

Article

Parasitoids Reduce Growth Rate of Oak-Feeding Caterpillars

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Abstract

Koinobiont parasitoids have been shown to both reduce and increase the growth rate of caterpillars. However, no comprehensive study has been conducted on several caterpillar hosts of a given plant species. Moreover, most of the existing case studies are on large caterpillars attacking crop plants. This may not be representative of the effect of parasitoids on the growth of caterpillars that feed on trees. We sampled caterpillar communities from the canopy of oak trees (*Quercus robur* and *Q. petraea*) in a forest in France and from one in Poland, measured their growth rate, and noted parasitoid exit. The details of the methods varied between study years and locations, and this was partially accounted for statistically. Across six species of Lepidoptera, parasitoids reduced caterpillar growth rate on average. The effect of parasitism appeared to vary widely within and across lepidopteran species, indicating diversity in the outcome of plant–herbivore–parasitoid interactions. Further studies should verify this result and determine if the reduced growth rate is accompanied by lower plant consumption rates. If so, plants would immediately benefit from attracting parasitoids when they are attacked by caterpillars, and forestry practices that increase parasitoid abundance could reduce folivory partly without delay.

Keywords: tri-trophic interactions; host manipulation; koinobiont; caterpillar growth curves; Hymenoptera; Lepidoptera



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1. Introduction

Parasitoids typically kill a significant proportion of herbivorous insects such as the caterpillars of Lepidoptera that feed on plants [1]. Some of these parasitoids paralyse their host permanently (idiobionts), but most paralyse their host only temporarily (koinobionts), so that the host can continue feeding [2]. Therefore, parasitoids may be regarded as providing less immediate benefit to individual plants than predators that kill herbivorous insects immediately. Plants that attract parasitoids (e.g., by emitting herbivore-induced plant volatiles [3]) may die or suffer reduced reproduction [4–6] before profiting from the delayed defence offered by the parasitoids. Moreover, neighbouring conspecific plants would equally profit, irrespective of whether they attracted parasitoids or not. Overall, the extent to which plants are under selection to attract parasitoids may depend strongly

on how parasitism affects herbivore feeding and growth. The immediate effects of parasitisation on caterpillar growth may also contribute to the effect that forestry practices that promote parasitoid abundance have on tree growth. If parasitoids reduce folivory directly, their benefit would be greater than if they only impact the next generation of herbivore populations; because such populations may operate over large distances and are thus hardly affected by local population dynamics.

Counterintuitively, parasitoids can both decrease and increase the growth of their hosts. The direction and extent of host growth manipulation are related to the relative size of host and parasitoid and whether the parasitoid is solitary or gregarious, with relatively large parasitoids requiring hosts to reach full size or grow larger than normal [7,8]. Parasitoid species may even adjust their host manipulation to different host species (e.g., [9,10]). Parasitoids can reduce caterpillar growth rate as a passive disease response or as active manipulation by the parasitoid and may also induce caterpillars to grow for a longer time and become larger (reviewed in [11]). To manipulate host growth, the adult parasitoid can inject factors along with the eggs into the host, such as endogenous viruses and venom [11]. Parasitoid larvae can also produce factors that affect host growth such as teratocytes (e.g., [12]). The reduced growth rate may be due to the parasitoid reducing the feeding rate of its host (e.g., [13,14]). Generally, a reduced growth rate is accompanied by a reduced leaf consumption rate. However, in the laboratory, overall leaf consumption may not be affected or can even increase if parasitoids prolong the host's development time (e.g., [15,16]). According to a recent review [11], many cases of both parasitoids increasing and decreasing growth of their host insects have been reported, but reduced growth appears more common. Notably, growth has not been quantified in a consistent way, often focusing on maximum size rather than growth rate. While maximum size may correlate best with total leaf consumption in captivity, growth rate is likely crucial in the field as reduced growth rate makes attaining larger sizes more difficult, exposes caterpillars to other causes of mortality for a longer time, and allows plants more time to build up defences in their leaves. Moreover, most of these case studies are on large caterpillars attacking crop plants. This may not be representative of the effect of parasitoids on the growth of caterpillars that feed on trees. No comprehensive study has been conducted on the effect of parasitoids on the growth rate in the community of caterpillar hosts of a given plant species.

