Reintroducing a nationally extinct predator, the forest caterpillar hunter (*Calosoma sycophanta*), for biocontrol of the invasive oak processionary (*Thaumetopoea processionea*) in Britain: considerations, benefits and risks

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No data were used or generated in this study.

Conflict of interest

The authors declare no conflict of interest.

Ethics approval statement

This project and subsequent publication was approved by Forest Researches ethics committee.

Abstract

1. Controlling invasive species remains one of the greatest challenges of the 21st century. Sustainably managing invasive pests like the oak processionary moth (*Thaumetopoea processionea*; OPM), which lacks natural enemies in Britain, may require the introduction, or reintroduction, of suitable biocontrol agents.

2. The forest caterpillar hunter (*Calosoma sycophanta*; FCH) is thought to have been historically native to Britain but is now possibly nationally extinct. A voracious predator of caterpillars, FCH could be an effective biocontrol agent of OPM, but we must first understand its ecology and natural history, which is scarcely recorded in patchy literature from the past century.

3. Here, we conducted a systematic review to inform a wider synthesis on the status of FCH in Britain and Europe, its known trophic interactions and habitat preferences, and the influence of climate on its current and future distributions. This informed discussion of the risks and benefits of reintroducing FCH to Britain.

4. Based on the records available, we stipulate that translocation of FCH populations to Britain should be based on the cautious assumption that it is a reintroduction following national extinction, likely due to poor prey availability. The biocontrol of various pest species by FCH, including OPM, is likely, and the suitability of Britain's climate may increase.

5. Reintroduction of FCH to Britain could aid management of OPM whilst also returning an important invertebrate predator to British forests. Further evidence of the wider direct and indirect interactions of extant FCH populations elsewhere, and deeper investigation into FCH's habitat requirements, are, however, required to safeguard the success and sustainability of prospective reintroduction.

Keywords: de-extinction, distribution, habitat preference, natural history records, prey availability, systematic review

Introduction

Invasive species are among the greatest threats to biodiversity in the 21st century (Simberloff *et al.*, 2013; Tercel *et al.*, 2023), but many species pose additional threats to public health (Marzano *et al.*, 2020; Backe *et al.*, 2021), increasing the perceived urgency of intervention. To control invasive insect species, large volumes of pesticides have traditionally been applied (Pimentel, 2014); however, the unsustainable costs, non-target effects and decreasing efficacy of pesticides have shifted focus toward sustainable integrated pest management strategies that incorporate nature-based solutions such as biocontrol (Barzman *et al.*, 2015). Classical biocontrol, in which non-native enemies of pests or invasives are released, can be highly effective (Stiling and Cornelissen, 2005), but can also significantly impact native biodiversity (Driesche and Hoddle, 2016; Heimpel *et al.*, 2024). Conservation biocontrol, whereby naturally occurring enemies of target species are maintained and promoted, offers a sustainable alternative (Shields *et al.*, 2019), but requires those natural enemies to co-occur with the target organism already. Local extinction of some natural enemies, increasingly likely in the Anthropocene, could destabilise the resilience of our ecosystems to invasive pests (Thomson, Macfadyen and Hoffmann, 2010; Thurman, Crowder and Northfield, 2017) and, in some cases, may have already occurred. Reintroducing biocontrol agents in such cases may be crucial for ensuring effective control of invasive pests but requires cautious assessment of the benefits and risks in much the same way as classical biocontrol given the potential for non-target impacts (Heimpel *et al.*, 2024).

The forest caterpillar hunter (FCH), *Calosoma sycophanta* (Linnaeus, 1758) is a large ground beetle (Coleoptera: Carabidae) found across much of the Western Palearctic, including most of Europe, areas of north-west Africa, and, western and central Asia (Stolbov *et al.*, 2018; Görn, 2019). A voracious polyphagous predator, FCH is thought to preferentially consume caterpillars of several common pest species such as spongy moth, *Lymantria dispar* (Linnaeus, 1758), pine processionary moth (PPM), *Thaumetopoea pityocampa* (Denis & Schiffermüller, 1775), and oak processionary moth (OPM), *Thaumetopoea processionea* (Linnaeus, 1758). Of these, OPM is considered a particularly notable pest

across much of Europe given its negative impacts to oak trees (Godefroid *et al.*, 2020) and, through large volumes of urticating hairs produced by larvae, public health through pseudo-allergenic reactions (Townsend, 2007; Marzano *et al.*, 2020). Current nature-based solutions to OPM populations in Britain are limited despite management focus shifting toward biocontrol (Miller *et al.*, 2025). Current biocontrol prospects for OPM in Britain are restricted to two larval parasitoids, *Carcelia iliaca* and *Pales processioneae,* which are both considered non-native but have proliferated since their respective first observations (Miller *et al.*, submitted). Despite the relative successes of each parasitoid locally, OPM has continued to spread, increasing demand for additional means for biocontrol and management. It is thought that FCH was once native to Britain and could therefore be considered for reintroduction to assist with biocontrol of OPM.

