



Host Gall Size and Temperature Influence Voltinism in an Exotic Parasitoid

Martin Aguirrebengoa*, María Eva Wong, Juan Ramón Boyero and Javier Quinto

Laboratorio de Entomología Agrícola, Centro IFAPA de Málaga, Instituto de Investigación y Formación Agraria, Pesquera, Alimentaria y de la Producción Ecológica, Málaga, Spain

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*Correspondence:

Martin Aguirrebengoa
martin.aguirrebengoa@
juntadeandalucia.es

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Insect phenology is highly temperature-dependent. Higher temperatures can lead to earlier emergence and lengthening of the active period, which enable many insect groups to complete more generations. Studies on the effects of climate change on insect populations are providing concerning evidence supporting this relationship. These kind of shifts in phenology and voltinism also occur in agricultural and forest insect pests and their natural enemies, with potential implications for biological control. The consequences derived from changing temperature regimes on tritrophic interactions remain poorly studied, particularly in gall-inducing insects and their parasitoids. Here we detail the occurrence of bivoltinism in the exotic parasitoid *Torymus sinensis*, previously categorized as univoltine, a widely introduced species to fight against the invasive Asian chestnut gall wasp *Dryocosmus kuriphilus* wherever this pest spread. This plasticity in voltinism has been observed in the southernmost European distribution of *D. kuriphilus*, and appears to be mediated by both temperature and gall traits, namely size or the number of gall chambers. Bivoltinism was most common at annual mean temperatures around 13.5°C and in galls with more chambers. Through this work, we intend to unravel the factors behind this phenomenon and discern the possible consequences on host-parasitoid interactions.

Keywords: biological control, *Castanea*, climate change, *Dryocosmus kuriphilus*, insect life-cycle, insect phenology, *Torymus sinensis*, phenotypic plasticity

INTRODUCTION

Temperature is one of the main drivers of insect phenology (Gutiérrez and Wilson, 2021). Changing temperatures can foster diverse effects on insect phenology, and main responses are driven by phenotypic plasticity and evolutionary changes (Forrest, 2016; Marshall et al., 2020; Rodrigues and Beldade, 2020). For example, warmer temperatures can increase estivation (dormant physiological state that takes place in summer in response to high temperatures), lead to earlier emergence from diapause (hormonally mediated delay in development in response to adverse environmental conditions) and/or advanced phenology (e.g., Saulich and Musolin, 2017; Davies, 2019; Marshall et al., 2020). Moreover, the associated lengthening of the active season enable many insect groups to complete more generations (voltinism) (e.g., Jönsson et al., 2009; Altermatt, 2010; Martín-Vertedor et al., 2010). Such changes can trigger multiple impacts on antagonistic interactions, such as phenological mismatches between natural enemies and their hosts

(Damien and Tougeron, 2019; Abarca and Spahn, 2021), or the alteration of community structure and food webs (Harvey et al., 2020; Lann et al., 2021), with detrimental consequences for pest control in agricultural and forest systems (Tougeron et al., 2020; Frank, 2021; Lann et al., 2021). In specialized host-parasitoid interactions, trophic levels often respond differently to thermal stress, but in general, parasitoids will be more constrained than hosts, not only by direct phenological shifts affecting their populations, but also by indirect bottom-up and top-down effects (Chidawanyika et al., 2019; Thierry et al., 2019; Tougeron et al., 2020). Despite their ecological and economic impacts, scarce attention has been paid to potential effects on plant–gall insect–parasitoid tritrophic interactions (but see Noe and Niinemets, 2020; Gil-Tapetado et al., 2021a), and further research is needed on this issue.

