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Aggregative oviposition varies with density in processionary moths—Implications for insect outbreak propensity

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Abstract

1. In gregarious insects, groups commonly originate from females laying eggs in masses and feeding groups are established as soon as larvae hatch. Some group-living insect species may aggregate beyond the individual parent level, such that offspring from two or more egg masses develop within a common resource.
2. Here we show that aggregative oviposition can vary with population density at oviposition and possibly be an important factor in outbreak dynamics of phytophagous insects.
3. We analysed density data with respect to egg mass aggregation for two species of pine processionary moths, *Thaumetopoea pinivora* (in Sweden 2005–2019) and *T. pityocampa* (in Spain 1973–1991). Both species lay their eggs in egg masses and feed in groups. During the study periods, insect population density for both species varied by at least an order of magnitude.
4. The two species showed strikingly similar patterns of egg mass aggregation. Egg masses were overdispersed at high population density, with few trees showing a high load of egg masses.
5. Our data suggest that aggregative oviposition can be important in explaining the previously documented higher propensity for outbreaks in insects laying eggs in clusters, compared with those laying individual eggs.

KEYWORDS
egg mass, gregariousness, group living, Lepidoptera, Notodontidae, *Thaumetopoea*

INTRODUCTION

Group living, or gregariousness, is a widespread trait among animals (Krause & Ruxton, 2002). In phytophagous insects, group living occurs in a wide range of taxa (Hunter, 2000). For example, in Lepidoptera, about 5% of North American butterfly species form larval aggregations (Stamp, 1980) and 8% of forest inhabiting moths in Canada have larvae with a gregarious lifestyle (Herbert, 1983). Several factors can explain the improved performance of large larval groups compared with smaller groups or solitary larvae, including better defence against enemies (Codella Jr. & Raffa, 1995; Hunter, 2000; Ronnås et al., 2010; Wilmoth & Fordyce, 2019), improved thermoregulation (Joos et al., 1988; Ronnås et al., 2010), and feeding facilitation (Allen, 2010; Denno & Benrey, 1997; Despland, 2019; Fordyce & Agrawal, 2001; Ghent, 1960).

The gregarious lifestyle is associated with a female depositing her eggs in an egg mass, which is typical of Lepidoptera (Costa & Pierce, 1997). The number of eggs per egg mass is an evolved trait that varies among species, from a few (e.g., *Battus polydamas*, Cisternas et al., 2020) to several hundred (Hinton, 1981). Lifetime group size can equal initial egg number, but due to mortality during larval development tends to be much smaller (e.g., Hunter, 1991). In general, larval groups need to be sufficiently large at egg hatch in order to compensate for mortality throughout the larval stage (Stamp, 1981). Thus, optimal group size varies among larval instars (Stamp, 1981), also because they are subject to dissimilar hurdles (Hunter, 1991). Aggregative oviposition, and subsequent merging of larval groups, can contribute to the maintenance of functional groups in late instars, despite mortality in earlier ones, in Lepidoptera but also in sawflies (e.g., Boevé, 1991; Campbell & Stastny, 2015; Codella Jr. & Raffa, 1995; Fitzgerald, 1995; Floater, 1996; Stamp, 1980; Sun & Underwood, 2011).

Insect species with a gregarious lifestyle appear more prone to outbreaks than species with a solitary lifestyle (Hanski, 1987; Hunter, 1991, 1995; Koricheva et al., 2012; Larsson et al., 1993; Nothnagle & Schultz, 1987; but cf. Cappuccino et al., 1995). Hanski (1987), in a short but thought-provoking article, has taken the life history perspective of gregariousness into a population perspective. He concluded that oviposition in egg masses should be considered as gambling ('risk-prone reproductive strategy'), whereas laying eggs singly should be seen as a form of risk-avoidance (also cf. Nothnagle & Schultz, 1987). It follows that species with a gregarious lifestyle show greater spatiotemporal variability in survival, or as Hanski puts it: 'the potential gain is high, but so is the possible loss'. Some patches, at a certain point in time, for whatever reason will be in a gain situation (e.g., low predation or disease incidence, favourable weather) that will increase or maximise group survival (Floater & Zalucki, 2000). Conversely, most patches typically experience a variety of factors that will reduce or limit group survival, and thus the population stays at endemic levels.

Processionary moths (Notodontidae: Thaumetopoeinae) constitute good models for analysing aggregative oviposition in a population dynamics context. As outbreaking defoliators, processionary moths are well known for their social behaviour that starts with the female laying all her eggs in an egg mass (Battisti et al., 2015). Larvae hatching from the egg mass are gregarious throughout their development. In addition, the colonies originating from different egg masses laid on the same tree can merge into larger groups on various parts of the tree, from where they move in lines between feeding sites and for pupation. Data from *Thaumetopoea pinivora* (Treitschke) in south Sweden showed larval colonies to be of larger size than expected based on the average number of eggs in an egg mass (Ronnås et al., 2010), which could have been the result of aggregative oviposition and/or fusion of larval groups. In addition, individuals in larger colonies benefited from a higher survival and growth rate compared with those living in smaller colonies 2013. A similar situation was observed by Pérez-Contreras et al. (2003) for *Thaumetopoea pityocampa* (Denis et Schiffermüller) in a field experiment manipulating group size.

