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noraceh@ceh.ac.uk

1 **Conservation of co-evolved interactions: understanding the *Maculinea-Myrmica* complex**

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3 J.A. Thomas^{1,2}, K. Schönrogge²

4 1 Department of Zoology, University of Oxford, Oxford, OX1 3SZ, United Kingdom

5 2 Centre for Ecology and Hydrology, Wallingford, OX10 8BB, United Kingdom

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11 Correspondence: jeremy.thomas@zoo.ox.ac.uk

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21 **Abstract**

22 1) The six papers in this Special Issue of *Insect Conservation and Biodiversity* are presented as a
23 *gedenkschrift* honouring ground-breaking contributions made by the late Graham Elmes towards
24 understanding the biology of *Myrmica* ants and their social parasites.

25 2) A common theme is that each research paper contributes new knowledge applicable to the future
26 survival of *Maculinea* (= *Phengaris*) species of butterflies, which have become flagships for insect
27 conservation across Europe. All *Maculinea* species are highly specialised, with larvae that feed briefly
28 on a specific foodplant before living underground for 11-23 months as social parasites of *Myrmica*
29 colonies.

30 3) This introductory overview provides a brief history of the research that has led to the current
31 collection, with emphasis on Graham Elmes' life and work. It is followed by three research papers
32 that illustrate the diversity, socio-biology and ecology of *Myrmica* ants. A fourth describes an
33 extreme adaptation that increases the efficiency with which some populations of *Maculinea* larvae
34 exploit the resources within *Myrmica* nests. A fifth, more theoretical, paper models the constraints
35 that typically lead to host specificity among social parasites, and explores why host switches are rare
36 and quick.

37 For over a century until the 1980s, nearly all attempts to conserve declining insects in protected
38 areas, or as targeted species, were ultimately disappointing, at least within the secondary or semi-
39 natural ecosystems that provide most species-rich habitats in the developed and developing world
40 (New *et al.*, 1995; Thomas, 1984a; Webb & Pullin, 1996). Indeed, extinction rates of rare butterflies
41 were often greater on UK Protected Areas than in neighbouring woodland or farmland (Thomas,
42 1984a, 1991). Success was achieved only when fresh approaches were applied, based on detailed
43 ecological knowledge of a threatened community, guild or species (New *et al.*, 1995; Thomas *et al.*,
44 2011). One key discovery was that many declining insects possess unexpectedly sedentary adult
45 phenotypes, ill-suited to persistence in modern fragmented landscapes (Hanski, 1999). Another was
46 that even apparent generalists may have specialised requirements at some (usually immature) stage
47 in their lives, involving close-knit interactions with other organisms and necessitating a narrow
48 definable niche to exist in sufficient abundance for their populations to experience optimum (or
49 positive) intrinsic growth rates (Thomas, 2016; Thomas *et al.*, 2001; Thomas *et al.*, 2011).
50 Compounding both constraints, different sets of genotypes may have co-evolved at local scales
51 and/or adapted to their local abiotic environment (Nash *et al.*, 2008; Schönrogge *et al.*, 2006;
52 Thompson, 2005), amplifying the challenge of conserving locally adapted subsets in a rapidly
53 changing world.

54 The endangered genus of *Maculinea* (= *Phengaris*) butterflies illustrates the above complexities in
55 extreme form. From mutualistic ancestors (Als *et al.*, 2004; Fiedler, 1998), their larvae evolved as
56 specialist social parasites that employ chemical and acoustical mimicry to infiltrate *Myrmica* ant
57 colonies, where the butterfly larvae prey upon ant brood or are fed directly by nurse ants (Akino *et*
58 *al.*, 1999; Barbero *et al.*, 2009; Elmes *et al.*, 1991; Thomas *et al.*, 2005). A cost of this life-style is a
59 high level of host specificity in most regional populations of each *Maculinea* species, albeit with
60 occasional host switches across their wider ranges and the existence of certain populations where
61 more than one host may be exploited (Tartally *et al.*, 2019a). Moreover, before exploiting ant
62 societies, the larva of each *Maculinea* species feeds briefly on one or two specific foodplants, which

63 must coexist in a suitable growth-form (Thomas & Elmes, 2001) within the 1-2 m foraging range of a
64 suitable *Myrmica* colony for the latter to be successfully parasitized (Als *et al.*, 2001; Elmes *et al.*,
65 1991; Kempe *et al.*, 2016; Patricelli *et al.*, 2015). Further complexity exists in certain populations,
66 where the *Maculinea* larvae themselves are hosts to equally specialised (and rarer) host-specific
67 ichneumonid parasitoids, each adapted to the larval demography and life-style of its particular host
68 (Anton *et al.*, 2007a; Anton *et al.*, 2007b; Thomas & Elmes, 1993; Thomas *et al.*, 2002). It is little
69 surprise, therefore, that early attempts to conserve Europe's dwindling populations of *Maculinea*
70 species failed, owing to inadequate knowledge of their specialised interactions and their wider
71 ecological needs (Thomas, 1980, 1984a).

72 This special issue of *Insect Conservation and Diversity* contains three original research papers that
73 illustrate the diversity, socio-biology and ecology of *Myrmica* ants. A fourth describes an extreme
74 adaptation that enables the larvae of *Maculinea* butterfly species to exploit the rich resources within
75 *Myrmica* colonies with increased efficiency after infiltrating their nests as social parasites. A fifth,
76 more theoretical, paper models the constraints that typically lead to host specificity among social
77 parasites with similar life-styles, and explores why host switches are rare and quick, while the sixth
78 paper – this introductory overview – provides a brief history of the research exploring these systems
79 that has led to the current collection. A common theme is that each research paper contributes new
80 knowledge applicable to the future survival of these endangered butterflies, which have become
81 flagships for insect conservation across Europe (Thomas & Settele, 2004). Another – and the
82 motivation for this volume - is that each paper is presented as a grateful tribute to G. W. Elmes
83 (1943-2017), an irreplaceable research colleague and mentor for fourteen of the authors and an
84 inspiration and fount of knowledge to all of them. Although Elmes had previously collaborated
85 fruitfully with three of us (Thomas, Schönrogge, Wardlaw), his main influence here stems from
86 contributing unmatched expertise in 2002-2010 on the biology and taxonomy of the genus *Myrmica*
87 during two pan-European EU Framework research programmes, MacMan (Settele *et al.*, 2005;
88 Settele *et al.*, 2002) and CLIMIT (<https://www.biodiversa.org/124>), both led by Josef Settele (UFZ

89 Helmholtz Institute, Germany). Both collaborations explored these interactions alongside the
90 application of this knowledge to nature conservation, as well as the putative impacts that climate
91 change might have on their specialised community modules. Together, these partnerships involved
92 more than 100 scientists from 18 institutions and 14 nations, including most authors here, and
93 trained a cohort of postgraduate students who were to become tenured research entomologists,
94 with expertise in the biology of ants and butterflies, at universities and research institutes across the
95 continent. In both cases, Elmes was the sole expert on ant biology among a team of theoreticians
96 and butterfly ecologists, and his legacy has been great immense.