The chalcid parasitoid *Torymus sinensis* (Hymenoptera: Torymidae), native to East Asia, is an effective biological control agent of the invasive Asian chestnut gall wasp *Dryocosmus kuriphilus* (Hymenoptera: Cynipidae), the most serious chestnut pest worldwide (Avtzis et al., 2019; EPPO, 2021). The use of this exotic natural enemy is a good example of successful classical biological control; this is the reason why it has been introduced wherever the pest spread over the past decades (Moriya et al., 1989; Avtzis et al., 2019; Marcolin et al., 2021). The life-cycle of *T. sinensis* is highly synchronized with that of its host *D. kuriphilus* (*T. sinensis* adults emerge from 1-year-old dry galls at the end of winter, shortly after the reactivation of *D. kuriphilus* larvae and subsequent gall induction, and parasitize larval stages growing inside the newly formed galls) and both species have been widely reported as univoltine (Moriya et al., 1989; Murakami et al., 1995; Cooper and Rieske, 2011; Ferracini et al., 2015). Although *T. sinensis* was traditionally considered as host-specific, an extensive tracking over the first 10 years after its introduction in mid-northern Italy demonstrated less strict monophagy and higher phenological plasticity than previously thought (Ferracini et al., 2017; about host specificity also see Gil-Tapetado et al., 2021b).

The phenology of exotic insect species may be subject to temperature-mediated alterations in their areas of introduction, particularly in their extreme distributional ranges. The southernmost distributional range of *Castanea sativa* chestnuts in continental Europe occurs in the southern Spanish province of Málaga, with the warmest European growing conditions (annual mean temperatures ranging from 13.1 to 16.0°C). *Dryocosmus kuriphilus* was first detected in 2014 in this area, and spread rapidly through the province, while *T. sinensis* has been yearly released in all affected localities since the year following the pest detection (Nieves-Aldrey et al., 2019; Wong et al., 2021). Climatic conditions in southern Spain could exert even greater selective pressure and lengthen the active period of both *D. kuriphilus* and *T. sinensis* in comparison to northern latitudes (Gil-Tapetado et al., 2021a; Quinto et al., 2021), therefore representing a suitable study area for further research into phenological shifts in *T. sinensis*. We predicted that bivoltinism in *T. sinensis* could occur in the warmest locations within the studied area, which would allow the occurrence of a first rapid life-cycle inside the newly formed fresh spring galls and likely start a second cycle on

the same *D. kuriphilus* cohort. With this aim, we sampled fresh spring *D. kuriphilus* galls across different locations and further assessed the influence of temperature variables. Given that gall traits can be related to temperature regimes and may play a crucial role in this host-parasitoid interaction (Gil-Tapetado et al., 2021a,c), we also evaluated the effect of the number of chambers per gall, which in turn is a proxy for gall size (László and Tóthmérész, 2013).

METHODS

Data Collection

Around 450 *D. kuriphilus* fresh spring galls were collected on 11-May-2021 from each of 17 chestnut sampling locations framed in three municipalities (Igualeja, Pujerra, and Jubrique) at the foothills of the Sierra de las Nieves mountainous enclave (Málaga, Spain; **Figure 1A**). Within each sampling location, leaf, bract, and basal galls were randomly collected from 8 to 10 trees, which were detached from shoots, and the leaf tissues cleaned. Twenty galls per sampling location were dissected and the mean number of chambers/gall (mean \pm SD: 4.81 ± 1.01 chambers/gall; range: 3.45–6.85) and of immature pre-dormant *T. sinensis* individuals per sampling location were determined. The estimation of immature *T. sinensis* individuals allowed to quantify the average parasitism by *T. sinensis* with a presumably univoltine life-cycle per sampling location:

univoltine *T. sinensis* parasitism (%) =

$$\frac{\text{number of immature } T. \text{ sinensis individuals}}{\text{number of dissected galls} \times \text{mean number of chambers/gall}} \times 100$$

