Extreme climatic events affect populations of Asian chestnut gall wasps, *Dryocosmus kuriphilus*, but do not stop the spread

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Abstract

1 Global climate change affects the frequency of extreme weather events that can influence plant–insect interactions.

2 We evaluated how the late-spring frost and severe drought that occurred in Spain in 2017 affected interactions between the invasive gall insect, *Dryocosmus kuriphilus*, and the native tree, *Castanea sativa*. We assessed effects on insect survival, fertility, population growth, and effects through changes in tree palatability and in other pests and pathogens.

3 Late-spring frost reduced *D. kuriphilus* to 25–40% of previous abundance. Wasp populations recovered rapidly (>7-fold in 3 years), consistent with density-dependence in population dynamics.

4 Larvae affected by freeze or drought were smaller. Female fecundity was affected by the freeze 1 year later.

5 Late-spring frosts and severe drought affected leaf size and physiology. Water content was higher within galls, but nitrogen was higher within galls in non-freeze plots after weather conditions improved.

6 Freezing also influenced the secondary chemistry of leaves. Phenol concentrations were lower, and terpenes higher, in frozen plots, while condensed tannins remained the same. Condensed tannins were reduced to half in the drought year.

7 Freezing had limited effects on damage from other pests and pathogens.

8 Our work expands understanding of how climate and weather affects forest pests.

Keywords Community interactions, density-dependence, drought, invasive pest, late-spring frost, secondary metabolites.

Introduction

There is a strong agreement that global climate change has important effects on forests and forest communities. Furthermore, pest and disease outbreaks are themselves important as sources of natural disturbance (Kirilenko & Sedjo, 2007; Ayres & Lombardero, 2018). Global climate change can influence forest disturbance caused by insects and pathogens through changes in temperature and precipitation that can affect their survival, reproduction, dispersal, and geographic distribution (Ayres & Lombardero, 2000; Bale *et al.*, 2002). However, climate change can involve not only shifts in average climate parameters, but also changes in the variability and predictability of weather patterns

(*e.g.*, more extreme weather events and reduced winter snow cover; Harris *et al.*, 2019; Wagner, 2020). The impact on insect populations may be even more dramatic when a growing season includes multiple climatic events. For example, the coincidence of spring frost and summer drought has been associated with general declines in insect abundance within a community of oak folivores (Marquis *et al.*, 2019).

One consequence of global climate change, at least in Mediterranean countries, is increased aridity and a higher frequency of extreme climatic events such as late-spring frosts and heat waves (Diffenbaugh *et al.*, 2005; Christensen *et al.*, 2007; Vitasse & Rebetez, 2018). Warming of temperatures in late winter and early spring tends to cause a general advancement of phenology (Menzel & Fabian, 1999; Parmesan & Yohe, 2003) including insects; shifts towards earlier seasonal

activity are widespread (Forrest, 2016). This can trigger the so called 'false spring' and induce earlier plant growth, which increases the risk of vulnerable plant tissues to subsequent spring frosts (Inouye, 2000; Bigler & Bugmann, 2018). Consequently, late-spring frosts, *i.e.*, below-freezing temperatures in late spring, are among the most critical extreme events in temperate and boreal regions (Zohner *et al.*, 2020). Late-spring frosts affect growth and reproduction of plants and may cause considerable economic losses. For example, the economic loss for agricultural crops after the 2007 late-spring frost in the U.S. was up to $112 million, with fruit crop loss of $86 million (Warmund *et al.*, 2008). Further examples of late-spring frost damage include 1995 in France (Ningre & Colin, 2007); 2010 in the NE of U.S.A. (Hufkens *et al.*, 2012); and 2011 and 2016 in Switzerland, south Germany, and northeastern France (Kreyling *et al.*, 2012; Vitasse *et al.*, 2018).

Late-spring frosts can kill foliage and therefore reduce photosynthesis and tree growth (Dittmar *et al.*, 2006; Bräuning *et al.*, 2016). Trees can partially compensate by producing new leaves (Kramer & Kozlowski, 1979; Neilson & Wullstein, 1983). However, refoliation is costly in resources and the length of the photosynthetic season is shorter nonetheless (Zohner *et al.*, 2019).

Late-spring frost may affect insect populations directly by killing eggs or early larvae exposed to the low temperatures, as well as by starvation when the tree foliage is killed (Meurisse *et al.*, 2012). Late-spring frost can also exert substantial impacts on trees, including increased mortality, altered morphology, decreased growth, changes in primary nutrients for insects (*e.g.*, N), and changes in leaf chemical defences (St. Clair *et al.*, 2009; Hufkens *et al.*, 2012; Man *et al.*, 2013). Consequently, late-spring frost may also influence the susceptibility of plants to insects or pathogens, although the number of studies that have examined the connection between freeze damage and insect susceptibility in trees is limited. Some authors suggest freeze as a predisposing factor to secondary insect pests and fungi (Wargo, 1996; Wolken *et al.*, 2009; La Spina *et al.*, 2013). Increased growth has been reported for insects feeding in tissue reflushed after freeze damage (Thomson *et al.*, 2001; Rubert-Nason *et al.*, 2017). The few studies of freeze-induced changes in phytochemistry and plant–insect interactions have reported an increase in phenolic glycosides and condensed tannins (St. Clair *et al.*, 2009) or mixed effects depending on the genotypes (Rubert-Nason *et al.*, 2017).

Rapid climate change tends to increase co-occurrence of extreme events as heat stress and drought (Mittler, 2006). The impact on insect communities of rising temperature has been broadly studied during the last 25 years (*e.g.*, Bale *et al.*, 2002; Estay *et al.*, 2014). Direct effects of warmer temperatures on insect physiology include rapid insect development and increased overwinter survival (Bale *et al.*, 2002). Nevertheless, warmer summer temperatures do not always reduce generation time (Forrest, 2016), and can result in increased mortality, smaller size, and lower dispersal capacity (Pineau *et al.*, 2017; Mech *et al.*, 2018).

Insects experience the effects of drought and heat directly but also indirectly through changes in host suitability (*e.g.*, phytochemistry) and changes in the broader biotic community (*e.g.*, competitors, enemies, and species that share common enemies) (Rouault *et al.*, 2006). Insect herbivores may be affected by drought because it can affect nutritional quality of plant tissue (Holopainen *et al.*, 2018) and reduced water content may interfere with nitrogen acquisition by insects (Huberty & Denno, 2004). However, the impact of drought on susceptibility of trees to insect infestations and mortality is unclear (McDowell *et al.*, 2011; Gely *et al.*, 2020). It has been suggested that plant nitrogen content can increase with moderate drought (Mattson & Haack, 1987; Kolb *et al.*, 2016) and decrease with severe drought (He & Dijkstra, 2014; but see Gely *et al.*, 2020). The effects of drought on tree resistance to pests may vary depending on the feeding guild of insect herbivores (Larsson, 1989; Jactel *et al.*, 2012). Moderate water-stress can limit woodborer performance (Lieutier *et al.*, 2004), but improve performance of defoliators due to increased concentration of soluble nitrogen in foliage (Mattson & Haack, 1987; Larsson, 1989). Nevertheless, experimental studies have found mixed responses of leaf-feeders to plant water stress (Rouault *et al.*, 2006; Castagneyrol *et al.*, 2018). This could be because the different sub-guilds within defoliators (*e.g.*, leaf chewers, gall formers, and leaf miners) may have different responses to plant water stress (Huberty & Denno, 2004; Jactel *et al.*, 2012). For leaf chewers and gall makers, survival, density, and overall performance have been found to decrease with drought (Huberty & Denno, 2004; Jactel *et al.*, 2012). Generalizations are further complicated because plant stress can have opposite effects on different life-stages of some galling insects (Bjorkman, 1998).

