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A phylogenetic test of the parasite-host associations between *Maculinea* butterflies (Lepidoptera: Lycaenidae) and *Myrmica* ants (Hymenoptera: Formicidae)

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Abstract. The parasitic caterpillars of *Maculinea* (Lepidoptera: Lycaenidae) need to be adopted and nursed by ants of the genus *Myrmica* (Hymenoptera: Formicidae). Each *Maculinea* species is locally associated with one or a few main and often several secondary host species. To determine whether the parasite-host associations bear marks of cophylogenetic constraints, we reconstructed phylogenies of *Maculinea* and *Myrmica* using DNA sequence data. We searched for evidence of cospeciation with a tree-independent (ParaFit) and tree-based (TreeFitter) method. This did not reveal any indication of phylogenetic host tracking in *Maculinea.* This agrees with earlier insights, which emphasise that as most of the potential host ant populations are never infested by *Maculinea*, the selective pressure of the butterflies on *Myrmica* is likely to be slight. Each *Maculinea* species also specialises on one or a few host plant species before adoption by ants. We suggest that *Maculinea* species have a substantial potential to accommodate evolutionarily to geographically changing ranges of potential *Myrmica* hosts, available at the oviposition sites of the butterflies. We use recently published evidence on geographically varying host ant species to discuss a suite of plausible scenarios of adaptive shifts to new *Myrmica* host species.

INTRODUCTION

Coevolution may be strictly defined as an evolutionary change in a trait of the individuals in one population in response to a trait of the individuals in a second population, followed by an evolutionary response by the individuals in the second population to the change in the individuals in the first population (Janzen, 1980; see also Thompson, 2005). For intimately associated parasites and hosts, where hosts have become allopatrically isolated, and parasites are unable to disperse to or survive on hosts phylogenetically distant to their natural host, coevolution may lead to cospeciation (Reed & Hafner, 1997). This is a process during which speciation in one group is paralleled by speciation in the other (Hafner & Nadler, 1988; Page, 1994; Hafner & Page, 1995; Page & Charleston, 1998). There is strong evidence for cospeciation if the phylogenetic trees of the two interacting groups show a pattern of shared evolutionary history (Futuyma & Slatkin, 1983).

Cospeciation has been demonstrated in many systems, e.g., between chewing lice and pocket gophers (Hafner & Nadler, 1988; Hafner & Page, 1995), nematodes and primates (Hugot, 1999), *Buchnera* bacteria and *Uroleucon* aphids (Clark et al., 2000) and lice and birds (Page et al., 2004; Hughes et al., 2007). Other studies report a partial or no fit between the parasite and host phylogenies in more complex situations, involving parasites infecting multiple hosts. This is the case for Monogenea and fish (Desdevises et al., 2002), lice and passerine birds (Johnson et al., 2002), chewing lice and toucans (Weckstein, 2004), and chewing lice and penguins (Banks et al., 2006).

Butterflies of the genus *Maculinea* (Lycaenidae) — now formally synonymised with *Phengaris* (Fric et al., 2007, but see Balletto et al., 2010) — show a remarkable parasitic association with their ant hosts. Caterpillars spend most of their life inside a *Myrmica* colony (Thomas et al., 1989; Elmes et al., 1991a). The caterpillars mimic host brood and are either actively fed by ants (cuckoo species, *Maculinea alcon*, *M. rebeli*; Elmes et al., 1991a, b) or prey on the ant brood (predatory species, *M. arion*, *M. arionides*, *M. nausithous*, *M. teleius*; Thomas & Wardlaw, 1992). After living inside a nest for up to two years (Schönrogge et al., 2000; Witek et al., 2006) the adult butterfly emerges inside the nest and escapes before being detected.

To survive in a host colony, *Maculinea* need to avoid being attacked by the host ant workers. The caterpillars possess a dorsal nectary organ, which produces secretions that are nutritious for ants and probably appease aggressive ants (Pierce et al., 2002; Wardlaw et al., 2000). To avoid being detected as aliens, caterpillars further engage in chemical mimicry or camouflage (Akino et al., 1999). *Maculinea rebeli*, for example, biosynthesise a cuticular hydrocarbon profile (CHC) similar to its main host, *Myr-*

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mica schencki (Akino et al., 1999), which ensures that the host workers react to caterpillars as if they were their own brood.

