in the northernmost part of its range, and bivoltine or multivoltine in the southern part of its distributional range (Jordan, 1995; Oishi & Sato, 2009; Yefremova et al., 2013). The leaf miner overwinters as larva inside a silk cocoon and pupates in early spring, resulting in a first generation of adults during the early season (Jordan, 1995). The oligophagous oak aphid *T. annulatus* (Aphididae) is a sap-sucking insect that is common on oak. It has multiple asexual generations during the early, middle and sometimes later parts of the growing season. The oak aphid reproduces sexually before overwintering (Stern, 2008). Oak trees in Europe are frequently attacked by the oak powdery mildew *E. alphitoides* (Desprez-Loustau et al., 2018). In autumn, this specialist biotrophic fungus produces overwintering structures (chasmothecia). In early spring, the sexual spores within the chasmothecia are released and infect oak leaves. The oak powdery mildew reproduces with asexual spores (conidia) during the remainder of the growing season, resulting

in multiple asexual generations (Faticov et al., 2020). For this study, all species were collected in the area of Stockholm (Sweden), and plant attackers were reared and maintained in colonies sustained on healthy seedlings of *Q. robur* within growth chambers before the experiments. Our study did not require ethical approval.

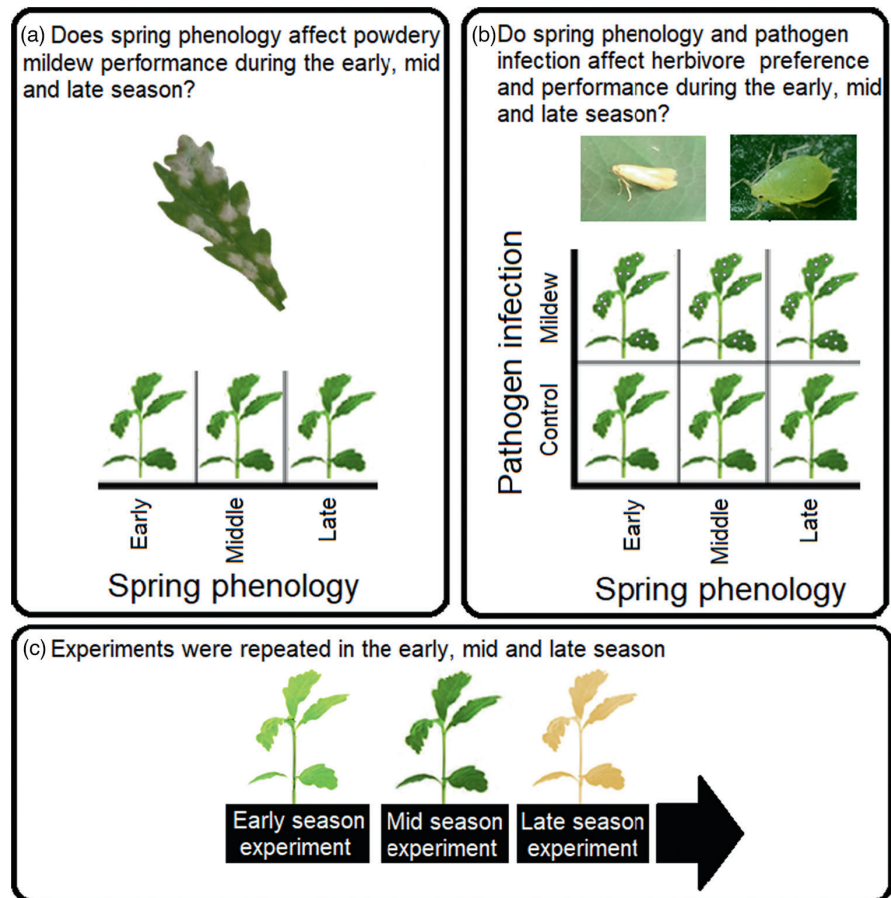
2.2 | Establishment of phenological treatments

To investigate the impact of germination date (henceforth the seedling-level trait 'spring phenology'; cf. Allstadt et al., 2015; Badeck et al., 2004; Flynn & Wolkovich, 2018; McClory et al., 2021) on pathogen infection and attack by the different generations of herbivores, we established groups of seedlings with early, middle and late phenology, matching the natural variation in phenology observed in Stockholm area, Sweden (Figure 1). We planted early phenology seedlings on 9 April 2019 ($n = 210$), middle phenology seedlings on 21 April 2019 ($n = 210$), and late phenology seedlings on 3 May 2019 ($n = 210$) from randomly collected acorns from multiple oak trees collected in Stockholm area. Since we were interested in the effects of changes in plant development during the growing season (rather than changes in the abiotic environment), we grew our study plants in a growth chamber at 23°C and 20h of light. Yet, in the end of August, we shortly induced leaf senescence by placing seedlings in a chamber with 12°C and 8 h of light per day for 10 days, as we regarded it as more reflective of natural plant development when leaf senescence was induced at the start of autumn. Importantly, leaf senescence was induced before conducting the late season experiment. Hence, temperature and light conditions were similar during the experiments conducted in the early, mid and late season. Each seedling was only used for a single experimental trial to avoid confounding effects. Seedlings were watered ad libitum to a tray placed underneath the plant pot, thereby avoiding direct contact between the water and the oak powdery mildew.

2.3 | The effect of spring phenology on pathogen performance

To assess the impact of spring phenology on oak powdery mildew performance, we infected 10 plants from each of the early, middle and late phenology treatments by gently brushing the upper leaf surface with asexual spores (Figure 1a). To investigate seasonal changes in the effect of spring phenology on pathogen infection, we repeated the same experiment during the early (28 May 2019), mid (14 July 2019) and late season (18 September 2019; Figure 1c). All leaves were scored 6, 9, 12, 16 and 20 days after infection. For each leaf, we visually estimated pathogen infection as the percentage of leaf surface covered by oak powdery mildew using the following categories: 0%, 1%–5%, 6%–10%, 11%–15%, 16%–20%, 21%–25%, 26%–30%, 31%–40%, 41%–60% and >60%. For statistical analyses, we calculated the infection level at the plant-level by averaging the midpoints of each category across the seedling's leaves.