Galling insects have an intimate relationship with their host plants (Price *et al.*, 1987; Stone *et al.*, 2002). The nutrition and defences of galling insects can depend upon their success in manipulating host plant morphology and physiology (Tooker *et al.*, 2008; Giron *et al.*, 2016; Oliveira *et al.*, 2016). There are three major hypotheses for the adaptive significance of gall induction and the evolution of gall morphology. The Nutritional Hypothesis states that galls provide a high-quality nutrient source with less plant defensive compounds than other feeding modes (Price *et al.*, 1987; Crespi *et al.*, 1997). The Microenvironment Hypothesis states that galls protect the insects from unfavourable abiotic conditions as temperature changes, desiccation, or ultraviolet radiation (Price *et al.*, 1987; Crespi *et al.*, 1997; Miller *et al.*, 2009). The Enemy Hypothesis argues that morphology and chemistry of the gall tissue protect the insect from predators, parasitoids and pathogens (Stone & Schonrogge, 2003).

The aim of this study was to assess how extreme climatic events, such as the late-spring frost of 2017, affected interactions between the native chestnut tree, *Castanea sativa* Mill., with its most important pest, the invasive gall insect *Dryocosmus kuriphilus* Yasumatsu, in Northern Spain. The year 2017 was also exceptionally warm (1.1 °C above the annual mean of the period 1981–2010; the warmest year since 1965) and was the year with the second most severe drought since 1965 (AEMET, 2017, 2018). Therefore, we also analysed how the warm temperatures and the severe drought may affect the plant–insect in that interaction. We evaluated direct effects of weather on insect performance by quantifying insect survival, fitness, and reproduction capacity. We also evaluated indirect effects of weather on *D. kuriphilus* population growth due to (i)
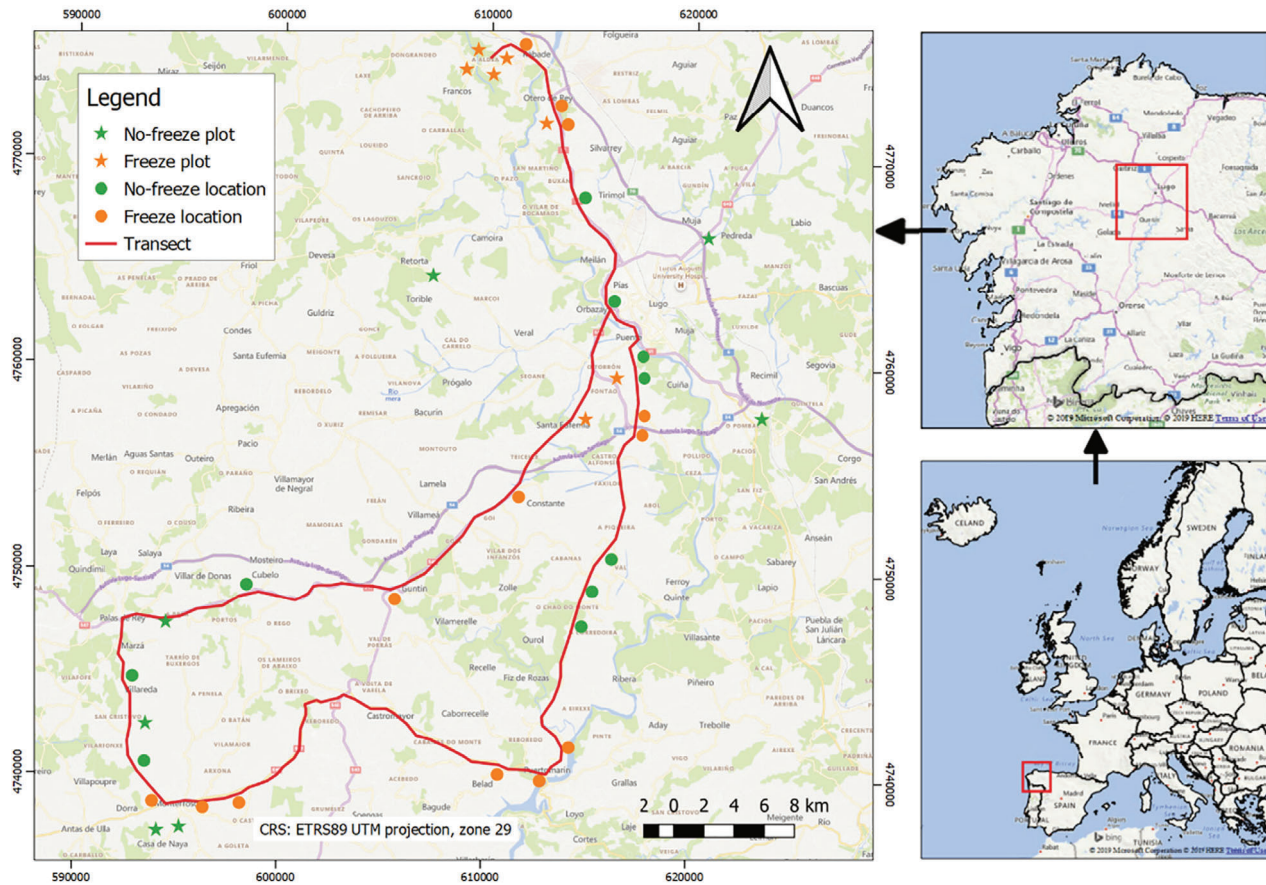
Figure 1 Locations visited after a late-spring frost in May 2017 in Galicia (NW of Iberian Peninsula). Fourteen of the 16 study plots are visible; the other two are located in the Northeast (Castroverde and Masoucos) and were not included in the figure to improve visualization of the survey transect.

changes in trees palatability, and (ii) changes in the associated communities of other insects and pathogens living in the same trees.

Material and methods

Study area

The study was carried out in Galicia (NW of Spain). From January to March of 2017, we established 16 study plots to follow the damage caused by *D. kuriphilus* on *Castanea sativa* in the study area. These plots were in the central area of Galicia (Fig. 1) with similar climatic conditions. All 16 study plots were private chestnut plantations with a double purpose: nut and wood production. The plots were discrete within a landscape matrix of agricultural and forest land. The plots had different owners and different agronomic histories which can influence the site index, even for plots located very close. In addition, spatial variability in local site conditions, involving microtopography and soil, can lead to large spatial variability in site quality (Skovsgaard & Vanclay, 2013). The quality of each plot for chestnut growth was assessed through the site index (the expected dominant height of the plot at a reference age of 45 years), according to the site index curves developed by Patricio and Nunes (2017). For our analyses,

we recognized eight high-quality sites and eight low-quality sites based on whether the height of dominant trees was greater than or less than 25 m at 45 years.

Study species

Sweet chestnut (*Castanea sativa*, Fagaceae) is a tree native to Southern Europe and Asia Minor. Sweet chestnut is a forest species of great interest in northwestern Spain for their economic value and for the area occupied, more than 100 000 ha, of which about 45 000 ha are in Galicia (MARM, 2011). The species is widely cultivated because it produces high-quality wood and edible seeds, the chestnuts, which have been used as human and animal food since ancient times (Conedera *et al.*, 2004).

Dryocosmus kuriphilus (Hymenoptera: Cynipidae) is originally from China and it is considered the most important insect pest of chestnuts worldwide (EPPO, 2005). It was first reported in Japan in 1941 damaging local chestnut orchards (Aebi *et al.*, 2006). The species was detected in Europe, in Italy in 2002 (Brussino *et al.*, 2002). Since then, it has spread throughout Europe reaching Spain in 2012 and Galicia in 2014 (Nieves-Aldrey *et al.*, 2019). Currently, it has spread throughout the territory (Gil-Tapetado *et al.*, 2021a).

