MINI REVIEW

Natural enemies and environmental factors affecting the population dynamics of the gypsy moth

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Abstract

The population densities of the gypsy moth (*Lymantria dispar*; Lepidoptera: Lymantriidae) may reach outbreak levels that pose considerable economic and environmental impacts to forests in Europe, Asia, Africa and North America. Compared with the situation in its native European range feeding damage by gypsy moth is often found to be more severe in North America and other parts of the world. Thus, the release from natural enemies can be interpreted as an important cause for high feeding damages. Natural enemies, especially parasitoids, can cause delayed density-dependent mortality, which may be responsible for population cycles. In North America where only few parasitoids have been introduced and the parasitism rates are considerably lower than in Europe, generalist predators play a larger role than in Europe. Many other factors seem to influence the population dynamics of the gypsy moth such as the host plants and weather. Nevertheless, much of the variability in population densities of the gypsy moth may be attributed to interacting effects of weather conditions and attack by natural enemies. In spite of the considerable number of studies on the ecology and population dynamics of the gypsy moth and the impact of their natural enemies, more quantitative information is required to predict the population dynamics of this pest species and to control its economic and ecologic impact.

Introduction

Worldwide, insect pests affect around 35 million hectares of forests each year (FAO 2010). The gypsy moth, *Lymantria dispar* L, is one of the pest species that can cause considerable problems in forests ecosystems. This foliage-feeding moth occurs naturally from Western Europe to the Central Asia to the Far East and across large parts of the Mediterranean (Giese and Schneider 1979; Grijpma 1989; Pogue and Schaefer 2007; Alalouni 2009; Avci 2009). It was introduced to New Zealand and North America (Glare et al. 1998; Pogue and Schaefer 2007; Orozumbekov et al. 2009). In North America, the species first appeared near Boston around 1868 and expanded its range across most of the north-eastern states in the United States and eastern provinces of Canada (Liebhold et al. 1992; Sharov et al. 2002a).

In order to understand the factors affecting the abundance and outbreaks of this economically and ecologically important pest, its population dynamics have been modelled to predict population dynamics for the development of management strategies (Campbell 1981; Sheehan 1989; Elkinton and Liebhold 1990; Berryman 1996; Novotny et al. 1998; McManus and Csóka 2007). The patterns of insect population dynamics are bewildering and are based on various density-dependent and density-independent factors (May 1974; Berryman and Stark 1985; Berryman et al. 1987; Wallner 1987). However, density-dependent factors have the major role in regulating populations (Berryman 1991b, 1996). Because most insect parasitoids act in a density-dependent manner, an understanding of their role in the dynamics of insect pests is important for predicting patterns

of population outbreaks in space and time (Royama 1977; Berryman 1996).

Data from native and invasive ranges suggest that the natural enemies of the gypsy moth may control its population dynamics (Turchin 1990; Berryman 1991a,b,c, 1998). It has been speculated that the escape from native natural enemies seems to be one reason of the invasion success and therefore higher feeding damages in the new range (Keane and Crawley 2002; Wolfe 2002; Clay 2003; Colautti et al. 2004).

Despite the economic and ecological importance of the gypsy moth, data on its ecology and population dynamics and the importance of its natural enemies are widely scattered in the literature. Here, we review the available information on the gypsy moth for Europe in comparison with other regions of the world. We especially focus on the comparison between natural enemies in the native and the new range of the species. We further complement this with information about host plants in the different parts of the range to account for further factors which may influence population dynamics. The ultimate aim of this study is to stimulate further research on factors that trigger population and outbreak dynamics of this ecologically and economic important pest species.

Population Dynamics and Outbreaks of the Gypsy Moth

The gypsy moth has univoltine life cycle, which affects its population dynamics (Montgomery and Wallner 1988). The insect diapauses in winter as an egg mass. Neonate larvae play a major role in the natural dispersal of the population through ballooning (Barbosa and Capinera 1978; Pogue and Schaefer 2007). While males have five instars, females usually have six which extends their period of exposure to natural enemies (Grijpma 1989). The pupae require approximately 2 weeks for development providing an ample opportunity for parasitoids and predators to attack (Leonard 1981).

Populations of the gypsy moth, like many other foliage-feeding forest insects, exhibit periodic gradations or population cycles (Varley et al. 1973; Leonard 1974; Berryman 1996; Kendall et al. 1999). These gradations seem to be localized at certain centres where conditions are presumed to be favourable. For example, cycles have occurred in the same forests of birch and alder in western Lithuania every 10 years since the 1970s (1971–1975, 1982–1983, 1993–1994; Zolubas et al. 2001). In Europe, the following terms are used to describe the various phases

of the cycle (see fig. 1): latency (when population is at low levels of density), progradation (population starts to erupt), culmination or outbreak (population reaches high levels of density) and post-gradation or retrogradation (population density decreases after outbreaks) respectively (Campbell 1981; Montgomery and Wallner 1988; Elkinton and Liebhold 1990; fig. 1). In North America, ecologists use the terms (innocuous or endemic, release phase, outbreak phase and decline phase (Elkinton and Liebhold 1990). The number of the egg masses per unit ground area or per tree in the spring before the hatch time usually gives an indicator of the gradation phase (Liebhold et al. 1994). The size of the egg masses and the proportion of the old egg masses can also give indications for the population phase (for more details, see also Liebhold et al. 1994).