To test if parasitoids reduce the average growth rate of caterpillars, we compared the growth rate of non-parasitised caterpillars with that of parasitised caterpillars collected from oak trees (*Quercus petraea* (Matt.) Liebl. and *Q. robur* L.) in two forests. We specifically tested the prediction that caterpillars that are parasitised have a lower growth rate than those that are not parasitised across caterpillar and parasitoid species, forests, and study years. These oaks are important components of forests in northern Europe and are known to host a wide variety of Lepidoptera [17], which in turn host a diverse parasitoid community [18]. They emit specific volatiles in response to herbivory that attract predators [19–21], but responses of parasitoids remain unclear [21].

2. Methods

2.1. Overview

We collected and reared spring-feeding caterpillars from the canopy of mature oak trees (*Q. petraea*, *Q. robur* and hybrids) in the Forêt de Rennes in Brittany, western France (2012 and 2019), and the Puszcza Zielonka forest in western Poland (2021 and 2022). Data on caterpillar growth were collected with other aims in mind, and methods differed between locations and years. In summary, we monitored the budburst phenology of selected oak trees, and sampled branches from the canopy shortly after budburst (Figure 1). We then

searched for caterpillars and reared each individually, assigning them to surrogate species. We then reared them to adulthood or parasitoid exit while measuring mass or length at least twice and attempted to identify them to species. We then calculated caterpillar growth rate and tested for effects of parasitism on caterpillar growth rate (Figure 1).

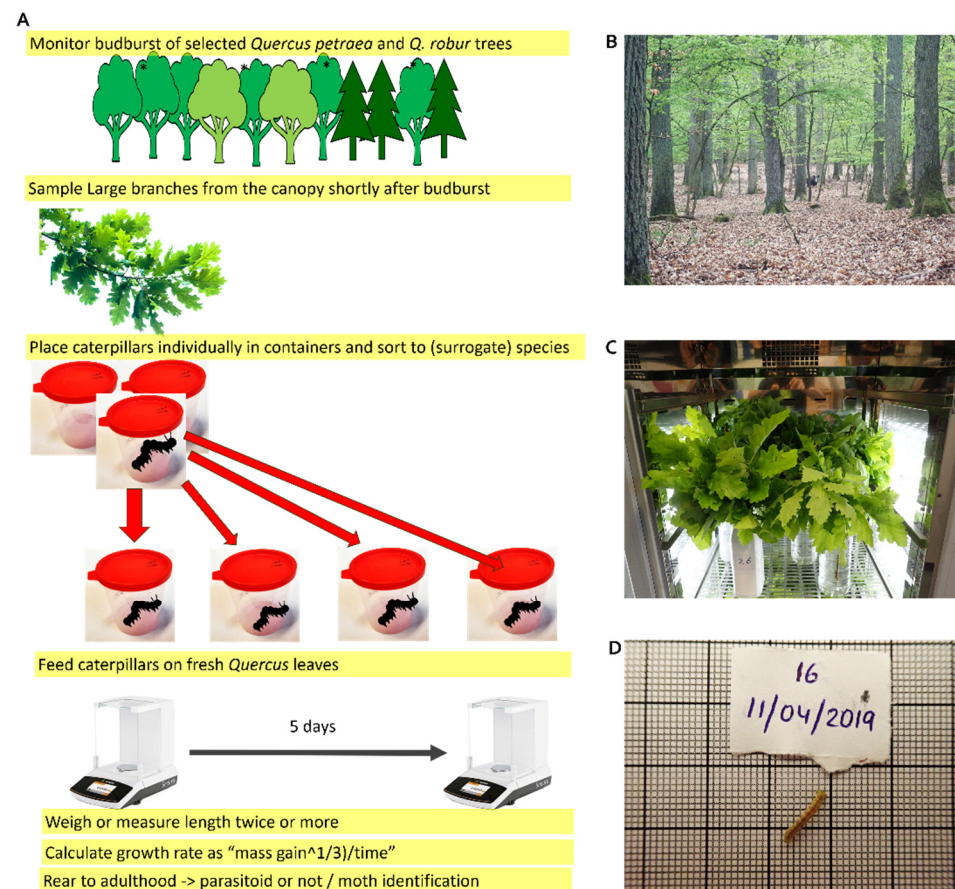


Figure 1. Overview of methods with (A) main steps, (B) Puszcza Zielonka forest in Poland in spring, (C) leaves kept fresh in growth chamber in Poland, and (D) caterpillar photograph for length measurement in France.