To examine putative aggregations in the processionary moths, we analysed data from two long-term monitoring studies involving ecologically similar *Thaumetopoea* species: (1) a 15-year study of the northern pine processionary moth *T. pinivora* in Sweden and (2) a 19-year study of the winter pine processionary moth *T. pityocampa* in Spain. By using yearly data on egg mass distribution and density for both species, we tested the hypothesis that aggregation of oviposition (at tree level) varies with population density. More specifically, we predicted that aggregation of egg masses increases with population density, resulting in larger larval colonies characterised by higher performance and potentially enhanced survival. Under conditions that promote group survival, such aggregative behaviour may represent an important factor for outbreak development.

MATERIALS AND METHODS

Study organisms

The northern pine processionary moth *T. pinivora* occurs as scattered populations from coastal areas along the Baltic Sea (Ronnås et al., 2011) to a few known sites in France, Germany and Spain (Cassel-Lundhagen et al., 2013; Hódar et al., 2016). The northernmost occurrence of *T. pinivora* is a small area in the southern part of Gotland Island in the Baltic Sea. *T. pinivora* has a two-year development cycle on Gotland. The adult emerges from the cocoons in the soil in mid to late July. Females are short-lived and oviposit on pine needles (100–200 eggs per female, Larsson et al., 2008). Eggs are laid in one or two egg masses, in the latter case, close to each other. The eggs hatch in late April the following year. In late July, the larvae leave the trees in head-to-tail processions to find suitable sites in the soil for cocoon spinning. The pupae overwinter and remain in the soil until emergence in July of the second year. The Gotland population has discrete year classes with higher egg densities in odd than in even years, which is noticeable at periods of high population density (Larsson et al., 2008). Although local peaks in density have been documented in a few populations throughout its range, the Gotland population is the only one for which a time-series of density is available.

The winter pine processionary moth, *T. pityocampa* is common all over the Mediterranean basin in southern Europe, northern Africa, and the Middle East. Throughout its range, *T. pityocampa* is a major pest of forests and ornamental trees, typically pines and cedars (Battisti et al., 2015). Outbreaks are recorded regularly in some parts of its range (Hódar et al., 2012; Li et al., 2015; Tamburini et al., 2013). *Thaumetopoea pityocampa* has one generation per year, with moths emerging from cocoons in the soil during the summer. The fecundity of a female varies from 100 to 300 eggs, depending on the population (Battisti et al., 2015). The short-lived females lay all their eggs in one mass on pine needles, and the larvae hatch in about 1 month. They immediately start to feed on pine needles and build a few silk 'tents' during the autumn, to spin the final winter tent in the apical parts of the tree (Uemura et al., 2021). From these conspicuous silk tents larvae have nightly forays to forage during winter whenever temperature conditions are met (Battisti et al., 2005). In spring, the larvae leave the tree in head-to-tail processions to pupate in the soil, where the pupae stay until summer (Uemura et al., 2020).

Study areas

The study area for *T. pinivora* is located a few metres above sea level in the southern part of Gotland Island, south Sweden (central

