



HAL
open science

Forward to the north: two Euro-Mediterranean bumblebee species now cross the Arctic Circle

Baptiste Martinet, Pierre Rasmont, Bjorn Cederberg, Dimitri Evrard, Frode
Odegaard, Juho Paukkunen, Thomas Lecocq

► **To cite this version:**

Baptiste Martinet, Pierre Rasmont, Bjorn Cederberg, Dimitri Evrard, Frode Odegaard, et al.. Forward to the north: two Euro-Mediterranean bumblebee species now cross the Arctic Circle. *Annales de la Société Entomologique de France*, 2015, 51 (4), pp.303-309. 10.1080/00379271.2015.1118357 . hal-01575789

HAL Id: hal-01575789

<https://hal.univ-lorraine.fr/hal-01575789>

Submitted on 8 Dec 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 **Forward to the North: two Euro-Mediterranean bumblebee species**
2 **now cross the Arctic Circle**

3 Baptiste Martinet¹, Pierre Rasmont¹, Björn Cederberg², Dimitri Evrard¹, Frode
4 Ødegaard³, Juho Paukkunen⁴ and Thomas Lecocq¹

5 ¹ University of Mons, Research institute of Biosciences, Laboratory of Zoology, Place
6 du Parc 20, 7000 Mons, Belgium

7 ² Swedish Species Information Centre, Swedish University of Agricultural Sciences,
8 PO Box 7007, 750 07 Uppsala, Sweden

9 ³ Norwegian Institute for Nature Research - NINA, Postal address: P.O. Box 5685
10 Sluppen, NO-7485 Trondheim, Norway

11 ⁴ Finnish Museum of Natural History, Zoology Unit, P.O. Box 17, FI-00014
12 University of Helsinki, Finland

13 * Corresponding author: Baptiste.martinet@student.umons.ac.be

14 **Abstract**

15 **In recent decades, several animal and plant species have been in regression**
16 **(population size decrease and geographical distribution shrinking). This loss of**
17 **biodiversity can be due to various factors such as the destruction and**
18 **fragmentation of habitat, urban development, pesticides or climate change.**
19 **However, some species benefit from these changes and expand their distribution.**
20 **Here we report observations of two Euro-Mediterranean bumblebee species:**
21 ***Bombus terrestris* for the first time and *Bombus lapidarius*, north of the Arctic**
22 **Circle in Fennoscandia.**

23 **Résumé**

24 Ces dernières décennies, de nombreuses espèces animales et végétales sont en
25 régression autant d'un point de vue de leur distribution qu'au niveau de leur effectif

26 de population. Cette perte de biodiversité peut être due à différents facteurs comme la
27 destruction et la fragmentation de l'habitat, le développement urbain, les pesticides ou
28 encore le changement climatique. Néanmoins, certaines espèces profitent de ces
29 perturbations pour étendre leur distribution. C'est ainsi que pour la première fois,
30 deux espèces Euro-Méditerranéennes de bourdons (*B. terrestris* et *B. lapidarius*) ont
31 été observées en 2013 et 2014 en Fennoscandie au-delà du Cercle Arctique.

32 **Keywords:** *Bombus terrestris*, biogeography, climate change, Fennoscandia, heat
33 wave

34

35 **Introduction**

36 Although bumblebees (genus *Bombus* Latreille) are distributed from Arctic tundra to
37 lowland tropical forest, they are clearly most abundant (relative abundance) in alpine
38 grassland habitats and cold and temperate regions of the Northern Hemisphere
39 (Williams 1998). Indeed, these robust hairy bees have thermoregulatory adaptations
40 involving facultative endothermy (Heinrich 1979), that enable them to live in the
41 coldest areas inhabited by insects such as the Himalayas (Williams 1991), the Andes
42 (Gonzalez *et al.* 2005) or north Greenland (Skorikov 1937), the Alps (Pradervand *et*
43 *al.* 2011) and the Pyrenees (Iserbyt & Rasmont 2012). They also reach a high
44 diversity in Arctic regions (e.g. Fennoscandia: Skorikov 1937; Løken 1973 or Alaska:
45 Williams 2014). In these high altitudes and latitudes, bumblebees are the only
46 remaining bee pollinators, supporting a large part of the pollination ecosystem service
47 (Shamurin *et al.* 1966; Kevan 1973). In recent decades, several animal and plant
48 species have been in regression (population size decrease and geographical
49 distribution shrinking). This loss of biodiversity can be due to various factors such as

50 the destruction and fragmentation of habitat, urban development, pesticides or climate
51 change.

52 However, their hotspot diversity areas (mountains, Arctic, Subarctic and Boreal
53 regions) are also regions most severely affected by global warming (IPCC 2007;
54 Franzén & Ockinger 2011; Franzén & Molander 2012), a phenomenon that will most
55 likely increase during the next decades (Berger 1991; Settele *et al.* 2005; Spangenberg
56 2012). Climate change poses a major threat to many bumblebee species (Rasmont *et*
57 *al.*, 2015), however, some are able to benefit and expand their ranges.

58

59 Current and expected global warming consequences are the focus of many research
60 projects (e.g. Parmesan & Yohe 2003). One of the major consequences of global
61 warming is species range displacement because organisms track their climatic niches
62 as observed in several organisms (Parmesan & Yohe 2003; Chen *et al.* 2011;
63 Kuhlmann *et al.* 2012). However, since thermo-tolerance is species specific, species
64 distribution shifts happen at different strength and speed (Klok & Chown 2003;
65 Franzén & Ockinger 2011) resulting in new species communities and new
66 interspecific interactions (Franzén & Molander 2012). For native species, the
67 interaction with climatic refugee species can lead to consequences similar to those
68 fostered by invasive species (Inoue *et al.* 2008; Kanbe *et al.* 2008; Yoon *et al.* 2009;
69 Nagamitsu *et al.* 2010; Meeus *et al.* 2011; Aizen *et al.* 2011; Thomas 2011; Arbetman
70 *et al.* 2013a; Murray *et al.* 2013; Arbetman *et al.* 2013b). Therefore, an early
71 detection of climatic refugee species through efficient faunistic surveys is important.