Because avoidance of detection requires highly specific chemical signals, most *Maculinea* are expected to associate with one host species (Thomas et al., 1989; Elmes et al., 2002). Nevertheless, *M. alcon* is found with three different host species in different parts of Western Europe (Elmes et al., 1994; Als et al., 2002). Indeed, recent studies have shown that each *Maculinea* species may use several hosts (Als et al., 2004 and references therein). Inside a non-optimal host colony, however, the CHC profile of *M. rebeli* caterpillars differs from that of the host workers (Schönrogge et al., 2004). Although aliens are tolerated in ant colonies when food is plentiful they are killed when conditions become stressful (Elmes & Wardlaw, 1983; Elmes et al., 2004). Therefore, when predation by the parasite caterpillar stresses the host colony, host workers may eliminate any aliens, including the caterpillar. Consequently, few of the *Maculinea* adopted by non-optimal *Myrmica* hosts survive (Thomas et al., 1989; Als et al., 2001).

Nash et al. (2008) suggest that local populations of *Maculinea alcon* and *Myrmica rubra* undergo a coevolutionary arms race with reciprocal CHC profile adaptation. If so, did *Maculinea* speciate in parallel with *Myrmica* diversification? This study aims to investigate whether the interaction of *Maculinea* with its *Myrmica* hosts has influenced its phylogeny. Here, we use DNA sequence data to reconstruct phylogenies of the *Maculinea* parasites and their *Myrmica* hosts. We then test congruence between these phylogenetic trees using tree- and distance-based methods that search for significant patterns of codiversification.

MATERIALS AND METHODS

Sequences of Cytochrome Oxidase I, tRNA-Leu and Cytochrome Oxidase II (COI, trnL, COII) and Elongation Factor 1α (EF-1α) were downloaded from GenBank for 32 *Maculinea* specimens (including two species of *Phengaris*, the genus to which all *Maculinea* formally belong; Fric et al., 2007) and outgroups *Pseudophilotes vicrama*, *Pseudophilotes baton* and *Pseudophilotes bavius* (data from Als et al., 2004). For *Myrmica*, we used Cytochrome Oxidase subunit I (COI), Cytochrome b (Cytb), ribosomal 28S extension region 2 (28S), Arginine Kinase (ArgK) exons 1 and 2, the F1 copy of Elongation Factor 1 alpha (EF-1α), and Long Wavelength Rhodopsine (LwRh) for a subset of species from our phylogenetic study of *Myrmica* (Jansen et al., 2010). Most *Myrmica* species recorded as host for *Maculinea* (Als et al., 2004 and references therein; Sielezniew & Stankiewicz, 2004, 2008) were included, except *Myrmica gallienii*, *M. salina* (Tartally, 2005) and *M. lonae* (Tartally et al., 2008), for which samples were unavailable. The outgroups were *Manica rubida* and *Manica invidia*. A list of taxa, with collection information and GenBank accession numbers is provided as supplementary material.

The sequences of *Maculinea* and *Myrmica* were aligned using Mafft 6.06b (Katoh et al., 2005). The respective alignments were 3173 and 3886 base pairs. The best-fitting models for the alignments of *Maculinea* and *Myrmica* were determined using the Akaike information criterion in Modeltest 3.7 (Posada & Crandall, 1998). Each alignment was analysed in MrBayes 3.1.2. (Ronquist & Huelsenbeck, 2003). The data were partitioned to genes and the appropriate substitution model (as chosen by AIC) was applied to each partition. For *Maculinea* two million generations were run, for *Myrmica* ten million, sampling every 1000th generation. 100,000 and 2 million generations were discarded as burn in, for *Maculinea* and *Myrmica*, respectively. A 50% majority rule consensus tree was calculated from 3,802 and 16,002 trees, respectively. The *Maculinea* tree was then simplified to contain one terminal for each species.

Currently available cophylogenetic methodologies either directly compare a priori defined host and parasite phylogenies (Page, 1994; Ronquist, 1995; Charleston, 1998; Brooks et al., 2001) or incorporate phylogenetic uncertainty into statistical tests (Huelsenbeck, 1997, 2000; Johnson et al., 2001; Legendre et al., 2002). To test whether two phylogenies are congruent Light & Hafner (2008) propose a research protocol involving three steps, which was adopted in this study.

To evaluate the possible congruence of the *Maculinea* and *Myrmica* phylogenies, the following were considered: (a) all records of parasite-host associations; (b) one host per parasite (i.e., the host traditionally considered most important in Europe, see Table 1) and (c) strategies similar to (a) and (b), but treating *M. alcon* and *M. rebeli* as one species (see Fig. 1 for a graphical representation of the associations). The associations were obtained from Als et al. (2004) and references therein and updated with the references cited in Table 1. Because there is geographical host differentiation in *M. alcon* (Elmes et al., 1998), a single main host could not be assigned; therefore the one-host-per-parasite-analyses were repeated (as in b), each time taking only one of the recorded hosts of *M. alcon* into account.

