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A framework for species translocation: prospects of returning the black-veined white butterfly to England

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Abstract

1. Insect translocations following historic extirpations and assisted colonisation into regions without historical records require assessment prior to species being released. We present a nine-step framework to assess translocations, and use this to evaluate the opportunity to reestablish the black-veined white butterfly, *Aporia crataegi*, in Britain, a century after its extinction.
2. The framework first establishes the rationale for translocation (step 1) and assesses whether a species will colonise naturally (step 2). It then assesses why a (reintroduced) species became extinct historically (step 3), whether the climate at proposed release sites is suitable (step 4) and if its habitat requirements are met (step 5). A risk assessment (step 6) is also required. For implementation, source populations are identified (step 7), followed by releases and monitoring (step 8), and ongoing reporting of outcomes and lessons learned (step 9).
3. *Aporia crataegi* seemingly meets all of the criteria. Unsuitable climate is likely to have led to extirpation but, despite 21st century climate and habitats now appearing to be suitable, natural and human-created barriers have prevented colonisation. The target area in England contains potential *A. crataegi* host plants and habitat that would accommodate dispersal across >100 km^2 of connected landscape. The risks are assessed as low, and potential source populations in western Europe have been identified using climate-matching analyses. Steps 6-9 are under continuing development.
4. The nine-step approach provides a convenient framework to assess translocations, and has potential to become a model to guide future translocation projects and inform future ‘best practice’ releases.

KEYWORDS: *Aporia crataegi,* Assisted colonisation, Biodiversity, Climate adaptation, Climate change, Conservation, Reintroduction, Resilience, Rewilding, Translocation

INTRODUCTION

Restoring or reintroducing species that became extinct a long time ago and introducing species to new regions in the context of climate change (assisted colonisation) involve a degree of uncertainty. Such translocations are becoming important, however, as the distributions of species respond to climate change (Chen et al., 2011; Thomas, Hill, et al., 2022). Some species are increasingly endangered by climate change (Thomas, Cameron, et al., 2004; Urban, 2015) and large numbers of species are unable to achieve their full potential distribution because of dispersal barriers. Hence, translocating species across natural (e.g., water for terrestrial species, land for freshwater species, or low elevations for montane species) and human created (e.g., intensive agricultural landscapes) barriers is, and will become, an increasing feature of conservation interventions (Hoegh-Guldberg et al., 2008; Thomas, 2011; IUCN/SSC, 2013; Gaywood et al., 2023; Gaywood, 2024). Such translocations need to be assessed to ensure that potential benefits are maximised and risks minimised.

Previous reintroductions of insects have proven successful, including successful butterfly introductions of species to unoccupied habitats within Britain (reviewed by Oates & Warren, 1990) with the greater success in locations where the climate is most suitable (Menéndez et al., 2006). The reestablishment of the large blue butterfly, *Phengaris arion*, in Britain has been successful (Thomas, Simcox & Clarke, 2009), and the habitat management linked to its reestablishment has favoured several other rare insect and plant species (Thomas, Simcox & Meredith, 2019). Likewise, the reestablishment of the chequered skipper *Carterocephalus palaemon* in England provided an impetus to the restoration of traditional woodland management that favours additional species (Bourn et al., 2024). However, both this specific butterfly literature and the wider translocation frameworks (below) also recognise many failures, most commonly attributed to inadequate habitat quality or quantity, or other environmental conditions for the stock released (Oates & Warren, 1990; Menéndez et al., 2006). Hence, this literature highlights the importance of assessing the habitat suitability of potential introduction sites, ensuring suitable climatic conditions, and obtaining stock that is derived from locations with equivalent environmental conditions elsewhere so as to minimise the risks of failure; although some level of uncertainty will always remain.

In this article, we lay out a framework (Table 1) to assess the merits and practicalities of reestablishment, or establishing an insect species in a region outside its current distribution. Developing such a framework enables researchers to identify information relevant to translocations, and its application also highlights gaps in knowledge that might hinder successful establishment of a target species. A number of different approaches to the translocation of species have been published, some of which are relatively broad assessments of ‘whether and why’ researchers and conservationists might wish to undertake translocations, and that vary from the more conceptual to practical (e.g., Hoegh-Guldberg et al., 2008; Invertebrate Link, 2010; IUCN/SSC, 2013; Van Kleunen et al., 2023; US Fish and Wildlife Service, 2024). Nonetheless, at a higher level, all of the frameworks consider the rationale and justification for translocation, evaluate the likelihood or feasibility of success, include an element of risk assessment, and some of them also consider release, monitoring and reporting options (Parts A-D of Table 1; see Table S1 for comparisons of frameworks). The framework we have developed builds on these, with greatest similarity to the comprehensive and broad US Fish and Wildlife Service (2024) approach. We recommend that those interested in developing possible translocation projects consider the range of frameworks available so as to select the elements most relevant to their specific situation. Our own framework draws on these and the wider literature to highlight issues that will be particularly relevant to the translocation of non-migratory plant-feeding insects of conservation concern, and to other non-migratory invertebrates (and other taxa) for which climatic conditions, habitat availability and connectivity represent constraints influencing their distributions.

Our framework is outlined in Table 1 and can be adjusted to suit different groups of non-migratory insects, other invertebrates and additional taxa. We illustrate how it can be used by assessing options to reintroduce the black-veined white butterfly, *Aporia crataegi*, to Britain, a century after the species' extinction. The framework represents a series of questions that consider the rationale behind the translocation, its likelihood of success, any potential negative as well as positive consequences of establishing a given species, and the logistics of the translocation and establishment process. It also provides a framework for learning from outcomes (both successes and failures) during the process, so as to increase the chances of future success.

METHODS

This study applies the translocation framework using a combination of literature review, field observation and climate suitability assessment. We adopt the following terminology: *reintroduction* as the process of returning a species to part of its historically-documented distribution, *reestablishment* when reintroductions successfully generate new populations, *assisted colonisation* when moving a species beyond its historically-documented distribution, and *translocation* as a broad term encompassing all three. Since the historical distributions (for example, over 200 years ago) of most terrestrial invertebrates are poorly known, *translocation* is a useful term in many instances. Geographically, the *United Kingdom* (UK) includes England, Wales, Scotland and Northern Ireland and is the UN member state that makes international commitments and reports to the Convention on Biological Diversity, and *Great Britain* (GB, or Britain) is the biologically-contiguous island comprising England, Wales and Scotland (apart from smaller offshore islands). However, most conservation matters are devolved to the four UK nations, and hence conservation regulations, assessments and approvals considered here are carried out for *England* (through Natural England, a government agency with the UK government Department for Environment, Food & Rural Affairs, Defra). Hence, we refer to the UK (international governance), GB (biological entity) and England (regional governance), as appropriate, throughout the manuscript.

Although referred to as ‘steps 1-9’, gathering information and drawing up plans that are relevant to different steps will typically develop simultaneously. Our case study is the potential translocation of *A. crataegi* to a proposed reestablishment area in Great Britain.

Literature review (relevant to steps 2-6 of Table 1). For our case study, we searched Google Scholar for the species proposed for translocation, here *Aporia crataegi* (searching for: "*Aporia crataegi*" OR "*A. crataegi*" OR "*A.crataegi*" OR "*black-veined white*" OR "*black veined white*"; search date 13 August 2024; no further relevant information was found beyond search results 250; and no additional relevant papers were found when revising the manuscript, repeating search 20 December 2024) retaining all publications from Europe westwards of longitude 20 °E (i.e., focussing on areas with a climatic match to the proposed reestablishment area). Once publications were identified, cited literature within them was also assessed; and grey literature was sought from online searches using the same search terms, geographic and date criteria, and considered for inclusion when information was considered to be ‘primary’ (e.g., direct oviposition and larval host plant reports, as opposed to derived information in field guides and online accounts which may include geographically undefined information not relevant to potential source populations). This literature was then subdivided into publications relevant to the different translocation assessment steps.

Field surveys. For our application of the framework to *A. crataegi*, selected sites were surveyed within an approximately 11 km x 9 km region in West Sussex, close to the south coast of England (location shown by the red triangle in Figure 1; site locations Table S2). This area contains a diversity of geologies, from the Wealden clays (at Knepp), through greensand (sandstone) to the chalk hills of the South Downs. The criteria used for assessing habitat suitability for the study species was based on literature review (for other species it may require additional quantitative habitat surveys within the current distribution).

Table 1. A nine-step framework for assessing proposed species translocations
PART A - Rationale and justification for translocation
1. What is the rationale for establishing a species outside its current distribution? This section considers legal commitments (e.g., to species reestablishment) as well as the biodiversity (e.g., endangerment of the translocated species, co-benefits for additional species), ecosystem (functions, services), social and economic rationale. What are the initial targets?
2. Will the species colonise without assistance? Step 2 considers the species' dispersal capacity, the availability of source populations, and barriers to dispersal. Translocation is unlikely to be required if the species is expected to colonise under its own volition within conservation planning timescales.
PART B - Evaluating the likelihood of establishing a viable new population
3. Why did the species become extinct historically? Relevant only for *re*introductions, step 3 considers the causes of previous extinctions, and whether they have been removed.
4. Is the climate suitable for the focal species? Climatic suitability needs to be considered for nearly all translocations (including reintroductions), given that the climate has changed everywhere. Relevant information includes the climatic sensitivity of a focal species, and the projected current and future climatic suitability of candidate release sites for the species.
5. Are the ecological requirements of the species and habitat available? Step 5 involves assessment of the basic habitat requirements (including other species) of all life stages of each species to ensure that releases are into potentially suitable environments.
PART C - Risk assessment
6. Are there risks associated with the translocation? Four key aspects of risk assessment involve: (i) ensuring that introduced species will not have adverse effects on existing ecological communities (e.g., via associated parasitoids and pathogens), or on the donor populations, (ii) assessing any commercial or social risks for people, (iii) evaluation of the legal and other steps that may be required, and (iv) assessment of the cost-effectiveness of the proposed project, including the need for financial support.
PART D - Releases and monitoring
7. Is suitable stock available for translocation? Step 7 involves identifying populations where the source material is likely to be well adapted to the target release sites, including consideration of their genetic attributes, adaptations (e.g., to host plants for herbivorous insects), and the climatic match between source and release sites.
8. Release and monitoring schedule What are the revised targets, given the information in steps 1-7? Projects should evaluate the most effective ways to undertake releases so as to minimise risks and maximise opportunities for success; includes monitoring to refine understanding of conditions that lead to population growth, to inform future releases.
9. Reporting on progress and lessons learned Communications may include providing reports to appropriate authorities and funders on progress against the initial (step 1) and revised (step 8) targets, and lessons learned, feedback to citizen scientists contributing to the project, public-domain scientific reports, planning media and other educational opportunities; aiming to improve the prospects for future conservation projects.

For *A. crataegi*, the most suitable habitat in western Europe was scattered hawthorn (*Crataegus monogyna*) bushes and suckering blackthorn (*Prunus spinosa*) scrub or hedgerow edges, and the availability of nectar plants with flowers in the blue/purple/red/pink spectrum, reported as favoured (see Results section 5). The aim of this fieldwork was to use these characteristics to identify the suitability of initial release sites, rather than assess the locations of *all* breeding habitats in the landscape.

Abundances of potential nectar sources were assessed using the DAFOR scale: D - Dominant >75% cover; A - Abundant 51-75%; F - Frequent 26-50%; O - Occasional 11-25%; R - Rare 1-10% (Groom et al., 2010). Overall DAFOR scores were then calculated by summing across plant species.

Climatic suitability. We summarised the existing climatic suitability information for the study species from the literature. We generated a mean Spring and Summer measure of Central England temperatures since 1850 (Parker et al. 1992; National Climate Information Centre, 2024) to assess climatic conditions during the period of regional extinction. We also undertook a climate similarity analysis of the match between the climate of the reestablishment area and existing populations elsewhere in Europe.

For the climate-matching analysis, we used bioclimatic indicators (Figure S1) for Europe downloaded from ECMWF Climate data store (available from Copernicus, Woulters, 2021). These data are available at a 1 km x 1 km resolution as a mean for 1979-2018 for the region shown in Figure 1. Downloaded bioclimatic variables are:

- Growing degree days (K day year^{-1}). Sum of daily degrees above the daily mean temperature of 278.15 K (5°C).
- Annual precipitation (mm year^{-1}). This indicator corresponds to the BIOCLIM variable BIO12, reflecting the annual mean of the daily precipitation *rate* (both liquid and solid phases). Given in units of m s^{-1}, this was converted to total precipitation sum over the year, a conversion factor of 3600x24x365x1000, giving mm year^{-1} values.