72 We here report the observations of two Euro-Mediterranean bumblebee species (*sensu*
73 de Lattin 1967) north of the Arctic Circle, a region hosting many bumblebee species

74 with restricted areas. Specifically, we hypothesize the potential trigger factors and the
75 potential consequences of the range shift to the North for Arctic biodiversity.

76 **Materials & Methods**

77 **Determination of original northern European bumblebee fauna**

78 We focused on the region north of the Arctic Circle in Fennoscandia. We determined
79 the original Arctic European bumblebee fauna (i.e. baseline dataset) according to (i)
80 literature (Løken 1973) and (ii) occurrence observations before 1973. The occurrence
81 observations were hosted by databases managed by B. Cederberg (Swedish Species
82 Information Centre (SSIC), Sweden); F. Ødegaard (Norwegian Biodiversity
83 Information Centre (NBIC) Norway); J. Paukkunen (Finnish Museum of Natural
84 History (MZH), Finland) and P. Rasmont & E. Haubruge (*Banque de Données*
85 *Faunique de Gembloux et de Mons* (BDFGM), Belgium). These occurrence datasets
86 were mapped using *Data Fauna Flora* software (Barbier *et al.* 2013)

87 **Detection of expanding species**

88 In order to assess potential changes in the northern European bumblebee fauna, we
89 collected samples beyond the Arctic Circle (see sampling map Fig. 1) in 2013 and
90 2014 using entomological sweep nets. All individuals were killed by freezing. Males
91 were prepared for chemotaxonomic analyses following De Meulemeester *et al.*
92 (2011).

93 The specific identification was verified by checking different morphological
94 diagnostic characters (Løken 1973, 1984; Rasmont 1984; Rasmont *et al.* 1986;
95 Pekkarinen & Kaarnama 1994). For the species belonging to the subgenus *Bombus*
96 *sensu stricto* (Cameron *et al.* 2007), a group with low morphological differentiation,
97 the morphological characters based on identification was assessed by comparing the
98 GC-FID chromatograms of cephalic gland labial secretions (Lecocq *et al.* 2011) with

99 reference specimens (*Bombus terrestris*: PRAS0006 from France, Var, Gonfaron
100 3.VII.2008, 43°18'N 06°18'E; *Bombus cryptarum*: PRAS0148 from Sweden,
101 Jämtland, Kvissle 15.VIII.2008, 63°16'N 13°56'E; PRAS0323 from Scotland, Wick,
102 Wireless 12.VIII.2009, 58°28'N 3°13'W, see Fig. 1) and with the list of compounds
103 given by Bertsch & Schweer (2012a,b). The cephalic gland labial secretions are
104 commonly used as diagnostic characters (Bertsch & Schweer 2012a). We followed
105 the preparation and analysis methods of De Meulemeester *et al.* (2011) and Lecocq *et*
106 *al.* (2011, 2014, 2015).

107 **Results**

108 A total of 756 specimens (17 species) were collected in the vicinity of Abisko
109 (Sweden), and Narvik (Norway) in 2013, 1159 specimens (20 species) from Abisko
110 (Sweden), Tarfala (Sweden) and Narvik (Norway) areas in 2014.

111 Among these specimens, we found two species previously unknown (unexpected)
112 north of the Arctic Circle: *B. lapidarius* and *B. terrestris*. Another species *B. wurflenii*
113 was observed far north of its baseline distribution (Løken 1973).

114 ***B. lapidarius* (Fig. 2A):** Abisko (Sweden), 68°21'10.3" N 18°48'53.7" E, altitude 388
115 m asl, 22 VII 2013, 1 ♂ on *Trifolium pratense*, leg. Martinet.

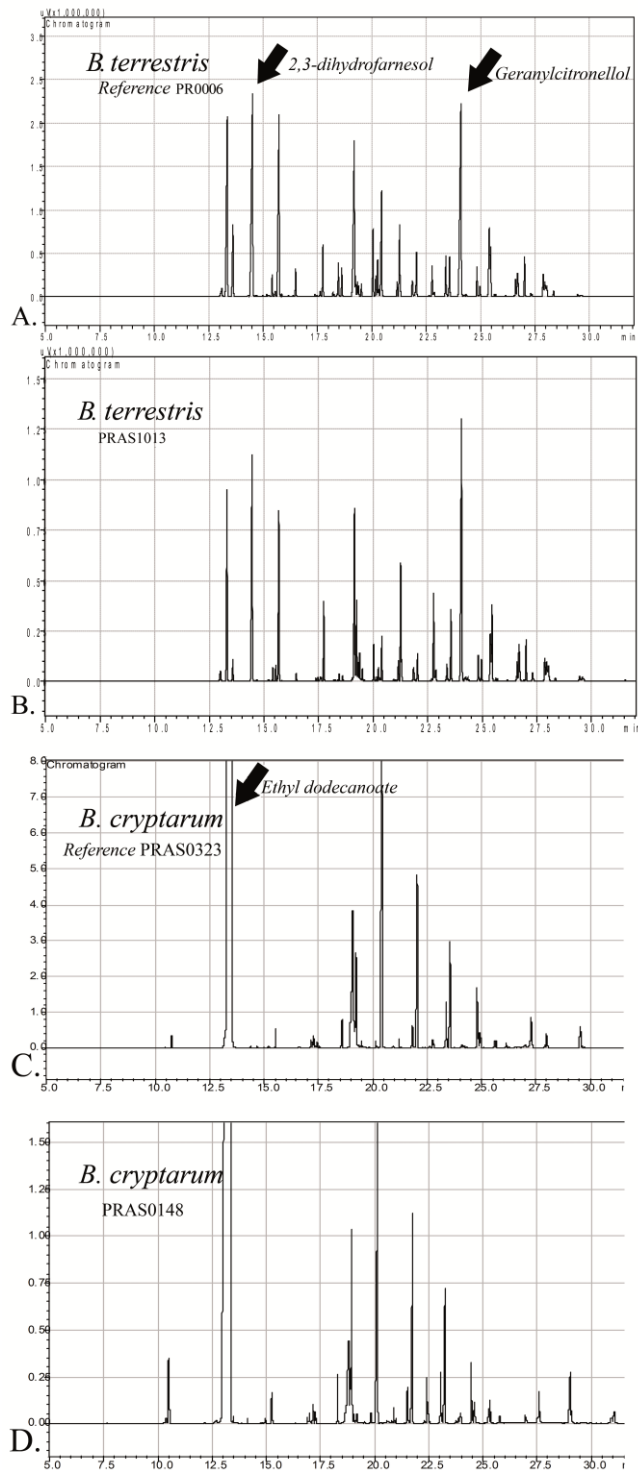
116 ***B. terrestris* (Fig. 2B):** Kiruna (Sweden), 67°49'38.6" N 20°20'26.9" E, 446 m asl, 15
117 VII 2013, 1 ♀ (BMAR0235) (Fig. 2B) on *Epilobium angustifolium*, leg. Martinet;
118 Björkliden (Sweden), 68°24'36.9" N 18°39'16.9"E, 565 m asl, 21 VII 2014, 1 worker
119 on *Astragalus alpinus*, leg. Rasmont; Narvik (Norway), Iptojávri, 68°06'23.8" N
120 17°29'20.4" E, 620 m asl, 27 VII 2014, 1 ♀ (PRAS1013) on *Epilobium angustifolium*,
121 leg. Rasmont & Martinet.

