Patterns of host use by brood-parasitic *Maculinea* butterflies across Europe

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Summary

The range of hosts exploited by a parasite is determined by several factors, including host availability, infectivity and exploitability. Each of these can be the target of natural selection on both host and parasite, which will determine the local outcome of interactions, and potentially lead to coevolution. However, geographical variation in host use and specificity has rarely been investigated. *Maculinea* (= *Phengaris*) butterflies are brood parasites of *Myrmica* ants that are patchily distributed across the Palæarctic and have been studied extensively in Europe. Here we review the published records of ant host use by the European *Maculinea* species, as well as providing new host ant records for more than 100 sites across Europe. This comprehensive survey demonstrates that while all but one of the *Myrmica* species found on *Maculinea* sites have been recorded as hosts, the most common is often disproportionately highly exploited. Host sharing and host switching are both relatively common, but there is evidence of specialization at many sites, which varies among *Maculinea* species. We show that most *Maculinea* display the features expected for coevolution to occur in a geographic mosaic, which has probably allowed these rare butterflies to persist in Europe.

1. Introduction

(a) Specificity in exploitative interactions

The vast majority of organisms have evolved to exploit the resources of other organisms, whether via herbivory, predation or parasitism [1]. Specialization on a small number of organisms can increase the efficiency of exploitation at the expense of generality [2], although there is still debate on the evolutionary mechanisms leading to such specialization [3, 4]. For parasites, which show long-term association with their hosts, the precise hosts that they exploit can be regarded as being determined by a series of proximate filters [5]. In turn, hosts must be encountered, infected and exploited [5, 6]. These filters can be the product of distribution, ecology and evolution. For example, hosts can only be encountered if their geographic distribution is included in the dispersal range of the parasite, and, all else being equal, more abundant hosts are more likely to be encountered than rare hosts. On the other hand, if parasites have evolved search strategies for particular hosts, this can change the “apparency” of hosts in the environment [7]. Whether a host can be infected may depend on general traits of the host unrelated to the parasite (such as physical or chemical barriers), or the evolution of particular parasite infection mechanisms [8]. Finally, exploitation of the host’s resources to produce new parasites may also be determined by general traits, such as immunocompetence and host vigour [9], or by specific interactions between the host and parasite phenotypes [10]. While some aspects of these filters may be entirely environmentally determined, others will have genetic components that are open to natural selection, and potentially coevolution.

(b) Brood parasites as models of coevolution

Although theories of coevolution are well developed [11], and diffuse coevolution is a likely explanation for much biological diversity [12, 13], demonstrating coevolution is far from straightforward. Avian brood parasites have been proposed to be an ideal system for exploring coevolution [14], for reasons most of which also apply to other brood parasites [15]. Chief among these shared properties are the direct nature of the exploitation and the relatively small number of species involved, which means that a single brood parasitic species normally exerts strong selection on one or a few host species, and that the coevolutionary traits involved are limited to those which are involved in brood care, and so are relatively straightforward to examine.

(c) The Geographic Mosaic of Coevolution

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†We dedicate this paper to the memory of Graham Elmes, who inspired so many *Maculinea* biologists to also consider the ants.

Genetic responses of both host and parasite, mediated by the environment (i.e. Gene × Gene × Environment interactions) are likely to lead to coevolution of parasites and hosts in a geographic mosaic [16]. This has several implications for the pattern of host use that is observed. One likely outcome of mosaic coevolution is that which and how many hosts a parasite exploits varies among populations, although this is an aspect of host-parasite interactions that is rarely explored. The geographic mosaic theory of coevolution rests on three principles; A) That there is geographical variation in the strength of coevolution among populations, which in the case of parasitism can be represented by the presence and abundance of alternative hosts. B) That there is geographical variation in the outcomes of coevolution, which in the case of parasitism implies a mosaic of populations that are locally adapted and locally maladapted to their hosts (although locally adapted populations may predominate as parasites generally adapt faster than their hosts because of shorter generation times and unequal selection pressure [17]), and C) That there is limited trait-remixing among populations, which implies that gene-flow between parasite and host populations is likely to be viscous. The combination of these features provides a mechanism for the maintenance of genetic diversity in coevolving species that would otherwise tend to be eliminated by selection, and is thought to be fundamental to the coevolutionary process {Thompson, 2005 #191}.

To examine the geographical mosaic of host specificity, we survey the variation in host use and specificity across Europe of *Maculinea* (= *Phengaris*) butterflies, which are well-known brood parasites of *Myrmica* ant colonies. The reliance of these butterflies on the sequential exploitation of both specific host plants and host ants means that they naturally occur in small, patchy populations that provide the ideal background for examining geographic mosaics. Using a database prepared from extensive field surveys and published studies, we set out to describe host use of *Maculinea* butterflies across Europe, and to test specific hypotheses associated with the potential geographic mosaic of coevolution in this system: H1) That there is variation among *Maculinea* populations in the species richness and community composition of *Myrmica*. H2) That the different *Maculinea* differ in their host use. H3) That viscous gene flow among populations may lead to geographical structure in host use (i.e. geographically closer populations may be adapted to the same hosts). H4) That *Myrmica* species are not simply exploited in the proportion available (i.e. that there has been selection leading to host specificity). H5) That most *Maculinea* populations are locally adapted to their *Myrmica* community, and exploit the most abundant host, but there are also some populations that show specificity that is maladaptive. H6) That when host-switching does occur, it may be to closely related hosts (since these may be more likely to share the traits used for exploitation).

To our knowledge, this study represents the most comprehensive analysis of geographic variation in host use for any parasite, and many of our results should be widely applicable to other brood parasite and general host parasite systems.

2. *Maculinea* butterflies and *Myrmica* ants

(a) The infection and exploitation of *Myrmica* colonies by *Maculinea* butterflies

Maculinea (abbreviated as “*Ma.*” hereafter) species are obligate brood parasitic lycaenid butterflies, whose caterpillars initially feed on the developing seeds of specific host plants, but are taken in and raised by *Myrmica* (“*My.*”) colonies in their final larval instar [18, 19]. The caterpillars develop within the host ant nest during the autumn and spring, exploiting the resources of the colony, and will then either pupate there, or continue development for an additional year[20].

Although many ant species have associations with lycaenid butterflies [21], the only confirmed host ants of *Maculinea* butterflies are all from the genus *Myrmica.* Thomas et al.[18, 22] gave an overview of misidentifications of the ant species and misinterpretations of captive observations and field data in some initial research. Yamaguchi [23] mentions *Aphaenogaster japonica* as a host of *Ma. teleius* and *Ma. arionides* in Japan, but these have subsequently been shown to be misidentifications of *Myrmica kotokui* [24-26].