The outbreaks of gypsy moth populations seem to be synchronized across large scales (Myers 1998; Johnson et al. 2005). Fifteen European countries (Austria, Czech Republic, France, Germany, Hungary, Italy, the Netherlands, Poland, Portugal, Russia, Spain, Romania, Serbia, Slovakia and Switzerland) experienced outbreaks between 1990 and 1995. Even small outbreaks occurred during this period in England, where the climate is rather unfavourable for this insect (Lipa and Kolk 1995; Wulf and Giraser 1996; Narang et al. 2001; Cannon et al. 2004). However,
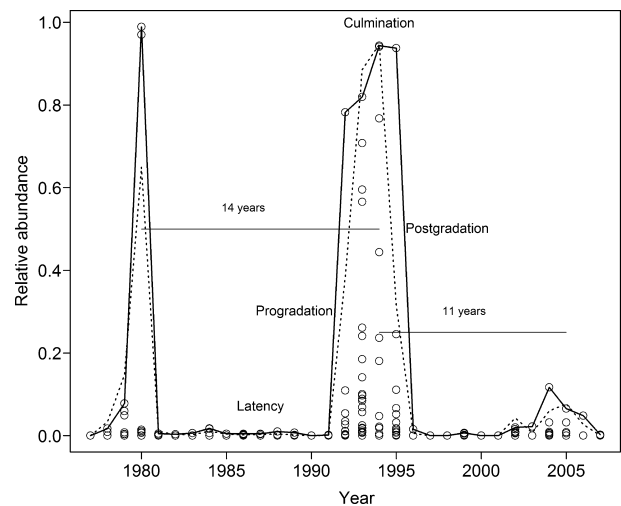

Fig. 1 Change in the realtive abundance of Gypsy moth in southern Germany to illustrate the terms used to describe the various phases of the population cycle. Open circles: relative abundance of gypsy moth to other moth species across sites; solid line: maximum density; dotted line: mean values (multiplied by 30). The insect needs 3 years to reach the culmination from the beginning of progradation period. (H. Hacker, unpublished data; see also Mueller et al. 2011).

there are some regional differences in the time span of two outbreaks, for example, in Slovakia and Germany, the period between two outbreaks can differ from 6 to 14 years (Grijpma 1989; Novotny et al. 1998; Delb 1999; Turcani et al. 2003b; see also fig. 1). The time between outbreaks' events can also vary across latitude and longitude (Weiser 1987; McNamara 1996). A period of three to 4 years between two outbreaks was observed in the Mediterranean and Balkan regions, whereas average of seven to 10 years was observed in Central Europe (Weiser 1987; McManus and Solter 2003). The damage caused by the insect in the Mediterranean and Balkan is more severe as well. The warmer and drier climate that provides larvae with favourable conditions for the development and survival might explain this short and intensive outbreak cycles (Weiser 1987; Grijpma 1989; McManus and Solter 2003). Furthermore, forest type (xeric soil, host plants) might shorten the cycle of outbreak compared with Central Europe.

In North America, the population dynamics of the gypsy moth were described in various terms, such as bimodal dynamics, population cycles, second-order lag correlations and spatial synchrony (Campbell and Sloan 1976; Montgomery and Wallner 1988; Liebhold 1992; Liebhold et al. 2000). In early studies, the evidence for cyclic fluctuations of population densities was not convincing in North America (Elkinton and Liebhold 1990; Liebhold and Kamata 2000). More recent studies, however, found population cycles with periods of 5 and 10 years between two outbreaks. Moreover, the period between two outbreak events differed with respect to the forest type (xeric, mesic; Johnson et al. 2005; Haynes et al. 2009; Bjornstad et al. 2010).

Explanations for why some foliage-feeding insects have population cycles have been widely discussed (Turchin 1990; Berryman 1991a,c; Murray 1999; Liebhold and Kamata 2000; Carey 2001). Many hypotheses have been proposed to explain this phenomenon, for example, maternal effects, changes in population genetics and the effects of host plant quality (Chitty 1967; Edelsteinkeshet and Rausher 1989; Ginzburg and Taneyhill 1994; Liebhold and Kamata 2000; Liebhold et al. 2000). Nevertheless, the delayed density-dependent mortality caused by natural enemies was supposed to be the main reason for population cycles in gypsy moth populations (Turchin 1990; Berryman 1991a,b; Liebhold and Elkinton 1991; Liebhold and Kamata 2000). In Central Europe, larval and pupal parasitoids can control abundance during outbreaks and postgradations (Maier 1995; Hoch et al. 2001; Turcani et al. 2001). Furthermore,

some tachinid parasitoids have generation times similar to that of their host. Thereby, the progradation phase seems to be as a result of the escape from these enemies (Montgomery and Wallner 1988; Berryman 1991b, 1996, 1998). In North America, rates of parasitism by tachinids are lower than in Europe. In spite of that, a delayed density dependence caused by introduced parasitoids was proposed as a factor controlling gypsy moth populations (Berryman 1991a,b, 1998). No evidence was found to support this proposal (Liebhold and Elkinton 1991; Liebhold et al. 2000). On the other hand, predation by small mammals appears to be the major cause of mortality in low-density populations, which slows down the increase of gypsy moth populations to outbreak levels (Liebhold et al. 2000). These observations led to the proposal that the changes in the density of generalist predators might be a determinant of the outbreak events (Liebhold et al. 2000; Johnson et al. 2006; Bjornstad et al. 2010). A recent study of the gypsy moth population cycles in North America suggested that even in the absence of the strong environmental changes, the behaviour of the gypsy moth population is controlled by trophic interactions (Allstadt et al. 2013).

The Effects of Natural Enemies on Population Dynamics

The gypsy moth encounters a diverse complex of natural enemies (Hoch et al. 2001). However, the effect of these enemies varies depending on the phase of gradation (Novotny 1989; Maier 1990, 1995; Novotny et al. 1998; Hoch et al. 2001; Turcani et al. 2001). More than 150 species of parasitoids are able to attack the gypsy moth in Europe (109 Hymenoptera, 56 Diptera; Grijpma 1989). The parasitism rates vary between 10% and 100% (Reardon 1981a). Despite this pool of parasitoids, efforts to establish parasitoids in the invasive range of the gypsy moth have been only partially successful, and only few parasitoid species can be considered as established (Campbell 1976; Reardon 1976; Montgomery and Wallner 1988; Glare et al. 1998).

