

Estimating expansion of the range of oak processionary moth (*Thaumetopoea processionea*) in the UK from 2006 to 2019

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- Abstract**
- 1 The expansion of oak processionary moth (OPM) in South-East England continues despite ongoing efforts to control the pest since its introduction in 2006.
 - 2 Using locations of OPM larval nests, supplied by the Forestry Commission and recorded as part of ongoing surveillance and control measures from 2006 onwards, we show that the expansion of the range of OPM in South-East England up to 2019 was biphasic with a higher rate of expansion from 2015 onwards.
 - 3 The maximum rate of OPM range expansion in the United Kingdom from 2006 to 2014 was estimated as 1.66 km/year (95% CI = [1.22, 2.09]), whereas the 2015–2019 expansion rate was estimated as 6.17 km/year (95% CI = [5.49, 6.84]). This corresponds to an estimated species range distribution area of 7077 km² in 2019.
 - 4 To explain the faster expansion of OPM range from 2015 onwards, we discuss potential reasons that include: natural capability of species of both short- and long-distance dispersal; external factors such as environmental heterogeneity; a reduction of active control.

Keywords Biological invasions, expansion rate, invasive forest pest, long-distance dispersal, oak processionary moth, range expansion, short-distance dispersal, spatial spread, *Thaumetopoea processionea*.

Introduction

Invasive insect pests have huge annual economic costs globally (Bradshaw *et al.*, 2016). Among invasive insects, tree and forest pests can have a particularly large long-term economic cost (Hill *et al.*, 2019) and a drastic impact on ecosystem services (Aukema *et al.*, 2011; Boyd *et al.*, 2013). The successful eradication of invasive forest pests is possible only if there is an adequate combination of surveillance and control (Boyd *et al.*, 2013), where each of these components should be based on thorough scientific understanding of the mechanisms of invasion and dispersal (Wilson *et al.*, 2009).

In this paper, we analyse the spread of oak processionary moth (OPM), *Thaumetopoea processionea* (Linnaeus, 1758) (Lepidoptera: Notodontidae), in South-East England (Fig. 1a). Oak processionary moth is a destructive pest of oak trees that can cause severe defoliation (Stigter *et al.*, 1997). Also, OPM larvae develop poisonous hairs (setae), which contain

the urticating toxin thaumetopoein (Lamy *et al.*, 1986) causing allergic reactions and irritations in humans and animals (Maier *et al.*, 2003; Gottschling & Meyer, 2006; Meurisse *et al.*, 2012; Mindlin *et al.*, 2012).

Oak processionary moth is a univoltine (*i.e.* producing a single brood in a season) Lepidoptera that feeds on *Quercus* species (Wagenhoff & Veit, 2011). It is naturally dispersed by female moths that lay eggs in the branches of the upper part of the crown of the tree (Groenen & Meurisse, 2012). The eggs hatch in spring (Wagenhoff *et al.*, 2013), and the larvae then go through six instars. Feeding and movements during the first three stages may occur during the daytime, whereas older larvae are active at night. Larval groups merge at later instars to form aggregates of up to 1000 individuals. These groups may emigrate from defoliated trees in search of new food sources. If there are no suitable hosts nearby the larvae may starve (Wagenhoff & Veit, 2011). Communal silk nests are constructed around the fifth or sixth instar in which the larvae congregate during the day. The larvae pupate in the nest; adult moths emerge from mid-July to mid-September and only live for 3–5 days (Townsend, 2013).

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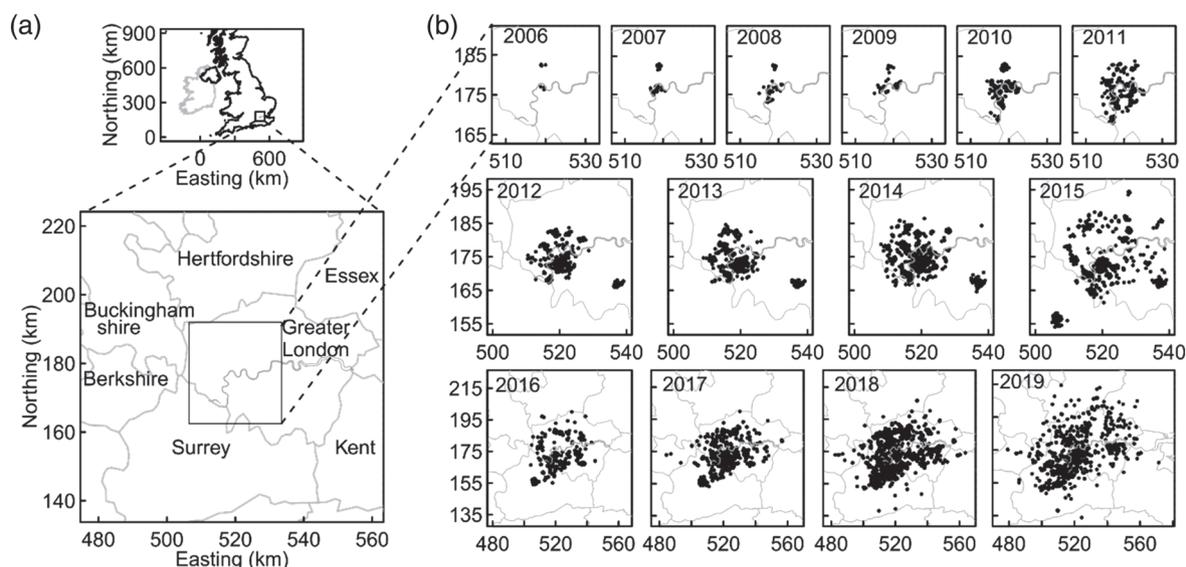


Figure 1 (a) Region in which oak processionary moth (OPM) has established in the United Kingdom (British National Grid). (b) Locations of new OPM larval nests from 2006 to 2019 recorded by the forestry commission as part of the OPM surveillance and control programme.

