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

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**Summary.** In recent decades, several animal and plant species have been in regression (population size decrease and geographical distribution shrinking). This loss of biodiversity can be due to various factors such as the destruction and fragmentation of habitat, urban development, pesticides or climate change. However, some species benefit from these changes and expand their distribution. Here we report observations (in 2013 and 2014) of two Euro-Mediterranean bumblebee species: *Bombus terrestris* for the first time and *Bombus lapidarius*, north of the Arctic Circle in Fennoscandia.

**Résumé.** Ces dernières décennies, de nombreuses espèces animales et végétales sont en régression autant d'un point de vue de leur distribution qu'au niveau de leur effectif de population. Cette perte de biodiversité peut être due à différents facteurs comme la destruction et la fragmentation de l'habitat, le développement urbain, les pesticides ou encore le changement climatique. Néanmoins, certaines espèces profitent de ces perturbations pour étendre leur distribution. C'est ainsi que pour la première fois, deux espèces Euro-Méditerranéennes de bourdons (*Bombus terrestris* et *Bombus lapidarius*) ont été observées en 2013 et 2014 en Fennoscandie au-delà du Cercle Arctique.

**Keywords:** *Bombus terrestris*; biogeography; climate change; Fennoscandia; heat wave

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

However, their hotspot diversity areas (mountainous, arctic, subarctic and boreal regions) are also regions most

severely affected by global warming (Core Writing Team et al. 2007; Franzén & Molander 2012; Franzén & Ockinger 2012), a phenomenon that will most likely increase during the next decades (Berger & Loutre 1991; Settele et al. 2005; Spangenberg et al. 2012). Climate change poses a major threat to many bumblebee species (Rasmont et al. 2015); however, some are able to benefit and expand their ranges.

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

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2013b). Therefore, an early detection of climatic refugee species through efficient faunistic surveys is important.

We here report the observations of two Euro-Mediterranean bumblebee species (*sensu de Lattin 1967*) north of the Arctic Circle, a region hosting many bumblebee species with restricted areas. Specifically, we hypothesize the potential trigger factors and the potential consequences of the range shift to the north for Arctic biodiversity.

## Materials and methods

### Determination of original northern European bumblebee fauna

We focused on the region north of the Arctic Circle in Fennoscandia. We determined the original Arctic European bumblebee fauna (i.e. baseline dataset) according to (i) literature (Løken 1973) and (ii) occurrence observations before 1973. The occurrence observations were hosted by databases managed by B. Cederberg (Swedish Species Information Centre (SSIC), Sweden); F. Ødegaard (Norwegian Biodiversity Information Centre (NBIC) Norway); J. Paukkunen (Finnish Museum of Natural History (MZH), Finland) and P. Rasmont & E. Haubruge (*Banque de Données Faunique de Gembloux et de Mons* (BDFGM), Belgium). These occurrence datasets were mapped using *Data Fauna Flora* software (Barbier et al. 2014).