122 ***B. wurflenii* (Fig. 2C):** Tromsø (Norway), 69°38'02.0" N 18°59'57.2" E, 427 m asl,
123 10 VII 2014, 2 workers on *Vaccinium uliginosum*, leg. Martinet & Evrard.

124 The comparison between the distribution of these species in the baseline dataset
125 (Løken 1973) and our new occurrence observations shows that *B. lapidarius* occurs
126 now 400 km north of its 1973 limits; *B. terrestris* occurs 800 km north of its 1973
127 limits and *B. wurflenii* now occurs 200 km north of its 1973 limits. All previous
128 reports of *Bombus lapidarius* and *B. terrestris* from north of the Arctic Circle (Fig.
129 2A, Fig. 2B) are of dubious provenance and remain unverified (see discussion).

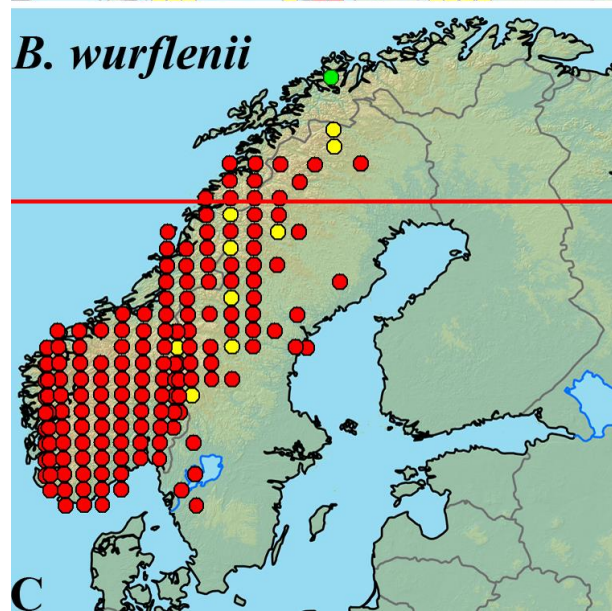
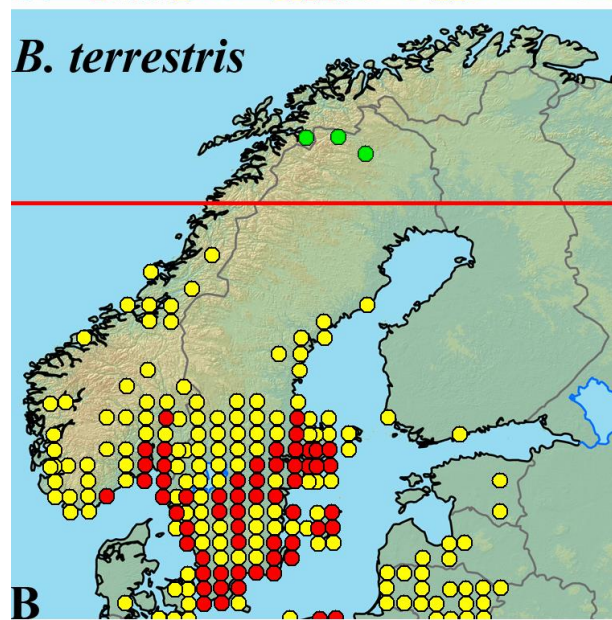
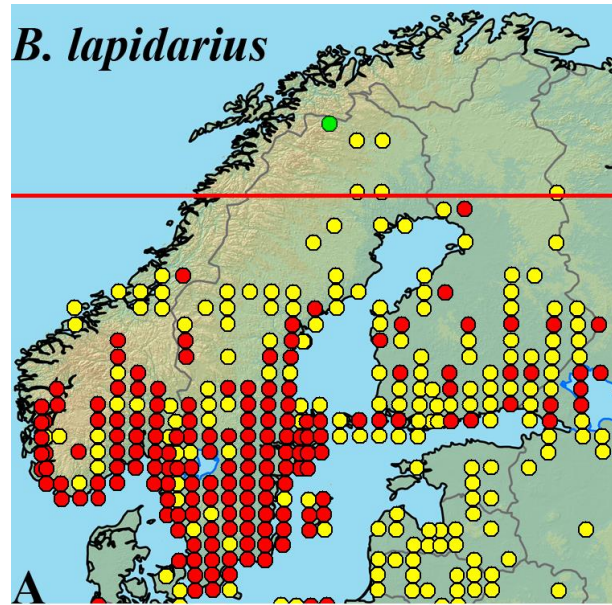
130

131



132

133 Figure 1. GC-FID chromatograms of *Bombus sensu stricto* males. (A) Reference
 134 specimen of *B. terrestris* (PRAS0006, Lecocq *et al.* 2013b). (B) *Bombus terrestris*
 135 male BMAR0235 (Kiruna). (C) Specimen of *B. cryptarum* male PRAS0323. (D) *B.*
 136 *cryptarum* male PRAS0148 (Jämtland, Sweden).