Dispersal of OPM between host trees can occur *via* one of three possible routes: short-distance movement of larvae, flight of females, and accidental human-mediated dispersal. The males are strong fliers and can disperse over distances of 50–100 km (Stigter *et al.*, 1997); however, the females usually lay their eggs near the site of emergence (Groenen & Meurisse, 2012).

Published estimates of the potential dispersal distance of females based on expert opinion vary between 5 and 20 km in continental Europe (Stigter *et al.*, 1997) and up to 7 km in the United Kingdom (Townsend, 2013). Analysis, reported by Groenen and Meurisse (2012), of the distribution and expansion of all recorded European populations of OPM indicated a mean (\pm SE) expansion rate of 4.29 (\pm 0.21) km/year from 1970 to 2009, and 7.50 (\pm 1.00) km/year from 1990 to 2009.

The first reports of breeding colonies (*i.e.* nests and larvae) of OPM in England were made in South-West London in June 2006 (Mindlin *et al.*, 2012; Tomlinson *et al.*, 2015). From 2006 to 2011, the government policy goal was to eradicate OPM from the United Kingdom (Conway *et al.*, 2016). However, by 2011 it became clear that OPM was established in the South-East of England surrounding the original distribution area, and eradication was no longer financially viable (Mindlin *et al.*, 2012; Tomlinson *et al.*, 2015). This led to changes in policy, which moved to containment of OPM within the known original outbreak area, and eradication of OPM elsewhere (Conway *et al.*, 2016). At the time of writing, the focus of control is to slow the rate of spread and minimize the impact of the pest in affected areas (Mindlin *et al.*, 2012; Tomlinson *et al.*, 2015; Conway *et al.*, 2016). However, despite ongoing attempts to contain OPM, the species' range has continued to expand (Straw *et al.*, 2019) (Fig. 1b). Moreover, in recent years, OPM appears to be spreading in the United Kingdom with increasing velocity (Straw *et al.*, 2019; Williams & Jonusas, 2019), which was not predicted by earlier studies (Cowley *et al.*, 2015; Conway *et al.*, 2016). Separate introductions of OPM that were identified and successfully eradicated in Leeds (in 2009), in Sheffield

(in 2010), and in Pangbourne (in 2010) (Townsend, 2013) are not considered in this study. Successful eradication of OPM in Pangbourne resulted from intensive management and strong control measures (Conway *et al.*, 2016). In Leeds and Sheffield, OPM populations also failed to establish (Sands, 2017) either due to the small initial populations (Townsend, 2013) or the relatively cool climate, which may be less suitable for OPM development, in Leeds and Sheffield compared with the South-East of England (Godefroid *et al.*, 2020).

Although eradication of OPM populations from the United Kingdom is no longer considered a feasible option, it is still important to slow the rate of spread and minimize the impact of the pest in affected areas. The current control policy consists of targeted control at the edge of the species' distribution area and locally managed control within known infested areas, which requires an understanding of both the current extent of the OPM population and the rate at which it is likely to expand. To facilitate the OPM management and control programme, in this paper we present a detailed analysis of annual surveillance data on OPM nest presence from which we infer the rate of OPM range expansion in the United Kingdom, and estimate the edge of the potentially infested area in subsequent years.

Methods

Distribution of larval nests of oak processionary moth

Annual reports of OPM larval nests have been recorded in London and the surrounding affected counties in the United Kingdom since 2006 (data collected by the Forestry Commission and other stakeholders as part of a UK Government OPM management and control programme, unpublished data used with permission, see Fig. 1b). The focus and extent of surveillance varied over time as the management strategy has developed from one of the initial attempts at eradication (2006–2011), through containment (no further spread) in 2011–2014, to the current strategy (from

the end of 2014 onwards) that aims to slow down the rate of expansion of the species range (Conway *et al.*, 2016). The data were collected by multiple contractors with the aim of directing management interventions (Cowley *et al.*, 2015; Conway *et al.*, 2016). Initially, surveillance was focused on supporting decisions for control actions and was not specifically designed to provide data for scientific research and analysis. Therefore, the initial survey effort was not evenly distributed or systematic and any negative findings were not recorded. The current management strategy (from the end of 2014) focuses surveillance on a 2 km buffer zone surrounding the known species range and all newly detected infested trees outside this area (Forestry Commission, 2015; Conway *et al.*, 2016). In later years (2018–2019), additional surveillance using radial transects extending outwards from the known edge of infestation was conducted with the aim of determining the true outer edge of the species range (see Supporting information, Fig. S1 for maps showing surveyed locations, Table S1). In addition, a portal was set up to enable members of the public to report sightings of OPM via the Forestry Commission Tree Alert System (forestry.gov.uk/treelert) to help identify OPM nests outside the recorded distribution area. Accordingly, we assume that recent data provide a sufficient estimate of the outer extent of OPM distribution, whereas the presence of OPM larval nests in the core zone is under-reported in the database.