97 Graham Elmes (Fig 1) himself had a remarkable and somewhat unorthodox career based at the UK
98 Natural Environment Research Council's Furzebrook Research Station in Dorset, later relocated to
99 NERC's Winfrith lab, both within 10 km of his birthplace, Wareham. Having left school aged 16 to
100 help support his family, he joined the then Nature Conservancy (now the Centre for Ecology &
101 Hydrology) at Furzebrook in 1961 as a junior assistant to M. V. Brian, the world's leading expert on
102 *Myrmica* biology of the time. Two decades later the baton passed to Elmes, who - after part time
103 study for high-school exams, a university degree and a PhD - was ultimately promoted five levels to
104 Senior Principal Scientific Officer, equivalent to a senior university chair.

105 Elmes' initial research helped to explain how differentiation in the development, behaviour and
106 physiology of *Myrmica* ants, combined with their ecological specialisations, social structures and the
107 dynamics - including queen numbers - of their colonies, encouraged the evolution of many subtly
108 different genotypes and species, enabling them to radiate as one of the three dominant ant genera
109 (with *Formica* and *Lasius*) of the Holarctic (e.g. Elmes, 1971, 1973, 1974, 1980, 1982, 1983, 1987,
110 1991; Elmes & Petal, 1990; Elmes & Wardlaw, 1981; Nielsen et al., 1999). A second lifelong passion
111 was to sample *Myrmica* colonies across the Palearctic in order to complement his experimental
112 studies with morphological analyses of numerous meticulously mounted series of the queens, males
113 and workers (Elmes, 1978; Elmes & Thomas, 1985). This resulted in the description of >40 new

114 species of *Myrmica* - and the synonymization of others - many in collaboration with Alex Radchenko,
115 thereby enlarging by ~40% the number of Red ant species recognised in the Palaearctic. With
116 Radchenko and in so-called 'retirement', Graham wrote the definitive monograph *Myrmica Ants*
117 (*Hymenoptera: Formicidae) of the Old World* (Radchenko & Elmes, 2010), a masterpiece for which
118 his name will be remembered long after the advances from >100 major peer-reviewed papers have
119 been absorbed into the anonymity of basic biological knowledge. Elmes' unique collection of
120 *Myrmica* specimens, consisting of several thousand series representing 240 of the c. 280 recognised
121 species in the genus, with paratypes of 80 species, are also conserved for perpetuity among the
122 Hope Entomological Collections in the University of Oxford's Natural History Museum.

123 Modern research on the interactions between *Maculinea* butterflies and *Myrmica* ants began in
124 1972, although the socially parasitic life-style of three species had been recognised in outline 50
125 years earlier (Chapman, 1916, 1918, 1919; Frohawk, 1916). In 1972, Jeremy Thomas was appointed
126 at Furzebrook to identify the factors driving 150 years of near continuous local extinction in national
127 populations of *M. arion*, by then reduced to a few individuals on a single UK site (Thomas, 1977,
128 1980, 1984a; Thomas *et al.*, 2009). Although not formally involved in the first decade of a
129 programme that focussed on the population dynamics, behaviour, ecological requirements and
130 evolutionary biology of *M. arion*, Elmes was an invaluable colleague whose own studies during the
131 1970s complemented and illuminated the former work. For example, while Thomas (1977) was
132 discovering that west European populations of *M. arion* were host specific to *Myrmica scabrinodis*
133 var *sabuleti*, and that this ant occupied a narrow thermophilous niche in grasslands that was seldom
134 generated under modern agriculture, Elmes was applying morphometrics to establish unequivocally
135 that *Myrmica sabuleti* was a true species, and that its larval development required warmer
136 temperatures than that of the other four commoner species of *Myrmica* inhabiting former *M. arion*
137 sites (Elmes, 1978, 1982; Elmes & Wardlaw, 1983).

138 By happy chance, Elmes' third interest, from the outset, was the evolutionary biology of inquiline
139 ants that parasitise *Myrmica* societies. He discovered, described and studied a new and rare species,
140 *Myrmica hirsuta*, whose miniature queens evolved from, and parasitise, *Myrmica sabuleti* societies
141 (Elmes, 1978, 1983), and provided key insights into the half-way house of microgyne queens found
142 in certain nests of *Myrmica rubra* (Elmes, 1976). It was thus a smooth transition to team up with his
143 good friend after JAT extended studies to the ecology and evolutionary biology of the five
144 recognised species of *Maculinea* on mainland Europe (Thomas, 1984b), aided at Furzebrook by
145 Judith Wardlaw, who meticulously maintained our lab experiments, and Ralph Clarke's modelling
146 and biometrical skills – a team that was further strengthened in 1999 when Karsten Schönrogge
147 joined, initially to study the adaptations of extreme dipteran social parasites, *Microdon mutabilis*
148 and *M. mymicæ* (Elmes *et al.*, 1999; Schönrogge *et al.*, 2002; Schönrogge *et al.*, 2006; Schönrogge *et*
149 *al.*, 2008). During the 1980s and 1990s, the UK team was able to advance knowledge on several
150 fronts (reviews: Thomas *et al.*, 1998a; Thomas *et al.*, 2005). We were most pleased to identify: (i) the
151 divergent host specificity of each *Maculinea* species, with each exploiting a different species of
152 *Myrmica* with different habitat requirements across the wide area of western Europe that was
153 initially sampled (Elmes *et al.*, 1998; Thomas *et al.*, 1989); (ii) the existence of occasional host shifts
154 between different sectors of the continent (Elmes *et al.*, 1994), more recently shown to be yet more
155 complex after massive pan-European sampling during MacMan (Tartally *et al.*, 2019a); (iii) how
156 *Maculinea* larvae employ chemical mimicry to infiltrate and exploit different species of *Myrmica*
157 (Akino *et al.*, 1999); (iv) major differences between the predatory-feeding strategies of *M. arion*, *M.*
158 *teleius*, and *M. nausithous* and the more efficient cuckoo-feeding of *M. alcon* and *M. rebeli* (Elmes *et*
159 *al.*, 1991; Thomas & Elmes, 1998; Thomas & Wardlaw, 1992), each with repercussions for host
160 specificity, population dynamics and resilience, and conservation (Thomas *et al.*, 1998a; Thomas *et*
161 *al.*, 2005); (v) the existence of an apparently fixed polymorphism of 1- and 2-year developing larvae
162 in certain populations of (especially) cuckoo species of *Maculinea* (Schönrogge *et al.*, 2000; Thomas
163 *et al.*, 1998b); and (vi) the remarkable specialisations of two genera of rare host-specific