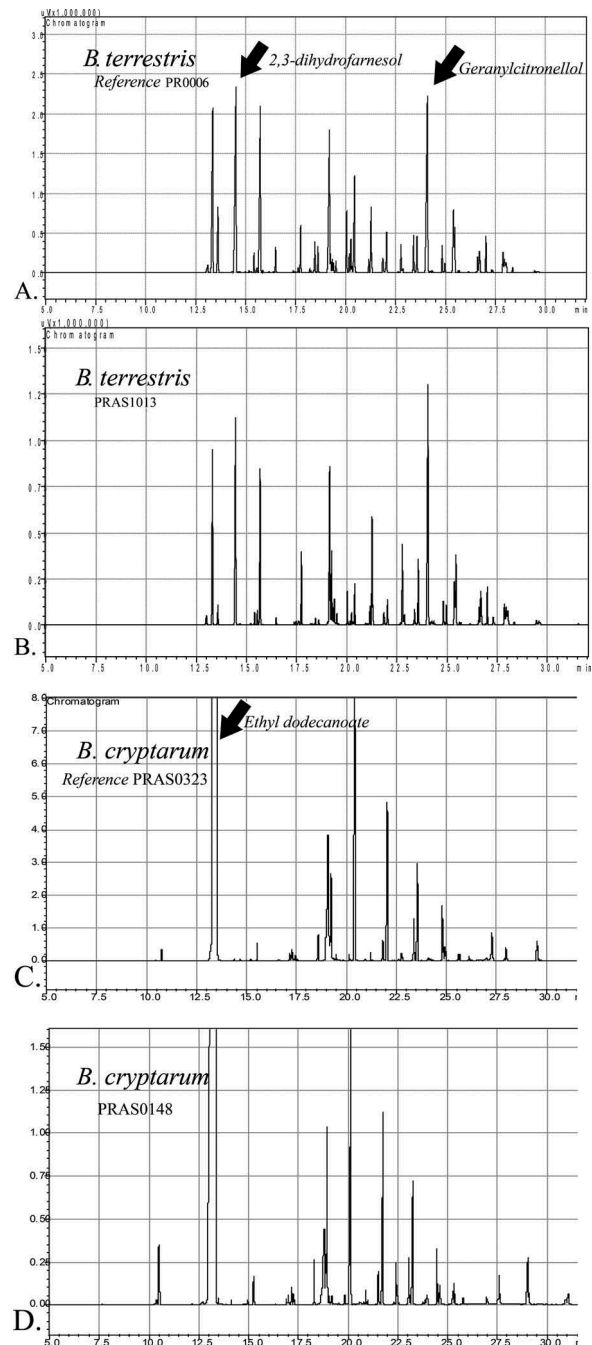
### Detection of expanding species

In order to assess potential changes in the northern European bumblebee fauna, we collected samples north of the Arctic Circle (see sampling map Figure 1) in 2013 and 2014 using entomological sweep nets. All specimens were individually killed by freezing. Males were prepared for chemotaxonomic analyses following De Meulemeester et al. (2011).

The specific identification was verified by checking different morphological diagnostic characters (Løken 1973, 1984; Rasmont 1984; Rasmont et al. 1986; Pekkarinen & Kaarnama 1994). For the species belonging to the subgenus *Bombus sensu stricto* (Cameron et al. 2007), a group with low morphological differentiation, the morphological characters based on identification were verified by comparing the GC-FID chromatograms of cephalic labial gland secretions (Lecocq et al. 2011) with reference specimens (*Bombus terrestris*: PRAS0006 from France, Var, Gonfaron 3.VII.2008, 43° 18'N 06°18'E; *Bombus cryptarum*: PRAS0148 from Sweden, Jämtland, Kvisle 15.VIII.2008, 63°16'N 13°56'E; PRAS0323 from Scotland, Wick, Wireless 12.VIII.2009, 58°28'N 3°13'W, see Figure 1) and with the list of compounds given by Bertsch and Schweer (2012a, 2012b). The cephalic labial gland secretions are commonly used as diagnostic characters (Bertsch & Schweer 2012a). We followed the preparation and analysis methods of De Meulemeester et al. (2011), Lecocq et al. (2011, 2015a, 2015b) and Brasero et al. (2015).

## Results

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



**Figure 1.** GC-FID chromatograms of *Bombus sensu stricto* males. **A**, Reference specimen of *B. terrestris* (PRAS0006, Lecocq et al. 2013b). **B**, *Bombus terrestris* male PRAS1013 (Narvik). **C**, Specimen of *B. cryptarum* male PRAS0323. **D**, *B. cryptarum* male PRAS0148 (Jämtland, Sweden).