The data were first analysed using ParaFit (Legendre et al., 2002). This statistical method does not depend on a priori defined phylogenies and is well suited to deal with multiple-host parasites. It uses genetic or patristic (summed branch lengths along a phylogenetic tree) distances to test significance of a global coevolutionary structure and of each parasite-host association. The method tests the null hypothesis that each parasite is associated with its host at random. If a parasite underwent a prolonged period of strict association with its host, there would be significant structure in the parasite tree mirroring that of the host. If one or both trees are unreliable, the program uses genetic distances instead of patristic distances. ParaFit takes as input a parasite-host association matrix (A), a matrix of principal coordinates calculated from pairwise genetic or patristic distances of the parasites (B) and a transposed matrix of principal coordinates for the host (C). The program compares a global trace statistic (ParaFitGlobal, Legendre et al., 2002) calculated from matrix D (D = CA'B) with the trace values obtained after a random permutation of the A matrix (keeping the same number of associations per parasite). The program tests individual associations in a comparable way.

To calculate pair wise distances in PAUP* (Swofford, 1998) the GTR+I and GTR+G+I models were used for the *Maculinea* and *Myrmica* COI alignments, respectively. Patristic distances were also calculated from the parasite and host trees in PAUP*. These matrices were then inserted into DISTPCOA (Legendre & Anderson, 1998), which yielded principal coordinates for the pairwise genetic and patristic distance matrices of the parasites and hosts. Finally, the significance of parasite-host associations was assessed with 9,999 permutations in ParaFit.

Then the data were analysed using a tree-based method implemented in TreeFitter (Ronquist, 1995). This tests the congruence between two phylogenetic trees by minimising a cost matrix. The user may specify costs associated with four evolutionary events (Ronquist, 1995; Page & Charleston, 1998): (1)

TABLE 1. Species of *Myrmica* recorded as hosts of the European *Maculinea* species; main host species are in bold. *Myrmica* species are ordered in an approximate sequence from the most xerotherm to oligotherm species. Country codes: A = Austria, CH = Switzerland, CZ = Czech, DK = Denmark, E = Spain, F = France, G = Germany, H = Hungary, LT = Lithuania, NL = The Netherlands, PL = Poland, RO = Romania, S = Sweden, SK = Slovakia, UA = Ukraine, UK = United Kingdom. References: [1]Elmes et al. (1998); [2]Sielezniew & Stankiewicz (2002); [3]Stankiewicz & Sielezniew (2002); [4]Höttinger et al. (2003); [5]Sielezniew et al. (2003); [6]Steiner et al. (2003) and references therein; [7]Sielezniew & Stankiewicz (2004); [8]Stankiewicz et al. (2005a); [9]Stankiewicz et al. (2005b); [10]Tartally (2005); [11]Tartally & Varga (2005); [12]Vályi-Nagy & Czősz (2007); [13]Sielezniew & Stankiewicz (2008); [14]Tartally & Varga (2008); [15]Tartally et al. (2008a); [16]Tartally et al. (2008b); [17]Witek et al. (2008); [18]Wynthoff et al. (2008); [19]Nash et al. (2008); [20]Munguira & Martin (1999).