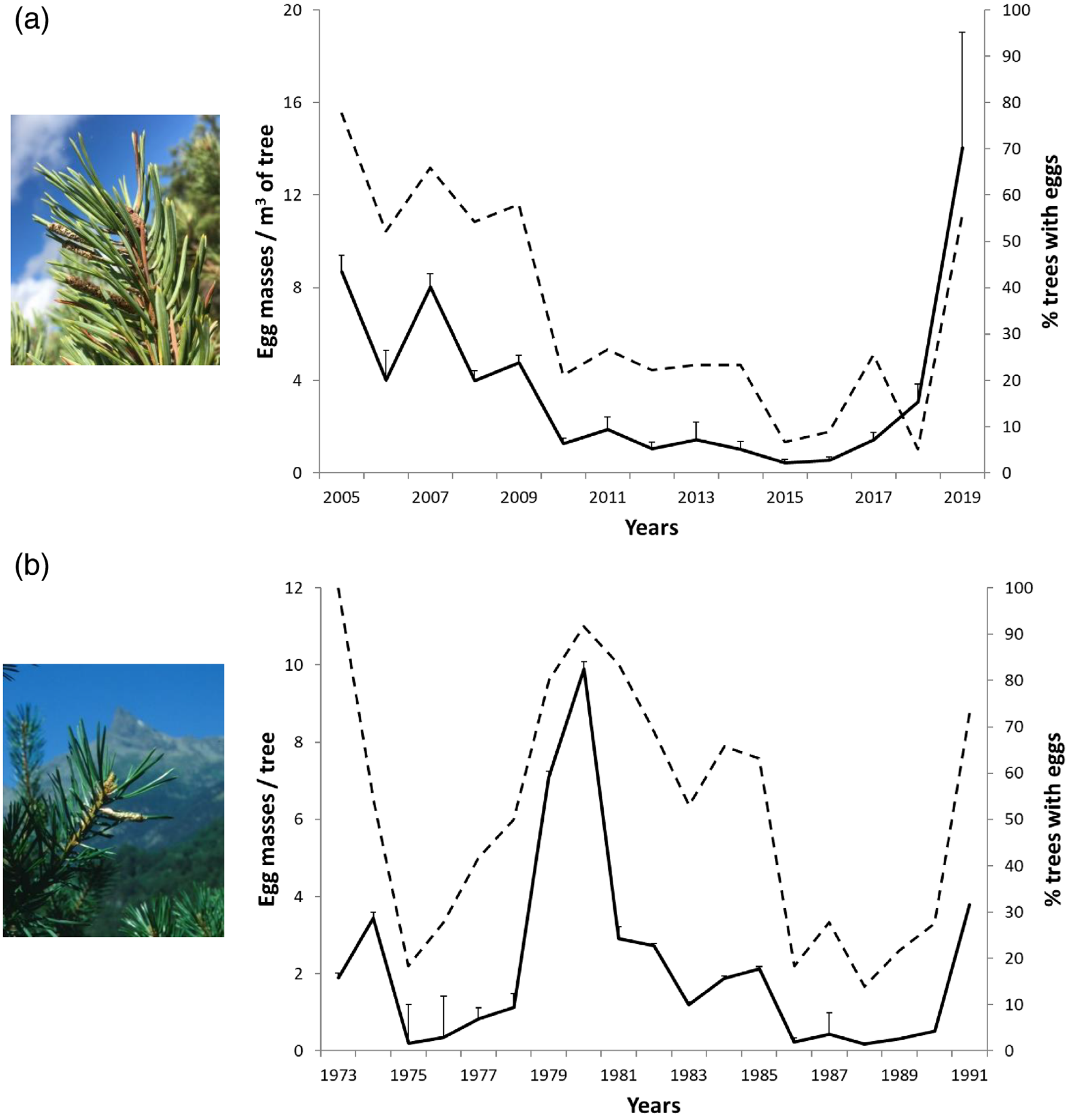

FIGURE 1 (a). Density of egg masses of *Thaumetopoea pinivora* per tree (standardised tree volume, solid line, left Y axis) and percentage of trees carrying egg masses (dotted line, right Y axis) in Gotland, Sweden. Each point is the mean of 90 trees occurring at three sites. Only positive standard error bars are shown to avoid overlapping. (b). Density of egg masses of *Thaumetopoea pityocampa* per tree (solid line, left Y axis) and percentage of trees carrying egg masses (dotted line, right Y axis) in Mora de Rubielos, Spain. Each point is the mean of 120 trees occurring at three sites. Only positive standard error bars are shown to avoid overlapping.

coordinates of the area: 56.94 N, 18.22 E). The area (ca 5000 ha) covers large patches of *Pinus sylvestris* woodlands, mixed with agricultural fields and coastal ecosystems. The climate is moderately cold, dry and sunny, with an average annual rainfall of 500.6 mm and 2137 h of sunshine (2002–2018, SMHI, Swedish Meteorological and Hydrological Institute, Hoburg weather station). In the same period, the average air temperature was 8.5°C, with mean monthly summer (June–September) temperatures of 16.4°C and mean monthly winter (December–March) temperatures of 1.2°C. During 2003–2009, the density of this population reached outbreak levels in approximately 3000 ha of the southernmost tip of the island (the Sudret area), for the most part in low-density, low-stature pine stands on poor soil ('alvar'). This resulted in extensive defoliation of the host trees (*P. sylvestris*) (Aimi et al., 2008), leading to health problems among people in the area due to the allergic response induced by the setae released by the larvae (Battisti et al., 2011).

The study area for *T. pityocampa* is located in Mora de Rubielos, in Teruel province, north-eastern Spain (40.30 N, 0.75 W) Demolin, 1970. The area covers approximately 13,000 ha of naturalised pine woodlands, dominated mostly by *Pinus nigra salzmannii*, *P. pinaster* and *P. sylvestris*. The site has a northern Mediterranean climate with cold, wet winters and hot, dry summers, receiving an average of 487 mm of rainfall (1971–2012, weather station at Mora de Rubielos) and 2639 h of sunshine annually (2012–2015, Teruel weather station, 35 km from Mora de Rubielos, data from AEMET, the Spanish Agency of Meteorology). The average air temperature was 10.4°C, with mean monthly summer temperatures of 21.5°C and mean monthly winter temperatures of 5.7°C. The elevation ranges from 1000 to 1800 m.

Monitoring of population density

For both species, population density was monitored annually by counting the number of egg masses per tree. An individual tree was the unit for the population density survey because it can receive eggs irrespective of previous defoliation. This is possible because both species defoliate the trees in winter (*T. pityocampa*) or spring (*T. pinivora*), thus before the new shoot of the year is produced. Egg masses are discrete, relatively conspicuous units, easily identified by visual inspection of the branches from the ground at least up to a height of about 3 m (Figure 1). Data on egg mass counts were collected independently in 2005–2019 (Sweden) and in 1973–1991 (Spain). Data from Sweden can be considered representative of the population density as trees were haphazardly chosen among those typically attacked by the moth. Data from Spain, however, came from a subset of trees, whereas the population is spread over a much larger area (about 12,000 ha) that includes trees of different heights and species (*P. pinaster*, *P. sylvestris*). To address this potential source of error, the density of egg masses on the study trees (*P. nigra*) was compared to the average index of defoliation for the whole area. The mean number of egg masses per study tree was positively correlated with the population density on a larger scale for all hosts and for *P. nigra* only (Supporting Information A).