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

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

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

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

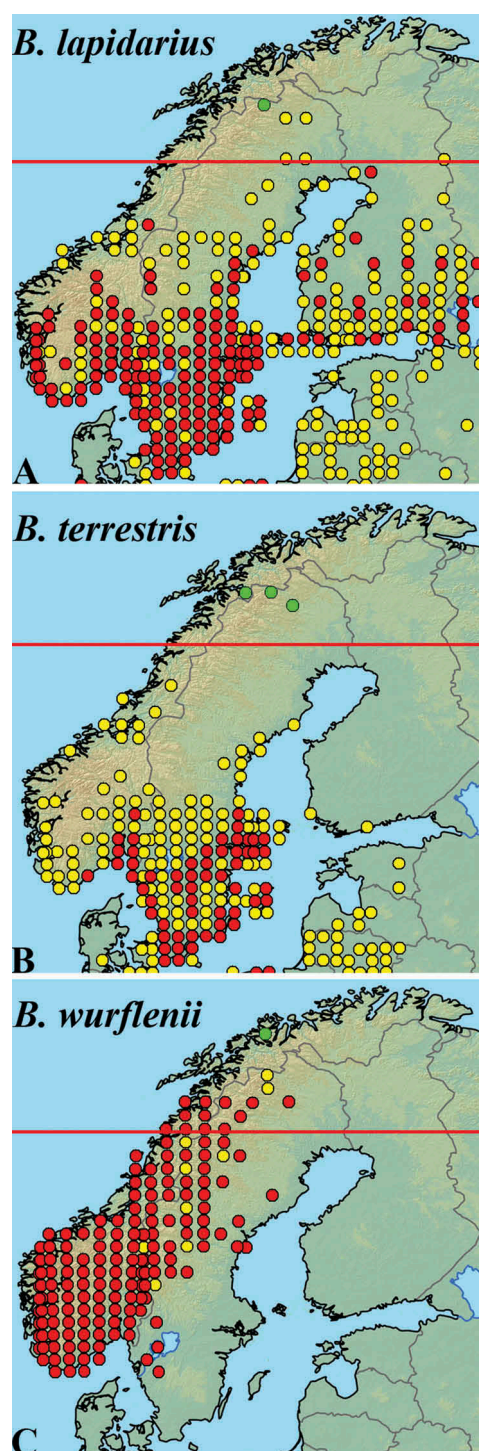
The comparison between the distribution of these species in the baseline dataset (Løken 1973) and our new occurrence observations shows that *B. lapidarius* occurs now 400 km north of its 1973 limits; *B. terrestris* occurs 800 km north of its 1973 limits and *B. wurflenii* now occurs 200 km north of its 1973 limits. All previous reports of *B. lapidarius* and *B. terrestris* from north of the Arctic Circle (Figures 2A and B) are of dubious provenance or unverified (see Discussion).

## Discussion

### Toward a new Arctic bumblebee fauna?

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

In Fennoscandia, our results show an obvious change in the northern European bumblebee fauna since the 1970s. The main change is the expansion of two Euro-Mediterranean species (*B. lapidarius* and *B. terrestris*) beyond the Arctic Circle. In the 1970s, the northern limit of *B. terrestris* barely reached north of Uppsala (60° N) in Sweden or Hamar (north Oslo, 60°50' N) in Norway, while *B. lapidarius* was reaching higher latitudes, at the southernmost margin of the boreal taiga forest (Løken 1973). Our recent observations show that both species now reach the 68° N latitude, whereby they have crossed the Arctic Circle. It is important to note that several specimens of *B. lapidarius* have been collected in north Sweden before our sampling in 1976 (Løken 1978). This year corresponds to the most extreme climatic event (heat



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



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

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

The expansion of *B. veteranus* and *B. wurflenii* beyond the Arctic Circle could most likely be explained by the cold adaptations of these species (Løken 1973; Reinig & Rasmont 1988) and climate change. In contrast, *B. lapidarius* and *B. terrestris* are Euro-Mediterranean bumblebees. Indeed, *B. terrestris* is abundant all around the Mediterranean coast and reaches its southern limits on the edges of the Sahara (Rasmont et al. 2008). *B. lapidarius* has not been found as far south and it does not live on the Mediterranean coast, but it reaches the Atlas Mountains in Morocco (Rasmont & Iserbyt 2014). Therefore, we suggest that the current global climate warming in northern regions could be the trigger factor of the expansion of such a species, as observed in other organisms (Rasmont et al. 2015).

An alternative hypothesis is that the Euro-Mediterranean species have not achieved equilibrium with their current environment (Svenning & Skov 2007) and are still continuing their post Ice-Age expansion (Lecocq et al. 2013a). However, the high dispersal ability of several bumblebee species such as *B. lapidarius* and *B. terrestris* (Kraus et al. 2009; Lepais et al. 2010), the long term occurrence of these species in surrounding regions (Rasmont & Iserbyt 2014), as well as their phylogeographic structure (i.e. endemic haplotypes and high genetic diversity in Fennoscandia at least for *B. lapidarius*; Lecocq et al. 2013a, 2013b) make this hypothesis unlikely. Further studies on bumblebee climatic

niches are needed to assess the role of climate change as a trigger factor of Euro-Mediterranean species expansion to cold regions. Higher temperature and successful reproduction probably also stimulate dispersal of queens. And finally, since *B. terrestris* is widely used and internationally traded for crop pollination, we cannot exclude that the collected *B. terrestris* individuals could have escaped from greenhouses. However, we did not observe any greenhouses in the surroundings of our study areas, the nearest ones being certainly more than 50 km distant.