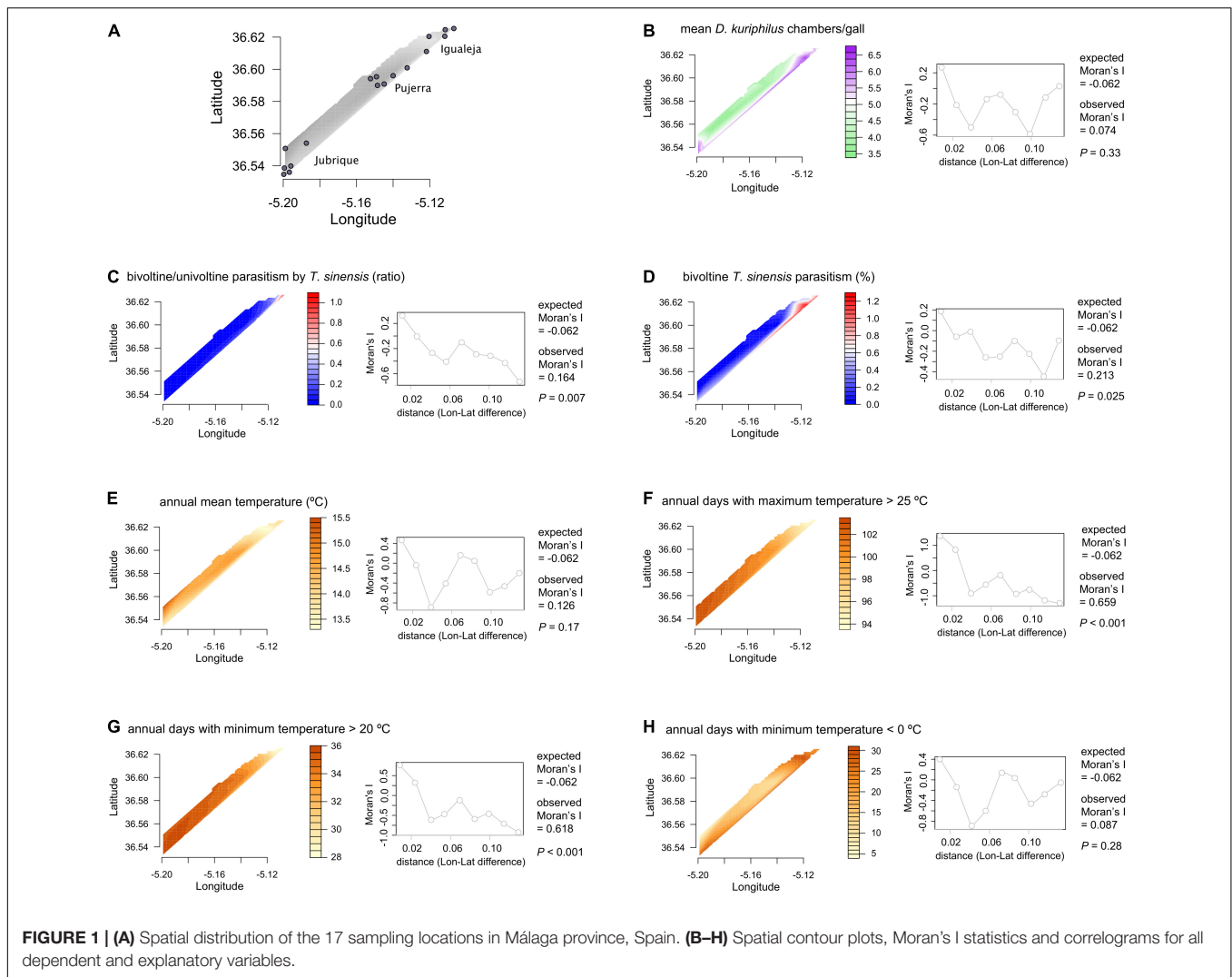
In addition, 435.38 ± 121.42 (mean \pm SD) fresh galls per sampling location (range: 260–691) with no previous exit holes were immediately stored in 75×7.5 cm sterilized cardboard tubes (one per location) with extractable tubes exposed to light. Tubes were maintained in laboratory conditions under natural daylight and ambient temperature and relative humidity. They were daily monitored for parasitoid emergence until late June, when no more parasitoids emerged after 10 days. Average bivoltine parasitism (parasitism hereafter) by *T. sinensis* across locations was calculated as:

bivoltine *T. sinensis* parasitism (%) =

$$\frac{\text{number of emerged } T. \text{ sinensis individuals}}{\text{number of stored galls} \times \text{mean number of chambers/gall}} \times 100$$

Besides, *T. sinensis* bivoltine/univoltine parasitism ratio per sampling location was calculated. The identity of immature and emerged *T. sinensis* individuals was corroborated using the keys provided by Nieves-Aldrey and Gil-Tapetado (2019).