Climatic events

April of 2017 in Galicia was characterized by two climatic events. There was a very warm period during early April due to the entrance of warm air from the North of Africa, raising temperatures above 30 °C in many areas and reaching a maximum of 34.3 °C on 9 April at Arnoia (Ourense). The exceptionally warm period promoted early growth in chestnuts as well as other plants. Then, a cold front penetrated Europe on 17 April, followed by a large incursion of dry polar air. Consequently, most of Europe experienced a series of nights that reached freezing temperatures. In Galicia, the coldest nights were from 27–29 April when temperature dropped to as low as −8.2 °C in Baltar (Ourense) (Meteogalicia, 2018).

The rest of 2017 was hot and dry in Galicia; the average temperature for 2017 was 0.8 °C above the mean for 1981–2010 while precipitation was 24% lower (966 *vs.* 1299 L/m²). Hydric balance was negative since April (−104.1 L/m²), and reached the lowest value in July (−148.9 L/m²) in the weather station of Campus de Lugo, in the vicinity of one of the study plots (data available at https://www.meteogalicia.gal/observacion/estacionshistorico/historico.action?idEst=10053).

In contrast, 2018 had relatively normal temperatures and precipitation that was 11% higher than the mean for 1981–2010 (Meteogalicia, 2018, 2019).

We did some additional measurements in 2020 (see Attack level and population growth section), which was also a warm year in Galicia but with near-average precipitation (5% lower than normal; Meteogalicia, 2021).

Effect of frost on Dryocosmus kuriphilus

Survival. To assess freeze damage directly to the insect pest, 3 days after the late-spring frost (2 May), we sampled along a transect of about 250 km through the study area. Along the way, we examined 39 chestnut plantations (including the 16 main study plots), 20 affected by the late-spring frost and 19 non affected (Fig. 1). In each plantation, we recorded the geographic coordinates (WGS 84, World Geodetic System 1984) with a GPS device and whether or not the plot suffered freeze damage. Given the variable topography, the study plots, frozen or not, were interspersed across landscape (Fig. 1). In 23 of these chestnut plantations (13 affected by late-spring frost and 10 non-affected), we collected 20 galls chosen haphazardly from within each of five different trees (total of 100 galls per plot). Galls were moved to the lab, stored in individual boxes within the refrigerator and dissected within 3 days to assess larval survival. Individual cell chambers containing ectoparasitoids were excluded from the estimations. We repeated this sampling in each of the next 3 weeks.

Attack level and population growth. In summer 2017, after freeze-damaged trees had flushed new shoots and leaves, we assessed gall abundance in the 16 main study plots. We selected two branches at random in each of 12–27 trees per plot. The number of trees varied among plots due to the availability of trees. On each branch, we located and examined the portion of the shoot that grew in the previous summer (2016). Within that length of shoot, we counted all the galls produced in the current year (2017). As a covariate representing variation in the size of shoots, we also counted the number of buds that were present at the end of previous year's growing season (2016). The branches were labelled, and thus we were able to repeat measurements on the same trees and branches in 2018 and 2020 (again using the previous year's buds as covariates). The resulting data allowed us to estimate galls/shoot for each plot in each year and *per capita* population growth rate between years.

Larval size and adult fecundity. To assess effects of the freeze event on *D. kuriphilus*, we weighed 145 late-instar larvae in 2017 from seven of the study plots (10–41 larvae/plot) and in 2018 we weighed 166 larvae from the same plots (21–27 larvae/plot). We also assessed female fecundity by counting the number of eggs produced by emerging female adults from galls collected in the same study plots (*n* = 57 and 107 females in 2017 and 2018, respectively). Galls were collected in the study plots and stored in individual boxes in the lab until females emerge. Eggs were counted by observing the dissected abdomen of the emerging females under the microscope. We compared these data with the only previous measurements of female eggs collected in the area. These data are from Lugo, the plot where the insect was detected in Galicia for the first time. The Lugo plot was among the 39 sites in the present study and was not affected by the frost. Thus, we had measurements of eggs per female in that location since 2015.

Gall characteristics. In 2018, at each of 16 main study sites, we collected and measured 51–160 galls of each of three types of galls based on the tissue where the gall is formed (shoot, leaf, or stipule). Variation in sample size among plots and gall types was due to the availability of trees and galls of the scarcest type (stipule galls). In the laboratory, we measured three perpendicular axes of each gall with digital callipers and averaged the three axes to estimate gall diameter. All of galls were subsequently dissected to measure gall wall thickness (with a calliper) and count the number of feeding chambers (each representing one gall wasp).

Effect of frost on tree nutritional quality and palatability

In June of 2017, after the leaves had re-flushed, we were able to collect and analyse 10 samples of ungalled leaves (each from a different tree) from each of six study plots (three plots that experienced freezing and three that did not). We avoided occasional leaves in the unfrozen plots that exhibited any signs of freezing damage. In the lab, we measured leaf size, nitrogen, and water content as well as total phenols, condensed tannins, and terpenes. In the same sampling, we also collected another sample of leaves with *D. kuriphilus* galls (one sample from each of five trees per plot). For each galled leaf, we analysed water and N content separately in the gall itself and in the leaf tissue surrounding the gall. We repeated this sampling in 2018 in the same six study plots.

To analyse water and N content, leaves were weighed fresh then oven-dried at 60 °C for 48 h. The dried samples were weighed again to estimate water content, milled to a fine

powder, and submitted to instant oxidation (as 0.1 g tissue samples); the gases released were quantified with an Elemental Analyser (LECO-TruSpec). Analyses were performed by the analytical unit of the University of Santiago de Compostela (RIAIDT).

To analyse concentrations of total terpenes, we followed Wainhouse *et al.* (1998). One gram of leaf or gall from each sample was cut in very small sections and terpene compounds were quantitatively extracted twice with n-hexane (with each extraction including 25 min in an ultrasonic bath). Later, the plant material was recovered by filtration using quantitative filter paper. Then, the solvent was evaporated at room temperature inside an extraction chamber, and the mass of the non-volatile terpene residue was measured with a precision scale.

Total leaf phenolics were determined following Sampedro *et al.* (2011). Phenolics were extracted from 0.5 g of leaf tissue with aqueous methanol (1:1 vol:vol) in an ultrasonic bath for 15 min, followed by centrifugation and subsequent dilution of the methanolic extract. Total phenolic content was determined colorimetrically using Folin–Ciocalteu in a BioTek Elx 850 microplate reader at 740 nm, quantified with a standard curve of tannic acid and expressed as mg tannic acid equivalents g^{-1} dry mass of plant tissue.

To analyse condensed tannins, the same extract was assayed with butanol – hydrochloric acid reagent (0.7 g ferrous sulphate heptahydrate in 50 mL concentrated HCl and n-butanol added to make 1 L), and absorbance was measured at 550 nm (Waterman & Mole, 1994) with the same microplate reader, using as standard purified condensed tannins of quebracho (*Schinopsis balansae* Engl., Unitan Saica, Buenos Aires).

Phytosanitary inventory

In summer 2018, we carried out an inventory of insect and fungi present in the same 266 study trees of the 16 main study plots (12–27 trees/plot). Identification was done to species level for the common organisms and to feeding guild for the unknown ones. For each pest or pathogen on each study tree, one of us (MJL) assessed severity of the damage on a scale from 0 to 5.

