

This is a repository copy of *Challenges and a call to action for protecting European red wood ants*.

White Rose Research Online URL for this paper:

<https://eprints.whiterose.ac.uk/187399/>

Version: Accepted Version

---

**Article:**

Balzani, Paride, Dekoninck, Wouter, Feldhaar, Heike et al. (7 more authors) (2022)  
Challenges and a call to action for protecting European red wood ants. *Conservation Biology*. e13959. ISSN 0888-8892

<https://doi.org/10.1111/cobi.13959>

---

**Reuse**

Items deposited in White Rose Research Online are protected by copyright, with all rights reserved unless indicated otherwise. They may be downloaded and/or printed for private study, or other acts as permitted by national copyright laws. The publisher or other rights holders may allow further reproduction and re-use of the full text version. This is indicated by the licence information on the White Rose Research Online record for the item.

**Takedown**

If you consider content in White Rose Research Online to be in breach of UK law, please notify us by emailing [eprints@whiterose.ac.uk](mailto:eprints@whiterose.ac.uk) including the URL of the record and the reason for the withdrawal request.

1 Accepted Conversation Biology, May 2022.

## 2 **Challenges and a call to action for protecting European red wood ants**

3 **Authors:** Paride Balzani, Wouter Dekoninck, Heike Feldhaar, Anne Freitag, Filippo, Frizzi, Filippo, Jan Frouz,,  
4 Alberto Masoni, Elva Robinson, Jouni Sorvari, Giacomo Santini

### 5 **Abstract**

6 Red wood ants (RWA) are a group of keystone species widespread in temperate and boreal  
7 forests of the Northern Hemisphere. Despite this, there is increasing evidence of local declines  
8 and extinctions. Here, we give an overview of the current protection status of RWA throughout  
9 Europe and review their IUCN threat classification. Only some RWA species have been  
10 assessed at a global scale, while not all national red lists of the countries where RWA are  
11 present include these species. In addition, different assessment criteria, inventory approaches,  
12 and risk categories are used in different countries, and data deficiency is frequent. The  
13 legislative protection is even more complex, with some countries protecting RWA implicitly  
14 together with the wildlife fauna, while others explicitly protect the whole group or particular  
15 species. This complexity often extends within countries, for example in Italy, where, outside  
16 of the Alps, only the introduced species are protected, while the native ones in decline are not.  
17 Therefore, an international, coordinated framework is needed for the protection of RWA.  
18 However, this firstly requires that the conservation target should be defined. Due to the similar  
19 morphology, complex taxonomy and frequent hybridization, protecting the whole RWA group  
20 seems a more efficient strategy than protecting single species, though with a distinction  
21 between autochthonous and introduced species. Second, an update of the current distribution  
22 of RWA species is needed throughout Europe. Third, a protecting law cannot be effective  
23 without the collaboration of forest managers, whose activity influences RWA habitat. Finally,  
24 RWA mounds offer a peculiar microhabitat, hosting a multitude of taxa, some of which are

25 obligate myrmecophilous species listed in the IUCN Red List. Therefore, RWAs' role as  
26 umbrella species could facilitate their protection if they are considered not only as target species  
27 but also as providers of species-rich microhabitats.

## 28 **Introduction**

29 With at least 13 species described in the Palearctic and up to 19 species reported in North  
30 America, red wood ants (RWA, i.e. species belonging to the *Formica rufa* group) are  
31 ecologically dominant species (Stockan et al., 2016). RWA are considered to be keystone  
32 species in temperate and boreal forests of Eurasia. Due to their large and long-lasting nests they  
33 impact functioning of mainly forest ecosystems in many ways and across several trophic levels,  
34 e.g. by controlling forest pest species (Trigos-Peral et al., 2021). Although RWA species are  
35 still abundant in many parts of their distribution range, their conservation raises increasing  
36 concerns (Dekoninck et al., 2010; Cherix et al., 2012; Breen, 2014; Mabelis & Korczyńska,  
37 2016). Indeed, there is evidence of local decline or even extinction. For example, *F. uralensis*  
38 went extinct in Switzerland (Cherix & Maddalena-Feller, 1986), while the scattered relict  
39 populations of this species in France, Germany and Poland are facing high extinction risks  
40 (Stankiewicz et al., 2005; Wegnez & Mourey, 2016). Moreover, local information is scattered  
41 and sometimes contradictory. For example, *F. pratensis* is reported as extinct in mainland  
42 Britain since at least 1988 (Nicholson, 1997). However, its presumed extinction is frequently  
43 erroneously dated to 2005, the year of the last update for this species on the Bees Wasps and  
44 Ants Recording Society (BWARS, [www.bwars.com](http://www.bwars.com)), although the page clearly reports that  
45 “The last known nest, near Wareham, died out in 1987”.