Egg parasitism

The gypsy moth egg parasitoids and hyperparasitoids have been recorded from six different families of Hymenoptera (Brown and Cameron 1982; table 1). *Anastatus japonicus* (Eupelmidae) and *Ooencyrtus kuvanae* (Encyrtidae) are considered the most important egg parasitoid species in Central Europe (Grijpma

1989). Other parasitoids including *Anastatus catalonicus*, *Anastatus bifasciatus* and *Anastatus japonicus* are important, for example, *A. catalonicus* attacked 40% of one egg mass in Germany (Maier 1995). *O. kuvanae, Anastatus disparis* and *A. bifasciatus* attack egg masses in Turkey, but *O. kuvanae* causes higher mortalities than the other two species (Avci 2009). The parasitism rates of egg parasitoids seem to fluctuate considerably in the native range of the gypsy moth. The rates vary between 0% and 10% in Central Europe and can reach more than 60% during an outbreak in Turkey (Maier 1995; Bathon 1996; Hoch et al. 2001; Turcani et al. 2001; Avci 2009). These data suggest that parasitism rates decrease with latitude (fig. 2a). Moreover, there is no correlation between the density of egg masses and parasitism rates in the native range, and the parasitism rates seem to be higher in repeatedly infested than in recently infested forests (Bathon 1996; Hoch et al. 2001; Turcani et al. 2001; Avci 2009).

In Asia (Korea and Japan), egg parasitoids seem to have little importance (Brown 1984; Schaefer et al. 1988). In North America, *A. disparis* and especially *O. kuvanae* are considered the main parasitoids of egg masses (Hoy 1976; Reardon 1981b). Together their parasitism rates can reach 20–40% (Brown and Cameron 1982; Brown 1984; McManus and Csóka 2007).

Although it is considered to cause higher mortality than *A. disparis*, *O. kuvanae* shows an extreme variability in parasitism rates as a result of the dependence on the size of the egg masses (Brown et al. 1983; Brown 1984).

At present, the available information allows no clear conclusions about the influence of egg parasitoids on the population dynamics of the gypsy moth. More comparative studies about the influence of egg parasitoids in the native and new range of the insect are needed.

### Larval and pupal parasitism

More than 23 species of parasitoids and hyperparasitoids have been recorded in Slovakia, Austria and Germany (table 2; Bathon 1993; Maier 1995; Hoch et al. 2001; Eichhorn 1996; Turcani et al. 2001). The tachinids *Parasetigena silvestris* and *Blepharipa sp.* cause the highest mortality rates. Together these species are the dominant tachinid parasitoids in Austria, Germany, Lithuania, Poland and Slovakia (Maier 1990, 1995; Eichhorn 1996; Hoch et al. 2001, 2006; Turcani et al. 2001; Zolubas et al. 2001; Sukovata and Fuester 2005). These two species are specialized and univoltine, which make their life span similar to their host (Montgomery and Wallner 1988; Maier 1990).

Table 1 The main invertebrate parasitoids and predators of the gypsy moth egg mass. Information compiled from (Brown and Cameron 1982; Mason and Ticehurst 1984; Villemant and Ramzi 1995; Hoch et al. 2001; Turcani et al. 2001, 2003b; Avci 2009; Camerini 2009)

	Order	Family and parasitism rates[1]	Species
Parasitoids	Hymenoptera	Encyrtidae 10–20% Central Europe and North America	*Ooencyrtus kuvanae*
		Eupelmidae 10–20% Europe	*Anastatus disparis*
			Anastatus bifasciatus
			Anastatus japonica
			Anastatus catalonicus
		Scelionidae	*Telenomus* sp.
		Torymidae	*Torymus anastativorus*
		Eulophidae	*Atoposomoidea ogimae*
		Pteromalidae	*Dibrachys cavus*
		Eulophidae	*Pediobius* sp.
Predators	Hymenoptera	Formicidae	*Aphaenogaster rudus rudus*
			Aphaenogaster tennesseensis
			Crematogaster cerasi
	Coleoptera	Dermestidae 1–10% North America 10–90% North Africa	*Dermestes lardarius*
			Trogoderma versicolor
			Anthrenus vladimiri
			Megatoma undata
			Cryptorhopalum ruficorne
		Trogossitidae	*Tenebroides maroccanus*
	Hemiptera	Pentatomidae	*Podisus* spp.

[1]Rough estimates of the parasitism's rates. These rates might vary considerably due to different factors.