- Mean temperature of coldest month (K). This was calculated by downloading monthly mean temperatures, and taking the minimum value.
- Temperature seasonality (K). Standard deviation of the monthly mean temperature multiplied by 100. This indicator corresponds to the BIOCLIM variable BIO04.

To exclude marine areas from climate surfaces, national boundaries were downloaded using the *geodata* package (Hijmans et al., 2023) and climate variables were masked to terrestrial boundaries.

To identify climate analogues, we took six potential reintroduction sites (Tables S2, S3), extracted the climate values and took the mean. The absolute difference between the mean climate value of the reintroduction sites and all other climate values within the dataset was calculated for each climate variable. The most similar cells (20%, 30%, 40% and 50% quantiles) were identified and plotted for each bioclimatic variable (reintroduction sites as red circle; Figure S2). An overall climate similarity map was produced by identifying cells which were within specific quantiles for *all* of the climate variables (Figure 4a). Based on the literature review, moisture availability is unlikely to be a limiting factor for the host plants or for *A. crataegi* in Britain (whereas it is in the Mediterranean), so we also estimated specific quantiles for *all* three of the temperature climate variables (Figure 4b).

To identify potential source populations, we downloaded *A. crataegi* presence records from Global Biodiversity Information Facility (GBIF; GBIF.org, 2024) and overlaid these on the climatic similarity maps (Figure 6). We carried out filtering of records by removing records that had: no coordinates, geospatial issues, zero counts, low coordinate precision (greater than or equal to 10 km), or records with low verification confidence. We additionally cleaned the records using the *coordinate cleaner* package (Zizka et al., 2019), and removed any stray UK records after 2000 as the species was confirmed extinct. All climatic suitability analysis was carried out using R version 4.3.2 (R Core Team, 2023). Code used for the climate similarity analysis is available on GitHub: https://github.com/charles-cunningham/translocationClimate.

It is important to recognise that each species, environmental situation and policy jurisdiction will require adjustments of methods to suit the ecological and social context of any proposed translocation. For this reason, our proposed framework in Table 1 is deliberately at a relatively high level so that it can be adjusted to particular circumstances.

RESULTS - THE FRAMEWORK ASSESSMENT

PART A. Rationale and justification for translocation.

1. *What is the rationale for establishing a species outside its current distribution?*

All translocation projects are likely to require an initial assessment of whether translocations (reintroductions and assisted colonisation) are consistent with national and other policy positions, guidelines and laws, and initial consideration of whether such a project would be environmentally, socially and / or economically beneficial.

Policy position. The UK is a signatory to the Convention on Biological Diversity (CBD) and the Bern Convention, providing a framework to consider the reestablishment of extirpated species. The CBD 2030 Target 4 states that signatories should "*Ensure urgent management actions to …* [aid] … *the recovery and conservation of species*" (Convention on Biological Diversity, 2022; our underlining). Furthermore, the CBD "*TARGET 8: Minimize the Impacts of Climate Change on Biodiversity and Build Resilience*" is relevant since we propose to translocate *A. crataegi* into a region of currently suitable and improving climate (below). The UK government 25-year plan for the environment (HM Government, 2018) makes provision by "*Providing opportunities for the reintroduction of native species*". *Aporia crataegi* is classified as Regionally Extinct (Figure 1) based on 2001 IUCN guidelines in the JNCC-sponsored Red Listing of British butterflies (Fox et al., 2010), updated in 2022 (Fox et al., 2022). As an extirpated native species in Britain, *A. crataegi* meets the 25-year plan criterion; reintroducing *A. crataegi* is in line with policy directives. Furthermore, under the Climate Change Act 2008, the National Adaptation Programme (Defra 2023) commits the UK government to "*provide areas for species to take refuge*" (for *A. crataegi* this would be from deterioration of climatic conditions in parts of Europe) and "*provide ecological networks for species to move*" (as in the landscape approach developed here).

Status in continental Europe. The species has declined in recent decades in north-western Europe primarily because of land use intensification. It is listed as extinct from the Netherlands and Czechia (Van Swaay et al., 2010), it no longer has breeding populations in Flanders (which includes the coastal regions of Belgium; Maes et al., 2016), and it is rare in the agriculturally intensive parts of north (eastern) France. It is prone to decline from increasing temperatures and drought in southern Europe (Carroll et al., 2009; below).

Co-benefits. Although the focus of translocating *A. crataegi* would initially be to reestablish one butterfly species, the associated landscape-scale management measures would generate a wide range of additional beneficiaries. *Aporia crataegi* is a representative species associated with scrub and 'edge' habitats, the encouragement of which is likely to favour many other British species including several rare and/or declining bird species: nightingales *Luscinia megarhynchos*, cuckoos *Cuculus canorus* and turtle doves *Streptopelia turtur*, and the regionally-extinct red-backed shrike *Lanius collurio*, which is also under consideration for GB reintroduction. There is a rich invertebrate fauna associated with the *C. monogyna* and *P. spinosa* food plants on which *Aporia crataegi* depends, such as the locally-distributed sloe pug moth *Pasiphila chloerata,* the sloe carpet moth *Aleucis distinctata*, and the scarce hawthorn jewel beetle *Agrilus sinuatus* that breeds in the trunks of veteran hawthorns. *Aporia crataegi* itself has been reported as carrying pollen, and moves within and between sites, and thus has the potential to act as a pollinator (Tables 2, 4; below), which could be beneficial in the context of recent declines in pollinator species (Biesmeijer et al., 2006).

There is also potential for social and economic benefits to be achieved through visitors and educational opportunities, as outlined under '*Costs and benefits*' in step 6 (below).

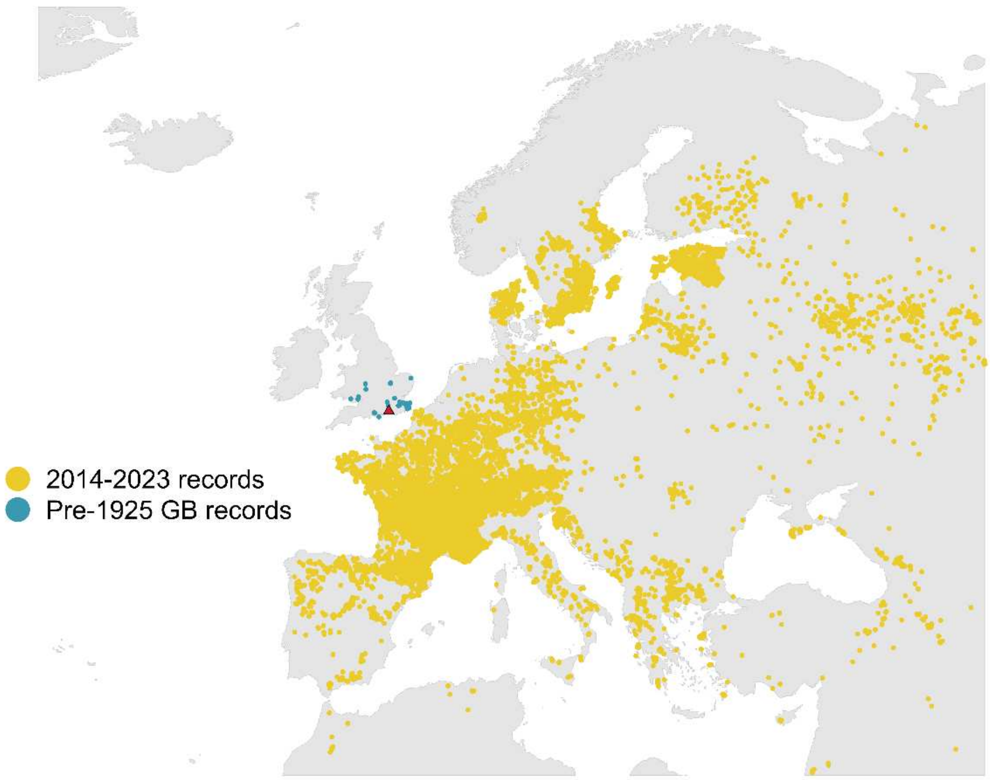

Figure 1. Black-veined white, *Aporia crataegi*, records from GBIF. All continental and African records from 2014-2023 are presented (yellow), with UK records prior to 1925 also shown (blue). The red triangle shows the proposed West Sussex translocation landscape in southern England. The map only shows records with sufficient spatial precision ($\leq$10 km) to plot.

Target. The initial target is to restore *A. crataegi* to a level whereby limited or no specific additional land management is required to maintain the species in at least one area of Britain, following its reintroduction. Once reestablished, *A. crataegi* could potentially be relatively easily encountered by the public, as it ranges widely and visits gardens in search of nectar sources, achieving potential wellbeing benefits. Established *A. crataegi* populations in southern England would provide naturally-dispersing individuals (and material for subsequent translocations) that would enable the species to extend its range northwards, and encourage support for similar reintroduction projects. The overall project targets (and thus assessments of success) are likely to develop iteratively in most translocation programmes, as knowledge of the species under consideration, environmental requirements and target landscapes increase over the assessment process; hence, the targets should be reviewed and updated at stage 8.

Conclusion. Successful translocation of *A. crataegi* would aim to (i) reverse a historical extinction in line with policy objectives, (ii) help secure the distribution of the species in western Europe, and provide opportunities for further expansion northwards, (iii) provide motivation to maintain habitats that will also benefit other species, and (iv) provide benefits to people. The initial target is to reestablish *A. crataegi* in Britain over the coming decade.

2. *Will the species colonise without assistance?*

In all instances of proposed translocations, it is important to evaluate whether a species is likely to colonise under its own volition (or because people will introduce it accidentally) over relevant conservation planning time scales. This requires consideration of the dispersal capacity of a species relative to both anthropogenic and natural barriers that may impede dispersal. It should also consider the potential for populations to establish in intervening locations between potential source and target sites. Translocations are unlikely to be required for migratory species, with the exception of the ‘special case’ where the aim is to establish new seasonal aggregations of migratory species, such as new overwintering sites.

Dispersal. Most recorded movements of *A. crataegi* have been of individuals recaptured within the same site where they were marked, and few individuals have been recorded moving further than 1 km (maximum 3.5 km) (Table 2). All studies also report that males are more mobile than females. The frequencies of within-site recaptures and modest between-patch distances (3 out of 94 recaptures were over 1 km; Lind *et al.,* 2007), especially for females, imply that long-distance dispersal events are infrequent.

The frequencies of movements over different distances can be estimated by fitting dispersal kernels to mark-release-recapture data. Baguette et al. (2000) found that the distribution of recorded dispersal distances best fitted a negative exponential model (analysing both genders together), Lind et al. (2007) reported a negative exponential fit for female movements separately (the gender relevant to the colonisation of new sites), and Jugovic, Crne & Luznik (2017) provide a mean distance estimate for female movements, from which it is also possible to estimate the negative exponential. Extrapolating these equations, we estimate that the chance of individuals moving 2 km or further are 0.0002% (genders combined), 0.05% (females) and 0.0017% (females), for the three studies respectively.

A challenge is that mark-release-recapture programmes underestimate the proportions of long-distance dispersers because individuals that move long distances are less likely to be detected; for example if they leave a given study area (e.g., Barrowclough, 1978; Wilson & Thomas, 2002). No assessment of the magnitude of this effect has been made for any of the published studies of *A. crataegi* dispersal, so we applied a numerical 'correction' (assuming a 22.5-fold under-estimate of longer distance movements) derived for another butterfly species that was estimated in a comparable patch network (Wilson & Thomas, 2002). Applying this 22.5-fold adjustment to the *A. crataegi* negative exponential relationships gave estimates of 0.0042%, 1.16% and 0.038% of individual movements being 2 km or more, for the three studies respectively. To give *a very approximate sense* of the implications for geographic-scale colonisation, we applied an arbitrarily-high 1,000-fold adjustment (increase) of longer-distance dispersal, and extrapolated to 4 km. These gave 0.00000034% (Baguette, combined-gender), 0.027% (Lind, female) and 0.000029% (Jugovic, female) chances of individual dispersal over 4 km. The empirical data and these 2 km and 4 km extrapolations indicate likely metapopulation connectivity among patches within a landscape, but are small enough to suggest that colonisation of Great Britain is unlikely without translocation.

Barriers to colonisation. Nearly all potential sources of colonists are small populations and distant from the English Channel; *A. crataegi* is extinct from the Netherlands (Van Swaay et al., 2010) and Flanders (coastal Belgium; Maes et al. 2016), and sparsely distributed in northern France. Intensively-farmed landscapes in this region are likely to constrain the species' potential northwards range extension. This is in addition to the natural geographic barrier of the English Channel (minimum width 32 km). Occasional individuals - nearly all males - may cross the Channel as vagrants, but they are unlikely to establish viable populations.