46 The main threats for these species have already been discussed in detail by Sorvari  
47 (2016). However, it is worth stressing that the relative importance of these threats varies  
48 considerably in different parts of their Palearctic distribution range. In the southernmost  
49 countries RWA are restricted to mountain areas, whereas at northernmost sites they also occur  
50 at lower altitudes (Stockan et al., 2016), and threatening factors may thus differ. Additionally,  
51 their problematic taxonomy, with some species identifiable only through molecular analysis

52 (Bernasconi et al., 2010), the presence of cryptic species (Bernasconi et al., 2011; Seifert, 1996,  
53 2021) and widespread hybridization (Seifert et al., 2010; Beresford et al., 2017), makes it  
54 difficult to efficiently assess population size and distribution.

55         Despite their ecological importance and widespread distribution, Hymenoptera, with  
56 the exception of wild bees (Kleijn et al., 2015; Drossart & Gérard, 2020), lag behind other  
57 insect taxa, like Lepidoptera or Coleoptera, as conservation targets (Leandro et al., 2017). Ants  
58 (particularly RWA) were an early group to be defined as vulnerable and worthy of protection  
59 (Wells et al., 1983). Given the importance of RWA in forest pest management, the European  
60 Council recommended as early as 1965 that all the member states adopt legal provisions for  
61 protecting these species, highlighting their decline and the need for their conservation (Pavan,  
62 1981). However, more than 50 years later there is no unique legal framework, and contradictory  
63 measures are sometimes taken. The importance of the focus on RWA protection extends  
64 beyond the conservation of these species per se. Indeed, they are important ecosystem  
65 engineers and umbrella species (e.g. Balzani et al., 2021a), so their conservation is relevant  
66 also for a wide range of other taxa. Moreover, RWA are perfect flagship species, providing an  
67 important example for the establishment of a supranational scheme aimed at the conservation  
68 of an invertebrate group. In this paper, we review the legal aspect of RWA protection and  
69 discuss how conserving these species must have support in national laws in Europe.

70         We will briefly review their position in the IUCN red list, then give an overview of their  
71 protection at the European level and, finally, we provide examples representative of the many  
72 contradictions and paradoxes that characterize the protection of these species. The main aim of  
73 this paper is to provide a wide overview of RWA protection in Europe by searching information  
74 for all the countries entirely included in Europe, with some in-depth analyses of specific cases,

75 of which the importance extends beyond their specific limitations, as they can be paradigmatic  
76 of the difficulties encountered in the protection of many other invertebrate taxa.

77

## 78 **Status quo of RWA protection in Europe**

### 79 *RWA protection at national level*

80 Several European countries protect RWA (Figure 1; Appendix S1). Some of them, such as  
81 Austria, implicitly protect them by protecting all the wildlife fauna, while others explicitly  
82 mention RWA, at least as a group. For example, in Estonia and Poland, all RWA are protected  
83 species, and in Hungary RWA are protected and their nests assigned a monetary value. In  
84 Switzerland, RWA are listed as protected since 1966 and all species are explicitly included in  
85 the Annex 3 of protected species in the Ordinance on the Protection of Nature and Landscape  
86 (OPN) of the Swiss Federal Council. In Germany, besides being protected by the Federal  
87 Nature Conservation Act (Bundesnaturschutzgesetz, BNatSchG) like all wildlife, all mound-  
88 building RWA are additionally listed as especially protected in Germany (like all wild bees and  
89 a few wasp species) under the Federal Species Protection Ordinance  
90 (Bundesartenschutzverordnung, BArtSchV), which includes a list of protected species. It is  
91 thus prohibited to disturb or destroy their nests or remove workers or other life-stages.  
92 Moreover, *F. polyclena* x *rufa* hybrids are implicitly protected as well since the parental species  
93 are protected. In Belgium, all RWA species were protected by a law of 1980. Later, Belgium  
94 legislation was organized at a Federal level and in 2009 the governments of the Flanders and  
95 Wallonia published a law in which three (for Flanders) and two (for Wallonia) species were  
96 protected, whereas Brussels protects only one species (*F. polyclena*). Finally, some other  
97 countries explicitly prioritize the protection of particular RWA species. In Bulgaria, some  
98 RWA species have been protected since 1959, though the obsolete scientific names included

99 have never been updated, and *F. rufa* is protected by the 2002 Bulgarian Biodiversity Act. In  
100 the United Kingdom, *F. pratensis* is a British Action Plan (BAP) 2007 priority species, i.e.  
101 those species “that were identified as being the most threatened and requiring conservation  
102 action”, being also listed in the Species of Principal Importance in England. Also, *F. aquilonia*  
103 is included in the Northern Ireland priority species list.