Surveillance involved visual inspection of host trees for the presence of OPM larval nests that were categorized as ‘new’ or ‘old’ based on expert opinion of contractors undertaking surveys. ‘New’ nests were either occupied at the time of observation or presumed to have been formed in the most recent OPM breeding season. ‘Old’ nests were presumed to be at least 1 year old, by which time nests were showing signs of decay, making detection more difficult and less reliable. Given the uncertainty over the age of ‘old’ nests, making it challenging to assign a year to a particular nest, and the inconsistency in recording the presence of ‘old’ nests with records only available from 2013 onwards, we confined our analysis to ‘new’ nests only (see Supporting information, Fig. S2 for maps showing locations of ‘old’ nests). ‘New’ nests were recorded at different times throughout the year. To specify the age of the nest, we assumed that ‘new’ nests recorded between emergence of larvae from the eggs in year N until emergence of larvae in year $N + 1$ represented nests with live larvae during the spring–summer of year N . Such nests are referred to as ‘nests in year N ’, where N refers to 2006–2019. Emergence of larvae in the South East of England normally occurs between mid-April and mid-May.

In total, the data consist of 40 048 unique locations in which OPM nests were recorded as present in 2006–2019, and 70 091 unique locations recorded as having no visible presence of OPM in 2013–2019 (surveyed pest-free locations were not recorded before 2013). Detailed information on search efforts (maps and tables characterizing surveyed locations in each year) are provided in the Supporting information Fig. S1 and Table S1.

Spatially distinct primary populations of OPM

In line with previous studies of OPM in the United Kingdom (Conway *et al.*, 2016), we assume the species’ distribution

observed between 2006 and 2015 arose from five spatially distinct primary populations. Two distinct populations, referred to in this paper as the northern and southern populations, identified in West London approximately 6 km apart in 2006 (Fig. 2a) were traced to the import and planting of infested saplings (Mindlin *et al.*, 2012). The northern and southern populations merged in 2010 but remained separate from other populations until 2015. The third population, referred to in this paper as the Croydon population (Fig. 1b: 2012, Fig. 3: 2015), was first recorded in 2012 with a large number of larvae observed in the grounds of Bethlem hospital in South-East London, which is sited at the border between the London Boroughs of Croydon and Bromley (Blatchley, 2013). Attempts to trace the source of the Croydon population were not successful; however, the absence of nest sites connecting this outbreak with the two original populations led to the conclusion that the cluster was formed either by independent introduction or by long-distance dispersal from populations in the original distribution area. The Croydon population remained separate until 2015 when it merged with the populations in West London. We used the available three time points in 2012–2014 to estimate the rate of spread of the Croydon population. A fourth distinct OPM population was identified in 2014 on the Olympic Park site in London (Conway *et al.*, 2016) (Fig. 1b: 2014, Fig. 3: 2015); however, this population merged with the northern and southern populations in 2016 and the two time points are not adequate to estimate the growth rate of the population using linear regression. In 2015, a fifth, distinct population of OPM was recorded in Guildford, south west of the original distribution area (Fig. 1b: 2015, Fig. 3: 2015).

In addition, from 2015 onwards, a number of potentially distinct populations were identified closer to the edges of the established populations through a combination of active and passive surveillance. The absence of recorded field evidence tracing the source of apparent new populations and the incomplete sampling of host trees between the known edge of species’ distribution area and newly identified nests means that there is no clear statistical method by which we can designate a non-contiguous location with OPM nests as a distinct satellite population. Therefore, we assume that all additional observations of OPM larval nests in 2015–2019 can be considered to be the result of expansion from the five original populations between 2006 and 2015 identified by Conway *et al.* (2016).

Maximum distance method

Following the analysis by Preuss *et al.* (2014), who compared the sensitivity of the predicted rate of range expansion to incomplete surveillance data for seven proposed models, we selected the maximum distance method as the most appropriate method for the OPM data since the data collection focused on the species range margins (especially in later years) (see Discussion). For each distinct OPM population (see, for example, populations in Fig. 2a–d), the centre of the population is calculated as the centre of the minimal circle that encompasses all initially recorded locations of nests. This minimal circle defines the initial boundary of the population range. New OPM nests are assigned to the population whose range boundary they are closest to. The centre of the range of each distinct population does not change