Fig. 2 Relationship between latitude and parasitism rates of the gypsy moth. (a) Correlation between latitude and the percentage of egg parasitism; (b) correlation between latitude and the rates of larval and pupal parasitism; (c) correlation between latitude and the number of insect species that parasitize the gypsy moth; and (d) correlation between the number of parasitoid species that attack the gypsy moth and the parasitism rates. For these plots, we collected information from different studies for different areas in the world (e.g. Germany, Slovakia, Turky…). However, we have to acknowledge that the phase of infestation, the sampling method and forests tree composition are different between the different studies, which may strongly influence this analysis. (Data sources: Bathon 1993, 1996; Pemberton et al. 1993; Maier 1995; Eichhorn 1996; Hoch et al. 2001; Zolubas et al. 2001; Lee et al. 2002; Turcani et al. 2003a,b; Avci 2009; Camerini 2009; Lee and Pemberton 2009; Saeidi 2011).
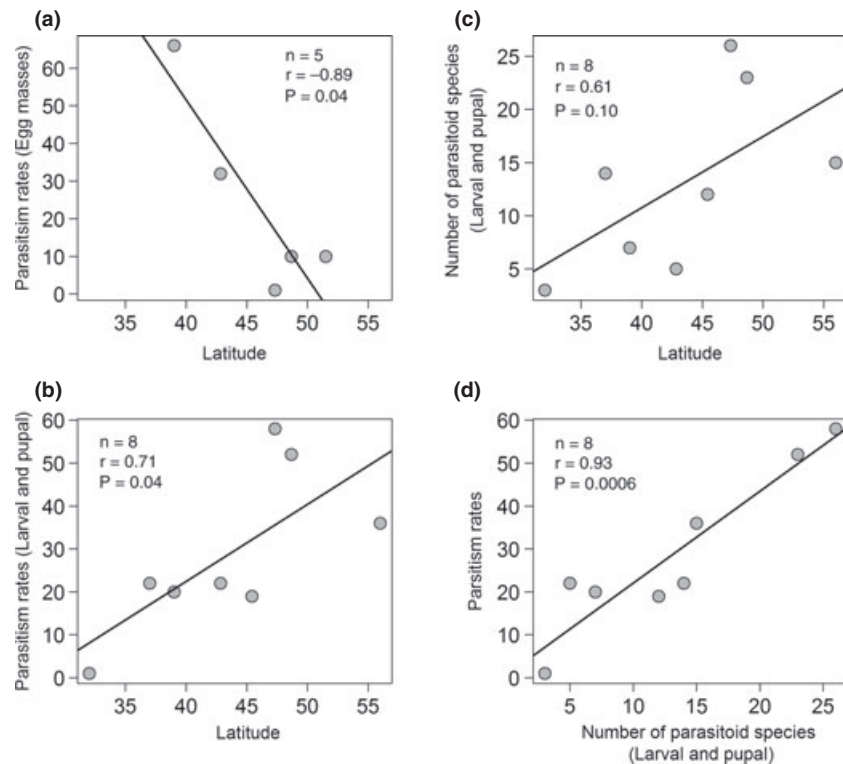
While *B. pratensis* place the egg on the consumed foliage, *Parasetigena silvestris* place it directly on old larvae resting in the trunk flaps (Odell and Godwin 1984; Gould et al. 1992). Therefore, the number of host-damaged leaf clusters and density of larvae significantly enhance oviposition and consequently the response for the changes in the host density (Odell and Godwin 1979, 1984; Williams et al. 1992). Other species of tachinids such as *Exorista* spp and *Compsilura* spp also are common in Europe. *Exorista segregate*, *Compsilura concinnata* and other species caused 20% of mortality for larvae and pupae during an outbreak period in Turkey (Avci 2009). *C. concinnata* also parasitized the gypsy moth during a period of low density in Italian willow forests (Camerini 2009).

Other important species that mainly belong to Braconidae, Ichneumonidae and Chalcididae also cause high rates of parasitism, but usually at low or increasing population levels (Maier 1995; Bathon 1996; Schopf and Hoch 1997; Hoch et al. 2001; Turcani et al. 2001; Zolubas et al. 2001). *Glyptapanteles liparidis* and *Glyptapanteles porthetriae* seem to be abundant in latency and progradations in Europe (Schopf and Hoch 1997; Hoch et al. 2001; McManus and Csóka 2007). *Phobocampe sp.* of the family Ichneumonidae cause considerable parasitism rates for the larvae and pupae in postgradations (Maier 1995; Zolubas et al. 2001). These species are oligo- or multivoltine. They

are also not specific to the gypsy moth that makes them less respondent to the changes in population densities and more active in low-density populations. For example, *Glyptapanteles liparidis* has excellent searching capacity, which makes this species effective in low density and in areas where populations increase (Schopf and Hoch 1997). However, like the other parasitoids, many factors influence the relationship between this gregarious endoparasitoid and the larvae. Such factors include: larval age, alternative hosts, host size and parasitoids complex (see also Schopf 1991; Schopf and Rembold 1993; Schopf and Steinberger 1996).

In the Asian range of the gypsy moth, tachinids, braconids and Ichneumonids comprise most of the parasitoid complex of the larvae and pupae (Lee et al. 2002; Lee and Pemberton 2009). Similar to Europe, the two species of tachinids *P. silvestris* and *Blepharipa sp* are the most effective parasitoids. On the other hand, *Phobocampe* spp. (Ichneumonidae) are considered effective parasitoids sometimes even more than tachinids (Pemberton et al. 1993; Lee and Pemberton 2009). A recent study in Central Asia showed that tachinids (e.g. *C. concinnata* and *Exorista larvarum)* do not play a large role in controlling high-density populations of *L. dispar* in orchards (Saeidi 2011). However, reports from that region are scarce. In North America, the established parasitoids such as *P. silvestris*

Table 2 Main parasitoids of the larvae and pupae of the gypsy moth. Information compiled from (Montgomery and Wallner 1988; Elkinton and Liebhold 1990; Maier 1990, 1995; Pemberton et al. 1993; Eichhorn 1996; Hoch et al. 2001, 2006; Turcani et al. 2001; Lee et al. 2002; Avci 2009; Camerini 2009; Lee and Pemberton 2009)