164 ichneumonid parasitoids which parasitise a few populations of *Maculinea* larvae, by employing - in
165 at least two species - agonistic semio-chemicals to storm the specific *Myrmica* nests that contain
166 caterpillars of their specific *Maculinea* hosts (Thomas & Elmes, 1993; Thomas *et al.*, 2002). During
167 the same period, JAT's other team applied and tested several key results in the field through
168 managing >50 UK sites to generate the deduced optimum habitat for *M. arion*, before re-introducing
169 it to the UK in 1983-1992 (Thomas *et al.*, 2009): 35 generations later the species had spread to ~40
170 UK Protected Areas, which today support the largest known populations of this globally Endangered
171 Species in Europe. Elmes and Thomas made similar recommendations based on the hosts and niches
172 we had identified of *M. nausithous* and *M. teleius* (Thomas, 1984b, 1991; Thomas & Elmes, 2001),
173 collaborating with Jan van der Made at Wageningen, who soon recruited Irma Wynhoff (1998) to
174 join his group. She ably extended these studies and, in 1990, successfully re-established these
175 nationally extinct butterflies to the Netherlands.

176 By the late 1990s, interest in the biology of the five recognised community modules of *Myrmica*-
177 *Maculinea*-foodplant-parasitoid had spread in Europe, amplified by a workshop organised by Irma
178 Wynhoff at Wageningen, which included a Special Issue of the papers in the *Journal of Insect*
179 *Conservation* (1998, volume 2). Soon, important advances to knowledge were being made at other
180 centres, notably in Copenhagen (e.g. Als *et al.*, 2001, 2002; Als *et al.*, 2004; Nash *et al.*, 2008) and
181 Leipzig-Halle (e.g. Geissler-Strobel *et al.*, 2000; Pfeifer *et al.*, 2000), providing the foundation for the
182 multi-centre collaborations of MacMan and CLIMIT that generated 66 original publications on these
183 systems in 2002-2005 (<http://www.macman.pensoft.net/>), and many since, as well as 90 short peer-
184 reviewed papers by 114 co-authors in the closing MacMan book (Settele *et al.*, 2005). It is beyond
185 the scope of this *gedenkschrift* to Graham Elmes to review the numerous papers published post-
186 MacMan. Sufficient to note that research on the *Maculinea* complex continues in at least thirteen
187 universities and institutes across Europe, including the seven represented here by the authors.

188 All five papers in this volume build on Elmes' legacy and confirm that the future of this field is in
189 good hands. The first, by Ebsen, Boomsma and Nash (2019), uses molecular techniques to reveal at
190 least one new cryptic species within the *Myrmica scabrinodis* group. This had been predicted when
191 Elmes *et al.* (1994) studied host specificity by *Maculinea alcon* in France and Spain, and noticed
192 clear-cut ecological and behavioural differences between two 'types' of *M. scabrinodis*, one
193 occupying dry niches and the other wet ones, which we labelled *scabrinodis* A and B but could not
194 separate on morphological criteria. Twenty-five years later, in an elegant study started during
195 MacMan, Ebsen and colleagues established that these forms were unquestionably two cryptic
196 species (they also show that various types of *M. sabuleti* are just that – types not species). These
197 results have an obvious application to conservation, since the large majority of Europe's *Maculinea*
198 populations are specific to a single host ant (Tartally *et al.*, 2019a), and each *Myrmica* species
199 occupies a different niche, requiring different management, within grasslands (Elmes *et al.*, 1998).

200 The second paper - The influence of colony traits on the collective behaviour of *Myrmica scabrinodis*
201 ants (Maák *et al.*, 2019) – extends Elmes' approach of investigating how social structure and factors
202 such as food supply collectively determine the physiological state of a *Myrmica* colony, which in turn
203 influences its tolerance (or intolerance) of intruders to the nest, including social parasites such as
204 *Maculinea* larvae, however close their chemical mimicry may be (Casacci *et al.*, 2019). This fine
205 team, led originally by Emilio Balletto at the University of Turin, has made remarkable advances in
206 understanding *Maculinea* systems post-MacMan, several in collaboration with our UK group and
207 many, as here, with Magda Witek and her outstanding group at the Polish Academy of Sciences.

208 Striking examples include describing how the larvae and pupae of *Maculinea* broadcast acoustical
209 signals that closely mimic the distinctive stridulations of (adult) *Myrmica* queens, thereby elevating
210 their status within host societies after penetration through chemical mimicry (Barbero *et al.*, 2009);
211 and how ovipositing female *Maculinea arion* select *Origanum* plants growing in close proximity to a
212 *Myrmica* nest through detecting an agonistic monoterpene volatile, carvacrol, that is released
213 when their foodplant's roots are disturbed (Patricelli *et al.*, 2015). The putative influence of

214 *Wolbachia* on relationships was also explored by Patricelli *et al.* (2013) and, most recently, di Salvo
215 *et al.* (2019) suggested that the bipartite *Myrmica* – *Maculinea* interaction might in fact be a
216 tripartite one, with direct or indirect involvement of the *Maculinea* microbiome.

217 The third paper represents the continuing collaboration post-MacMan between excellent teams at
218 the Universities of Debrecen and Copenhagen. In this example, Tartally *et al.* (2019b) studied the
219 impacts of changes to traditional farming practices on *Myrmica* densities in former hay meadows in
220 the mountains of north-east Hungary, that support the xerophilous Alcon blue. Although these
221 meadows contain some unusual *M. alcon* X (*sensu* Tartally *et al.*, 2019a) populations in which
222 species-level host specificity has not been demonstrated, the effects of 10 year's abandonment were
223 found to be detrimental to the status of all *Myrmica* populations sampled. The study highlights the
224 need to maintain low-intensity pastoral farming by mowing or grazing to avoid the decline of
225 biodiversity, reversing a trend that has become widespread in Transylvania and other mountainous
226 regions of eastern Europe, which remain a stronghold for *Maculinea* populations alongside many
227 other threatened insect species.

228 The fourth paper completes an unfinished draft begun by Graham Elmes fifteen years ago but set
229 aside when writing his monograph on *Myrmica* (Radchenko & Elmes, 2010). It represents the fifth
230 paper in a sequence studying the polymorphism in growth in certain populations of (especially)
231 cuckoo species of *Maculinea*, whereby some larvae take 1 year and others 2 years to develop within
232 the same ant nests. The first three papers (Schönrogge *et al.*, 2000; Thomas *et al.*, 1998b; Witek *et*
233 *al.*, 2006) described the phenomenon, and include data that suggested that the polymorphism might
234 be fixed rather than plastic. If confirmed, this would be exceedingly unusual in the animal kingdom,
235 having previously been described only in salmonid fish. Putative benefits of such a strategy were
236 explored in a theoretical model by Hovestadt *et al.* (2007), who concluded that the phenomenon
237 could evolve owing to the ergonomic benefits that ensued if certain assumptions prevailed, such as a
238 need for individual females to lay a mixture of eggs that were genetically pre-determined as fast- or

239 slow-developing individuals, and that the ratio of slow-developers could not exceed 50%. The
240 current paper describes a series of lab experiments made by Elmes and Thomas that confirm both
241 the existence of a fixed polymorphism and Hovestadt's theoretical predictions of the attributes
242 required for this to evolve.