Statistical analysis

Population abundance, measured as galls per shoot, was analysed with a general linear model that included site quality, freezing in 2017 or not, and their interaction as fixed effects, site nested within site quality and freezing as a fixed effect, tree nested within site as a random effect, the number of buds per shoot at the end of previous year's growing season (potential sites for galls) as a continuous variable, and no intercept.

Larval size and adult fecundity were analysed with an analysis of variance (ANOVA) that included year, freezing, year x freezing, and plot nested within freezing.

Leaf size, terpenes, phenols, and condensed tannins were analysed with an ANOVA that included year, freezing, and their interaction as fixed effects. Each replicate sample represented a different tree. Water and nitrogen content were analysed with an ANOVA that included year, tissue type (ungalled leaf, ungalled portion of galled leaf, or gall), freezing or not in 2017, their 2-

and 3-way interactions, and plot nested within freeze and year; tree was a random effect nested within plot and year.

The size and wall thickness of galls were analysed with an ANOVA that included freezing, site quality, gall type, and their interactions as fixed effects, and plot nested within freezing and site quality as a random effect. Cells per gall were log-transformed prior to analysis to improve normality and homoscedasticity.

Damage levels from common pests and pathogens were analysed with an ANOVA that included freezing, site quality, and their interaction as fixed effects, and plot nested within freezing x site quality as a random effect. Regression models were used to compare attack level of *D. kuriphilus* with the severity of other insects and pathogens.

Statistical analyses were performed with the package JMP (SAS Institute Inc.).

Results

Impact of extreme climatic events on Dryocosmus kuriphilus

At the time of the freeze, chestnut trees in all plots were growing shoots and expanding leaves. Trees from plots affected by the freeze lost their crowns completely (Fig. 2), while the non-affected plots either suffered no visible damage or only had some leaves that were partially frozen. Due to local topography, the freeze had variable effects across our study plots: seven were affected and nine were not (Table 1).

Freezing effects on *D. kuriphilus* varied with gall type. Frozen galls in leaves dropped with the leaves within a few days and larvae of *D. kuriphilus* presumably died inside (Fig. 2b). Frozen galls in shoots showed less initial damage (Fig. 2c) and the larvae remained alive longer. Shoot galls sampled 3 days after the frost contained 96% of the larvae alive. A week after the frost, survival was still 87% (Fig. 2d), but gall tissue deteriorated progressively, and larval survival declined accordingly. Larval survival dropped to 68% and then only 25% over the next 2 weeks as the shoot galls rotted (Fig. 2e,f). We did not observe larval mortality in plots not affected by the late-spring frost.

When new leaves grew back in the plots affected by the late-spring frost some contained galls. By the end of larval development in 2017, surviving galls per shoot in frozen plots was only 25–50% of that in unfrozen sites, with stronger reductions in plots that were best for chestnut growth (Fig. 3). In 2018, galls per shoot were still lower in plots that had been frozen, but less so than in 2017. By 2020, gall abundance had fully recovered in frozen plots on high-quality sites and was even higher than unfrozen plots on low-quality sites where wasp densities averaged almost 7 galls per chestnut shoot (Fig. 3). In 2017 and 2020, average gall densities were significantly higher in low-quality sites for chestnut ($F_{1295} = 14.03$, $P < 0.001$, and $F_{1,67} = 4.28$, $P = 0.042$, respectively).

The rapid recovery of *D. kuriphilus* populations in frozen plots was attributable to strong density-dependence, with *per capita* growth rate of *D. kuriphilus* being high when they were relatively rare and decreasing as abundance increased (Fig. 4). In plots with low abundance, growth rates corresponded to population doubling times of just over 3 years ($R \approx 2.25$ galls/gall/year). The

Figure 2 (a) Freeze damage on chestnut leaves and shoots. (b) *Dryocosmus kuriphilus* larvae inside the frozen gall. (c) Bud gall apparently not affected by frost. (d) Gall inner tissue showing necrosis while the larvae was still alive. (e, f) Larvae alive inside the gall 3 weeks after the frost.

apparent equilibrium abundance (K) was about 5 galls/shoot; plots with <5 galls/shoot tended to increase and those with more tended to decrease (Fig. 4). The deterministic density-dependent function in Fig. 4 predicts recovery from low abundance (0.1 galls/shoot) to 90% of equilibrium in ~5 years.

The mass of late instar larvae differed conspicuously between years; larvae of the same developmental stage were about 30% larger in 2018 than in 2017 (Fig. 5, upper; $F_{1,297} = 183.03$, $P < 0.0001$). There was also an effect of frost but only in 2017 when larvae from frozen plots were about 13% smaller than

Table 1 Characteristics of the 16 main study plots. Site index (mean $\pm$ SE) for low- and high-quality sites were 23.3 $\pm$ 0.3 and 26.2 $\pm$ 0.4 m, respectively

Locality	Latitude (°N)	Longitude (°E)	Elevation (m.a.s.l.)	Frost damage	Minimum temp. (°C)	Site quality	Site index (m)
Carballal	42.871	7.883	524	No	1.4	High	25.6
Castroverde	43.101	7.338	534	No	−1.0	High	27.2
O Corgo	42.912	7.504	518	No	−1.9	High	28.2
Rumín	42.854	7.870	549	No	1.4	High	25.8
Verín II	42.760	7.868	574	No	1.4	High	25.4
Gaioso	43.126	7.669	403	Yes	−3.3	High	25.4
Uriz I	43.117	7.649	414	Yes	−3.3	High	26.2
Uriz II	43.114	7.651	407	Yes	−3.3	High	25.5
Buratai	42.994	7.508	448	No	−1.9	Low	23.7
Calde	42.953	7.611	571	No	−1.9	Low	23.0
Masoucos	42.996	7.276	683	No	−0.6	Low	24.6
Torible	43.023	7.681	544	No	−1.9	Low	24.2
Verín I	42.760	7.869	580	No	1.4	Low	23.0
Casa Laranxa	43.118	7.660	411	Yes	−2.8	Low	22.6
Esperante	42.964	7.598	520	Yes	−2.8	Low	23.6
Robra	43.089	7.613	407	Yes	−3.3	Low	22.2

those from unfrozen plots (Fig. 5, upper; main effect of freeze: $F_{1,297} = 8.69$, $P = 0.003$; year x freeze interaction: $F_{1,297} = 7.48$, $P = 0.007$).

In the year of the frost, fecundity did not differ among females, but in the next year, adult females in frozen plots had barely half the fecundity as those in unfrozen plots or the previous year (Fig. 5, lower; year x freeze interaction: $F_{1,155} = 9.36$, $P = 0.0026$). The low fecundity of females in frozen plots 1 year after the freeze was a notable pattern in our study population. It contrasts with the stability of fecundity over 3 years in our oldest study site (Lugo, not affected by the freeze), which is where the gall wasp has been established the longest (first detected in 2014): mean $\pm$ SE = 125 $\pm$ 6, 116 $\pm$ 6, and 138 $\pm$ 8 in 2015, 2017 and 2018, respectively; $F_{2,102} = 2.40$; $P = 0.09$.

Impact of extreme climatic events on chestnut leaves and galls

There was severe damage to chestnut trees in the plots that froze in 2017. All leaves and shoots that were expanding at that time were destroyed and dropped within few days (Fig. 2a). Trees responded with refoliation but the length of leaves in 2017 was reduced in frozen plots: mean $\pm$ SE = 9.7 $\pm$ 0.9 vs. 14.3 $\pm$ 0.9 cm, respectively ($F_{1,38} = 10.34$; $P = 0.003$). Leaf size in frozen plots was still 26% smaller in 2018: 14.3 $\pm$ 1.0 vs. 19.5 $\pm$ 0.8 cm, respectively ($F_{1,38} = 20.14$; $P < 0.0001$). Leaf size may also have been affected by the drought because leaf length was less in 2017 than in 2018: 12.0 $\pm$ 0.6 vs. 17.3 $\pm$ 0.6 cm, respectively ($F_{1,77} = 27.76$; $P < 0.0001$ for a year effect).