#### 104 *The Italian paradox*

105 Italy is paradigmatic of what happens in the countries at the southern limit of RWA distribution,  
106 where less information is available, and public awareness is lower. In Italy, these species are  
107 typical dwellers of the Alps (Pavan et al., 1971), where they occur at elevations between 450  
108 and 2000 meters. However, this information dates back to several decades ago and it is to be  
109 taken cautiously, since a shift of the distribution area towards higher elevations due to warming  
110 as documented in other insect taxa (Hagen et al., 2007; Moret et al., 2016) is possible. Further  
111 south, the situation is more complex. The only autochthonous species outside of the Alps is  
112 *Formica pratensis*, occurring also in the Apennine mountains. The actual distribution and  
113 abundance of this species are however unknown, and the few existing reports are outdated  
114 publications (Pavan et al., 1971), personal observations, and sparse, often unconfirmed notes  
115 on citizen science platforms (e.g. iNaturalist). It is clear, however, that some of the Apennine  
116 populations have recently disappeared or significantly decreased in number (G. Santini  
117 personal observation). This declining trend is in line with the tendency observed in other  
118 countries, such as Switzerland, Belgium, Romania and Turkey (Dekoninck et al., 2003; Freitag  
119 et al., 2008; Kiss & Kobori, 2010; Çamlitepe & Aksoy, 2019), as well as the British mainland  
120 (Nicholson, 1997).

121 This situation is further complicated by the fact that since the 1950s to 1980s, several  
122 introductions were carried out by transplanting entire RWA nests (mostly belonging to the

123 species *F. paralugubris*; Masoni et al., 2019) from the Alps to the Apennine mountains as  
124 biological control agents (Pavan, 1959). These introductions had varying success, with some  
125 populations that are developing traits of invasiveness, impacting the native fauna (Frizzi et al.,  
126 2018; Balzani et al., 2021b), but also other taxa (Di Nuzzo et al. 2022).

127         In Italy, no national law protects RWA (nor any other ant), despite an aborted attempt  
128 to include the whole group in a law in 2001 (N. 5013 – Rules for the protection of the  
129 heterotherm fauna), which was not approved. Instead, each local Authority (Region) legislates  
130 on the matter. Several Regions grant some type of protection (Appendix S2) either by generally  
131 protecting ant nests, mentioning the “*Fomica rufa* group”, or specifying the names of some  
132 species (sometimes with misspelled names). Interestingly, one regional law currently grants  
133 protection to other ant species, including *Formicoxenus nitidulus*, an obligate myrmecophilous  
134 ant listed as “Vulnerable” at a Global level (IUCN Red List) cohabiting within the nests of  
135 various RWA species (Härkönen & Sorvari, 2017). Similarly, in the United Kingdom, *F.*  
136 *nitidulus* is a BAP priority species for conservation, but its wood ant hosts are not protected.  
137 How to protect an obligate myrmecophile without protecting its host ant is unfortunately not  
138 specified.

139         The most peculiar situation occurs in the Regions straddling the Tuscan-Emilian  
140 Apennine, where both the native *F. pratensis* and the introduced *F. paralugubris* occur, the  
141 former declining and the latter spreading. Quite surprisingly, protection laws were formulated  
142 for the introduced species, and protection started soon after the first introductions in the 1950s  
143 (Pavia, Prefectoral Decree 6<sup>th</sup> April 1956). Moreover, efforts to increase public awareness of  
144 the introduced species have been done, whereas the declining *F. pratensis* did not receive  
145 comparable attention.

146 *RWA protection at international level*



147 According to the IUCN Red List (accessed 8<sup>th</sup> October 2021), RWA species are classified as  
148 “Near Threatened” at a global level, but only some species (*F. rufa*, *F. lugubris*, *F. polycтена*,  
149 *F. aquilonia*, *F. pratensis*, and *F. uralensis*) have been assessed. Previous assessments (from  
150 1983 to 1994) classified all the above RWA species as “Vulnerable” except *F. uralensis* that  
151 was classified as “Indeterminate” (from 1986 to 1994).