243 The final paper of this special issue describes the results from another Hovestadt *et al.* (2019) model.
244 It extends an approach very satisfying to Elmes (and us), of collaborating with talented theoreticians
245 who constructed models to explore questions which were impractical to test experimentally given
246 existing techniques or resources. Typically, we supplied fragments of empirically-derived knowledge
247 to ground the models in realism, and generally the simulations rejected some of our pet speculations
248 while generating new testable ideas: previous examples include Hochberg *et al.* (1994), Clarke *et al.*
249 (1997), and Hovestadt *et al.* (2007; 2012). Here, Hovestadt presents a population-genetic model that
250 explores the putative link between multi-host use and host switching in host-parasite interactions,
251 such as those of *Maculinea*. He concludes: (i) that host-shifting may proceed so rapidly that multiple
252 host-use is unlikely to be observed, (ii) back and forth transition in host-use can exhibit a hysteresis-
253 loop, (iii) the parasites' host-use may not be proportional to local host frequencies but under certain
254 conditions may be restricted to the rarer host, and (iv) that a substantial decline in parasite
255 abundance may typically precede a shift in host-use.

256 The above papers, written in memory of Graham Elmes, represent just five aspects of a burgeoning
257 body of research into *Maculinea-Myrmica* community modules from across Europe. Results to date
258 have revealed not only the remarkable adaptive complexities that can evolve within specialised
259 networks of interacting species, but are also providing essential knowledge on which to base
260 conservation regimes across Europe (e.g. Andersen *et al.*, 2013; Johst *et al.*, 2006; Kajzer-Bonk *et al.*,
261 2016; Klein *et al.*, 2013; Korosi *et al.*, 2012; Nowicki *et al.*, 2015; Nowicki *et al.*, 2014; Sielezniew *et*
262 *al.*, 2012; Skorka *et al.*, 2013; Soares *et al.*, 2012; Vanden Broeck *et al.*, 2017; Vilbas *et al.*, 2015;
263 Vrabec *et al.*, 2017). The validity of this approach is already exemplified by the long-term restoration

264 and spread of *Maculinea arion* in the UK (Thomas *et al.*, 2009; Thomas *et al.*, 2011) and of *M.*
265 *nausithous* and *M. teleius* in the Netherlands (Wynhoff *et al.*, 2017; Wynhoff *et al.*, 2011). This ‘large
266 blue management’, in turn, has benefited other declining species in two ways (Elmes & Thomas,
267 1992): (i) through the restoration of continuity of disappearing seral stages within grasslands and
268 across landscapes, and (ii) through the direct impacts of keystone *Myrmica* populations, for
269 example, through the dispersal of plants with elaiosome-bearing seeds (some of which are
270 specifically attractive to *Myrmica*) and their deposition in enemy-free patches of loose soil around
271 the ant nests (Randle *et al.*, 2005).

272 In summary, studies of *Maculinea*–*Myrmica* systems in the western Palaearctic have made
273 fundamental contributions to evolutionary-, behavioural-, population- and community ecology,
274 while providing the knowledge base for successful evidence-led conservation. Historical drivers, such
275 as the land use changes that precipitated the extinction of *M. arion* in the UK, are an increasing
276 challenge, now amplified by changing climates (Thomas, 2016). In closely coupled systems, different
277 tolerances by species to abiotic factors, such as temperature, can lead to desynchronization,
278 population declines, and detrimental trophic cascades, as exemplified by the winter moth
279 *Operophtera brumata* and its oak host around the millennium (van Asch & Visser, 2007; Visser &
280 Holleman, 2001), although in this case strong selection caused the moth’s phenology to adapt,
281 compensating for the mismatch within a few generations (van Asch *et al.*, 2012). With regard to
282 *Maculinea*, we have much to learn about their adaptive potential to their abiotic environment and
283 their biological interactions under multiple selection pressures (e.g. Casacci *et al.*, 2019; Hovestadt *et*
284 *al.*, 2019; Nash *et al.*, 2008; Tartally *et al.*, 2019a). Thus, important areas of research remain:
285 population genetics, regional adaptations, phylogeny, and the status of putative cryptic species; the
286 precise mechanisms by which larvae manipulate host societies by ever closer post-adoption
287 chemical mimicry and, perhaps, by sophisticated acoustical communication; whether the few
288 populations recorded as exploiting more than one *Myrmica* species are generalist social parasites or
289 co-existing populations of cryptic species, sub-species or hybrids, or simply pseudo-sinks or artefacts

290 from nest-switches during the *Maculinea* pupal stage (Tartally *et al.*, 2019a); on dispersal, meta-
291 population structure and population dynamics within sites; the roles of Wolbachia and microbiomes
292 in *Maculinea* interactions and dynamics; and the biology and conservation of their endangered
293 ichneumonid parasitoids. Land management for conservation should be based on such knowledge,
294 and future measures might involve assisted migration, as in the UK and Netherlands, or the
295 introduction of relevant trait response norms through targeted breeding, as recently proposed for
296 species of tree (Cannon & Petit, 2019). Finally, having sampled *Myrmica* populations across the
297 Palearctic, it would please Graham Elmes much to learn of similar studies on these systems now
298 occurring beyond Europe, for example in Japan (Ueda *et al.*, 2016) and in China (Gao *et al.*, 2016).