The yearly count of egg masses of *T. pinivora* was conducted within the outbreak area described in more detail by Aimi et al. (2008). Thirty isolated, small-statured (mean height: 1.6 m) trees, among those originally used in the experiment by Aimi et al. (2008), were selected at each of three sites representative of the insect population in the area and located about 2 km from each other. Egg mass density was monitored on selected trees for 5 years (starting with eggs laid in 2005), until trees were too large to allow easy access for counting. Therefore, a second cohort of trees was selected in 2010, similar in height to those in the same general area from 2005. Trees from this cohort were used for 5 years and thereafter, in 2015, replaced by a third cohort of trees of suitable height until the study was terminated after the 2019 oviposition. Thus, we collected data from three cohorts spanning 90 trees at each of the three sites during the 15-year period; data for 2006, however, are based on a lower number of trees ($N = 18$, six per site) due to limitations to field work in that year. Yearly searches for egg masses were most often performed in autumn (10 years), but in 5 years (2011, 2013, 2014, 2018, 2019), they had to be done in the spring before egg hatch. The spring assessments may underestimate the true density if egg masses disappear during winter due to predation by passerine birds; however, the birds rarely remove entire egg masses (pers. obs. by Stig Larsson). In most situations, the egg masses were easy to find (Figure 1). We acknowledge that, occasionally, some egg masses could have remained undiscovered on some trees. The error is likely to be small because the size of the trees allowed a thorough inspection. The accuracy of the method was examined in a supplementary study in 2012/2013: 75 egg masses were detected on 120 trees in the fall count (September), with only eight additional egg masses detected in the spring recount (May).

The yearly count of egg masses of *T. pityocampa* was performed in Mora de Rubielos at three selected study sites (Alto de Mora, Bajo de Mora and Valle de Cabra) within a radius of 3 km, with an elevation ranging from 1182 to 1317 m. An area of approximately 0.25 ha was selected within each site, and 40 trees of *P. nigra* were chosen within this area, separated at a minimum distance of 5 m from each other. Average height of trees was 2.7 m at the beginning of the study period in 1973 and 3.2 m by 1981, but unfortunately, the final height in 1991 was not measured. The selected trees were all of similar height to avoid differences in vulnerability to attack, as tree height (apparency) has been suggested to be a critical factor determining the likelihood of attack (Demolin, 1969; Dulaurent et al., 2012), and to facilitate sampling of egg masses. By the end of summer, once the eggs have hatched, egg masses are systematically searched for and collected. Their spotting was made easier by the occurrence of early feeding symptoms, as the needles partly consumed by the newly hatched larvae turn yellow-brown. Sampling was performed for different purposes (see Cayuela et al., 2014); here we use only the number of egg masses per tree on a year basis. A total of 4925 egg masses were sampled throughout the study period on a total of 2280 tree observations, with only 22 tree observations missing over 19 years.

Data analysis

To track the density of egg masses per tree through time, standardisation of egg masses per unit volume of tree foliage was required, especially for *T. pinivora*, where three different cohorts of trees were used in the 15-year period. This was achieved by calculating the volume of the tree crown, to account for variation in tree size and shape. The volume of the crown was calculated at the start of each cohort by assuming a spindle-like shape for the tree crown, measuring total height, height to the lowest green branch, and height from the ground to the widest part of the tree. Volumes were determined again at the end of the 5 years of tree observations for each cohort. The volume growth was equally divided among the 5 years, so that the number of egg masses refers to the estimated volume of the tree in each year of observation. For each of the three sites, the mean number of egg masses per unit tree ($N = 30$ trees) was used to calculate the general mean of egg mass density in each year. For *T. pityocampa*, standardisation was not possible because data on tree size at the beginning and end of the census period was not available.

The percentage of trees with egg masses was calculated for each species in each year. The distribution of the number of egg masses per tree was determined by pooling all the trees of the sites and ranking them based on the number of egg masses. Female moths of *T. pinivora* often split their egg load into two egg masses laid on nearby shoots (see Supporting Information B), and therefore the average egg load of one female was considered the sample unit. In *T. pityocampa*, one female lays all her eggs in one egg mass (Battisti et al., 2015).

