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Parasitoids and pathogens in a collapsing *Lymantria dispar* (Lepidoptera: Erebidae) population in Lower Austria

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Abstract

A local population outbreak of the spongy moth, *Lymantria dispar* L. (Lepidoptera: Erebidae), in Lower Austria, resulted in the defoliation of an oak forest in 2018 and 2019. In the study year 2020, the population density was still high but was expected to decline. In the present work, the role of parasitoids and pathogens in the collapse of the population was investigated. In total, 20 egg masses, 680 larvae and 12 pupae of *L. dispar* were collected in the field from April to July 2020 and reared until the emergence of adult moths or death. Causes of mortality were determined based on emerging parasitoids and on microscope inspection of non-parasitized cadavers. Stage-specific mortality rates were calculated for eggs, larval stages (L1–L6) and pupae. Seven parasitoid species and three pathogens were responsible for the premature death of spongy moths. The egg parasitoid *Anastatus disparis* (Hymenoptera: Eupelmidae) emerged from 19% of all eggs. Larval parasitoids caused stage-specific mortality rates from 15% to 61%. The dominant parasitoid of young and intermediate instars was the solitary wasp *Glyptapanteles porthetriae* (Hymenoptera: Braconidae). Mature larvae were mainly parasitized by the parasitic flies *Blepharipa pratensis* (Diptera: Tachinidae) and *Parasetigena silvestris* (Diptera: Tachinidae). Pathogens caused stage-specific mortality rates from 11% to 41%. The nuclear polyhedrosis virus (*Ld*NPV; Lefavirales: Baculoviridae) was the dominant pathogen in all instars. The introduced fungus *Entomophaga maimaiga* (Entomophthorales: Entomopthoraceae)—detected for the first time in Austria in 2019—caused low mortality rates in older larvae. Starting from high egg mass densities in spring, the spongy moth population declined to negligible levels until summer.

KEYWORDS
entomopathogens, forest ecology, Lymantria dispar, natural enemies, parasitoids

1 | INTRODUCTION

The spongy moth, *Lymantria dispar* (Lepidoptera: Erebidae), is a univoltine-defoliating forest pest. Although the larvae are highly polyphagous, they show considerable host preferences (Wellenstein & Schwenke, 1978). In Central Europe, *Quercus robur*, *Quercus cerris* and *Quercus petraea* are the primary host plants (Alalouni et al., 2013). As in many other forest pest insects, the population dynamics of *L. dispar* are characterized by population cycles, which are synchronized over large parts of continents and

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typically comprise periods of 8–13 years in Central Europe (Hlásny et al., 2016). The regulation of these dynamics is very complex and not fully understood yet (Hlásny et al., 2016; Johnson et al., 2005). Several field studies highlighted the importance of natural enemies in these population dynamics in Europe (e.g. Fuester et al., 1983; Hoch et al., 2001; Zúbrik & Novotný, 1997). The complex of natural enemies of the spongy moth is very diverse in its Palearctic native area, including numerous parasitoids (Alalouni et al., 2013; Žikić et al., 2017), predators (Gschwantner et al., 2002; Smith & Lautenschlager, 1978) and pathogens (Novotný, 1989; Weiser, 1998). According to investigations in Austria and other Central European countries, egg parasitoids of *L. dispar* play a subordinate role (Alalouni et al., 2013; Fuester et al., 1983; Hoch et al., 2001; Zúbrik & Novotný, 1997), while larval and larval-pupal parasitoids are very abundant. The specialized and univoltine tachinids *Parasetigena silvestris* and *Blepharipa pratensis* (Diptera: Tachinidae) are considered to be the most important parasitoid species. Especially in periods of high host densities (Alalouni et al., 2013), they consistently cause high parasitization rates (Alalouni et al., 2014; Eichhorn, 1996; Fuester et al., 1983; Hoch et al., 2001; Kalbacher, 2008; Maier, 1990; Turcáni et al., 2001). Oligo- or multivoltine braconid and ichneumonid wasps are particularly important in periods of low population densities (Alalouni et al., 2013), with *Glyptapanteles liparidis*, *Cotesia melanoscela* (Hymenoptera: Braconidae) and *Phobocampe* sp. (Hymenoptera: Ichneumonidae) as the dominant species in Austria (Eichhorn, 1996; Fuester et al., 1983; Hoch et al., 2001; Kalbacher, 2008). In its invasive range in North America, the natural enemy complex is less diverse (Žikić et al., 2017). While generalist parasitoids, like the polyphagous tachinid *Compsilura concinnata* (Diptera: Tachinidae), are of great importance in the invasive range, they are largely insignificant in Central Europe (Alalouni et al., 2013; Griffiths, 1976; Hoch et al., 2001; McManus & Csóka, 2007). Pathogens cause high mortality rates, particularly in dense populations of *L. dispar* (Alalouni et al., 2013; Hoch et al., 2001). The nuclear polyhedrosis virus *Ld*NPV (Lefavirales: Baculoviridae) is essentially involved in the collapse of virtually all spongy moth outbreaks (Alalouni et al., 2013; Doane, 1970; Weiser, 1998; Wellenstein & Schwenke, 1978). In the past decade, *Entomophaga maimaiga* (Entomophtorales: Entomophtoraceae) spread rapidly throughout much of Europe after its release in Bulgaria in 1999 (Holuša et al., 2020) and was first detected in Austria in 2019 (Hoch et al., 2019). Multiple infection cycles and rapid host death make *E. maimaiga* often a superior competitor in case of co-infections with other pathogens or parasitoids (Elkinton et al., 2019). The fungus has displaced *Ld*NPV as the dominant pathogen of *L. dispar* in wide parts of North America in the past decades (Hajek et al., 2015). Negative correlations between the prevalence of *E. maimaiga* and parasitism rates were shown in North America (Hajek et al., 2015) and are supported by first results from Europe (Georgiev et al., 2013; Tabaković-Tošić et al., 2014; Zúbrik et al., 2016). Increasing conidial densities of *E. maimaiga* in the progressing season are often associated with higher mortality rates in late spongy moth instars (Hajek, 1999). Parasitoids associated with late host instars, especially tachinids, are therefore particularly prone to competition (Georgiev et al., 2013; Tabaković-Tošić et al., 2014; Zúbrik et al., 2016).