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302 **References**

- 303 Akino, T., Knapp, J.J., Thomas, J.A., & Elmes, G.W. (1999) Chemical mimicry and host specificity in the
304 butterfly *Maculinea rebeli*, a social parasite of *Myrmica* ant colonies. *Proceedings of the*
305 *Royal Society B-Biological Sciences*, **266**, 1419-1426.
- 306 Als, T.D., Nash, D.R., & Boomsma, J.J. (2001) Adoption of parasitic *Maculinea alcon* caterpillars
307 (Lepidoptera: Lycaenidae) by three *Myrmica* ant species. *Animal Behaviour*, **62**, 99-106.
- 308 Als, T.D., Nash, D.R., & Boomsma, J.J. (2002) Geographical variation in host-ant specificity of the
309 parasitic butterfly *Maculinea alcon* in Denmark. *Ecological Entomology*, **27**, 403-414.
- 310 Als, T.D., Vila, R., Kandul, N.P., Nash, D.R., Yen, S.H., Hsu, Y.F., Mignault, A.A., Boomsma, J.J., &
311 Pierce, N.E. (2004) The evolution of alternative parasitic life histories in large blue butterflies.
312 *Nature*, **432**, 386-390.
- 313 Andersen, A., Simcox, D.J., Thomas, J.A., & Nash, D.R. (2013) Assessing reintroduction schemes by
314 comparing genetic diversity of reintroduced and source populations: A case study of the
315 globally threatened large blue butterfly (*Maculinea arion*). *Biological Conservation*, **175**, 34 -
316 41.
- 317 Anton, C., Musche, M., & Settele, J. (2007a) Spatial patterns of host exploitation in a larval parasitoid
318 of the predatory dusky large blue *Maculinea nausithous*. *Basic and Applied Ecology*, **8**, 66-74.
- 319 Anton, C., Zeisset, I., Musche, M., Durka, W., Boomsma, J.J., & Settele, J. (2007b) Population
320 structure of a large blue butterfly and its specialist parasitoid in a fragmented landscape.
321 *Molecular Ecology*, **16**, 3828-3838.
- 322 Barbero, F., Thomas, J.A., Bonelli, S., Balletto, E., & Schönrogge, K. (2009) Queen ants make
323 distinctive sounds that are mimicked by a butterfly social parasite. *Science*, **323**, 782-785.
- 324 Cannon, C.H. & Petit, R.J. (2019) The oak syngameon: more than the sum of its parts. *New*
325 *Phytologist*.
- 326 Casacci, L.P., Schönrogge, K., Thomas, J.A., Balletto, E., Bonelli, S., & Barbero, F. (2019) Host
327 specificity pattern and chemical deception in a social parasite of ants. *Scientific Reports*, **9**.

328 Chapman, T.A. (1916) What the larva of *Lycaena arion* does during its last instar. *Transactions of the*
329 *Entomological Society of London*, **1915**, 291 - 297.

330 Chapman, T.A. (1918) On the life history of *Lycaenaalcon* F. . *Etudes de Lépidoptérologie Comparée*,
331 **16**, 277 - 300.

332 Chapman, T.A. (1919) Contributions to the life history of *Lycaena euphemus* Hb. *Transactions of the*
333 *Entomological Society of London*, **1919**, 450 - 465.

334 Clarke, R.T., Thomas, J.A., Elmes, G.W., & Hochberg, M.E. (1997) The effects of spatial patterns in
335 habitat quality on community dynamics within a site. *Proceedings of the Royal Society B-*
336 *Biological Sciences*, **264**, 347-354.

337 Di Salvo, M., Calcagnile, M., Tala, A., Tredici, S.M., Maffei, M.E., Schönrogge, K., Barbero, F., &
338 Alifano, P. (2019) The Microbiome of the *Maculinea-Myrmica* Host-Parasite Interaction.
339 *Scientific Reports*, **9**.

340 Ebsen, J.R., Boomsma, J.J., & Nash, D.R. (2019) Phylogeography and cryptic speciation in the
341 *Myrmica scabrinodis* Nylander, 1846 species complex (Hymenoptera: Formicidae), and their
342 conservation implications. *Insect Conservation and Diversity*.

343 Elmes, G.W. (1971) Experimental Study on Distribution of Heathland Ants. *Journal of Animal Ecology*,
344 **40**, 495-&.

345 Elmes, G.W. (1973) Observations on density of queens in natural colonies of *Myrmica rubra* L.
346 (Hymenoptera-Formicidae). *Journal of Animal Ecology*, **42**, 761-771.

347 Elmes, G.W. (1974) Effect of Colony Population on Caste Size in 3 Species of *Myrmica* (Hymenoptera-
348 Formicidae). *Insectes Sociaux*, **21**, 213-229.

349 Elmes, G.W. (1976) Some Observations on Microgyne Form of *Myrmica Rubra* L (Hymenoptera,
350 Formicidae). *Insectes Sociaux*, **23**, 3-21.

351 Elmes, G.W. (1978) Morphometric Comparison of 3 Closely Related Species of *Myrmica* (Formicidae),
352 Including a New Species from England. *Systematic Entomology*, **3**, 131-145.

353 Elmes, G.W. (1980) Queen Numbers in Colonies of Ants of the Genus *Myrmica*. *Insectes Sociaux*, **27**,
354 43-60.

355 Elmes, G.W. (1982) The Phenology of 5 Species of *Myrmica* (Hym Formicidae) from South Dorset,
356 England. *Insectes Sociaux*, **29**, 548-560.

357 Elmes, G.W. (1983) Some Experimental observations on the parasitic *Myrmica hirsuta* Elmes.
358 *Insectes Sociaux*, **30**, 221-234.

359 Elmes, G.W. (1987) Temporal Variation in Colony Populations of the Ant *Myrmica sulcinodis*. 1.
360 Changes in Queen Number, Worker Number and Spring Production. *Journal of Animal*
361 *Ecology*, **56**, 559-571.

362 Elmes, G.W. (1991) The social biology of *Myrmica* ants. *Insectes Sociaux*, **7**, 17 - 34.

363 Elmes, G.W., Barr, B., Thomas, J.A., & Clarke, R.T. (1999) Extreme host specificity by *Microdon*
364 *mutabilis* (Diptera : Syrphidae), a social parasite of ants. *Proceedings of the Royal Society B-*
365 *Biological Sciences*, **266**, 447-453.

366 Elmes, G.W. & Petal, J. (1990) Queen Number as an Adaptable Trait - Evidence from Wild
367 Populations of 2 Red Ant Species (Genus *Myrmica*). *Journal of Animal Ecology*, **59**, 675-690.

368 Elmes, G.W. & Thomas, J.A. (1985) Morphometrics as a tool in identification: a case study of a
369 *Myrmica* in France (Hymenoptera, Formicidae). *Insect Sociaux*, **2**, 97 - 108.

370 Elmes, G.W. & Thomas, J.A. (1992) Complexity of species conservation in managed habitats -
371 Interaction between *Maculinea* butterflies and their ant hosts. *Biodiversity and*
372 *Conservation*, **1**, 155-169.

373 Elmes, G.W., Thomas, J.A., Hammarstedt, O., Munguira, M.C., Martin, J., & van der Made, J.G. (1994)
374 Differences in host-ant specificity between Spanish, Dutch and Swedish populations of the
375 endangered butterfly *Maculinea alcon* (Schiff.) (Lepidoptera). *Zoologica Memorabilia*, **48**, 55
376 - 68.

377 Elmes, G.W., Thomas, J.A., & Wardlaw, J.C. (1991) Larvae of *Maculinea rebeli*, a Large Blue butterfly,
378 and their *Myrmica* host ants - Wild adoption and behavior in ant nests. *Journal of Zoology*,
379 **223**, 447-460.

