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

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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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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.