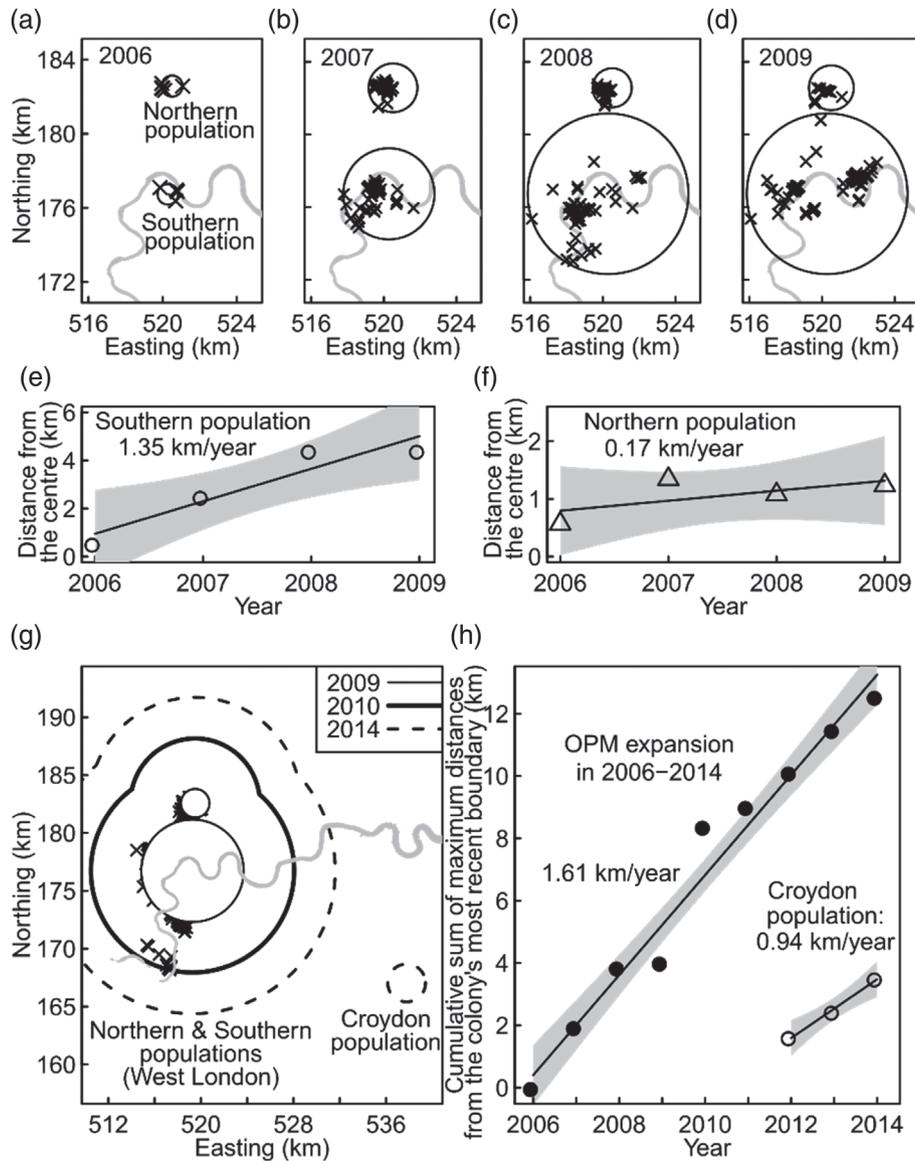


Figure 2 Expansion of OPM populations in the United Kingdom in 2006–2014 originating from two known primary populations. To distinguish the two primary populations, we refer to these in the text as the ‘Southern’ and ‘Northern’ populations based on relative location. (a–d) spread of OPM from the two primary populations from 2006 to 2009: Circles around each population are the modelled boundaries of the populations; crosses denote known locations of larval nests. Linear regression and 90% confidence interval are shown for the spread of: (e) the southern population, and (f) the northern population. (g) The modelled boundary of the initially distinct populations is shown for 2009, 2010, and 2014. Crosses show the location of larval nests recorded in 2010 that were located between boundaries in 2009 and 2010. (h) Linear regression and 90% confidence interval for the global estimate of the expansion rate for 2006–2014 (filled circles; $r^2 = 0.97$; $P < 0.001$; 90% CI = [1.40, 1.81]); and the same for the expansion of the Croydon population (open circles; $r^2 = 0.99$; $P = 0.048$; 90% CI = [0.49, 1.39]).

in successive years. Each year, for each distinct population, the maximum distance between the centre of the population’s range and all nests assigned to that population is calculated (Fig. 2a–d) and used, *via* linear regression, to estimate the expansion rate (Fig. 2e–f). The maximum distance is used to define the current boundary of the population’s range by updating the radius of the boundary. All analyses were carried out using the statistical software R (R Core Team, 2021).

In using the maximum distance method, we assume that the rate of dispersal is the same in all directions, as might be expected

for natural, diffusive dispersal if there are no limits due to host availability. The advantage and disadvantage of ignoring local asymmetries are addressed in the discussion section.

A population is considered as a distinct population only while its boundary does not intersect the boundaries of other populations, otherwise those populations are considered to have merged. When two or more populations merge, the maximum distance method is adjusted as follows: the expansion of the merged population is considered relative to the boundary of the range of the merged populations (rather than introducing a