Finally, to test whether the temperature is determinant of *T. sinensis* bivoltinism, we obtained fine-scale spatial temperature values (annual mean temperature, annual number of days with maximum temperature $> 25^\circ\text{C}$, annual number of days



with minimum temperature > 20°C, and annual number of days with minimum temperature < 0°C) for each of the 17 sampling locations from the 1971 to 2000 Iberian Climatic Atlas of AEMET (State Meteorological Agency of Spain), which provides georeferenced data with an accuracy of 1 km².

Statistical Analyses

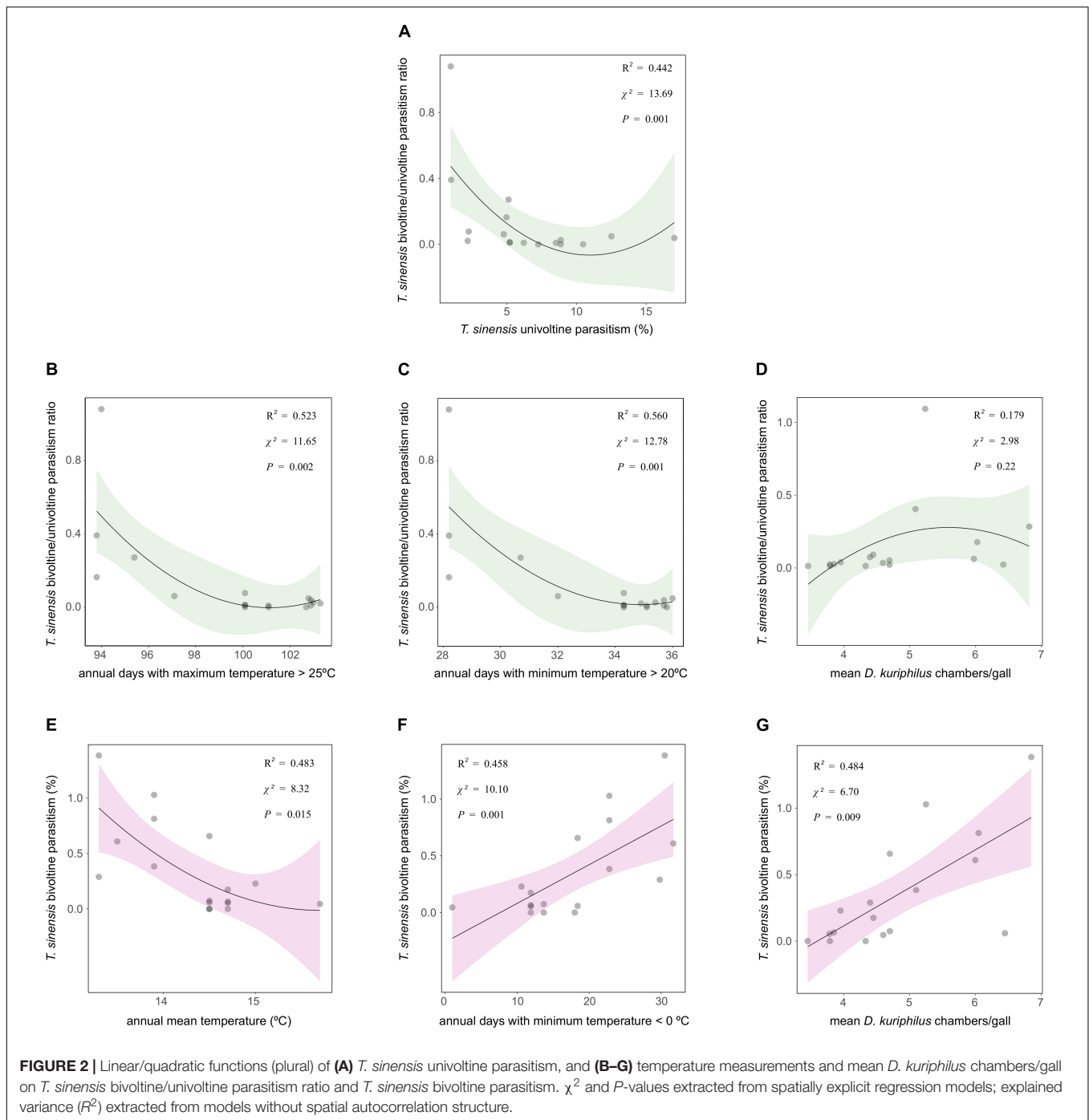
We used the statistical program R version 3.5.2 for the analyses (R Core Team, 2020). First, we tested the occurrence of spatial autocorrelation for all dependent (*T. sinensis* bivoltine/univoltine parasitism ratio and *T. sinensis* bivoltine parasitism) and explanatory variables (*T. sinensis* univoltine parasitism, temperature measurements, and mean *D. kuriphilus* chambers/gall), based on Moran's I correlation coefficient for distance matrices (Griffith and Chun, 2014; Hansen et al., 2020). Moran's I correlation coefficients were calculated with the package *ape* (Paradis and Schliep, 2019), and we used the package *pgirmess* (Giraudoux, 2021) for plotting the correlograms and