Of the four currently recognized species of *Maculinea* found in Europe [27] (see also below), *Ma. nausithous* and *Ma. teleius* initially develop on the flowers of great burnet (*Sanguisorba officinalis*), albeit in slightly different successional stages [21, 28] and positions on the plant [29-31], but may co-occur on the same sites. *Ma. alcon* develops on gentians (*Gentiana* spp. and *Gentianella* spp.), and *Ma. arion* develops on either thyme (*Thymus* spp.) or wild marjoram (*Origanum vulgare*) [19, 32]. After developing through three larval instars on these plants, the newly-moulted fourth instar exits the plant and descends to the soil surface where it awaits discovery by a foraging *Myrmica* worker [19, 33, 34].

Infection of *Myrmica* colonies (usually referred to as “adoption”[33, 35]) involves the larva being picked up by a worker ant and taken back to the ant nest, where it is placed amongst the ant brood. While the first foraging worker of any species of *Myrmica* to encounter a *Maculinea* larva under its food plant will almost always pick it up and take it back to the nest [33, 36], transfer to the brood chamber and initial integration may be highly species specific [35]. This specificity is largely mediated by the cuticular hydrocarbons that the fourth instar larvae produce, which mimic those of their host ants [37-40], with better-matching mimics achieving greater infection [40, 41]. However, in some populations that use multiple host ant species, this mimicry is imperfect, and seems to represent a compromise between mimicking different host *Myrmica* [40, 42]. Prior to adoption *Ma. arion* and *Ma. teleius* show a prolonged stereotypical sequence of behaviours before being picked up [31, 34, 36, 43], which may also convey non-chemical (e.g. tactile [34] or acoustic [44]) information , while *Ma. alcon* and *Ma. nausithous* are picked up quickly and with simpler behavioural sequences [31, 33, 35, 43].

Once inside the nest, *Maculinea* caterpillars have two *Myrmica* ant exploitation strategies. *Ma. teleius* and *Ma. arion* larvae feed as predators on the ant brood, while larvae of the *Ma. alcon* group (see below) have a more efficient “cuckoo” strategy where they are mainly fed by trophallaxis by the worker ants as if they were ant larvae [33, 45], but are also able to prey directly on the ant brood. While the larvae of *Ma. nausithous* are also predatory, they share some characteristics with the cuckoo species, feeding mostly on *Myrmica* eggs and small larvae [46]. Exploitation by *Maculinea* caterpillars severely reduces host ant fitness [40, 47-49], so there is strong selection on ants to identify these virulent parasites, which has in turn led to sophisticated strategies to misdirect the ants. Much closer chemical mimicry [50], involving additional species-specific secretions, is achieved after 4-6 days by caterpillars in the nests of their primary host species, while those adopted by secondary or non-host *Myrmica* species supress this second phase of secretions and depend, usually unsuccessfully, on the chemical camouflage [50] afforded by simply acquiring nest odours from the host [38, 42, 51]. Caterpillars and pupae also mimic sounds produced by *Myrmica* queens [52], which increase their perceived value to the ant colony, although these signals are not specific within the genus *Myrmica* [53]. Despite these sophistications, *Maculinea* larvae and pupae are frequently killed by their host ants [6, 45, 54], especially under food stress [55].

The coevolutionary process requires that both hosts and parasites evolve traits in direct response to the presence of and traits evolved by the other species. While the adaptation of *Maculinea* butterflies to their host ants in terms of mimicry of cuticular hydrocarbons is well established, it has also been shown that *Myrmica* ants in populations parasitized by *Maculinea* vary in their response to butterflies from different populations [35], and both diverge in their cuticular hydrocarbons (presumably to avoid mimicry; [40]) and become stricter in recognizing nestmates [56] compared with non-parasitized populations. This is consistent with an on-going coevolutionary arms race between *Maculinea* butterflies and their *Myrmica* hosts.

(b) Previous studies on host ant specificity of *Maculinea* and the scope of this study

Initial results from Western Europe [18] suggested that each *Maculinea* species is adapted to exploit a different *Myrmica* host ant species. However, further work in the region quickly demonstrated that *Ma. alcon* shows geographical shifts in host ant specificity [57]. Over the last twenty years there have been a plethora of publications describing host ant use by *Maculinea* butterflies in Europe (table S1), which has more than doubled the number of *Myrmica* species that are known to be exploited, and blurred the clear patterns that were initially thought to exist, leading some to question whether there really was any specificity [58].

The establishment of the MacMan EU research network [59] provided a unique opportunity to study host ant specificity at a pan-European scale, and to implement some more standardized methods of data collection, including the avoidance of artefacts that bedevilled certain early reports [22]. This study therefore aims to both synthesize the published information on host ant use by these butterflies, and to add original data collected during and after the MacMan project.

(c) Conservation considerations

The occurrence of *Maculinea* butterflies in small, patchy populations, which are naturally vulnerable to extinction [60], together with changes in land use over the last century, have led to rapid declines of many populations and extinctions in several European countries [61, 62]. All *Maculinea* species in Europe were considered as vulnerable to global extinction in the first European data book for butterflies [63] and although many have been reclassified in the latest version [64], declines have continued in many countries [65]. An understanding of the ant host use of *Ma. arion* in the U.K. has proven critical in both working out why it became extinct [61] and in its successful reintroduction [66]. However, the type of geographical variation in host specificity that we examine here means that the lessons from the populations in the U.K. may not be directly applicable elsewhere in Europe, and other reintroduction programs have been less immediately successful [62]. We hope that by highlighting the geographic mosaic of coevolution between *Maculinea* butterflies and their host ants we will aid future conservation efforts for these butterflies across Europe.

3. Methods

(a) The database and sites included

This study was based on a database derived from fieldwork conducted by the authors, combined with already published host ant studies (summarized in table S1). Protocols for collecting host ant data were drawn up during the MacMan project, and the initial data collected together at the end of that network in 2006. Construction of the database was then undertaken by the first author during a postdoctoral fellowship in Copenhagen (2009-2011), and expanded over the next seven years. In this database, the unit of replication was the site, defined as a distinct area in which a discrete population of one of the European *Maculinea* species was present, and specifically the part of that area where its host plant occurred.

This was straightforward for *Ma. teleius* and *Ma. nausithous*, since patches of *Sanguisorba officinalis* are usually well defined. For *Ma. arion*, both *Thymus* and *Origanum* occur on many areas where the butterfly is found, so these were not distinguished. However, for *Ma. alcon* there are at least two distinct types of habitat used by the butterfly, primarily associated with two different host plants in the genus *Gentiana*. Some populations are found on wet heathlands and boggy meadows, and mostly use the marsh gentian, *G. pneumonanthe* as a host, while others are found on much drier areas, often at higher elevations, and mostly use the cross-leaved gentian *G. cruciata*. These two types of populations of *Ma. alcon* have been considered as two separate species in the past (*Ma. alcon* and *Ma. rebeli* respectively), but recent molecular studies have found no phylogenetic differentiation [67-71]. Nevertheless we treat them separately here, since they occur in very different habitats, which are likely to have very different *Myrmica* communities, and because where examined each type secretes a distinctive pre-adoption chemical profile regardless of the local host ant species [72]. We will refer to the mostly *G. pneumonanthe*-using, hygrophilic form, as *Ma. alcon H*, and the mostly *G. cruciata*-using, xerophilic form as *Ma. alcon X*. Both these forms of *Ma. alcon* may also lay eggs on other gentian plants, particularly in central Europe and the Pyrenees, where the willow gentian, *Gentiana asclepiadea,* and various *Gentianella spp*. may be used as initial food plants [68, 73-75], but the distinction between wet and dry sites is usually clear. It has also become apparent in recent years that the specific name *Ma. rebeli* (originally described as a subspecific form of *Ma. alcon* [76]) has been incorrectly applied to the *G. cruciata*-using form of *Ma. alcon* [77], and should be associated with *Ma. alcon* from another distinct habitat - above the treeline in the Alps. Some data are now available on the host ant use of such alpine populations (putative *Ma. alcon* form *rebeli*), which have been found to lay their eggs exclusively on *Gentianella rhaetica* [78], so we will discuss these separately where appropriate, and we also treat one record from the literature as belonging to this form (see below). These sites were not included in the main analyses.

