

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/id/eprint/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 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

7

8

9

10

11

12

13

14

15

16

17

18

19

20

21

22

23

24

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

- 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
- but also as providers of species-rich microhabitats.

Introduction

28

29

30

31

32

33

34

35

36

37

38

39

40

41

42

43

44

45

46

47

48

49

50

51

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

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

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

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

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

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

77

78

79

80

81

82

83

84

85

86

87

88

89

90

91

92

93

94

95

96

97

98

Status quo of RWA protection in Europe

RWA protection at national level

Several European countries protect RWA (Figure 1; Appendix S1). Some of them, such as Austria, implicitly protect them by protecting all the wildlife fauna, while others explicitly mention RWA, at least as a group. For example, in Estonia and Poland, all RWA are protected species, and in Hungary RWA are protected and their nests assigned a monetary value. In Switzerland, RWA are listed as protected since 1966 and all species are explicitly included in the Annex 3 of protected species in the Ordinance on the Protection of Nature and Landscape (OPN) of the Swiss Federal Council. In Germany, besides being protected by the Federal Nature Conservation Act (Bundesnaturschutzgesetz, BNatSchG) like all wildlife, all moundbuilding RWA are additionally listed as especially protected in Germany (like all wild bees and a few wasp species) under the Federal **Species** Protection Ordinance (Bundesartenschutzverordnung, BArtSchV), which includes a list of protected species. It is thus prohibited to disturb or destroy their nests or remove workers or other life-stages. Moreover, F. polyctena x rufa hybrids are implicitly protected as well since the parental species are protected. In Belgium, all RWA species were protected by a law of 1980. Later, Belgium legislation was organized at a Federal level and in 2009 the governments of the Flanders and Wallonia published a law in which three (for Flanders) and two (for Wallonia) species were protected, whereas Brussels protects only one species (F. polyctena). Finally, some other countries explicitly prioritize the protection of particular RWA species. In Bulgaria, some RWA species have been protected since 1959, though the obsolete scientific names included have never been updated, and *F. rufa* is protected by the 2002 Bulgarian Biodiversity Act. In the United Kingdom, *F. pratensis* is a British Action Plan (BAP) 2007 priority species, i.e. those species "that were identified as being the most threatened and requiring conservation action", being also listed in the Species of Principal Importance in England. Also, *F. aquilonia* is included in the Northern Ireland priority species list.

The Italian paradox

99

100

101

102

103

104

105

106

107

108

109

110

111

112

113

114

115

116

117

118

119

120

121

122

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

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

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

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

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

RWA protection at international level

According to the IUCN Red List (accessed 8th October 2021), RWA species are classified as "Near Threatened" at a global level, but only some species (*F. rufa, F. lugubris, F. polyctena, F. aquilonia, F. pratensis*, and *F. uralensis*) have been assessed. Previous assessments (from 1983 to 1994) classified all the above RWA species as "Vulnerable" except *F. uralensis* that was classified as "Indeterminate" (from 1986 to 1994).

147

148

149

150

151

152

153

154

155

156

157

158

159

160

161

162

163

164

165

166

167

168

169

170

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

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

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

Suggestions for a strategic approach for a future European conservation framework