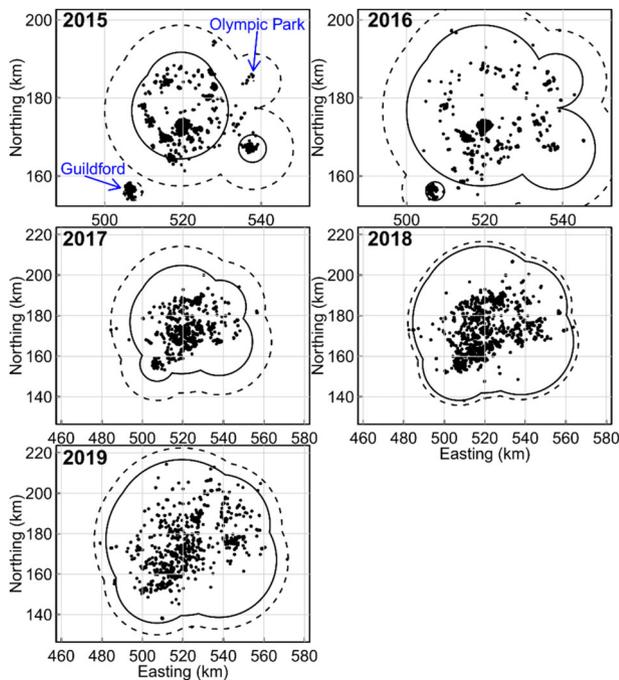


Figure 3 Estimation of the expansion rate of OPM larval nests from 2015 to 2019 using the maximum distance method, and assuming that the Guildford population is the only new distinct population to occur after 2014. Black dots represent locations of OPM larval nests recorded as 'new' in the forestry commission dataset in each year from 2015–2019; the estimated boundaries of expanding known populations in the specified year (*i.e.* the same year as nests) are shown by dashed lines, and in the previous year – by thin solid line. Note for presentation purposes 2015, 2016 data are plotted on a different scale to the 2017–2019 data.

single centre of the merged population) and is calculated in the following way. Let N be the year corresponding to when the populations were distinct and separate for the last time (*cf.* Fig. 2d,g, $N = 2009$ – thin line). In year $N + 1$ (*cf.* crosses Fig. 2g), we calculate the perpendicular distance from the year N boundaries to all newly identified nests that lie outside the year N boundaries. The maximum of these distances is used to define the new 'merged' population boundary: the boundary of the merged population in year $N + 1$ is created by expanding outwards from the original boundaries by this distance (Fig. 2g: thick line denotes the boundary of the merged population in year $N + 1$). When the merged population continues to expand, its boundary is updated according to the same maximum distance method, for example see Fig. 2g where the dashed line around the merged northern and southern populations shows the population's boundary in 2014.

Estimating the rate of spread of OPM from 2006 to 2019

Using the maximum distance method, in our global estimate of the expansion rate for 2006–2014, we calculated the maximum dispersal distance for all populations each year and then chose the largest out of these to represent the dispersal distance for that year when calculating the global expansion rate (Fig. 2h, filled circles). A linear regression analysis was applied to these data

points to obtain the average annual rate of spread of the OPM population in West London from 2006 to 2014.

In 2015, the already merged northern and southern populations merged with the Croydon population, and a new OPM population in Guildford was detected. We assume that no new satellite populations are introduced after 2015 and that all newly observed OPM larval nests are the result of continued expansion of previously identified populations. Specifically, the northern and southern populations detected in 2006; the Croydon population detected in 2012 in South-East London; the population detected in 2014 at the Olympic Park; and the population detected in 2015 in Guildford. The boundary of the species' range in 2014 is given by the boundaries of merged northern and southern populations together with the Croydon population and OPM populations at the Olympic Park. Starting from the boundaries of the range of OPM in 2014, and using data on new nests in each successive year, we estimated the boundary of the range of the merged OPM populations from 2015 to 2019 (see Fig. 3) using the same method as described above. For clarity, in Fig. 3 we show only new nests observed in each year for 2015–2019 together with the calculated boundary of OPM populations in that year and in the previous year. To obtain the expansion of the range of OPM in the United Kingdom from 2006 to 2019, the distances of annual expansion of the boundary of the species' range from 2015 to 2019 were added cumulatively to distances that characterize OPM expansion from 2006 to 2014.

To estimate the species' range expansion rate, we compared linear and segmented regression (Mugge, 2003, 2008, 2016, 2017) where the latter assumed a single breakpoint. The models were compared using both residual standard error (RSE) and the Akaike information criterion (AIC) (Akaike, 1974). The segmented regression analysis was selected due to lower values of RSE and AIC. See Supporting information Fig. S3 for details of this comparison.

Estimating the potentially infested area (one-year prediction)

To facilitate the management and control programmes, a prediction of subsequent year's species range area is often required. We predict species range area using the maximum distance method presented above, where the boundary of the species' range was obtained as a part of estimation of the expansion rate (see boundaries of populations shown in Fig. 3). To test how well this method performs in predicting the expansion of OPM range, we removed data for 2019, re-ran the segmented regression, and estimated the 95% prediction interval (PI) for 2019. This estimate was compared with the observed data for 2019.

According to the underlying assumption of diffusive spread (*i.e.* the expansion is symmetric in all directions independently of other factors such as, for example, local host density or control efforts), the estimation based on the maximum distance method described above is likely to overestimate the spread of OPM in certain areas. Hence, the estimated range of OPM is likely to be an overestimate of the actual range. We also introduce an alternative approach in the Supporting information Note S1 that provides an estimate of the range of OPM within the 'core population' by using statistical methods to distinguish the core from isolated satellite populations. The implications