380 Elmes, G.W., Thomas, J.A., Wardlaw, J.C., Hochberg, M.E., Clarke, R.T., & Simcox, D.J. (1998) The
381 ecology of *Myrmica* ants in relation to the conservation of *Maculinea* butterflies. *Journal of*
382 *Insect Conservation*, **2**, 67-78.

383 Elmes, G.W. & Wardlaw, J.C. (1981) The quantity and quality of overwintered larvae in 5 Species of
384 *Myrmica* (Hymenoptera, Formicidae). *Journal of Zoology*, **193**, 429-446.

385 Elmes, G.W. & Wardlaw, J.C. (1983) A comparison of the effect of temperature on the development
386 of large hibernated larvae of 4 Species of *Myrmica* (Hym-Formicidae). *Insectes Sociaux*, **30**,
387 106-118.

388 Fiedler, K. (1998) Lycaenid-ant interactions of the *Maculinea* type: tracing their historical roots in a
389 comparative framework. *Journal of Insect Conservation*, **2**, 3-14.

390 Frohawk, F.W. (1916) Further observations on the last stage of the larva of *Lycaena arion*.
391 *Transactions of the Entomological Society London*, **1915**, 313 - 316.

392 Gao, K., Li, X.S., Chen, F.Y., Guo, Z.Y., & Settele, J. (2016) Distribution and habitats of *Phengaris*
393 (*Maculinea*) butterflies and population ecology of *Phengaris teleius* in China. *Journal of*
394 *Insect Conservation*, **20**, 1-10.

395 Geissler-Strobel, S., Kaule, G., & Settele, J. (2000) Biotope networks - an endangerment for animals?
396 Long-term study of a meta-population of the butterfly *Glaucopsyche nausithous* and
397 discussion of general aspects. *Naturschutz und Landschaftsplanung*, **32**, 293 - 299.

398 Hanski, I. (1999) *Metapopulation Ecology*. Oxford University Press, Oxford.

399 Hochberg, M.E., Clarke, R.T., Elmes, G.W., & Thomas, J.A. (1994) Population-dynamic consequences
400 of direct and indirect interactions involving a Large Blue butterfly and its plant and Red ant
401 hosts. *Journal of Animal Ecology*, **63**, 375-391.

402 Hovestadt, T., Mitesser, O., Elmes, G.W., Thomas, J.A., & Hochberg, M.E. (2007) An evolutionarily
403 stable strategy model for the evolution of dimorphic development in the butterfly *Maculinea*
404 *rebeli*, a social parasite of *Myrmica* ant colonies. *American Naturalist*, **169**, 466-480.

405 Hovestadt, T., Thomas, J.A., Mitesser, O., Elmes, G.W., & Schönrogge, K. (2012) Unexpected benefit
406 of a social parasite for a key fitness component of its ant host. *American Naturalist*, **179**,
407 110-123.

408 Hovestadt, T., Thomas, J.A., Mitesser, O., & Schönrogge, K. (2019) Multiple host use and the
409 dynamics of host switching in host-parasite systems. *Insect Conservation and Diversity*.

410 Johst, K., Drechsler, M., Thomas, J., & Settele, J. (2006) Influence of mowing on the persistence of
411 two endangered large blue butterfly species. *Journal of Applied Ecology*, **43**, 333-342.

412 Kajzer-Bonk, J., Skorka, P., Nowicki, P., Bonk, M., Krol, W., Szpilyk, D., & Woyciechowski, M. (2016)
413 Relative contribution of matrix structure, patch resources and management to the local
414 densities of two Large Blue butterfly species. *Plos One*, **11**.

415 Kempe, C., Nowicki, P., Harpke, A., Schweiger, O., & Settele, J. (2016) The importance of resource
416 distribution: spatial co-occurrence of host plants and host ants coincides with increased egg
417 densities of the Dusky Large Blue *Maculinea nausithous* (Lepidoptera: Lycaenidae). *Journal of*
418 *Insect Conservation*, **20**, 1033-1045.

419 Klein, M., Weddeling, K., & Lamm, J. (2013) Ursachenanalyse zum Rückgang des Dunklen
420 Wiesenknopf-Ameisenbläulings *Maculinea nausithous* am Eifelfuss im westlichen Rhein-Sieg-
421 Kreis - Einfluss von Wirtsameisen, Vegetationsstruktur und Habitatmanagement.
422 *Decheniana*, **166**, 55 - 72.

423 Korosi, A., Orvosy, N., Batary, P., Harnos, A., & Peregovits, L. (2012) Different habitat selection by
424 two sympatric *Maculinea* butterflies at small spatial scale. *Insect Conservation and Diversity*,
425 **5**, 118-126.

426 Maák, I., Camera, J., Casacci, L.P., Barbero, F., Trigos-Peral, G., Ślipiński, P., Bonelli, S., Zaccagno, M.,
427 & Witek, M. (2019) The influence of colony traits on the collective behaviour of *Myrmica*
428 *scabrinodis* ants. *Insect Conservation and Diversity*.

429 Nash, D.R., Als, T.D., Maile, R., Jones, G.R., & Boomsma, J.J. (2008) A mosaic of chemical coevolution
430 in a large blue butterfly. *Science*, **319**, 88-90.

431 New, T.R., Pyle, R.M., Thomas, J.A., Thomas, C.D., & Hammond, P.C. (1995) Butterfly conservation
432 management. *Annual Review of Entomology*, **40**, 57-83.

433 Nielsen, M.G., Elmes, G.W., & Kipyatkov, V.E. (1999) Respiratory Q10 varies between populations of
434 two species of *Myrmica* ants according to the latitude of their sites. *Journal of Insect*
435 *Physiology*, **45**, 559-564.

436 Nowicki, P., Marczyk, J., & Kajzer-Bonk, J. (2015) Metapopulations of endangered *Maculinea*
437 butterflies are resilient to large-scale fire. *Ecohydrology*, **8**, 398-405.

438 Nowicki, P., Vrabec, V., Binzenhofer, B., Feil, J., Zaksek, B., Hovestadt, T., & Settele, J. (2014) Butterfly
439 dispersal in inhospitable matrix: rare, risky, but long-distance. *Landscape Ecology* **29**, 401 -
440 412.

441 Patricelli, D., Sielezniew, M., Ponikwicka-Tyszko, D., Ratkiewicz, M., Bonelli, S., Barbero, F., Witek M.,
442 Buś M.M., Rutkowski R. & Balletto, E. (2013). Contrasting genetic structure of rear edge and
443 continuous range populations of a parasitic butterfly infected by *Wolbachia*. *BMC*
444 *Evolutionary Biology* **13**, 14.