Analyses of leaves without galls showed variable effects from freezing on phytochemistry (Fig. 6). In frozen plots compared to unfrozen plots, total phenols were significantly lower ($\approx$23%), and total terpenes were significantly higher ($\approx$26%) ($F_{1,63} = 4.32$ and 4.70, respectively; $P < 0.04$). Condensed tannins were similar between frozen and unfrozen plots but were more than twice as high in 2018 as in 2017 ($F_{1,63} = 4.70$, $P = 0.03$). ANOVAS of the data in Fig. 6 revealed no other significant main effects or interactions.

Galls always had higher water content than the surrounding leaf tissue in galled leaves or than ungalled leaves (Fig. 7, upper; least square means $\pm$ SE = 82.1 $\pm$ 0.4, 63.3 $\pm$ 0.4, and 64.4 $\pm$ 0.4%; $F_{2,167} = 647.07$, $P < 0.0001$, Table 2). Water content of leaves and galls was higher in 2018 compared with the drought year of 2017 (least square means $\pm$ SE = 72.9 $\pm$ 0.4 vs. 66.9 $\pm$ 0.4%; $F_{1,75} = 113.38$; $P < 0.0001$); this was especially true in the ungalled leaves and galled leaves. In 2017, water content of ungalled leaves and galled leaves was markedly higher in frozen plots (which had reflushed leaves) than in unfrozen plots (63–65% vs. 55–59%, Fig. 7) but this was not true in 2018 (66–68%; freeze x year interaction: $F_{1,75} = 24.86$, $P < 0.0001$). There was also a frost x tissue type interaction ($F_{2,167} = 8.01$; $P = 0.0005$) because ungalled leaves and the ungalled part of galled leaves had particularly low water content in unfrozen plots in 2017 (Fig. 7, upper).

Years were similar with respect to average nitrogen content of leaves and galls, but there were patterns with respect to tissue types and exposure to freezing (Fig. 7, lower; Table 2). The highest N concentrations in 2017 were in the relatively small reflushed leaves (with and without galls) in plots that froze (2.96–3.16%). However, N content of the galls themselves was relatively low in these samples. In 2018, N content tended to be lower in the frozen plots than the unfrozen plots, especially in galls and the ungalled portion of leaves with galls.

In 2018, galls were of similar size in plots that froze or not in 2017: mean diameter $\pm$ SE = 9.16 $\pm$ 0.15 vs. 9.16 $\pm$ 0.13 mm, respectively ($F_{1,12} = 2.82$, $P = 0.12$). Shoot galls were larger than leaf galls, which were larger than stipule galls: 11.19 vs. 9.44 vs. 7.44 mm (SE = 0.13 for all; $F_{2,1887} = 526$, $P < 0.0001$); this range was greater in good quality sites than poor quality sites: 7.24 to 11.33 mm vs. 7.64 to 11.04 mm (site quality x gall type: $F_{2,1887} = 4.42$, $P = 0.012$). The number of chambers per gall was positively related to gall size and showed similar patterns as gall size: no effect from the freeze ($F_{1,12} = 0.00$, $P = 0.95$), and stronger differences between gall types on good quality sites (1.28 to 2.62 vs. 1.28 to 2.06 cells/gall for stipule galls to bud galls; site quality x gall type: $F_{2,1887} = 8.66$, $P = 0.0002$). The average thickness of galls walls was about 2.45 $\pm$ 0.06 mm
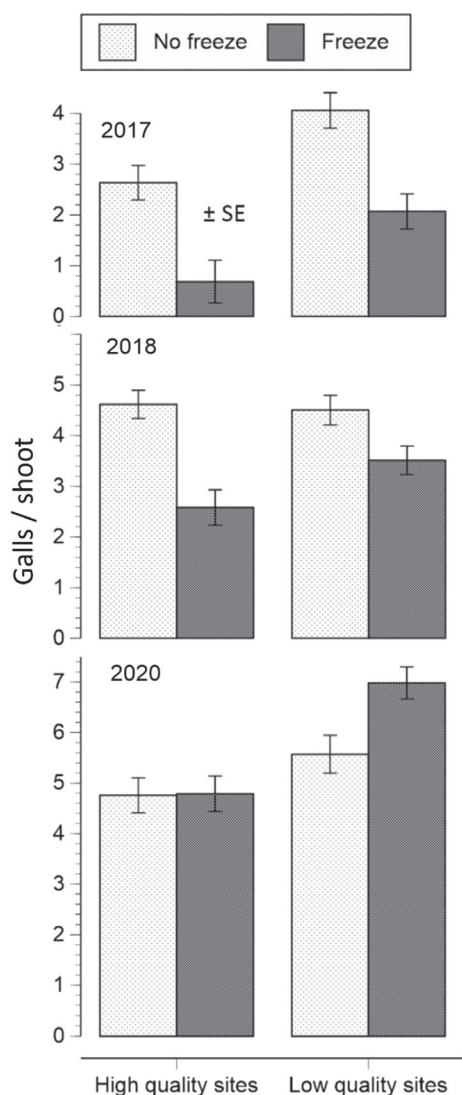
Figure 3 The abundance of *Dryocosmus kuriphilus* galls in plots that were and were not frozen in the year of the late-spring frost (2017), the following year, and 2 years later. Data are grouped by sites that were low *vs.* high quality for growth of chestnut trees.

Figure 4 *Per capita* change in the abundance of *Dryocosmus kuriphilus* from 2017 to 2018 as a function of density in 2017. Each point represents a plot. Some plots were frozen in spring of 2017 and some were not. There was additional variation among plots in initial density due to time since invasion by *D. kuriphilus*. The relationship was log-linear and suggests an equilibrium (*K*) of about 5 galls/shoot (with an average annual shoot being 25 cm long and containing 5 buds).

Figure 5 Larval mass (a) and fecundity (b) of *Dryocosmus kuriphilus* in 2 years in plots that were and were not frozen in spring of 2017.

irrespective of freezing, site quality, or any of their interactions ($P > 0.12$).