FIGURE 1 Overview of the experimental design. (a) To investigate the impact of spring phenology on oak powdery mildew performance, we established three treatments in early spring: (1) early phenology, (2) middle phenology and (3) late phenology plants. (b) To investigate the joint impact of spring phenology and pathogen infection on the preference and performance of leaf miners and aphids, we established six treatments in early spring: (1) early phenology, no infection, (2) early phenology, infection, (3) middle phenology, no infection, (4) middle phenology, infection, (5) late phenology, no infection and (6) late phenology, infection. (c) As the influence of spring phenology on pathogen infection and herbivore preference and performance might change during the growing season, we repeated the experiment in the early, mid and late parts of the growing season



2.4 | The effect of spring phenology and pathogen infection on herbivore preference and performance

To investigate the impact of spring phenology and pathogen infection on the preference and performance of different generations of multivoltine herbivores, we infected 90 seedlings from each phenological treatment with oak powdery mildew and left 90 seedlings from each phenological treatment uninfected. We carried out inoculations by gently brushing the upper part of the leaves with mildew spores when the seedling had its first developed leaves (van Dijk et al., 2020). As inoculations for all phenological treatments were carried out when the plant was most susceptible (i.e. when the first leaves developed), all phenological treatments had similar levels of pathogen infection. Our multifactorial design consisted of six treatment combinations by crossing the three phenology states (early, middle, late) with infection (infected or uninfected; Figure 1b). For both the leaf miner (*T. ekebladella*) and aphid (*T. annulatus*), we conducted preference and performance experiments during the early (28 May 2019), mid (14 July 2019) and late season (18 September 2019; Figure 1c). While both species are known to have multiple generations, each species has a distinct life-history, thereby dictating differences in the exact timing and methods of the experimental trials. Below, we describe the experimental details separately for the two species.

2.4.1 | Preference and performance of the leaf miner *Tischeria ekebladella*

To assess oviposition preference and larval performance of the leaf miner, we placed six oak seedlings (one seedling per treatment combination) and one moth pair ($\delta\phi$) in a 40×30×50cm rearing cage. As it is uncommon for eggs of *T. ekebladella* not to develop a mine (Gripenberg et al., 2010; Tack et al., 2010, 2012), we assessed oviposition preference as the presence of leaf mines on each plant after 12 days. We repeated the experiment in the early ($n = 7$ cages), mid ($n = 9$) and late ($n = 9$) season with the three subsequent herbivore generations. To assess larval performance, we recorded mine size and larval survival on the plants from the preference experiment. We calculated mine size as the mine length × mine width, and monitored larval survival for the first and second generation (the third generation larvae overwinter).

2.4.2 | Preference and performance of the aphid *Tuberculatus annulatus*

To assess aphid preference, we placed six oak seedlings (one seedling per treatment combination) in a rearing cage and placed five wingless nymphs on each plant ($n = 10$ rearing cages). After 6 days, we scored preference by recording the number of aphids

on each plant. We scored aphid preference after 6 days because it is a time frame too short for reproduction (Stern, 2008), avoiding confounding aphid preference with performance. To assess aphid performance, we conducted a separate experiment, where we placed five wingless nymphs on plants from each treatment combination that were individually covered with a pollination bag ($n = 10$ plants per treatment combination). As a measure of performance, we recorded aphid population size after 21 days. Each experiment was carried out in the early, mid and late season in the growth chamber.

2.5 | Statistical analyses

To analyse the effect of spring phenology on pathogen performance, and the joint effects of phenology and pathogen infection on herbivore performance, we ran likelihood ratio χ^2 tests using the framework of (generalized) linear mixed effects models using the functions *glm*, *lmer* and *glmer* from the *base* and *LME4* packages in R (Bates et al., 2015; R Development Core Team, 2020). All the predictors were categorical. We assessed model fit using the diagnostic tools in the *sjPlot* and *DHARMA* packages (Hartig, 2020; Lüdtke, 2020), tested for statistical significance using the function *Anova* in the *CAR* package (Weisberg, 2019), and selected final models by backward selection with a cut-off *p*-value of 0.05 (Crawley, 2013). We conducted post-hoc comparisons using the function *pairs* in the R-package *LSMEANS* (Lenth, 2016). The model structures, transformations and link functions are summarized in Table S1.

2.5.1 | The effect of spring phenology on pathogen performance

To investigate the effect of spring phenology on pathogen performance during the early, mid and late season, we modelled the percentage infection on each plant as a function of spring phenology, days after infection and season. To assess whether the effect of spring phenology on pathogen infection changed with days after infection, we included the interaction between spring phenology and days after infection. As the effects of spring phenology and days after infection on pathogen infection levels may differ between the early, mid and late season, we included all two and three-way interactions between spring phenology, days after infection and season. We included *plantID* as a random factor to account for repeated measures on the same set of plant individuals (i.e. 6, 9, 12, 16 and 20 days after infection).

2.5.2 | The effect of spring phenology and pathogen infection on herbivore preference

To analyse the impact of spring phenology and pathogen infection on the preference of leaf miners and aphids during the early, mid

and late season, we modelled the presence of mines (1/0) and the number of aphids as functions of spring phenology, presence of pathogen infection and season. As the effect of spring phenology on the preference of herbivores may depend on pathogen infection, we included the interaction between spring phenology and presence of pathogen infection. As the effect of spring phenology and pathogen infection on herbivore preference may differ between the early, mid and late season, we included the two- and three-way interactions between spring phenology, presence of pathogen infection and season. For the presence of mines, we specified a binomial distribution with a logit link, and for the number of aphids, we specified a Poisson distribution with a log link. To account for the shared environment in each cage, we included *CageID* as a random factor.

2.5.3 | The effect of spring phenology and pathogen infection on herbivore performance

To analyse the impact of spring phenology and pathogen infection on the performance of leaf miners and aphids during the early, mid and late season, we modelled mine size, larval survival of the leaf miner and population size of the aphid, as functions of spring phenology, presence of pathogen infection and season. We included the interaction between spring phenology and presence of pathogen infection, as well as the two- and three-way interactions between spring phenology, presence of pathogen infection and season. For mine size, we specified a Gaussian distribution with identity link, for larval survival a binomial distribution with a logit link, and for aphid population size a Poisson distribution with a log link. As we had instances with multiple mines on the same plant, we included *PlantID* as a random factor in the mine size model. To account for non-independence and overdispersion, we included *CageID* as a random effect in the larval survival model, and *PlantID* in the aphid population size model, respectively.