138 Figure 2. Maps summarizing the expansion toward the north of *B. lapidarius* (A), *B.*
139 *terrestris* (B) and *B. wurflenii* (C). Red dots represent the presence of the species
140 before 1974 (mainly Løken (1973) for Fennoscandia and Elfving (1968) for Finland)
141 and yellow dots represent records from new sites of the species since 1974, which
142 include data from BDFGM, MZH, NSIC, SSIC, Pekkarinen *et al.* (1981). Red dots
143 are also used, if records from both periods (>1974 and ≤ 1974) are known from the
144 same area (grid cell). Green dots represent our records of 2013 and 2014. The red line
145 represents the Arctic Circle.

146 **Discussion**

147 **Toward a new Arctic bumblebee fauna?**

148 The eco-climatic ranges (e.g. geographical distribution) of different species are
149 currently undergoing significant modifications. In bumblebees, many species are in
150 regression (e.g. Williams 1986; Rasmont *et al.* 2005a; Cameron *et al.* 2011) while few
151 species are expanding their distribution (e.g. *B. semenoviellus*: van der Smissen &
152 Rasmont, 2000; Sima & Šmetana 2012; *B. hypnorum*: Roberts 2012; *B. haematurus*:
153 Jenič *et al.* 2010; *B. moderatus*: Owen *et al.* 2012).

154 In Fennoscandia, our results show an obvious change in the northern European
155 bumblebee fauna since the 1970s. The main change is the expansion of two Euro-
156 Mediterranean species (*B. lapidarius* and *B. terrestris*) beyond the Arctic Circle. In
157 the 1970s, the northern limit of *B. terrestris* barely reached Uppsala (60° N) in
158 Sweden or Hamar (north Oslo, 60°50' N) in Norway, while *B. lapidarius* was
159 reaching higher latitudes, at the southernmost margin of the boreal taiga forest (Løken
160 1973). Our recent observations show that both species now reach the 68° N latitude,
161 whereby they have crossed the Arctic Circle. It is important to note that several
162 specimens of *B. lapidarius* have been collected in north Sweden before our sampling

163 in 1976 (Løken 1978). This year corresponds to the most extreme climatic event (heat
164 waves) of the last century in most of west Europe including the north of Fennoscandia
165 (Klein 2009). Our hypothesis is that *B. lapidarius* is probably rare with a patchy
166 distribution in the north of the Fennoscandia. However when the weather conditions
167 are favourable for this species (temperature increase) it becomes more visible, perhaps
168 more abundant or simply is more resistant to heat waves than the other species. So the
169 sampling likelihood of *B. lapidarius* is higher during a particularly hot summer such
170 as in 1976. The years 2013 and 2014 also provided heat waves in the north of
171 Fennoscandia (Finnish Meteorological Institute 2013, 2014).

172 The expansion of Euro-Mediterranean bumblebee taxa toward the north has already
173 been recorded in other regions. In Great Britain, *B. terrestris* was only recorded by
174 Alford (1975) at the maximum latitude of Aberdeen (57° N), while currently it
175 reaches the northern coast of the Scotland (60° N) (Roberts 2012 and Rasmont pers.
176 obs.) and the Shetland (Macdonald 2014). In Russia, Panfilov (1957) observed only
177 few specimens of *B. terrestris* in only one location in the Moscow region, while
178 recently Levchenko (2012) found a large number of specimens in nearly all surveyed
179 locations of this region. Such expansion has also been observed for *B. veteranus*
180 which now crosses the Arctic Circle in Finland, Russia (e.g. in the Murmansk Oblast,
181 Paukkunen & Kozlov 2015) and in Sweden (Cederberg 2013).

182 The expansion of *B. veteranus* and *B. wurflenii* beyond the Arctic Circle could most
183 likely be explained by the cold adaptations of these species (Løken 1973, Reinig
184 1988) and climate change. In contrast, *B. lapidarius* and *B. terrestris* are Euro-
185 Mediterranean bumblebees. Indeed, *B. terrestris* is abundant all around the
186 Mediterranean coast and reaches its southern limits on the edges of the Sahara
187 (Rasmont *et al.* 2008). *B. lapidarius* has not been found as far south and it does not

188 live on the Mediterranean coast, but it reaches the Atlas Mountains in Morocco
189 (Rasmont & Iserbyt 2014). Therefore, we suggest that the current global climate
190 warming in northern regions could be the trigger factor of the expansion of such a
191 species, as observed in other organisms (Rasmont *et al.* 2015).

192 An alternative hypothesis is that the Euro-Mediterranean species have not achieved
193 equilibrium with their current environment (Svenning & Skov 2007) and are still
194 continuing their post Ice-Age expansion (Lecocq *et al.* 2013a). Nevertheless the high
195 dispersal ability of several bumblebee species such as *B. lapidarius* and *B. terrestris*
196 (Kraus *et al.* 2009, Lepais *et al.* 2010), the long term occurrence of these species in
197 surrounding regions (Rasmont & Iserbyt 2014), as well as their phylogeographic
198 structure (i.e. endemic haplotypes and high genetic diversity in Fennoscandia at least
199 for *B.lapidarius*; Lecocq *et al.* 2013a; Lecocq *et al.* 2013b) make this hypothesis
200 unlikely. Further studies on bumblebee climatic niches are needed to assess the role of
201 climate change as a trigger factor of Euro-Mediterranean species expansion to cold
202 regions. And finally, since *B. terrestris* is widely used and internationally traded for
203 crop pollination, we cannot exclude that the collected *B. terrestris* individuals could
204 have escaped from greenhouses. However, we did not observe any greenhouses in the
205 surroundings of our study areas, the nearest ones being certainly more than 50 km
206 distant.