Impact of weather and gall wasps on other pests and pathogens

Our survey of 266 trees carried out in 2018 and distributed across 16 plots revealed frequent occurrences of three types of folivorous insects (defoliators, leaf miners, and leaf skeletonizers) and four types of fungi (*Cryphonectria parasitica*, *Mycosphaerella maculiformis*, *Gnomoniopsis* sp., and *Phomopsis* sp.) Damage from one or more of these agents were evident in 17–96% of the trees. Most trees showed damage from at least one of the insect groups and one of the fungal groups (97% and 87%, respectively). The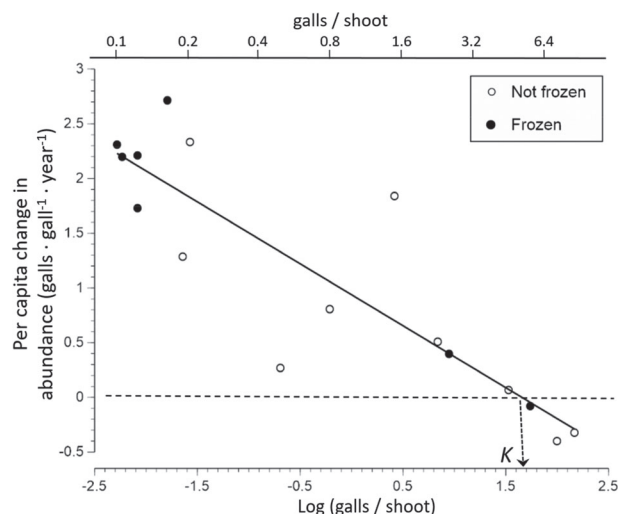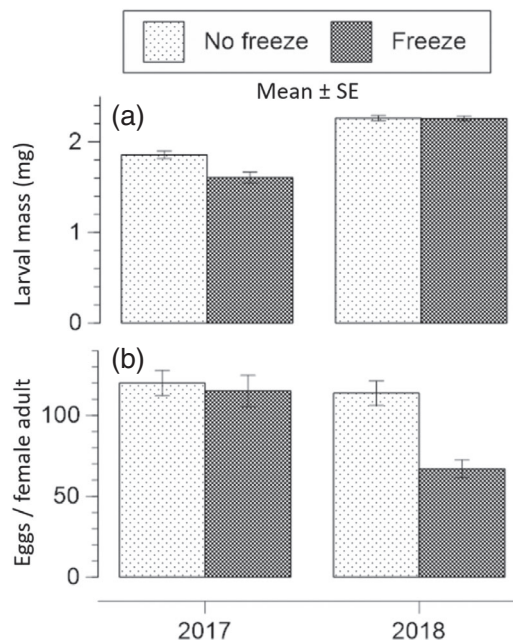re were no significant correlations among the seven agents in their damage levels (|r| < 0.26 for 22 pairwise comparisons, $n = 266$).

There was only limited evidence for effects of freezing in 2017 on damage from pests and pathogens in 2018. Leaf miner damage was higher in previously frozen plots: mean damage score ± SE = 0.30 ± 0.03 *vs.* 0.08 ± 0.03, respectively ($F_{1,7.8} = 26.47$, $P < 0.0001$), and skeletonizer damage was lower
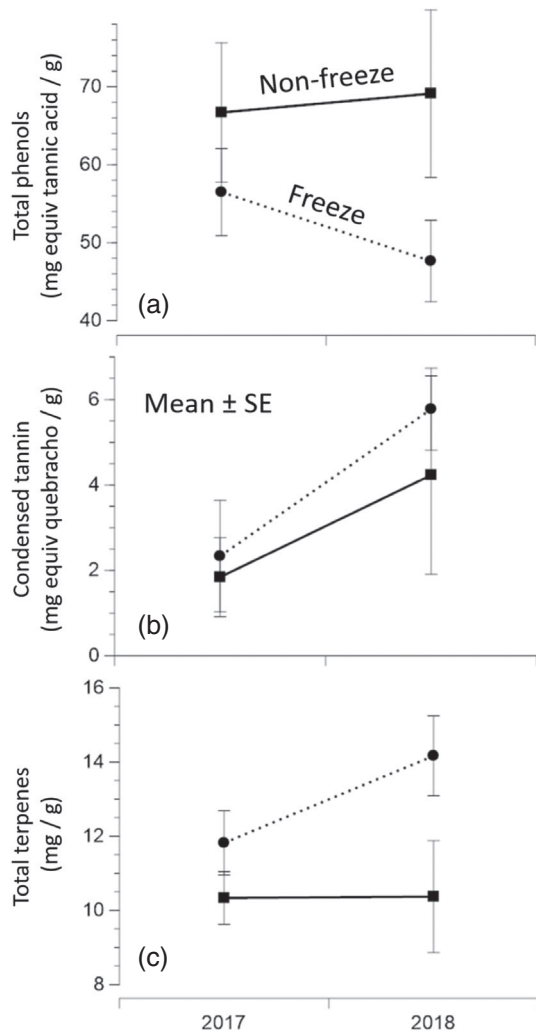
Figure 6 Foliar concentrations of (a) Total phenols, (b) Condensed tannins, and (c) Terpenes in 2 years in plots of chestnut that were and were not frozen in spring of 2017.

Figure 7 Foliar concentrations of water (upper) and nitrogen (lower) in 2 years in plots of chestnut that were and were not frozen in spring of 2017. Measurements included control leaves, leaf tissue around galls in galled leaves, and the galls themselves.

Discussion

The late-spring frost of April 2017 caused severe freezing damage to both natural and cultivated vegetation though Europe (Vitasse & Rebetez, 2018). There were catastrophic consequences for fruit growing and viticulture. Economic losses were estimated at €3.3 bn mainly for fruit and wine growers – especially in Italy, France, Germany, Poland, Spain and Switzerland (Munich Re, 2017).

The major damage in Galicia occurred in wine and chestnut plantations (DOGA, 2017). Altitude, even just a few meters, made big differences among sites; plots located at lower altitude suffered more damage. In clear nights with temperature inversions, colder near-ground temperatures bring greater frost damage at lower topographic areas (Clarke, 1946).

The late-spring frost strongly affected chestnut trees, but also populations of *Dryocosmus kuriphilus*. Abundance after the frost was reduced to 25–50% of the previous abundance in plots that froze (Fig. 3). Presumably, most larvae died by starvation because they were unable to leave their deteriorating gall tissue. Surprisingly, in plots where trees lost completely the crown, trees flushed back with galls in leaves and shoots, most likely because some buds were not yet developed by the end of April. We cannot reject the possibility that *D. kuriphilus* lays some eggs in dormant or adventitious buds, as is known in other gall makers when abundance is high and oviposition sites are limited (Hails & Crawley, 1991). However, plots with low attack levels, and presumably limited competition, also showed galls after refoliation. It could be adaptive for females so spread

in previously frozen plots: damage score $= 0.15 \pm 0.06$ *vs.* 0.48 ± 0.05, respectively ($F_{1,12.6} = 15.89$, $P = 0.002$). There were no significant effects of the 2017 freeze on any of the other five agents ($P > 0.18$). There were no significant effects for any of the seven agents from site quality or freeze x site quality. There was a tendency for variation in attack severity by fungi among replicate plots (Wald's P value $= 0.03$, 0.03, 0.06, and 0.07 for *Cryphonectria*, *Gnomoniopsis*, *Mycosphaerella*, and *Phomopsis*, respectively). None of the insect groups showed variation in attack levels among replicate plots.

Damage from skeletonizers tended to decrease with increasing damage from gall wasps ($P = 0.002$, $n = 260$; regression of residuals from above ANOVA *vs.* % crown damage from gall wasps). However, damage from *Gnomoniopsis* and *Mycosphaerella* tended to decrease with increasing damage from gall wasps ($P = 0.0002$ and $P = 0.02$, respectively, n = 260). The other four agents of damage showed no relationship to abundance of gall wasps.