3 | RESULTS

3.1 | The effect of spring phenology on pathogen performance

Pathogen infection was higher during the early and mid season than during the late season (Figure 2; Table 2; Table S2). Infection differed among phenological classes, with late phenology plants sustaining higher infection levels (Figure 2; Table 2; Table S3). The impact of plant spring phenology on pathogen infection differed among seasons (Figure 2; Table 2; Table S4). In the early season, mildew infection levels were highest on the late phenology seedlings, whereas infection levels were similar for early and middle phenology seedlings (Figure 2a; Table S4). In the mid season, mildew infection levels were highest on middle and late phenology plants, whereas none of the early phenology seedlings became infected (Figure 2b; Table S4). During the late season, mildew infection levels were highest on late

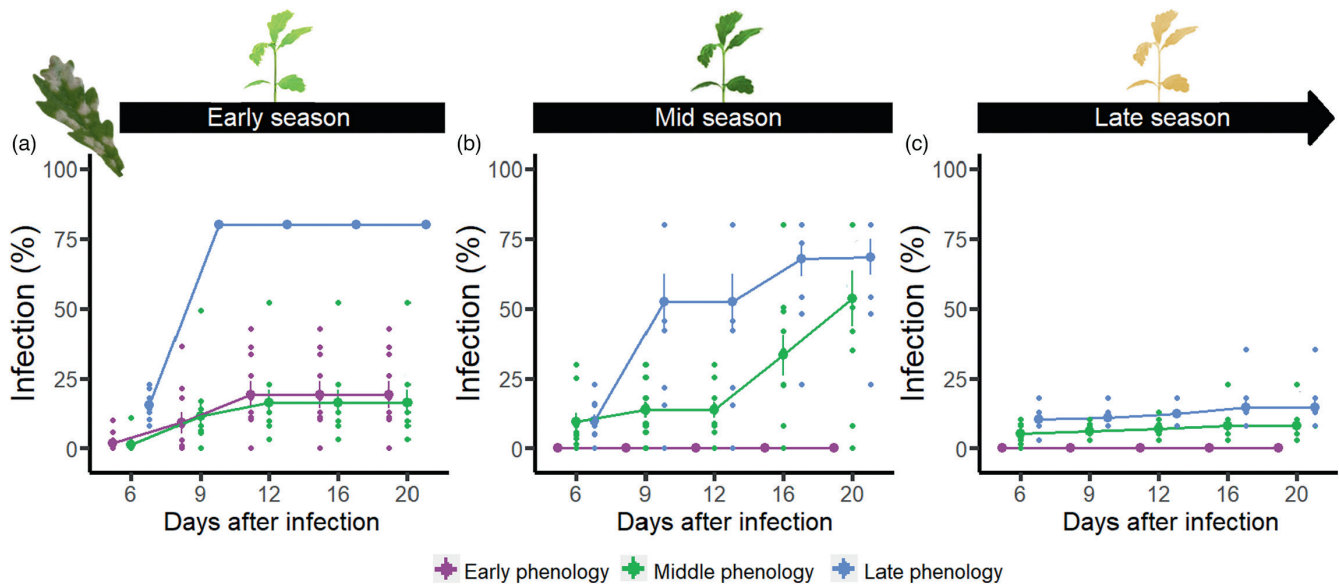


FIGURE 2 The effect of spring phenology (early, middle and late) on the infection dynamics of the oak powdery mildew *Erysiphe alphitoides* on seedlings of the pedunculate oak *Quercus robur*, separately for the (a) early, (b) mid and (c) late season. Circles represent mean infection percentages (based on the raw data) for each combination of treatment and days after infection (6, 9, 12, 16 and 20), and vertical lines represent standard errors. The maximum infection percentage was 80%, as we used the mid-points of the categories to calculate the mean

phenology seedlings and intermediate on middle phenology seedlings, whereas none of the early phenology seedlings became infected (Figure 2c; Table S4).

3.2 | The effect of spring phenology and pathogen infection on herbivore preference

The proportion of plants with leaf mines was higher in the early and mid season than in the late season (Figure 3; Table 2; Table S5). However, neither the impact of spring phenology nor the impact of pathogen infection on oviposition preference changed with the progression of the growing season (Table 2). Moth preference changed with plant spring phenology, with a higher number of mines on middle and late phenology plants than on early phenology plants (Figure 3; Figure S1; Table 2; Table S6). Pathogen infection consistently affected moth preference throughout the growing season, with female moths preferring healthy plants over infected plants (Figure 3; Figure S1; Table 2). We did not detect an interactive effect between spring phenology and pathogen infection on the preference of the leaf miner (Table 2).

During the aphid preference experiment, most of the aphids released in the cages were found back on plants in the early and mid season, whereas the majority of aphids left their host plants during the late season (Figure 4; Table 2; Table S7). The effect of spring phenology and pathogen infection on the number of aphids differed between the early, mid and late season (Figure 4; Table 2). In the early season, aphids preferred late phenology plants without pathogen infection (Figure 4a; Tables S8 and S9), in the mid season aphids preferred healthy plants but had no preference for plant phenology

(Figure 4b; Tables S8 and S9), and in the late season aphids preferred middle phenology plants, but did not distinguish between healthy and infected plants (Figure 4c; Tables S8 and S9). We did not find an interactive effect between spring phenology and pathogen infection on aphid preference (Table 2).

3.3 | The effect of spring phenology and pathogen infection on herbivore performance

Mine size differed among the seasons, with larger mines during the mid season than during the early season (Figure 3; Table 2; Table S10). We detected an interactive effect between spring phenology and pathogen infection on mine size, where mine size was larger on infected than healthy individuals for the middle phenology plants, but larger on healthy than infected individuals for the late phenology plants (Figure 3; Figure S2; Table 2; Table S11). Larval survival was not significantly affected by spring phenology or pathogen infection during any part of the growing season (Figure S3; Table 2).

Aphid performance decreased as the season progressed, with population growth in the early season, population maintenance in the mid season and population decline in the late season (Figure 4; Table 2; Table S12). Aphid population size was higher on healthy plants than on infected plants during the entire growing season (Figure 4; Figure S4; Table 2). We also detected an interactive effect of spring phenology and pathogen infection on aphid population size, with a particularly high aphid population size on healthy as compared to infected individuals for the early phenology plants (Figure 4; Figure S4; Table 2; Table S13).