Conclusion. The rarity of dispersal distance over 1 km by females (the colonising gender), limited source populations, the need for colonists to cross the English Channel, and the additional need for (rare) immigrants to find suitable habitats once they arrive make unassisted recolonisation of Britain unlikely within the foreseeable future.

Table 2. Dispersal studies	
Belgium: 58% of recaptures were relatively short, within-patch movements. The maximum recorded dispersal distance was 1.59 km. Immigration and emigration rates were highest for the small patches.	Baguette, Petit & Quéva (2000)
France, Normandy: Males were more mobile than females. Individuals moved between meadows.	Ratto (2008)
Sweden, Öland island: mean dispersal distances 315 m for males and 182 m for females (over 2.5 days average). Three of 94 recaptures were over 1 km.	Lind et al. (2007)
Slovenia: Most recaptures within sites. Male median distance was 604 m, max 3.5 km; the only between-site movement for a female was 1.4 km, with mean daily movements of females at 13.3 m.	Jugovic, Crne & Luznik (2017)

To summarise Part A, justification for translocating *A. crataegi* to Britain appears to exist from statutory, ecological and social perspectives (step 1), and the species seems unlikely to be able to colonise without assistance (step 2).

PART B. Is translocation likely to result in the establishment of a viable new population of the species?

3. *Why did the species become extinct historically?*

For species for which a reintroduction is being considered, understanding its previous distribution and why that species became extinct from a particular site or region is valuable, given that reintroducing a species is unlikely to be successful if it is to an area where the environmental pressures that led to its original disappearance are still in operation. However, the causes of extinction are inevitably likely to be fairly speculative for invertebrates that died out a long time ago (as in *A. crataegi*), in which circumstances greater emphasis should be placed on the current suitability of the environment for establishment.

Historical status and distribution. Aporia crataegi occurred across southern Britain (Pratt, 1983, Eeles, 2023; Figure 1), with some colonies recorded as far north as Yorkshire, but it disappeared ~100 years ago. Populations declined and the distribution shrank severely in the late 19th century, Allan (1948) suggesting that the persistence of this species in Britain beyond 1880 was due to its temporary reestablishment or reinforcement from imported continental stock. This hypothesis received some support from genetic analyses, which found that 3 specimens (in 1888, 1908 and 1924) were apparently of European rather than British stock (Whitla et al., 2024). The last records of *A. crataegi* in Britain were from the early 1920s, both 1923 (but note the 1924 specimen) and 1925 being listed as possible years of the last sighting (Pratt,1983; Eeles, 2023). A number of unsuccessful small-scale reintroductions have been attempted since, but these were likely at too small a scale, with too few adults released over too short a period of time, in too small a habitat patch or inadequate habitat conditions (Oates & Warren, 1990), or potentially when the climate was not as suitable as at present.

Potential causes of extinction. The main hypothesis for the species' extinction is that the British climate was unsuitable for *A. crataegi* in the late 19th and early 20th centuries, including a series of wet Septembers (Allan, 1948; Pratt, 1983; Eeles, 2023); although the precise reasons for extinction are unknown. Specific weather events would be unlikely to cause regional extinction unless the background climatic conditions were already marginal, however. In the absence of certain causation, a century after the species' disappearance, it is at least possible to say that the decline and subsequent extinction of *A. crataegi* coincided with a series of cold years in England (Figure 2, below). There are signs from museum specimens of genetic erosion in *A. crataegi* in Britain (Whitla et al., 2024), but this seems likely to be a consequence of the butterfly's low numbers, rather than the primary cause.

Conclusion. The species is thought to have become regionally extinct due to unsuitable climatic conditions. Many different environmental changes have taken place over the century since *A. crataegi*'s extinction from Britain, so the focus is primarily on whether the climate and habitats are suitable today (steps 4-5, below).

4. Is the climate suitable for the focal species?

Given the levels of climate change that have already taken place everywhere in the world, and that future climate change will continue to take place, all translocations should consider the climatic suitability of potential release sites. For example, attempting to relocate a species to an area where the climate is projected to 'deteriorate' for that species is unlikely to be a cost-effective use of conservation funds, even if that area supported populations of the species historically.

Sensitivity of populations to climate. The distribution of *A. crataegi* across Europe as a whole (Figure 1) suggests that it is largely a montane species in the south, but occurs in the lowlands further north. This implies that climate, specifically temperature, is an important determinant of the species' distribution.

Table 3. Climatic limits and responses	
Spain, Sierra de Guadarrama: Apparently avoids areas with high temperatures at low elevation: they lay eggs on the 'shady' (cooler) side of host plant bushes at low elevations, abundance per host plant and larval survival increased with elevation. Lack of suitable host plants at high elevation limit the capacity of *A. crataegi* to colonise higher elevations.	Merrill et al. (2008)
Spain, Sierra de Guadarrama: *A. crataegi* did not show population declines at higher or lower elevations in central Spain.	Caro-Miralles & Gutiérrez (2023)
Spain: *A. crataegi* emerged earlier in the year in 2017-2022, compared to 1985-2005, but did not exhibit an increase in elevation; in mountains in central Spain.	Goded et al. (2024)
Spain, Catalonia: Periodic population crashes, likely related to unsuitable climatic conditions.	Ubach et al. (2022)
Greece: *A. crataegi* showed a substantial decline in abundance between 1998 and 2011/2012 in a National Park during a period when the regional climate warmed by 0.95°C (in contrast, low elevation butterfly species tended to increase).	Zografou et al. (2014)
England / Europe: Climate / distribution modelling reveals that central, southern and eastern England are climatically suitable for *A. crataegi* and projected to be amongst the most suitable climatic areas for the butterfly in Europe, with declines projected in lowland / southern Europe (Figure 3).	Carroll et al. (2009)

Merrill et al. (2008) concluded that *A. crataegi* was adversely affected by high temperatures at low elevations in the Sierra de Guadarrama in central Spain (Table 3). Although *A. crataegi* has apparently not declined in this region in recent years (Caro-Miralles & Gutiérrez, 2023; Goded et al., 2024), extreme population fluctuations of *A. crataegi* in Catalonia may be linked to climatic variation (Ubach et al., 2022). It has declined in Greece, in line with regional warming (Zografou et al., 2014), and has also shifted phenology in response to climate warming (Goded et al., 2024). Together, these results suggest climate sensitivity and potential vulnerability to hotter climates in the Mediterranean region (Table 3).

Climate at the time of extinction from England, and today. The Central England Temperature (CET) record (National Climate Information Centre, 2024) is consistent with the hypothesis that the decline of *A. crataegi* was linked to low temperatures towards the end of the 19th and in the early 20th centuries. The late 1870s through to 1892 were particularly cold, with further cool spells in 1907-1909, and cold years in 1922-1924 (Figure 2), immediately prior to the butterfly's final records, in 1923-1925. The average daily spring and summer temperature of the period 1990-2023 inclusive is 12.65 °C, or 1.15 °C hotter per day than the 1875-1925 average.

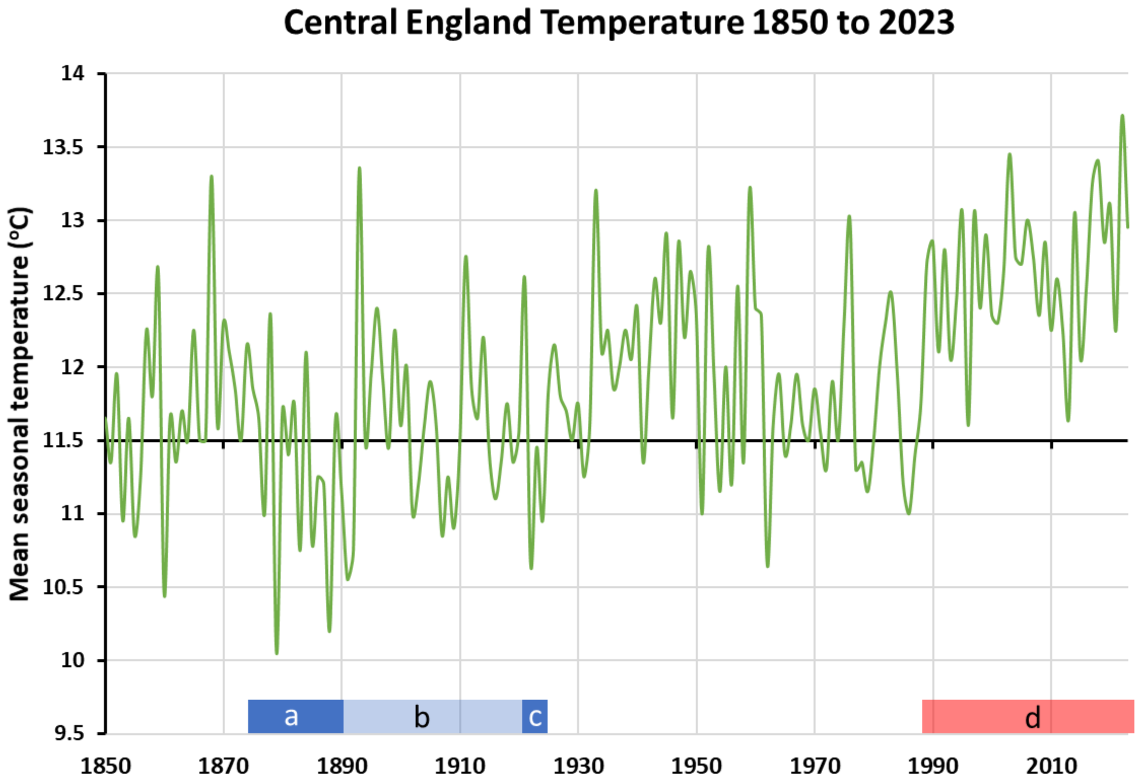

Figure 2. Central England Temperature (CET) average of seasonal daily temperatures for spring (March-May) and summer (June-August) for 1850-2023. The horizontal line shows the average daily temperature of spring and summer in the CET from 1875-1925 inclusive, at 11.5°C: (a) represents a cold period when *Aporia crataegi* decline was noted, (b) uncertain status, (c) last reported sightings, and (d) the most recent 35 years, when the spring/summer mean temperature has been higher than the 1875-1925 average in every year.

The average current spring and summer climate (2017-2023 inclusive) is 13.07 °C, some 1.57 °C warmer than during 1875-1925 (National Climate Information Centre, 2024). Spring sunshine hours *in England* have also increased (by ~15% between the 1910s and 2010s), while summer sunshine hours have remained stable or increased very slightly (Met Office, 2024). Increased sunshine hours facilitate the capacity of gregarious larvae of other butterfly species to thermoregulate in the cooler parts of species' distributions (Bryant et al. 2000), increasing development rates (Bryant et al. 1998), and thus may potentially increase the developmental rate of gregarious *A. crataegi* larvae under present-day spring conditions in lowland England.

Climate matching and distributional potential. Carroll et al. (2009) modelled the recent distribution of the species across Europe in relation to climate variables (Figure 3).

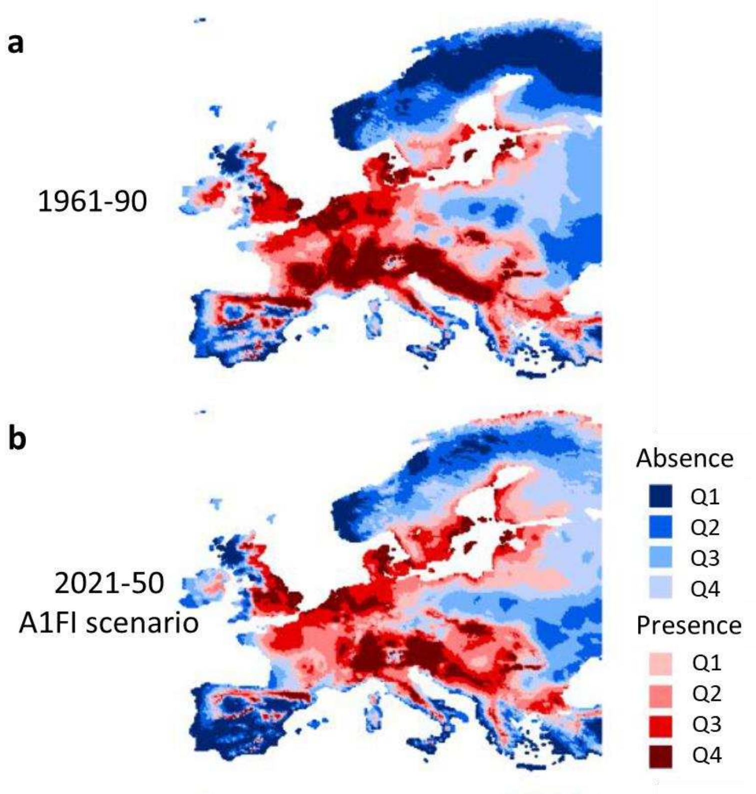

Figure 3. Modelled (GAM) climate suitability of Britain and Europe for *Aporia crataegi* for (a) the late-20th century and (b) for a 2021-2050 climate scenario (selected panels from Figure 2 in Carroll et al. 2009; ©Elsevier Ltd). Reds and pinks indicate predicted presence of *A. crataegi*, while blue shades indicate predicted absence. Presences and absences are divided into quartiles (Q), from darkest red (highest projected climatic suitability) to darkest blue (lowest projected suitability). Pale colours are of intermediate projected suitability.