2.2. Caterpillar Rearing in France 2012

We sampled branches from 19 oak trees (*Q. petraea*–*Q. robur* hybrids) shortly after budburst (11 April to 11 May 2012 as timing of budburst varies between trees [22]). We transported the branches in plastic bags to the lab and reared the associated caterpillars individually in Petri dishes at room temperature using locally obtained *Q. robur* leaves. We photographed the caterpillars every alternate day on graph paper (Figure 1D) and then determined their length from the photographs (24 April to 24 May). We assigned the caterpillars to surrogate species and linked these later to species using individuals that we reared to adulthood and identified. We noted when a parasitoid exited from a caterpillar or if the caterpillar pupated.

2.3. Caterpillar Rearing in France 2019

We collected branches from 24 oak trees (*Q. petraea*–*Q. robur* hybrids) in spring (26 March to 23 May 2019) and reared the caterpillars in the lab (part of these data were used in [22]). We reared all caterpillars separately in Petri dishes in a climate room mimicking the average diurnal changes in temperature, daylight, and relative humidity of the study forest. We fed the caterpillars with freshly emerged *Q. robur* leaves. The caterpillars were weighed on a semi-microbalance on average twice a week. In addition to

classifying caterpillars into surrogate species and linking these to reared adults, we used DNA barcoding [23] to provisionally identify caterpillars that did not reach adulthood. Samples were processed following the laboratory and bioinformatic pipeline described by Kortmann et al. [22]. Briefly, DNA was extracted from homogenised specimens, and a mitochondrial COI minibarcode was amplified using high-throughput-sequencing-adapted primers, followed by sequencing on an Illumina MiSeq platform. Sequences were quality filtered and clustered into operational taxonomic units (OTUs), which were compared against reference sequences from the Barcode of Life Data System (BOLD), with assignments additionally checked against NCBI. Because whole specimens were analysed and could contain DNA from parasitoids or other associated organisms, multiple taxa could be recovered from an individual sample. Moth identity was therefore assigned from the lepidopteran sequence matching the reference database.

2.4. Caterpillar Rearing in Poland 2021

We collected branches from the canopy of four sessile oak trees (*Q. petraea*) shortly after budburst (14 May 2021). We cut the branches into pieces and transported them to the laboratory in plastic bags. The next day, we searched the branches for caterpillars and placed each individually in a 50 mL cup. *Operophtera brumata* (L.) (Geometridae) caterpillars could be putatively recognised, and other morphologies were given surrogate-species names. We reared the caterpillars individually on leaves from these trees in a climate chamber with a constant temperature of 20 °C and relative humidity of 75%. Three days later, we removed the frass and placed a new leaf inside each cup. We weighed the caterpillars the day after collection before adding food, and six days later, as they were transferred to a new cup. Thus, on both occasions, caterpillars could not feed for a few hours before weighing, removing variation caused by stomach content. Caterpillars were henceforth fed *Q. petraea* leaves taken from the sampled trees, and we noted death, parasitoid exit, pupation, and eclosion dates. We identified all eclosed Lepidoptera to species using dissection of genitalia when needed [24–27] to then link caterpillar surrogate species to species.

2.5. Caterpillar Rearing in Poland 2022

This study in 2022 was similar to that in 2021, but sampling ten trees (six on 11 May and four on 16 May 2022), and caterpillar mass change was measured over a five-day period (described in more detail in [28]). Unfortunately for the current purpose, this time, we avoided rearing caterpillars that appeared parasitised.

2.6. Data Analysis

To estimate caterpillar mass from their length (data from France 2012), we assumed that caterpillars had a cylindrical shape and thus utilised the formula ' $\pi \times (\text{height}/2)^2 \times \text{length}$ ' to calculate their volume [29,30]. For each species, we inferred height from length by determining the height–length ratio from several lateral photographs of caterpillars found online. We thus estimated that the height–length ratios were 0.1563 for *Cosmia trapezina* (L.) (Noctuidae), 0.1364 for *O. brumata*, and 0.1507 for *Orthosia cruda* (Den. & Schiff.) (Noctuidae). We finally assumed that the mass density of the caterpillars is similar to water to translate estimated volume into estimated body mass.