TABLE 2 The impact of spring phenology, days after infection, season and their interactions on infection by the oak powdery mildew *Erysiphe alphitoides*, and the impact of spring phenology, pathogen infection, season and their interactions on the preference and performance of the leaf miner *Tischeria ekebladella* and the aphid *Tuberculatus annulatus*. The number of replicates is shown between brackets below each response variable. Shown are χ^2 -values and degrees of freedom for the final models after backwards model selection (with empty cells reflecting predictors that were excluded from the final model). Estimates from predictors and variance components of random factors are shown in Tables S14–S18

Oak powdery mildew (<i>Erysiphe alphitoides</i>)						
	Spring phenology	Days after infection	Season	Spring phenology × days after infection	Spring phenology × season	Days after infection × season
Infection percentage (n = 90 plants)	$\chi^2 = 253.58$ df = 2 $p < 0.0001$	$\chi^2 = 463.21$ df = 4 $p < 0.0001$	$\chi^2 = 102.60$ df = 2 $p < 0.0001$	$\chi^2 = 283.43$ df = 8 $p < 0.0001$	$\chi^2 = 90.47$ df = 4 $p < 0.0001$	$\chi^2 = 242.38$ df = 8 $p < 0.0001$
						$\chi^2 = 195.83$ df = 16 $p < 0.0001$
Leaf miners (<i>Tischeria ekebladella</i>)						
	Spring phenology	Pathogen infection	Season	Spring phenology × Pathogen infection	Spring phenology × Season	Pathogen infection × Season
Presence of mines (n = 96 plants)	$\chi^2 = 15.77$ df = 2 $p < 0.0001$	$\chi^2 = 9.89$ df = 1 $p = 0.002$	$\chi^2 = 7.90$ df = 2 $p = 0.019$			
Mine size (n = 533 mines)	$\chi^2 = 1.16$ df = 2 $p = 0.561$	$\chi^2 = 0.27$ df = 1 $p = 0.604$	$\chi^2 = 14.60$ df = 2 $p < 0.0001$	$\chi^2 = 5.10$ df = 1 $p = 0.024$		
Larval survival (n = 32 plants)						
Aphids (<i>Tuberculatus annulatus</i>)						
	Spring phenology	Pathogen infection	Season	Spring phenology × Pathogen infection	Spring phenology × Season	Pathogen infection × Season
Number of aphids (n = 180 plants)	$\chi^2 = 6.20$ df = 2 $p = 0.045$	$\chi^2 = 16.42$ df = 1 $p = 0.0001$	$\chi^2 = 54.07$ df = 1 $p < 0.0001$		$\chi^2 = 33.76$ df = 4 $p < 0.0001$	$\chi^2 = 11.26$ df = 2 $p = 0.004$
Aphid population size (n = 180 plants)	$\chi^2 = 8.85$ df = 2 $p = 0.012$	$\chi^2 = 23.77$ df = 1 $p < 0.0001$	$\chi^2 = 403.34$ df = 2 $p < 0.0001$	$\chi^2 = 6.81$ df = 2 $p = 0.033$		

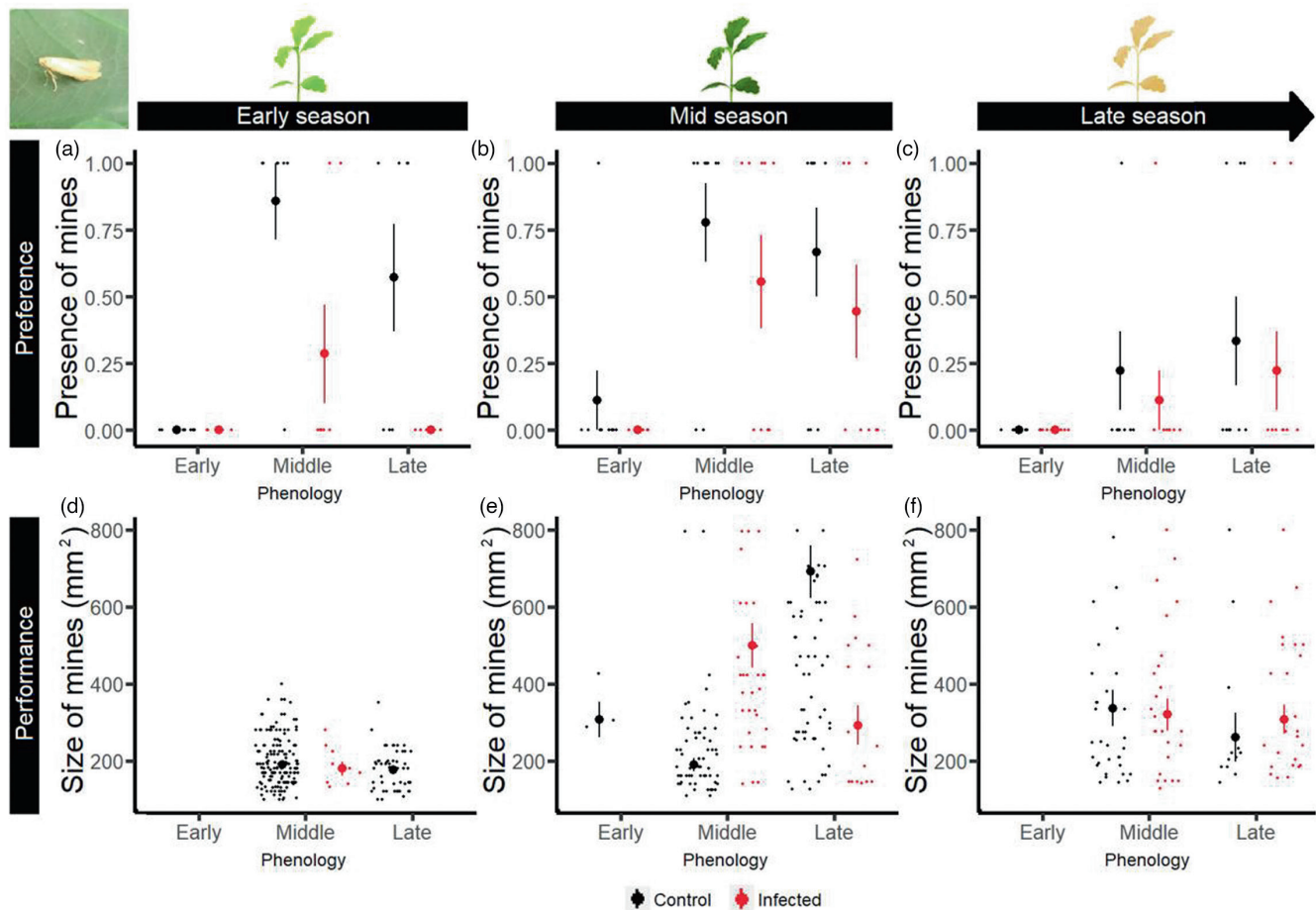


FIGURE 3 The effect of spring phenology (early, middle and late) and pathogen infection on (a–c) preference and (d–f) performance of the leaf miner *Tischeria ekebladella* on seedlings of the pedunculate oak *Quercus robur*, separately for the early, mid and late season. Shown on the ordinate is the proportion of plants of each treatment combination that had mines of *T. ekebladella* after 12 days (preference) or the size of mines (performance). Circles and vertical lines represent means and standard errors (based on the raw data), respectively

4 | DISCUSSION

We used multifactorial growth chamber experiments to examine the impact of spring phenology on the performance of a plant pathogen, and the independent and interactive effects of spring phenology and pathogen infection on the preference and performance of two herbivores in the early, mid and late season. For the oak powdery mildew pathogen, infection levels were consistently high on late phenology plants. While the leaf miner consistently preferred late phenology and healthy seedlings, aphids changed their preference during the growing season. We found an interactive effect of spring phenology and pathogen infection on both leaf miner and aphid performance, which did not change across the growing season. Our findings suggest that spring phenology of the host plant has a major impact on pathogen infection, with higher infection levels on late phenology plants, irrespective of whether infection takes place in the early, mid or late season. The effect of spring phenology on insect preference and performance was also apparent throughout the growing season, even though the exact pattern of preference and performance depended on the species, biotic context (pathogen infection) and period of the growing season.