Based on this analysis, the climate in most of England (apart from the South-West and Lake District) and parts of eastern Scotland were already expected to be suitable under past (1961-1990) climatic conditions (red over most of lowland England in Figure 3a), and future climates (2021-2050); with a corresponding decline in southern and central Europe, where it is expected to become increasingly montane (Figure 3b). These scenarios suggest that England has some of the most suitable climates in Europe for the species.

It is instructive to consider the match between proposed reestablishment sites and climatic conditions elsewhere within the species' range. Presented as climate surfaces for four climate variables, Figure S1 shows that southern England falls within the range of climatic conditions where current populations of the species exist within continental Europe (Figure 1). Using a climate matching approach (see Methods), Figure S2 shows the locations of the areas in Europe with the most similar recent climates to the proposed establishment area for each of the four climate variables considered separately. Combining these variables (overlap of the four panels of Figure S2) highlights the climatic similarity of the proposed reestablishment sites to the climate of northern France to the Netherlands, and to localised mid-elevation areas in southern France and the Iberian Peninsula (Figure 4a). However, the main consideration is whether conditions are warm enough in lowland England, given that *A. crataegi* was hypothesised to die out in Britain following several cold periods (Figure 2), and that the species occurs in parts of Europe that are wetter as well as areas that are drier than lowland England (Figures 1, S1, S2). If we consider the three thermal variables (winter cold, growing degree days, thermal seasonality), similar areas are highlighted (Figure 4b). This provides a greater range of locations with climates similar to the proposed reestablishment sites, albeit still with a focus on north-western Europe and Iberian Peninsula mountain ranges.

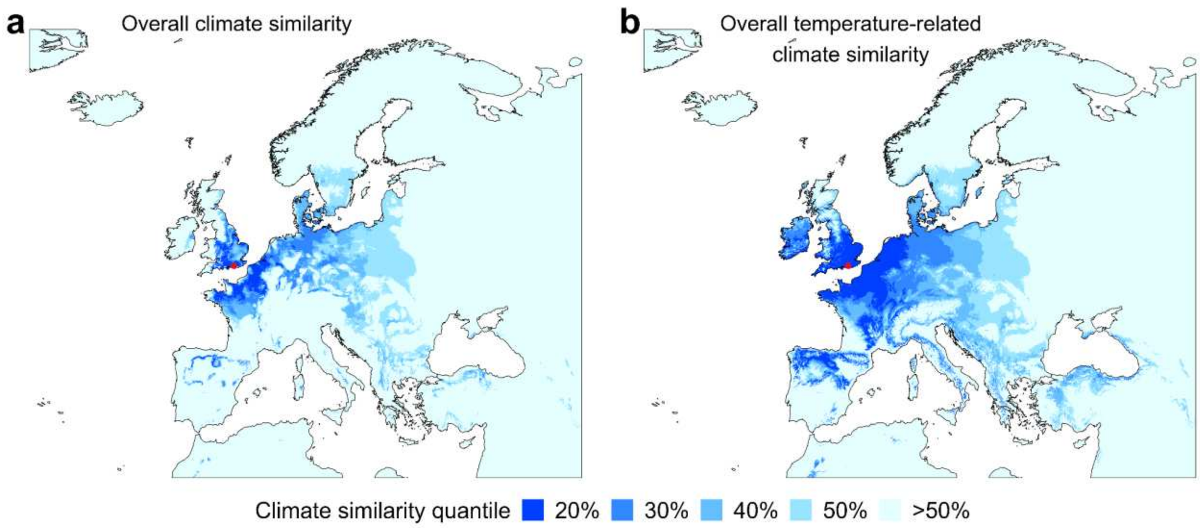

Figure 4. Overlap between the climatic match (a) for all four climate variables considered and (b) for the three temperature-related variables to the potential West Sussex translocation sites (red spot in the south of England). 20% corresponds to locations in the top 20% similarity for all variables considered: darker blue indicates closer match.

Conclusion. Overall, the current climate over much of southern Britain appears to be suitable for *A. crataegi*, and recent studies suggest that it will remain suitable for *A. crataegi* in the future (Carroll et al., 2009). Reestablishment would facilitate readjustment of the species' distribution to align more closely with suitable current and future climatic conditions.

5. *Are the ecological requirements of the species and habitat available?*

For most non-migratory invertebrate species, local habitat conditions are likely to be important determinants of whether populations will establish. The details of such assessments will vary among taxa, but will normally include consideration of the requirements of both the immature and adult stages of the life cycle. This will commonly include reviewing likely interactions with other species and with the physical environment. Depending on the species and environments considered, bespoke methodologies will be required pertinent to each situation, wherever possible adopting the same or similar criteria and quantitative methodologies within source regions and target establishment sites. In practice, different methodologies are likely to have been adopted in previous studies already reported in the literature, and hence a mixture of qualitative and quantitative approaches may be required. For *A. crataegi*, this involved an assessment of adult resources, larval host plants, habitats, and any structural elements of the habitat (e.g., plant growth forms and microclimates) that may affect suitability.

Adult resources. As with most temperate-zone butterfly species, selection of nectar plants is relatively flexible, although *A. crataegi* is often reported as visiting purple, red and pink flowers (Table 4). Several such species are widespread in the British countryside, including *Centaurea*, *Trifolium* and *Vicia* species. The reestablishment of *A. crataegi* could contribute to pollination; in Sweden, Lind et al. (2007) report *A. crataegi* as one of the most important *potential* pollinators of the pyramidal orchid, *Anacamptis pyramidalis*, which also occurs on the chalk of the South Downs (Table S2 sites 4-5).

Table 4. Nectar sources / pollination	
France, Normandy: purple flowers, especially *Symphytum uplandicum* (comfrey), *Trifolium pratense* (red clover), *Centaurea nigra* (common knapweed) and *Vicia cracca* (tufted vetch).	Ratto (2008)
Sweden, Öland island: *A. crataegi* was one of two high frequency carriers of pollinia of the pyramidal orchid, *Anacamptis pyramidalis*.	Lind et al. (2007)
Slovenia: Nine plant species used for nectar, with >80% feeding events on *Knautia illyrica* (an Adriatic scabious) and *Vicia* ag. *cracca* (tufted vetch).	Jugovic, Crne. & Luznik (2017)

Larval host plants. The primary larval host plants in candidate western European regions (Northern France, Belgium and Spain) where stock might be sourced (below) are *Crataegus monogyna* and *Prunus spinosa* (Table 5a). The only exception was a report that *Rosa* species may be used rarely in the mountains of Central Spain, but larvae from egg batches experimentally transferred to *Rosa* in that region failed to survive (Merrill et al., 2008).

Table 5. Oviposition and larval host plants	
a) Northern France, Belgium and Spain (potential translocation source areas)	
Belgium: Larvae feed on young shoots of *Prunus spinosa* and *Crataegus monogyna.*	Baguette, Petit & Quéva (2000)
France, Normandy: 50 egg batches, all on *P. spinosa* and *C. monogyna*.	Ratto (2008)
Spain, Cadiz: *C. monogyna*.	Verdugo Páez & Verdugo Páez (1985)
Spain, Sierra de Guadarrama: Main host plants are *C. monogyna*, *P. spinosa,* very rarely *Rosa* sp. Of 10 egg batches transplanted to *Rosa*, none survived (3 of 5 control transplants onto *C. monogyna* did survive).	Merrill et al. (2008)
b) Additional records (outside of translocation source areas)	
France, South-East: film shows oviposition and larval feeding on *Crataegus*, *Prunus spinosa* and wild *Pyrus amygdaliformis.*	Kan-van Limburg Stirum & Kan-van Limburg Stirum (2014)
Italy: regarded as polyphagous in the early 20th century, with the chief food-plant being the wild pear, *Pyrus* (where it occurred on pear, apple, plum, cherry, apricot, it is reported as not causing serious crop reduction). Italian specimens differ genetically from the extinct British specimens.	Martelli (1931) Todisco et al. (2020)
Germany: *Aporia crataegi* egg batch obtained from *Crataegus monogyna*.	Geervliet, Vet & Dicke (1996)
Germany: Mirabelle plum trees, *Prunus insititia.*	Jancke (1942)
Sweden: *Sorbus acuparia* and *Cotoneaster integerrinus.*	Wiklund (1984)
Slovenia: Main host plants *Prunus spinosa* and *Crataegus monogyna*.	Jugovic, Crne & Luznik (2017)
Slovenia: Larval groups most frequent on *Prunus spinosa* (52.4% of plants), *Crataegus monogyna* (46.5% of plants), and infrequent on *Rosa* sp. and rock cherry, *Prunus mahaleb* (2 plants each out of 362 plants with batches across all hosts).	Jugovic, Grando & Genov (2017)
Slovenia: *Crataegus monogyna* (N=13) and rarely on *Prunus mahaleb* (N=1).	Jugovic & Kržič (2019)
Morocco, Middle Atlas: Larval group feeding on *Crataegus laciniata.*	Thomas & Mallorie (1985)

Slovenian *A. crataegi*, which belong to the Belgium-France-Spain clade (as do the extinct British specimens; Todisco et al., 2020), also mainly use *C. monogyna* and *P. spinosa* (Table 5b). Earlier historical records (Pratt, 1983) and records further east indicate that a wider range of host plants in the Rosaceae are used under different environmental conditions / by different genotypes (Table 5b).

Habitats and structural elements of host plants. *Aporia crataegi* uses a wide range of habitats, ranging from dry grasslands to woodland edges and rides (Table 6). In each case, habitats are characterised by scattered, and typically small, host plants. These may be relatively isolated host plants (of *C. monogyna*) and suckering stems (of *P. spinosa*) in areas with scattered scrub, along hedgerows or at woodland edges. In some regions, host plants growing in sheltered conditions are especially favoured. This is likely to be the case in Britain, where summers are relatively cool.

Table 6. Habitat / growth form of host plants	
Belgium: Larvae feed on young shoots of *P. spinosa* and *C. monogyna* growing at the margins of chalk grasslands.	Baguette, Petit & Quéva (2000)
France, Normandy: Meadows and hedgerows where 44 out of 50 egg batches were laid on plants under 2.5 m high; especially on relatively isolated plants in shelter/sun.	Ratto (2008)
Sweden, Öland island: Various habitats including woodland / grassland / alvar steppe.	Lind et al. (2007)
Spain, Sierra de Guadarrama: Grassland, scrub and woodland, with a positive effect of host plant density on *A. crataegi* occurrence. Eggs were laid on the warmer south side of host plants at high elevation, and on the shady northern side at lower elevations.	Merrill et al. (2008)
Slovenia: Dry karst meadows and hedgerows with suitable nectar plants, and *P. spinosa* and *C. monogyna* larval hosts, and *Prunus mahaleb* and *Rosa* spp. Eggs were laid on the upper side of the leaves of, and groups of larvae found on, relatively small host plants, in particular microclimates.	Jugovic, Crne & Luznik (2017), Jugovic, Grando & Genov (2017), Jugovic & Kržič (2019)

Habitat at potential sites for establishment. *Crataegus monogyna and P. spinosa* scrub has increased at the potential reestablishment sites, and elsewhere in Britain. This is due to a combination of reduced rabbit populations due to myxomatosis, and reduced frequencies of hedgerow management (cutting). Additional scrublands have developed as a consequence of recent (re)wilding projects (Figure 5a) and other extensive grazing conservation projects. Hence, parts of southern England likely have higher habitat availability than at the time of the species' extinction.