### Consequences for Arctic species conservation

Besides the understanding of factors triggering expansion, the consequences of the expansion of *B. terrestris* and *B. lapidarius* should be taken into account in local bumblebee conservation management. It remains to assess how *B. lapidarius* and *B. terrestris* could compete with the original high latitude bumblebee fauna where they forage side-by-side. However, both species are known for their large colonies (Holm 1960; Velthuis & van Doorn 2006) and for their high opportunism in foraging plant selection (Ruszkowski 1971; Teräs 1985; Rasmont 1988; Teper 2004). On the other hand, Arctic bumblebee species only establish small colonies with a low number of offspring (Løken 1973; Richards 1973; Berezin 1994, 1995). Therefore, Arctic bumblebee species already impacted by climatic stress (Franzén & Molander 2012; Franzén & Ockinger 2012; Martinet et al. 2015) could suffer from a drastic competition from the new Euro-Mediterranean invaders. As we are at the very initial stages of colonization of these species, it is, as yet, difficult to project the future situation.

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## References

- Aizen MA, Lozada M, Morales CL. 2011. Comparative nectar-foraging behaviors and efficiencies of an alien and a native bumble bee. *Biological Invasions*. 13:2901–2909.
- Alford DV. 1975. *Bumblebees*. London: Davis-Poynter; 352 p.
- Arbetman MP, Meeus I, Morales CL, Alzen MA, Smagghe G. 2013a. Co-introduction and spillover of parasites by invasive *Bombus terrestris*. Bumblebee's chauffer hitchhike alien parasites when traveling to Patagonia, Argentina. *Biological Invasions*. 15:489–494.
- Arbetman MP, Meeus I, Morales CL, Alzen MA, Smagghe G. 2013b. Alien parasite hitchhikes to Patagonia on invasive bumblebee. *Biological Invasions*. 15:489–494.
- Barbier Y, Rasmont P, Dufrene M, Sibert JM. 2014. Data fauna flora [Internet]. Mons (Belgique): Université de Mons-Hainaut. Available from: <http://hdl.handle.net/2268/148255>
- Berezin MV. 1994. Social organization of the bumblebees (Hymenoptera, Apoidea, *Bombus*) in the Arctic (Wrangel island). In: Lenoir A, Arnold G, Lepage M, editors. *Les insectes sociaux*, 12th Congress of the IUSSI-UIEIS, Paris, p. 320.
- Berezin MV. 1995. Geographical diversity, species correlation, population structure and cenotic interactions of Arctic bumble bees (Apidae, *Bombus*). In: Grönlund E, Melander O, editors. *Swedish-Russian tundra ecology. Expedition-94*. Stockholm: Swedish Polar Research Secretariat; p. 205–215.
- Berger A, Loutre MF. 1991. Insolation values for the climate of the last 10 million years. *Quaternary Science Reviews*. 10:297–317.
- Bertsch A, Schweer H. 2012a. Male labial gland secretions as species recognition signals in species of *Bombus*. *Biochemical Systematics and Ecology*. 40:103–111.
- Bertsch A, Schweer H. 2012b. Cephalic labial gland secretions of males as species recognition signals in bumblebees: are there really geographical variations in the secretions of the *Bombus terrestris* subspecies? (Hymenoptera: Apidae: *Bombus*). *Beiträge zur Entomologie*. 62:103–124.
- Brasero N, Martinet B, Urbanová K, Valterová I, Torres A, Hoffmann W, Rasmont P, Lecocq T. 2015. First chemical analysis and characterization of the male species-specific cephalic labial-gland secretions of South American bumblebees. *Chemistry & Biodiversity*. 12:1535–1546.
- Cameron SA, Hines HM, Williams PH. 2007. A comprehensive phylogeny of the bumble bees (*Bombus*). *Biological Journal of the Linnean Society*. 91:161–188.
- Cameron SA, Lozier JD, Strange JP, Koch JB, Cordes N, Solter LF, Griswold TL. 2011. Patterns of widespread decline in North American bumble bees. *Proceedings of the National Academy of Sciences*. 108:662–667.
- Cederberg B. 2013. Artfaktblad *Bombus veteranus sandhumla* [Internet]. Uppsala (Sweden): Artdatabanken, SLU; [cited 2015 Sept 16]. Available from: <http://artfakta.artdatabanken.se/taxon/102704>