Maculinea	***Myrmica***	**Host evaluation, comments, references**
arion	*hellenica*	eastern PL, at this site, *sabuleti* was not used and the nest density of *Myrmica* was very low[13]
	rugulosa	eastern PL, at this site, *sabuleti* was not used and the nest density of *Myrmica* was very low[13]
	schencki	eastern PL, at this site, *sabuleti* was not used and the nest density of *Myrmica* was very low[13]
	sabuleti**	**main host** F, UK, S[1]
	scabrinodis	minor host F, UK, S[1]
	lobicornis	a single pupa found[4]
rebeli	*specioides*	secondary host A[6]; occasionally H, RO[14]
	rugulosa	one nest (+ in the only *sabuleti* nest found)[8]
	schencki**	**main host** F, E[1]; **exclusive host** LT[9]; **one of two main hosts** H[12]; **one of the three species mainly used** H, RO[15]; secondary host PL[6]
	sabuleti	**main host** PL, A, G[6]; **one of two main hosts** H[12]; **one of the three species mainly used** H, RO[15]; rarely a host F, E[1]
	lonae	occasionally H, RO[15]
	scabrinodis	**one of the three species mainly used** H, RO[15]; secondary host PL[6]; rarely a host F, E[1]
	sulcinodis	secondary host CH[6]
	ruginodis	rarely a host F, E[1]
alcon	***salina***	**main host** at the northeast. H, nearby populations use *scabrinodis*[10]; occasionally a host H, RO[15]
	rubra**	**one of the two main hosts** DK, S[19], **host** S[1]; secondary host NL[1]
	scabrinodis**	**only host** E, F[1]; PL, UA, A[2, 4, 17]; **main host** H, RO[12, 15]; **main host** with *vandeli*, south. PL[7]
	vandeli	**main host** with *scabrinodis*, southern PL[7]; occasionally a host H, RO[15]
	ruginodis**	**main host** NL[1]; **one of the two main hosts** DK, S[19]
teleius*	*specioides*	found once in H, RO[14]
	rugulosa	PL, CZ, SK, UA, at most sites not possible to distinguish primary host (5 spp)[17]
	sabuleti	minor host F, PL[1]
	salina	locally important at a few sites H, RO[14]
	gallienii	PL, CZ, SK, UA, at most sites not possible to distinguish primary host (5 spp)[17]; secondary host (same frequency as in *scabrinodis*) PL[3]; locally important host (few sites) H, RO[14]
	rubra	**main host at western sites** H, RO[14]; **highest frequency** in PL[3]; PL, CZ, SK, UA, at most sites not possible to distinguish primary host (5 spp)[17]; minor host F, PL[1]; minor host, in same nest with *nausithous* in western H[11]
	scabrinodis**	**only host** NL[18]; **main host** F, PL[1]; **main host at eastern sites** H, RO[14]; secondary host PL[3]; PL, CZ, SK, UA, at most sites not possible to distinguish primary host (5 spp)[17]
	vandeli	minor host F, PL[1]; found once in H, RO[14]
	ruginodis	PL, CZ, SK, UA, at most sites not possible to distinguish primary host (5 spp)[17]; one nest PL[3]
nausithous	***rubra*****	**only host** F, E, PL, NL[1, 3, 18]; **main host** in western H[11]; **main host** in PL, UA[17]
	scabrinodis	the **only** "potential" **host** in two isolated populations in RO[16]; two nests, Kraków region PL[17]; host E[20]
	ruginodis	two nests, Kraków region PL[17]

* In northern Mongolia, *Maculinea teleius* is recorded from *Myrmica kamtschatica*, *M. forcipata* and *M. angulinodis* nests (Woyciechowski et al., 2006). ** Traditionally considered to be the main host and used as such in the analysis of cospeciation .

cospeciation (C): parasite speciation parallel to host; (2) duplication (D): parasite speciation independent of host; (3) host switching (H): parasite adopted secondary host(s); (4) sorting (S): parasite disappeared from host lineage (e.g., through extinction). These costs are optimised in a generalised parsimony framework: the optimal fit has the lowest global cost. TreeFitter is able to explore the optimal cost settings for a specified range; an interval between zero and four was chosen for all cost categories. The *Maculinea-Myrmica* associations were analysed using (1) a set of cost settings penalising each of the events in turn, (2) the default settings (C = 0, D = 0, H = 2, S = 1), (3) the maximum codivergence settings (C = –1, D = 0, H = 0, S = 0) and (4) a high cost for codivergence and switching to investigate independent parasite evolution (C = 10, D = 0, H = 10, S = 1). Ten thousand permutations of the parasite tree were used to determine whether the empirical associations were significantly less costly than associations by chance alone.

RESULTS

For *Maculinea* a well resolved tree was recovered. *Maculinea arion* + *M. arionides* and *M. teleius* + *M. nausithous* were separate, well-supported sister clades (posterior probability, PP = 100; Fig. 1). *Maculinea alcon* and *M. rebeli* formed a polytomy without any well supported monophyletic groups. Their relationship to other *Macu-*