207 **Consequences for Arctic species conservation**

208 Besides the understanding of factors triggering expansion, the consequences of the
209 expansion of *B. terrestris* and *B. lapidarius* should be taken into account in local
210 bumblebee conservation management. It remains to assess how *B. lapidarius* and *B.*
211 *terrestris* could compete with the original high latitude bumblebee fauna where they
212 forage side-by-side. However, both species are known for their large colonies (Holm

213 1960; Velthuis & van Doorn 2006) and for their high opportunism in foraging plant
214 selection (Ruszkowski 1971; Teräs 1985; Rasmont 1988, Teper 2004). On the other
215 hand, Arctic bumblebee species only establish small colonies with a low number of
216 offspring (Løken 1973; Richards 1973; Berezin 1994, 1995). Therefore, Arctic
217 bumblebee species already impacted by climatic stress (Franzén & Ockinger 2011;
218 Franzén & Molander 2012; Martinet et al. 2015) could suffer from a drastic
219 competition from the new Euro-Mediterranean invaders. As we are at the very initial
220 stages of colonisation of these species, it is, as yet, difficult to project the future
221 situation.

222 **Acknowledgements**

223 The authors thank the Abisko and Tarfala scientific stations (Sweden) for their
224 welcome and their help in material collection. We acknowledge all the people that
225 helped us in our journey to the Abisko and Tarfala stations: Peter Läkare and Gunhild
226 Ninis Rosqvist (University of Stockholm), Magnus Augner and Linnéa Wanhatalo
227 (Abisko Station), Hannele Savela (Oulu University, Interact administration), Josefine
228 Strand and Therese Wikström (Länsstyrelsen i Norrbottens län Naturvårdsenheten,
229 Luleå). The research has received funding from the European Community's Seventh
230 Framework Programme (FP7/2007-2013) under grant agreement no 244090, STEP
231 Project (Status and Trends of European Pollinators, www.step-project.net) and from
232 the INTERACT FP-7 EU project. Special thanks to M. Franzen, Alrun Siebenkäs
233 (UFZ, Halle) for their help. Thomas Lecocq has been working as a post-doc in the
234 BELBEES project funded by the Belgian Scientific Politic (BELSPO,
235 BR/132/A1/BELBEES).

236 **References**

- 237 Aizen MA, Lozada M, Morales CL. 2011. Comparative nectar-foraging behaviors and
238 efficiencies of an alien and a native bumble bee. *Biological Invasions* 13:
239 2901–2909. doi: 10.1007/s10530-011-9972-3.
- 240 Alford D V. 1975. *Bumblebees*. London: Davis-Poynter, 352 p.
- 241 Arbetman MP, Meeus I, Morales CL, Alzen MA, Smagghe G. 2013a. Co-introduction
242 and spillover of parasites by invasive *Bombus terrestris*. *Bumblebee's chauffer*
243 hitchhike alien parasites when traveling to Patagonia, Argentina. *Biological*
244 *Invasions. Biodiversity Conservation* 15: 489–494.
- 245 Arbetman MP, Meeus I, Morales CL, Alzen MA, Smagghe G. 2013b. Alien parasite
246 hitchhikes to Patagonia on invasive bumblebee. *Biological Invasions* 15: 489–
247 494. doi: 10.1007/s10530-012-0311-0.
- 248 Barbier Y, Rasmont P, Dufrêne M, Sibert JM. 2014. Data fauna flora, Mons,
249 Belgique : Université de Mons-Haintaut, <http://hdl.handle.net/2268/148255>
- 250 Berezin MV. 1994. Social organization of the bumblebees (Hymenoptera, Apoidea,
251 *Bombus*) in the Arctic (Wrangel island), p. 320 in: Lenoir A., Arnold G.,
252 Lepage M. (Ed.), *Les insectes sociaux*, 12th Congress of the IUSSI-UIEIS,
253 Paris.
- 254 Berezin M V. 1995. Geographical Diversity, Species Correlation, Population
255 Structure and Cenotic Interactions of Arctic Bumble Bees (Apidae, *Bombus*),
256 p. 205–215 in: Grönlund E., Melander O., *Swedish-Russian Tundra Ecology.*
257 *Expedition-94*. Stockholm: Swedish Polar Research Secretariat.
- 258 Berger A, Loutre M F. 1991. Insolation values for the climate of the last 10 million
259 years. *Quaternary Science Reviews* 10: 297–317.

260 Bertsch A, Schweer H., 2012a. Male labial gland secretions as species recognition
261 signals in species of *Bombus*. *Biochemical Systematics and Ecology* 40
262 (2012) 103–111

263 Bertsch A, Schweer H., 2012b. Cephalic labial gland secretions of males as species
264 recognition signals in bumblebees: are there really geographical variations in
265 the secretions of the *Bombus terrestris* subspecies? (*Hymenoptera: Apidae:*
266 *Bombus*). *Beiträge zur Entomologie*, 62(1): 103-124.

267 Cameron SA, Hines H.M., Williams P.H. 2007. A comprehensive phylogeny of the
268 bumble bees (*Bombus*). *Biological Journal of the Linnean Society* 91: 161–
269 188.

270 Cameron SA, Lozier J D, Strange J P, Koch J B, Cordes N, Solter L F, Griswold T L.
271 2011. Patterns of widespread decline in North American bumble bees.
272 *Proceedings of the National Academy of Sciences* 108(2): 662–667.

273 Cederberg B, 2013. Artfaktblad *Bombus veteranus sandhumla*. Artdatabanken, SLU,
274 Uppsala, Sweden.
275 http://www.artfakta.se/artfaktblad/Bombus_Veteranus_102704.pdf (accessed
276 16.XII.2014).