152 RWA (and in general, ants) are not included in the European Red List  
153 ([https://ec.europa.eu/environment/nature/conservation/species/redlist/index\\_en.htm](https://ec.europa.eu/environment/nature/conservation/species/redlist/index_en.htm), accessed  
154 11<sup>th</sup> October 2021). On the national or regional level, the situation is more complex. Not all  
155 European countries include ants, or even insects, in national red lists  
156 (<https://www.nationalredlist.org/>, accessed 11<sup>th</sup> October 2021). For example, in Ireland, no red  
157 list has been produced that covers ants at all, even though all RWA species present are in urgent  
158 need of local protection (Breen, 2014). Moreover, when RWA are considered, there is no  
159 consensus across different national red lists on which species to include, assessment criteria  
160 differ, some risk categories are not fully comparable, and data deficiency is frequent (Appendix  
161 S3). In addition, it is unclear how hybrids, an often-occurring phenomenon in RWA, should be  
162 treated. For example, only the provisional Red List of the ants of Flanders explicitly assessed  
163 hybrids (*F. rufa x polycтена*; Dekoninck et al., 2003, 2005).

164 The lack of a comprehensive assessment of the risks faced by RWA species is not  
165 surprising, as all ants suffer from the same lack of information. Only 149 out of the  
166 approximately 14,000 globally known living ant species  
167 (<https://www.antweb.org/statsPage.do>, accessed 4th January 2022) are listed in the IUCN Red  
168 List. For all of them, the last official assessment dates back to 1996, and needs therefore to be  
169 updated. RWA currently face increasing threats throughout their distribution range, but the  
170 available information on both threats and distributions is highly variable (Sorvari, 2016). The

171 situation may be particularly critical in the countries at the southern margin of their distribution  
172 (Italy, Greece, Turkey), where the effects of climate change are probably stronger (Rebetez &  
173 Reinhard, 2008), and information limited (Kovats et al., 2014). Since in these regions RWA  
174 are restricted to high elevations, the upward shift of populations will progressively be limited  
175 by a lower habitat availability. Moreover, only species included in official Red Lists (following  
176 the IUCN criteria) can be protected by law in some countries (e.g. Belgium). Despite their  
177 ecological importance, RWA protection receives limited attention, and no effort has been made  
178 to standardize protection measures at least in Europe. The complexity of the legal status  
179 between and within countries, and the diversity of protection measures taken by different States  
180 necessitate the development of broad-scale conservation actions and the deployment of  
181 common, coordinated strategies.

182

### 183 **Suggestions for a strategic approach for a future European conservation framework**

#### 184 *RWA species as conservation targets*

185 One key decision point is whether to focus conservation efforts on single species or to consider  
186 the entire group as a target. Protecting single species has the great advantage of allowing for  
187 individually tailored protection policies based on the specific needs of species or local  
188 populations. This approach, however, has the associated cost of the harmonization of legal  
189 frameworks across countries and requires considerable and informed expertise to support the  
190 legal actions. The examples provided here suggest that this is not always the case and that  
191 establishing legal protection across the entire group is a by far simpler task. Moreover,  
192 protection at the species level also faces the many difficulties stemming from the taxonomy of  
193 these species, starting from the fact that species identification may prove difficult. Furthermore,  
194 should we protect hybrids? Hybridization occurs frequently in RWA and is probably one of the

195 mechanisms promoting speciation (Bernasconi et al., 2011). As pointed out by Robinson and  
196 Stockan (2016), conservation measures should allow the preservation of evolutionary processes  
197 like this, but how to translate it into laws? Targeting the group could be an easier way to cope  
198 with such problems, although care should be taken into distinguishing between autochthonous  
199 and introduced species, as the case *F. pratensis* – *F. paralugubris* in Italy shows.

200         Moreover, the existence of a law protecting RWA does not guarantee effective  
201 protection, as it is often difficult to define what the right protective measures are or should be.  
202 When nests are located in areas where work is to be carried out (road widening, new  
203 construction, etc.), the ant nests are usually moved. Unfortunately, the success rate of these  
204 translocations is often low (Serttaş et al., 2020). Forestry practices must also be considered.  
205 Even if nests are not directly destroyed during logging, their survival can be hampered by  
206 indirect effects resulting from damages to their habitat (Sorvari & Hakkarainen, 2007; Sorvari,  
207 2016). However, these effects should be carefully considered case by case, as different species  
208 can show different tolerance towards anthropogenic habitat disturbances (Fitzpatrick et al.,  
209 2021). On the other side, the natural closure of the forest canopy can eliminate the habitat  
210 suitable for RWA species (Vandegehuchte et al., 2017; Fitzpatrick et al., 2021). Viable  
211 solutions must therefore be proposed to foresters to reconcile logging and the protection of the  
212 RWA. In particular, to achieve effective conservation results, there is the need to train foresters  
213 to apply ecologically sound management plans that take into account specific RWA needs on  
214 a local base. Examples are the creation of forest gaps and clearings where canopy closure is  
215 excessive or, at the other extreme, reducing the extensions of clearcut areas to facilitate the  
216 recolonization of disturbed sites. Also, RWA colony foundation can sometimes rely on  
217 temporary social parasitism of colonies of species belonging to the subgenus *Serviformica*  
218 (Maeder et al., 2016). The protection of these species could, therefore, facilitate the successful  
219 establishment of new RWA colonies.