445 Patricelli, D., Barbero, F., Occhipinti, A., Berteà, C.M., Bonelli, S., Casacci, L.P., Zebelo, S.A., Crocoll, C.,
446 Gershenzon, J., Maffei, M.E., Thomas, J.A., & Balletto, E. (2015) Plant defences against ants
447 provide a pathway to social parasitism in butterflies. *Proceedings of the Royal Society B-*
448 *Biological Sciences*, **282**.

449 Pfeifer, M.A., Andrick, U.R., Frey, W., & J., S. (2000) On the ethology and ecology of a small and
450 isolated population of the Dusky Large Blue Butterfly *Glaucopsyche (Maculinea) nausithous*
451 (Lycaenidae). *Nota Lepidopterologica*, **23**, 147 - 172.

452 Radchenko, A.G. & Elmes, G.W. (2010) *Myrmica ants (Hymenoptera: Formicidae) of the Old World*.
453 Natura Optima Dux Foundation, Warsaw.

454 Randle, Z., Simcox, D.J., Schönrogge, K., Wardlaw, J.C., & Thomas, J.A. (2005) *Myrmica* ants as
455 keystone species and *Maculinea arion* as an indicator of rare niches in UK grasslands.

456 Schönrogge, K., Barr, B., Wardlaw, J.C., Napper, E., Gardner, M.G., Breen, J., Elmes, G.W., & Thomas,
457 J.A. (2002) When rare species become endangered: cryptic speciation in myrmecophilous
458 hoverflies. *Biological Journal of the Linnean Society*, **75**, 291-300.

459 Schönrogge, K., Gardner, M.G., Elmes, G.W., Napper, E.K.V., Simcox, D.J., Wardlaw, J.C., Breen, J.,
460 Barr, B., Knapp, J.J., Pickett, J.A., & Thomas, J.A. (2006) Host propagation permits extreme
461 local adaptation in a social parasite of ants. *Ecology Letters*, **9**, 1032-1040.

462 Schönrogge, K., Napper, E.K.V., Birkett, M.A., Woodcock, C.M., Pickett, J.A., Wadhams, L.J., &
463 Thomas, J.A. (2008) Host recognition by the specialist hoverfly *Microdon mutabilis*, a social
464 parasite of the ant *Formica lemani*. *Journal of Chemical Ecology*, **34**, 168-178.

465 Schönrogge, K., Wardlaw, J.C., Thomas, J.A., & Elmes, G.W. (2000) Polymorphic growth rates in
466 myrmecophilous insects. *Proceedings of the Royal Society B-Biological Sciences*, **267**, 771-
467 777.

468 Settele, J., Kühn, E., & Thomas, J.A. (2005) *Studies in the Ecology & Conservation of Butterflies in*
469 *Europe II* Pensoft, Sofia.

470 Settele, J., Thomas, J.A., Boomsma, J.J., Kuehn, E., Nash, D.R., Anton, C., Woyciechowski, M., &
471 Varga, Z. (2002) *MACulinea* butterflies of the habitats directive and European red list as
472 indicators and tools for conservation and MANagement (MacMan). *Verhandlungen der*
473 *Gesellschaft für Ökologie*, **32**, 63.

474 Sielezniew, M., Rutkowski, R., Ponikwicka-Tyszko, D., Ratkiewicz, M., Dziekanska, I., & Svitra, G.
475 (2012) Differences in genetic variability between two ecotypes of the endangered
476 myrmecophilous butterfly *Phengaris (=Maculinea) alcon* - the setting of conservation
477 priorities. *Insect Conservation and Diversity*, **5**, 223-236.

478 Skorka, P., Nowicki, P., Lenda, M., Witek, M., Sliwinska, E.B., Settele, J., & Woyciechowski, M. (2013)
479 Different flight behaviour of the endangered scarce large blue butterfly *Phengaris teleius*
480 (Lepidoptera: Lycaenidae) within and outside its habitat patches. *Landscape Ecology*, **28**,
481 533-546.

482 Soares, P.O., Crespi, A.L., Rodrigues, M.C., & Arnaldo, P.S. (2012) The habitat vegetational structure
483 and the success of the blue alcon, *Maculinea alcon* (Denis & Schiffermuller). *Plant*
484 *Biosystems*, **146**, 1-6.

485 Tartally, A., Thomas, J.A., Anton, C., Balletto, E., Barbero, F., Bonelli, S., Brau, M., Casacci, L.P., Csoz,
486 S., Czokes, Z., Dolek, M., Dziekanska, I., Elmes, G., Furst, M.A., Glinka, U., Hochberg, M.E.,
487 Hottinger, H., Hula, V., Maes, D., Munguira, M.L., Musche, M., Nielsen, P.S., Nowicki, P.,
488 Oliveira, P.S., Peregovits, L., Ritter, S., Schlick-Steiner, B.C., Settele, J., Sielezniew, M., Simcox,
489 D.J., Stankiewicz, A.M., Steiner, F.M., Svitra, G., Ugelvig, L.V., Van Dyck, H., Varga, Z., Witek,
490 M., Woyciechowski, M., Wynhoff, I., & Nash, D.R. (2019a) Patterns of host use by brood
491 parasitic *Maculinea* butterflies across Europe. *Philosophical Transactions of the Royal Society*
492 *B-Biological Sciences*, **374**.

493 Tartally, A., Nash, D.R., Varga, Z., & Lengyel, S. (2019b) Changes in host ant communities of Alcon
494 Blue butterflies in abandoned mountain hay meadows. *Insect Conservation and Diversity*.

495 Thomas, J.A. (1977). *Ecology and conservation of the large blue butterfly*. Institute of Terrestrial
496 Ecology, Cambridge.

497 Thomas, J.A. (1980) Why did the Large Blue become extinct in Britain. *Oryx*, **15**, 243.

498 Thomas, J.A. (1984a). The conservation of butterflies in temperate countries: past efforts and lessons
499 for the future. In *Biology of butterflies* (ed. by R.I. Vane-Wright & P. Ackery), Vol. 11, pp. 333
500 - 353. Academic Press, London.

501 Thomas, J.A. (1984b) The behavior and habitat requirements of *Maculinea nausithous* (the Dusky
502 Large Blue butterfly) and *Maculinea teleius* (the Scarce Large Blue) in France. *Biological*
503 *Conservation*, **28**, 325-347.

504 Thomas, J.A. (1991) Rare species conservation: case studies of European butterflies. In The scientific
505 management of temperate communities for conservation (ed. by I. Spellerberg, B. Goldsmith
506 & M.G. Morris), Vol. 29, pp. 149 - 197. Blackwells, Oxford.

507 Thomas, J.A. (2016) Butterfly communities under threat. *Science*, **353**, 216-218.

508 Thomas, J.A., Bourn, N.A.D., Clarke, R.T., Stewart, K.E., Simcox, D.J., Pearman, G.S., Curtis, R., &
509 Goodger, B. (2001) The quality and isolation of habitat patches both determine where
510 butterflies persist in fragmented landscapes. *Proceedings of the Royal Society B-Biological
511 Sciences*, **268**, 1791-1796.