From 2017, temporally synchronized local population outbreaks of the spongy moth were observed in large parts of Central Europe, including Austria (Hoch et al., 2021), Germany (Lemme et al., 2019) and Slovakia (Zúbrik et al., 2021). With approximately 4000 hectares, the forest area defoliated by *L. dispar* in 2018 was the largest ever recorded in Austria; similar levels occurred in 2019, but dropped to zero in 2020 (Hoch et al., 2021). After detecting *E. maimaiga* at the study site in 2019, our aim was to investigate the role of the single mortality factors and the nature of the mortality agents during the collapse of a local outbreak.

2 | MATERIALS AND METHODS

2.1 | Investigation site

Insects were collected in an isolated mixed oak forest of about 100 hectares at 330 m altitude, surrounded by agricultural land and settlement areas (Eggenburg, Lower Austria; 48°38′20″N, 15°49′40″E). The forest was chosen as one of two locations in Austria where *E. maimaiga* was detected in the previous year (Hoch et al., 2019). While earlier studies on natural enemies of *L. dispar* in Austria have been conducted in the very east of the country (Burgenland), this is the first investigation in Lower Austria, located about 100 km north-west. The dominant tree species at the study site is *Quercus petraea*, with *Quercus cerris*, *Pinus sylvestris*, *Acer platanoides*, *Robinia pseudoacacia*, *Quercus robur* and *Prunus avium* as cooccurring tree species. The tree age is 50–70 years. The forest is located in the warm-arid Pannonian subcontinental climate zone, with an average annual temperature of 10.0°C and an average annual precipitation of 500 mm. Air temperatures at the investigation site were recorded with data loggers from early April to the end of July 2020, precipitation data were derived from the nearest meteorological station in Krems (ZAMG, 2020). An unprecedented spongy moth outbreak was observed in the forest in 2018, resulting in total defoliation in 2018 and 2019. The number of egg masses per tree was estimated as 8–13 in 2018 and 4–5 in 2019 (Schafellner, 2020). In the study year 2020, the population density was still high in spring, but collapsed completely by summer.

2.2 | Sampling and rearing methods

Population density was estimated in early spring by counting the number of new egg masses on 400 tree stems within an area of 10 hectares covering the outbreak centre in the previous years. On 7 April, 20 egg masses were collected from randomly chosen trees within the observation area. The number of eggs per egg mass was counted, transparent eggs were visually classified as unfertilized. The eggs were stored at room temperature. Spongy moth hatching and emergence of egg parasitoids were documented for each egg mass individually. Between 14 May and 30 July, 680 spongy moth larvae were collected on 10 dates (Table 1). First and second instars (L1, L2) were collected from branches with beating nets, third and fourth instars (L3, L4) were also from tree trunks. Final instars (L5, L6) and pupae were plucked from tree stems, but mostly from burlap bands on 72 oak trees. The intended sample size was at least 100 larvae per instar. From the fourth instar, this goal could no longer be achieved due to the declining population. Despite an intensive search on four dates in July, we found only 12 pupae. All sampled insects were kept under semi-field conditions protected from precipitation in Vienna. The larval stages were determined by the width of the head capsules. Oviposition of tachinids with macrotype eggs (*P. silvestris*) was documented by the presence of eggs on the host cuticle at the time of collection. Larvae were transferred to 250 cm^3 plastic boxes and fed oak leaves from the investigation site. First and second instars were kept in groups of 10. Although group rearing can spread pathogen infection among individuals, solitary rearing of spongy moth larvae is associated with increased stress levels (Pavlushin et al., 2019) and reduced survival rates (Wang et al., 2021), especially in early instar larvae from dense populations (Ponomarev et al., 2021). Third and later instar larvae were kept individually. Both larvae and pupae were reared until death or moth eclosion.

2.3 | Determination of mortality agents

Death by parasitization was observed through the emergence of parasitoids from any host stage. Cocoons and puparia of the parasitoids (Zúbrik, 1998) were used for the first determination of the species and later secured with adult individuals whenever possible. The morphological identification of the species was done with the key of Simons et al. (1979). Dead spongy moth larvae without apparent signs of parasitism were dissected and examined for viral occlusion bodies, fungal spores and microsporidia using phase contrast microscopy. Bacteria were not assumed as a primary cause of mortality, because their direct pathogenicity is often questionable (Novotný, 1989).

2.4 | Data analysis

Mortality rates were calculated stage-specifically as the proportion of individuals killed by a single mortality factor out of all individuals collected in the given stage. The significance of differences in mortality rates between individuals collected in different developmental stages or on different dates was tested using Fisher's exact test. Egg mass density and egg numbers per egg mass were calculated as means ± standard deviation.