277 Chen I-C, Hill JK, Ohlemüller R, *et al.* 2011. Rapid range shifts of species associated
278 with high levels of climate warming. *Science* 333: 1024–1026. doi:
279 10.1126/science.1206432.

280 Core Writing Team, Pachauri R K and Reisinger A (Eds.). IPCC. 2007. Contribution
281 of Working Groups I, II and III to the Fourth Assessment Report of the
282 Intergovernmental Panel on Climate Change, Geneva, Switzerland. 104p.

283 de Lattin G. 1967. *Grundriss der Zoogeographie*. Iena, Stuttgart: Gustav Fisher, 602 p.

284 De Meulemeester T., Gerbaux P., Boulvin M., Coppée A., Rasmont P. 2011. A
285 simplified protocol for bumble bee species identification by cephalic secretion
286 analysis. *Insectes Sociaux* 58: 227–236.

287 Elfving R. 1968. Die Bienen Finnlands. *Fauna Fennica* 21: 1–69.

288 Finnish Meteorological Institute 2013. June was exceptionally warm.
289 <http://en.ilmatieteenlaitos.fi/press-release/730379> (accessed 13.02.2015).

290 Finnish Meteorological Institute 2014. An exceptionally long heatwave .
291 <http://en.ilmatieteenlaitos.fi/press-release/10014539> (accessed 13.02.2015).

292 Franzén M, Ockinger E. 2011. Climate-driven changes in pollinator assemblages
293 during the last 60 years in an Arctic mountain region in Northern Scandinavia.
294 *Journal of insect conservation* 16: 227–238.

295 Franzén M, Molander M. 2012. How threatened are alpine environments? a cross
296 taxonomic study. *Biodiversity and Conservation* 21: 517–526.

297 Gonzalez VH, Ospina M, Bennett D. 2005. Abejas altoandinas de Colombia: Guía de
298 campo. Bogotá : Instituto de Investigación de Recursos Biológicos Alexander
299 von Humboldt, 80p.

300 Heinrich B. 1979. Bumblebee economics. Cambridge, Massachussets: Harvard
301 University Press, 256p.

302 Holm SN. 1960. Experiments on the domestication of bumblebees (*Bombus* Latr.) in
303 particular *B.lapidarius* L. and *B.terrestris* L. Royal Veterinary and Agriculture
304 College Copenhagen Yearbook 1960: 1–19.

305 Inoue MN, Yokoyama J, Washitani I. 2008. Displacement of Japanese native
306 bumblebees by the recently introduced *Bombus terrestris* (L.) (Hymenoptera:
307 Apidae). *Journal of Insect Conservation* 12: 135–146.

- 308 Iserbyt S, Rasmont P. 2012. The effect of climatic variation on abundance and
309 diversity of bumblebees: a ten years survey in a mountain hotspot. *Annales de*
310 *la Société entomologique de France* (n.s.) 48: 261–273.
- 311 Jenič A., Gogala A., Grad J. 2010. *Bombus haematurus* (Hymenoptera: Apidae), new
312 species in the Slovenian bumblebee fauna. *Acta entomologica slovenica* 18(2):
313 168–170.
- 314 Kevan P G. 1973. Flowers, insects, and pollination ecology in the Canadian high
315 Arctic. *Polar Record* 16: 667–674.
- 316 Kanbe Y, Okada I, Yoneda M, *et al.* 2008. Interspecific mating of the introduced
317 bumblebee *Bombus terrestris* and the native Japanese bumblebee *Bombus*
318 *hypocrita sapporoensis* results in inviable hybrids. *Naturwissenschaften* 95:
319 1003–1008.
- 320 Klein T. 2009. Comparaison des sécheresses estivales de 1976 et 2003 en Europe
321 occidentale à l'aide d'indices climatiques. *Bulletin de la Société géographique*
322 *de Liège* 53 : 75-86.
- 323 Klok JC, Chown S.L. 2003. Resistance to temperature extremes in sub-Antarctic
324 weevils, interspecific variation, population differentiation and acclimation.
325 *Biological Journal of the Linnean Society* 78: 401–414.
- 326 Kraus FB, Wolf S, Moritz RFA. 2009. Male flight distance and population
327 substructure in the bumblebee *Bombus terrestris*. *Journal of Animal Ecology*
328 78: 247–252.
- 329 Kuhlmann M, Guo D, Veldtman R, Donaldson J. 2012. Consequences of warming up
330 a hotspot: Species range shifts within a centre of bee diversity. *Diversity and*
331 *Distributions* 18: 885–897.

332 Lecocq T, Lhomme P, Michez D, Dellicour S, Valterová I, Rasmont P. 2011.
333 Molecular and chemical characters to evaluate species status of two cuckoo
334 bumblebees: *Bombus barbutellus* and *Bombus maxillosus* (Hymenoptera,
335 Apidae, Bombini). *Systematic Entomology* 36: 453–469.

336 Lecocq T, Dellicour S, Michez D, Lhomme P, Vanderplanck M, Valterova I, Rasplus
337 JY, Rasmont P. 2013a. Scent of a break-up: phylogeography and reproductive
338 trait divergences in the red-tailed bumblebee (*Bombus lapidarius*). *BMC*
339 *Evolutionary Biology* 13:263. doi: 10.1186/1471-2148-13-263

340 Lecocq T, Vereecken N, Michez D, Dellicour S, Lhomme P, Valterová I, Rasplus JY,
341 Rasmont P. 2013b. Patterns of genetic and reproductive traits differentiation in
342 Mainland vs. Corsican populations of bumblebees. *PLoS One* 8:e65642. doi:
343 10.1371/journal.pone.0065642

344 Lecocq T, Brasero N, De Meulemeester T, Michez D, Dellicour S, Lhomme P, de
345 Jonghe R, Valterová I, Urbanová K, Rasmont P. 2014. An integrative
346 taxonomic approach to assess the status of Corsican bumblebees: implications
347 for conservation. *Animal Conservation*. in press. DOI: 10.1111/acv.12164.