- Chen IC, Hill JK, Ohlemüller R, Roy DB, Thomas CD. 2011. Rapid range shifts of species associated with high levels of climate warming. *Science*. 333:1024–1026.
- Core Writing Team, Pachauri RK, Reisinger A, editors. 2007. *Contribution of working groups I, II and III to the fourth assessment report of the Intergovernmental Panel on Climate Change*. Geneva (Switzerland): IPCC, 104 p.
- de Lattin G. 1967. *Grundriss der Zoogeographie*. Iena (Stuttgart): Gustav Fisher; 602 p.
- De Meulemeester T, Gerbaux P, Boulvin M, Coppée A, Rasmont P. 2011. A simplified protocol for bumble bee species identification by cephalic secretion analysis. *Insectes Sociaux*. 58:227–236.
- Elfving R. 1968. Die Bienen Finnlands. *Fauna Fennica*. 21:1–69.
- Finnish Meteorological Institute. 2013. June was exceptionally warm [cited 2015 Feb 13]. Available from: <http://en.ilmatieenlaitos.fi/press-release/730379>.
- Finnish Meteorological Institute. 2014. An exceptionally long heatwave [cited 2015 Feb 13]. Available from: <http://en.ilmatietaenlaitos.fi/press-release/10014539>.
- Franzén M, Molander M. 2012. How threatened are alpine environments? A cross taxonomic study. *Biodiversity and Conservation*. 21:517–526.
- Franzén M, Ockinger E. 2012. Climate-driven changes in pollinator assemblages during the last 60 years in an Arctic mountain region in Northern Scandinavia. *Journal of Insect Conservation*. 16:227–238.
- Gonzalez VH, Ospina M, Bennett D. 2005. *Abejas altoandinas de Colombia: Guía de campo*. Bogotá: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt; 80 p.
- Heinrich B. 1979. *Bumblebee economics*. Cambridge (MA): Harvard University Press; 256 p.
- Holm SN. 1960. Experiments on the domestication of bumblebees (*Bombus* Latr.) in particular *B. lapidarius* L. and *B. terrestris* L. Copenhagen: Royal Veterinary and Agriculture College, Yearbook 1960, p. 1–19.
- Inoue MN, Yokoyama J, Washitani I. 2008. Displacement of Japanese native bumblebees by the recently introduced *Bombus terrestris* (L.) (Hymenoptera: Apidae). *Journal of Insect Conservation*. 12:135–146.
- Iserbyt S, Rasmont P. 2012. The effect of climatic variation on abundance and diversity of bumblebees: a ten years survey in a mountain hotspot. *Annales de la Société entomologique de France* (n.s.). 48:261–273.
- Jenič A, Gogala A, Grad J. 2010. *Bombus haematurus* (Hymenoptera: Apidae), new species in the Slovenian bumblebee fauna. *Acta entomologica slovenica*. 18:168–170.
- Kanbe Y, Okada I, Yoneda M, Goka K, Tsuchida K. 2008. Interspecific mating of the introduced bumblebee *Bombus terrestris* and the native Japanese bumblebee *Bombus hypocrita sapporoensis* results in inviable hybrids. *Naturwissenschaften*. 95:1003–1008.
- Kevan PG. 1973. Flowers, insects, and pollination ecology in the Canadian high Arctic. *Polar Record*. 16:667–674.
- Klein T. 2009. Comparaison des sécheresses estivales de 1976 et 2003 en Europe occidentale à l'aide d'indices climatiques. *Bulletin de la Société géographique de Liège*. 53:75–86.
- Klok CJ, Chown SL. 2003. Resistance to temperature extremes in sub-Antarctic weevils, interspecific variation, population differentiation and acclimation. *Biological Journal of the Linnean Society*. 78:401–414.
- Kraus FB, Wolf S, Moritz RFA. 2009. Male flight distance and population substructure in the bumblebee *Bombus terrestris*. *Journal of Animal Ecology*. 78:247–252.
- Kuhlmann M, Guo D, Veldtman R, Donaldson J. 2012. Consequences of warming up a hotspot: species range shifts within a centre of bee diversity. *Diversity and Distributions*. 18:885–897.
- Lecocq T, Brasero N, De Meulemeester T, Michez D, Dellicour S, Lhomme P, de Jonghe R, Valterová I, Urbanová K, Rasmont P. 2015a. An integrative taxonomic approach to assess the status of Corsican bumblebees: implications for conservation. *Animal Conservation*. 18:236–248.