Quantifying caterpillar growth rate is complicated because caterpillar growth occurs in phases, and absolute mass gain increases with body size. Specifically, growth pauses during moulting (change of instar), and caterpillars lose considerable body mass while preparing to pupate [31]. Detailed studies showed that caterpillar growth rate can be approximated as ' $(\text{final mass} - \text{initial mass})^{1/3} / \text{development time}$ ' [31]. We visualised the growth curves of oak-feeding caterpillars in our study for individuals with at least three size measurements (France 2012 and 2019). To calculate growth rate, we took the

first measurement as the initial mass. In an attempt to avoid the mass loss associated with pupation, we selected the final mass as the measurement before mass gain decreased when multiple measurements were available for an individual (2012 and 2019). For 2012, we also excluded caterpillar measurements that were longer than 16 mm, as caterpillars then approach pupation. When we had only two measurements (Poland 2021, 2022), we used a short period (five days in 2022, six days in 2021) over which to calculate growth rate to avoid inclusion of mass loss in preparation for pupation. We finally excluded caterpillars that lost rather than gained mass from analysis. Caterpillars that experienced mass loss may have been pupating or unhealthy but possibly also included instances of mass loss induced by parasitoids. We also excluded the few instances of dipteran parasitoids, as they might not manipulate caterpillar growth [32].

We compared growth rates of non-parasitised caterpillars that reached the pupal stage with those recorded as parasitised. Because the data originated from studies conducted in different years using different methodologies, calculated growth rates are not directly comparable among years. Our inference therefore focused on comparisons between parasitised and non-parasitised individuals within species $\times$ year combinations, where individuals were subject to the same study-specific methodology. We used generalised estimating equations (GEEs), implemented in the *geepack* package in R [33–35], with species $\times$ year combinations as clusters and an exchangeable correlation structure. This approach accounts for correlation among observations within species $\times$ year combinations but does not eliminate potential heterogeneity in the effect of parasitism among studies. We therefore complemented the overall analysis with separate within-species $\times$ year comparisons for combinations containing at least three individuals in each parasitism category using Welch's two-sample *t*-test.

3. Results

Overview

We analysed the growth rate of 246 non-parasitised and 34 parasitised caterpillars belonging to five species and one unidentified surrogate species (Table 1). These were *Acrobasis repandana* (Fabr.) (Pyralidae), *C. trapezina*, *Eudemis profundana* (Den. & Schiff.) (Tortricidae), *Op. brumata*, *Or. cruda*, and an unidentified leaf roller (probably Tortricidae). The growth curves of individuals that were measured more than twice show both mass gains and losses. The development time often spanned several months, but most of the growth occurred during the first weeks after collection (Figure 2). The absolute mass gain often increased with time initially (Figure 2), consistent with detailed studies of caterpillar growth patterns [31]. By measuring caterpillars at only two points in time, the growth rate data are thus noisy, even if precautions were taken. However, in most cases, the first section of the growth was typically steady in non-parasitised caterpillars, so that using the first five or six days to calculate growth rate over, will generally avoid the mass loss associated with pupation as intended.

The parasitoids were koinobiont Hymenoptera. The caterpillar growth rates we calculated varied considerably within species, both for non-parasitised and parasitised caterpillars (Figure 3). Across the combined dataset, parasitised caterpillars had an estimated 14% lower growth rate than non-parasitised caterpillars (GEE: $p = 0.006$; Table 2). Nevertheless, some parasitised caterpillars showed growth rates as high as or higher than the average of non-parasitised individuals. *Op. brumata*, often one of the main herbivores on these oak trees, was the most common species in our data and showed a significant reduction in larval growth rate (Figure 3; GEE effect estimate = -0.0057 , $p < 0.001$). The within-species $\times$ year analyses were broadly consistent with the overall negative association: four of the five species $\times$ year combinations with sufficient replication had lower

mean growth rates in parasitised caterpillars (Table 3). Effect sizes nevertheless varied considerably among combinations, including one positive estimate, indicating substantial heterogeneity in the association between parasitism and growth rate. Of the 62 caterpillars that lost mass (excluded from the above analyses), 12 were recorded as parasitised.

Table 1. Overview of sample sizes for growth rate of parasitised and non-parasitised caterpillars.

		<i>A. repandana</i>	<i>C. trapezina</i>	<i>E. profundana</i>	<i>Op. brumata</i>	<i>Or. cruda</i>	Species A	Total
France	Non-Parasitised		9		11	2		22
2012	Parasitised		3		1	1		5
France	Non-Parasitised			10	48	2		65
2019	Parasitised			4	6	1		12
Poland	Non-Parasitised				4		65	69
2021	Parasitised				1		8	9
Poland	Non-Parasitised	52		18	17	6		93
2022	Parasitised	3		1	1	1		6
Total		55	12	33	89	13	73	281

Table 2. Results of generalised estimating equation model for effect of parasitisation on caterpillar growth rate with family set as Gaussian, id as interaction between species and year, correlation structure as exchangeable, and link as identity. Number of clusters was 100, with a maximum cluster size of 60. *p*-values smaller than 0.05 are in bold font.