Six sites were initially identified as meeting habitat criteria, based on their host plant, growth form, nectar sources, shelter and landscape (area, connectivity) attributes (Table S2). These include regenerating scrubland within the Knepp Wildland project area (Figure 5a), which has extensive grazing by cattle, ponies, pigs and wild ungulates; Frenchland Barn that provides openings within woodland and successional meadows with deer browse (Figure 5b); and chalk sites in the South Downs, mainly characterised by extensive grazing management and rabbits (Figures 5c, d). Dispersal data (above) suggest that *A. crataegi* would form a patchy population or metapopulation, and hence a landscape approach to the reestablishment is required; the greater the dispersal rate of a species the more important it is that suitable habitats are available beyond the release sites themselves. The sites identified are located in a landscape containing additional suitable habitats and are within or abut a wider de-intensification and nature recovery corridor of at least 200 km^2 in Sussex (Weald to Waves, 2024).

Conclusion. Multiple sites are available that meet the specified adult resources (nectar), host plant and other habitat requirements of *A. crataegi*, and there is potential for a regional metapopulation to establish.

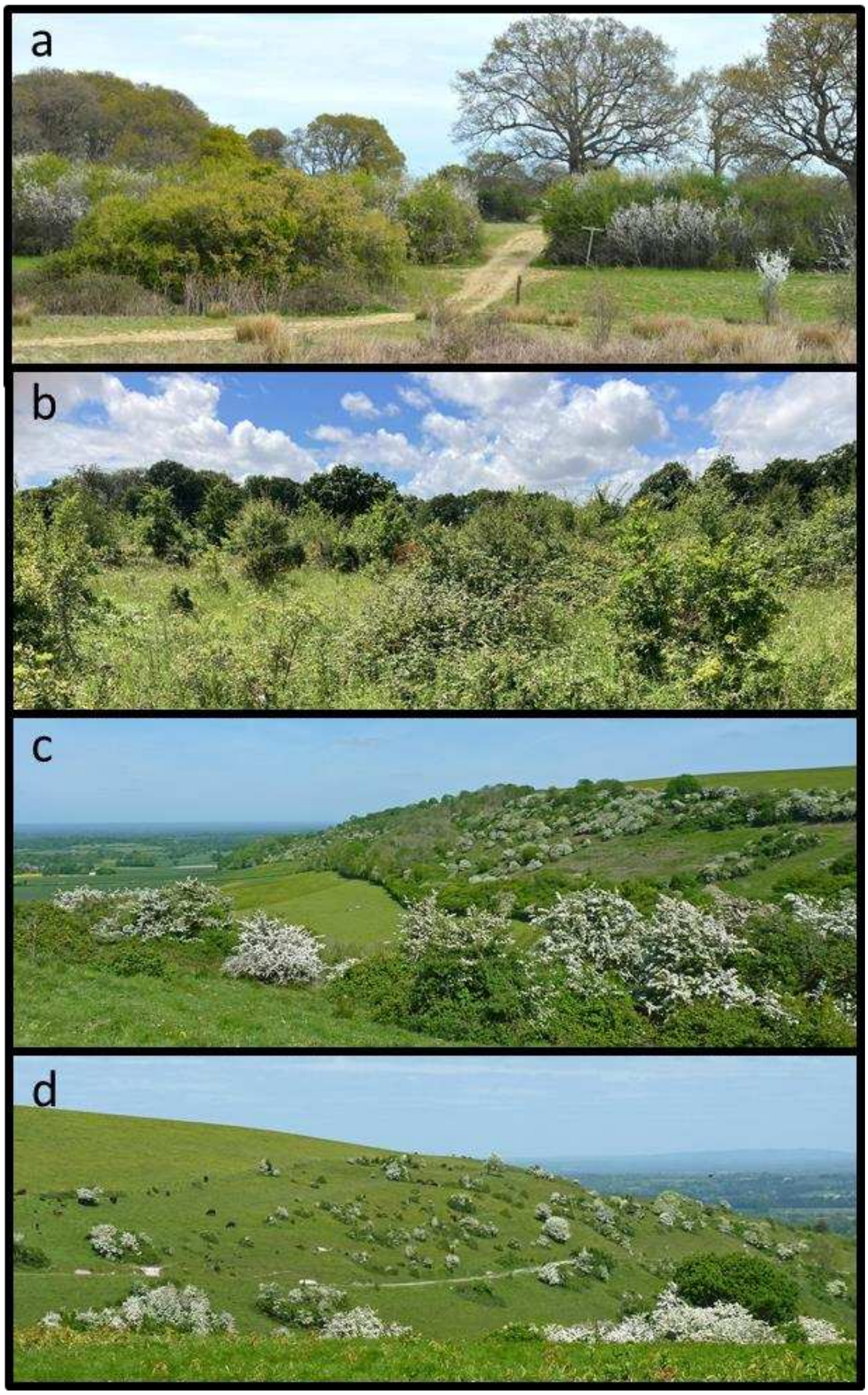

Figure 5. Proposed release sites: (a) Overgrown hedgerows and scattered white-flowering *Prunus spinosa*, with fresh green growth of *Crataegus monogyna*, at Knepp Wildlands; (b) Scattered *C. monogyna* scrub in successional meadows with *P. spinosa* in hedgerows, at Frenchland Barn; (c) Scattered flowering *C. monogyna* on the South Downs escarpment of West Sussex; view from Sullington Hill towards Barnsfarm Hill; (d) Sullington Hill, West Sussex, with flowering bushes of *C. monogyna*. Photos: a, b © Chris Thomas; c, d © Neil Hulme.

PART C. Risk assessment.

6. *Are there risks associated with the translocation?*

Risk assessments associated with reintroductions, and particularly with translocations outside historically-known distributions, will include biological, social and economic components. The details will inevitably be situation and taxon specific. Biologically, there is consideration of whether introduced species will have adverse effects on existing ecological communities (e.g., via associated parasitoids and pathogens), which will be unlikely for most instances of reintroductions. Equally concerning may be the potential impacts on donor populations, hence the importance of selecting appropriate large populations to source stock (see step 7, below). It is also important to consider the balance between any social, commercial or economic costs and the beneficial consequences of translocations, evaluation of the legal basis for any releases (mainly considered in step 1), and assessment of the cost-effectiveness of the proposed project. Such risks may include the need for financial support, and consideration of whether resources would be more cost-effective if allocated to other conservation projects.

Community effects - natural enemies. Studies of parasitoids associated with *A. crataegi* in the region are provided in Table S4. The most frequently named parasitoid is *Cotesia glomerata*, which commonly attacks the large white butterfly *Pieris brassicae*, and is already widely established in Britain. All remaining known parasitoids of *A. crataegi* (Table S4) are also established in Britain, typically specialising either on the butterfly family Pieridae (the whites and yellows), to which *A. crataegi* belongs, or on a wider range of Lepidoptera (Broad, Shaw & Godfray, 2016; Tschorsnig, 2017). It is unlikely that the *A. crataegi* populations in Britain could result in the establishment of any new parasitoid species.

Other natural enemies (pathogens, including viruses and bacteria) are also most likely to be shared with other species in the Pieridae. Native resident British species in the Pieridae are *P. brassicae*, the small white *P. rapae*, the green-veined white *P. napi*, the orange-tip

Anthocharis cardamines, the wood white *Leptidea sinapis*, and the brimstone *Gonepteryx rhamni*; with the clouded yellow *Colias croceus* visiting annually. GBIF records show that all of these species co-exist widely with *A. crataegi* across western Europe, making it unlikely that disease or parasitoid-mediated interactions between *A. crataegi* and other pierids would have negative impacts on their distributions.

Three of these pierids are migrants, with many thousands of individuals moving naturally from continental Europe to Britain annually (Williams, 1935; Baker, 1969; Hu et al., 2016; Hawkes et al., 2024). Hence, pathogens for which adult pierid butterflies are vectors will have been transferred by this means already. Commercial imports of living *Crataegus* plants from continental Europe have likely numbered in the millions in the recent past (Whittet et al., 2016; Ryan, 2023; EFSA et al, 2023). Hence, it is unlikely that plant-surface and plant-transferred pathogens exist in continental areas of western Europe without having already arrived in Britain. Overall, the proposed reintroduction is unlikely to introduce pathogens not already present in Britain.

Infection with *Wolbachia* bacteria is one potential concern since they can potentially have either positive or negative impacts on insects, including butterflies (Ahmed et al., 2015), ranging from providing resistance to viruses, parasitoids and insecticides, hormonally improving host plant quality, increasing pupal weight, host survival and reproduction, maintaining sex ratios, through to generating cytoplasmic incompatibility, increasing individual mortality and generating highly biased sex ratios, culminating in either increased or decreased population sizes (Hyder et al., 2024; Shao et al., 2024). Information is limited for *A. crataegi*, although a study in central Asia found no evidence that *Wolbachia* had negative "*effects on* A. crataegi *fitness and no reproductive abnormalities* [were] *induced*" (Bykov et al., 2021). Family-level gender ratios and fertility/survival will be monitored during the captive breeding programme (see step 8, below).

Commercial and social effects. The species used as larval host plants are all in the Rosaceae, and this family includes *Malus* (apples), *Pyrus* (pears), and *Prunus* (plums, cherries). Historically, the butterfly was noted as a potential orchard pest, but it has proven difficult to track down records that distinguish between *A. crataegi* larvae as sometimes being observed on fruit trees, and the larvae having commercially significant consequences. Martelli (1931), for instance, noted that Italian populations did not cause “serious injury” to orchard trees in the early 20th century (Table 5). We found no evidence of the species being regarded as an orchard pest in Europe (westwards of longitude 20°E) in the last 75 years in either the ecological or horticultural literatures. Studies of insect pests of apple orchards in the Rhône valley in France do not mention *A. crataegi* (Simon et al., 2011); neither does a review of integrated crop management and organic systems for apple production in Europe as a whole (Tresnik & Parente, 2007). There is no mention of *A. crataegi* in three companion papers on the control of pests of apples and pears in northern and central Europe (Cross et al., 1999a, 1999b; Solomon et al., 2000), or in a more recent study of the control of invertebrate pests of pears across Europe (Shaw, Nagy & Fountain, 2021). Nor could we find any recent mention of the butterfly as a pest of cultivated *Prunus*, cherries or plums, in the region under consideration (e.g., Jaastad et al., 2004; Quero-García et al., 2017). We conclude that *A. crataegi* is not a pest of orchards and fruit production under modern horticultural practices in western Europe (Table 5).

Costs and benefits. It is considerably easier to assess the direct costs than the potential social and financial benefits of any specific project, which will likely generate additional wildlife tourism income to the region, and increase the sense of wellbeing in those concerned about the future of butterflies. Knepp specifically is visited by thousands of wildlife-enthused visitors annually. Numbers for the latest single years for which records are available (Rachel Greaves, *personal communication*) are 10,000 visitors on ‘wildlife safaris’ (in 2024), 5,697 paying campers (2023), and 5,645 visitors accessing public footpaths (2022), with the Knepp Wildland Foundation collaborative programmes providing additional educational opportunities (e.g., reaching 40,500 through green careers events in 2024). More broadly, there are approaching 38,000 members of the Sussex Wildlife Trust and over 40,000 members of the NGO Butterfly Conservation, who are likely to obtain particular pleasure (and hence in principle an increase in wellbeing) from the species' reestablishment. The total pool of people who might derive pleasure is much larger, but hard to quantify: there are around 0.9 million members of Wildlife Trusts nationally, 3-4 million BBC *Countryfile* viewers weekly, 1.2 million RSPB members and 5.4 million National Trust members (these memberships and viewing figures overlap with one another).

The provisional budget for the project, up to and including the first phase of releases, is £75,500 (at 2024 rates) consisting of: Project Officer for 3 days/week (£24,000), Project Officer UK site visits (£1,000), Assistant to Project Officer to oversee the captive breeding programme (£6,000), collection of egg batches from a minimum of 2 continental sites (£5,000), captive breeding equipment (£4,500), and veterinarian support for 5 months to carry out a Disease Risk Pathway analysis (£35,000). Advice from butterfly ecologists and researchers is being provided gratis, and most of the rearing and monitoring will be undertaken by volunteers. Regulatory procedures account for the majority of the expenditure. Project Officer time is required to compile the considerable amount of information required by national authorities (Defra, 2021) prior to translocations (including reintroduction of species to the UK) taking place, and an independent veterinary risk assessment (paid for by government agency Natural England, in this instance) is mandatory to ensure that any disease, parasitoid and other risks are assessed and minimised (Sainsbury & Vaughan-Higgins, 2012; Suarez et al., 2017; Bourn et al., 2024).