- Lecocq T, Dellicour S, Michez D, Dehon M, Dewulf A, De Meulemeester T, Brasero N, Valterová I, Rasplus JY, Rasmont P. 2015b. Methods for species delimitation in bumblebees (Hymenoptera, Apidae, *Bombus*): towards an integrative approach. *Zoologica Scripta*. 44:281–297.
- Lecocq T, Dellicour S, Michez D, Lhomme P, Vanderplanck M, Valterova I, Rasplus JY, Rasmont P. 2013a. Scent of a break-up: phylogeography and reproductive trait divergences in the red-tailed bumblebee (*Bombus lapidarius*). *BMC Evolutionary Biology*. 13:263.
- Lecocq T, Lhomme P, Michez D, Dellicour S, Valterová I, Rasmont P. 2011. Molecular and chemical characters to evaluate species status of two cuckoo bumblebees: *Bombus barbutellus* and *Bombus maxillosus* (Hymenoptera, Apidae, Bombini). *Systematic Entomology*. 36:453–469.
- Lecocq T, Vereecken N, Michez D, Dellicour S, Lhomme P, Valterová I, Rasplus JY, Rasmont P. 2013b. Patterns of genetic and reproductive traits differentiation in Mainland vs. Corsican populations of bumblebees. *PLoS One*. 8: e65642.
- Lepais O, Darvill B, O'connor S, Osborne JL, Sanderson RA, Cussans J, Goffe L, Goulson D. 2010. Estimation of bumblebee queen dispersal distances using sibship reconstruction method. *Molecular Ecology*. 19:819–831.
- Levchenko TV. 2012. Materialy po faune pchel (Hymenoptera: Apoidea) Moskovskoj oblasti. 3. Semejstvo Apidae. Rod *Bombus* Latreille, 1802 [Contributions to the fauna of bees (Hymenoptera: Apoidea) of Moscow Province. 3. Family Apidae. Genus *Bombus* Latreille, 1802]. *Eversmannia*. 31/32:72–88. (In Russian).
- Løken A. 1973. Studies on Scandinavian bumble bees (Hymenoptera, Apidae). *Norsk Entomologisk Tidsskrift*. 20:1–218.
- Løken A. 1978. Notes on the Scandinavian fauna of social Aculeates (Hym., Vespidae and Apidae s.s.). *Norwegian Journal of Entomology Tidsskrift*. 25:165–170.
- Løken A. 1984. Scandinavian species of the genus *Psithyrus* Lepeletier (Hymenoptera: Apidae). *Entomologica Scandinavica*. suppl. 23:1–45.
- Macdonald MA. 2014. Buff-tailed Bumblebee *Bombus terrestris* in Shetland. *BWARS Newsletter*. 20:20–22.
- Martinet B, Lecocq T, Smet J, Rasmont P. 2015. A protocol to assess insect resistance to heat waves, applied to bumblebees (*Bombus Latreille*, 1802). *PLOS ONE*. 10:e0118591.
- Meeus I, Brown MJF, De Graaf DC, Smagge G. 2011. Effects of Invasive Parasites on Bumble Bee Declines. *Conservation Biology*. 25:662–671.
- Murray TE, Coffey MF, Kehoe E, Horgan FG. 2013. Pathogen prevalence in commercially reared bumble bees and evidence of spillover in conspecific populations. *Biological Conservation*. 159:269–276.
- Nagamitsu T, Yamagishi H, Kenta T, Inari N, Kato E. 2010. Competitive effects of the exotic *Bombus terrestris* on native bumble bees revealed by a field removal experiment. *Population Ecology*. 52:123–136.
- Owen RE, Otterstatter MC, Carter RV, Farmer A, Colla SR, O'toole N. 2012. Significant expansion of the distribution of the bumble bee *Bombus moderatus* (Hymenoptera: Apidae) in Alberta over twenty years. *Canadian Journal of Zoology*. 90:133–138.
- Panfilov DV. 1957. Shmeli (Bombidae) Moskovskoj oblasti [The bumble bees (Bombidae) of the Moscow province]. *Uchenye Zapiski moskovskogo gorodskogo pedagogicheskogo instituta V.P. Potemkina* 65(6):191–219. (In Russian).