Infection levels of the oak powdery mildew *E. alphitoides* were higher on late phenology seedlings. This matches previous studies on the infection of oak leaves with oak powdery mildew in early spring, which showed that young leaves are more susceptible to oak powdery mildew infection (Edwards & Ayres, 1982; Marçais & Desprez-Loustau, 2014). Importantly, and not previously reported on, late phenology plants were still more susceptible towards the end of the growing season. Mechanistically, these findings match the observation by Feeny and Bostock (1968) that oak leaves acquire the ability to reduce spore germination by increasing their tannin content with age. The lower infection levels when inoculating the plants at the end of the season might reflect the fact that all leaves were senescent by that time. While comparative studies are lacking, we tentatively conclude that the effect of spring phenology on pathogen infection may have a pronounced and underappreciated impact on disease dynamics during the middle, and even towards the end, of the growing season.

Spring phenology and pathogen infection had independent effects on leaf miner preference, with higher oviposition rates on later phenology and healthy seedlings, a pattern that was consistent during the early, mid and late season. The effects of

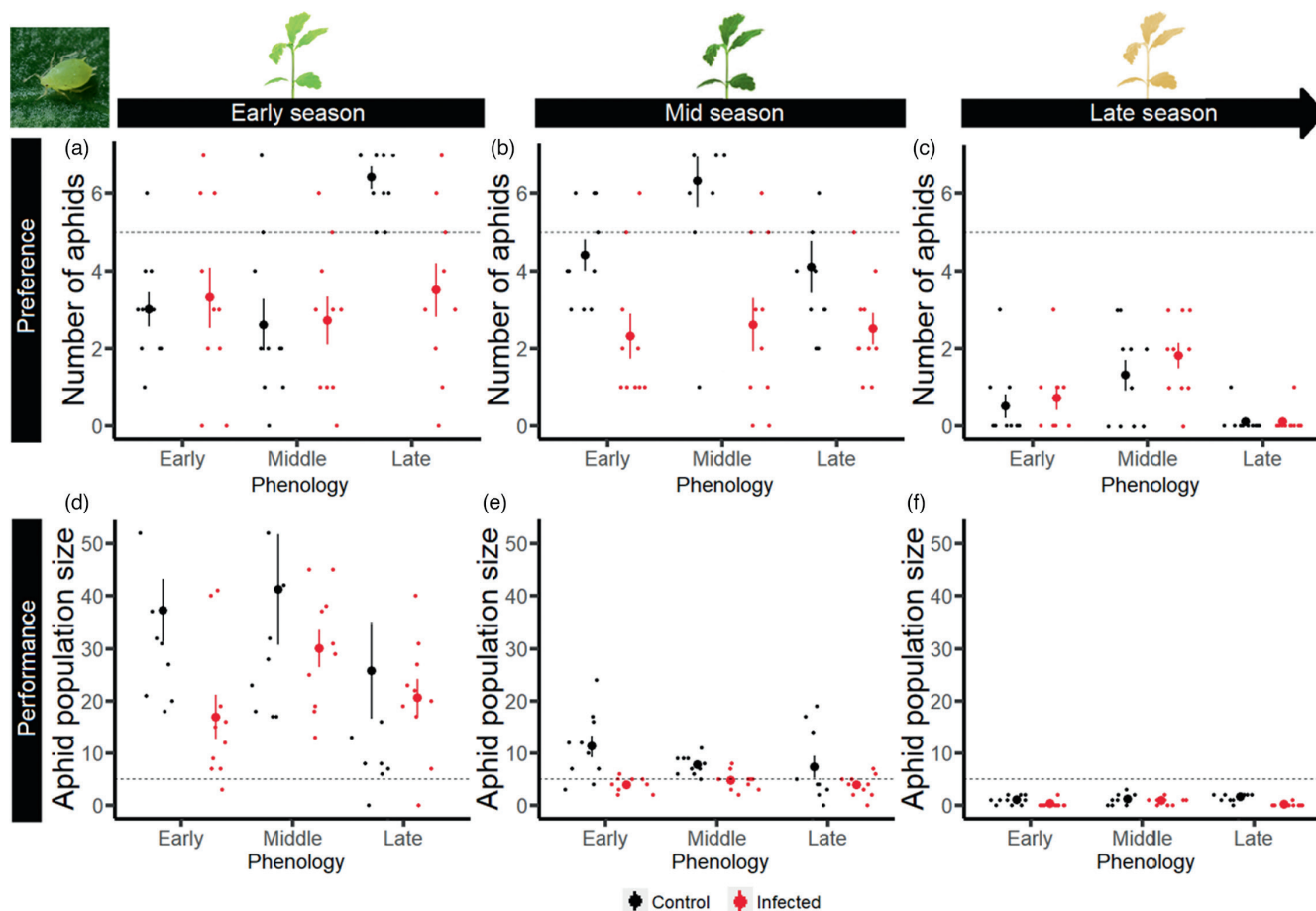


FIGURE 4 The effect of spring phenology (early, middle and late) and pathogen infection on (a–c) preference and (d–f) performance of the aphid *Tuberculatus annulatus* on seedlings of the pedunculate oak *Quercus robur*, separately for the early, mid and late season. Shown on the ordinate is the number of aphids (preference) and the aphid population size (performance). Circles and vertical lines represent means and standard errors (based on the raw data), respectively, and the dashed line represents the initial number of aphids per plant ($n = 5$)