The level of aggregation of egg masses at tree level in each year was analysed using different statistics. The coefficient of dispersion, or variance-to-mean ratio (Sokal & Rohlf, 1995), of the mean number of egg masses per tree (egg mass density) in each year was related to the egg mass density, which is a proxy of overall population density (Supporting Information A). Other indices of spatial aggregation available from literature, such as the Taylor's Power Law (Taylor, 1961; Taylor, 2017) and the Lloyd's mean crowding (Lloyd, 1967; Wade et al., 2018), called also Morisita's I index (Iwao, 1968), were used for comparison. All these indices include a bias associated with the natural increase of the variance with the mean, and the comparison with the baseline data was done by the analysis of covariance for each study area, using the first year of the series as reference (1973 for Spain and 2005 for Sweden) and simulating a regular increase of the mean. The analysis of covariance was also used to compare slopes of the two study areas. The occurrence of temporal autocorrelation in the time-series of dispersion indices was tested using the R package gretl (Baiocchi & Distaso, 2003), specifically designed for the analysis of autocorrelation in time-series data. The software was run for the whole datasets of *T. pinivora* and *T. pityocampa*, and for the same datasets where trees with no eggs were removed. The occurrence of spatial autocorrelation of egg density among trees was tested using the geoR suite for the dataset of *T. pinivora*, as tree coordinates were not available for *T. pityocampa*. One year in the *T. pinivora* dataset stood out in the series because of the occurrence of an anomalous tree; Cook's distance was calculated and the point was excluded from the analysis whenever the value was >5. The analyses were run using the R software programme (R Core Team, 2020).

RESULTS

The *T. pinivora* population in Sweden and the *T. pityocampa* population in Spain showed strikingly similar patterns of egg mass aggregation. For both systems, aggregation increased with the population density of the moth.

During the study periods, insect population density at both sites varied by at least an order of magnitude. Density, expressed as the mean number of egg masses per tree, was generally related to the percentage of trees carrying egg masses. In *T. pinivora* (Figure 1a), the density was high at the beginning of the study period, with heavy defoliation of the pine trees, and then decreased to very low levels for 8 years. During the last 2 years (2018–2019), the density increased to levels close to those of the outbreak years. Density was not spatially correlated in any of the years considered in the study. In *T. pityocampa* (Figure 1b), the density was low at the beginning of the study period, although most trees were carrying eggs, and then increased to high levels with a distinct peak in 1980. This was followed by a rapid decline in density, which extended until 1990, when the density again increased.

Density of egg masses per tree varied enormously at both sites. In many cases, trees had no egg masses (780 out of 1186, i.e., 65.7% for *T. pinivora*; 1090 out of 2258, i.e., 48.3% for *T. pityocampa*), although all trees received at least one egg mass in the periods of observation. When trees were carrying egg masses, their distribution showed a very long tail (Figure 2). In *T. pinivora*, the number of cases in which trees received eggs from one female moth was conservatively estimated at 206 (see Supporting Information B). In the other 200 cases, trees received eggs from two or more female moths, indicating a tendency of the latter to aggregate on some trees for oviposition. In *T. pityocampa*, 461 trees were chosen by only one female, whereas in 706 cases, trees were carrying more than one egg mass.

The level of aggregation of egg masses at tree level for each year, measured by the coefficient of dispersion, was positively related to egg mass density in both species (Figure 3), with a slope marginally higher ($p = 0.063$) for *T. pinivora* than for *T. pityocampa*. The coefficient values were significantly higher than those expected based on the natural increase of the variance with the mean for both species ($p < 0.01$ for *T. pinivora* and $p = 0.029$ for *T. pityocampa*). In *T. pinivora*, the year 2018 stands out as an outlier because one tree at one of the sites received many more egg masses ($N = 48$) than those found on all other trees combined ($N = 5$) at that site. There was no autocorrelation of the dispersion coefficient of the egg masses in the time series for both species, irrespective of whether trees with no eggs were included in the models or not (*T. pinivora*: $Q_{lag14} = 9.19$, $p = 0.82$; $Q_{lag14} = 10.39$, $p = 0.73$. *T. pityocampa*: $Q_{lag18} = 13.5$, $p = 0.76$; $Q_{lag18} = 13.6$, $p = 0.75$). The other indices of spatial aggregation provided similar results (Supporting Information C).

DISCUSSION

Egg mass aggregation increased with the density of the insect population in both *T. pinivora* in Sweden and *T. pityocampa* in Spain. This is one of the few field studies, if not the first, to document invertebrates building larger groups as population density increases (Krause & Ruxton, 2002). The variation in population density was substantial, although not extreme (Fitzgerald, 1995; Li et al., 2015), and probably reflects a common situation in populations of *Thaumetopoea* spp. and other phytophagous insect species.

The aggregation levels observed for each species conform to Taylor's Power Law (the variance V of a non-negative random variable is a power function of its mean M; i.e., $V = a\ M^b$), as verified for many organisms, including moths (Taylor, 2017). Although mechanisms can differ among models, they seem to be context-independent and related to population dynamic patterns (Giometto et al., 2015). All the statistics used to test for aggregation of the egg masses at tree level confirm the pattern for both *Thaumetopoea* species, with slightly different outcomes. The dispersion coefficient and the Lloyd's mean crowing, or Morisita's I, indicated a stronger aggregation of the egg