Order	Family	Species
Diptera	Tachinidae	*Parasetigena silvestris* (Rob.-Desv)
		Blepharipa pratensis (Meigen)
		Compsilura concinnata (Meigen)
		Zenillia libatrix (Panzer)
		Siphona borealis (Mesner)
		Blepharipa schineri (Mesnil)
		Palexorista sp.
		Carcelia gnava (Meigen)
		Drino incospicua (Meigen)
		Senometopia separata (Rondani)
		Exorista lavarum (L.)
		Exorista segregate (Rondani)
		Aphantorhaphopsis samarensis (Villeneuve)
		Pales pavida (Meigen)
	Sarcophagidae	*Parasarcophaga uliginosa* (Kramer)
Hymenoptera	Braconidae	*Apanteles xanthostigma* (Haliday)
		Glyptapanteles liparidis (Bouché)
		Glyptapanteles porthetriae (Muesebeck)
		Cotesia melanoscela (Ratzeburg)
		Meteorus pulchricornis (Wesmael)
		Cotesia ocneriae (Ivanov)
		Apanteles sp.
		Rogas sp.
Hymenoptera	Ichneumonidae	*Gelis areator* (Panzer)
		Hyposoter tricoloripes (Viereck)
		Phobocampe lymantriae (Gupta)
		Phobocampe unicincta (Gravenhorst)
		Phobocampe disparis (Viereck)
		Pimpla hypochondriaca (Ratzeburg)
		Lymantrichneumon disparis (Poda)
		Theronia atalantae (Poda)
	Chalcididae	*Monodontomerus* sp.
		Brachymeria intermedia (Nees)

and *Blepharipa* spp. and braconids, such as *Cotesia melanoscela,* can cause considerable mortality rates (Elkinton and Liebhold 1990; McManus and Csóka 2007).

The existing studies and reports agree that the tachinids species play a major role in the dynamics of the gypsy moth due to the high mortality they cause. They can reduce the density during outbreak significantly. Furthermore, parasitism rates on the larvae and pupae of the gypsy moth seem to increase towards northern latitudes (fig. 2b,c,d). Montgomery and Wallner (1988) noticed that the response of tachinid species to the change in the gypsy moth density is delayed, which might explain the high density of them in postgradations. During low densities of gypsy moth, other generalist parasitoids might have the major role to keep population from eruption (table 3).

Predation

The populations of many phytophagous insects are largely determined by their predators and hosts (Price et al. 1980; Wallner 1987). Predators are often generalists that feed on a wide range of prey species. Therefore, it is difficult to determine the impact of an individual predator on prey populations (Smith 1985; Liebhold et al. 2000). The relative importance of predation on the population dynamics of the gypsy moth seems to differ according to the attacked stage of the insect (egg masses, larvae or pupae), characteristics of predators, forests type and climate. Nevertheless, egg

Table 3 Important parasitoids of the larvae and pupae during various population phases in middle Europe and some parts of Asia. The values in the table represent the range between the lowest (zero value means that these parasitoids can be absent in some phases or regions) and the highest possible parasitism rates. (Pemberton et al. 1993; Maier 1990, 1995; Eichhorn 1996; Schopf and Hoch 1997; Hoch et al. 2001, 2006; Turcani et al. 2001; Zolubas et al. 2001; Lee et al. 2002; Avci 2009; Camerini 2009; Lee and Pemberton 2009)

Population phase	Species	Span of parasitism rates (%)
Latency	*Parasetigena silvestris*	0–20
	Blepharipa sp.	0–17
	Glyptapanteles liparidis	0–47
	Glyptapanteles porthetriae	0–28
	Cotesia melanoscela	0–25
	Hyposoter tricoloripes	0–14
	Phobocampe sp.	0–10
Progradation	*Parasetigena silvestris*	0–77
	Blepharipa sp.	0–57
	Glyptapanteles liparidis	0–23
	Glyptapanteles porthetriae	0–10
	Hyposoter tricoloripes	0–20
	Phobocampe sp.	0–21
Outbreak	*Parasetigena silvestris*	0–95
	Blepharipa sp.	0–65
	Glyptapanteles liparidis	0–18
	Glyptapanteles porthetriae	0–18
	Cotesia melanoscela	0–59
	Phobocampe sp.	0–24
Postgradation	*Parasetigena silvestris*	0–97
	Blepharipa sp.	0–95
	Phobocampe sp.	0–22

predation by invertebrates is considered to be one of the main factors influencing the population dynamics of the gypsy moth in North Africa (Flaval and Villemant 1997). Seventeen insect species feed on egg masses in cork oak forests in Morocco causing mortalities between 25% and 90%. The climatic conditions combined with the biological and trophic characteristics of the predators enable them to attack egg masses during the 9-month egg stage (Villemant and Ramzi 1995; Villemant and Andrei-Ruiz 1999).

Among invertebrates, both the adults and larvae of *Calosoma sycophantha* (Carabidae) are the main predator of larvae and pupae of the gypsy moth (Weseloh 1993; Weseloh et al. 1995; McManus and Csóka 2007). In Germany, Austria and Slovakia, the abundance of coleopteran predators increase with the increase in gypsy moth populations (Bathon 1996; Hoch et al. 2006). However, the role of beetles in regulating the populations of the gypsy moth needs more attention (Weseloh 1985a,b; Montgomery and Wallner 1988; Elkinton and Liebhold 1990).

In Europe, vertebrates probably cause more mortality than invertebrates (i.e. in Slovakia, invertebrates caused 38% of the egg mass predation, whereas vertebrates caused 62%; Turcani et al. 2003a). Birds seem to be the most important predators (Reichart 1959; Higashiura 1989; Turcani et al. 2001, 2003a). For example, 77% of the egg masses are damaged in Slovakia (Turcani et al. 2001). In Japan, bird predation on egg masses varied between 4% and 70% and was density independent (Higashiura 1989).

In North America, invertebrate predators of egg masses seem to be not important as a mortality factor. Dermestids (*Cryptorhopalum ruficorne)* can attack 3–10% of the egg masses (Mason and Ticehurst 1984). Predation by vertebrate seems to be more effective, for example, predation rates of egg masses by birds are between 65% and 89% (Cooper and Smith 1995; McManus and Csóka 2007).

Small mammals seem to have an important impact on populations of the gypsy moth. Mice cause high mortalities, for example, 98% of deployed gypsy moth pupae were destroyed within 72 h in Ukraine (McManus and Csóka 2007). Mice also caused more than 45% mortality in an artificial population of gypsy moth pupae in Austria (Gschwantner et al. 2002). The predation by small mammals plays also an important role in gypsy moth dynamics in natural oak forests in Asia (Liebhold et al. 1998). Nevertheless, the abundance of small mammals and predation rates are affected by forest types and elevation (Liebhold et al. 1998, 2005). In general, data from Europe and Asia suggest that predation by small mammals is able to

keep gypsy moth populations at low density levels (Liebhold et al. 1998; Gschwantner et al. 2002).