the package *akima* (Akima and Gebhardt, 2020) for plotting the spatial contour plots.

Next, we tested the relationship between the dependent and explanatory variables. Given the overall high spatial autocorrelation observed for both explanatory and dependent variables (higher than expected in all cases; **Figures 1B–H**), we performed spatially explicit regression models with the package *spaMM* (Rousset and Ferdy, 2014), set to linear or quadratic functions based on model fit (**Supplementary Table 1**). Regarding the different temperature measurements, we used the ones that showed the best model fit in each case (**Supplementary Table 1**). We used the packages *ggplot2* (Wickman, 2016) and *rms* (Harrell, 2019) for graphing the scatterplots and 3D plots.

RESULTS

A total of 144 *T. sinensis* individuals emerged from the fresh spring galls collected in May 2021. This implies a *T. sinensis* bivoltine parasitism of 0.34 ± 0.41% (mean ± SD; range:

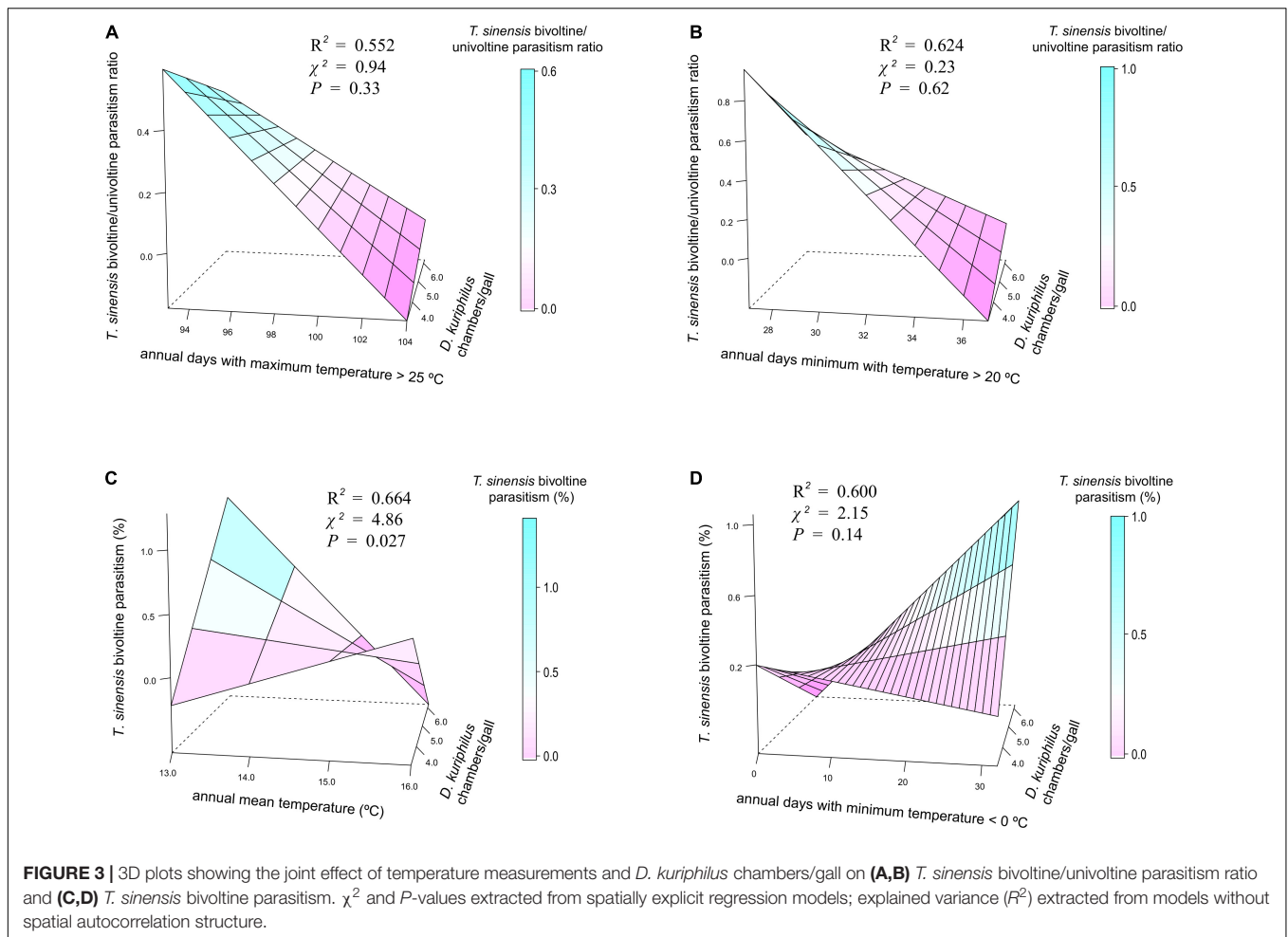


0–1.38%). *Torymus sinensis* univoltine parasitism was $6.54 \pm 4.24\%$ (mean \pm SD; range: 0.95–17.02%), whereas *T. sinensis* bivoltine/univoltine parasitism ratio was 0.13 ± 0.26 (mean \pm SD; range: 0–1.08).