220 *RWA as providers of species-rich microhabitats*

221 RWA host many myrmecophiles that thrive within their nest mounds (e.g. Frizzi et al., 2020),  
222 some of which are obligate mutualists and cannot survive outside RWA nests (Robinson et al.,  
223 2016). Some of these obligate guest species are listed in the IUCN Red List. Clearly, conserving  
224 RWA is integral to protect these organisms, most of which belong to invertebrate groups even  
225 less likely to have been assessed for conservation than the Hymenoptera (Parmentier et al.,  
226 2014; Robinson et al., 2016). Since the conservation of a species strongly depends on the  
227 conservation of its habitat, a thorough revision of the conservation status of myrmecophilous  
228 species could be very useful in updating the conservation status of RWA. Considering RWA  
229 not only as target species but also as providers of species-rich microhabitats might prove a key  
230 strategy to conserve not only them, but all their associated guest species.

231

### 232 **The need for updated information on distribution patterns**

233 Establishing a common and unambiguous legal framework is, however, only the first step  
234 toward the effective protection of RWA. One of the main difficulties in achieving effective  
235 conservation strategies is the non-systematic, and sometimes anecdotal information on their  
236 distribution, making it impossible to monitor populations over time. In turn, the lack of such  
237 data hinders the compilation of Red Lists based on the IUCN criteria. Moreover, habitat  
238 requirements are often recorded at a local scale from presence-only recording, running into  
239 false absence biases (but see Vandegehuchte et al., 2017). Switzerland is an important  
240 exception, as a mapping of RWA mounds (especially *Formica lugubris* and *F. paralugubris*)  
241 was carried out within the fourth National Forest Inventory  
242 ([https://www.waldwissen.net/en/forest-ecology/forest-fauna/insects-invertebrates/red-wood-  
243 ants-in-switzerland#c97108](https://www.waldwissen.net/en/forest-ecology/forest-fauna/insects-invertebrates/red-wood-ants-in-switzerland#c97108)). However, these data are incomplete, as the sampling design -

244 oriented to trees - did not allow the obtaining of suitable data for less frequent species such as  
245 *F. rufa* and *F. polycтена*, or species living outside forests such as *F. pratensis*. Of course, public  
246 engagement and citizen science projects contribute greatly to mapping efforts in particular  
247 because RWA nests are usually conspicuous. Successful cases are the Swiss “Ameisenzeit”  
248 (<https://www.ameisenzeit.ch/>) and “Opération fourmis” (Avril et al., 2019; Freitag et al., 2020),  
249 Nest Quest in the United Kingdom ([https://www.buglife.org.uk/get-involved/surveys/nest-](https://www.buglife.org.uk/get-involved/surveys/nest-quest/)  
250 [quest/](https://www.buglife.org.uk/get-involved/surveys/nest-quest/)), and the results obtained by Sorvari (2021) in Finland. Furthermore, the activities of  
251 amateur associations such as the Ameisenschutzwerke (<https://www.ameisenschutzwerke.de/>)  
252 in Germany contribute to the RWA mapping. However, to enable a European-level risk  
253 assessment a common, standardized international monitoring strategy for RWA would be vital  
254 and would allow the collection of data on RWA habitat requirements in each country. Indeed,  
255 RWA occurrence correlates with many environmental features (e.g. Berberich et al., 2016;  
256 Vandegehuchte et al., 2017). Furthermore, such a scientifically coordinated monitoring scheme  
257 would allow reducing the inevitable bias related to any survey involving lay organizations. This  
258 will finally allow the determination of whether common protection strategies can be applied,  
259 or more fine-grained strategies are needed (e.g. between Northern and Southern countries).

260           We hope with this work to ignite the construction of an international network aimed at  
261 the conservation of this important group, at least at the European level.