RWA species as conservation targets

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

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

195

196

197

198

199

200

201

202

203

204

205

206

207

208

209

210

211

212

213

214

215

216

217

218

219

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

RWA as providers of species-rich microhabitats

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

231

232

233

234

235

236

237

238

239

240

241

242

243

220

221

222

223

224

225

226

227

228

229

230

The need for updated information on distribution patterns

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

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

244

245

246

247

248

249

250

251

252

253

254

255

256

257

258

259

260

261

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

Supporting Information

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

267

268

262

263

264

265

266

Literature cited

- 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.
- Balzani P et al. 2021a. CO₂ biogeochemical investigation and microbial characterization of red
- 273 wood ant mounds in a Southern Europe montane forest. Soil Biology and Biochemistry:
- **274** 108536.
- Balzani P et al. 2021b. Plasticity in the trophic niche of an invasive ant explains establishment
- 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.
- 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
- identification in red wood ants (*Formica rufa* group). Systematic Entomology 35: 243-249.
- Bernasconi C, Cherix D, Seifert B, Pamilo P. 2011. Molecular taxonomy of the Formica rufa
- group (red wood ants) (Hymenoptera: Formicidae): a new cryptic species in the Swiss Alps.
- 288 Myrmecological News 14: 37-47.
- 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 Çamlıtepe Y, Aksoy V. 2019. Distribution and Conservation Status of the European Red Wood
- 293 Ant Species Formica pratensis Retzius, 1783 (Hymenoptera, Formicidae) in (European)
- 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
- 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
- situation et perspectives de monitoring. Schweizerische Zeitschrift fur Forstwesen 163: 232-
- 300 239.
- 301 Dekoninck W, Vankerkhoven F, Maelfait JP. 2003. Verspreidingsatlas en voorlopige Rode
- 302 Lijst van de mieren van Vlaanderen. Rapport van het Instituut voor Natuurbehoud, Brussel.
- 303 191.

- Dekoninck W, Maelfait JP, Vankerkhoven F, Grootaert P. 2005. Remarks on the distribution
- and use of a provisional red list of the ants of Flanders (Formicidae, Hymenoptera). JNCC
- 306 Report 367: 74-85.
- 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
- measures and bringing together the actors. Insects, 11(9), 649.
- 314 Fitzpatrick BR, Baltensweiler A, Düggelin C, Fraefel M, Freitag A, Vandegehuchte ML,
- Wermelinger B, Risch AC. 2021. The distribution of a group of keystone species is not
- associated with anthropogenic habitat disturbance. Diversity and Distributions 27: 572-584.
- 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.
- 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.
- 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.

- Frizzi F et al. 2020. A comparative study of the fauna associated with nest mounds of native
- and introduced populations of the red wood ant Formica paralugubris. European Journal of
- 328 Soil Biology 101: 103241.
- Hagen SB, Jepsen JU, Ims RA, Yoccoz NG. 2007. Shifting altitudinal distribution of outbreak
- zones of winter moth *Operophtera brumata* in sub-arctic birch forest: a response to recent
- 331 climate warming? Ecography 30: 299-307.
- 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).
- 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.
- Kleijn D et al. 2015. Delivery of crop pollination services is an insufficient argument for wild
- pollinator conservation. Nature communications, 6(1), 1-9.
- 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
- 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,
- 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.
- 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
- 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
- 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
- of imported red wood ant populations in the Campigna Biogenetic Nature Reserve (Foreste
- 355 Casentinesi National Park, Italy). Conservation Genetics Resources 11: 231-236.
- 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.
- Nicholson A. 1997. Dorset heaths Natural Area profile. English Nature, Arne, Wareham.
- Parmentier T, Dekoninck W, Wenseleers T. 2014. A highly diverse microcosm in a hostile
- world: a review on the associates of red wood ants (Formica rufa group). Insectes Sociaux, 61:
- 362 229-237.
- Pavan M. 1959. Attivitá 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.
- Pavan M. 1981. Perché formiche e uccelli nella lotta biologica? In: Studi sulle formiche utili
- alle foreste. Collana verde, Ministero dell'Agricoltura e delle foreste.

- Rebetez M., Reinhard M. 2008. Monthly air temperature trends in Switzerland 1901–2000 and
- 371 1975–2004. Theoretical and Applied Climatology 91: 27-34.
- 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.
- 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 polyctena x*
- rufa wood ants (hymenoptera: Formicidae) abound under conditions of forest fragmentation.
- 385 Evolutionary Ecology 24: 1219-1237.
- Seifert B. 2018. The ants of central and north Europe. Lutra Verlags- und Vertriebsgesellschaft,
- 387 407 pp.
- 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 Serttas 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
- ant ecology and conservation. Cambridge University Press.
- 396 Sorvari J. 2021. Distribution of Finnish mound-building Formica ants (Hymenoptera:
- 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
- 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.
- Vandegehuchte ML et al. 2017. Distribution and habitat requirements of red wood ants in
- 407 Switzerland: Implications for conservation. Biological Conservation 212: 366-375.
- 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.
- Wells SM, Pyle RM, Collins NM. 1983. The IUCN Invertebrate Red Data Book. IUCN,
- 412 Gland.

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