On sites where multiple *Maculinea* were known to fly, identification of *Maculinea* larvae found in nests followed [79], although it is not possible to distinguish between pupae of *Ma. nausithous* and *Ma. teleius* based on morphology. Unless their identities were confirmed by rearing to adulthood, the small number of pupae found on sites that were known to support both of these *Maculinea* were therefore excluded from the database and our analysis. The set of *Maculinea* known to occur on each of the sites in our database was summarized using an UpSet diagram [80], which provides an accurate quantitative way of summarizing intersecting sets when more than three elements are involved [81]. The UpSet was implemented in the *UpSetR* package [82] in *R* version 3.5.1 [83].

For newly collected data, the main method of assessing the *Myrmica* community close to food plants was the excavation of nests. Although there were small variations in methods used among groups, the majority of data was collected in the late spring or early summer, when food plants could be reliably identified and when fully grown *Maculinea* larvae and pupae were present in nests (see also the following section). Patches of food plants were identified (taking into account any information on where butterflies were flying and laying eggs the previous year), plants randomly selected, and then a circular area with a radius of 2 m searched for all *Myrmica* nests, which were subsequently excavated. To examine the wider geographical variation in the encounter filter (and because excavation of nests was not always practical or permitted on some sites), it was also measured on additional sites by setting out ant baits (sugar and/or protein) in areas within two meters of host plants. Baits were always placed more than 2 m, and usually more than 4 m, apart, so each bait that attracted *Myrmica* workers was assumed to correspond to a separate nest. Data added to the database from the literature were collected in various ways, ranging from simple records of a host *Myrmica* species being used on a particular site to comprehensive surveys that published data equivalent in detail to the newly collected data. Data from each source was coded based on the type of data available (table S1), so that data could be included or excluded from each analysis as appropriate.

Myrmica ants were generally identified following [84, 85] or [86], but if an identification was doubtful, specimens were sent to *Myrmica* experts (Sándor Csősz, Graham Elmes, Alexander Radchenko or Bernhard Seifert) for identification. *Myrmica* species names follow the revision published in [87]. Where latitude, longitude or altitude of sites were not provided directly, they were estimated using www.mapcoordinates.net.

In order to investigate how different populations of *Maculinea* parasites have adapted to exploit their *Myrmica* ant hosts, ideally one should be able to examine how the three filters on host use (encounter, infection and exploitation) differ among sites. However, distinguishing between infection and exploitation in the field has proved impractical on a large scale, so the combined effect of these two filters was examined.

(b) The encounter filter

The use of specific host plants by the first three larval instars of *Maculinea* butterflies provides a constraint for the encounter filter. Only *Myrmica* colonies that are within ant worker foraging range of the larval food plants will be encountered by the fourth instar *Maculinea* larvae. As a general rule of thumb, it is usually assumed that the foraging range of *Myrmica* workers is largely restricted to within two meters of the nest [88], so that for this study we defined the encounter filter as the community of *Myrmica* ants that is present within two meters of host plants. The encounter filter is, of course, also open to change if either the parasites have evolved mechanisms to preferentially exploit host plants closer to host ant nests, or if *Myrmica* ants do not forage randomly with respect to host plants. Many other lycaenid butterflies that associate with specific ants use these ants as an oviposition cue [89-91], but the evidence for the use of ant-dependent oviposition in *Maculinea* has been controversial [30, 92-96]. The most recent evidence suggests that while *Maculinea* butterflies may lay their eggs in response to the presence of *Myrmica* ants, they do not distinguish among different species of *Myrmica* [97]. Hence our use of *Myrmica* distribution relative to overall host plant distribution as a measure of the encounter filter may underestimate the rate of encounters[41], but not the potential hosts that are encountered. Ovipositing female *Maculinea* butterflies do, however, select the buds of their food plants that are in particular growth-forms or phenological stages [30, 92, 98], and these may occur in microhabitats that may be associated with particular *Myrmica* species [30]. Ideally, therefore, the encounter filter should be the *Myrmica* community found around food plants on which eggs have been laid [41], although this effect is likely to be small, especially in comparison with difference in *Myrmica* communities between areas with and without food plants [88, 99, 100]. On the other hand, females may avoid plants on which others have laid eggs [101], which will lead to a more even distribution of eggs (and larvae) relative to *Myrmica* nests [93, 96]. Larvae leaving plants may also time their exit to maximize the chances of being encountered by *Myrmica* workers rather than any other ants, but this does not influence which *Myrmica* species they encounter [36]. Overall, we therefore believe that our measure of the number of nests close to food plants provides a good approximation of the encounter filter.

The sets of *Myrmica* species found on different sites were summarized using an UpSet. To examine variation among *Maculinea* populations in the species richness of *Myrmica* (hypothesis H1), the number of species was compared using Generalized Linear Models (GLZs) with Poisson errors in JMP v14.1 (® SAS Institute, 2018). In order to get a reliable estimate of the total *Myrmica* community on a site, a minimum number of samples of *Myrmica* nests is necessary. We estimated this minimum number by calculating the difference between the bias-corrected Chao-1 estimate of true *Myrmica* species richness [102] and the observed *Myrmica* species richness for each site, and compared this with the number of nests examined (either the number excavated or the number of baits that attracted *Myrmica* workers). Differences in the *Myrmica* community among sites (i.e β-diversity) were compared by using Non-metric Multi-Dimensional Scaling (NMDS) ordination based on Bray-Curtis dissimilarities in the *R* package *vegan* [103], to reduce the data a small number of uncorrelated variables. These new variables were then used in discriminant analyses in JMP to test differences in *Myrmica* communities among the different *Maculinea*.