	Estimate	S. e.	Wald	<i>p</i> -Value
Intercept	0.028	0.0016	312.3	<0.001
Parasitisation	−0.004	0.0016	7.6	0.006
Estimated scale parameters:				
Intercept	0.00027	<0.001		
Estimated correlation parameters:				
Alpha	0.787	0.0842		
Effect estimates				
Effect size:	−14%	Standardised effect:		−0.24

Table 3. Results of Welch’s two-sample *t*-test for year–species combinations with at least 3 observations per category, with Hedges’ *g* effect estimates. *p*-values smaller than 0.05 are in bold font. See Table 1 for sample sizes.

Year	Species	Mean Growth Rate		T	DF	<i>p</i> -Value	<i>g</i>
		Non	Par				
2012	<i>Cosmia trapezina</i>	0.0373	0.0347	0.16	2.25	0.887	−0.148
2019	<i>Eudemis profundana</i>	0.0136	0.0198	−0.94	4.95	0.39	0.556
2019	<i>Operophtera brumata</i>	0.0151	0.0097	2.61	8.96	0.028	−0.754
2021	Species A	0.0305	0.0289	0.50	10.1	0.628	−0.152
2022	<i>Acrobasis repandana</i>	0.0472	0.0227	2.88	2.02	0.101	−5.01