spring phenology and pathogen infection on aphid preference were likewise independent, but their effects changed during the growing season. Regarding spring phenology, aphids preferred late phenology plants during the early season, were unaffected by spring phenology during the mid season, and preferred mid phenology plants during the late season. Regarding pathogen infection, aphids preferred healthy plants during the early and mid season, while pathogen infection did not affect aphid preference during the late season. The dependency of insect preference on spring phenology and infection status is likely due to changes in primary and secondary leaf chemistry, plant volatiles or physical leaf traits (Copolovici et al., 2014; Hunziker et al., 2021; Tikkanen & Julkunen-Tiitto, 2003). We found that neither leaf miner nor aphid preference was affected by the interaction between spring phenology and pathogen infection, suggesting that preference-related changes in plant traits due to spring phenology are not modulated by pathogen infection. As another general pattern, the overall negative impact of plant pathogens on the preference of both the leaf miner and aphids matches the findings from a meta-analysis by Fernandez-Conradi et al. (2018) on the effect of pathogen infection on phytophagous insects. More idiosyncratically,

spring phenology had a different impact on the preference of the leaf miner and aphid during the mid and late parts of the growing season, suggesting that either guilds (leaf miners vs. sap-sucking insects) or species within guilds respond differently to seasonal variation in spring phenology-related plant traits. Taken together, our results highlight that spring phenology and pathogen infection independently affect the preference of phytophagous insects across the full growing season.

Both leaf miner and aphid performance were affected by the interaction between spring phenology and pathogen infection. This implies that performance-related changes in plant traits due to spring phenology are – in contrast to traits relevant for preference – modulated by pathogen infection. The different impacts of spring phenology, pathogen infection and their interaction on preference versus performance related plant traits indicates that climatic-induced changes in spring phenology and pathogen infection might change the relationship between preference and performance (Gripenberg et al., 2010). For example, while leaf miner preference and performance were strongly matched on late phenology plants with regards to infection status during the mid season, this relationship was inverted on middle phenology plants. Notably,

we also detected a strong main effect of pathogen infection on aphid performance, but not on leaf miner performance. This matches a meta-analysis of Fernandez-Conradi et al. (2018), which showed that performance is reduced more strongly for aphids than for other herbivores in response to infection of plants by biotrophic pathogens. The salicylic acid pathway provides a more efficient defence against sap-sucking herbivores than against leaf miners and is often induced by biotrophic fungi such as the oak powdery mildew (Fernandez-Conradi et al., 2018).

We found that late phenology plants had higher infection levels in all parts of the growing season and that the effect of spring phenology on herbivore preference and performance was dependent on a combination of spring phenology, biotic environment (pathogen infection) and season. One important message from this study is that the effect of spring phenology – which is often expected to be of relevance only in spring – leaves a pronounced impact on disease dynamics and attack by different herbivore guilds also during the middle and late parts of the growing season. This implies that microbial and insect attackers during the middle of the summer and autumn can also act as selective agents on spring phenology, a phenomenon that is rarely (if ever) taken into account in evolutionary studies on spring phenology. For the oak system, we speculate that warmer springs and plant attackers select for early phenology oaks but that this selection might be counteracted by abiotic factors, such as early frost events (Deans & Harvey, 1996). From a natural history perspective, we used oak seedlings to run our experiments, and it would be important to generalize our findings (or refute generalization) to different ontogenetic stages and other plant systems in future work. From a methodological perspective, we decided to use similar environmental conditions when conducting the early, mid and late season experiments, and induced leaf senescence before the late season experiment. While these controlled environmental conditions by and large allowed us to isolate the effects of the experimental factors from experimental conditions and seasonal variation in climate, we hope that future studies will integrate these studies into a more natural (and by necessity more complex) environmental context and quantify the relative importance of spring phenology, pathogen infection, seasonal variation in temperature and experimental conditions, both under controlled and field conditions. Understanding the ecological and evolutionary consequences of changes in spring phenology and pathogen infection on herbivores throughout the season in plant-based food web is particularly timely because of the documented effects of climate change on insect voltinism, plant spring phenology and disease dynamics.

AUTHOR CONTRIBUTIONS

Álvaro Gaytán, Karl Gotthard and Ayco J. M. Tack conceived the ideas and designed methodology; Álvaro Gaytán collected, analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

This work was supported by the Bolin Centre for Climate Research and the Swedish Research Council (2015-03993 and 2021-03784 to A.J.M.T.). We thank M. Faticov and L.J.A. van Dijk for help with the collection of insects.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.2547d7wtn> (Gaytán et al., 2022b).

ORCID

Álvaro Gaytán  <https://orcid.org/0000-0001-9827-4664>

Karl Gotthard  <https://orcid.org/0000-0002-4560-6271>

Ayco J. M. Tack  <https://orcid.org/0000-0002-3550-1070>

REFERENCES

- Ahanger, R. A., Bhat, H. A., Bhat, T. A., Ganie, S. A., Lone, A. A., Ganai, S. A., Haq, S., Khan, O. A., Junaid, J. M., & Bhat, T. A. (2013). Impact of climate change on plant diseases. *Animal Science*, 1, 105–115.
- Allstadt, A. J., Vavrus, S. J., Heglund, P. J., Pidgeon, A. M., Thogmartin, W. E., & Radeloff, V. C. (2015). Spring plant phenology and false springs in the conterminous US during the 21st century. *Environmental Research Letters*, 10, 104008. <https://doi.org/10.1088/1748-9326/10/10/104008>
- Altermatt, F. (2010). Climatic warming increases voltinism in European butterflies and moths. *Proceedings of the Royal Society B: Biological Sciences*, 277, 1281–1287. <https://doi.org/10.1098/rspb.2009.1910>
- Badeck, F., Bondeau, A., Böttcher, K., Doktor, D., Lucht, W., Schaber, J., & Sitch, S. (2004). Responses of spring phenology to climate change. *The New Phytologist*, 162, 295–309. <https://doi.org/10.1111/j.1469-8137.2004.01059.x>
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Bellemin-Noël, B., Bourassa, S., Despland, E., De Grandpré, L., & Pureswaran, D. S. (2021). Improved performance of the eastern spruce budworm on black spruce as warming temperatures disrupt phenological defences. *Global Change Biology*, 27, 3358–3366. <https://doi.org/10.1111/gcb.15643>
- Chen, Y., & Poland, T. M. (2009). Interactive influence of leaf age, light intensity, and girdling on green ash foliar chemistry and emerald ash borer development. *Journal of Chemical Ecology*, 35, 806–815. <https://doi.org/10.1007/s10886-009-9661-1>
- Copolovici, L., Vaartnou, F., Estrada, M. P., & Niinemets, U. (2014). Oak powdery mildew (*Erysiphe alphitoides*)-induced volatile emissions scale with the degree of infection in *Quercus robur*. *Tree Physiology*, 34, 1399–1410. <https://doi.org/10.1093/treephys/tpu091>
- Coyle, D. R., Jordan, M. S., & Raffa, K. F. (2010). Host plant phenology affects performance of an invasive weevil, *Phyllobius oblongus* (coleoptera: Curculionidae), in a northern hardwood forest. *Environmental Entomology*, 39, 1539–1544. <https://doi.org/10.1603/EN09381>
- Crawley, M. J. (2013). *The R book*. Wiley.
- Deans, J., & Harvey, F. (1996). Frost hardiness of 16 European provenances of sessile oak growing in Scotland. *Forestry*, 69, 5–12. <https://doi.org/10.1093/forestry/69.1.5>