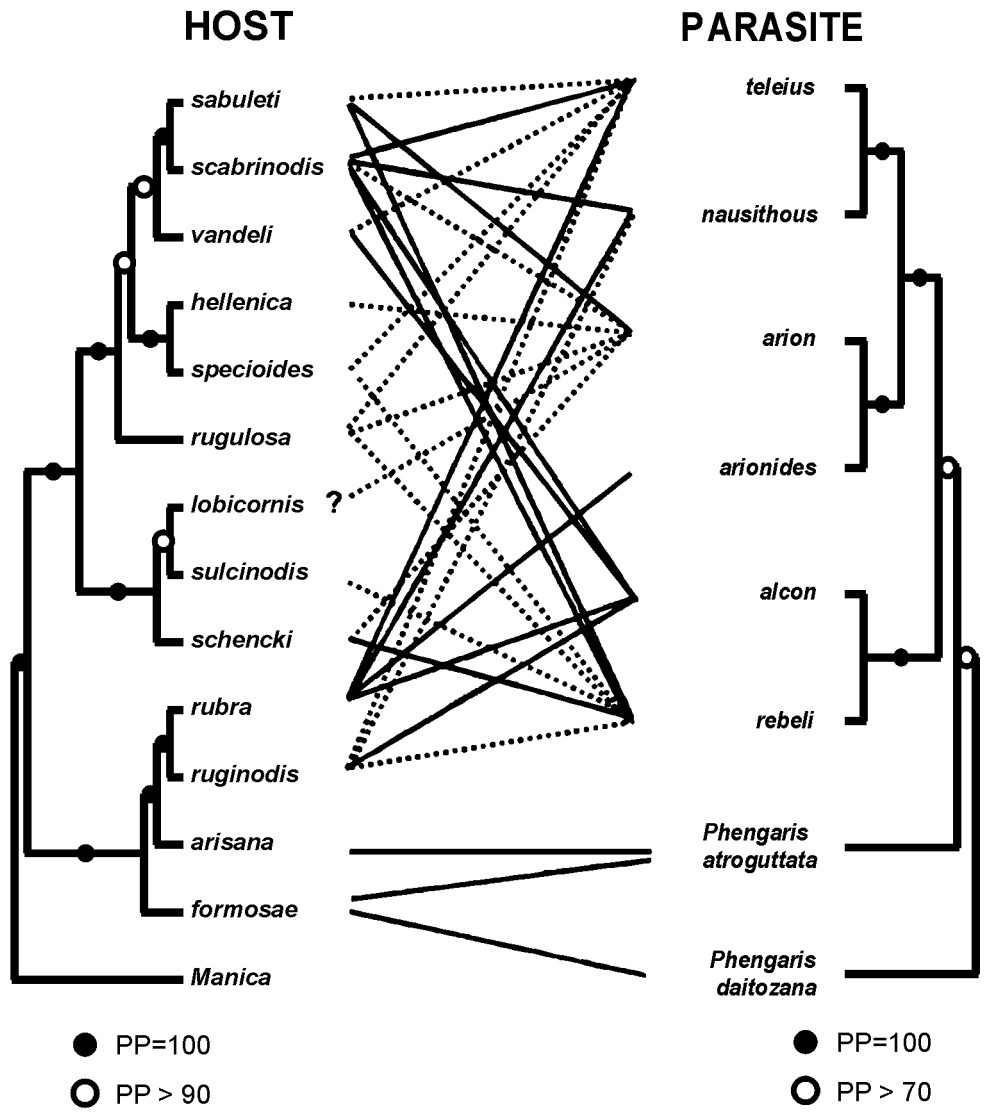

Fig. 1. Graphical representation of the associations of *Maculinea* parasites and two closely related oriental *Phengaris* species (right) with their *Myrmica* hosts (left). The *Myrmica* and *Maculinea* phylogenies are the result of Bayesian analyses of data partitioned to genes and an appropriate model chosen by AIC applied to each partition. The analyses were run for two (burn in 10,000) and ten million (burn in 2 million) generations. Full lines indicate main host associations for each species; dashed lines represent secondary or rarely used hosts; for a comprehensive summary of the host species recorded for European *Maculinea* species, see Table 1. Filled circles indicate 100% posterior probability; unfilled circles represent a posterior probability higher than 90% for *Myrmica* and higher than 70% for *Maculinea*. Note that these phylogenies are based on previous data of one or several specimens per species, the details of which are not presented. Notably, the species in the *alcon-rebeli* clade were not reciprocally monophyletic.

linea received moderate support (PP = 76). The phylogeny was not investigated further, as our results are identical to those of Als et al. (2004) and the Bayesian tree in Fric et al. (2007). The *Myrmica* tree was completely resolved, received high support at every node (Fig. 1) and also agrees with the one presented in Jansen et al. (2010). Morphologically known species groups were recovered as monophyletic: scabrinodis (the clade containing *M. sabuleti* and *M. rugulosa*), lobicornis (*M. lobicornis* and *M. sulcinodis*), and rubra (*M. rubra*, *M. ruginodis* and *M. arisana*).