With both adults and larvae capable of consuming 4-11 larvae per day, FCH has strong potential as a biocontrol agent of various pests (Weseloh, 1988). Due to the high quantities of prey consumed, FCH has a history of being released as a biocontrol agent to successfully control populations of *Lymantria dispar* in North America through classical biocontrol, and *Thaumetopoea pityocampa* in Turkey through augmentative biocontrol (Weseloh, 1990; Kanat and Mol, 2008). The combination of previous successes, high frequency prey consumption and being widely distributed has brought attention to FCH as a possible biocontrol option for OPM in northern Europe, including in Britain. The release of FCH to augment native populations, which have previously suffered crashes in the mid-1900s, has been proposed as a nature-based solution for managing OPM in Belgium and the Netherlands (Crevecoeur, Willems and Jamers, 2021). This would replicate the model of release in Turkey, which has a consistent impact on annual PPM numbers (Kanat and Mol, 2008) and has led to recent success in breeding FCH for a prospective breed-and-release scheme (Crevecoeur, 2024). There is hypothetically scope for a similar approach in Britain since OPM has been rapidly spreading as an invasive pest in Britain since 2006. The evidence underpinning FCH's historic native status and potential for biocontrol in Britain is, however, weak and fragmented, and the feasibility of reintroduction is poorly understood.

Given the significant potential of FCH for the biocontrol of OPM in Britain, a review is necessary to update our understanding of FCH's status in Britain and the factors underpinning its potential as a sustainable solution to OPM's ecological invasion. Here, using a systematic review and synthesis based on adjacent examples and literature, we provide a summary and discussion of: (i) the historic and current status of FCH in Britain; (ii) the current status of FCH across Europe; (iii) the known trophic interactions of FCH; (iv) the known habitat preferences of FCH; (v) climate as a potential driver of FCH distributions; and (vi) the balance of risks and benefits involved in prospectively reintroducing FCH to Britain (Figure 1). By providing this synthesis, we hope to stimulate further investigation of the potential for reintroducing FCH to enhance the evidence available and ensure that any reintroduction is robust, sustainable and effective.

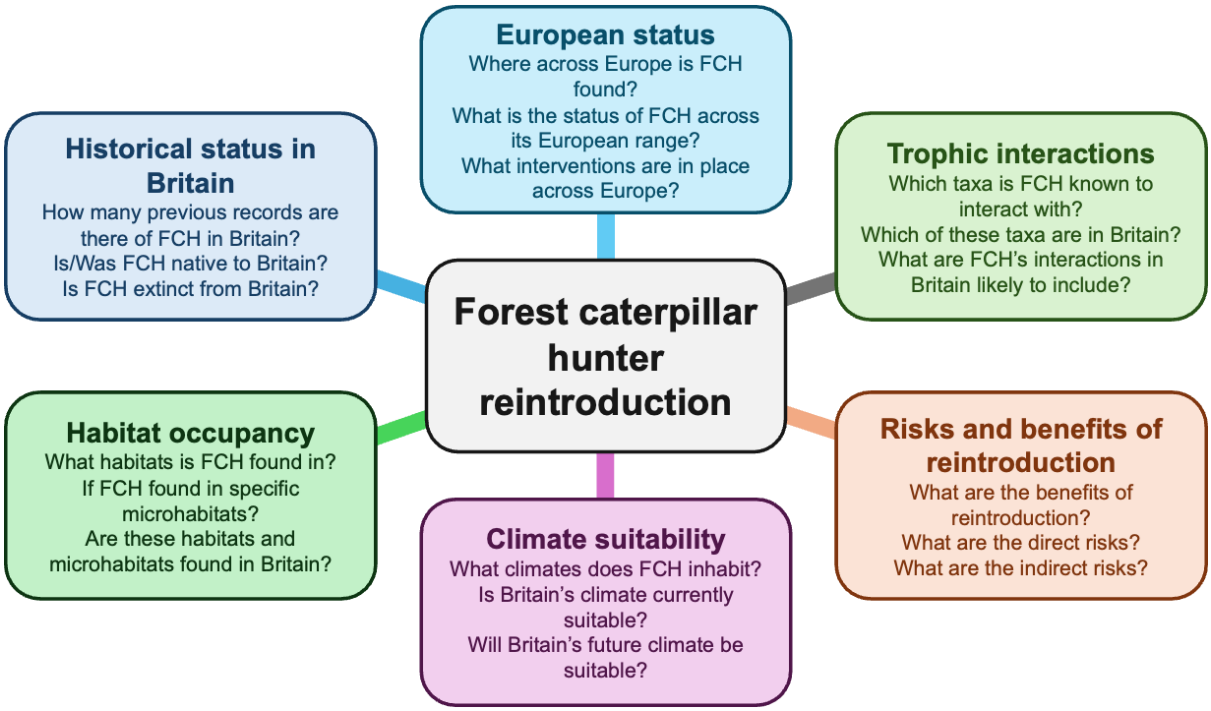

Figure 1: A summary of the key topics and questions addressed by this review. The evidence across each of these topics is used to discuss the prospective reintroduction of FCH to Britain for the biocontrol of OPM.