- Despland, E. (2018). Effects of phenological synchronization on caterpillar early-instar survival under a changing climate. *Canadian Journal of Forest Research*, 48, 247–254. <https://doi.org/10.1139/cjfr-2016-0537>
- Desprez-Loustau, M.-L., Massot, M., Toigo, M., Fort, T., Kaya, A. G., Boberg, J., Braun, U., Capdevielle, X., Cech, T., Chandelier, A., Christova, P., Corcobado, T., Dogmus, T., Dutech, C., Fabreguettes, O., d'Arcier, J. F., Gross, A., Jung, M. H., Iturrirxa, E., ... Tack, A. J. M. (2018). From leaf to continent: The multi-scale distribution of an invasive cryptic pathogen complex on oak. *Fungal Ecology*, 36, 39–50.
- Edwards, M. C., & Ayres, P. G. (1982). Seasonal changes in resistance of *Quercus petraea* (sessile oak) leaves to *Microsphaera alphitoides*. *Transactions of the British Mycological Society*, 78, 569–571. [https://doi.org/10.1016/S0007-1536\(82\)80174-5](https://doi.org/10.1016/S0007-1536(82)80174-5)
- Ekholm, A., Tack, A. J. M., Bolmgren, K., & Roslin, T. (2019). The forgotten season: The impact of autumn phenology on a specialist insect herbivore community on oak. *Ecological Entomology*, 44, 425–435. <https://doi.org/10.1111/een.12719>
- Ekholm, A., Tack, A. J. M., Pulkkinen, P., & Roslin, T. (2020). Host plant phenology, insect outbreaks and herbivore communities – The importance of timing. *The Journal of Animal Ecology*, 89, 829–841. <https://doi.org/10.1111/1365-2656.13151>
- Faticov, M., Ekholm, A., Roslin, T., & Tack, A. J. M. (2020). Climate and host genotype jointly shape tree phenology, disease levels and insect attacks. *Oikos*, 129, 391–401. <https://doi.org/10.1111/oik.06707>
- Feeny, P., & Bostock, H. (1968). Seasonal changes in the tannin content of oak leaves. *Phytochemistry*, 7, 871–880. [https://doi.org/10.1016/S0031-9422\(00\)84845-1](https://doi.org/10.1016/S0031-9422(00)84845-1)
- Fernandez-Conradi, P., Jactel, H., Robin, C., Tack, A. J. M., & Castagneyrol, B. (2018). Fungi reduce preference and performance of insect herbivores on challenged plants. *Ecology*, 99, 300–311. <https://doi.org/10.1002/ecy.2044>
- Flynn, D. F. B., & Wolkovich, E. M. (2018). Temperature and photoperiod drive spring phenology across all species in a temperate forest community. *The New Phytologist*, 219, 1353–1362. <https://doi.org/10.1111/nph.15232>
- Fowler, S. V., & Lawton, J. H. (1984). Foliage preferences of birch herbivores: A field manipulation experiment. *Oikos*, 42, 239. <https://doi.org/10.2307/3544799>
- Gaytán, Á., Gotthard, K., & Tack, A. J. M. (2022a). Strong impact of temperature and resource specialisation on patterns of voltinism within an oak-associated insect community. *Ecological Entomology*, 47, 544–552. <https://doi.org/10.1111/een.13139>
- Gaytán, A., Gotthard, K., Tack, A. J. M. (2022b). Data from: Spring phenology and pathogen infection affect multigenerational plant attackers throughout the growing season. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.2547d7wtn>
- Gripenberg, S., Mayhew, P. J., Parnell, M., & Roslin, T. (2010). A meta-analysis of preference-performance relationships in phytophagous insects. *Ecology Letters*, 13, 383–393. <https://doi.org/10.1111/j.1461-0248.2009.01433.x>
- Hartig, F. (2020). *DHARMA: Residual diagnostics for hierarchical (multi-level/mixed) regression models*. R package version 0.4.5. <http://florihartig.github.io/DHARMA/>
- Hunziker, P., Lambert, S. K., Weber, K., Crocoll, C., Halkier, B. A., & Schulz, A. (2021). Herbivore feeding preference corroborates optimal defense theory for specialized metabolites within plants. *Proceedings of the National Academy of Sciences of the United States of America*, 118, e2111977118. <https://doi.org/10.1073/pnas.2111977118>
- Isaev, A., Shoukhovolsky, V., Tarasova, O., Palnikova, E., & Kovalev, A. (2018). *Forest insect population dynamics, outbreaks and global warming effects*. Scrivener Publishing, Wiley.
- Jain, A., Sarsaiya, S., Wu, Q., Lu, Y., & Jingshan, S. (2019). A review of plant leaf fungal diseases and its environment speciation. *Bioengineered*, 10, 409–424.
- Jordan, T. (1995). Biologie und Parasitoidenkomplex der Eichenminiermotte *Tischeria ekebladella* (Bjerkander, 1795) (Lep., Tischeriidae) in Norddeutschland. *Journal of Applied Entomology*, 119, 447–454. <https://doi.org/10.1111/j.1439-0418.1995.tb01317.x>
- Lehmann, P., Ammunét, T., Barton, M., Battisti, A., Eigenbrode, S. D., Jepsen, J. U., Kalinkat, G., Neuvonen, S., Niemelä, P., Terblanche, J. S., Økland, B., & Björkman, C. (2020). Complex responses of global insect pests to climate warming. *Frontiers in Ecology and the Environment*, 18, 141–150. <https://doi.org/10.1002/fee.2160>
- Lenth, R. V. (2016). Least-squares means: The R package lsmeans. *Journal of Statistical Software*, 69, 1–33. <https://doi.org/10.18637/jss.v069.i01>
- Lüdecke, D. (2020). *sjPlot: Data visualization for statistics in social science*. R package version 2.8.11. <https://CRAN.R-project.org/package=sjPlot>
- Marçais, B., & Desprez-Loustau, M.-L. (2014). European oak powdery mildew: Impact on trees, effects of environmental factors, and potential effects of climate change. *Annals of Forest Science*, 71, 633–642. <https://doi.org/10.1007/s13595-012-0252-x>
- Mattson, W. J. (2012). *The role of arthropods in Forest ecosystems*. Springer Science & Business Media.
- McClory, R. W., van Dijk, L. J. A., Mutz, J., Ehrlén, J., & Tack, A. J. M. (2021). Spring phenology dominates over light availability in affecting seedling performance and plant attack during the growing season. *Forest Ecology and Management*, 495, 119378. <https://doi.org/10.1016/j.foreco.2021.119378>
- Menzel, A., Sparks, T. H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kübler, K., Bissolli, P., Braslavská, O., Briede, A., Chmielewski, F. M., Crepinsek, Z., Curnel, Y., Dahl, Å., Defila, C., Donnelly, A., Filella, Y., Jatczak, K., Måge, F., ... Züst, A. (2006). European phenological response to climate change matches the warming pattern. *Global Change Biology*, 12, 1969–1976. <https://doi.org/10.1111/j.1365-2486.2006.01193.x>
- Nanninga, C., Buyarski, C. R., Pretorius, A. M., & Montgomery, R. A. (2017). Increased exposure to chilling advances the time to budburst in north American tree species. *Tree Physiology*, 37, 1727–1738.
- Niemelä, P. (1983). Seasonal patterns in the incidence of specialism: Macrolepidopteran larvae on Finnish deciduous trees. *Annales Zoologici Fennici*, 20, 199–202.
- Oishi, M., & Sato, H. (2009). Life history traits, larval habits and larval morphology of a leafminer, *Coptotriche japoniella* (Tischeriidae), on an evergreen tree, *Eurya japonica* (Theaceae), in Japan. *Journal of the Lepidopterists' Society*, 63, 7.
- O'Neill, B. F., Bond, K., Tyner, A., Sheppard, R., Bryant, T., Chapman, J., Bell, J., & Donnelly, A. (2012). Climatic change is advancing the phenology of moth species in Ireland: Warming is advancing moth phenology. *Entomologia Experimentalis et Applicata*, 143, 74–88. <https://doi.org/10.1111/j.1570-7458.2012.01234.x>
- Petit, R. J., Csaikl, U. M., Bordacs, S., Burg, K., Coart, E., Cottrell, J., van Dam, B., Deans, J. D., Dumolin-Lapegue, S., Fineschi, S., Finkeldey, R., Gillies, A., Glaz, I., Goicoechea, P. G., Jensen, J. S., König, A. O., Lowe, A. J., Madsen, S. F., Matyas, G., ... Turchini, D. (2002). Chloroplast DNA variation in European white oaks: Phylogeography and patterns of diversity based on data from over 2600 populations. *Forest Ecology and Management*, 22, 5–26.
- Posledovich, D., Toftegaard, T., Wiklund, C., Ehrlén, J., & Gotthard, K. (2015). The developmental race between maturing host plants and their butterfly herbivore – The influence of phenological matching and temperature. *The Journal of Animal Ecology*, 84, 1690–1699. <https://doi.org/10.1111/1365-2656.12417>
- Price, P. W. (1997). *Insect ecology* (3rd ed.). Wiley, University of Minnesota.
- R Development Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <http://www.R-project.org>