3 | RESULTS

3.1 | Weather conditions and phenology of *L. dispar*

Spring 2020 was extraordinarily dry until the end of May. The temperature was 2.5°C above the long-term average in April and 2.5°C below the average in May (ZAMG, 2020). The mean monthly temperatures were 12.5°C for both April and May (Figure 1). June was characterized by high precipitation (Figure 3). The weather in July largely corresponded to the long-term average of the nearest weather stations (Retz and Krems; ZAMG, 2020). Spongy moth hatching started on April 7th. The development of younger instars was strongly delayed, due to the low temperatures in May. First and second instars were present in the field over unusually extended periods (7 and 6 weeks, respectively). From June, the development of third and older instars accelerated with the increasing temperatures (Figure 1). The majority of the spongy moth larvae pupated in July and moth eclosion peaked around August 1st.

3.2 | Egg mass density and egg mortality of *L. dispar*

Egg mass density at the investigation site was 13.0 ± 12.6 egg masses per tree ($n = 400$), the egg masses contained 222 ± 125 eggs. Only 1.0% of the 4433 eggs were visually identified as unfertilized,

TABLE 1 Stage-specific sample sizes and sampling dates at the investigation site in 2020.

	April	May		June				July					
Stage	7th	14th	26th	2nd	16th	23rd	30th	7th	16th	21st	30th	Total	
Eggs	4.433	–	–	–	–	–	–	–	–	–	–	4.433	
L1	–	99	–	–	–	–	–	–	–	–	–	99	680
L2	–	238	–	–	–	–	–	–	–	–	–	238	
L3	–	–	50	88	11	–	–	–	–	–	–	149	
L4	–	–	–	45	35	4	–	–	–	–	–	84	
L5	–	–	–	–	7	–	26	17	6	8	–	64	
L6	–	–	–	–	–	2	13	12	11	6	2	46	
Pupae	–	–	–	–	–	–	–	2	5	1	4	12	
Total	4.433	337	50	133	53	6	39	31	22	15	6	5.125	

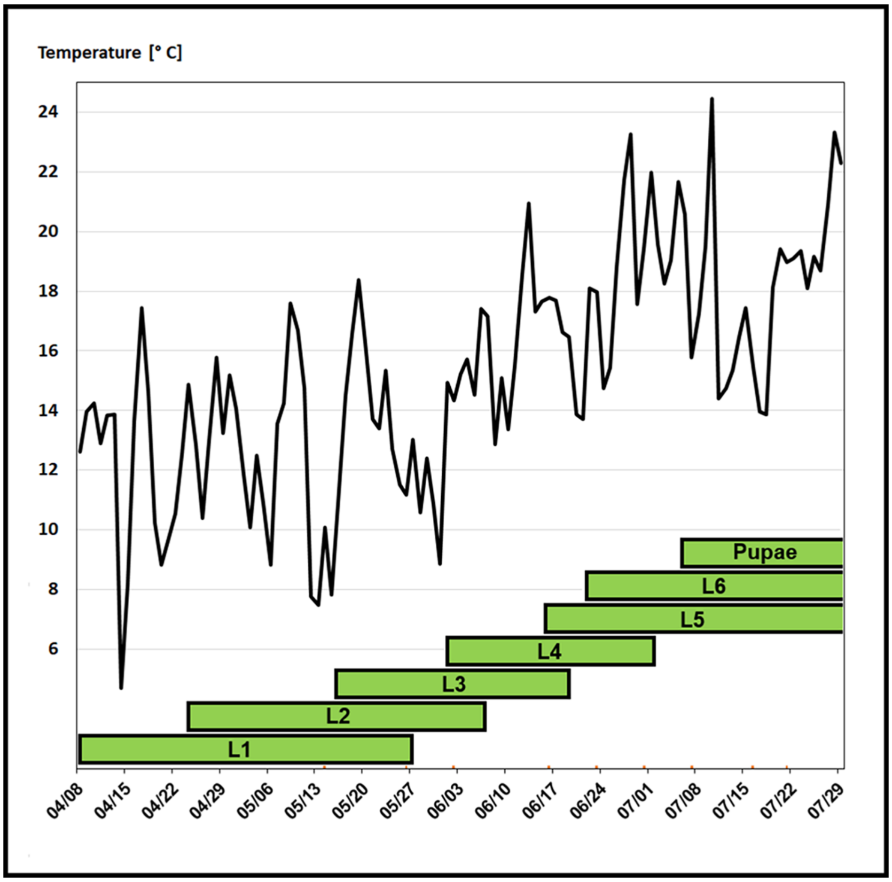

FIGURE 1 Mean daily temperature and phenology of *L. dispar* in the field at the study site in 2020.

but spongy moth larvae hatched from only 53.2%. Instead, wasps emerged from 19.2% of the eggs and were identified exclusively as the chalcid egg parasitoid *Anastatus disparis* (Hymenoptera: Eupelmidae). From 27.7% of all eggs, neither wasps nor spongy moth larvae emerged. Unhatched eggs contained spongy moth larvae as well as pharate adult wasps in a ratio strongly varying among individual egg masses. Parasitization rates of individual egg masses varied between 2.8% and 46.0%. Two egg masses did not hatch at all; these eggs contained only dead spongy moth larvae, but no parasitoids.

3.3 | Larval and pupal mortality

Six parasitoid species (the braconid wasps *Glyptapanteles porthetriae*, *G. liparidis*, *Cotesia* sp., the ichneumonid wasp *Hyposoter tricoloripes*, the tachinid flies *Parasetigena silvestris* and *Blepharipa pratensis*) and three pathogens (*Ld*NPV, *Entomophaga maimaiga*, *Endoreticulatus schubergi*) were identified as mortality factors of *L. dispar* larvae and pupae (Table 2). While pathogens (*Ld*NPV, unidentified fungi) were the predominant mortality factors of first instar larvae (41%), parasitoids were the dominant mortality agents in all other instars (Figure 2). The main cause of death of second to fourth instars was the braconid wasp *G. porthetriae* (23%–37%). The ichneumonid wasp *H. tricoloripes* (4%–8%) and the tachinid fly *P. silvestris* (10%–11%) became more abundant mortality factors in intermediate instars (L3, L4) compared to younger instars (Table 2). The most important mortality agents of late instar larvae (L5, L6) were the tachinid flies *P. silvestris* (24%–28%) and *B. pratensis* (19%–37%; Figure 2). No distinct pupal parasitoids of the spongy moth were recorded. Pupal mortality was exclusively induced by the larval-pupal parasitoid *B. pratensis* (17%) or due to unknown causes (25%).