- Parmesan C, Yohe G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature*. 421:37–42.
- Paukkunen J, Kozlov MV. 2015. Stinging wasps, ants and bees (Hymenoptera: Aculeata) of the Murmansk region, Northwest Russia. *Entomologica Fennica*. 26:53–73.
- Pekkarinen A, Kaarnama E. 1994. *Bombus terrestris* auct. new to Finland (Hymenoptera, Apidae). *Sahlbergia*. 1:11–13.
- Pekkarinen A, Teräs I, Viramo J, Paatela J. 1981. Distribution of bumblebees (Hymenoptera, Apidae: *Bombus* and *Psithyrus*) in eastern Fennoscandia. *Notulae Entomologicae*. 61:71–89.
- Pradervand JN, Pellissier L, Rossier L, Dubuis A, Guisan A, Cherix D. 2011. Diversity of bumblebees (*Bombus* Latreille, Apidae) in the Alps of the canton Vaud (Switzerland). *Mitteilungen der Schweizerischen Entomologischen Gesellschaft*. 84:45–66.
- Rasmont P. 1984. Les bourdons du genre *Bombus* Latreille *sensu stricto* en Europe Occidentale et Centrale (Hymenoptera, Apidae). *Spixiana*, München. 7:135–160.
- Rasmont P. 1988. Monographie écologique et zoogéographique des Bourdons de France et de Belgique (Hymenoptera, Apidae, Bombinae) [Thèse de doctorat en Sciences Agronomiques]. Gembloux: Faculté des Sciences agronomiques de l'Etat; 310 + LXII p.
- Rasmont P, Coppée A, Michez D, De Meulemeester T. 2008. An overview of the *Bombus terrestris* (L. 1758) subspecies (Hymenoptera: Apidae). *Annales de la Société Entomologique de France* (n. s.). 44:243–250.
- Rasmont P, Franzen M, Lecocq T, Harpke A, Castro L, Cederberg B, Dvorak L, Fitzpatrick U, Gonseth Y, Haubruge E, et al. 2015. Climatic risk and distribution atlas of European bumblebees. Sofia: Pensoft; 236 p.
- Rasmont P, Iserbyt S. 2014. Atlas of the European Bees: genus *Bombus*. 3d Edition. STEP Project. Status Trends Eur Pollinators, Atlas Hymenoptera, Mons, Gembloux. Available from: <http://www.zoologie.umh.ac.be/hymenoptera/page.asp?ID=169>.
- Rasmont P, Pauly A, Terzo M, Patiny S, Michez D, Iserbyt S, Barbier Y, Haubruge E. 2005. The survey of wild bees (Hymenoptera, Apoidea) in Belgium and France [Internet]. Roma: Food and agriculture organization of the United Nations. Available from: <http://www.gembloux.ulg.ac.be/entomologie-fonctionnelle-et-evolutive/wp-content/uploads/2012/07/1597.pdf>
- Rasmont P, Scholl A, De Jonghe R, Obrecht E, Adamski A. 1986. Identité et variabilité des mâles de bourdons du genre *Bombus* Latreille *sensu stricto* en Europe occidentale et centrale (Hymenoptera, Apidae, Bombinae). *Revue Suisse de Zoologie*. 93:661–682.
- Reinig WF, Rasmont P. 1988. Beitrag zur Kenntnis der Bergwaldhummel *Alpigenobombus wurfleini* (Radoszkowski, 1859) (Hymenoptera, Apidae, Bombinae). *Spixiana*, München. 11:37–67.
- Richards KW. 1973. Biology of *Bombus polaris* Curtis and *B. hyperboreus* Schönherr at lake Hazen, Northwest Territories (Hymenoptera: Bombini). *Quaestiones entomologicae*. 9:115–157.
- Roberts S. 2012. Information sheet: tree bee (*Bombus hypnorum*) [Internet]. Hymettus (BWARS). [cited 2015 Oct 31]. Available from: [http://www.bwars.com/sites/www.bwars.com/files/info\\_sheets/03\\_Bombus\\_hypnorum\\_20120321.pdf](http://www.bwars.com/sites/www.bwars.com/files/info_sheets/03_Bombus_hypnorum_20120321.pdf)
- Ruszkowski A. 1971. Food plants and economical importance of *Bombus terrestris* (L.) and *B. lucorum* (L.). *Pamiętnik Pulawski*. 47:215–250.