The tree-independent method (ParaFit) returned a non significant ParaFitGlobal statistic and non significant individual associations, except for *M. teleius* and *Myrmica rubra* (P = 0.018). The analysis was repeated, taking into account only the traditional main host for each parasite species, which did not yield a significant global statistic, nor any statistically significant individual association. Changing the main host for *M. alcon* or treating *M. alcon* and *M. rebeli* as one species did not alter the results. Finally, the use of patristic distances was to no avail. No similarity could be found between the parasite and host phylogenies.

In the tree-based analysis (TreeFitter), the exploration of the cost space (all possible combinations of values between zero and four for each parameter) did not yield a single optimal solution and no solution received a P-value below 0.06. Therefore, there was no objective criterion to

select one cost setting over another. When taking into account all recorded parasite-host associations, the global cost of the optimal reconstruction was never significantly lower than costs obtained after 10,000 random rearrangements of the parasite tree. All reconstructions implied a number of switches, unless a very high cost was set for switching. The above analysis was repeated, considering only the traditional main host for each parasite species. Again, the cost estimation failed to produce a significant solution. This did not change when the data were analysed using different hosts for *M. alcon* or when *M. alcon* and *M. rebeli* were treated as one species. The parasite tree was fitted using the same settings as before, and failed to recover any significant coevolutionary signal in the *Maculinea* tree. Evidently, the parasite-host associations are random and not shaped by cospeciation.

DISCUSSION

Clearly, the *Maculinea* and *Myrmica* phylogenies were not congruent. Incongruent parasite and host phylogenies, however, do not imply that coevolution did not occur in the evolutionary history of the parasites and their hosts. Literature abounds with examples why coevolution is not detected. For example, cophylogenetic methods may fail to recover a significant pattern because of phylogenetic uncertainty (Johnson et al., 2002) or multiple-host parasites (Banks & Paterson, 2005).

The *Maculinea* tree obtained in this study is congruent with that recorded in the literature (Als et al., 2004; Fric et al., 2007) and received good support. The *Myrmica* phylogeny was derived from several gene fragments and corroborated most morphologically defined species groups (Seifert, 1988; Radchenko 1995; Radchenko & Elmes, 2001; Jansen et al., 2010). Thus, incorrect host or parasite trees do not explain their mutual incongruence. If each *Maculinea* species uses *Myrmica* species belonging to at least the same species-group clade then this would support the co-speciation hypothesis. Visual inspection of the tanglegram (Fig. 1) reveals that this is not the case; even the main host species tend to belong to more than one *Myrmica* species group. Nevertheless, to accommodate the possibility of phylogenetic uncertainty, a ParaFit with distance data was applied. This method estimates coevolutionary statistics independent of any a priori defined phylogenetic structure (Legendre et al., 2002). Again, no congruence was found.

Maculinea species are obligately dependent on their *Myrmica* host species, but only a minute proportion of the potential host colonies are infected with this parasite (Elmes et al., 1998). However, until recently the cospeciation hypothesis seemed plausible; still in the early 2000s it was believed that *Maculinea* species are mainly dependent on a single host species (Thomas et al., 2005). Currently, however, a great diversity of host species is recorded (Table 1), although the significance of many of the host species for the survival of *Maculinea* populations is poorly documented. As emphasised by Thomas et al. (2005), successful rearing of *Maculinea* in a nest of *Myrmica*, or finding caterpillars close to pupation in a field nest, does not prove that that specific host species could maintain the local parasite population. To prove this, more detailed life-history and survival studies are needed.

In spite of these uncertainties, the high diversity of host species reported recently (Table 1) suggests that host ant exploitation by *Maculinea* is fairly flexible, even locally, indicating a potential for shifting to a new main host. The current pattern is one of geographical variation in the use of the main host species and there is no reason why the potential for host shift should be only historical (as would be the case if cospeciation had occurred).

Notably, even though the presence of the right host species is vital for any *Maculinea* population, their main limiting resource seems to be their host plant, each species usually using locally or even globally only one or a few closely related food plant species in the period prior to their adoption by the host ant (Munguira & Martin, 1999). The availability of food plants rather than the presence of ant nests determine the oviposition patterns of *Maculinea* species (Thomas & Elmes, 2001). Because the species composition of *Myrmica* nesting close to the obligate food plant may differ geographically (Thomas et al., 1998), there probably is strong selection for *Maculinea* to adapt to the regional or local *Myrmica* species nesting close to the food plants of the caterpillars of the butterfly. This geographical variation in host use may thus be interpreted as a result of coevolutionary dynamics (as defined by Janzen, 1980 and Thompson, 2005) involving locally restricted arms races (Nash et al., 2008). The results presented demonstrate that coevolution and cospeciation are evolutionarily distinct phenomena and the former does not necessarily imply the latter.