Systematic review

In accordance with PRISMA guidelines, pre-defined search terms were queried against recognised literature databases to identify the available relevant literature concerning FCH, its known distribution, historical distribution records with a focus on records from Britain, causes of population decline, habitat preferences, and dietary preferences. The search string used was: (Calosoma OR "Calosoma sycophanta") AND (Diet OR prey OR habitat OR extinction OR "population decline" OR climate OR distribution). This was queried against Scopus on 21/05/2024, returning 77 articles, of which 30 were removed when screening titles and abstracts for article relevance against the aforementioned topics. From the remaining articles, 10 were removed when screening whole papers, and from the remaining articles 37 were used to inform this review.

Historical British *Calosoma sycophanta* records

Records of FCH in the British Isles are sparse but continuous. The Natural History Museum London holds six British specimens, including the first dated record of FCH in Britain. Three of these specimens are part of the Stephens Collection which is dated 1790-1850, although the FCH specimens are not themselves dated and the collection was posthumously expanded by Thomas Marsham (Max Barclay, pers. Comm.; Figure 2). The first dated individual was collected in 1862 from St Leonards, Sussex. The second specimen was collected from Carlisle in 1913. The final dated specimen comprises four elytra (thus representing at least two individuals) extracted from an undescribed animal pellet from Thetford Forest, Suffolk in 1997 (Miquel, 2005); this was speculated to be a breeding population but subsequent surveys failed to find any individuals. The National Biodiversity Network Atlas also includes nine records dating back to 1903, although three records from 1992 are identical and may be duplicated entries (NBN Trust, 2025; Table 1). Overall, these records indicate that, whilst uncommon, FCH has consistently been recorded in the British Isles for a significant period, but has not been recorded in recent years despite concerted efforts. This strongly indicates that FCH is nationally extinct and, even

if small populations do persist, supplementary releases may be necessary to generate sufficient population sizes for effective biocontrol of the OPM and other invasives or pests.

Figure 2: Photos of the three FCH specimens held at the Natural History Museum London. Upper Left: Collected in St, Leonards, Sussex, 1862. Upper Right: Collected in Carlisle, 1913. Lower Left: Collected in Thetford Forest, Suffolk, 1997.

Table 1: List of FCH specimens collected in the UK and stored at the Natural History Museum London.

Date of record	**Status of individual**	**Location**
1903	Live adult	Battle, Sussex
1905	Not stated	Hastings, Sussex
1951	Not stated	Jersey
1963	Not stated	Dungeness

1986	Not stated	St Ives, Cambridgeshire
1992	Not stated	Thursley Common, Surrey
1992	Not stated	Thursley Common, Surrey
1992	Not stated	Thursley Common, Surrey
2018	Not stated	Portland, Dorset

The European status of *Calosoma sycophanta*

The distribution of FCH broadly spans much of the Palearctic, where it inhabits both deciduous and coniferous open forests (see individual European country statuses in Table S1 Stolbov *et al.*, 2018). Both adults and larvae feed on a variety of large caterpillar larvae, particularly Noctuidae, with males exhibiting preference for arboreal hunting whereas females are more likely to hunt on the ground (Burgess, 1911). Following overwintering underground, adults typically emerge in summer months, often June and July, before breeding and then returning to overwinter underground (Burgess, 1911). Additionally, adults exist as one of two colour morphs, metallic green or black, and the factors influencing this are unknown. While green morphs are present across the whole range, black morphs (examples of which can be seen in Figure S1) appear limited to Mediterranean regions (Crevecoeur, 2024). Larvae eclose at a similar time to emerging adults before moulting through three instars and finally pupating underground to eclose the following summer as adults (Burgess, 1911). Individuals can live for up to four years and can be active each summer or enter a diapause, spending a summer underground, which is thought to be linked to prey availability (Spieles and Horn, 1998).

Despite its broad distribution, FCH has relatively low population densities across its range (Schwenke, 1966; Görn, 2019) and has suffered large population declines, particularly in western Europe where it has been declared locally extinct in many areas (Görn, 2019). Görn (2019) documented the fluctuations of FCH populations in Germany, stating that FCH was relatively common at the start of the 20th century but is extinct in five federal states as of 2019, critically endangered in an additional five states, endangered in two states, and vulnerable in another. Trautner (1996) stated that similar trends had been observed in the 20th century for FCH in France, Switzerland, Austria, Luxembourg, Belgium, the Netherlands and Denmark, the latter four of which have identified FCH among the most endangered invertebrates in their countries. Additionally, Trautner (1996) went on to hypothesise the causes of FCH declines across Europe. Firstly, the increase in pesticide application during the 20th century, particularly those targeted toward outbreaks of lepidopteran pests, is linked to severe population losses of FCH, both due to active deleterious effects on FCH larvae by pesticides but also due to the indirect effect of reduced prey availability (Crevecoeur, Willems and Jamers, 2021). This is highlighted by a loss of ~6000 FCH in a cork oak (*Quercus suber*) forest on the Spanish Costa Brava after the pesticide DDT had been aerially sprayed to combat an undescribed moth infestation (Trautner, 1996). Recent legal protections at both the regional and international scales have allowed some recovery, but records in western and northern Europe remain uncommon. This has led to calls to bolster FCH populations in both Germany and Belgium (Trautner, 1996; Crevecoeur, Willems and Jamers, 2021).