(c) The infection and exploitation filters

If *Maculinea* larvae successfully infect and exploit a *Myrmica* colony, they will develop within the nest during the autumn and winter. We therefore assessed the success of infection and exploitation by examining the presence and number of live fully grown larvae and pupae in the excavated nests. Comparison of the community of *Myrmica* ants within 2 m of host plants that housed overwintered *Maculinea* larvae and pupae with the total community was used as a measure of the specificity of these infection and exploitation filters. There are several potential pitfalls to measuring host use by examining the presence of parasites within nests [22]. Critically, we restricted sampling to full-grown larvae, pupae, or emerging adults to measure only those individuals that had successfully exploited a *Myrmica* colony. However, we will still have recorded caterpillars that survived occasionally in rare benign nests of a host species to which they are ill-adapted[66]. Our datasets will inevitably also contain a few false positives, especially for predatory species of *Maculinea* [104], where the final depletion of ant brood caused a host ant colony to desert its parasitized nest site to be replaced by an offshoot from a different but neighbouring *Myrmica* species before the butterfly emerged [22, 47]. However, our sampling was so extensive, both geographically and quantitatively, that we are confident that the broad patterns that emerge are unequivocal.

The different *Myrmica* hosts used by each *Maculinea* were collated and described using area-proportional Euler diagrams using ellipses [81], as implemented in the *R* package *eulerr* [105]. The number of hosts used by different *Maculinea* (hypothesis H2) was compared using Generalized Linear Models (GLZs) with Poisson errors in JMP. To examine geographical similarity in host use (hypothesis H3), spatial autocorrelation analysis was carried out in GenoDive 2.0b27 [106] separately for each *Maculinea* by comparing a matrix of pairwise distances between sites that hosted that *Maculinea* with a matrix of *Jaccard* similarities in their community of host ants. Distances were divided into ten classes for each *Maculinea* so that each contained 10% of the sample pairs. Moran's *r* was then used to examine how the similarity of hosts changed with geographical distance.

To examine whether *Maculinea* butterflies show local ant host specificity (hypothesis H4), the distribution of the number of nests that were found to contain *Maculinea* larvae or pupae was compared with the distribution of nests that did not contain *Maculinea* using contingency tables. For sites with only a single potential host ant species present, host ant specificity cannot be examined. For sites with two or more potential host ant species present, the significance of the deviation from homogeneity in the contingency table was tested using a χ^2 statistic, the probability of which was tested by random reassignment of the number of nests to each cell in the table 100,000 times, with the constraint that marginal total were retained. The observed value of the χ^2 statistic was then compared with the distribution of χ^2 statistics generated from the 100,000 permutations.

If specialization on one or a few hosts is favoured by natural selection, as appears to be the case in *Maculinea* brood parasites, then all else being equal, butterflies will benefit most by specializing on the most abundant host (hypothesis H5). This implies that they should exploit common hosts more frequently than expected based on their encounter rate, and fail to successfully exploit less abundant hosts [40, 107] – a form of frequency-dependent selection. To examine this, we plotted the proportional exploitation of each host used (i.e. the proportion of nests containing overwintered *Maculinea* larvae or pupae for each site that belonged to that host) against the proportional availability of that host (i.e. the proportion of *Myrmica* nests excavated that belonged to that host). If host *Myrmica* were exploited in the proportion available, sites would lie along the 1:1 line. To test whether there were deviations from the 1:1 line, 1-proportion Z-tests were carried out comparing the proportion of points that were above or below the 1:1 line for each *Maculinea* with the null hypothesis that there would be equally many above and below the line, subdividing the x-axis into those *Myrmica* that were more abundant (> 50% of the nests available) and those that were less abundant (<50% of available nests) at each site.

(d) Host switching and host sharing

In cases where multiple host ants are used on the same site, there may still be specificity that reflects coevolution with hosts, particularly if hosts share similar parasite defence mechanisms. All else being equal, we might expect more phylogenetically related hosts to have more similar defence mechanisms, so that host sharing and switching between hosts may be modulated by *Myrmica* phylogeny (hypothesis H6). To test this we calculated the Phylogenetic Species Evenness index [108] for each site on which multiple *Myrmica* hosts were used both for the complete *Myrmica* community and the community of *Myrmica* nests that supported overwintered *Maculinea* larvae or pupae, using the R package *picante* [109]. This index provides a measure of phylogenetic diversity within a community that takes species abundances into account and should be independent of species richness, and ranges between 0 (species are highly related and/or there is very high skew in their abundances) to 1 (all species are unrelated and equally abundant). For the analysis, which requires a phylogenetic tree with branch lengths, a modified version of the *Myrmica* tree produced by [110] was used, with the species that they did not include added based on relationships inferred from [111]. The values of this index for the encountered and exploited *Myrmica* communities at each site were then compared with a paired t-test separately for every *Maculinea* which had multiple sites where more than one *Myrmica* was exploited simultaneously.

4. Results and discussion

In total we collected data on *Myrmica* host ant availability from 419 sites (figure 1, table S1), of which 214 also provided direct records of host ant use. Most sites (83.3%) only supported a single *Maculinea*, but 70 sites supported up to four different *Maculinea* (figure 1), most notably *Ma. teleius* and *Ma. nausithous*, which co-occurred on 53 of these sites. The sites on which each *Maculinea* occurred provided a good sample of their known European distributions (figure S1). All *Maculinea* were generally found at lower altitudes towards the north, and in more mountainous areas towards the south (ANCOVA on log(altitude); latitude: $F_{1,487} = 251.7$, $p < 0.0001$; figure S2), but the characteristic altitude for each *Maculinea* varied ($F_{4,187} = 9.93$, $p < 0.0001$, *Maculinea* × latitude interaction: $F_{4,487} = 5.89$, $p = 0.0001$), with *Ma. alcon X* being found at significantly higher altitudes (Least-square mean = 377 m) than the other *Maculinea* (*Ma. alcon H* = 199 m, *Ma. arion* = 247 m, *Ma. nausithous* = 199 m, *Ma. teleius* = 257 m). This compared with a mean altitude of 1450 m for the three sites with *Ma. alcon* form *rebeli*.

(a) The encounter filter – *Myrmica* communities on *Maculinea* sites

A total of 17 different *Myrmica* species were found on *Maculinea* sites across Europe (figure 2, figure S3), with the number on any particular site varying from 1 to 9 (figure 2). These belonged to four of the species groups currently recognized within *Myrmica* [87] and well supported by recent phylogenetic analyses [110-112] (the *rubra*, *scabrinodis*, *lobicornis* and *schencki* groups). Members of the *lobicornis* group tended to be rare, but the other three groups all included very common species (figure 2). The most common species across sites was *My. scabrinodis* (more than 10,000 nests examined), and the rarest was *My. tulinae* (6 nests among over 2,400 *Myrmica* nests examined at Krakow in Poland) although the identification of this latter species should be treated with caution [87] and molecular data suggest that the morphological traits used to classify it apply to individuals from a range of species, and may represent aberration or hybridization [111].