3.3.1 | Mortality from pathogens

The overall larval mortality from pathogens declined from 41% in first instars to 12% in second instars and morality rates remained below 20% throughout larval development (Table 2). Host death from *Ld*NPV occurred within 10 days after collection in 50% of the first instar larvae, in 47% more than 14 days after collection. *Ld*NPV was clearly the dominant agent, causing 70% of the overall pathogen-induced mortality. Virus particles were found in all larval stages, with the highest mortality rates in first instar larvae and low levels in subsequent instars (7%–13%). The entomopathogenic fungus *E. maimaiga* was rarely detected in fourth, fifth or sixth instar larvae, causing stage-specific mortality below 5% (Table 2). The first fungal infection was found in one out of 133 (0.7%) larvae collected on June 2nd. After heavy rains in early June, mortality from *E. maimaiga* significantly increased in the second half of the month (6% on June 16th, 17% on June 23rd; Figure 3). While cadavers of larvae collected until June 16th contained exclusively conidia, cadavers collected on June 23rd or later contained both conidia and

TABLE 2 Percentage parasitism and other mortality factors of *L. dispar* eggs, larvae (L1–L6) and pupae by developmental stage at time of sampling.

Mortality-agent	Eggs ($n=4433$)	L1 ($n=99$)	L2 ($n=238$)	L3 ($n=149$)	L4 ($n=84$)	L5 ($n=64$)	L6 ($n=46$)	Pupae ($n=12$)	Total ($n=5125$)
A. disparis	**19.2** (849)	–	–	–	–	–	–	–	**19.2** (849)
Larval Parasitism	–	**15.2**^{a} (15)	**43.3**^{bc} (103)	**52.3**^{cd} (78)	**45.2**^{bcd} (38)	**50.0**^{cd} (32)	**60.9**^{d} (28)	**16.7**^{ab} (2)	**42.8** (296)
Braconidae									
G. porthetriae	–	**10.1**^{a} (10)	**35.7**^{bc} (85)	**31.5**^{c} (47)	**22.6**^{cd} (19)	–	–	–	**23.0** (159)
G. liparidis	–	–	–	**0.7**^{a} (1)	–	**1.6**^{a} (1)	–	–	**0.3** (2)
Cotesia sp.	–	–	–	**0.7** (1)	–	–	–	–	**0.1** (1)
Ichneumonidae									
H. tricoloripes	–	**1.0**^{a} (1)	**2.1**^{a} (5)	**4.0**^{ab} (6)	**8.3**^{b} (7)	–	–	–	**2.7** (19)
Tachinidae									
P. silvestris	–	–	–	**10.7**^{a} (16)	**9.5**^{a} (8)	**28.1**^{b} (18)	**23.9**^{b} (11)	–	**7.7** (53)
B. pratensis	–	**4.0**^{a} (4)	**5.0**^{a} (12)	**4.7**^{a} (7)	**4.8**^{a} (4)	**18.8**^{b} (12)	**37.0**^{c} (17)	**16.7**^{abc} (2)	**8.4** (58)
Unidentified tachinids	–	–	–	**1.3**^{a} (2)	–	**1.6**^{a} (1)	–	–	**0.4** (3)
Pathogens	–	**41.4**^{a} (41)	**11.8**^{b} (28)	**10.7**^{b} (16)	**13.1**^{b} (11)	**18.8**^{b} (12)	**15.2**^{b} (7)	–	**16.6** (115)
*Ld*NPV	–	**34.3**^{a} (34)	**7.1**^{b} (17)	**8.1**^{b} (12)	**7.1**^{b} (6)	**12.5**^{b} (8)	**6.5**^{b} (3)	–	**11.6** (80)
E. maimaiga	–	–	–	–	**3.6**^{a} (3)	**4.7**^{a} (3)	**4.3**^{a} (2)	–	**1.2** (8)
E. schubergi	–	–	–	–	–	–	**2.2** (1)	–	**0.1** (1)
Unidentified fungi	–	**5.1**^{a} (5)	**4.6**^{a} (11)	**2.7**^{a} (4)	**1.2**^{a} (1)	–	**2.2**^{a} (1)	–	**3.2** (22)
Mixed infections	–	**2.0**^{a} (2)	–	–	**1.2**^{a} (1)	**1.6**^{a} (1)	–	–	**0.6** (4)
Unidentified factors	**27.7** (1.228)	**19.2**^{a} (19)	**19.7**^{a} (47)	**8.7**^{bd} (13)	**6.0**^{bc} (5)	**1.6**^{c} (1)	**10.9**^{abcd} (5)	**25.0**^{ab} (3)	**13.4** (93)
Total mortality	**46.9** (2.077)	**75.8**^{ac} (75)	**74.8**^{ac} (178)	**71.8**^{ab} (107)	**64.3**^{bd} (54)	**70.3**^{abd} (45)	**87.0**^{c} (40)	**41.7**^{d} (5)	**72.8** (504)

Note: Numbers in bold represent per cent mortality, and numbers in parenthesis represent absolute numbers. Superscript letters indicate significant stage-specific differences in mortality rate caused by the corresponding mortality factor (Fisher's exact test: $\alpha=0.05$). Stages with a common superscript letter showed no significant differences, those without a common letter differed significantly.