The trophic interactions of *Calosoma sycophanta*

Whilst it is known that FCH is a predatory carabid and regularly consumes the larvae and pupae of several lepidopteran species, it is vital that its broader trophic interactions are considered prior to reintroduction to Britain. Many of the species FCH has been observed predating are high profile pest species such as spongy moth, OPM and PPM, all of which currently pose a threat to British forests or are predicted to in the near future (Forest Research, 2022a, 2022b, 2022c). The additional biocontrol potential of FCH in Britain could therefore be significant; however, it remains unclear which non-target species FCH might predate and what factors influence individual foraging dynamics and trophic interactions in FCH. Due to its widespread use as a biocontrol agent, the literature surrounding FCH natural diet is relatively well developed compared to other aspects of FCH ecology. Publications from the early 1900s describe the trophic interactions of FCH in the USA. At this time, FCH was often incorrectly considered a specific predator of spongy moth (Bess, 1961; Campbell, 1975) despite research from Burgess (1911) demonstrating that FCH would feed on a broad range of prey species, including forest tent caterpillar (*Malacosoma disstria*), eastern tent caterpillar (*Malacosoma americana*), brown-tail moth (*Euproctis chrysorrhoea*) and fall webworm (*Hyphantria cunea*; Table 2).

Table 2: All known prey items of FCH that are recorded in the literature.

Order	Family	Species	Life stage predated by FCH	Status in Britain	Observer
Lepidoptera	Erebidae	*Euproctis chrysorrhoea*	Larvae	Distributed in the south and south-east	(Kanat and Mol, 2008)
Lepidoptera	Erebidae	*Hyphantria cunea*	Larvae	Occasional immigrant	(Kanat and Mol, 2008)
Lepidoptera	Erebidae	*Lymantria dispar*	Larvae, Pupae	Common around Greater London area, patchy distribution on the south-east coast	(Kanat and Mol, 2008)
Lepidoptera	Erebidae	*Lymantria monacha*	Larvae	Common in the southern half of Britain	(Kanat and Mol, 2008)
Lepidoptera	Erebidae	*Dasychira pudibunda*	Larvae	Commonly distributed in England and Wales	(Kanat and Mol, 2008)
Lepidoptera	Geometridae	*Bupalus pinianus*	Larvae	Common across Britain	(Schwenke, 1966)
Lepidoptera	Lasiocampidae	*Malacosoma disstria*	Larvae	Not present	(Burgess, 1911)
Lepidoptera	Lasiocampidae	*Malacosoma americana*	Larvae	Not present	(Burgess, 1911)
Lepidoptera	Notodontidae	*Thaumetopoea processionea*	Larvae, Pupae	Locally abundant around	(Görn, 2019)

				Greater London area	
Lepidoptera	Notodontidae	*Thaumetopoea pityocampa*	Larvae, Pupae	Not present but at risk of establishing	(Kanat and Mol, 2008)
Lepidoptera	Notodontidae	*Thaumetopoea solitaria*	Larvae, Pupae	Not present	(Kanat and Mol, 2008)
Lepidoptera	Notodontidae	*Phryganidia californica*	Larvae	Not present	(Beblese, 1916)
Lepidoptera	Noctuidae	*Helicoverpa zea*	Larvae	Occasional immigrant	(Beblese, 1916)
Lepidoptera	Pyralidae	*Galleria mellonella*	Larvae, Pupae	Established in Britain	(Spieles and Horn, 1998)
Lepidoptera	Tortricidae	*Tortrix viridana*	Larvae	Common across Britain	(Kanat and Mol, 2008)
Hymenoptera	Diprionidae	*Diprion sp.*	Larvae	Some species present in Britain	(Schwenke, 1966)

Weseloh (1988) represents much of the contemporary literature from America but largely focuses on specific aspects of trophic interactions with spongy moth (e.g. FCH's capacity to discriminate between life stages and sexes of spongy moth prey). The larvae of FCH exhibit a preference for female spongy moth pupae (Weseloh, 1988). If FCH exhibits a similar bias toward female OPM, this could generate large local impacts to OPM populations given that female OPM exhibit higher site fidelity as adults (Townsend, 2013) and are therefore more likely to sustain co-occurrence with FCH. From Europe, two key publications identify potential FCH trophic interactions. Kanat and Mol (2008) provide the most comprehensive list of recorded prey from Turkey which includes *Thaumetopoea sp*, *Euproctis chrysorrhoea, Hyphantria cunea, Lymantria dispar* and *Tortrix viridana* (Table 2). Görn (2019) also provides an extensive list of prey species from Germany, including *Thaumetopoea sp.,* spongy moth, nun moth (*Lymantria monacha*) and brown-tail moth (Table 2). These species are, importantly, predominantly considered pests, and wider interactions with other species are undescribed, so it remains uncertain whether FCH could have any detrimental impacts, such as targeting species of conservation concern.