512 Thomas, J.A., Clarke, R.T., Elmes, G.W., & Hochberg, M.E. (1998a). Population dynamics in the genus
513 *Maculinea* (Lepidoptera: Lycaenidae). In *Insect Populations in Theory and in Practice* (ed. by
514 J.P. Dempster & I.F.G. McLean), Vol. 19, pp. 261-290. Chapman & Hall, London.

515 Thomas, J.A. & Elmes, G.W. (1993) Specialized searching and the hostile use of allomones by a
516 parasitoid whose host, the butterfly *Maculinea rebeli*, inhabits ant nests. *Animal Behaviour*,
517 **45**, 593-602.

518 Thomas, J.A. & Elmes, G.W. (1998) Higher productivity at the cost of increased host-specificity when
519 *Maculinea* butterfly larvae exploit ant colonies through trophallaxis rather than by
520 predation. *Ecological Entomology*, **23**, 457-464.

521 Thomas, J.A. & Elmes, G.W. (2001) Food-plant niche selection rather than the presence of ant nests
522 explains oviposition patterns in the myrmecophilous butterfly genus *Maculinea*. *Proceedings
523 of the Royal Society B-Biological Sciences*, **268**, 471-477.

524 Thomas, J.A., Elmes, G.W., & Wardlaw, J.C. (1998b) Polymorphic growth in larvae of the butterfly
525 *Maculinea rebeli*, a social parasite of *Myrmica* ant colonies. *Proceedings of the Royal Society
526 B-Biological Sciences*, **265**, 1895-1901.

527 Thomas, J.A., Elmes, G.W., Wardlaw, J.C., & Woyciechowski, M. (1989) Host specificity among
528 *Maculinea* butterflies in *Myrmica* ant nests. *Oecologia*, **79**, 452-457.

529 Thomas, J.A., Knapp, J.J., Akino, T., Gerty, S., Wakamura, S., Simcox, D.J., Wardlaw, J.C., & Elmes,
530 G.W. (2002) Parasitoid secretions provoke ant warfare. *Nature*, **417**, 505-506.

531 Thomas, J.A., Schönrogge, K., & Elmes, G.W. (2005). Specializations and host associations of social
532 parasites of ants. In *Insect Evolutionary Ecology* (ed. by M.D.E. Fellowes, G.J. Holloway & J.
533 Rolff), pp. 475 - 514. Royal Entomological Society, London.

534 Thomas, J.A. & Settele, J. (2004) Evolutionary biology - Butterfly mimics of ants. *Nature*, **432**, 283-
535 284.

536 Thomas, J.A., Simcox, D.J., & Clarke, R.T. (2009) Successful conservation of a threatened *Maculinea*
537 butterfly. *Science*, **325**, 80-83.

538 Thomas, J.A., Simcox, D.J., & Hovestadt, T. (2011) Evidence based conservation of butterflies. *Journal*
539 *of Insect Conservation*, **15**, 241-258.

540 Thomas, J.A. & Wardlaw, J.C. (1992) The capacity of a *Myrmica* ant nest to support a predacious
541 species of *Maculinea* butterfly. *Oecologia*, **91**, 101-109.

542 Thompson, J.N. (2005) *The Geographic Mosaic of Coevolution*. University of Chicago Press, Chicago.

543 Ueda, S., Komatsu, T., Itino, T., Arai, R., & Sakamoto, H. (2016) large blue butterflies (*Phengaris* spp.,
544 Lepidoptera: Lycaenidae) in Japan. *Scientific Reports*, **6**.

545 van Asch, M., Salis, L., Holleman, L.J.M., van Lith, B., & Visser, M.E. (2012) Evolutionary response of
546 the egg hatching date of a herbivorous insect under climate change. *Nature Climate Change*,
547 **484**, 55 - 61.

548 van Asch, M. & Visser, M.E. (2007) Phenology of forest caterpillars and their host trees: the
549 importance of synchrony. *Annual Review of Entomology*, **52**, 37-55.

550 Vanden Broeck, A., Maes, D., Kelager, A., Wynhoff, I., WallisDeVries, M.F., Nash, D.R., Oostermeijer,
551 J.G.B., Van Dyck, H., & Mergeay, J. (2017) Gene flow and effective population sizes of the
552 butterfly *Maculinea alcon* in a highly fragmented, anthropogenic landscape. *Biological*
553 *Conservation*, **209**, 89-97.

554 Vilbas, M., Teder, T., Tiitsaar, A., Kaasik, A., & Esperk, T. (2015) Habitat use of the endangered
555 parasitic butterfly *Phengaris arion* close to its northern distribution limit. *Insect Conservation*
556 *and Diversity*, **8**, 252-260.

557 Visser, M.E. & Holleman, L.J.M. (2001) Warmer springs disrupt the synchrony of oak and winter moth
558 phenology. *Proceedings of the Royal Society B-Biological Sciences*, **268**, 289-294.

559 Vrabec, V., Kulma, M., Bubova, T., & Nowicki, P. (2017) Long-term monitoring of *Phengaris*
560 (Lepidoptera: Lycaenidae) butterflies in the PA (TM) elou surroundings (Czech Republic): is
561 the waterway construction a serious threat? *Journal of Insect Conservation*, **21**, 393-400.

562 Webb, M.R. & Pullin, A.S. (1996) Larval survival in populations of the large copper butterfly *Lycaena*
563 *dispar batavus*. *Ecography*, **19**, 279-286.

564 Witek, M., Sliwiska, E.B., Skorka, P., Nowicki, P., Settele, J., & Woyciechowski, M. (2006)
565 Polymorphic growth in larvae of *Maculinea* butterflies, as an example of biennialism in
566 myrmecophilous insects. *Oecologia*, **148**, 729-733.

567 Wynhoff, I. (1998) Lessons from the reintroduction of *Maculinea teleius* and *M. nausithous* in the
568 Netherlands. *Journal of Insect Conservation*, **2**, 47-57.

569 Wynhoff, I., Kolvoort, A.M., Bassignana, C.F., Berg, M.P., & Van Langevelde, F. (2017) Fen meadows
570 on the move for the conservation of *Maculinea (Phengaris) teleius* butterflies. *Journal of*
571 *Insect Conservation*, **21**, 379-392.

572 Wynhoff, I., van Gestel, R., van Swaay, C., & van Langevelde, F. (2011) Not only the butterflies:
573 managing ants on road verges to benefit *Phengaris (Maculinea)* butterflies. *Journal of Insect*
574 *Conservation*, **15**, 189-206.

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580 Fig 1. Graham Wakely Elmes (1943-2017). Expert on the biology and diversity of *Myrmica* ants, and
581 on the social parasites that infiltrate their societies.