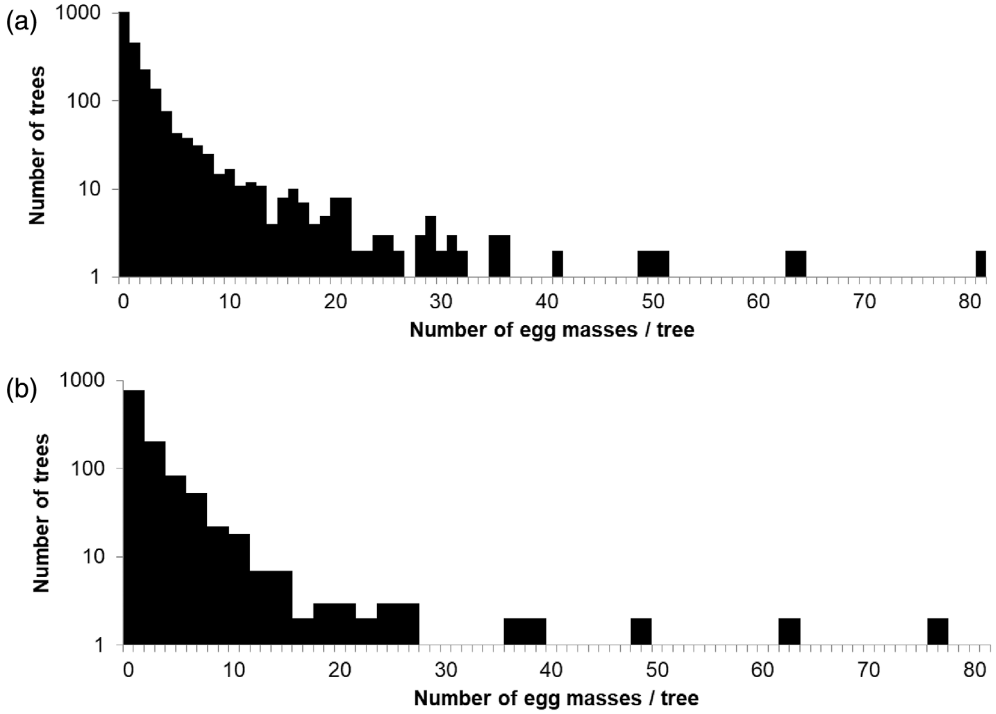

FIGURE 2 (a). Frequency of trees hosting *Thaumetopoea pinivora* egg masses in Gotland, Sweden. Trees from the entire study period pooled ($n = 1186$). The Y axis is in log scale to better show the occurrence of trees with high egg mass load. (b). Frequency of trees hosting *Thaumetopoea pityocampa* egg masses in Mora de Rubielos, Spain. Trees from the entire study period pooled ($n = 2258$). The Y axis is in log scale to better show the occurrence of trees with high egg mass load.

masses for *T. pinivora*, which is possibly explained by the oviposition behaviour of ovipositing for two egg masses (Supporting Information B).

The mechanisms behind the aggregations that we see in our data are not obvious. Selection of oviposition sites in phytophagous insects is commonly thought to be governed by the characteristics of the host plant that increase offspring development and survival ('preference-performance hypothesis', e.g., Thompson & Pellmyr, 1991), that is, females select high-quality plants (Floater & Zalucki, 2000). Capital breeders sensu Tammaru and Haukioja (1996) are less mobile and selective in relation to the oviposition substrate, whereas *Thaumetopoea* species seem to be an exception in this regard (Battisti et al., 2015) (Figure 1). *Thaumetopoea* species, however, are highly social organisms, and this special behaviour may affect their dynamics. It is possible that trees with many egg masses of *Thaumetopoea* spp. are recognised as high-quality hosts (due to nutrients, secondary chemicals, needle morphology, enemy-free space). However, there is little support for the notion that tree characteristics are important for egg-laying in *T. pityocampa* (Stastny et al., 2006). The fact that a large proportion of the trees had no egg masses, even in the years of high population density, implies that aggregation was unlikely due to the shortage of (suitable) host trees. In the processionary moths considered in this study, the current year's needles are not eaten by the larvae and can be used for oviposition even if they are smaller compared to those produced by undefoliated trees (Battisti, 1988 and Supporting Information D). A second possibility is that the aggregation of egg masses is due to ovipositing females responding to cues from egg masses already deposited on the tree by one or several other females ('conspecific hypothesis'), which may affect the ovipositing females negatively (to avoid competition, Nufio & Papaj, 2001) or positively (Campbell & Stastny, 2015; Steiger & Stöckl, 2017; Sun & Underwood, 2011). The latter could result in aggregations, such as those seen in our data, but no experimental evidence in *Thaumetopoea* species supports the conspecific hypothesis. A third possibility is that the aggregated distribution of the pupae in the soil, and thus the emerging moths, determines female oviposition behaviour as female moths are short lived and with limited dispersal capacity (Demolin, 1969; Robredo, 1963) ('local density hypothesis'). Larval groups in processions search for a suitable pupation site in the ground (Battisti et al., 2015; Robredo, 1963), producing sites with very high densities of pupae (Bonsignore et al., 2019) and, eventually, emerging moths that may communally oviposit on nearby trees. However, at least for *T. pinivora*, the lack of spatial autocorrelation offers little (indirect) evidence that pupation sites underlie egg mass aggregation.