Above a sample of 24 nests, most sites had reached a stable estimate of the *Myrmica* community (figure S4), so a minimum sample of 25 nests was used to compare ant communities (which reduced the number of sites with sufficient data to 199). Somewhat surprisingly given the known European distribution of *Myrmica* species [87, 113] and their overall distribution across sites (figure S3), the number of *Myrmica* species recorded on a site in this dataset did not vary significantly with latitude, longitude or altitude (GLZ: *Likelihood-ratio (L-R)* $\chi^2 = 0.179$, *d.f.* = 1, $p = 0.672$; *L-R* $\chi^2 = 0.874$, *d.f.* = 1, $p = 0.350$; *L-R* $\chi^2 = 0.678$, *d.f.* = 1, $p = 0.410$ respectively). The size of the *Myrmica* community was, however, significantly different among sites occupied by the different *Maculinea* (hypothesis H1: *L-R* $\chi^2 = 12.82$, *d.f.* = 4, $p = 0.0122$, figure 2).

NMDS adequately reduced the *Myrmica* community data to three axes (stress value of 0.134). Discriminant analyses based on these axes showed that the *Myrmica* community on sites occupied by different *Maculinea* could be split into two major divisions by the first NMDS axis: those found on drier sites occupied by *Ma. arion* and *Ma. alcon X*, and those found on the wetter sites occupied by *Ma. nausithous*, *Ma. teleius* and *Ma. alcon H* (*Wilks'* $\lambda_{3,248} = 0.371$, $p < 0.0001$, 91.3% correctly classified), with no difference within the xerophilic group (*Wilks'* $\lambda_{3,248} = 0.997$, $p = 0.971$, 53.4% correctly classified) and a small but significant difference between *Ma. nausithous* and the other *Maculinea* in the hygrophilic group (*Wilks'* $\lambda_{3,248} = 0.841$, $p < 0.0001$, 65.9% correctly classified), although there was some overlap of all groups (figure 2).

(b) The infection and exploitation filters – *Myrmica* specificity

Of the 17 *Myrmica* species found on *Maculinea* sites, overwintered larvae or pupae were found in the nests of all but one (*My. lobulicornis;* figure S6). However, the number of hosts used on any site was generally low (figure 2), with 70% of sites examined having only a single host ant. *My. scabrinodis* was the only ant species recorded as a host for all five *Maculinea*. There was significant variation among *Maculinea* in the number of hosts used (hypothesis H2: Poisson GLZ; *L-R* $\chi^2 = 15.27$, *d.f.* = 4, $p = 0.004$), and patterns of host use differed geographically within some *Maculinea* (hypothesis H3; figure 3, see below).

As has been suggested previously [114], *Ma. nausithous* has the smallest range of hosts, being restricted to a single host (either *My. rubra* or *My. scabrinodis*) on all but one site, where it was found in the nests of four *Myrmica* species (one being *My. tulinae*, so this record should be treated with caution). However, there was little spatial structure in this pattern, with the less common host (*My scabrinodis*) being used across Europe.

Ma. alcon H was only found in the nests of more than two *Myrmica* species on a single site (figure 3) and was generally split into two geographically distinct groups (figure 3). Those in the north-west of Europe exploited species within the *rubra* species group (*My. rubra* and *My. ruginodis*), while in the remainder of Europe, ants from the *scabrinodis* species group (*My. scabrinodis*, *My. aloba, My. slovaca* and *My vandeli*) were hosts. The only exception to this was one site in Belgium where *My. scabrinodis* was used as a host on a site where *My. rubra* and *My. ruginodis* were the main hosts. This pattern was reflected in the spatial autocorrelation analysis which shows that hosts were very similar among sites up to 1000 km apart, but significantly different beyond this. There has been one report of a *My. schencki* nest housing the only *Ma. alcon* found on a Polish site in 2013 [115], but in a more extensive survey at the same site the following year only *My. scabrinodis* nests were found to be exploited, and in larger numbers [115], so we consider that this record (of a prepupa) was probably a case of nest-takeover [22], and have not included it in the database.

Ma. alcon X generally exploited *My. sabuleti* or *My. schencki*, with all other recorded hosts being exploited on sites where one of these two species was also a host (except for two sites where *My. specioides* was the only host). Host communities were less similar beyond a distance of around 800 km, but sites towards the extreme south west and north east all used *My schencki* as a host. An outwardly similar pattern was found in *Ma. teleius*, except in this case the two main hosts were *My. rubra* and *My. scabrinodis,* and there were two sites where *My. slovaca* was a host (in one case shared with *My. specioides*), but there was no real spatial structure in host use.

Ma. arion sites tended to fall into two groups which exploited *scabrinodis* group ants (*My. lonae*, *My. sabuleti, My. scabrinodis* or *My. specioides*) in most of Europe, and *My. schencki* (sometimes in combination with other species) in north-east Europe (although one site where *My. schencki* is used as a host is known from Italy). The relatively small area where *My. schencki* dominates is reflected in the spatial autocorrelation results, where communities go from being significantly similar to significantly dissimilar over a distance of around 400 km, but whether this is representative of the whole range of *Ma. arion* is unclear, as the *My. schencki*-using populations of this butterfly are on the eastern border of the area we covered. Distinguishing between the closely related *My. sabuleti* and *My. lonae* can be problematic in northern Europe [87] and sharing of mitochondrial haplotypes suggests that they may not be separate species [111]. Hence it is unclear whether the apparent switch from using *My. sabuleti* to using *My. lonae* observed in the most northern sites is genuine, or reflects a cline in host morphology [87].

The putative *Ma. alcon* form *rebeli* populations from above the tree-line in the Austrian Alps have been shown to use *My. sulcinodis* as a host [78], which is the most common *Myrmica* species recorded on the two sites examined (table S1). It is notable that another record of an *Ma. alcon* group caterpillar found in a *My. sulcinodis* nest was made by David Jutzeler in the 1980’s in the Swiss Alps at a site above the tree-line, where eggs were found on plants in the *Gentianella germanica* complex [116, 117]. This site was subsequently destroyed in a landslide (Jutzeler, personal communication), but we consider it highly likely that this was also the putative form *rebeli*.

The probability that the pattern of host ant use found simply reflected host ant availability (hypothesis H4) was often low, being below the conventional $a = 0.05$ in 55 out of 160 cases where it could be calculated (figure 4). The (log-transformed) probability that *Myrmica* nests were infected and exploited in the proportion encountered was negatively correlated with the log of the number of *Myrmica* nests in which *Maculinea* larvae or pupae were found on a site (ANCOVA; $F_{1,150} = 54.6$, $p < 0.0001$) and differed among the different *Maculinea* ($F_{4,150} = 6.05$, $p = 0.0002$; *Maculinea* × log(number of infected nests): $F_{4,150} = 2.33$, $p = 0.058$; figure 4), with *Ma. alcon X* and *Ma. arion* showing a greater proportion of sites showing specificity than the other four *Maculinea*. However, for all *Maculinea*, the proportion of sites where significant ($\alpha < 0.05$) specificity was found was higher than the 5% predicted by chance except when only a single infested nest was found (figure 4).