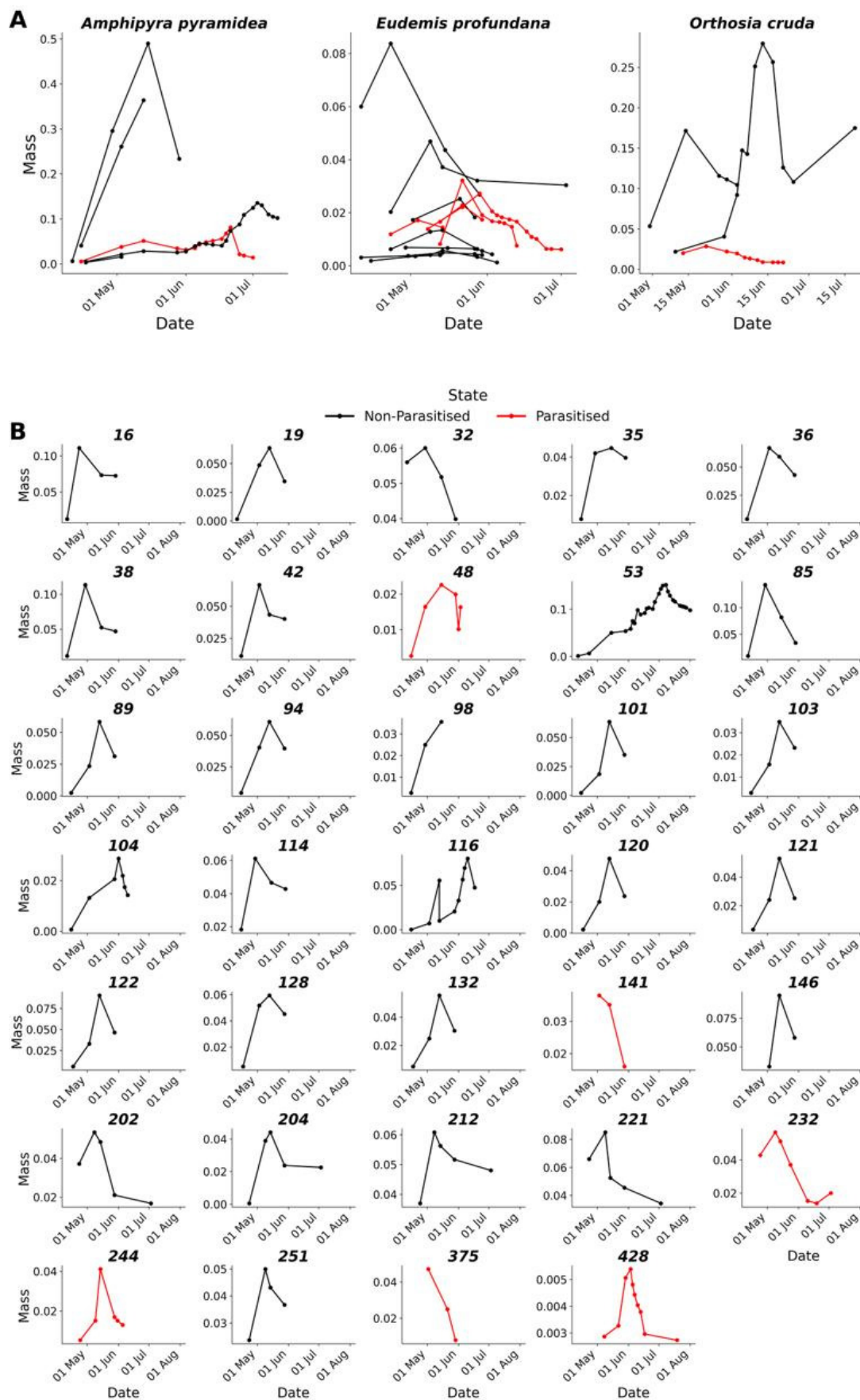


Figure 2. Growth curves of individual caterpillars (in black, non-parasitised individuals; in red, parasitised individuals) for three species (**A**) and winter moth *Operophtera brumata* (**B**) reared in France. Mass is expressed in grams. Numbers in (**B**) represent individual ID numbers.