A noteworthy observation by Görn (2019) is that FCH preferentially enters the nests of processionary moths to attack larvae and pupae, which may lead to unintended non-target impacts to the parasitoids currently controlling OPM populations. The two parasitoids of OPM recorded in Britain, *C. iliaca* and *P. processioneae*, will be present in nests during the latter part of the OPM lifecycle where they inhabit pupal chambers inside OPM nests prior to their eclosure. Predation within nests may therefore lead to undesirable intraguild interactions between FCH and these parasitoids with net negative consequences since any parasitised OPM are already likely to die. This does, however, remain hypothetical and requires further investigation and validation.

Spieles and Horn (1998) highlighted the importance of prey identity for the fecundity and behaviour of FCH, specifically demonstrating that predation of spongy moth larvae leads to greater emergence and breeding success compared to predation of an alternative prey, *Galleria mellonella*. This appears to be consistent with findings from Burgess (1911) which found adult FCH to be more active in areas where spongy moth are more abundant. Similarly, Weseloh (1993) found that insufficient spongy moth abundances when FCH emerge from overwintering will cause adult FCH to re-enter the soil within a

few weeks. It should be noted, however, that these findings are derived from studies in the United States of America, which lacks many of the prey species present in Europe such as OPM and PPM, which may reduce the relevance of these findings to reintroduction of FCH in Britain.

Overall, the diet of FCH is partially recorded, mostly based on direct observations, with many common FCH prey known to be prominent pest species, several of which are present in Britain or are likely to be present in the near future. The wider diet of FCH still, however, remains unknown, so potential non-target impacts may be unpredictable in the event of a reintroduction to Britain based on the current evidence base. This highlights a need to understand more fully the wider diet of FCH to be able to truly evaluate the benefits and risks of any potential reintroduction. Together, the current evidence nevertheless suggests that FCH could provide a significant contribution to biocontrol in Britain if introduced to areas with relevant prey, but this must also be dictated by the availability of appropriate habitats.

Habitat occupancy of *Calosoma sycophanta*

Within both its British and European ranges, several clear habitat preferences can be derived from existing records and studies. Whilst, as its name suggests, FCH is known to inhabit forests, very little information on habitat occupancy within those forests is described in the literature. FCH does not appear to be limited to certain forest types; for example, it is found in both deciduous and coniferous forests (Burgess, 1911; Kanat, Toprak and Akbulut, 2005; Miquel, 2005). Similarly, FCH is known to predate a range of prey species that are found exclusively in certain forest types, such as OPM (deciduous) and PPM (coniferous). The breadth of habitats occupied by FCH makes it difficult to understand the specific requirements of FCH. Common habitat requirements of other ground beetles include suitable shelter for pupation, diapause or overwintering, an appropriate climate for survival and development, and prey availability (Koivula, 2011; Jowett et al., 2021).

FCH is known to pupate and overwinter underground; however, there is currently no information available regarding the soil conditions required for either of these processes to complete successfully beyond the need for moderately shaded, moist ground (Burgess, 1911; Weseloh, 1996). Properties like soil type, moisture, pH, average temperature and density are all important factors for healthy adult emergence in other beetles; for example, Ellis *et al* (2004) show that dry soil resulted in complete failure to pupate in *Aethina tumida* Murray, 1867 (Coleoptera: Nitidulidae). Similarly, Hiiesaar *et al* (2006) showed that overwintering Colorado potato beetle, *Leptinotarso decemlineata*, Say, 1824 (Coleoptera: Chrysomelidae) were more likely to survive in clay sand compared to those in loamy clay soil. The uncertainties around the requirements of FCH make formal habitat predictions and management difficult.

Climatic factors underpinning *Calosoma sycophanta* presence

FCH inhabits a diverse range of climates, with a distribution ranging from Scandinavia to the Levant, which suggests that FCH is tolerant of a wide range of conditions (Sheth and Angert, 2014). Literature detailing the climatic requirements of FCH are, however, sparse. Its tolerance of a wide range of conditions may make FCH a suitable resident for most of the northern hemisphere, with previous limits to its range likely associated with physical boundaries rather than climatic (Stolbov *et al.*, 2018; Sutton *et al.*, 2023). The expansion of FCH at its north-eastern range in western Siberia may corroborate this (Stolbov *et al.*, 2018); whilst this could be explained by climate change, the 25 new records coincide spatially with the range expansion of outbreaks of spongy moth and nun moth. Average summer temperatures in Western Siberia are similar to areas across the same longitude, where FCH is already present, which suggests that the new outbreaks of prey items may be the dominant driver of FCH

spread (Stolbov *et al.*, 2018). It may be that increasing temperatures are allowing FCH prey to expand into new areas, which then facilitates concurrent FCH range expansion but there is no definitive evidence supporting either hypothesis and range shifts of different prey within FCH's current range may render FCH range shifts erratic and unpredictable.