(c) Local adaptation

The pattern of host exploitation expected from local adaptation (hypothesis H5; figure 5) was indeed seen for *Ma. alcon H* and *Ma. arion*, with over-exploitation of common hosts (Single proportion *Z*-test; $Z = +3.92$, $p < 0.001$; $Z = +3.15$, $p < 0.001$ respectively) and under-exploitation of rare hosts ($Z = -5.82$, $p < 0.001$; $Z = -6.67$, $p < 0.001$ respectively). *Ma. alcon X*, *Ma. nausithous* and *Ma. teleius* all under-exploited rare hosts ($Z = -3.86$, $p < 0.001$; $Z = -2.97$, $p = 0.002$; $Z = -3.05$ $p = 0.001$ respectively) but did not overexploit common hosts ($Z = -0.816$, $p = 0.793$; $Z = +0.242$, $p = 0.404$; $Z = +0.756$, $p = 0.775$ respectively). The general under-exploitation of rare hosts across all *Maculinea* is not unexpected, since populations that continue to exploit only rare hosts are unlikely to persist, particularly in the predatory species *Ma. arion* and *Ma. teleius*, which have the greatest effect on host colony fitness [45]. It has been shown that that a minimum of 50% [45] to 68% [66] of the larval population of these *Maculinea* must be adopted by the main host (in host-specific populations) for intrinsic growth rates to be positive. Nevertheless, some apparently maladapted populations are also found (occupying the top left of figure 5), for example at one isolated Polish site [118], the rare *My. lobicornis* is the main host, despite only making up 13% of the available *Myrmica* nests [119]. In the more efficient and less virulent cuckoo-feeding species *Ma. alcon H* and *Ma. alcon X* this threshold is expected to be considerably lower and has been shown empirically to be as low as 13% [45]. It must be remembered that which *Myrmica* species are rare or abundant close to food plants is likely to change over time, both in response to environmental changes and in response to the selection pressure exerted by *Maculinea* [99, 120, 121]. The failure of *Ma. alcon X* and *Ma. nausithous* to adapt to use the most common hosts therefore could indicate that host switching may be more difficult for these *Maculinea*, or alternatively that their host ants respond more rapidly to exploitation. Even if, overall, the most commonly available hosts tend to be overexploited and the less abundant hosts avoid parasitism, suggesting local adaptation by *Maculinea*, there are still several cases where local maladaptation (specialization on a locally rare host) is evident for all *Maculinea*.

(d) Host sharing and host switching

Pairwise comparison of the Phylogenetic Species Evenness index between the host *Myrmica* community and the entire *Myrmica* community on sites showed that these differed significantly for *Ma. alcon H* (Paired *t*-test; $t = -3.55$, *d.f.* = 11, $p = 0.0053$), but not for the other *Maculinea* (*Ma. alcon X*: $t = +0.432$, *d.f.* = 17, $p = 0.671$; *Ma. arion*: $t = -0.180$, *d.f.* = 8, $p = 0.862$; *Ma. teleius*: $t = +1.34$, *d.f.* = 13, $p = 0.206$). This suggests that shared hosts are not generally more closely related for three of the four *Maculinea* where it could be tested. For *Ma. alcon H*, this pattern arises from the two areas of Europe with very distinct host use (figure 3), where hosts are confined to particular *Myrmica* species groups, even though *Myrmica* from the other groups are encountered. Comparison of species groups for the other *Maculinea* shows that shared hosts are usually also from the same *Myrmica* species group in *Ma. arion*, but in *Ma. alcon X* and *Ma. teleius* there are many sites where hosts are shared among *Myrmica* from different species groups. In both cases, however, this is dominated by sharing between two particular pairs of species, *My. sabuleti* and *My. schencki* in *Ma. alcon X*, and *My. scabrinodis* and *My. rubra* in *Ma. teleius*. This latter pairing in particular contrasts with *Ma. alcon H*, where these two species tend not be shared. One possible reason for this could be that the very common *My. scabrinodis* appears to consist of at least two cryptic species that are morphologically indistinguishable, but are genetically quite distinct [111, 122] and differ in their ecology and behaviour [88].

A recent theoretical model of the evolution of host use in *Maculinea* [123] explored the roles of *Myrmica* species abundance and similarity in host phenotypes on the evolution of specificity. This came to the conclusion that two stable strategies are likely to exist: 1) specialization on a single, abundant host, or 2) use of multiple hosts when host abundance is lower and hosts at least partially share phenotypes related to *Maculinea* infection ability. This is generally supported by the patterns that we have found here, with the majority of populations specializing on a single, abundant host. Where hosts are shared, it is still unclear whether this represents some similarity in infection-related phenotypes. Infection and exploitation of *Myrmica* colonies by *Maculinea* butterflies critically depends on circumventing the ants' self-/non-self-recognition system by mimicking their cuticular hydrocarbons [37, 39-41, 51]. These cuticular recognition cues are generally species-specific in *Myrmica*, but also show some similarities among species [39-41, 124]. Hence it is expected that sharing of, or switching between, certain hosts may be more easily achieved if they have more similar sets of hydrocarbons, even if some degree of specificity is maintained. For example, different populations of *Ma. alcon H* in Denmark exploit *My. rubra* or *My. ruginodis*, or both species simultaneously, but never exploit *My. scabrinodis*., although it is relatively common [125] and is exploited almost exclusively in most of Europe (figure 3). This is because the closely related *My. rubra* and *My. ruginodis* have much more similar cuticular hydrocarbons than either has with *My. scabrinodis*. Although producing a hydrocarbon profile that is a reasonable mimic of both *My. rubra* and *My. ruginodis* may have costs in terms of somewhat reduced infectivity[40], this step is still within the levels of natural variability found in Danish *Ma. alcon H* populations, whereas the hydrocarbons of *My. scabrinodis* are not [40]. Does this pattern hold for the other *Maculinea* butterflies across Europe? Pre-adoption larvae of *Ma. alcon X* in eastern Austria that simultaneously exploit *My. sabuleti* and *My. schencki* have been shown to produce a set of cuticular hydrocarbons that simultaneously match different portions of the cuticular profile of these rather distantly related *Myrmica* [42]. Although, in general, cuticular hydrocarbons of ants tend to evolve rather slowly [126], when the cuticular hydrocarbons of different *Myrmica* are compared, they generally show rather little phylogenetic similarity [124]. This may be because of the additional roles of ant cuticular hydrocarbons in species [127] and possibly mate [128, 129] recognition, which may lead to selection on their divergence during speciation. Whether host sharing and switching is related to cuticular hydrocarbon similarity therefore remains an open question, but an interesting examples is provided by *My. vandeli* which has cuticular hydrocarbons practically indistinguishable from *My. scabrinodis* [124]. It is thought that *My. vandeli* may act as a temporary social parasite of *My. scabrinodis* [87], and therefore has evolved a similar set of hydrocarbons to itself integrate into colonies of this host. Hence it is notable that we only found *My. vandeli* being exploited by *Maculinea* on sites on which they also exploit *My. scabrinodis* (figure 3).