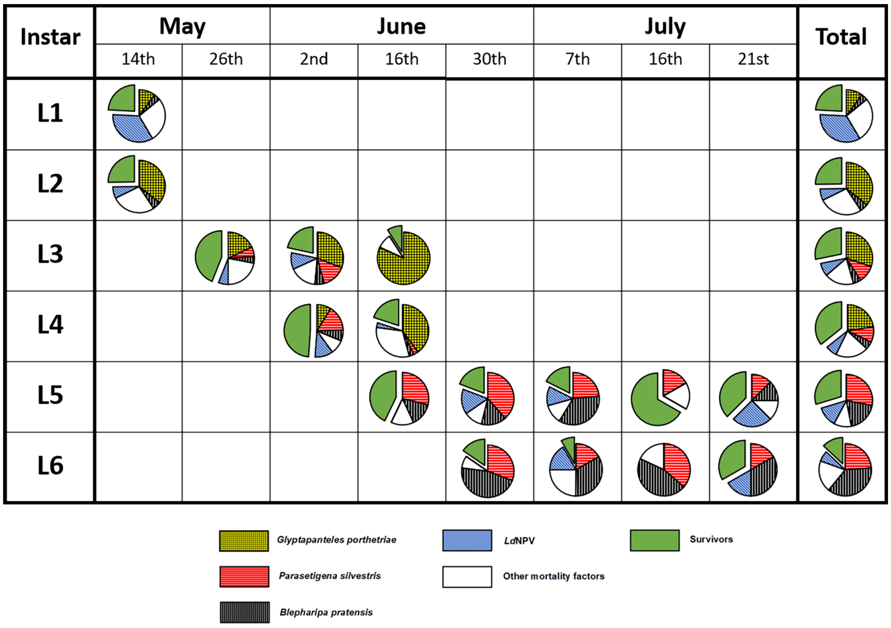

FIGURE 2 Proportion of *L. dispar* larvae that developed into adult moths (survivors) or were killed by the four major mortality factors: *G. porthetriae*, *P. silvestris*, *B. pratensis*, and *Ld*NPV, specific for each sampling date and instar. The samples taken on June 23rd and July 30th are not shown due to the small sample size.

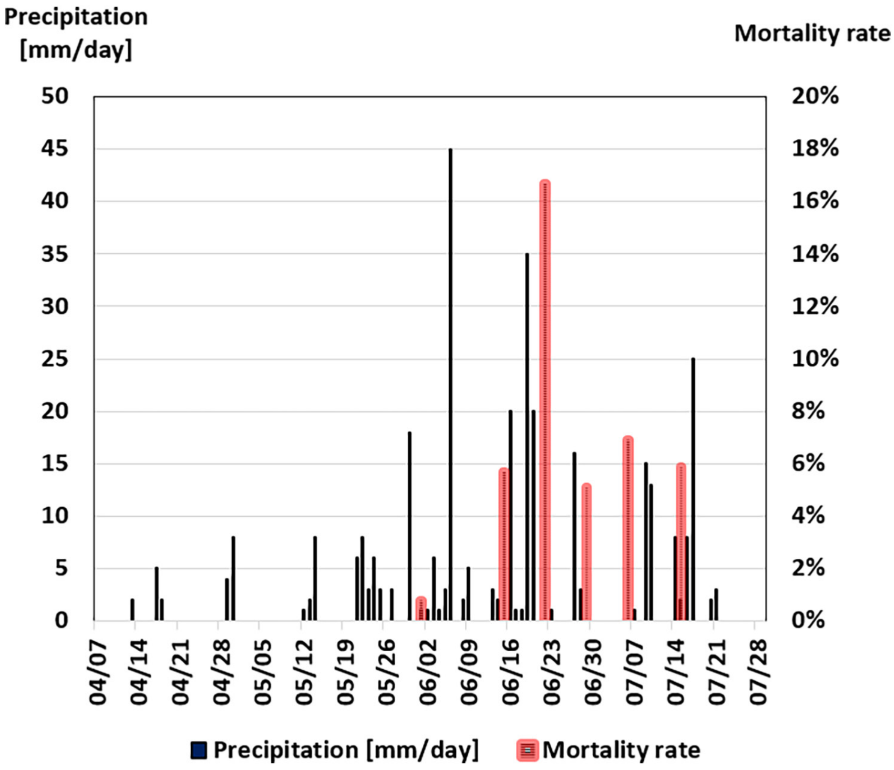

FIGURE 3 Precipitation data and mortality rates from *Entomophaga maimaiga* by collection date.

azygospores. A single sixth instar individual was evidently killed by the microsporidium *E. schubergi* (Glugeida: Encephalitozoonidae). Unidentified fungal spores were observed in a low number of larvae.

3.3.2 | Mortality from parasitic wasps

Mortality from the braconid wasp *G. porthetriae* was highest in larvae collected as second instars (36%) and remained at high levels in third (32%) and fourth instar larvae (23%) as well (Table 2). Wasp larvae emerged from their hosts over a period of 6 weeks (mid-May to early July) with a peak observed in larvae collected on June 16th, when 81% of all third instars and 40% of all fourth instars were killed by the braconid wasp (Figure 2). In contrast, larvae parasitized by *G. liparidis* and *Cotesia* sp. were only sporadically collected. *Cotesia* sp. emerged from a single third instar larva on June 16th, *G. liparidis* emerged from two host individuals, one collected as third instar larva on June 3rd and another as fifth instar larva on July 16th, respectively.