262 **Supporting Information**

263 Additional information is available online in the Supporting Information section at the end of  
264 the online article. The authors are solely responsible for the content and functionality of these  
265 materials. Queries (other than absence of the material) should be directed to the corresponding  
266 author.

267

268 **Literature cited**

269 Avril A, Dépraz A, Schwander T, Freitag A. 2019. Opération Fourmis, le premier recensement  
270 participatif des fourmis vaudoises - contexte, méthodologie et bilan préliminaire. Bulletin de  
271 la Société vaudoise des Sciences naturelles 98: 109-120.

272 Balzani P et al. 2021a. CO<sub>2</sub> biogeochemical investigation and microbial characterization of red  
273 wood ant mounds in a Southern Europe montane forest. Soil Biology and Biochemistry:  
274 108536.

275 Balzani P et al. 2021b. Plasticity in the trophic niche of an invasive ant explains establishment  
276 success and long-term coexistence. Oikos 130: 691-696.

277 Berberich G, Grumpe A, Berberich M, Klimetzek D, Wöhler C. 2016. Are red wood ants  
278 (*Formica rufa*-group) tectonic indicators? A statistical approach. Ecological Indicators 61:  
279 968-979.

280 Beresford J, Elias M, Pluckrose L, Sundström L, Butlin RK, Pamilo P, Kulmuni J. 2017.  
281 Widespread hybridization within mound-building wood ants in Southern Finland results in  
282 cytonuclear mismatches and potential for sex-specific hybrid breakdown. Molecular ecology  
283 26: 4013-4026.

284 Bernasconi C, Pamilo P, Cherix D. 2010. Molecular markers allow sibling species  
285 identification in red wood ants (*Formica rufa* group). *Systematic Entomology* 35: 243-249.

286 Bernasconi C, Cherix D, Seifert B, Pamilo P. 2011. Molecular taxonomy of the *Formica rufa*  
287 group (red wood ants) (Hymenoptera: Formicidae): a new cryptic species in the Swiss Alps.  
288 *Myrmecological News* 14: 37-47.

289 Breen J. 2014. Species dossier, range and distribution data for the Hairy Wood Ant, *Formica*  
290 *lugubris*, in Ireland. *Irish Wildlife Manuals*, No. 68. National Parks and Wildlife Service,  
291 Department of the Arts, Heritage and the Gaeltacht, Ireland.

292 Çamlitepe Y, Aksoy V. 2019. Distribution and Conservation Status of the European Red Wood  
293 Ant Species *Formica pratensis* Retzius, 1783 (Hymenoptera, Formicidae) in (European)  
294 Turkey. *Journal of the Entomological Research Society* 21: 199-211.

295 Cherix D, Maddalena-Feller C. 1986. Disappearance of Swiss ant species or the need for new  
296 data. In: Velthuis HHW (Ed.), *Proceedings of the 3rd European Congress of Entomology, Part*  
297 *3*, pp. 413–416.

298 Cherix D, Bernasconi C, Maeder A, Freitag A. 2012. Fourmis des bois en Suisse: état de la  
299 situation et perspectives de monitoring. *Schweizerische Zeitschrift für Forstwesen* 163: 232-  
300 239.

301 Dekoninck W, Vankerhoven F, Maelfait JP. 2003. *Verspreidingsatlas en voorlopige Rode*  
302 *Lijst van de mieren van Vlaanderen*. Rapport van het Instituut voor Natuurbehoud, Brussel.  
303 191.

304 Dekoninck W, Maelfait JP, Vankerkhoven F, Grootaert P. 2005. Remarks on the distribution  
305 and use of a provisional red list of the ants of Flanders (Formicidae, Hymenoptera). JNCC  
306 Report 367: 74-85.

307 Dekoninck W, Hendrickx F, Grootaert P, Maelfait JP. 2010. Present conservation status of red  
308 wood ants in north-western Belgium: Worse than previously, but not a lost cause. European  
309 Journal of Entomology 107: 209-218.

310 Di Nuzzo L et al. 2022. Red wood ants shape epiphytic lichen assemblages in montane silver  
311 fir forests. iForest-Biogeosciences and Forestry 15: 71-76.

312 Drossart M, Gérard M. 2020. Beyond the decline of wild bees: Optimizing conservation  
313 measures and bringing together the actors. Insects, 11(9), 649.

314 Fitzpatrick BR, Baltensweiler A, Düggelin C, Fraefel M, Freitag A, Vandegehuchte ML,  
315 Wermelinger B, Risch AC. 2021. The distribution of a group of keystone species is not  
316 associated with anthropogenic habitat disturbance. Diversity and Distributions 27: 572-584.