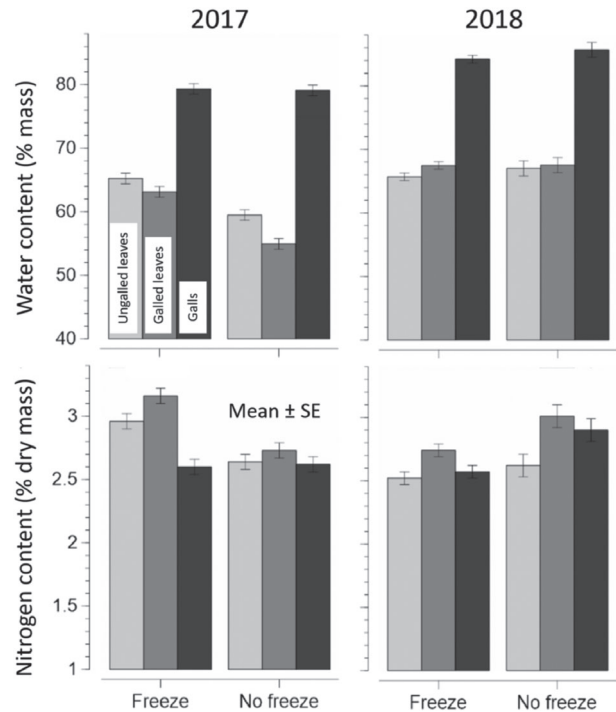**Table 2** ANOVA results comparing water and nitrogen content of three tissue types (ungalled leaves, galled leaves, and galls) in 2017 and 2018 from a total of 88 trees within plots that were frozen in spring of 2017 and those that were not. Corresponds to data in Fig. 7

Source	df num.	df den.	Water content		Nitrogen content	
			F	P	F	P
Year	1	75	113.38	<0.0001	1.45	0.23
Tissue type	2	167	647.07	<0.0001	21.56	<0.0001
Year*tissue type	2	167	7.36	0.0009	9.85	<0.0001
Freeze	1	75	11.03	0.0014	0.00	0.97
Year*freeze	1	75	24.87	<0.0001	23.46	<0.0001
Tissue type*freeze	2	167	8.01	0.0005	7.67	0.0006
Year*tissue type*freeze	2	167	4.41	0.014	3.05	0.050
Plot[year, freeze]	9	75	7.69	<0.0001	4.01	0.0003

their eggs among different bud types as a bet hedging strategy (Hopper, 1999).

Effects of the late frost were most dramatic on sites best for chestnut growth, where populations were reduced to a quarter compared with non-freeze plots (Fig. 3, high-quality sites). It remains unclear why wasp population declined more in better sites for chestnut. Population levels were higher in low-quality sites and the proportion of leaf gall *vs.* shoot galls was similar among sites as well as bud density. There were no differences in gall wall thickness due to site quality. Neither did we observe an effect of site quality on water content of the galls that could explain differences in turgidity and therefore susceptibility to frost. Rocha *et al.* (2013) suggested that the presence of a gall wasp induces physiological changes on plant foliage increasing plant defence mechanisms against cold. If this was true in our system we would have expected differences in crown damage due to the freeze in plots with higher wasp abundance, but crown damage was similar in all the freeze plots, independently of the site quality.

In spite of dramatic effects on abundance, wasp populations recovered very quickly in frozen plots. One year after the freeze (2018), even though the statistical effect of freeze remained, wasp populations in freeze-plots had increased by 7.5-fold in high-quality sites and 1.6 in low-quality plots (Fig. 3). Increases in abundance in non-freeze plots were more moderate (Fig. 3). This is consistent with density-dependent growth in wasp population dynamics (Fig. 4). Three years after the late-spring frost (2020), populations had fully recovered in the freeze plots, which was consistent with simple extrapolations from the density-dependent function. In general, intraspecific competition is a leading candidate to produce rapid density dependence (Berryman *et al.*, 1987; Royama, 1992); this is also likely in our study system since the number of buds available for oviposition decreased in sites with high gall wasp density (Gil-Tapetado *et al.*, 2021b).

The initially higher densities of *D. kuriphilus* in low-quality sites were again evident by 2020. This is consistent with the hypothesis that environments less suitable for plant growth tend to favour high abundance of gall makers (Fernandes & Price, 1992).

Results supported the hypothesis that chestnut trees affected by the late-spring frost of 2017 compensated by allocating resources to produce new leaves (Rubert-Nason *et al.*, 2017). However, they did not compensate fully in that leaves were smaller in plots that froze. Even a year later, leaves were still 27% smaller in freeze plots than non-freeze plots. Refoliation after freezing varies among species both in extent and in character – some species respond with an increase in leaf size (St. Clair *et al.*, 2009) while others tend to increase leaf number (Prozherina *et al.*, 2003). Leaf size was also affected by drought, since leaves were 30% bigger in 2018 compare with 2017. Plant plasticity to drought stress varies within genera, species and even cultivars (Sanchez-Blanco *et al.*, 2002). Many studies have shown a reduction in leaf size and increase in leaf number with the increase of water stress (Bosabalidis & Kofidis, 2002; Bhusal *et al.*, 2020).

Results supported the hypothesis that both freeze and drought influenced leaf phytochemistry. In the summer of the freeze, the smaller reflushed leaves in plots that froze had higher water content, perhaps due to reduced leaf water loss (Wang *et al.*, 2019). Water content of ungalled leaves was higher in 2018 compared with the drought year of 2017 – especially in non-freeze plots (Fig. 7). Nitrogen concentrations of ungalled leaves were also higher in freeze plots *vs.* non-freeze plots. This could be related to the smaller size of leaves in freeze plots, but this cannot be the only explanation because differences disappeared in 2018 when leaves from freeze plots were still smaller. Opposite to our results, St. Clair *et al.* (2009) found a reduction in N content of about 25% in aspen leaves that reflushed after freeze, but in that case the reflushed leaves were larger rather than smaller compared to leaves on unfrozen trees. The nitrogen content of ungalled leaves was more affected by freeze than drought because non-freeze plots were similar among years (Fig. 7 lower). This contradicts the hypothesis that total nitrogen is generally increased by drought stress (Mattson & Haack, 1987) but aligns with the model of Gutbrodt *et al.* (2011).

Results supported the hypothesis that galls provide shelter from physical environment. Water content was always higher in the gall tissue than in the surrounding leaf tissue (galled leaves) or ungalled leaves both in 2017 – the drought year – and in 2018 when rain recovered to normal values (Fig. 7). Our data thus support the Microenvironment Hypothesis for explaining the adaptive significance of gall induction and the evolution of gall morphology (Price *et al.*, 1987; Crespi *et al.*, 1997; Stone & Schonrogge, 2003; Miller *et al.*, 2009). Even under the severe drought of 2017, water content of the galls was much higher than ungalled leaf tissues. However, our data seem inconsistent

with the Nutritional Hypothesis that galls provide a higher quality nutrient source than other feeding modes (Price *et al.*, 1987; Crespi *et al.*, 1997). In 2017, N content within the gall was similar to the surrounding leaf tissue or the control leaves in non-freeze plots and was even significantly lower in the galls of the freeze plots that have to reflush the leaves (Fig. 7). In 2018, N content within the gall tissue was higher than ungalled leaves, but only in the non-freeze plots. In freeze plots, N content remained the same as the year before. This suggests that the nutritive hypothesis is only supported under conditions of high resources or that N is not limiting to insect nutrition. In 2018, after recovery to normal climatic conditions, N content was higher in the galls from plots not exposed to frost, but in frozen plots N content remained the same as in the previous year. In ring-porous trees (including chestnuts), the development of earlywood vessels begins some 2–3 weeks before the development of leaves (Sass-Klaassen *et al.*, 2011; González-González *et al.*, 2014). Earlywood development draws on reserves accumulated in the previous growing season (Ermich, 1959). Consequently, these trees may have lower carbohydrate reserves because they had to use them to reflush the leaves. Trees may compensate by increasing photosynthesis rates or by increasing their autumnal productivity (Zohner *et al.*, 2019), but both possibilities would have been limited in our study by the severe drought of 2017. Therefore, our results suggest that galls are nutrient sinks only when the growing conditions are good and N availability is relatively high. Thus, we find no clear evidence of manipulation of phytochemistry by *D. kuriphilus* as has been described for other gall-making species (Wool *et al.*, 1999; Giron *et al.*, 2016; Oliveira *et al.*, 2016).