Conclusion. The risks of new pests and diseases, or other 'adverse' ecological interactions, arising from reintroduction of *A. crataegi* appear to be very small. Legal and financial considerations appear to be surmountable, as considered further in the Discussion. Step 6 of the framework is ongoing.

PART D. Releases and monitoring.

7. ***Is suitable stock available for translocation?***

This aspect of the assessment involves consideration of the provenance of the source material, identifying populations likely to be well adapted to the climates and other environmental conditions at the target release sites. This will involve liaising with researchers and conservation organisations in the areas where source stock may be obtained, both to facilitate collections and ensure that source populations are sufficiently large to sustain proposed levels of removal; where appropriate, source population sizes should be monitored before and after collecting. The potential to 'bulk up' many insect species over one to three generations in captivity (but not more, to prevent inbreeding or adaptation to captivity) typically enables stock to be obtained with minimal impact on the source populations, although some taxa will undoubtedly be much harder than others to culture in captivity.

Genetics and population sources. The source material considered for reintroduction is from the butterfly clade represented in western Europe, which is the same clade as the historical specimens recorded from Britain over a century ago (Todisco et al., 2020). Egg laying and larvae are confined to *P. spinosa* and *C. monogyna* in the region from which source material might be obtained (Table 5a), both of which are extremely abundant in the landscape proposed for releases (Figure 5). To increase genetic diversity in the introduced population, the aim is to source materials from more than one population in western Europe.

Availability of source locations with climates similar to south-central England. The climatic similarity of northern France and mid-elevation areas in southern France and the Iberian Peninsula (Figure 4) highlight locations from which potentially suitable stock could be sourced. The locations of documented populations within these matching climatic zones include parts of Brittany and Normandy in France, mid-elevations in the eastern Pyrenees in Spain (reported to support large populations; Constanti Stefanescu, *personal* *communication*) and the Massif Central in France (Figure 6; populations in other areas of western Europe also have matching climate, especially in France). The butterflies from these locations have the same haplotypes (evolutionary lineage) as historical specimens of the extinct British material (Todisco et al., 2020), and egg laying and larval feeding is on *C. monogyna* and *P. spinosa* (Table 5).

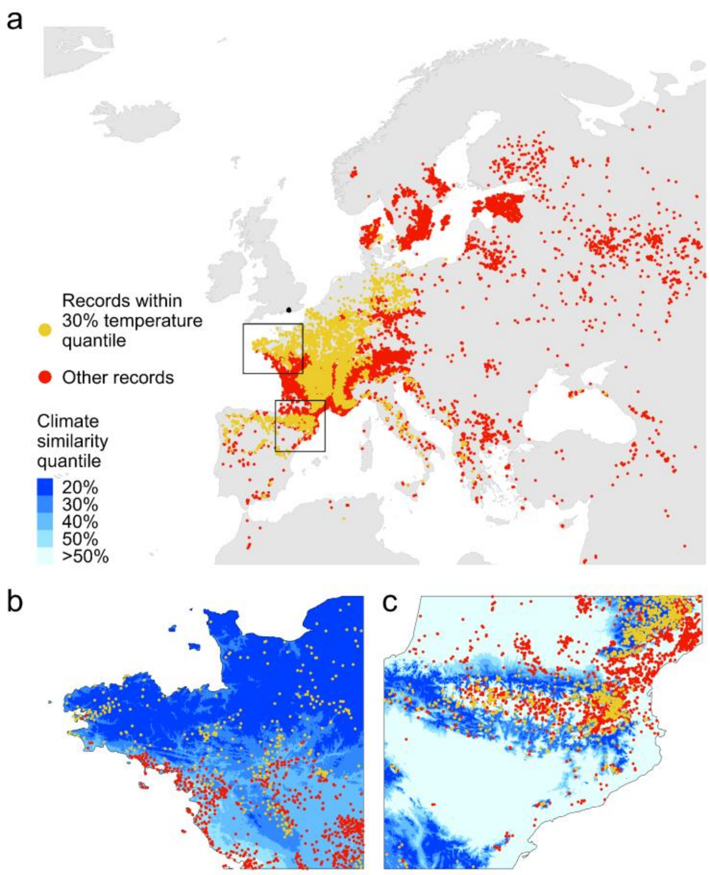

Figure 6. (a) Climatic match of the West Sussex (black spot) potential reintroduction sites, illustrating areas of overlap of distributional records of the species in 2014-2023 (from GBIF) with the temperature match (30% most similar) of the area from Figure 5b. Species records with similar (yellow) and different (red) climatic conditions are shown. Northwestern France (b) and the Pyrenees (c) illustrate areas of overlap in greater detail (underlying darker blue shading indicating greater climatic match).

Conclusion. Populations can be identified with suitable genetics (matching extinct British specimens) and ecological (larval host plants) attributes within areas where the climate is similar to that in the proposed reintroduction area. Further progress is now required to obtain material compliant with appropriate UK (England), source country and regional regulations (see Discussion).

8/9. Releases and reporting.

Translocation programmes then require the development of collecting, potentially captive breeding, and release and monitoring programmes. Ideally, projects will be established in such a way whereby release locations have somewhat contrasting local conditions, enabling researchers and managers to gather data that will improve the success of future projects. This information should then be collated into accessible reports (preferably publications) and disseminated to all partners. Opportunities for public appreciation and involvement in the establishment, conduct, and monitoring of projects should normally be communicated widely.

The practicalities of collecting, captive breeding, release and designing the monitoring schedule (step 8) for *A. crataegi* are still being prepared at the time of writing in December 2024, but are not insurmountable. The variation in different soils, mixtures of *P. spinosa* and *C. monogyna*, alternative nectar sources and different browsing regimes will enable the monitoring of any initial experimental release programme to generate new knowledge that will inform priorities when identifying subsequent release sites and management options. It will only be possible to confirm some of the details of captive breeding, releases and monitoring once the initial stock is obtained, since the amount of material obtained and ease of bulking numbers up in captivity are unlikely to be known precisely before the programme actually starts. Information currently under consideration for inclusion in the monitoring programme are host plant and microclimate use, flower visitation relative to the availability of different flowering species, pre- and post-diapause survival (of families during captive breeding and following release), dispersal of males and females, exchanges of individuals between release sites and the colonisation of new sites, gender ratios (e.g, associated with potential *Wolbachia* incidence for captive-bred families and post-release populations), population growth rates, and retention of samples to track genetic variation and microbial incidence. Reporting on progress and lessons learned (step 9) is expected to follow.

Given the information on dispersal (step 2), climate and habitat (steps 3-5), the updated targets are to achieve restoration at the landscape-scale (>100 km^2), containing at least 10 breeding concentrations (>25 ha total) within ten years of the first major releases, with the potential for further geographic expansion thereafter. The longer-term aspiration is that *A. crataegi* becomes fully established (i.e., classified as Least Concern in the UK) over several decades, not requiring further conservation interventions to maintain viable breeding populations thereafter.

DISCUSSION

The framework outlined here (Table 1) has been useful in assessing the reintroduction of a species long after it became extinct, and would also be appropriate for translocating a species outside its known historical range (assisted colonisation). Using this approach, we find that there is considerable potential to reestablish the black-veined white butterfly, *Aporia crataegi*, in lowland England. There is a sound rationale for reintroducing *A. crataegi*: translocation will contribute to UK policy targets, benefit the species itself, provide multiple benefits for other taxa through associated habitats, and act as a socially-positive example of species reestablishment (step 1); and we assess that the species is very unlikely to recolonise Britain without assistance (step 2). As in all cases when introducing a species to a new area for the first time, or to an area from which it has been absent for a long period, there are nonetheless considerable uncertainties. Hence, it is important to design release programmes in a way (e.g., releases in contrasting local habitat conditions) that maximises the capacity to learn from initial attempts to establish new populations of a species.

The species became extinct historically at a time when England’s climate was colder (the likely cause of regional extinction; step 3), and both the current climate (step 4) and habitats (step 5) in the proposed reestablishment area are deemed to be suitable. The climate of lowland southern, central and eastern England today is considerably warmer (and hence more suitable) than in the years immediately preceding the species’ extinction from Britain, and is projected to be one of the most climatically suitable regions of Europe in the coming decades (Figure 3). Furthermore, the proposed landscape for reestablishment contains many sites that meet the habitat, host plant and nectar requirements of the butterfly (Tables 4-6, Table S2), at a spatial scale relevant to the dispersal and population connectivity of the species (Table 2). All potential indicators suggest that a substantial and extensive metapopulation could be established. Assessing risks (step 6), sourcing breeding stock (step 7), planning captive breeding programmes, release and monitoring (step 8), and then reporting (step 9) are still under development for this project, and will be considered in greater detail in future publications.

In addition to this nine-step framework, all projects of this kind must operate within the legal requirements of all countries / states / provinces involved, including land ownership and permissions, national and local conservation designations governing donor populations (we have provisionally identified source populations and engaged with entomologists and conservationists in continental Europe to obtain materials) and recipient sites, and constraints around the transport of species across national and other administrative boundaries. For the UK, this is especially contentious because the climate-driven movement of many species northwards from continental Europe into Britain is likely to be prevented by the barrier of the English Channel. This means that specific decisions will likely have to be made around the arrival of many species, rather than unaided colonisation taking place via conservation corridors or other connectivity projects. As such, approval from the government agency Natural England is required (Defra, 2021) as well as an independent veterinary risk disease and parasite assessment (Sainsbury & Vaughan-Higgins, 2012; Suarez et al., 2017;

Bourn et al., 2024). For *A. crataegi*, the aim will be to minimise the risk of introducing new parasitoids and diseases (e.g., by collecting healthy gravid females, or keeping wild-collected egg batches in sealed containers to avoid the accidental release of egg parasitoids). Such ‘enemy free’ stock will also provide opportunities for rapid population growth in the first few years (=generations) after release, before they accumulate parasitoids and pathogens, which are shared with other, already-resident species in the family Pieridae.

While this current regulatory rationale is understandable, the formal process generates a financial barrier. The approval and veterinary assessment costs represent three-quarters or more of the total ~£75,500 initial budget (see step 6, above), and these additional costs appear to be less enticing to external funders than the direct costs of the reintroduction programme. This total amount is modest by vertebrate reintroduction standards (for example, the total cost of the Scottish Beaver Trial was ~£1,573,000; Scotlink, 2021), and it is miniscule relative to the £1.8 billion planned 2025/26 government expenditure on environmental land management schemes (Defra, 2024). Given that bespoke management for *A. crataegi* is unlikely to be required following its successful reestablishment, this would appear to be relatively good value for an ~1.6% increase in the British butterfly fauna. Nevertheless, budgets of up to ~£100,000 will likely prevent most insect translocations across national borders from ever happening; unless they are prioritised and funded by national conservation bodies or major NGOs. Government agency Natural England is generously covering the veterinary assessment costs for *A. crataegi*.

This support is extremely unlikely to be available at present for the assisted colonisation of a species for which there are no historical records in Britain. Streamlined protocols, international priority lists and multinational agreements need to be developed if insect translocations across national or other boundaries are to be scaled-up. Unless this happens, risk-averse procedures of individual nations (and Convention on Biological Diversity concerns over biological invasions) are likely to prevent most potential assisted colonisations from taking place. Such a project would be unlikely to be sanctioned in the UK context, even if a species is endangered in continental Europe and the climate and habitats of the UK might provide a refuge.

These regulatory and financial barriers may encourage unscrupulous actors to undertake illegal releases. Indeed, an apparent clandestine introduction of *A. crataegi* was reported in 2023 (BBC, 2023), with further reports of the species being present at the same site in 2024 (Butterfly Conservation, 2024). This is seriously problematic because it (i) generates a negative impression of butterfly conservationists acting outside the law, (ii) provides no useful information to inform future releases because the manner of release is undocumented, and it is unknown whether any of the 2024 observations of adult butterflies represent breeding success since 2023 or further 2024 releases (the May 20th date of observations in 2024 implies the latter), and (iii) may not represent appropriate source material (e.g., if inbred through captive breeding). These events also result in ‘experts’ highlighting all of the possible negative consequences of the reestablishment of the species, as highlighted in the BBC (2023) headline “*Illegal reintroduction of extinct species is harmful for environment, experts warn*”, which is unlikely to be true and jeopardises support for the legitimate reintroduction of appropriate material of the same species at suitable sites (as in the case developed here). These clandestine releases are damaging, regardless of the outcome. If the butterflies establish, the illegal reintroduction will appear to reduce the case (and financial support) for the introduction of more suitable stock elsewhere. If unsuccessful, it may be taken as evidence that other reintroduction attempts will be unsuccessful and thus weaken the case (and financial support) for the introduction of genetically-appropriate material to networks of higher quality habitats elsewhere. If barriers to translocations were reduced, properly managed translocation programmes could demonstrate viable pathways for translocation and reduce the appeal of counterproductive clandestine releases.