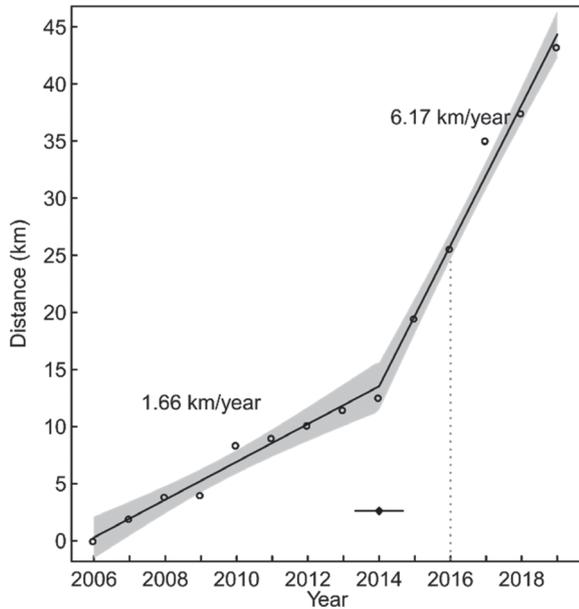


Figure 4 Rates of OPM range expansion in 2006–2019 (segmented regression, 95% CI). A single black dot and the horizontal line in 2014 show the identified breakpoint and boundaries of its 95% confidence interval. The vertical dotted line marks the 2016 year, which is the first year when the impact from the 2015 shift in management policy could be observed in data.

for surveillance and control scenarios using estimates for range expansion based upon the full (maximum distance) and core populations are briefly considered in the discussion section.

Results

Estimated expansion rate of OPM

The segmented regression analysis of surveillance data for OPM nests (Fig. 1) revealed an abrupt increase in the expansion rate of the range of OPM from 2015 onwards (Fig. 4). The breakpoint was estimated as 2014, 95% CI = [2013.33, 2014.67]. The expansion rate of the species' range in 2006–2014 was estimated as 1.66 km/year (Fig. 4; $r^2 = 0.99$; $P < 0.001$; 95% CI = [1.22, 2.09]), and the expansion rate in 2015–2019 was estimated as 6.17 km/year (Fig. 4; $r^2 = 0.99$; $P < 0.001$; 95% CI = [5.49, 6.84]).

Estimated potentially infested area in 2019 (one-year prediction)

Assuming diffusive spread and estimating the range according to the maximum distance method using all new nests in 2015 onwards, except for the new population in Guildford in 2015 (Fig. 3), we removed data for 2019 and estimated the expansion rate for 2019 by linear regression of the 2015–2018 data. The predicted extent of expansion in 2019 (7.95 km, 95% PI = [3.51, 12.38]) agreed with the observed expansion (5.79 km) (Fig. 5); the area of the predicted potentially infested area in 2019 was estimated as 7747 km² (95% PI = [6403, 9214]) which agreed

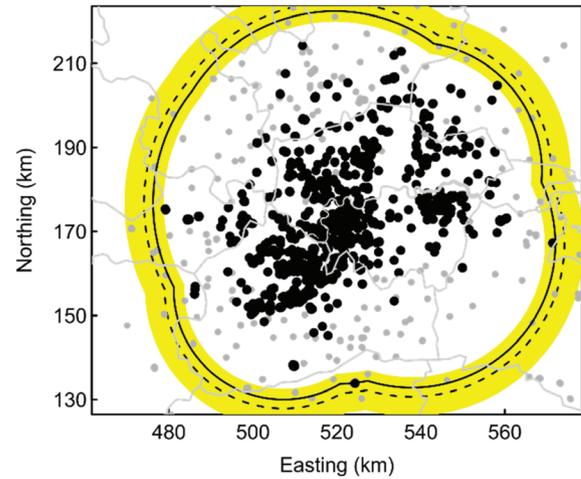


Figure 5 Comparison of the predicted boundary of the potentially infested area using only 2006–2018 data with the estimated boundary using all data. Locations of OPM nests in 2019 are shown as black dots; pest-free locations in 2019 are shown as grey dots. The boundary estimated from the data (solid line) and predicted from the pre-2019 data (mean value is shown by dashed line, 95% PI is shown by the yellow area) are shown, see the main text for numerical values. In total, the data for 2019 consists of 7696 locations with OPM nests (black dots), and 4590 pest-free locations (grey dots).

with the area of 7077 km² inferred from the observed data for 2019. Considering the core distribution area separately from potential isolated satellite populations, the core distribution area for 2019 was predicted as 2948 km² (95% PI = [2815, 3080]) (see Fig. S5 in Supporting information Note S1).

Discussion

Eradication of OPM from the United Kingdom is no longer considered a feasible option. The current strategy aims to slow the rate of spread of the pest *via* targeted control at the edge of the infested zone, and locally managed control to mitigate the impact on tree health and human activity in heavily infested areas. Surveillance and control for OPM are costly, and decisions on where to target resources require an understanding of both the current extent of the pest and the rate at which it is likely to spread. Having an up-to-date estimation of the expansion rate helps to optimize surveillance and control strategies.

We have analysed data for reports of OPM larval nest presence from the start of the outbreak in South-East England in 2006 up to 2019. The segmented regression analysis suggested that the expansion of OPM range can be separated into two phases, with a faster expansion rate observed from 2015 onwards.

Here, we review the assumptions underpinning the results, and discuss potential reasons for the faster expansion of OPM range in recent years.

Limitations

The analysis presented in this paper assumes that the recorded data capture the true extent of the species' range each year.