Despite strong links between foliar chemistry, environmental conditions, and herbivore performance (Mattson, 1980; Barbehenn & Constabel, 2011), few studies (*e.g.*, St. Clair *et al.*, 2009; Selig & Bohne, 2016) have evaluated the impacts of freeze damage on the chemistry of tree foliage. In our study, freeze had variable effects depending on the secondary metabolites. Phenol concentrations were lower in freeze plots and total terpenes were higher, while condensed tannins remained the same (Fig. 6). Previous studies have reported that increased phenolic glycosides and decreased condensed tannins in aspen leaves after a freeze (Rubert-Nason *et al.*, 2017), and that the effects of freezing on condensed tannins varied with damage severity and tree size (St. Clair *et al.*, 2009).

In our study trees, condensed tannins were strongly related to drought in that concentrations were less than half in the drought year than in 2018. Some previous work has reported reductions of terpenes and phenolics during drought (Koricheva *et al.*, 1998; Julkunen-Tiitto *et al.*, 2015), but other studies have reported that moderate drought resulted in higher concentrations of total polyphenolics (Nogues *et al.*, 2014; Rivas-Ubach *et al.*, 2014).

The special conditions of 2017 including changes in plant chemistry seemed to influence *D. kuriphilus* performance. Larvae feeding in galls from freeze plots were significantly smaller compared with larvae from unfrozen plots, but this effect disappeared in 2018. In general, larvae feeding during the drought conditions of 2017 were smaller compared with 2018, when precipitation was normal (Fig. 5 upper). These differences were not explained by differences in N content because N content within galls was similar for frozen and unfrozen plots in 2017. Furthermore, differences in larval size disappeared in 2018 even though the N content of galls from freeze plots was significantly lower than from non-freeze plots but similar to the previous year when larvae were clearly smaller (Figs 5 upper and 7).

There seemed to be an effect of climatic events on female fecundity because the number of eggs was dramatically reduced in 2018 in females emerging from the freeze plots (Fig. 5 lower). Exposure of insects to low temperature shock can decrease adult fecundity (Levie *et al.*, 2005; Pandey & Johnson, 2005), but in our study, the pattern in fecundity was only evident in 2018, and not the previous year for females surviving after the frost in 2017. Nitrogen concentrations of the galls in 2018 may help to explain differences in fecundity because N content of galls from freeze plots was significantly lower than the N content in non-freeze plots. But N concentration in galls from freeze plots in 2018 was similar to the 2017 galls, when there were no differences in female fecundity. Previous work reported that a female insect encountering a poor-quality host plant may modify her oviposition behaviour either by reducing the number of eggs she lays or adjusting the size or nutritional content of the eggs (Leather & Burnand, 1987). However, *D. kuriphilus* is a parthenogenetic species and we measured recently emerged females from current year galls before they had encountered a new host. Fecundity of gall-midges (Diptera: Cecidomyiidae) tends to decrease with increasing gall size due to intraspecific competition within the gall (Weis *et al.*, 1983; Ehler & Kinsey, 1990). Similarly, Kato and Hijii (1993) found that gall wasps (Hymenoptera, Cynipidae) from large clutches were less fecund because their mother provisioned less resources to individual progeny. However, we did not see differences in gall size or number of chambers within galls that were related to the freeze. Indeed, *D. kuriphilus* females have shown very stable fecundity since 2015 (in the Lugo plot where the insect was firstly detected) in spite of general population increases in the area (Fig. 3).

We analysed the effect of abiotic damage (frost and drought) on leaf secondary chemistry but did not measure rapid inducible defences or characterize the individual components of phenolics, tannins, terpenes (Yarnes *et al.*, 2008; Lombardero *et al.*, 2016). Thus we cannot reject the possibility that other plant defences may underlie the observed pattern in insect fecundity (Awmack & Leather, 2002; Peterson *et al.*, 2020). However, this is made less likely for gall insects because inner gall tissue where the insects actually feed are enhanced sinks for photosynthates and commonly have low concentrations of secondary compounds (Price *et al.*, 1987; Allison & Schultz, 2005; Motta *et al.*, 2005). Rehill and Schultz (2012) found a positive relationship between condensed tannin concentration and the reproductive performance of a galling aphid. However, in our system, condensed tannins increased in both freeze and non-freeze plots in 2018 while female fecundity dropped only in freeze-plots.

Extreme weather events can dramatically impact populations of individual insect species. Our phytosanitary surveys allowed us to test hypotheses regarding responses of the community of chestnut pests and pathogens. Freeze events can cause shifts in host plant palatability and suitability for insect herbivores and increase susceptibility of trees for future damage (Wargo, 1996;

Rubert-Nason *et al.*, 2017). However, we observed limited effect from freezing in 2017 on damage from pest and pathogens in 2018. Damage of leaf miners was higher in previously frozen plots. Leaf miners have been reported to be influenced by specific leaf area and mean annual rainfall (Bairstow *et al.*, 2010) as well as foliar N concentrations (Giron *et al.*, 2007). Nevertheless, this pattern was the opposite of that found in our system as leaves were still smaller, and N concentrations lower, in freeze plots a year after the freeze. Lower phenols in freeze plots could be a potential explanation for greater damage from leaf miners but phenols have been reported to play a minor role in the resistance of other leaf miners (Ramiro *et al.*, 2006).

Opposite the case for leaf-miners, damage from leaf skeletonizers was lower in previously frozen plots. There is little information on determinants of diet quality in leaf skeletonizers, but they have been reported to do better in plants under stress (Wills & Farr, 2017). In our study, damage by skeletonizers tended to decrease with increasing damage from gall wasps. This is consistent with the hypothesis that galling insect species may indirectly affect the incidence and consumption of folivorous insects by changing phenolic concentrations (Pascual-Alvarado *et al.*, 2008).

Fungal damage was not affected by frost as has been previously reported (Osorio & Mcgee, 1992, but see Reich & Vanderkamp, 1993). However, damage by *Mycosphaerella maculiformis* and *Gnomoniopsis* sp. tended to decrease with increasing damage from gall wasps. Previous work showed that *Gnomoniopsis* sp. causes necrosis in the galls, negatively affecting the survival of *D. kuriphilus* (Vannini *et al.*, 2016).

Late-spring frost events are a feature of mid-latitude weather systems around the world. Historical weather data, tree ring information and projections from general circulation models can be combined to better understand past and future patterns in spring frost events. Projections of late-spring frosts risk under a climate change scenario indicate that the change in the risk will be region-specific (Zohner *et al.*, 2020). In the case of the northern Iberian Peninsula, it has been reported that about one third of beech forests experienced at least one late frost defoliation event during 2003–2018 (Olano *et al.*, 2021) and the frequency increased since the 1990s (Sangüesa-Barreda *et al.*, 2021), suggesting an on-going frost risk rise.

Our work expands understanding of how climate change can alter the impact of forest pests (Ayres & Lombardero, 2018) directly by affecting insect populations and indirectly by affecting tree palatability. Effects can include changes in the community structure of herbivorous insects (Lavergne *et al.*, 2010; Walther, 2010) and other species living in the same trees (Forchhammer *et al.*, 2008; Ims *et al.*, 2008; Villalpando *et al.*, 2009). Our results state that late-spring frost and summer drought can influence forest pest abundance (Fig. 3), phytochemistry of trees (Figs 6 and 7), and the broader community of forest insects. The effects of these climatic events were large but transient, as other studies have previously pointed out (Marquis *et al.*, 2019). It remains unknown if or when frosts and droughts can produce lasting changes in forests. Further knowledge will require more studies that are structured around weather events that cannot be easily planned or predicted.

Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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