317 Freitag A, Dischinger C, Cherix D. 2008. *Formica pratensis* (Hyménoptères: Formicidae) dans  
318 le canton de Vaud: état des peuplements et importance des talus de routes comme milieu de  
319 substitution. Bulletin de la Société Vaudoise des Sciences Naturelles 91: 47-68.

320 Freitag A, Schwander T, Broennimann O, Dépraz A. 2020. Opération Fourmis, les résultats du  
321 premier recensement participatif des espèces de fourmis vaudoises. Bulletin de la Société  
322 Vaudoise des Sciences Naturelles 99: 13-27.

323 Frizzi F, Masoni A, Quilghini G, Ciampelli P, Santini G. 2018. Chronicle of an impact foretold:  
324 the fate and effect of the introduced *Formica paralugubris* ant. Biological Invasions 20: 3575-  
325 3589.



326 Frizzi F et al. 2020. A comparative study of the fauna associated with nest mounds of native  
327 and introduced populations of the red wood ant *Formica paralugubris*. European Journal of  
328 Soil Biology 101: 103241.

329 Hagen SB, Jepsen JU, Ims RA, Yoccoz NG. 2007. Shifting altitudinal distribution of outbreak  
330 zones of winter moth *Operophtera brumata* in sub-arctic birch forest: a response to recent  
331 climate warming? Ecography 30: 299-307.

332 Härkönen SK, Sorvari J. 2017. Effect of host species, host nest density and nest size on the  
333 occurrence of the shining guest ant *Formicoxenus nitidulus* (Hymenoptera: Formicidae).  
334 Journal of Insect Conservation 21: 477-485.

335 Kiss K, Kóbori OT. 2010. *Formica pratensis* supercolony in the Hoia Forest (Cluj Napoca,  
336 Romania). Acta Scientiarum Transylvanica 18/1.

337 Kleijn D et al. 2015. Delivery of crop pollination services is an insufficient argument for wild  
338 pollinator conservation. Nature communications, 6(1), 1-9.

339 Kovats RS, Valentini R, Bouwer LM, Georgopoulou E, Jacob D, Martin E, Rounsevell M,  
340 Soussana J-F. 2014. Europe. In: Barros VR, Field CB, Dokken DJ, Mastrandrea MD, Mach  
341 JK, Bilir TE, Chatterjee M, Ebi KL, Estrada YO, Genova RC, Girma B, Kissel ES, Levy AN,  
342 MacCracken S, Mastrandrea PR, White LL (Eds.), Climate Change 2014: Impacts, Adaptation,  
343 and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth  
344 Assessment Report of the Intergovernmental Panel on Climate Change Cambridge University  
345 Press, pp. 1267-1326.

346 Leandro C, Jay-Robert P, Vergnes A. 2017. Bias and perspectives in insect conservation: a  
347 European scale analysis. Biological Conservation 215: 213-224.

348 Mabelis AA, Korczyńska J. 2016. Long-term impact of agriculture on the survival of wood  
349 ants of the *Formica rufa* group (Formicidae). Journal of insect conservation 20: 621-628.

350 Maeder A, Cherix D, Bernasconi C, Freitag A, Ellis S. 2016. Wood ant reproductive biology  
351 and social systems. In: Stockan & Robinson (Eds.), Wood ant ecology and conservation.  
352 Cambridge University Press.

353 Masoni A, Frizzi F, Natali C, Bernasconi C, Ciofi C, Santini G. 2019. Molecular identification  
354 of imported red wood ant populations in the Campigna Biogenetic Nature Reserve (Foreste  
355 Casentinesi National Park, Italy). Conservation Genetics Resources 11: 231-236.

356 Moret P, Arauz MDLA, Gobbi M, Barragán Á. 2016. Climate warming effects in the tropical  
357 Andes: first evidence for upslope shifts of Carabidae (Coleoptera) in Ecuador. Insect  
358 Conservation and Diversity 9: 342-350.

359 Nicholson A. 1997. Dorset heaths Natural Area profile. English Nature, Arne, Wareham.

360 Parmentier T, Dekoninck W, Wenseleers T. 2014. A highly diverse microcosm in a hostile  
361 world: a review on the associates of red wood ants (*Formica rufa* group). Insectes Sociaux, 61:  
362 229-237.

363 Pavan M. 1959. Attività italiana per la lotta biologica con formiche del gruppo *Formica rufa*  
364 contro gli insetti dannosi alle foreste.