However, surveillance and control practices evolved over the course of the outbreak with data recording in the initial stages of the outbreak driven by practical aims of identification and eradication rather than as part of a designed experiment to track expansion rates. Negative finds started to be recorded only in 2013. This reduced the uncertainty in whether absence of positive recordings can be taken to mean an absence of nests. The availability of negative as well as positive results led to a significant improvement in our confidence in the interpretation of the data. Active surveillance for OPM is costly, limiting the number of locations that can be targeted as part of a designed surveillance strategy. As the size of the species' range has grown, the distance between sampling points has by necessity increased, leading to coarser granularity in the data. In addition, as management of OPM has been taken over by local public and private landowners, local records of OPM populations do not necessarily feed into the Forestry Commission database. A particular issue with managing tree pests and diseases is the multiple stakeholder involvement, which was exacerbated for OPM by the urban environment where access to private land can limit surveillance and delay control (Tomlinson *et al.*, 2015).

We have assumed that the separate OPM populations in 2006–2015 as reported in Conway *et al.* (2016) represent distinct OPM populations whose edges can be estimated accurately from the data. This assumption is supported by recordings in 2013–2015 that show sufficiently large nest-free areas between the populations (Figs 1 and S1), together with a relatively sharp decrease of the number of OPM larval nests as a function of distance from the centre of each population (not shown). The origins of the distinct populations observed after 2006 are unclear with no evidence of infested nursery stock imported from continental Europe found to explain the large outbreaks in Croydon and Guildford (Conway *et al.*, 2016). This suggests some form of long-distance dispersal from within the United Kingdom such as human-mediated spread of infested material such as planting of infested saplings taken from the outbreak area or disposal of infested waste from tree culling (Wilson *et al.*, 2009). An additional possibility is dispersal of the female moths on wind currents associated with extreme weather events (Stigter *et al.*, 1997).

The estimated rate of expansion is affected by both the method used to capture the observed range expansion and the intensity and distribution of sampling (Preuss *et al.*, 2014). Alternative methods for describing range expansion include: area-based measures using grid occupancy (*e.g.* used by Conway *et al.*, 2016, to study the OPM outbreak in the United Kingdom); distance measures characterizing the central tendency (mean, or median as in Annex 12 in Conway *et al.*, 2016); and, distance measures characterizing range margin statistics (such as 95th gamma quantile, marginal mean, maximum). Incomplete sampling affects the reliability of all methods of estimation. Preuss *et al.* (2014) found that the method that best estimates the true rate of spread varies according to the characteristics of the sampling that generated the data. The current management strategy for OPM focuses surveillance on a buffer zone surrounding the original distribution area (Conway *et al.*, 2016). With the absence of evidence to the contrary, we assumed that the data provide a sufficient estimate of the outer extent of the range of OPM, whereas the presence of larval nests in the core zone is probably

under-reported. Preuss *et al.* (2014) showed that the maximum distance method is the most appropriate method for the data with such properties: the method is robust with respect to incomplete sampling, and it does not require intensive sampling within the core zone. Consequently, we applied the maximum distance method and modified it for the case of merging populations. Such modification allowed the measurements of maximum distance and consequent estimation of the expansion rate to be carried out every year even when new distinct populations appeared and when merging populations had different ages. When comparing rates of OPM range expansion estimated using different methods, one should note that according to Preuss *et al.* (2014) 'distance-based methods calculated from the central tendency (mean and median) and the area-based method of grid occupancy' provide estimates that are often 'roughly half those calculated from the range margin'. However, 'this need not always be the case because long-distance dispersers at the range margin are likely to comprise a disproportionately small proportion of the population (and thus have a relatively small influence on the mean and median), despite having potentially large effects on range margin statistics' (Preuss *et al.*, 2014).

By using the maximum distance method, we characterize the expansion of a population by a single rate of expansion, ignoring potential local asymmetry of spread in different directions that may be caused by a range of factors such as local impacts from applied control measures; heterogeneities in the distribution of hosts in the landscape; or, directed long-distance dispersal caused, for example, by environmental factors such as strong, persistent winds. Effectively, the maximum distance method estimates the maximum among all rates of spread in different directions. Hence, this can result in overestimation of the actual rate of range expansion in some directions (where the actual rate might be lower due to, for example, the absence of hosts or due to sufficiently effective surveillance and control measures); whereas the 'true' maximum rate will be underestimated if the furthest nest from the centre of the population's range is not detected (Preuss *et al.*, 2014).

The advantage of using a single maximum rate in all directions is that the method takes into account that OPM's spread could be undetected in some directions due to incomplete data on host locations (Cowley *et al.*, 2015) and under-sampling. Such undetected spread could not be reduced by improving control measures alone – even an application of 100% effective control measures to all detected infested trees would not stop OPM from spreading from sites that were not detected. Hence, the estimation of the species' range expansion should account for possible undetected spread, and the maximum distance method satisfies this requirement. However, when applying the maximum distance method to estimate the potentially infested area, the resulting estimated area can be overestimated – *i.e.* it can include large areas where no OPM nests were reported during surveillance. For a more nuanced overview of the likely range of OPM, we also derived an estimate for the OPM range that represents the expansion of the core population (details of the method are given in Supporting information Note S1). The additional analysis allowed us to distinguish the expansion of the core OPM population from long-distance isolated satellite populations that may have arisen by trade, or other introductions from elsewhere. The derivation of a range expansion for the

core population provides policy makers and regulators with a smaller target area in which to deploy limited resources for control, albeit in the knowledge that some more distant satellite populations will be missed. Although it is beyond the scope of the present paper, it would be possible to analyse the comparative cost effectiveness for surveillance and control scenarios under fixed budgets for the full (core and satellites) and core range of expansion of OPM.