In studies on a few species laying eggs in masses, aggregative oviposition has been defined as female insects preferring to lay egg masses on leaves or branches previously colonised by other females and to position their egg masses adjacent to existing ones (Campbell & Stastny, 2015; Desurmont & Weston, 2010; Sun & Underwood, 2011). We conclude that our data are in line with this definition, although we have no direct observations of females ovipositing in sequence. Such observations are not easy to obtain in nature.

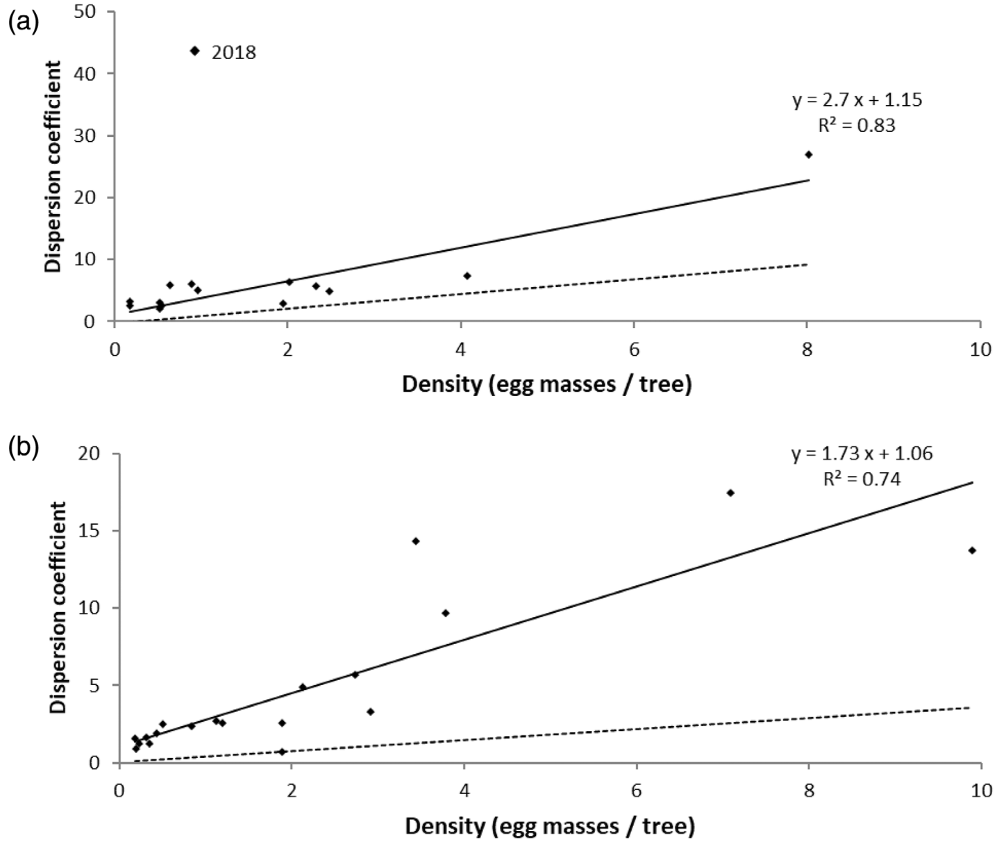

FIGURE 3 (a). Dispersion coefficient of *Thaumetopoea pinivora* egg masses per tree (ratio between variance and mean of the 90 trees measured in each year) as related to density of egg masses per tree in each of the 15 years of the study period (2005–2019) in Gotland, Sweden. The point of 2018 stands as an outlier and it is explained by a single tree that received many egg masses in a year of low density. The regression line does not include the point of 2018. The dotted line shows the increase of the dispersion coefficient expected based on the increase of the mean, simulated from data of the first year. (b). Dispersion coefficient of *Thaumetopoea pityocampa* egg masses per tree (ratio between variance and mean of the 120 trees measured in each year) as related to density of egg masses per tree in each of the 19 years of the study period (1973–1991). The dotted line shows the increase of the dispersion coefficient expected based on the increase of the mean, simulated from data of the first year.

When aggregated, egg masses in our study were often, but not always, found on the same branch or on nearby shoots of another branch in the same tree. Because experimental trees were small statured, we considered all egg masses in the same tree to constitute one aggregate, allowing us to easily define the unit of aggregation. We do not know to what extent larval groups arriving from other trees may contribute to aggregation, but it seems reasonable that the great majority of mature larvae are from the same natal tree, at least during non-outbreak conditions.

Few studies have documented aggregative oviposition under field conditions. Studies on the viburnum leaf beetle convincingly showed that the beetles oviposited in an aggregated way, but this conclusion was achieved through field studies combined with experimental studies in the laboratory (Desurmont et al., 2014; Desurmont & Weston, 2010, 2011). We know of no other experimental studies that have documented aggregative oviposition in nature (cf. Boevé, 1991; Campbell & Stastny, 2015; Codella Jr. & Raffa, 1995; Fitzgerald, 1995; Floater, 1996; Stamp, 1980; Sun & Underwood, 2011). Controlled experiments in the laboratory, however, clearly show that gravid females, when given a choice, may prefer to oviposit on plants, or plant parts, already oviposited on by another female (Raitanen et al., 2014; Yan et al., 2018), even if the opposite, that is, avoidance of ovipositing on plants with conspecific eggs, may be the norm (e.g., Nufio & Papaj, 2001).