Torymus sinensis bivoltine/univoltine parasitism ratio showed a non-linear correlation with *T. sinensis* univoltine parasitism: the relationship was negative, but only when *T. sinensis* univoltine parasitism was lowest (Figure 2A). *Torymus sinensis* bivoltine/univoltine parasitism ratio was negatively correlated with the annual number of days with a maximum temperature > 25°C and with a minimum temperature > 20°C (Figures 2B,C),

whereas no significant correlation with the mean number of *D. kuriphilus* chambers/gall was detected (Figure 2D). *Torymus sinensis* bivoltine parasitism showed no correlation with *T. sinensis* univoltine parasitism ($\chi^2 = 1.78$, *P* = 0.18), whereas it was negatively correlated with annual mean temperature (Figure 2E), and conversely, positively correlated with annual days with a minimum temperature < 0°C and with the mean number of *D. kuriphilus* chambers/gall (Figures 2F,G).

Temperature patterns and *D. kuriphilus* chambers/gall did not show significant interactive effects on *T. sinensis* bivoltine/univoltine parasitism ratio (Figures 3A,B), but had a



synergistic interactive effect on *T. sinensis* bivoltine parasitism (Figure 3C). The highest bivoltinism rate took place in those locations in which the number of *D. kuriphilus* chambers/gall was higher (≥ 5) and where the coolest annual mean temperature occurred ($\leq 14^\circ\text{C}$). When annual days with a minimum temperature $< 0^\circ\text{C}$ was taken as the measure of temperature, such an interactive effect was not observed (Figure 3D).