Given the lack of field-based evidence for the climatic niche of FCH, evidence from captive breeding programmes may provide a valuable analogue. Weseloh (1996) provides details on conditions suitable for breeding adults and raising larvae, finding that keeping breeding adults and larvae at 25 °C enhances adult survival and enables larval growth. It is, however, likely that the temperatures used in this study are higher than necessary for FCH larvae to develop, with other studies showing that ground beetle larvae are capable of growing at lower temperatures such as 15 °C and 16 °C (Lopatina *et al.*, 2011; Vesović *et al.*, 2023). Additionally, FCH is known to inhabit northern areas of Europe with marine west coast or humid continental climates that have average June temperatures of ~20 °C; since this is the month in which FCH is known to emerge and lay eggs, it is unlikely they are experiencing 25 °C (Burgess, 1911). Similarly, Weseloh (1996) stored overwintering adults at 4 °C, which is above the average winter temperature for many northern European countries. These overwintered adults were, however, given peat moss as a substrate which may not thermally resemble substrates available to wild FCH. Weseloh (1996) also provided moist peat moss to adult FCH and larvae as substrate during the summer, which was suitable for gravid females to lay eggs and for larvae to grow successfully. Wet and dry paper towels were also tested as suitable substrate; however, these were less effective than peat moss, with wet paper towels being slightly suitable and dry paper towels being largely unsuitable, with many larvae desiccating. Ultimately, Weselohs (1996) did not produce perfect analogue for FCH requirements in the wild; however, they do show that larvae need suitably moist substrate to survive. This is also reflected in the previously mentioned studies that indicate carabid larvae require moist soil conditions to survive.

Based on inference from previous records of FCH found in locations across Britian ranging from Carlilse to Norfolk and associated literature, Britain is likely to be climatically suitable for FCH in the coming decades, and might only become more suitable (i.e., closer to current FCH population climates) under current climate warming predictions (Met Office Hadley Centre, 2018). Climate does not, however, appear to be a limiting factor for FCH across much of Europe, suggesting that the presence of prey items is a driver of occurrences. Britain may be marginally climatically suitable for FCH and that its mild climate with low temperature seasonality may explain why FCH has never been common if previously native.

Benefits, risks and feasibility of reintroduction

The benefits of reintroducing FCH are apparent: the enhanced biocontrol of OPM and the return of an ecologically significant predatory beetle to Britain. The risks are, however, somewhat more insidious to predict. From the evidence compiled through systematic review, it seems likely that poor prey availability will have driven population declines and potential extinctions of FCH in Britain. This limitation to their population growth may be addressed by the increasing prevalence of OPM, making this a likely low-risk and high-benefit reintroduction. Given the recency of FCH's records in Britain, its reintroduction is unlikely to have any severe impacts to non-target species beyond its previous interactions, which are not known to have had any profound effects on other species. It is, of course, noteworthy though that reintroduction focused on biocontrol of OPM would likely mean introducing FCH to sites that it may not have previously occupied, with potentially previously unobserved interactions and consequent impacts as a result.

It is also important to note that the invasion by OPM has introduced new species and interactions to the invaded systems beyond just OPM. Most notably, the two parasitoids of OPM recorded in Britain, *C. iliaca* and *P. processionea*, will almost certainly be impacted by both exploitation competition for OPM larvae and direct predation of parasitised caterpillars by FCH, especially if it does engage in nest raiding behaviour (Görn 2019). Whilst this is likely to increase the pressure on OPM, potentially mitigating its population increases and spread, it could have unpredictable consequences for parasitoid-driven biocontrol, resulting in greater future dependence on FCH for biocontrol of OPM, therefore reducing the robustness of this control. Such risks will be difficult to predict from studies of other ecosystems containing FCH, and may be best addressed by continuous monitoring of smaller-scale reintroductions at discrete OPM-infested locations, although containment of released populations to release sites will likely be impractical.

Following the framework developed by Heimpel et al. (2024), which is designed for assessing benefit-risk tradeoffs for classical biocontrol, it may be possible to quantify the potential risk of FCH reintroduction. Although it is impossible to account for every possible risk, those described above (e.g., competition, non-target predation) are the most likely. Our capacity to quantify the benefits and risks in this framework is currently limited by a lack of quantitative data related to the broader impacts of FCH on a wide range of taxa beyond the pests focal to most of the current literature. To use this quantitative framework effectively, we first need to understand: (i) the broader trophic interactions of FCH; (ii) the wider ecological network FCH is part of, including its indirect interactions such as competition; (iii) the taxa available and therefore at risk in OPM-infested areas, and their ecological and functional roles. These data can be derived from targeted study of FCH populations in its existing European distribution, perhaps using broader spectrum methods like dietary metabarcoding to characterise FCH's interactions and those of potential competitors more broadly than has traditionally been achieved. Such evidence will introduce significantly more confidence in the outcomes of reintroduction of FCH.