365 Pavan M, Ronchetti G, Vendagna V. 1971. Corologia del gruppo *Formica rufa* in Italia  
366 (Hymenoptera: Formicidae). Collana verde 30, Ministero dell'agricoltura e delle foreste,  
367 Roma.

368 Pavan M. 1981. Perché formiche e uccelli nella lotta biologica? In: Studi sulle formiche utili  
369 alle foreste. Collana verde, Ministero dell'Agricoltura e delle foreste.

370 Rebetz M., Reinhard M. 2008. Monthly air temperature trends in Switzerland 1901–2000 and  
371 1975–2004. *Theoretical and Applied Climatology* 91: 27-34.

372 Robinson EJ, Stockan J. 2016. Future directions for wood ant ecology and conservation. In:  
373 Stockan & Robinson (Eds.), *Wood ant ecology and conservation*. Cambridge University Press.

374 Robinson EJ, Stockan J, Iason GR. 2016. Wood ants and their interaction with other organisms.  
375 In: Stockan & Robinson (Eds.), *Wood ant ecology and conservation*. Cambridge University  
376 Press.

377 Ronchetti G, Groppali R. 1995. Quarantacinque anni di protezione forestale con *Formica*  
378 *lugubris* zett. (hym. formicidae): l'esperienza di Monte d'Alpe (Appennino ligure in provincia  
379 di Pavia). Istituto di entomologia dell'Università.

380 Seifert B. 1996. *Formica paralugubris* nov. spec.-a sympatric sibling species of *Formica*  
381 *lugubris* from the western Alps (Insecta: Hymenoptera: Formicoidea: Formicidae).  
382 *Reichenbachia* 31: 193-201.

383 Seifert B, Kulmuni J, Pamilo P. 2010. Independent hybrid populations of *Formica polycтена* x  
384 *rufa* wood ants (hymenoptera: Formicidae) abound under conditions of forest fragmentation.  
385 *Evolutionary Ecology* 24: 1219-1237.

386 Seifert B. 2018. *The ants of central and north Europe*. Lutra Verlags- und Vertriebsgesellschaft,  
387 407 pp.

388 Seifert B. 2021. A taxonomic revision of the Palaearctic members of the *Formica rufa* group  
389 (Hymenoptera: Formicidae) – the famous mound-building red wood ants. *Myrmecological*  
390 *News* 33: 133-179.

391 Serttaş A, Bakar Ö, Alkan UM, Yılmaz A, Yolcu HI, Ipekdal K. 2020. Nest Survival and  
392 Transplantation Success of *Formica rufa* (Hymenoptera: Formicidae) Ants in Southern  
393 Turkey: A Predictive Approach. *Forests* 11(5): 533.

394 Sorvari J. 2016. Threats, conservation and management. In: Stockan & Robinson (Eds.), Wood  
395 ant ecology and conservation. Cambridge University Press.

396 Sorvari J. 2021. Distribution of Finnish mound-building *Formica* ants (Hymenoptera:  
397 Formicidae) based on using a citizen science approach. *European Journal of Entomology* 118:  
398 57-62.

399 Stankiewicz AM, Sielezniew M, Borowiec ML, Czechowski W. 2005. *Formica uralensis*  
400 Ruzsky (Hymenoptera: Formicidae) in Poland. *Fragmenta Faunistica* 48: 175-180.

401 Stockan J, Robinson EJ, Trager JC, Yao I, Seifert B. 2016. Introducing wood ants: evolution,  
402 phylogeny, identification and distribution. In: Stockan & Robinson (Eds.), Wood ant ecology  
403 and conservation. Cambridge University Press.

404 Trigos-Peral G, Juhász O, Kiss PJ, Módra G, Tenyér A, Maák I. 2021. Wood Ants: Important  
405 Components of the Forest" Immunity System". <https://doi.org/10.21203/rs.3.rs-200088/v1>.

406 Vandegehuchte ML et al. 2017. Distribution and habitat requirements of red wood ants in  
407 Switzerland: Implications for conservation. *Biological Conservation* 212: 366-375.

408 Wegnez P, Mourey F. 2016. *Formica uralensis* Ruzsky, 1895 une espèce encore présente en  
409 France mais pour combien de temps? (Hymenoptera: Formicidae). *Bulletin de la Société royale*  
410 *belge d'Entomologie* 152: 72-80.

411 Wells SM, Pyle RM, Collins NM. 1983. The IUCN Invertebrate Red Data Book. IUCN,  
412 Gland.

413 **Figure legends**

414 **Figure 1.** Map of red wood ant (RWA) protection status across European countries.