Predation by small mammals is considered one of the most important factors affecting the population dynamics of the gypsy moth in North America (Campbell 1975; Campbell and Sloan 1977; Elkinton et al. 1989; Grushecky et al. 1998; Hastings et al. 2002). It seems that mammals do not regulate the populations in a density-dependent fashion. The predation rate is mostly determined by the variation in predator densities, which is closely linked to the production of acorns (the major food for predators in winter) and not by the gypsy moth densities (Elkinton et al. 1989, 1996; Jones et al. 1998; Liebhold et al. 2000). Furthermore, the distribution and abundance of small mammals are determined by forest types and elevation among other factors (Yahner and Smith 1991). If small mammal predators are abundant, they are able to control the populations of the gypsy moth at low densities, but this is not sufficient to induce population collapse during outbreaks or to control increasing populations of the insect (Elkinton et al. 1996; Liebhold et al. 2000). Thus, density fluctuations of small mammal predators might be a probable factor of the synchronization in gypsy moth populations. Overall, the available information suggests that the density of small mammal predators along with the proportion of susceptible tree species is an important factor for the gypsy moth population cycles (Sharov and Colbert 1996).

Pathogens

Entomopathogenic micro-organisms have a considerable impact on Eurasian populations of the gypsy moth (Weiser 1987, 1998; Novotny 1989; table 4). In Central Europe, the mortality caused by pathogens is higher than the mortality caused by parasitoids (Bathon 1993; Hoch et al. 2001; Turcani et al. 2001). Probably the often reported unknown mortality factors are due to pathogens. For example, the average mortality caused by unknown factors in a 6-year study in Slovakia was 24%, which was larger than any other factor (Turcani et al. 2001). Microsporidia and pathogens such as fungi, bacteria and nematodes also have an effect on European populations of the gypsy moth (Weiser 1998; Maddox et al. 1999; Solter et al. 2009). In the Asian native range of the gypsy moth, fungi may cause epizootics in *L. dispar* populations. Mixed infections of *E. maimaiga* and *Paecilomyces canadensis* were found in 20% of the dead larvae in Japan (Aoki 1974; Hajek 1999). In North America, the nuclear polyhedrosis virus (NPV) is the most important factor causing the collapse of gypsy moth

Table 4 The most important pathogens of gypsy moth larvae (Hajek et al. 1990; Novotny et al. 1998; Weiser 1998; Hoch et al. 2001; McManus and Solter 2003; Turcani et al. 2003a,b; Pilarska et al. 2006; Saeidi 2011)

Pathogen	Type of organism	Geographical area
Nuclear polyhydrosis virus (NPV)	Virus	North America, Europe, Asia
Bacillus thuringiensis var. kurstaki	Bacterium	North America, Europe, Asia
Entomophaga maimaiga (Humber, Shimazu and Soper)	Fungus	North America, Eastern Europe
Entomophthora aulicae (Reich)	Fungus	Europe
Beauveria bassiana	Fungus	Central Asia
Nosema muscularis (Weiser)	Microsporidium	Europe
Nosema lymantriae (David and Weiser)	Microsporidium	Europe
Thelohania similis (Weiser)	Microsporidium	Europe
Thelohania disparis (Timofejeva)	Microsporidium	Europe
Plistophora schubergi (Zwölfer)	Microsporidium	Europe

populations (McManus and Csóka 2007). *E. maimaiga* also caused a dramatic epizootic in larval gypsy moth populations throughout many areas of the northeastern United State (Andreadis and Weseloh 1990; Hajek et al. 1990).

The significance of pathogens depends on the density of the gypsy moth. During outbreaks, NPV infects stressed larvae causing high mortality (Campbell and Podgwait 1971; Novotny 1989). Therefore, high densities of larvae, non-preferred hosts and a moist and cold climate are optimal conditions for the virus (Wallis 1957; Campbell and Podgwait 1971; Murray et al. 1989; Woods et al. 1991). Moreover, most NPV infections start from a few egg masses. Thereafter, the contaminated environment is the major factor for transgenerational transmission (Doane 1970; Woods and Elkinton 1987; Murray and Elkinton 1989).

NPV is an important mortality factor of the gypsy moth in the native and invasive ranges. It causes the collapse of the population during the outbreaks, and its effects decrease in low populations. No evidence was found to support the hypothesis that the interaction between the larva and the virus is the reason for population outbreaks (Vezina and Peterman 1985; Bowers et al. 1993).

The Effects of Other Factors

Host plants

More than 300 tree species of different families serve as host plants of the gypsy moth (Grijpma 1989;

Liebhold et al. 1995). Many of the tree species belonging to families of Fagaceae, Salicaceae, Betulaceae and Rosasceae are the hosts throughout the native and invasive ranges (Lechowicz and Mauffette 1986; Pogue and Schaefer 2007). The preference of tree species by larvae varies considerably owing to the regional and local composition of the vegetation (Lechowicz and Jobin 1983; Mauffette et al. 1983; Mauffette and Lechowicz 1984). In Central Europe, the primary hosts of the gypsy moth are *Quercus petraea, Quercus cerris* and *Quercus robur* (Fagaceae) (Bogenschutz et al. 1989; Grijpma 1989; Twery 1990). In the Balkans and the Mediterranean areas (Spain, Portugal, Sardinia and the southern regions of France), other species of this genus, that is, *Quercus suber, Quercus pubescens* and *Quercus ilex* are the primary hosts (Serrão 2002; McManus and Csóka 2007). Near the northern limits of its range in Lithuania, birch (*Betula* spp.) and alder (*Alnus* spp.) are the primary hosts (Zolubas et al. 2001). *Salix alba* is attacked in the southern range margins (Italy; Camerini 2009). There further seems to be a current trend towards an expansion of the host range. *Pinus brutia* and *Cedrus libani* have recently been reported as host plants in Turkey (Avci 2009). Moreover, the gypsy moth at high densities attacks fruit trees, for example, apple, pear and stone fruit trees in Germany (Montgomery and Wallner 1988; Vogt and Dickler 1993; Orozumbekov et al. 2004; Alalouni 2009; Saeidi 2011).