(e) Fitting the patterns together – The geographic mosaic of coevolution

There is considerable variation in host use of all the European *Maculinea*, but this does not imply lack of specificity in their interactions with *Myrmica* ants at a population level [58]. The different initial host plants used by the different *Maculinea* are found in different types of habitat, which correlate with the different *Myrmica* communities found there (figure 2), and set the boundaries of the encounter filter for the *Maculinea* butterflies. However, there is still a lot of variation and overlap in *Myrmica* communities, so that even very close sites rarely have precisely the same community present. This fulfils one of the three main tenets of the geographical mosaic theory of coevolution [16], that there should be a mosaic of hot-spots and cold-spots for coevolution. Coevolution between *Maculinea* butterflies and any particular *Myrmica* species can only take place when that *Myrmica* species is present at a particular site. The second tenet of geographic mosaic theory is that there should be geographical variation in the outcome of coevolution. At the majority of sites, *Maculinea* butterflies appear to be locally adapted to their host *Myrmica*, in that they are effectively exploiting the most abundant *Myrmica* host. The identity of this abundant host varies geographically, however, and overall, but with a fair number of exceptions, we found that each *Maculinea* exploits a constant host ant species on multiple sites across areas of thousands rather than hundreds of km^2 in Europe, with major host switches occurring in each species at greater distances (figure 3). Small, population-scale switches as found for *M. alcon H* in Denmark [40] and for *Ma. alcon X* in Poland, Italy and parts of central Europe [38, 41, 68, 107] are comparatively unusual, but quite apparent within the snapshot of time sampled during this study. However, there are a substantial minority of sites where *Maculinea* populations seem to be maladapted, and are specialized on a rare *Myrmica*. This is precisely what is expected if there is ongoing coevolution between

Maculinea butterflies and their *Myrmica* hosts, because there is also expected to be selection on hosts to avoid infection and exploitation, and the lack of parasitism of a common *Myrmica* species can be seen as local adaptation of the host to avoid parasitism. The third component of the geographic mosaic theory is (limited) trait-remixing among populations. This is also a characteristic of *Maculinea* populations. Although *Maculinea* are quite limited in their dispersal when examined using mark-release-recapture techniques or behavioural observations [130-133], their genetic structure suggests occasional long-distance dispersal [134-137], so allowing the maintenance of the genetic diversity required for coevolution across a wide geographic area.

5. Conclusion

The life cycle of *Maculinea* butterflies makes them entirely dependent on *Myrmica* ants, which suffer serious fitness losses as a consequence. Both sides in the interaction are therefore expected to impose severe selection pressure on the other, so providing the basic conditions for coevolution. In this paper we have looked at *Maculinea* evolution in terms of how they exploit and are adapted to different *Myrmica* species, however it must also be borne in mind that coevolution *within* species pairs is likely to be the norm [40], and that the patterns we examine here can only be interpreted in the framework of (albeit very tight) diffuse coevolution. The variety of exploitation strategies used, however, mean that whether and how coevolution proceeds is likely to be different for the different *Maculinea*, which is reflected in our results.

The "cuckoo"-feeding *Ma. alcon* group are more dependent on integration within the *Myrmica* colony, as they need to constantly interact with the ants that feed them [45], which requires sustained deception [38, 39]. This seems to have led to large scale geographic mosaic of exploitation, in which the same or related hosts are used over distances of a thousand kilometres or so. Specificity is generally high within sites, but local adaptation is variable. It is frequent in *M. alcon H*, but much less so in *Ma. alcon X*, which generally interacts with a larger potential host community.

The best-known predatory *Maculinea*, *Ma. arion*, shows a somewhat similar pattern, but on a smaller spatial scale, which tends to lead to local adaptation to the most common *Myrmica* host. However, it also seems to be able to exploit the nests of other *Myrmica* on the same sites, albeit so inefficiently that a population cannot be supported by the presence of the maladapted host species alone[66], which leads to generally lower apparent specificity. This is taken to a further extreme by *Ma. teleius*, which has the largest host range, largely exploits *Myrmica* in much the same proportion as they are encountered, and shows no apparent geographical structure in its host use, giving little evidence of ongoing coevolution. It should be recalled, however, that our data will contain more false positives for these latter species, caused by ants switching nest sites during the pupal stage following the disproportionate damage inflicted through carnivory on the typically small nests of their main hosts. For example, roughly half the instances for *Ma. arion* emerging from nests occupied by *My. scabrinodis* in the UK resulted from nest-takeover and half from genuine survival with this normally unsuitable host [47, 66]

Ma. nausithous is unusual in many ways. Its hosts seem to be very limited compared with the other *Maculinea*, which has led to an apparent lack of local adaptation in its host use. Despite using the same major hosts as *Ma. alcon H*, it does not seem to be able to use the related *Myrmica* species in the same way, suggesting that it does not rely on the same type of cuticular mimicry to gain access to its food [138]. This is possibly because its apparent need, when small, to eat ant eggs in the heavily protected host chambers that contain queens [46] requires closer host-specific mimicry of its main host that is simply ineffective with other *Myrmica* species. Essentially there is also little evidence of coevolution between this species and its *Myrmica* hosts, but for completely different reasons to *Ma. teleius*, which are at opposite ends of the host specificity spectrum. In the case of *Ma. nausithous*, there is little geographic variation in outcomes, while in the case of *Ma. teleius*, we seem to lack coevolutionary hotspots.

It is clear that the idea of "one *Myrmica* for one *Maculinea*" does not hold across Europe as a whole but is often true in smaller regions within the continent. It is equally clear that different *Maculinea* have different propensities for using multiple *Myrmica* hosts or shifting host. Such alternation in the use of a network of hosts by parasites is expected to be a common outcome of antagonistic coevolution [139]. Similar patterns to those shown by *Maculinea* butterflies and their *Myrmica* hosts have also been suggested for other brood parasites [140], but not documented in such detail. Host defences and in what ways parasites overcome them is critical to how such antagonistic coevolution proceeds. The variability found within the genus *Maculinea* is potentially very useful for exploring this aspect of coevolution, but we still need to learn more about exploitation and defence strategies of both partners. In particular, the difference between the patterns of host use by *Ma. alcon* that occur in dry and wet habitats is an intriguing pattern that merits further investigation, although it seems that somewhat different chemical deception strategies may be involved [72]. What leads to the very limited host range of *Ma. nausithous* compared to the closely related *Ma. teleius* is also unclear and should be investigated in more detail.