Group living has both benefits and costs for phytophagous insects, with an optimum size that varies among species. Many insect species benefit from group living in early instars when predation pressure is intense (Despland, 2019; Hunter, 2000; Wilmoth & Fordyce, 2019), including the processionary moths, as shown by Floater and Zalucki (1999) for *Ochrogaster lunifer* and by Ronnås et al. (2010) for *T. pinivora*. The latter species also benefits from group living as neonate larvae through improved thermoregulation in basking groups (Ronnås et al., 2010). The benefit from group living tends to be less important in older instars for many species (Costa & Ross, 2003), and some species even change to a solitary life as they grow older (Despland, 2013; Despland & Hamzeh, 2004). Processionary moths, however, benefit from large groups throughout all larval instars. For instance, the larvae of *Thaumetopoea pityocampa* feed during winter and stay protected in silk tents built in the canopy, and the quality of these tents is positively related to the number of larvae in the group (Battisti et al., 2005; Pérez-Contreras et al., 2003; Poitou et al., 2021). In addition, the larvae from the third instar are protected against vertebrate predators by the urticating setae, which are also released into the soil at the pupation time and can persist there for a long time (Battisti et al., 2017). Thus, the maintenance of a large colony size in *Thaumetopoea* spp. probably improves survival through their entire development, from neonate larvae until emergence of the adult moths.

The increased aggregation of egg masses at higher insect population densities can have consequences for population dynamics. For example, one could argue that clumped larval colonies at high population density could lead to overexploitation of the resource and possible negative feedback on insect density. Long-term data on the population dynamics of *T. pityocampa*, however, indicate that populations generally thrive around low mean densities, far below outbreak densities (Hódar et al., 2012; Li et al., 2015; Tamburini et al., 2013). Even at outbreak peaks, complete defoliation is rare; a regional study by Hódar et al. (2012) showed that less than half of the pine plots experienced strong defoliation, and less than 1% of the plots were completely defoliated. Aggregations of early instars may also carry negative consequences via induced responses by the host trees or increased cues and apparency to predators (Mumm & Hilker, 2006). It should be noted, however, that group size will decline as the feeding season progresses due to larval mortality, and by far the greatest needle biomass will be consumed by late instars, as in other lepidopterans (Scriber & Slansky Jr., 1981). With fewer individuals per colony, predation and other causes of mortality will also reduce the number of viable colonies. From a carrying capacity point of view, the optimum group size can therefore be quite large for early instars. Positive effects of increased group size include increased survival due to better protection against predators (Costa & Pierce, 1997, cf. Stamp, 1981 about higher rates of parasitism) and better thermoregulation (Battisti et al., 2005; Poitou et al., 2021; Ronnås et al., 2010). In order to maintain a functional group size, colonies may merge and the total number of colonies will decrease. Such merging can occur during the first instar in *T. pinivora* (Ronnås et al., 2010) but becomes more common during later instars in *T. pityocampa* (Uemura et al., 2021). When food is not limited, larger colonies may have positive effects on survival, as discussed in the previous paragraph. Thus, in general, the group size dynamics in *Thaumetopoea* spp. following aggregative oviposition suggests a positive feedback on population density.

In terms of outbreak dynamics, aggregative oviposition can be important when insect populations go from endemic to epidemic density. Spatiotemporal variability in patch quality is thought to initiate outbreaks (Floater & Zalucki, 2000; Hanski, 1987), as high-quality patches promote survival. Most likely, favourable conditions across patches (few predators, favourable weather, low host resistance) are sporadic and ephemeral. Insect species laying eggs in large masses, such as *Thaumetopoea* spp., can take advantage of such windows of opportunity to trigger local population growth. The phenomenon of aggregative oviposition would add not only numbers of larvae to the patch but also opportunities for larval groups to regroup, merge, and thus maintain the benefits of gregariousness. As populations shift from endemic to epidemic, aggregative oviposition could be critical in reducing larval mortality, triggering positive feedback and thus increasing the probability of an outbreak. Admittedly, our data refer to population density and aggregations at the tree level whereas the Hanski (1987) model of outbreak propensity refers to the situation at the patch level. Future experimental studies, controlling population density and oviposition events at larger spatial scales, will be needed to further corroborate our suggested link between aggregative oviposition and outbreak propensity.

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CONFLICT OF INTEREST

There are no disputes over the ownership of the data presented in this paper and all contributions have been attributed appropriately. The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data generated and analysed for the study are available from the University of Padova repository https://researchdata.cab.unipd.it/id/eprint/727

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1 Supporting information.

Relationships between egg mass density on the experimental trees and the defoliation index at the Spanish site of Mora de Rubielos.

Fecundity and splitting of the eggs of *Thaumetopoea pinivora* in egg masses.

Aggregation of the egg masses (Taylor's Power Law, Lloyd's mean crowding and Morisita's I).

Defoliation and tree selection.

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