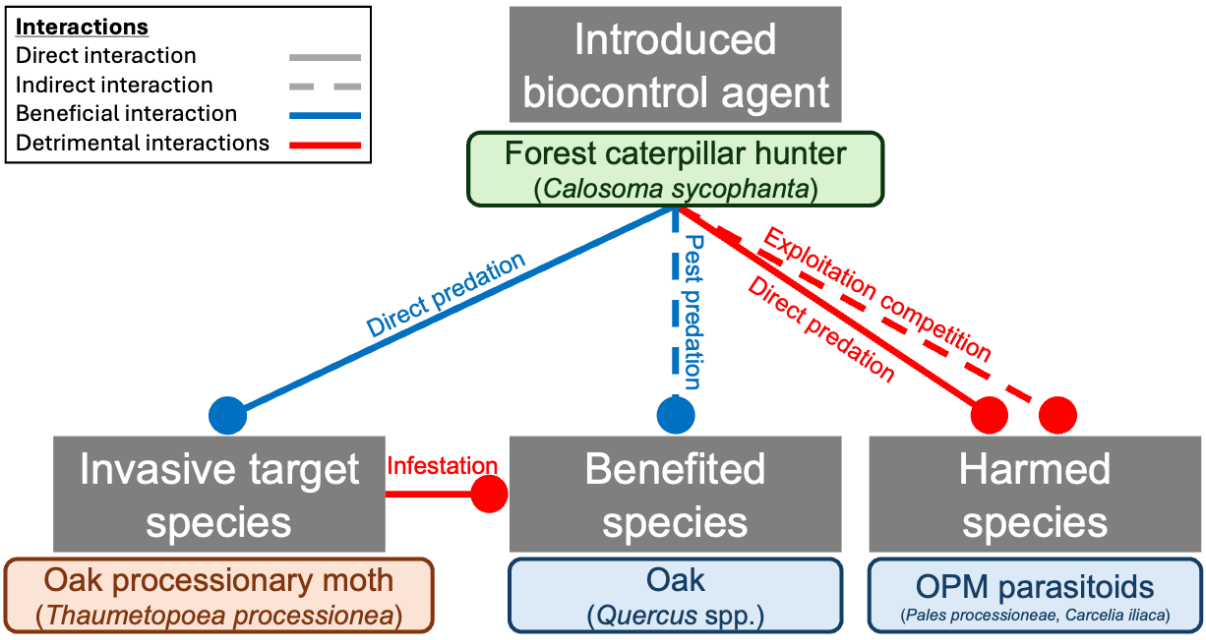

Figure 4: The risks and benefits of FCH reintroduction based on the framework proposed by Heimpel et al. (2024). Quantitative information can be integrated through further study of FCH's direct (e.g., trophic) and indirect (e.g., competition) ecological interactions in its current European range.

Discussion

Arguably the most conclusive aspect of this review is the compilation of previous trophic interactions of FCH, which is well documented to require large caterpillars for successful larval development and for adults to breed. These caterpillars are often Noctuidae larvae, which include many prominent pest species. Several of the prey of FCH are increasingly abundant in Britain, suggesting that a wide range of prey would now be available to a reintroduced population of FCH. It is unknown whether the diet of FCH includes the consumption of species aside from these caterpillars and, if so, what those prey might be, which is especially important for determining non-target and indirect impacts of reintroducing FCH to Britain. To understand this fully and elucidate whether an FCH population in Britain would have an impact on, for example, species of conservation concern, broader spectrum dietary data are needed from natural populations, which molecular methods like dietary metabarcoding could provide (Cuff *et al.*, 2022).

Regarding potential local drivers of FCH extinctions, despite the scarcity of available data, prey availability is consistently identified as a local challenge for FCH populations (Stolbov *et al.*, 2018). An abundant prey source is strongly associated with successful FCH populations in most recorded cases. For instance, in studies investigating drivers of local FCH extinctions, heavy pesticide use decimating lepidopteran larval populations is stipulated as the predominant driver alongside a loss of open forest habitat, with more resolved habitat occupancy data being absent in the literature (Görn, 2019). Importantly, the phenology of FCH is thought to be linked to outbreaks of preferred prey, such as spongy moth and PPM (Stolbov *et al.*, 2018; Schweiger, Nützel and Koch, 2020). Any further work toward reintroducing FCH or using it for classical or augmentative biocontrol should consider long term prey availability and open forest habitat availability since these appear to be critical for sustainable populations of FCH.