348 Lecocq T, Dellicour S, Michez D, Dehon M, Dewulf A, De Meulemeester T, Brasero
349 N, Valterová I, Rasplus JY, Rasmont P. Methods for species delimitation in
350 bumblebees (Hymenoptera, Apidae, *Bombus*): towards an integrative
351 approach. *Zoologica Scripta*. in press.

352 Lepais O, Darvill B, O'Connor S, Osborne JL, Sanderson RA, Cussans J, Goffe L,
353 Goulson D. 2010. Estimation of bumblebee queen dispersal distances using
354 sibship reconstruction method. *Molecular Ecology* 19: 819–831.

355 Levchenko TV. 2012. Materialy po faune pchel (Hymenoptera: Apoidea) Moskovskoj
356 oblasti. 3. Semejstvo Apidae. Rod *Bombus* Latreille, 1802. [Contributions to

357 the fauna of bees (Hymenoptera: Apoidea) of Moscow Province. 3. Family
358 Apidae. Genus *Bombus* Latreille, 1802]. *Eversmannia* 31/32: 72-88 (In
359 Russian).

360 Løken A. 1973. Studies on Scandinavian bumble bees (Hymenoptera, Apidae). *Norsk*
361 *Entomologisk Tidsskrift* 20: 1–218.

362 Løken A. 1978. Notes on the Scandinavian fauna of social Aculeates (Hym., Vespidae
363 and Apidae s.s.). *Norwegian Journal of Entomology Tidsskrift* 25: 165-170

364 Løken A. 1984. Scandinavian species of the genus *Psithyrus* Lepeletier
365 (Hymenoptera: Apidae). *Entomologica Scandinavica*, suppl. 23: 1-45.

366 Martinet B, Lecocq T, Smet J, Rasmont P. 2015. A protocol to assess insect resistance
367 to heat waves, applied to bumblebees (*Bombus* Latreille, 1802), PLOS ONE, in
368 press

369 Macdonald MA. 2014. Buff-tailed Bumblebee *Bombus terrestris* in
370 Shetland. *BWARS Newsletter* 20: 20-22.

371 Meeus I, Brown MJF, De Graaf DC, Smagghe G. 2011. Effects of Invasive Parasites
372 on Bumble Bee Declines. *Conservation Biology* 25: 662–671.

373 Murray TE, Coffey MF, Kehoe E, Horgan FG. 2013. Pathogen prevalence in
374 commercially reared bumble bees and evidence of spillover in conspecific
375 populations. *Biological Conservation* 159: 269–276. doi:
376 10.1016/j.biocon.2012.10.021.

377 Nagamitsu T, Yamagishi H, Kenta T, Inari N, Kato E. 2010. Competitive effects of
378 the exotic *Bombus terrestris* on native bumble bees revealed by a field
379 removal experiment. *Population Ecology* 52: 123–136.

380 Owen R. E, Otterstatter MC, Carter RV, Farmer A, Colla SR, O'Toole
381 N. 2012. Significant expansion of the distribution of the bumble bee *Bombus*

382 *moderatus* (Hymenoptera: Apidae) in Alberta over twenty years. Canadian
383 Journal of Zoology 90: 133–138.

384 Panfilov D.V. 1957. Shmeli (Bombidae) Moskovskoj oblasti. [The bumble bees
385 (Bombidae) of the Moscow province]. Uchenye Zapiski moskovskogo
386 gorodskogo pedagogicheskogo instituta V.P. Potemkina 65(6): 191–219 (In
387 Russian).

388 Paukkunen J. & Kozlov, M. V. 2015. Stinging wasps, ants and bees (Hymenoptera:
389 Aculeata) of the Murmansk region, Northwest Russia. – Entomologica
390 Fennica 26, in press.

391 Parmesan C, Yohe G. 2003. A globally coherent fingerprint of climate change
392 impacts across natural systems. Nature 421: 37–42. doi: 10.1038/nature01286.

393 Pekkarinen A, Teräs I, Viramo J, Paatela J 1981. Distribution of bumblebees
394 (Hymenoptera, Apidae: *Bombus* and *Psithyrus*) in eastern
395 Fennoscandia. Notulae Entomologicae 61: 71–89.

396 Pekkarinen A, Kaarnama E. 1994. *Bombus terrestris* auct. new to Finland
397 (Hymenoptera, Apidae). Sahlbergia 1: 11–13.

398 Pradervand J-N, Pellissier L, Rossier L, Dubuis A, Guisan A, Cherix D. 2011.
399 Diversity of bumblebees (*Bombus* Latreille, Apidae) in the Alps of the canton
400 Vaud (Switzerland). Mitteilungen der Schweizerischen Entomologischen
401 Gesellschaft 84: 45–66.

402 Rasmont P. 1984. Les bourdons du genre *Bombus* Latreille *sensu stricto* en Europe
403 Occidentale et Centrale (Hymenoptera, Apidae). Spixiana, München 7 : 135–
404 160.

405 Rasmont P, Scholl A, De Jonghe R, Obrecht E, Adamski A. 1986. Identité et
406 variabilité des males de Bourdons du genre *Bombus* Latreille *sensu stricto* en

407 Europe occidentale et centrale (Hymenoptera, Apidae, Bombinae). Revue
408 suisse de zoologie 93: 661–682.

409 Rasmont P. 1988. Monographie écologique et zoogéographique des Bourdons de
410 France et de Belgique (Hymenoptera, Apidae, Bombinae). Thèse de doctorat
411 en Sciences Agronomiques, Gembloux : Faculté des Sciences agronomiques
412 de l'Etat, 310 + LXII p.