Biphasic expansion

The first phase of expansion of OPM in the United Kingdom between 2006 and 2014 (mean 1.66 km/year, standard error = 0.20) was much slower than reported rates of expansion in other countries. Groenen and Meurisse (2012) reported a mean (\pm SE) expansion rate of 4.29 (\pm 0.21) km/year from 1970 to 2009, and 7.50 (\pm 1.00) km/year from 1990 to 2009 (Groenen & Meurisse, 2012). However, in the second phase of the OPM expansion, the rate of 6.17 (\pm 0.30) km/year is closer to reported expansion rates of OPM range in other countries (Groenen & Meurisse, 2012). The rates of spread of OPM estimated in this paper are also consistent with those observed for the closely related pine processionary moth *Thaumetopoea pityocampa* (Denis & Schiffermüller, 1775) (*Lepidoptera: Notodontidae*) ranging from a lower estimate of the early spread rate of 1.36 km/year (Godefroid *et al.*, 2016) up to a rate of 5.6 km/year (Battisti *et al.*, 2005) as observed in natural conditions, with the maximum flying distance of females on the flight mill observed as 10.5 km (Robinet *et al.*, 2012).

As in the case of some other invasive insect and bird species (Shigesada & Kawasaki, 1997), one could consider two main potential explanations for the apparent biphasic expansion of OPM in the United Kingdom:

- 1 'Stratified diffusion': OPM may be capable of both short- and long-distance dispersal. The first phase of the expansion may be dominated by short-distance dispersal with minimal intra-specific competition, whereas the faster rate of expansion in the second phase is driven by long-distance dispersing individuals that create new satellite populations. The expansion in the second phase is linear with satellite populations created not very far from the parental population that quickly merge with it (Shigesada & Kawasaki, 1997).
- 2 *External factors*: OPM may disperse only *via* short-distance dispersal, but the rate of expansion is influenced by environmental heterogeneity and a reduction of active control at the boundaries of the species' range. Annual variation in climatic conditions may also affect emergence and reproduction of OPM.

The detection of potential satellite populations provides, in principle, some support for the case of 'stratified diffusion' in 2015–2019. Also, in the case of 'stratified diffusion', the creation of such satellite populations would be intensified due to the potentially weaker control in the core zone and therefore higher population density and higher number of moths capable of dispersing at large distances. However, the ambiguity in the detection of such satellite populations remains – many apparent satellites may be due to lack of surveillance or reporting

in the surrounding areas. There is strong evidence that environmental heterogeneity affects the rate of spread of OPM with the flight path of both males and females, driven by attraction to host plant volatiles (Williams & Jonusas, 2019) and an apparent preference for open woodland (Sands, 2017). The role of habitat connectivity on the spread of OPM in the United Kingdom was studied by Cowley *et al.* (2015), who used 2006–2012 data on OPM invasion in the United Kingdom and applied a patch-based model based on electric network theory. Cowley *et al.* (2015) predicted the expansion of OPM after 2012 towards the North-East and South-West from initial populations, which is in line with the observations in consequent years – see panels for 2017–2019 in Fig. 1. Stigter *et al.* (1997) observed a dependence of dispersal distance of OPM on the quality and structure of the habitat crossed by moths. Also, quantitative analysis by Saura *et al.* (2014) investigated range expansion of invasive species using a generalized network model of habitat connectivity. Their work suggests that a better-connected habitat network would result in faster spread of invasive species such as OPM.

A reduction of active control at the boundaries of the range of OPM, which inevitably would occur given the limited resources and the growth of the range, may also have contributed towards the faster rate of spread in 2015–2019. Since the end of 2014, the control strategy began to focus on slowing the rate of spread instead of full containment of infestation within the known outbreak area (Conway *et al.*, 2016). Such a shift would affect the dispersal of moths during the flight period of 2015 and later years, and therefore this would change the number of live nests during summer of 2016 and later. However, if we assume that there would have been a constant rate of expansion in the absence of a strategy change, then the segmented regression analysis suggests that the change to the overall control strategy from 2015 onwards (see Fig. 4: vertical dotted line) did not reduce the rate of expansion of the range margin. In this work, we did not study whether the changes in control strategy had a significant impact on OPM abundance in the buffer zone and closer to the core distribution area. One possible explanation for the apparent lack of success of the control strategy in slowing the spread of OPM from 2016 onwards is the decision to apply a 2 km buffer zone around new infested locations outside the known outbreak area (Forestry Commission, 2015), which is not sufficient to intercept an infestation that is spreading by approximately 6 km per year. However, active surveillance for OPM is costly, limiting the number of locations that can be visited each year meaning that as the range increases the spatial density of sampling points decreases and cases on the edge of the species range are likely to be missed.

Considering that the dispersal can be influenced by multiple various factors such as characteristics of invading organisms, host landscape and environmental factors, and the impact of control measures (Hastings *et al.*, 2005; Cowley *et al.*, 2015; Conway *et al.*, 2016; Parnell *et al.*, 2017; Prospero & Cleary, 2017), further research is needed to identify reasons for the apparent increased rate of OPM range expansion in the United Kingdom in 2015–2019. Understanding these reasons will enable development of reliable range expansion models needed for optimization of surveillance and control strategies.

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Data availability statement

The data that support the findings of this study are available from Forestry Commission, UK.

Supporting information

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

Appendix S1: Supporting information

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