The ichneumonid wasp *H. tricoloripes* killed 1% of the larvae collected as first instars, 2% and 4% of larvae collected as second and third instars and 8% of larvae collected as fourth instars (Table 2). The peak of parasitization occurred in fourth instar larvae collected on June 16th (14.3%). Host death occurred in the third or fourth instar, almost exclusively in June. Individuals collected as first and second instars died an average of 26 days after sampling, while almost all individuals collected as third or fourth instars died within 10 days. Adult wasp eclosion peaked on 17 June.

3.3.3 | Mortality from tachinid flies

Tachinid flies played a subordinate role as a mortality factor in young (L1, L2) larvae (4%–5%), but parasitization rates increased in intermediate (L3, L4) instars (14%–17%). In late instars (L5, L6) they became the dominant mortality factor (50%–61%; Figure 2). Macrotype eggs of *P. silvestris* were observed on 13% of all larvae, with a peak of 34% in larvae collected as third instars. This proportion was significantly higher than in any other stage. Oviposition peaked in June, while larvae collected in May and July carried *P. silvestris* eggs much less frequently. However, mortality caused by *P. silvestris* was significantly higher in larvae collected as fifth (28%) or sixth instars (24%) than in preceding instars (Table 2). Host death from *P. silvestris* occurred from the fourth to the sixth instar, almost exclusively in July. Superparasitism was observed in 11% of *L. dispar* larvae killed by *P. silvestris*; in these cases, two maggots emerged from each host individual.

The tachinid fly *B. pratensis* caused low but constant mortality rates around 5% in larvae collected as first to fourth instars. In fifth and sixth instars, *B. pratensis* became a significant mortality factor, causing host death rates of 19% and 37%, respectively (Table 2). Host death almost exclusively occurred during the pupal stage, between July 13th and August 21st. Superparasitism was observed in 7% of the host larvae, all of them collected as sixth instars. The puparia of *B. pratensis* were dissected in autumn 2020 in order to identify the species and differentiate *B. pratensis* from *Blepharipa schineri*. Dissections revealed that 24% of the puparia were hyperparasitized by the chalcid wasps *Perilampus ruficornis* and *Perilampus aeneus* (Hymenoptera: Perilampidae).

4 | DISCUSSION

This study investigated the contribution of parasitoids and pathogens in the collapse of a local gypsy moth population in Austria. One of the main peculiarities compared to previous Central European studies (Alalouni et al., 2013; Hoch et al., 2001; Zúbrik & Novotný, 1997) was the observed high rate of egg parasitism (19%), which was exclusively caused by the eupelmid wasp *A. disparis*. By contrast, Hoch (1995) did not find any egg parasitoid in a 2-year-study conducted in Burgenland (Austria). In the largest survey conducted in Central Europe, egg parasitism was recorded at different sites in Slovakia over 4 years (Zúbrik & Novotný, 1997). Only one site showed egg parasitization rates of 10% in a single year. In all other 21 site-year combinations, egg parasitization rates were below 2%. More recently, negligible rates of egg parasitism were observed in Germany (Alalouni et al., 2014) and Italy (Camerini, 2009). Reports of similar or even higher parasitization rates than in our study originate from Serbia in the 1970s (Milanović et al., 1998) and earlier from several parts of Europe (Burgess & Crossman, 1929; Kurir, 1944). Since local and periodic oscillations in the abundance of *A. disparis* are well known (Burgess & Crossman, 1929; Wellenstein & Schwenke, 1978), the significance of results from a single study site and year is limited. One factor that may have contributed to the high abundance at our investigation site is the phase of the population cycle, as *A. disparis* is typically most abundant during host population collapse (Bathon, 1993; Kurir, 1944; Wellenstein & Schwenke, 1978; Zúbrik & Novotný, 1997).

Compared to previous reports (Hoch, 1995; Wellenstein & Schwenke, 1978; Wermelinger, 1995; Zúbrik & Novotný, 1997), the number of eggs with larvae that did not hatch was unusually high. This can have different reasons, for example, sublethal pathogen infections (Akhanaev et al., 2020; Goertz, 2004; Goertz & Hoch, 2008; Weiser, 1998), a low nutrient supply for larvae in the previous year (Ilyinykh et al., 2017) or predatory activities, for example, by mites (Bathon, 1993; Camerini, 2009; Saeidi, 2011). Eventually, *A. disparis* contributed to the embryonic mortality of its host. Females of *A. disparis* are known to feed on *L. dispar* eggs (Parker, 1933). Furthermore, host egg abortion without successful wasp emergence is a frequently underestimated aspect of the regulatory capacity of egg parasitoids (Abram et al., 2016).