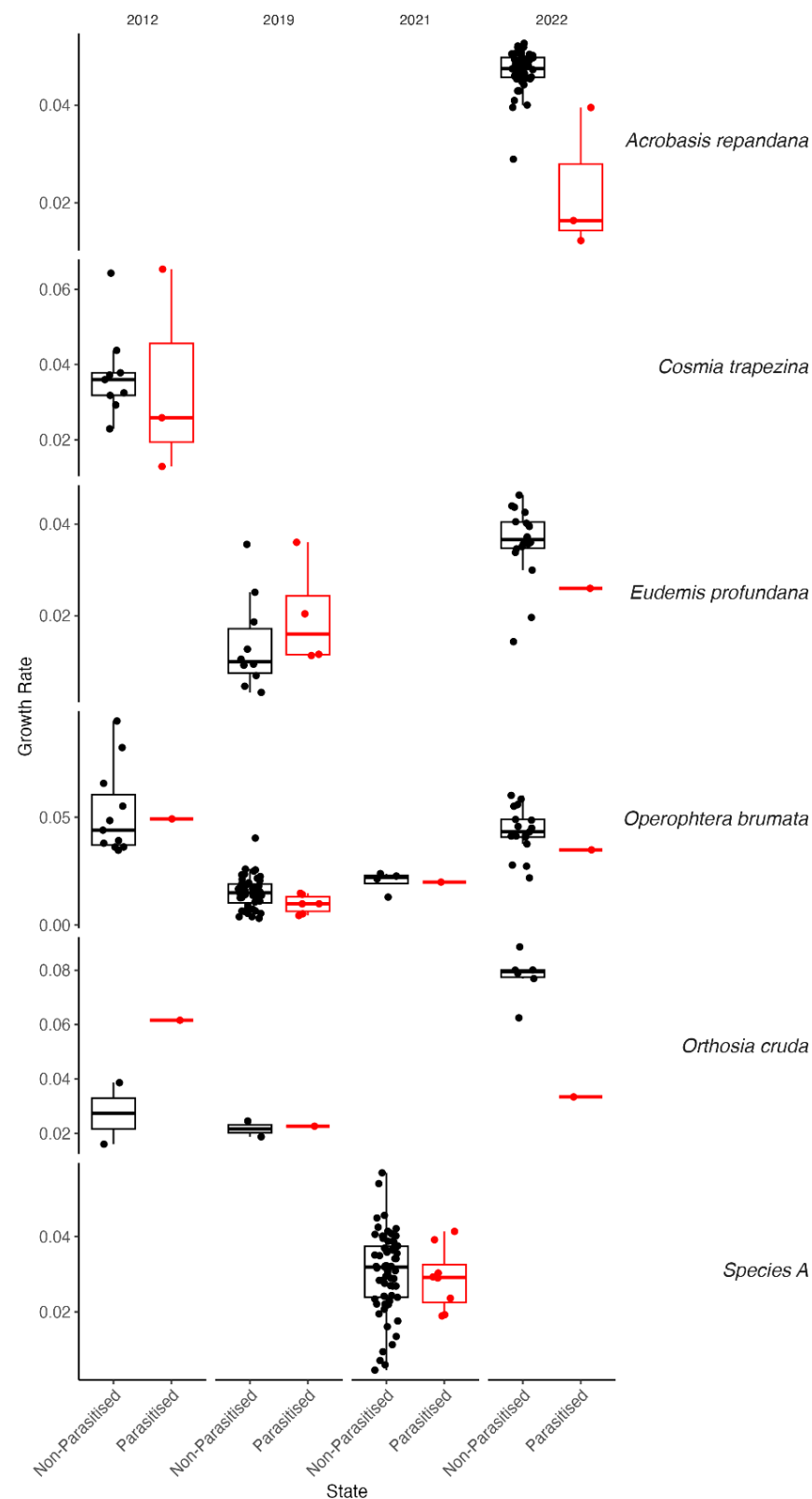


Figure 3. Scatter plot and boxplots of growth rate (mass increase ($\text{mg}^{1/3}$)/time interval (days)) of non-parasitised (in black) and parasitised (in red) caterpillars reared during four springs (France 2012, 2019, Poland 2021, 2022). The central line within each box represents the median, the box boundaries denote the interquartile range, and the whiskers extend to the smallest and largest values within 1.5 times the interquartile range. Data points beyond this range are displayed as outliers. Boxplots for species with few data points need to be interpreted with caution.

4. Discussion

We measured the growth rate of non-parasitised and parasitised spring caterpillars collected from oak trees (*Q. robur* and *Q. petraea*) in France and Poland, and we found that, across six species of Lepidoptera, parasitised caterpillars had an estimated 14% lower growth rate on average. However, some parasitised caterpillars showed growth rates as high as or higher than the average of non-parasitised ones. Notably, by excluding caterpillars that lost rather than gained mass, and in 2022 excluding caterpillars that appeared parasitised, we probably excluded some cases in which parasitoids severely reduced caterpillar growth rate, so that our analysis likely underestimates the average reduction in caterpillar growth rate. Even though we detected a reduction in the growth rate on average, there was extensive variation in the effects of parasitism on the growth rate within and across caterpillar species. This indicates that this tri-trophic interaction has diverse outcomes. Such diversity is consistent with the broader concept of continua in the outcomes of biotic interactions [36] and with evidence that parasitoids can vary markedly in their effects on host growth, ranging from growth suppression to growth promotion [11].

Our study has several limitations. The data were compiled from studies conducted in different years and using somewhat different methodologies. We minimised this problem by basing inference on comparisons between parasitised and non-parasitised caterpillars within species $\times$ year combinations. Nevertheless, this design assumes that study-specific conditions affect the two groups similarly within each species $\times$ year combination. However, methodological or environmental differences among studies could also modify the effect of parasitism, which cannot be resolved statistically with the present data. Specifically, the response of caterpillars to parasitism may depend on leaf quality and on rearing temperature [37]. Leaf quality likely varied between years in response to weather, and rearing temperature varied between the years, except between the two years in Poland. Long-term trends in leaf chemistry in response to N deposition and changes in CO₂ concentration have been observed in Europe (1990–2016 [38]), and droughts have been shown to affect leaf quality in our study species on an annual scale (2004–2021 [39]). Within our study, 2019 was a drought year, but this was mainly during the summer before and after the spring during which we conducted the study. In addition, leaf chemistry responds to weather at a much shorter temporal scale (up to 12 days [40]). Notably, there is also much variation in leaf quality related to canopy position and leaf age [41–43] that may allow herbivorous insects to partly avoid such temporal differences by choosing particular leaves. This may help explain why, in a long-term study, insect herbivory did not increase with increasing average foliar N concentration [39]. However, our caterpillars had no choice as they were fed leaves in captivity. In addition, in a short-term study, foliar N was not affected, but mainly the partitioning of that nitrogen among biochemical compounds [40], so that the effect of weather on caterpillar nutrition may have been limited. To address such potential inter-annual differences in the effects of parasitism on caterpillar growth, multi-year studies that measure leaf chemistry and caterpillar growth in a detailed and uniform manner are needed. Due to the confounding of inter-annual variation in weather and methods of measuring caterpillar growth, the limited number of study years per site, and limited sample size per year, our data are not suited to address this issue. The estimated overall effect should therefore be interpreted as an average association across the heterogeneous studies represented in our dataset rather than as a universal effect size.