413 Rasmont P, Pauly A, Terzo M, Patiny S, Michez D, Iserbyt S, Barbier Y, Haubruge
414 E. 2005. The survey of wild bees (Hymenoptera, Apoidea) in Belgium and
415 France. Roma: Food and agriculture organization of the United Nations,
416 [http://www.gembloux.ulg.ac.be/entomologie-fonctionnelle-et-evolutive/wp-](http://www.gembloux.ulg.ac.be/entomologie-fonctionnelle-et-evolutive/wp-content/uploads/2012/07/1597.pdf)
417 [content/uploads/2012/07/1597.pdf](http://www.gembloux.ulg.ac.be/entomologie-fonctionnelle-et-evolutive/wp-content/uploads/2012/07/1597.pdf).

418 Rasmont P, Coppée A, Michez D, De Meulemeester T. 2008. An overview of the
419 *Bombus terrestris* (L. 1758) subspecies (Hymenoptera: Apidae). Annales de la
420 Société entomologique de France (n. s.) 44 (2): 243–250.

421 Rasmont P, Iserbyt S. 2014. Atlas of the European Bees: genus *Bombus*. 3d Edition.
422 STEP Project. Status Trends Eur Pollinators, Atlas Hymenoptera, Mons,
423 Gembloux. <http://www.zoologie.umh.ac.be/hymenoptera/page.asp?ID=169>.

424 Rasmont P, Franzen M, Lecocq T, Harpke A, Castro L, Cederberg B, Dvorak L,
425 Fitzpatrick U, Gonseth Y, Haubruge E, Mahé G, Manino A, Neumayer J,
426 Ødegaard F, Roberts SPM, Paukkunen J, Pawlikowski T, Reemer M, Straka J,
427 Schweiger O. 2015. Climatic Risk and Distribution Atlas of European
428 Bumblebees. Sofia: Pensoft, 236p.

429 Reinig WF, Rasmont P. 1988. Beitrag zur Kenntnis der Bergwaldhummel
430 *Alpigenobombus wurfleini* (Radoszkowski, 1859) (Hymenoptera, Apidae,
431 Bombinae). Spixiana, München 11(1): 37–67.

432 Richards K W. 1973. Biology of *Bombus polaris* Curtis and *B. hyperboreus*
433 Schönherr at lake Hazen, Northwest Territories (Hymenoptera: Bombini).
434 Quaestiones entomologicae. 9: 115–157.

435 Roberts S. 2012. Information sheet: Tree bee (*Bombus hypnorum*). Hymettus
436 (BWARS).

437 Ruszkowski A. 1971. Food plants and economical importance of *Bombus terrestris*
438 (L.) and *B. lucorum* (L.). Pamietnik Pulawski 47: 215–250.

439 Settele J & al. (Alarm Project). 2005. Alarm: Assessing Large-scale environmental
440 Risks for biodiversity with tested Methods. Ecological Perspectives for
441 Science and Society 14(1): 69–72.

442 Shamurin V F. 1966. Rol' nasekomikh-opilitelei v tundrovikh soobshchestvakh. [*The*
443 *role of insects in tundra communities*]. Organizmi iprirodnayasreda. Voprosi
444 geographii. 69: 98–117. (in Russian).

445 Skorikov AS. 1937. Die grönländischen Hummeln im Aspekte der
446 Zirkumpolarfauna. Entomologiske Meddelelser 20: 37–64.

447 Šima P, Smetana. 2012. *Bombus (Cullumanobombus) semenoviellus* (Hymenoptera:
448 Apidae: Bombini) new species for the bumble bee fauna of Slovakia.
449 Klapalekiana 48: 141–147.

450 Spangenberg J H, Carter T R, Fronzek S, Jaeger J, Jylhä K, Kühn I, Omann I, Paul A,
451 Reginster I, Rounsevell M, Stocker A, Sykes M T, Settele J. 2012. Scenarios
452 for investigating risks to biodiversity. Global Ecology and Biogeography
453 21(1): 5–18.

454 Svenning J-C, Skov F. 2007. Could the tree diversity pattern in Europe be generated
455 by postglacial dispersal limitation? Ecological Letters 10: 453–60. doi:
456 10.1111/j.1461-0248.2007.01038.x.

457 Teper D. 2004. Comparison of food plants of *Bombus terrestris* L. and *Bombus*
458 *lapidarius* L. based on pollen analysis of their pollen loads. Journal of
459 Apicultural Science 49 (2): 43–50.

460 Teräs I. 1985. Food plants and flower visits of bumblebees (*Bombus*: Hymenoptera,
461 Apidae) in southern Finland. Acta Zoologica Fennica 179: 1–120.

462 Thomas C D. 2011. Translocation of species, climate change, and the end of trying to
463 recreate past ecological communities. Trends in Ecology and Evolution 26(5):
464 216–221.

465 van der Smissen, J. & P. Rasmont. 2000. *Bombus semenoviellus* Skorikov 1910, eine
466 für Westeuropa neue Hummelart (Hymenoptera: *Bombus*,
467 *CullumanoBombus*). Bembix 13: 21–24.

468 Velthuis HHW, van Doorn A. 2006. A century of advances in bumblebee
469 domestication and the economic and environmental aspects of its
470 commercialization for pollination. Apidologie 37: 421–451.

471 Williams PH. 1986. Environmental change and the distribution of British bumble bees
472 (*Bombus* Latr.). Bee world. 67(2): pp.50-61.

473 Williams PH. 1991. The bumble bees of the Kashmir Himalaya (Hymenoptera:
474 Apidae, Bombini). Bulletin of the British Museum of Natural
475 History (Entomology). 60: 1–204.

476 Williams PH. 1998. An annotated checklist of bumble bees with an analysis of
477 patterns of description (Hymenoptera: Apidae, Bombini). Bulletin of the
478 British Museum (Natural History). 67: 79–152.

479 Williams PH., Thorp R, Richardson L, Colla S. 2014. Bumble Bees of North
480 America. New Jersey: Princeton University Press, 208 p.

481 Yoon HJ, Sohn MR, Choo YM, Li J, Sohn HD, Jin BR. 2009. Defensing gene
482 sequences of three different bumblebees, *Bombus* spp. Journal of Asia-Pacific
483 Entomology 12: 27-31.