The likelihood of a host shift depends on the specific lifestyle of the parasite. There are striking differences between the predatory and cuckoo-feeding *Maculinea* species in their relations with their host ants, but for different reasons, both predatory and cuckoo-feeding species have evolved a more or less general *Myrmica*-like CHC profile. The cuckoo-feeding caterpillar is taken by host workers to the brood chamber, where it is fed by nurse ants. In the nest of secondary hosts, in benign situations, the caterpillar keeps a general *Myrmica*-like profile, probably acquired passively from the host (Schönrogge, 2004). However, after isolation from the host nest the same caterpillars are able to synthesise additional compounds that cannot be acquired from the secondary host, but resemble the CHC of the main host (Schönrogge et al., 2004). Thus it is likely that these compounds can be produced by the caterpillar, but their production is suppressed in secondary host colonies. However, in food-stressed colonies the caterpillars probably synthesise the main-host-specific CHCs to facilitate begging for food. In this case close mimicry of the main host would prove fatal for the parasite, whereas in stressed nests of the main host the synthesis of the same compounds elevates the status of the caterpillar, probably to a level equivalent to that of the host queen (Thomas et al., 2005).

When predatory *Maculinea* caterpillars are taken into a host nest, they attach a patch of silk to the roof of an outer

chamber, from where they make short foraging bouts to the brood chamber to feed on large ant larvae. Unfortunately, there is little information on the changes in the CHC profiles of predatory *Maculinea* species, but their less intimate association with host ants compared to the cuckoo species may theoretically exert a lower selective pressure to match the CHC profile of the host.

In summary, the main difference between the two *Maculinea* strategies seems to be a higher risk of the cuckoo-feeding caterpillars being killed in food-stressed colonies of secondary hosts, potentially leading to higher host specificity of cuckoo species. However, this expectation is not supported by field data, as the predatory *M. nausithous* are the most host-specific *Maculinea* (Tartally, 2008a). This may be explained by the mitigating effect of an additional adaptation. Recently, Barbero et al. (2009a, b) showed that the caterpillars and pupae of both a cuckoo-feeding and a predatory *Maculinea* species mimic the stridulation of the queen of their main host and so achieve a high status within the ant society. Notably, the sounds made by queens of the three *Myrmica* species studied were indistinguishable. Given the possible universal efficiency of acoustic communication, the close chemical adaptation of cuckoo-feeding *Maculinea* species could still be a strong selective force in stressed nests of secondary host species effectively working against host shifts.

For predatory *Maculinea* not specialising chemically to beg food in continuous close contact with the host, selection against host specialisation could still occur because their lifestyle requires a much larger number of host colonies than the cuckoo-feeding species (Thomas et al., 2005). In spite of the differences in the life-styles of predatory and cuckoo-feeding species, host shifts are recorded for species in both groups (Table 1). Below are presented a set of hypothetical adaptive mechanisms that could operate in both groups of *Maculinea* subject to selection to shift between hosts, e.g., when next to food plants of the caterpillar a secondary host species outnumbers the traditional, locally rare main host. The models are classified on the basis of plausible parasite-host scenarios.

One stable main host and the evolutionary potential for increasing the exploitation of that host

When colonies of the main host are abundant, then adaptation to that host species is expected to become evolutionarily fixed. This outcome is recorded for cuckoo-feeding *Maculinea* species over large geographical areas along with the connate ability to synthesise a host-species mimicking odour. However, because "a species, like a sponge, soaks up heterozygous (recessive) mutations while remaining from first to last externally (phenotypically) homogeneous" (Chetverikov, 1926), populations maintain genetic potential for adaptive evolution (Schmalhausen, 1949; Lewontin, 1974; Wilkins, 2001). Hence, the expectation is that *Maculinea* populations with one stable host maintain a high standing genetic variation.

Traditional main host scarce, but secondary host abundant

When the habitat of a specific host species changes (e.g., when moving from one geographical region to another, or locally over long periods of time), the vital spatial correlation between the locations of the nests of the main host and the caterpillar's host plant may break down, and other potential host species may occupy the space close to the host plants. Then, there will be a strong selective pressure that favours those genetic variants that have CHC patterns close to those of the new, numerically dominant host species. Even though chemical closeness of the old and new host species is expected to facilitate a host shift, serendipitous adaptation may take place. For example, Hojo and coworkers (Akino, 2008; Hojo et al., 2009) described that *Camponotus japonicus* (the only host of the lycaenid *Niphanda fusca)* brings caterpillars to its nest and after adoption, these caterpillars synthesise CHCs that are more similar to those of the male ants than worker ants with which the caterpillars live, which is an unexpected but efficient means of raising the status of the caterpillars within the ant colony.