Mortality rates from pathogen infections must be interpreted with caution due to the possibility of infection transmission, especially when the larvae are kept in groups. The extended period from collection to the NPV-induced host death in many first instar larvae indicates a high proportion of infections during rearing (Yerger & Rossiter, 1996). Compared to previous studies, NPV-induced mortality was high in young larvae, but low in older larvae (Hoch et al., 2001, 2019; Maier, 1990; Turcáni et al., 2001). Due to the longer exposure time (Godwin & Shields, 1984; Reardon & Podgwaite, 1976) and increased environmental contamination with occlusion bodies, NPV prevalence typically increases with larval maturation (Murray et al., 1989) and causes a second wave of high mortality (Woods & Elkinton, 1987). April 2020 was warm (Figure 1), very dry (Figure 3), and had the most sunshine hours ever recorded in Lower Austria (ZAMG, 2020). High temperatures at the time of hatching of spongy moth are positively correlated with NPV prevalence (Hajek & Tobin, 2011). Sunlight is assumed to be the most important abiotic factor affecting NPV epizootiology as the virus occlusion bodies are very sensitive to UV radiation (Ment et al., 2018). NPV-infected larvae often die at elevated sites (Murray & Elkinton, 1992) where they are exposed to high radiation from the sun, particularly when the canopy is not fully developed in spring. Precipitation would have mitigated this effect, as rainfall shifts occlusion bodies down to shadier areas of the crown (Ment et al., 2018). Therefore, the weather conditions in the study year may have induced unusually high rates of inactivation of the viral occlusion bodies that were excreted from early-instar cadavers. Merely considering mortality rates is, however, likely to underestimate the impact of NPV as well as other pathogens on spongy moth population dynamics. For example, sublethal NPV infections result in significantly reduced female fecundity and increased embryonic mortality in eggs from the infected females (Akhanaev et al., 2020; Il'inykh et al., 2009; Myers et al., 2000).

In 2019, the introduced entomopathogenic fungus *E. maimaiga* caused high mortality in the spongy moth population at the investigation site (Hoch et al., 2019). Its low prevalence in the study year 2020 can be attributed to dry spring weather conditions. Sufficient soil moisture is a prerequisite for the germination of the resting spores (azygospores) of *E. maimaiga* and thus for the initial infections within the host population (Reilly et al., 2014). Additionally, humidity correlates positively with the formation, discharge and germination of the conidia (Hajek, 1999). The germination of azygospores was apparently inhibited by low soil moisture in spring until the dry period was ended by several consecutive days with rainfall at the end of May. The presence of the different types of fungal spores allows conclusions to be drawn about the source of infection of individual larvae. While cadavers infected by soilborne azygospores only produce conidia, cadavers infected with airborne conidia are capable of producing both azygospores and conidia (Hajek, 1999). The absence of azygospores in larvae infected in the first half of June indicates that these infections originated from soilborne azygospores. This also explains why *E. maimaiga* was not detected in third instar larvae, although they were still widespread at the onset of the infections (Figures 1 and 3). In contrast to fourth and older instars, which often rest in soil litter during the day, third instar larvae are rarely found on the ground (Weseloh, 1990), where infections from azygospores are most likely (Hajek, 1999, 2001). While *E. maimaiga* can go through six to seven (Malakar et al., 1999), occasionally nine infection cycles within a single generation of host larvae (Hajek & Shapiro-Ilan, 2018), the late onset of primary infections in the study year reduced the number of possible infection cycles significantly. Consequently, despite favourable conditions for infections from June onwards, airborne conidia density did not reach levels high enough to induce high mortality rates.

In most European studies examining spongy moth populations in comparable periods of the population cycle, *G. porthetriae* played an insignificant role or was completely absent (Fuester et al., 1983; Hoch et al., 2001; Kalbacher, 2008; Maier, 1990; Sukovata & Fuester, 2005; Turcáni et al., 2001; Zolubas et al., 2001). In Austria, *G. porthetriae* has never been reported as the dominant larval parasitoid. In our study, the wasp caused unusually high rates of parasitization, particularly in intermediate instars (Eichhorn, 1996; Fuester et al., 1983; Hoch et al., 2001; Kalbacher, 2008). Contrary to previous reports (Burgess & Crossman, 1929; Čapek, 1988; Fuester et al., 1983; Griffiths, 1976; Marktl et al., 2002), a second generation of wasps was apparently able to develop in third and fourth instar spongy moth larvae. This is supported by a two-peak distribution of wasp emergence dates from their hosts (mid-May and mid-June; Figure 2) and the long period in which the wasps emerged from their hosts. The low temperatures in May delayed the development of the spongy moth larvae, allowing the wasps to find suitable hosts for several weeks. As surprising as the high abundance of *G. porthetriae* was the low abundance of *Cotesia* sp. and in particular *G. liparidis*, which were the predominant larval parasitoids observed in spongy moth populations in earlier studies in Austria (Eichhorn, 1996; Fuester et al., 1983; Hoch, 1995). An explanation for these differences comes from the very high rates of hyperparasitism of the braconid cocoons from chalcidid wasps, recorded at the study site in 2020 as well as in the year before (Dorfmann, 2020). Specifically, the cocooned larvae of *C. melanoscela* overwinter under natural conditions for several months and are particularly prone to hyperparasitism (Griffiths, 1976; Weseloh, 1983). On the contrary, the gregarious development of *G. liparidis* should reduce the per capita risk of hyperparasitism compared to the solitary *G. porthetriae* (Vyas et al., 2020). Eventually, the high prevalence of *E. maimaiga* at the investigation site in 2019 (Hoch et al., 2019; Schafellner, 2020) has contributed to the low abundance of *G. liparidis* in 2020. While *G. porthetriae* is typically associated with young spongy moth larvae (Nussbaumer & Schopf, 2000), *G. liparidis* induces highest parasitization rates in its second generation that emerges from late instar hosts (Fuester et al., 1983). Furthermore, the number of *G. liparidis* progenies per host individual increases with the host age (Schopf & Hoch, 1997). Compared to *G. porthetriae*, *G. liparidis* prefers older larval stages, which significantly increases competition with *E. maimaiga* for host larvae.