Understanding the historical status of FCH in Britain is difficult with the evidence available. No genetic studies have been conducted on the available specimens to compare them to other European populations despite this being a viable pathway to identifying relatedness and possibly the approximate timescale of separation. The only evidence available is therefore the specimens themselves and consultation with relevant natural historians. The earliest recorders of FCH in the 19th century concluded that FCH should have been considered an “often occurring immigrant” due to the majority of records occurring in coastal regions such as the coast of East Kent, the Isle of Wight and Plymouth, and the scarcity of records at the time (Fowler, 1887). Similarly, during the 20th century, records were sparse; however, records began to appear much further inland than typical for channel migrants, such as in Carlisle (1913) and Thetford Forest, Surrey (1997). Telfer (2016) presents two possibilities for these records: (i) they represent individuals from established populations, particularly for Thetford Forest, which has had more than one individual recorded; or (ii) that there have been unregulated releases of FCH in these locations, the motive for which would be unclear. It should also be noted that, where FCH has been found in Britain, there have been no repeated records after the date of the initial record. The only known location where attempts at further captures has taken place was Thetford Forest, Surrey, where both diurnal and nocturnal surveys took place but were unsuccessful (Telfer, 2016).

With no current fossil record evidence and expert opinion split over whether to consider FCH a frequent immigrant or an under-recorded native, it is difficult to conclude whether FCH have previously held established populations in Britain and thus can be considered native. What can be said is that FCH has a long association with Britain spanning at least 170 years with records continuously appearing. This may indicate the presence of small, localised populations that are under-recorded and have suffered similar local extinctions as European populations. With the establishment of OPM in Britain,

it seems only a matter of time before FCH is able to sustainably remain in affected areas if prey availability has been a limiting factor for FCH historically. Regardless of the potential persistence of small undetectable local populations, we advise, based on the evidence above, that the addition of FCH populations to Britain is considered a reintroduction to ensure that it proceeds through a thorough process with full consideration of both the risks and benefits of doing so for the native fauna. We do, however, believe that the above evidence highlights the strong potential of doing so for mitigating the spread and establishment of the rapidly increasing invasive, OPM.

Conclusions

We have demonstrated that, based on previous records, FCH is likely to have been native to Britain, but should likely now be considered nationally extinct, at least from the perspective of introducing populations from elsewhere. Given the climatic suitability of Britain (although slightly lower than much of Europe) and the presence of the open forest habitats that FCH broadly occurs in, it is likely that poor availability of suitable prey was the cause of national extinction, and the greatest constraint for prospectively reintroduced populations. Given the rapidly increasing populations of OPM in Britain, this presents a serendipitous opportunity to sustainably control these populations whilst simultaneously reintroducing an ecologically significant species to Britain's entomofauna.

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Supplementary Information

Figure 1: A collection of both green and black morph FCH specimens from different regions in Europe kept at the Natural History Museum London.

Table S1: List of countries with records of FCH and the status of FCH in that country.

Country	**Status**	**Most Recent Date**
Albania	Native	Continuous
Algeria	Native	Continuous
Armenia	Native	Continuous
Austria	Native	Continuous
Azerbaijan	Native	Continuous
Belarus	Native	Continuous
Belgium	Native	Continuous

Bosnia-Erzegovina	Native	Continuous
Bulgaria	Native	Continuous
Canada	Introduced	Continuous
China	Native	Continuous
Croatia	Native	Continuous
Cyprus	Native	Continuous
Czech Republic	Native	Continuous
Denmark	Native	Continuous
Estonia	Native	Continuous
Finland	A few records through accidental introduction	1983
France	Native	Continuous
Georgia	Native	Continuous
Germany	Native	Continuous
Greece	Native	Continuous
Hungary	Native	Continuous
Iran	Native	Continuous
Israel	Native	Continuous
Italy	Native	Continuous
Kazakhstan	Native	Continuous
Kosovo	Native	Continuous
Kyrgyzstan	Native	Continuous
Latvia	Native	Continuous
Lebanon	Native	Continuous
Liechtenstein	Native	Continuous
Lithuania	Native	Continuous
Luxembourg	Native	Continuous
Macedonia	Native	Continuous
Mauritania	Not recorded	-
Moldova	Native	Continuous
Montenegro	Native	Continuous

Morocco	Native	Continuous
Netherlands	Native	Continuous
Norway	Single specimen	1921
Poland	Native	Continuous
Portugal	Native	Continuous
Romania	Native	Continuous
Russia	Native	Continuous
Serbia	Native	Continuous
Slovakia	Native	Continuous
Slovenia	Native	Continuous
Spain	Native	Continuous
Syria	Native	Continuous
Sweden	Native	Continuous
Switzerland	Native	Continuous
Tajikistan	Native	Continuous
Tunisia	Native	Continuous
Turkey	Native	Continuous
Turkmenistan	Native	Continuous
Ukraine	Native	Continuous
United Kingdom	Undetermined	2018
United States	Introduced	Continuous
Uzbekistan	Native	Continuous