Maximising the chances of success. Successful establishment is never guaranteed, particularly when a species disappeared a long time ago, or for assisted colonisation projects into regions from which there are no historic records. The framework used here enables those involved to consider the merits of different possible strategies to increase the chances of success. It enabled us to identify the climatic and habitat requirements of the species and target landscape, and the availability of potential source populations.

The information available for this project suggests that the current climate of southern and eastern Britain is unlikely to be a major constraint for *A. crataegi* (Figures 2, 3, 4, 6), and that the climate there now is likely much more suitable than during the period when *A. crataegi* disappeared. Nonetheless, the 'weather' or 'bad years' can still be an issue (environmental stochasticity). The high variability in between-year population growth rates characteristic of many insect species (Palmer et al., 2017) can result in temporary periods of negative population growth, so release programmes should consider undertaking releases over several years. This increases the chance of coinciding with at least one 'good year'. Where feasible, releasing hundreds to thousands of individuals can mitigate against environmental stochasticity (good- and bad-weather years), Allee effects (deterministic reductions in population growth at very low densities in some species, for example caused by rapid emigration from release sites resulting in low mating success), and demographic stochasticity, given the low egg-to-adult survival of most insects and the particular susceptibility of species with egg/larval groups (as in *A. crataegi*) to high levels of population variability (Kuussaari et al., 2004). Hence, the source material may need to be 'bulked up' in captivity for a generation or two (as we plan for *A. crataegi*).

There is also uncertainty about the best habitat conditions and management for reestablishments to succeed. So, it is sensible to undertake releases at several heterogeneous sites. Researchers and conservation practitioners will then be able (via monitoring) to quantify the characteristics of sites that provide, for example, the greatest adult residence and larval survival in relation to nectar sources, host plants, shelter and the presence of browsing animals. These data will come together to identify the rates of population growth and population spread associated with different release conditions, informing subsequent releases and management options.

Gathering dispersal data and understanding the population dynamics of a species is valuable because it helps set the spatial scale of a particular project. Given the dispersal behaviour of *A. crataegi* (above), and its variable population dynamics (it may not survive for long in a small isolated habitat patch), the likelihood of success will be higher if habitat occurs over substantial areas of the landscape; as in the wider landscape considered here.

Identifying suitable source populations also benefits from considering factors such as the climatic similarity, host plant use that minimises risk and, if available and relevant, knowledge of the genetic similarity of extant populations to historical populations. However, all populations evolve, and genotypes adapted to 21st century conditions may be more successful than those that are closest to the historical populations that became extinct decades or centuries ago. In the project described here, we could identify suitable genetic material associated with *C. monogyna* and *P. spinosa* host plants, within the same overall clade as the extinct British forms. We favour combining genotypes from two or more source populations to increase genetic diversity within the reestablishment region, and hence provide evolutionary capacity within the resulting population.

In conclusion, reviewing the information gathered here (steps 1-7), we consider that there is a realistic prospect of reestablishing *Aporia crataegi* in Britain, a century after its regional extinction. We are in favour, therefore, of monitored releases of our target species being undertaken to evaluate population growth, host plant use, and rates of colonisation away from release sites, aiming to develop knowledge to inform future best practices for releases. As a conspicuous species able to visit flowers in gardens, as well as in wilder habitats, we believe that this is likely to be widely supported by conservationists and by the public.

The framework used here could be adopted for a wide range of insect translocations globally, although consideration should also be given to additional factors which may apply in different circumstances; as identified by other frameworks, including the US Fish and Wildlife Service (2024) approach (Table S1). Nearly all study systems are likely to have a number of case-specific considerations, so we would encourage researchers and managers to be relatively flexible so as to focus on the constraints, risks and opportunities most relevant to those systems. The framework could also be adopted for additional translocations to the UK, but it is only likely to be extended to assisted colonisation (as opposed to reintroductions) if current national regulations and priorities are adjusted to facilitate the regulatory approval of translocations that would bring (global) conservation benefits. Calls for increasing numbers of translocations are likely to grow in coming decades, as the impacts of climate change on the distributions of species become increasingly difficult to accommodate within 'static' conservation programmes. It is important that '*trans situ*' approaches to conservation (complementing *in situ* and *ex situ* conservation; Thomas, 2020) are sufficiently well developed that it becomes increasingly feasible (socially, politically and empirically) to undertake priority translocations over the coming decades. Generating methodologies and experience to enable these to be assessed and conducted in a systematic way should facilitate the process.

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AUTHOR CONTRIBUTIONS

All authors contributed to the development of the project. CDT devised and drafted the manuscript and other authors commented. CAC undertook the climate-matching analysis, MO, NACH and NADB provided expertise and information on butterfly ecology and introductions, ECC and NACH conducted habitat surveys, and BGM, PG and NACH provided information on the proposed translocation landscapes in West Sussex. PG and BGM provided coordination with Natural England. We thank Rachel Greaves for providing visitor numbers to Knepp.

CONFLICT OF INTEREST

Two of the authors (ECC, PG) were employed by the Knepp Estate at the time the work reported here was conducted, and one (BGM) is employed by the Knepp Wildland Foundation - two of the six potential release sites considered here are in the Knepp Wildland areas of the Knepp Estate.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available from the following sources. Bioclimatic indicators data for Europe from the ECMWF Climate data store (available from *Copernicus*, Woulters, 2021), national boundaries to distinguish land/sea were downloaded using the geodata package (Hijmans et al., 2023), and code for the climate similarity analysis is available on GitHub: *https://github.com/charles-cunningham/translocationClimate*. Central England temperature data since 1850, v2.0.1.0 (April 2023 release) are available from the National Climate Information Centre (2024), *https://hadleyserver.metoffice.gov.uk/hadcet/*. *Aporia crataegi* presence records from Global Biodiversity Information Facility (GBIF.org, 2024). Site host plant and nectar plant abundances are provided in Table S3, and sources of information in Tables 2-6 are accompanied by corresponding citations of the original research papers.

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SUPPLEMENTARY FIGURES AND TABLES

Table S1. *Examples* of published approaches to reintroductions and translocations. Steps and considerations suggested in publications are listed beneath the four higher-level categories identified in the current paper.

PART A - Rationale and justification for translocation		**PART B - Evaluating the likelihood of establishing a viable new population**			**PART C - Risk Assessment**	**PART D - Releases and monitoring**			
1. What is the rationale for establishing a species outside its current distribution?	2. Will the species colonise without assistance?	3. Why did the species become extinct historically?	4. Is the climate suitable for the focal species?	5. Are the ecological requirements of the species and habitat available?	6. Are there risks associated with the translocation?	7. Is suitable stock available for translocation?	8. Release and monitoring schedule	9. Reporting on progress and lessons learned	**Current paper**
1. Is there a high risk of decline or extinction under climate change?	2. Will the organisms arrive on their own to new habitat?	3. Are translocation and establishment of species technically possible?			4. Do benefits of translocation outweigh the biological and socioeconomic costs and constraints?				Hoegh- Guldberg et al. (2006)
1. The case for translocations in the context of a changing environment 2. Aims, purposes and objectives		3. Biological principles and feasibility studies			4a Availability of… stock and relevant legal considerations 5. Social and political considerations	4b Availability of suitable release stock and … legal considerations	6. Monitoring		Invertebrate Link (2010)
1. Deciding when translocation is an acceptable option 2. Planning a translocation		3. Feasibility and design			4. Risk assessment	5. Release and implementation 6. Monitoring and continuing management		7. Dissemination of information	IUCN/SSC (2013).
1. Identify management objectives for multispecies conservation	2. Identify or forecast species that are being introduced into an ecosystem	3. Predict which resident species will interact with the newly introduced species 4a. Predict introduced species establishment success and consequences for resident species population dynamics and ecosystem services 5a. Evaluate consequences for multiple management objectives and their trade-offs under uncertainty			4b, 5b. Assess trade-offs under uncertainty and identify strategies that avoid worst-case scenarios			6. Improve future predictions	Van Kleunen et al. (2023)
1. Decision framing and engagement	2. Identifying objectives	3. Feasibility assessment (including habitat and climate suitability) 4. Developing alternatives 5a. Risk assessment and prediction of outcomes			5b. Risk assessment and prediction of outcomes	6. Deciding course of action 7. Implementation		8. Outcomes assessment, dissemination	US Fish and Wildlife Service (2024)

Sequential numbering listed here retains the order to steps in each published framework. In some instances, the original numbers have been changed where certain numbered parts of the original publication are not formal steps in the framework (e.g., some of the numbered sections in the Invertebrate Link (2010) framework represent a mixture of general information and considerations around releases, rather than specific steps). Where steps fall under two different categories, they are listed as 1a, 1b etc, with the relevant component underlined here.

Table S2. Candidate sites considered for analyses of the climate match between possible reestablishment locations in West Sussex, England, and climatic conditions across Europe. Further site details are provided in Table S3.

ID	**Site**	**OS GridRef**	**Easting**	**Northing**	**Longitude**	**Latitude**
1	**Knepp Wildland**	TQ136209	513600	120900	-0.38326538	50.976317
2	**Knepp Wildland**	TQ144205	514400	120500	-0.37200088	50.972563
3	**Frenchland Barn**	TQ146161	514600	116100	-0.37053724	50.932974
4	**Steyning**	TQ165112	516500	111200	-0.34507367	50.888549
5	**Steyning**	TQ168104	516800	110400	-0.34106586	50.881298
6	**Sullington Hill**	TQ095121	509500	112100	-0.44428369	50.898007

Table S3. Potential initial reestablishment sites in West Sussex, England

Site & OS Grid Ref	Habitat attribute	
1. Knepp Wildland[$] **'Hampshire 1'** **TQ136209**	Host plants	>200 scattered *Crataegus monogyna*, >200 scattered *Prunus spinosa*, with suitable shelter.
	Nectar plants*	Highest summed DAFOR score. *Prunella vulgaris* F, *Odontites vernus* F, *Geranium dissectum* F, *Centaurium erythraea* F, *Cirsium vulgare* O, *Convolvulus arvensis* O, *Persicaria hydropiper* O, *Mentha arvensis* O.
	Landscape connectivity	Adjacent to 'Shooting Ground'[$] & other Knepp sites.
	Dist to Site 1	N/A
2. Knepp Wildland[$] **'Honeypools Barn'** **TQ144205**	Host plants	70 scattered *Crataegus monogyna*, 150 scattered *Prunus spinosa*, with suitable shelter.
	Nectar plants*	*Prunella vulgaris* F, *Centaurium erythraea* F, *Geranium dissectum* O, *Epilobium* sp. O. Also *Trifolium repens* A.
	Landscape connectivity	Good connections via thorny scrub across the entire Southern Block. Corridor along blackthorn-rich road margins and thorn-rich hedgerows cross-country towards Frenchland Barn scrub meadow (below).
	Dist to Site 1	0.9 km
3. Frenchland Barn **'Scrub meadow'** **TQ146161**	Host plants	~4 ha sheltered, scrubby meadow with abundant *Prunus spinosa*.
	Nectar plants*	*Cirsium* A, and otherwise nectar-rich.
	Landscape connectivity	Additional sheltered woodland glades (one with abundant *P. spinosa*) to the immediate East, connected by wide rides. Good connections southward to Chanctonbury Ring and SSE-ward towards the Steyning sites via thorny hedgerows, some scrubby fields and laggs.
	Dist to Site 1	4.9 km, equidistant stepping-stone between Knepp and the South Downs.
4. Steyning Downland Scheme **'Steyning Rifle Range'** **TQ165112**	Host plants	Warm, sheltered coombe with abundant scattered and clustered *Crataegus monogyna*; abundant *Prunus spinosa* as scattered stands and dominant in peripheral hedgerows and woodland margins.
	Nectar plants*	Widespread nectar sources, with abundant *Trifolium pratense* and plenty of *Knautia arvensis.*
	Landscape connectivity	Connections occur westward along the Downs, to the Sullington Hill site and beyond; *Crataegus monogyna* is extremely widespread along the escarpment, and more

		locally available on the dip slope of the South Downs.
	Dist to Site 1	10.0 km
5. Steyning Downland Scheme **‘Steyning Round Hill’** **TQ168104**	Host plants	Sheltered multi-aspect chalk grassland slopes and a *Prunus spinosa*-rich chalk pit. Scattered *Crataegus monogyna* and *Prunus spinosa* stands.
	Nectar plants*	Adequate nectar sources, with some *Knautia arvensis*.
	Landscape connectivity	Steyning Rifle Range 1 km to the North; and westward connections to Sullington Hill and beyond.
	Dist to Site 1	11.0 km
6. Sullington Hill **Sullington Manor Farm** **TQ095121**	Host plants	Deep, sheltered chalk coombe with abundant scattered *Crataegus monogyna* over >8 ha, together with localised *Prunus spinosa* stands.
	Nectar plants*	*Knautia arvensis*, with *T. pratense*, *P. vulgaris* and *Cirsium* abundant.
	Landscape connectivity	Suitable habitat east at Barnsfarm Hill (towards the Steyning sites) and to the west at Chantry Hill and beyond.
	Dist to Site 1	9.8 km

Footnotes:

$ Additional habitat is available scattered throughout the >400 hectares of the Knepp Estate ‘southern block’, with reestablishment potential also in the wider, surrounding landscape.