In North America, a wide range of tree species are hosts of the gypsy moth (Mauffette et al. 1983; Lechowicz and Mauffette 1986; Liebhold et al. 1995). Many hypotheses have been proposed to explain the host preferences of the gypsy moth in North America, for example, phylogeny (host trees in North America should be closely related to those in Europe), plant traits, dynamics of the gypsy moth and climatic conditions (Lechowicz and Jobin 1983; Montgomery 1990; Liebhold et al. 1995). In spite of that, it was suggested that the leaf quality and the timing of eclosion relative to leaf emergence on different hosts appear more likely to determine the host preferences (Lechowicz and Mauffette 1986).

Forest susceptibility and host trees are important factors influencing the dynamics of the gypsy moth (Barbosa and Greenblatt 1979). Susceptible species provide an easily digestible and balanced diet for the gypsy moth during the different stages of the larvae (Twery 1990). Thereby, outbreaks occur more frequently on xeric sites having many susceptible host species. Such sites help to increase the insect development and to avoid natural enemies (Campbell and Sloan 1977; Montgomery 1990). For example, the

estimated time span between two outbreaks in xeric forests with susceptible hosts (i.e. oak and pine) is four to 5 years, while it is nine to 10 years in mesic forests with less-susceptible hosts (i.e. mix of oak, maple, beech, birch; Johnson et al. 2006; Haynes et al. 2009; Bjornstad et al. 2010). On the other hand, the change in the chemistry and the nutritional quality of foliage during the defoliation lead to the decline of the population (Wallner and Walton 1979; Schultz and Baldwin 1982; Rossiter 1987). Additionally, spatial variations, feeding and synchrony of the egg hatch with leaf emergence of host plants are interactive factors contributing to the change of population densities (Leonard 1974; Valentine and Houston 1984; Montgomery and Wallner 1988; Hunter and Elkinton 2000).

The phenology of host plants and herbivores is mainly influenced by environmental factors. The variations in response to temperature and photoperiod determine the synchrony of host and herbivores (Van Asch and Visser 2007). Insects also need to adapt with spatial and temporal variations to achieve synchrony with the host plants (see also Scheiner 1993; Van Dongen et al. 1997; Kawecki and Ebert 2004; Mopper 2005). Hunter (1993) suggested that the phenological synchrony has little effect on the fluctuation in the populations of the gypsy moth. The net effects of phenology on the growth of the gypsy moth population largely depend on natural-enemy effects (Hunter and Elkinton 2000). In spite of the limited evidence, the synchrony of hosts and herbivores is speculated to influence the population dynamics of univoltine insects (see Watt and Woiwod 1999; Forkner et al. 2008).

Weather

Weather, especially temperature and precipitation affect directly and indirectly the population dynamics of the gypsy moth and the synchronization of the outbreaks (Leonard 1974; Montgomery and Wallner 1988; Elkinton and Liebhold 1990; Van Asch and Visser 2007). Temperature was frequently reported to influence the hatch of egg masses, larval and pupal development and females' fecundity. Leonard (1974) reported detailed information about the influence of winter and spring temperature on the hatch time of egg masses. Winter-survived eggs and the phenology of egg hatch in spring depend on temperature (Andresen et al. 2001). Temperature can also affect the population size of the gypsy moth' larvae and pupae considerably, for example, high temperatures help larvae and pupae to develop faster, thereby escaping

from some natural enemies (Leonard 1974; Montgomery and Wallner 1988). Precipitation reduces the ability of neonate larvae to spread and could increase spread of diseases between gypsy moth larvae (Leonard 1974). Precipitation can also be the responsible factor for the synchronization of the gypsy moth populations over large areas directly or indirectly (see Haynes et al. 2013).

Favourable weather (dry-warm) seems to support outbreaks (Delb 1999). However, there is also a lack of the short- and long-term studies regarding the potential role of weather for the population dynamics of the gypsy moth. We speculate that much of the variability in population densities of the gypsy moth may be attributed to interacting effects of weather conditions and attack by natural enemies.

Ecological and Economic Impact of the Gypsy Moth

The ecological effects of the gypsy moth vary depending on the defoliation levels. These levels are usually related to the susceptibility of the host species, the amount of foliage removed and the number of consecutive episodes of defoliation (Muzika and Gottschalk 1995; USDA 1995; Davidson et al. 2001). Defoliation by the gypsy moth may cause dramatic changes in tree species composition, which influences also wildlife species through changes in habitat characteristics (Twery 1990; Muzika and Gottschalk 1995; Webb et al. 1995). For example, North American woodpeckers may take advantages of the habitat changes caused by defoliation of the gypsy moth (Koenig et al. 2011). Furthermore, intense defoliation can indirectly affect birds, small mammals and even fish (Witter et al. 1992; Thurber et al. 1994; USDA 2012). One of the effects on birds is the increase in the abundance of non-game bird species due to the change in habitat characteristics (increased habitat diversity, habitat suitability and food supply; Whitmore and Greer 1991). The defoliation may also change the biological diversity as well as food web dynamics (Muzika and Gottschalk 1995). Many wildlife species depend on the host trees as a food supply. The loss of this food supply owing to tree mortality after defoliation reduces the capacity of an area to support some species, that is, the loss of acorns for grey squirrels (Gorman and Roth 1989; Twery 1990). On the other hand, defoliation and frass decomposition can influence the soil nutrient dynamics (Hollinger 1986; Chapman et al. 2003). Recent study suggested increasing soil total C, total N and the soil NH_4 pool by frass deposition. Additionally, herbivory

increases soil respiration and decreased total soil N relative to 'undamaged' controls independent of frass deposition (see Frost and Hunter 2004). However, there are inconsistent results about the influence of frass deposition on soil dynamics (see e.g. Lightfoot and Whitford 1990; Lovett and Ruesink 1995; Reynolds et al. 2000; Reynolds and Hunter 2001).