Main local host species varies in abundance in time

Sometimes the main host becomes rare because of the effect the parasite has on the survival of its colonies, whereas a secondary host may be temporally unaffected. If the CHC profiles of two temporally alternating potential host species are relatively similar, genetic variation may allow tracking of the available host species. Such see-sawing between two adaptive peaks seems to fit the shifting host use of *Myrmica rubra* and *M. ruginodis* by *Maculinea alcon* in Denmark, reported by Nash et al. (2008).

No reliable single host, but a combination of two hosts might suffice

If the combined nest density of two permanent host species is sufficient to maintain the parasite population, but that of one of the species would not, selection may favour an individual-level CHC profile that is a mix of the CHC patterns of the hosts. Such a tactic is close to that described by Schlick-Steiner et al. (2004). In Central Europe the cuckoo-feeding *Maculinea rebeli* has one main and several secondary host species, and rather than emitting a general *Myrmica*-like odour the pre-retrieval caterpillars synthesise an aggregate odour containing specific compounds of at least two host species. Because fine-tuned active synthesis of host-specific CHC starts in the cuckoo-feeders only several days after adoption by the host ant, it is unlikely that the fine-tuning could result in the production of CHC profiles of more than one host species. Such a system would be very costly and after adoption there is no selection for aggregate-odour mimicry. The pre-retrieval mixed synthesis could, however, facilitate the evolution of fine-tuned mimicry of the realised host after adoption, when more than one host species is needed to maintain the population.

Adaptation to the realised host species of a set of more or less equally probable host species is theoretically plau-

sible, hence future studies should concentrate on finding such situations in natural populations. A prerequisite to individual developmental flexibility of fine-tuned adaptation is an environmental signal that reliably correlates with the realised host species. In *Maculinea*, such a signal would be the odour (CHC pattern) of the host colony. Then selection could act on the available genetic variation in the parasite, such that a cuckoo-feeding caterpillar's CHC synthesis is switched to mimicking the CHC of the realised host.

A flexible norm of reaction, a concept that includes phenotypic plasticity of CHC profile expression in insects, by which an organism with a specific genotype undergoes adaptive modifications triggered by environmental factors (Schmalhausen, 1949; Levins, 1968), is a wide-spread phenomenon in the animal and plant kingdoms (West-Eberhard, 2003). For example, in the water strider *Gerris odontogaster*, wing length (short or long wings) and mode of reproduction (direct or post-diapause reproduction) are determined by photoperiod with temperature as a modifying environmental cue (no genetic switch). Notably, developmental plasticity in water striders may vary among individuals, populations and species, depending on how genetic switches and environmental cues interact in determining the physiological and morphological features of the phenotype, and as a result the life-history of a species is also contingent on the geographical location of the population (for a review, see Vepsäläinen, 1978).

Currently little is known about the reaction norms of *Maculinea*, and as far as we are aware nothing is known about potential switch mechanisms in the context of chemical mimicry, although the fact that host switching may be successful under certain conditions may be deduced from the data provided by Schönrogge et al. (2004). The concept of reaction norms provides intriguing testable hypotheses of chemical host exploitation by these parasites. The great variety of different chemical tactics used by parasites to break in to host domains — see reviews by Lenoir et al. (2001) and Akino (2008) — however, indicate a variety of potential case-specific switch mechanisms. Hopefully the studies referred to in Table 1 (e.g., Sielezniew & Stankiewicz, 2008; Tartally et al., 2008a, b) will encourage a theoretically and empirically broader approach to studies of adaptive shifts and modifications of the chemical mimicry of *Maculinea* of potential host species.

Thus, in order to study the adaptive pathways in *Maculinea* species associated with their host use, locally paired samples of *Maculinea* and their realised *Myrmica* host species need to be collected in various geographical regions, where it is known that *Maculinea* show differences or variation in host use (cf. Nash et al., 2008 for Denmark), i.e., shift the focus to the population level in those regions where strong selection favouring exploitation of a new host is expected or has been realised. Both *Maculinea* and *Myrmica* phylogenies should then be reconstructed to determine whether there are cryptic species (in both host and parasite) and whether adaptive evolution has occurred in the parasite and the host through host shifts. Furthermore, to shed light on the adaptation of *Maculinea* caterpillars to the local host species they exploit, the CHC profiles of local parasite-host pairs should be analysed following the experimental design of Schönrogge et al. (2004), including both the pre-adoption and post-adoption CHC profiles of the caterpillars.

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