* Flower species in purple/blue/red/pink spectrum, using DAFOR (not showing R species) for Knepp sites.

Table S4. Natural enemies	
The Netherlands and Germany: *Cotesia glomerata* (sourced from the Netherlands) listed as a parasitoid of *A. crataegi* (sourced from Germany). *Cotesia glomerata* preferred *Aporia crataegi*-infested hawthorn leaves over uninfested hawthorn.	Geervliet, Vet & Dicke (1996)
Germany, Rhineland: *Apanteles glomeratus* parasitism reached a maximum of ~20-30% in 1955, and ~60-80% in 1956. Some 60-75% of the *Apanteles* cocoons failed to give rise to adults, mainly owing to (hyper)parasitism.	Wilbert (1959)
Germany, Rhineland: Parasitised by generalist *Apanteles glomeratus* and *A. pieridis.* Parasitism was variable and ranged from 0 to 28%.	Wilbert (1960)
Unknown location, literature review: generalist *Apanteles glomeratus* identified as parasitoid.	Laing & Levin (1982)
France, South-East: Film of *Cotesia glomerata* parasitising *A. crataegi*.	Kan-van Limburg Stirum & Kan-van Limburg Stirum (2012)
Germany: Parasitoids *Apanteles glomeratus* and *A. pieridis* caused high mortality in some places.	Blunck & Wilbert (1962)
Germany: *Pimpla instigator* and *Apechthis compunctor* parasitized up to 7 and 12% of the pupae, respectively, in 1956.	Blunck & Wilbert (1962)
Italy: Parasitoids recorded were *Apanteles difficilis*, *Pimpla instigator*, *A. spurius*, *Brachymeria scirropoda*, *Tricholyga segregata*, *A. glomeratus* and *Pteromalus puparum*. Populations reduced by polyhedral virus.	Martelli (1931)
Serbia: *Ceromasia rubrifrons* reared from pupa.	Stanković et al. (2014)
Unknown location: cited report that *Bacillus thuringiensis* is highly virulent in *Aporia crataegi.*	Steinhaus (1951)

Taxonomic revisions mean that few of the published names of *A. crataegi* parasitoids correspond to their current names. Pathogen identification is somewhat uncertain (nearly all accounts are historical; prior to the development of newer molecular methods) and most records are from outside our focal area (i.e., in Asia).

Cotesia glomerata (=*Apanteles glomeratus*) is already widely established in Britain. *Cotesia* (=*Apanteles*) *pieridis* is regarded as a synonym of *C. glomerata* (Broad, Shaw & Godfray 2016).

Pimpla instigator which is a synonym of *Pimpla rufipes*; a major host of this species is also *P. brassicae* and this parasitoid is widespread in the UK.

Apechthis compunctor is a Lepidopteran parasitoid that already occurs with scattered records from Cornwall to Norfolk, and north to North Wales and Yorkshire.

Apanteles difficilis corresponds to *Cotesia cajae* (=*Cotesia perspicua*, =*Cotesia ofella*), all of which are reported already from England (Broad, Shaw & Godfray 2016).

Apanteles spurius corresponds to *Cotesia spuria*, which is known already from England, Scotland, Wales and the Isle of Man (Broad, Shaw & Godfray 2016).

Brachymeria scirropoda is a synonym of *Brachymeria tibialis*, which also parasitises a range of Lepidoptera and occurs in England.

Tricholyga segregata (=*Exorista segregata*) is apparently *Exorista fasciata*, a polyphagous tachinid parasitoid of Lepidoptera (Tschorsnig, 2017) which occurs in England, Wales, Scotland and Ireland.

Pteromalus puparum is a pupal parasitoid of Pieridae and Papilionidae butterflies, found in England, Wales and Scotland.

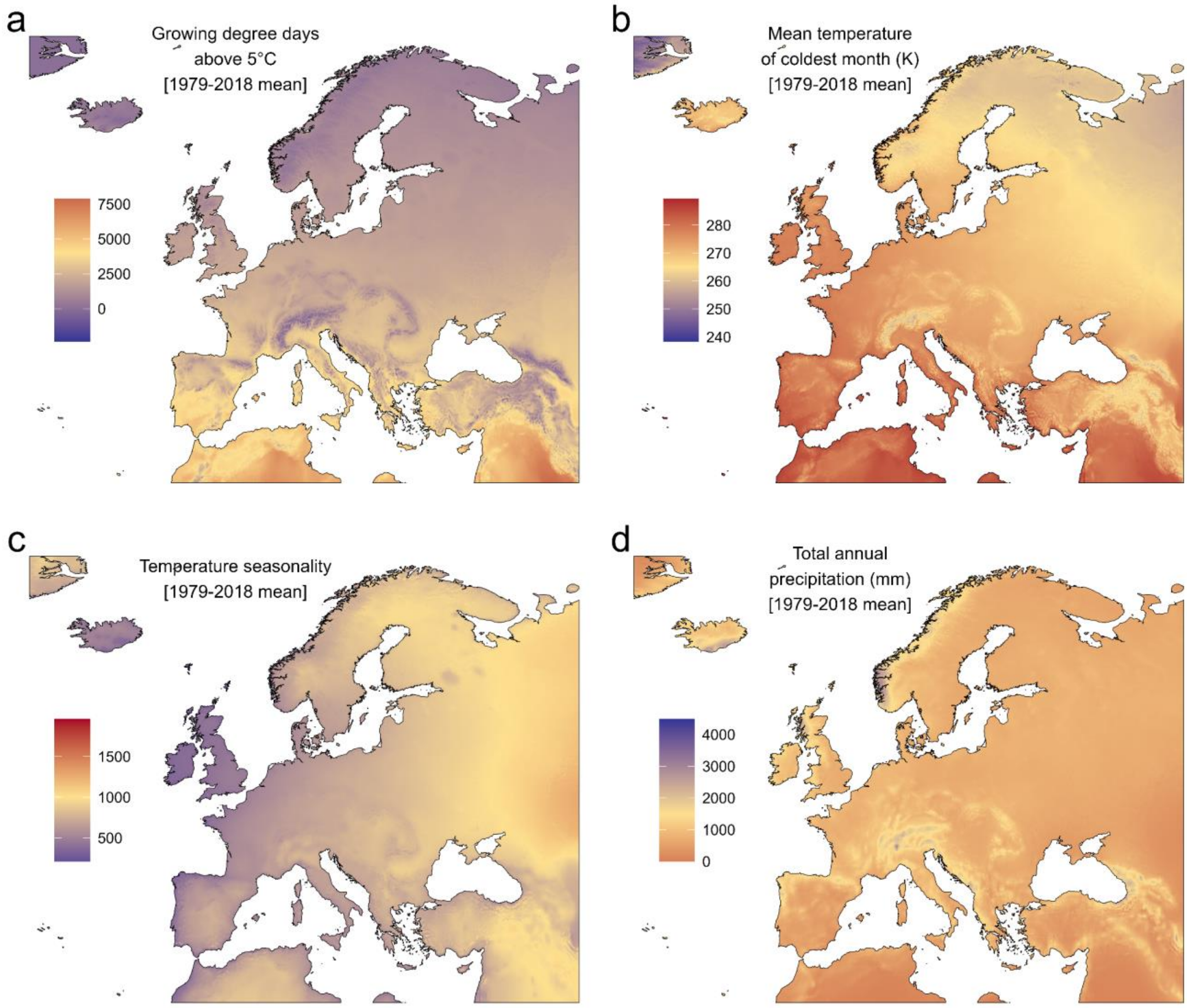

Figure S1. Distribution of four climate variables across Europe.

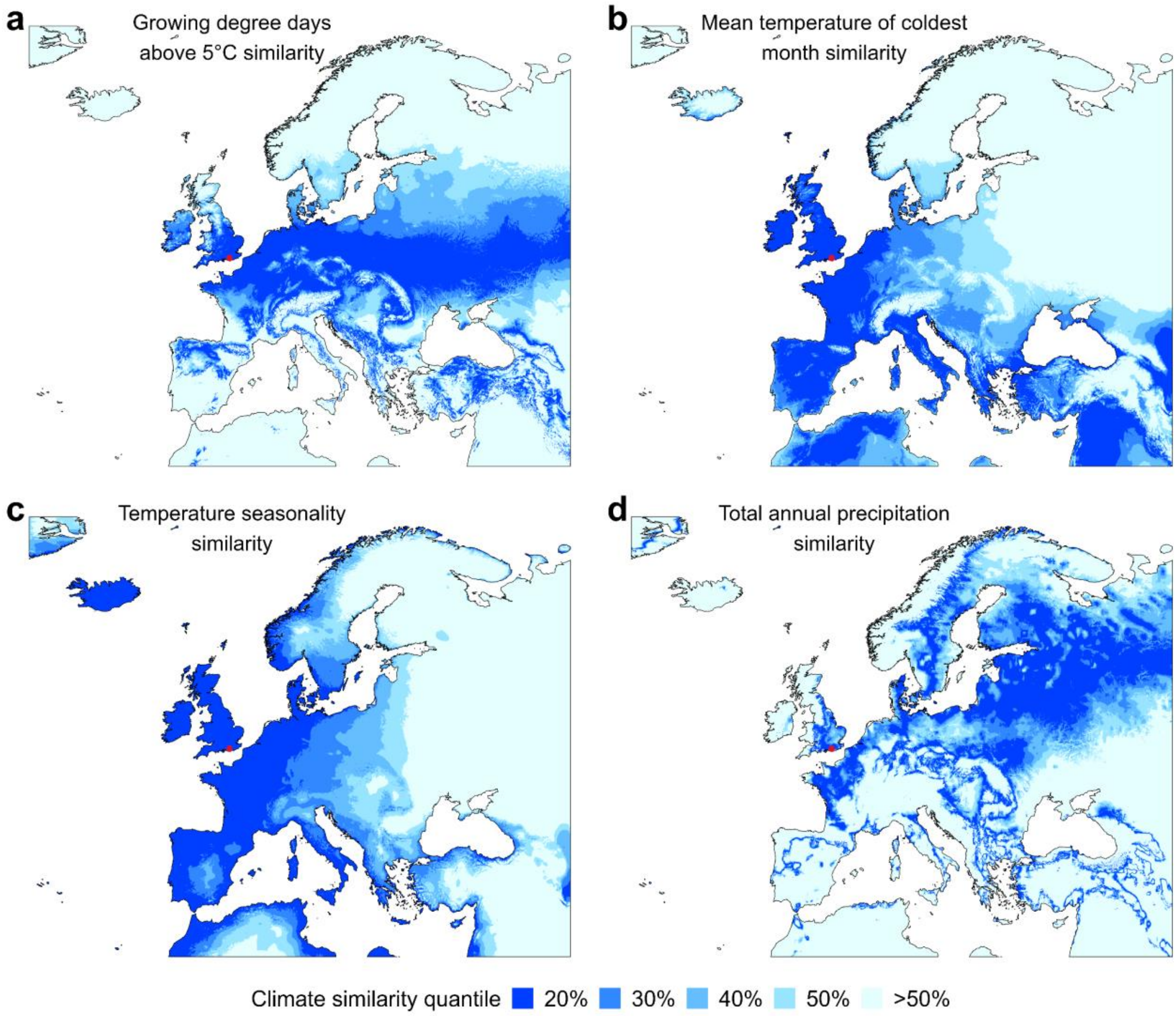

Figure S2. Similarity in quantiles of four climate variables to the West Sussex translocation sites (red dot), England. All four climate variables indicate climate similarity of West Sussex to areas of continental Europe that support populations of *Aporia crataegi* (Figure 1), as well as to other areas in southern, central and eastern England.