- Real, L. A., & Brown, J. H. (2012). *Foundations of ecology: Classic papers with commentaries*. University of Chicago Press.
- Scheirs, J., Bruyn, L. D., & Verhagen, R. (2002). Seasonal changes in leaf nutritional quality influence grass miner performance: Plant phenological age hypothesis. *Ecological Entomology*, 27, 84–93. <https://doi.org/10.1046/j.1365-2311.2002.0378a.x>
- Schwartzberg, E. G., Jamieson, M. A., Raffa, K. F., Reich, P. B., Montgomery, R. A., & Lindroth, R. L. (2014). Simulated climate warming alters phenological synchrony between an outbreak insect herbivore and host trees. *Oecologia*, 175, 1041–1049. <https://doi.org/10.1007/s00442-014-2960-4>
- Southwood, T. R. E. (1961). The number of species of insect associated with various trees. *The Journal of Animal Ecology*, 30, 1. <https://doi.org/10.2307/2109>
- Stern, D. L. (2008). Aphids. *Current Biology*, 18, R504–R505. <https://doi.org/10.1016/j.cub.2008.03.034>
- Tack, A. J. M., Gripenberg, S., & Roslin, T. (2012). Cross-kingdom interactions matter: Fungal-mediated interactions structure an insect community on oak: Fungus–plant–insect interactions. *Ecology Letters*, 15, 177–185. <https://doi.org/10.1111/j.1461-0248.2011.01724.x>
- Tack, A. J. M., Ovaskainen, O., Pulkkinen, P., & Roslin, T. (2010). Spatial location dominates over host plant genotype in structuring an herbivore community. *Ecology*, 91, 22.
- Tikkanen, O.-P., & Julkunen-Tiitto, R. (2003). Phenological variation as protection against defoliating insects: The case of *Quercus robur* and *Operophtera brumata*. *Oecologia*, 136, 244–251. <https://doi.org/10.1007/s00442-003-1267-7>
- Toftegaard, T., Posledovich, D., Navarro-Cano, J. A., Wiklund, C., Gotthard, K., & Ehrlén, J. (2019). Butterfly–host plant synchrony determines patterns of host use across years and regions. *Oikos*, 128, 493–502. <https://doi.org/10.1111/oik.05720>
- van Dijk, L. J. A., Ehrlén, J., & Tack, A. J. M. (2020). The timing and asymmetry of plant–pathogen–insect interactions. *Proceedings of the Royal Society B: Biological Sciences*, 287, 20201303. <https://doi.org/10.1098/rspb.2020.1303>
- Weisberg, F. (2019). *An R companion to applied regression* (3rd ed.). Sage.
- Yefremova, Z. A., Yegorenkova, E. N., & Mishchenko, A. V. (2013). Eulophid wasps (Hymenoptera, Eulophidae), parasitoids of leaf-mining moths (Lepidoptera: Gracillariidae, Nepticulidae, Tischeriidae) on the English oak in the Middle Volga Area. *Entomological Review*, 93, 309–315. <https://doi.org/10.1134/S0013873813030044>

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Gaytán, Á., Gotthard, K., & Tack, A. J. M. (2022). Spring phenology and pathogen infection affect multigenerational plant attackers throughout the growing season. *Journal of Animal Ecology*, 91, 2235–2247. <https://doi.org/10.1111/1365-2656.13804>