- Settele J, Hammen V, Hulme P, Karlson U, Klotz S, Kotarac M, Kunin W, Marion G, O'connor M, Petanidou T, et al. 2005. Alarm: assessing large-scale environmental risks for biodiversity with tested methods. *Ecological Perspectives for Science and Society*. 14:69–72.
- Shamurin VF. 1966. Rol' nasekomikh-opilitelei v tundrovikh soobshchestvakh [The role of insects in tundra communities]. *Organizmi iprirodnayasreda. Voprosi geographii*. 69:98–117. (In Russian).
- Šima P, Smetana V. 2012. *Bombus* (Cullumanobombus) *semenoviellus* (Hymenoptera: Apidae: Bombini) new species for the bumble bee fauna of Slovakia. *Klapalekiana*. 48:141–147.
- Skorikov AS. 1937. Die grönländischen Hummeln im Aspekte der Zirkumpolarfauna. *Entomologiske Meddelelser*. 20:37–64.
- Spangenberg JH, Carter TR, Fronzek S, Jaeger J, Jylhä K, Kühn I, Omann I, Paul A, Reginster I, Rounsevell M, et al. 2012. Scenarios for investigating risks to biodiversity. *Global Ecology and Biogeography*. 21:5–18.
- Svenning J-C, Skov F. 2007. Could the tree diversity pattern in Europe be generated by postglacial dispersal limitation? *Ecology Letters*. 10:453–460.
- Teper D. 2004. Comparison of food plants of *Bombus terrestris* L. and *Bombus lapidarius* L. based on pollen analysis of their pollen loads. *Journal of Apicultural Science*. 49:43–50.
- Teräs I. 1985. Food plants and flower visits of bumblebees (*Bombus*: Hymenoptera, Apidae) in southern Finland. *Acta Zoologica Fennica*. 179:1–120.
- Thomas CD. 2011. Translocation of species, climate change, and the end of trying to recreate past ecological communities. *Trends in Ecology & Evolution*. 26:216–221.
- van der Smitsen J, Rasmont P. 2000. *Bombus semenoviellus* Skorikov 1910, eine für Westeuropa neue Hummelart (Hymenoptera: *Bombus*, *CullumanoBombus*). *Bembix*. 13:21–24.
- Velthuis HHW, van Doorn A. 2006. A century of advances in bumblebee domestication and the economic and environmental aspects of its commercialization for pollination. *Apidologie*. 37:421–451.
- Williams PH. 1986. Environmental change and the distributions of British bumble bees (*Bombus* Latr.). *Bee World*. 67:50–61.
- Williams PH. 1991. The bumble bees of the Kashmir Himalaya (Hymenoptera: Apidae, Bombini). *Bulletin of the British Museum of Natural History (Entomology)*. 60:1–204.
- Williams PH. 1998. An annotated checklist of bumble bees with an analysis of patterns of description (Hymenoptera: Apidae, Bombini). *Bulletin of the British Museum (Natural History)*. 67:79–152.
- Williams PH, Thorp R, Richardson L, Colla S. 2014. *Bumble bees of north America*. Princeton (NJ): Princeton University Press; 208 p.
- Yoon HJ, Sohn MR, Choo YM, Li J, Sohn HD, Jin BR. 2009. Defensin gene sequences of three different bumblebees, *Bombus* spp. *Journal of Asia-Pacific Entomology*. 12:27–31.