While our study estimated an overall effect of parasitoids on caterpillar growth rate, the parasitoids were in most cases not identified beyond order, so that we could not compare the effects of growth rate of various clades of parasitoids, or e.g., correlations with the degree of host specialisation. In Poland, eclosed parasitoids were used to characterise the parasitoid community associated with oaks using DNA metabarcoding [21], so that

links with particular caterpillars were lost. With more data, we could also ask whether certain caterpillar traits (e.g., host–plant specialisation, phenology, size, abundance) make them more or less prone to growth rate reduction (e.g., [44]). It is also important to note that our methods could not fully avoid noise in the data due to the pauses in growth during moulting and mass loss before pupation as well as reduced growth rates that may be due to pathogens or even parasitoids that developed inside caterpillars but never exited them. The difficulty of measuring growth rate from field-collected caterpillars is illustrated by the mass trajectories of individuals that were measured more than twice (Figure 2). Moreover, some of the caterpillars were shelter builders (*A. repandana*, *E. profundana*, and species A), so by breaking their shelters when we weighed or fed them, their growth rates were probably reduced [45]. This extra stress might, for example, exacerbate the effect of parasitoids on growth rate. Occasional host-plant switching (in France from *Q. petraea* to *Q. robur*) could have added more noise to the data.

A further source of noise may be the stomach content, which may have varied considerably among the caterpillars in France that were removed from their food right before weighing. In Poland, caterpillars had been kept without food for several hours before weighing so that their digestive systems were probably empty, reducing this source of noise. Measuring caterpillar length may avoid this source of noise but has its own limitations due to caterpillar stretchability and changing allometry during ontogeny. Finally, further noise was probably introduced when attempting to identify caterpillars that died based on surrogate species (e.g., [28]). Indeed, we had an unidentified leaf roller.

Perhaps this field-based study can inspire similar studies in this and other systems that avoid methodological pitfalls identified here as much as possible and thus verify our results and determine their generality. To obtain more accurate data on how parasitoids affect larval growth rate, we need controlled experiments in which caterpillars are weighed frequently, their development is monitored in short intervals, and caterpillars are infected with known parasitoid species during specific stages (e.g., [15,46,47]), but this is hardly feasible for a diverse caterpillar–parasitoid community associated with a species of tree. Nevertheless, we believe that our results are robust to methodological particularities because methods of rearing and measuring growth were the same for both categories within years, and study year and species identity were at least partially accounted for statistically. Overall, our data indicate that parasitoid wasps on average reduce the caterpillar growth rate of caterpillars associated with oak trees in western and northern Europe.

Further studies need to address to what extent the reduced growth rates of parasitised caterpillars result in reduced leaf consumption. If slower-growing caterpillars indeed consume less leaf material, parasitoids would immediately benefit the individual plant, albeit this benefit being smaller than that of attracting predators that kill caterpillars immediately. Even if slower-growing caterpillars consume more by increasing development time, in the field, the slower growth rate will expose them to other natural enemies and the elements for a longer period. This can also lead to reduced total leaf consumption on average. Moreover, as leaves become more defended as they develop [48], slower growth will lead to spring caterpillars experiencing decreased food quality, further reducing their growth and survival rate. Notably, the time spent feeding also affects mortality as caterpillars are more likely to be attacked during feeding [49], but we have little insight into how parasitoids affect caterpillar feeding behaviour (e.g., [13,50]). Overall, reduced growth rate with extended development time could still reduce the overall leaf damage under field conditions. Therefore, to establish the link between parasitoids manipulating host growth and the resulting leaf consumption, we need both matching data on leaf consumption and growth (e.g., [14,15]), as well as on caterpillar mortality in the field (e.g., [51,52]). If reduced growth rate is indeed accompanied by reduced leaf consumption in the field, our results

suggest that individual trees have an immediate benefit from recruiting parasitoids and would thus be selected to do so. Future studies will need to test this.

Author Contributions: F.M. developed the initial concept of this study, participated in the fieldwork and caterpillar rearing in Poland, supervised data analysis, and wrote the first draft of the manuscript. A.T. performed the data analyses and visualisations. S.M. helped collect data in 2019 and curated the data from France, S.L. collected data in 2012, and A.P. initiated and helped with data collection in France (2012 and 2019). U.W. participated in the fieldwork, weighed the caterpillars in Poland, and identified adult Lepidoptera reared from caterpillars in Poland. All authors contributed to the manuscript writing. All authors have read and agreed to the published version of the manuscript.

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