Forest trees have been categorized according to their susceptibility to defoliation. Generally, a single year of defoliation is sufficient for killing a conifer attacked by gypsy moth, while two or three successive years of defoliation are usually needed for the death of deciduous trees (Johnson and Lyon 1991). A considerable number of trees die due to the attack by other organisms after defoliation (Davidson et al. 1999, 2001). The heavy attacks of *Agrilus biguttatus* (Col., Buprestidae) on oak in France was recorded after an exceptional outbreak of the gypsy moth in the previous years (Landmann 1996; Moraal and Hilszczanski 2000). In this context, different biotic and abiotic stresses may increase the susceptibility to defoliation by gypsy moths in European forests, especially in oak forests (Gottschalk and Wargo 1996; Führer 1998; Moraal and Hilszczanski 2000).

Clearly, the current management strategies have impacts on native biota (Sample et al. 1996). Products of *Bacillus thuringiensis* var. *kurstaki* (BTK) probably affect different species of moths more than the outbreak moth species (Schweitzer 2004). Furthermore, some chemicals, such as diflubenzuron (or Dimilin, an insect growth regulator) persist in the environment for long time thereby affecting the forest environment and species (Sundaram et al. 1991; Lischke 1993; USDA 1995). Reports on human health and ecological assessment of the various products are also available (e.g. Forster et al. 1993; Gericke and Schellschmidt 1993; USDA 1995).

Published information on the economic impacts of the gypsy moth in its native range is limited. Some data alluding to the economic impact of the gypsy moth indirectly point to the high cost of control measures. Infested stands in Slovakia covering 18 000–22 000 ha during 1992–1994 were treated with BTK (Turcani et al. 2001b, 2003a,b). In Germany in 1994, around 5200 ha were treated with diflubenzuron, and around 2000 ha were treated with BTK (Seeman 1999). The gypsy moth seems to have also considerable economic impact on orchards. Since the 1980s, the annual defoliation of pistachio, walnut and apple orchards ranged between 17 000 and 52 000 ha in Kyrgyzstan (Orozumbekov et al. 2004). The gypsy moth caused considerable damage to poplar plantations, oak forests (1 471 839 ha) and evergreen ecosystems (3 153 882 ha) in Greece, and it was controlled using chemicals and bio-insecticides (Avtzis 2001). Nevertheless, it is important to mention that no control measures have been used in some areas of Europe, for example, in Austria since the early 1960s (Hoch et al. 2001) and in some infested stands in Germany (Seeman 1999).

In North America, more than 34 million ha have been defoliated by the gypsy moth since 1924 (McManus 2007). The estimated timber loss in 1981 in Pennsylvania alone had a value of 72 million dollars (Montgomery and Wallner 1988). Huge budgets were released to develop strategies to control this pest and to limit its spread, such as the 'Slow the spread' programme, one of the largest programmes in the USA (Sharov et al. 2002a,b). The recently estimated costs of loss caused by the gypsy moth and other foliage feeders in the USA and the government expenditures to manage these pests range between 4 and 120 million dollars annually (see Aukema et al. 2011).

Many studies predict an increase in the potential economic and ecological damage caused by forest pests in the future due to climate change, which may increase the likelihood of pest establishment in new locations as well as the impacts of both native and introduced pests (Logan et al. 2003; Regniere et al. 2009; FAO 2010). This prediction includes the gypsy moth. A modelling study (Vanhanen et al. 2007) indicated a shift in the distribution boundaries of the gypsy moth and the nun moth (*Lymantria monacha*) in Central Europe; in this model, the northern boundary will shift ca. 500–700 km to the north, and the southern boundary will shift ca. 100–900 km to the north. This shift threatens forests in the new areas (Vanhanen et al. 2007).

Conclusions

The damage and defoliation caused by the gypsy moth in its native range are less severe than that caused in its new ranges. This can be interpreted as a result of the release from natural enemies in the new ranges. Natural enemies are considered to be the dominant mortality factor in insect populations (Cornell et al. 1998).They could cause local extinction of native populations if these populations are vulnerable (Hochberg and Ives 1999). Pathogens, especially NPV in periods of outbreaks cause the highest mortality rates in all populations of the gypsy moth (Novotny 1989; Woods et al. 1991). Parasitoids can also cause high mortality rates. Tachinids are thereby the major parasitoids with a potential influence on the population dynamics of gypsy moth. While Tachinids

contribute to the collapse of the population of the gypsy moth during outbreaks, parasitoids of other families contribute to regulating the populations at low densities. Parasitoids of the egg masses do not seem to cause sufficient mortality levels that influence the population of the insect. Predators cause considerable mortality rates, with birds and small mammals causing higher mortalities than invertebrates, at least in North America. Studies evaluating the other biotic and abiotic factors influencing the dynamics of gypsy moth are rare and especially with respect to the phenologies of host plants and the insect.

In spite of several decades of research on the ecology, population dynamics and the importance of natural enemies, we have little quantitative information to predict the population dynamics of this important forest pest species and to control its impact. More research about the interaction between environmental factors, host plants and parasitoids complex would help to understand more about the reasons of this insect eruption and the synchrony over large areas in Europe and North America.

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