Mortality of spongy moth larvae from ichneumonid wasps was induced by a single species, the oligovoltine *H. tricoloripes*. By contrast, the univoltine *Phobocampe* species were more abundant in previous Austrian studies (Fuester et al., 1983; Hoch et al., 2001). *H. tricoloripes* is likely dependent on alternative hosts and its scattered distribution is well known (Fuester et al., 1983). According to the literature, *H. tricoloripes* prefers the youngest instars of the spongy moth (Fusco, 1981), while in the present study, parasitization rates were highest in fourth instar larvae. However, the short period between collection and host death in intermediate instars (L3, L4) indicates that they were already attacked in earlier stages. The low parasitization rates in the young larvae are probably due to competition, particularly with *G. porthetriae*, which develops much faster inside the host than the ichneumonid wasp. In the case of multiparasitism, faster development often correlates with competitive superiority (Marktl et al., 2002).

It is consistently reported in the literature that parasitization success of the tachinid fly *P. silvestris* increases with host age and that first and second instar larvae of *L. dispar* are unsuitable hosts for *P. silvestris*. Reports on host suitability of third instar larvae, however, differ (Godwin & Odell, 1984; Maier, 1990; Pemberton et al., 1993). *P. silvestris* attaches its macrotype eggs to the host cuticle; when the host moults, the eggs are shed with the exuvia. The presence of eggs on the host surface indicates the stage at which the larva was infested. We collected third instar larvae with no tachinid eggs attached, which were later found to be killed by *P. silvestris*. This shows clearly that successful parasitization also occurs in second instar hosts. Third instar larvae apparently allowed for a high degree of parasitization success. In the fourth instar larvae collected in early

June, several larvae were killed by *P. silvestris*, although at the time of collection, only one larva carried a tachinid egg. In contrast, 33% of all fourth instar larvae collected in mid-June had an egg attached, but *P. silvestris* emerged from only a single larva. Apparently, the environmental conditions (temperature) had a stronger influence on the parasitization success of *P. silvestris* than the host stage. After oviposition, the maggots hatch within 3 to 8 days before entering the host's haemocoel (Herting, 1960). If the host moults before the parasitic fly hatches, the egg is eliminated. Both the timing of hatching of *P. silvestris* and the time between moults of the host larvae are affected by temperature. However, the latter is disproportionally stronger influenced by low temperatures (Limbu et al., 2017; Prell, 1915). Obviously, the cool weather in May and the associated strongly delayed development of the second and third instar larvae favoured the parasitization success of *P. silvestris* in these early host stages. In contrast, the fourth instars progressed much faster due to high temperatures in June (Figure 1), resulting in a high proportion of *P. silvestris* eggs being lost due to the moulting host larvae.

As an oviposition strategy, *B. pratensis* uses microtype eggs attached to the leaf surface and ingested by the host with food. The probability of egg ingestion increases with the leaf area consumed by the host (Godwin & Odell, 1981). This explains the significant increase in the parasitization rate of the final instars. Food consumption of female hosts during their final (i.e. sixth) instar is higher than the total amount of food consumed by males throughout their immature development (i.e. five instars; Leonard, 1966). *B. pratensis*, recovered from host larvae collected as third or fourth instars, suffered particularly from hyperparasitization by *Perilampus* spp. This suggests an oviposition preference of *Perilampus* for middle-aged host larvae.

Collection of larvae under burlap bands was reported to increase parasitism from *P. silvestris*, *B. pratensis* and *C. melanoscela* (Maier, 1990; Reardon, 1976). However, this was observed in dense populations with accumulations of numerous larvae under each burlap band, which was not the case in the present study. Gould et al. (1992) found lower parasitization rates by *P. silvestris* under burlap bands, but an accumulation of eggs on some larvae, probably those that rested at the periphery of the bands. According to Fuester et al. (1983), the collection technique had no effect on the parasitization rates or the species composition. The prevalence of *Ld*NPV was reported to be underestimated by the use of burlap bands (Murray & Elkinton, 1992). This may also be the case for *E. maimaiga*. Larvae resting at the tree trunk have a significantly lower risk of infection than larvae resting in the litter (Hajek, 2001). Burlap bands provide hiding places for the larvae and thus may artificially reduce the number of larvae that rest in the litter. The predatory beetle *Calosoma sycophanta* (L.; Coleoptera: Carabidae) was very abundant at the study site and also regularly observed under burlap bands. However, no pupae with the characteristic feeding damages (Gschwantner et al., 2002) were found.

According to reports of earlier outbreaks (Hoch et al., 2001) and critical egg mass numbers in the literature (Wellenstein & Schwenke, 1978), the egg mass density in spring would have been sufficient to completely defoliate the trees at the study side. Despite this, hardly any leaf damage was observed and by summer 2020 the population had completely collapsed. Infections of the youngest larvae by *Ld*NPV and parasitization of late larval stages by the tachinid flies *P. silvestris* and *B. pratensis* were the most prominent mortality factors of the spongy moth population. These results are consistent with those from previous studies in Central Europe. The main peculiarities of the present study regard the high egg parasitization rate and the clear dominance of the braconid wasp *G. porthetriae* as antagonist of younger larvae. The latter was very likely favoured by specific weather conditions, which resulted in the presence of young larvae in the field for an extended period of time. On the contrary, the weather conditions were unfavourable for the introduced pathogen *E. maimaiga*, which suffered from the very dry spring conditions. Our results highlight the crucial role of abiotic conditions in the complex interactions between the spongy moth and its numerous natural enemies.

AUTHOR CONTRIBUTIONS

Thomas Zankl: Investigation; writing – original draft; visualization; methodology; conceptualization. **Christa Schafellner:** Conceptualization; writing – original draft; project administration; supervision; resources; methodology. **Gernot Hoch:** Conceptualization; project administration; resources; supervision; methodology.

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CONFLICT OF INTEREST STATEMENT

The authors declare they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in KNB Data Repository at DOI:10.5063/F18S4NC5.

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SUPPORTING INFORMATION

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