DISCUSSION

We demonstrate the occurrence of bivoltinism in the widely introduced biological control agent *T. sinensis* in southern Spain. A small but significant proportion of the population (mean: 13%) was able to complete a rapid immature development in less than 3 months and emerge in May–June from fresh galls, instead of estivating in larval stage during summer and overwintering as last larval or early pupal stage (Ferracini et al., 2015; Borowiec et al., 2018).

Contrary to what we predicted, bivoltinism was favored in locations with larger galls and cooler temperatures (annual mean temperatures around 13.5°C ; Figures 2, 3). Several gall size-derived indirect effects could explain the positive relationship

between large galls and bivoltinism. On the one hand, more *D. kuriphilus* larvae can escape from parasitism in larger galls, i.e., with more chambers (Bonsignore and Bernardo, 2018; Gil-Tapetado et al., 2021c), which could determine higher availability of hosts for a potential second generation of *T. sinensis*. Gall size is also positively related with *D. kuriphilus* population densities (Kato and Hijii, 1993), since a greater number of eggs/bud are laid at higher densities, which leads to the formation of larger galls. On the other hand, larger galls could more strongly buffer the impact of abiotic factors (Price et al., 1987; Miller, et al., 2009), delaying the immature development of *D. kuriphilus*, thus becoming potential prey for the offspring of *T. sinensis* individuals emerging from spring galls. Further evidence supporting the effect of temperature on gall size was recently reported by Gil-Tapetado et al. (2021a), who highlighted that larger galls are formed in the Mediterranean region than in cooler conditions in the Eurosiberian region. Regarding temperatures, the offspring of those *T. sinensis* emerging from spring galls in May could be able to parasitize the same cohort of *D. kuriphilus*, specifically individuals remaining in L3 stage (Quinto et al., 2021). However, the duration of the immature development of *D. kuriphilus* could be shortened and the adult phenology advanced in the warmest locations, consequently

reducing the likelihood of parasitization by a second generation of *T. sinensis*.

Several aspects raised in this study require further research. First, it should be delved into the high spatial autocorrelation observed for bivoltinism (Figure 1), which could be partially attributed to local microenvironmental conditions. Second, large-scale studies assessing the potential emergence of *T. sinensis* from fresh spring galls throughout its entire distributional range are needed to understand how thermal regimes influence on this phenomenon, including different chestnut species and genotypes. Third, the persistence of bivoltinism and its long-term ecological and evolutionary consequences for the components of this specialized plant–gall inducing host–parasitoid tritrophic interaction must be thoroughly analyzed. The existence of two generations per year *a priori* could lead to increased population levels (making this strategy potentially beneficial and selectable for the species) and enhanced pest control. Nevertheless, the individuals of *T. sinensis* that emerged from fresh galls were somewhat smaller than those that emerge from dry galls (personal observation). Hence, the potential consequences for the population dynamics of *T. sinensis* may be negative, since a smaller adult size is generally associated to lower fertility and ultimately fitness (temperature-size rule; Honěk, 1993; Kingsolver and Huey, 2008; Verberk et al., 2021). Additionally, intraspecific competition could limit this rapid generation (with presumably shorter ovipositor) to oviposit on unparasitized host larvae in the innermost chambers. Increased temperatures due to climate change could also reduce the occurrence of bivoltinism in this area, although it is cannot be ruled out that the competitiveness of this rapidly developing generation of *T. sinensis* may increase over the years. Lastly, the high phenological plasticity observed in this species reinforce the need to study its potential environmental risks: hybridization with native species and attack on non-target species.

Host gall size and temperature influence the ratio of bivoltinism at the southernmost European distribution of *T. sinensis*. Long-term and large-scale upcoming studies are needed to gain knowledge about the extent, applicability and implications of voltinism changes in this important biological control agent of *D. kuriphilus*.

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DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

MA analyzed the data. MA and JQ led the writing of the manuscript. All authors agreed with the last draft of the manuscript, and planned, designed, and performed the research and collected the data, and executed data interpretation.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2022.784111/full#supplementary-material>

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