Many of the patterns that we have shown here have also been described for other brood parasites, particularly the common cuckoo, *Cuculus canorus*, the host interactions of which have been examined over a long period and in many populations [141]. Cuckoo populations also vary in the hosts that they parasitize, and tend to specialize on more abundant hosts at a regional scale [142]. However, the evidence for specialization on locally abundant hosts is equivocal [143-145], and as far as we are aware no studies have been carried out systematically examining the effects of the relative abundance of alternative hosts, but different studies suggest both adaptive (e.g. [143]) and maladaptive (e.g. [146, 147]) specialization. This is consistent with the pattern expected from an ongoing geographic mosaic of coevolution. The rate of adaptation of cuckoos and other avian brood parasites to their hosts is surprisingly fast [148], but their hosts can also respond quickly, as they have comparable generation times. This may lead to a higher proportion of apparently maladapted avian brood parasite populations compared with *Maculinea* populations. Specialization on hosts in the common cuckoo seems to be largely under genetic control, and is specifically associated with the genotypes of females, who belong to "gentes" that are associated with both host choice and often with host egg mimicry [149], and which are maintained even in close sympatry [150]. While it has been suggested that such host race specalization may also occur within *Maculinea* populations [151], this has not been supported by more recent ecological and genetic studies [70, 125]. This study has confirmed most of the key predictions of the geographic mosaic theory of coevolution {Thompson, 1999 #11} over a large area, and across several hundred populations. It is gratifying that patterns and relationships that have been observed locally also generally apply across larger geographic regions, but it is also apparent that some only emerge when the large scale is considered. Avian brood parasites are generally better dispersers than *Maculinea* butterflies, and are frequently migratory, so the most useful geographic scale to examine their potential coevolutionary mosaics may be correspondingly larger. Conversely, many other host-parasite system are much more restricted geographically, and smaller scale geographic analyses of these may prove very fruitful.

Within the lycaenid butterflies, ant brood parasitism is a very uncommon strategy [152], despite most lycaenid butterflies having some sort of symbiotic relationship with ants, most commonly mutualistic interactions in which nutritious secretions are traded for protection [153]. Despite its rarity, brood parasitism has evolved multiple times within the *Lycaenidae*, but has rarely led to diverse lineages [152, 153], suggesting that it is a strategy that does not persist long over evolutionary time spans. The genus *Maculinea* is relatively young (ca. 2.5 MYA) compared with other lycaenid genera [67], and the conservation concern over all its constituent species reflects its natural rarity and vulnerability to local extinction. However, such local extinctions are also likely to be a natural part of the geographic mosaic in which these butterflies coevolve with *Myrmica* ants. The propensity for host ant switching shown by all *Maculinea* is likely to be the key to their persistence on regional and continental scales. Whether this continues to be the case under increased pressure from human activities and climate change remains to be seen.

6. Figure legends

Figure 1. Summary of the 419 *Maculinea* sites examined in this study. *a)* Map showing the distribution of the sites colour-coded according to the *Maculinea* present on each site. Where more than one *Maculinea* occurs on a site, symbol areas are proportional to the number, and dissected according to the *Maculinea* present. *b)* The intersecting sets of *Maculinea* across all sites visualized as an "UpSet". The matrix at the bottom of the diagram shows all combinations of *Maculinea* across the sites, with the bars above the combinations showing the frequency of that combination, and those to the left of the butterfly names showing the frequency of each group.

Figure 2. Diversity of the *Myrmica* species community found on *Maculinea* sites. *a)* The seventeen *Myrmica* species, belonging to four *Myrmica* species groups found on *Maculinea* sites, showing their phylogenetic relatedness [110, 111] and overall abundance (total number of nests) across all sites. *b)* Histograms showing the numbers of *Myrmica* species recorded from sites that supported each *Maculinea*. Counts are based on sites where at least 25 nests were excavated or 25 baits attracted *Myrmica* ants. Sites supporting more than one *Maculinea* are counted separately for each. *c)* NMDS ordination plot of the *Myrmica* communities found on sites supporting the different *Maculinea*, based on Bray-Curtis dissimilarities for sites where more than 25 nests were excavated or 25 baits attracted *Myrmica* ants. Convex hulls define the extent of the communities associated with each *Maculinea*. Sites supporting more than one *Maculinea* are counted separately for each. The further apart two sites are on the ordination plot, the more different their community of *Myrmica* ants. The ordination scores of the *Myrmica* species are also plotted. *d)* Histograms showing the numbers of *Myrmica* species whose nests contained overwintered *Maculinea* larvae or pupae recorded from sites that supported each *Maculinea*. Sites supporting more than one *Maculinea* are counted separately for each.

Figure 3. Host use across the five main *Maculinea* groups. For each *Maculinea* the top panel shows the geographical distribution of all sites where overwintered larvae or pupae were found in excavated nests ("host nests"). Each symbol is a pie diagram showing the proportion of host nests that belonged to each *Myrmica* species, with size proportional to the number of host nests examined. The central panel shows an area-proportional Euler diagram with the set of host *Myrmica* used by each *Maculinea*. The area of the ellipse assigned to each *Myrmica* species is approximately proportional to the number of sites where that ant was a host. The bottom panel shows a spatial autocorrelogram showing how the similarity between the host community used on different sites (based on Jaccard similarity indices) varies with distance between sites. Pairs of sites are grouped into 10 distance classes with equal sample size (which are therefore different for each *Maculinea*). Markers are placed at the maximum distance for each class and are coloured depending on whether the correlation among communities (Moran's r) is significantly different from zero ($p < 0.05$; filled circles) or not (open circles).

Figure 4. Relationship between specificity and sampling effort for each *Maculinea*. Specificity was tested by comparing the distribution of *Myrmica* nests of each species found close to food plants with that of the nests of those species found to contain overwintered larvae or pupae of *Maculinea* for all sites where more than one *Myrmica* species was recorded. Each point in the graph represents the estimated probability that hosts are used in the proportion available for each *Maculinea* at one site, coloured according to the *Maculinea* present. Least-squared regression lines are shown in the same colour for each *Maculinea*. Note that for clarity, the y-axis is reversed so that sites showing greater specificity are further from the x-axis. The conventional level of statistical significance ($\alpha = 0.05$) is indicated by a dashed line, and all points above this can be considered to show significant specificity. Where each regression line crosses this threshold gives an estimate of the number of nests containing overwintered *Maculinea* caterpillars or pupae needed to achieve a 50% probability of detecting significant specificity.

Figure 5. Comparison of proportional availability and proportional exploitation of *Myrmica* nests for each *Maculinea*. Each point represents one *Myrmica* species on one site where more than one potential host *Myrmica* species was recorded. The x-axis represents the relative abundance of that *Myrmica* species at the site, and the y-axis is the proportion of all host nests at that site of that *Myrmica* species. If *Myrmica* species are exploited in the proportion that they are available, points should be evenly distributed above and below the 1:1 diagonal (shown as a dashed line). Points below this line (in the grey area) represent under-exploitation, while points above the line represent over-exploitation. The relationship is visualized for each *Maculinea* with a LOWESS regression line (smoothing parameter $\alpha = 0.4$).

Additional Information

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Ethics
All novel research for this project was carried out in accordance with the regulations operating in the specific European counties where sites were located, including obtaining local permits to work in protected areas where appropriate.

Data Accessibility
The dataset supporting this article has been uploaded as part of the Supplementary Material.

Authors' Contributions
AT, JAT and DRN conceived the study. AT compiled the database, with input from all other authors. DRN carried out the analysis and wrote the manuscript, with input from JAT and AT. All authors read, corrected and approved the submitted version of the manuscript. Original data for the manuscript was provided by all authors, whose contributions are given in detail in table S1.

Competing Interests
The authors declare no competing interests

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