

Endangered by laws: potential consequences of regulations against thistles on bumblebee conservation

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1 Endangered by laws: potential consequences of regulations against thistles

2 on bumblebee conservation

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Summary

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- Many Bumblebee (*Bombus*) species are undergoing a strong decline in Europe due to, 30 amongst other things, a decrease of food resources. While leguminous plants (Fabaceae) are 31 32 considered to be one of the main pollen sources of bumblebees, thistles (Asteraceae tribe Cardueae) have been suggested to be important for male diet. Yet, several European countries 33 apply strict regulations against thistles since they are considered to be one of the principal 34 35 weeds in agricultural landscapes. Such regulations could impact bumblebee conservation through disruption of male diet and ecology. Here, we assess the male-depending importance 36 37 of thistles for bumblebee species based on field observations across countries where a legal regulation against thistles is in effect. We ultimately aim to evaluate the potential 38 consequences of these regulations on bumblebee conservation. Our results confirm that most 39 40 of floral visit observations of males occur on thistles (mainly *Cirsium* spp. and *Carduus* spp.) 41 and some species are almost exclusively observed on them. Thistle removal is thus most likely a threat for bumblebees. Therefore, we advocate repealing the thistle removal acts to 42 43 make way for alternative thistle regulations which reconcile biodiversity conservation and agricultural requirements. 44
- 45 Résumé. Menacé par des lois : les conséquences potentielles des législations
- 46 d'échardonnage sur la conservation des bourdons.
 - Les bourdons sont en régression en Europe, en partie à cause d'une diminution de leurs ressources alimentaires. Alors que les légumineuses sont considérées comme étant une des principales sources de pollen pour les bourdons, les chardons (Asteraceae, tribu des Cardueae) ont été suggérés comme étant importants pour l'alimentation des mâles. Pourtant, plusieurs pays européens appliquent des règles législatives strictes contre les chardons car ils sont considérés comme étant des « mauvaises herbes » majeures dans le paysage agricole. De

telles régulations pourraient avoir un impact sur la conservation des bourdons à travers la perturbation de l'alimentation et de l'écologie des mâles. Ici, nous estimons l'importance des chardons pour les mâles d'espèces de bourdons en se basant sur des observations sur le terrain dans les différents pays où un règlement d'échardonnage est en vigueur. Notre objectif est d'évaluer les conséquences potentielles de ces règlements sur la conservation des bourdons. Nos résultats confirment que la plupart des visites florales des mâles sont observées sur les chardons (principalement *Cirsium* spp. et *Carduus* spp.) et que certaines espèces sont presque exclusivement observées sur ces plantes. La suppression des chardons constitue donc très probablement une menace pour les bourdons. Par conséquent, nous préconisons d'abroger les lois d'échardonnage pour faire place à des réglementations alternatives qui concilient la conservation de la biodiversité et les besoins agricoles.

- **Keywords**: *Bombus*, Cardueae, *Carduus*, *Cirsium*, floral resources, pollinator conservation,
- 65 weed control legislation.

Introduction

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Almost 90 percent of all flowering plant species are pollinated by animals (Ollerton et al. 67 2011). In cold and temperate regions of the Northern Hemisphere, the social species group of 68 69 bumblebees (*Bombus* spp.) is the main pollinating agent (Heinrich 1979). However, many 70 species are experiencing a strong population decline and range contraction fostered by landscape modifications and fragmentation, intensive use of agrochemicals, pathogen 71 72 infections, competition with alien species, climate change, reduction in floral resources, and interactions between all these factors (Goulson et al. 2005). Conservation actions have been 73 developed to ensure bumblebee survival and to avoid a major disruption of pollination 74 service. One strategy aims to mitigate the current qualitative and quantitative reduction in 75 floral resources (e.g. Carvell et al. 2007; Kleijn & Raemakers 2008; Scheper et al. 2014) 76 77 because bumblebees require a long term flowering and a large diversity in plant species (Persson & Smith 2013; Rundlöf et al. 2014). Determining the most important plants for 78 bumblebee diet and ecology is therefore essential to plan efficient conservation management. 79 Several studies based on field observations have pointed out that leguminous plants 80 (Fabaceae) are among the main pollen sources for bumblebees, especially for scarcer species 81 82 (Rasmont & Mersch 1988; Goulson et al. 2005, 2008). However, most of these assessments consider only the worker caste. Since workers are often the most abundant caste during field 83 studies, floral preferences of other castes could be blurred. Yet, other caste requirements are 84 thought to be different (Goulson 2010). For instance, some studies have suggested the 85 importance of thistles (Asteraceae tribe Cardueae; Tree of Life Web Project 2009) for male 86 87 diet at regional scales (e.g. Croxton et al. 2002; Pywell et al. 2005; Carvell et al. 2006). Yet, several European countries apply strict legal regulations against thistles, aimed at curbing 88 flowering, development and seed dispersal since they are considered to be noxious weeds in 89 90 the agricultural landscape (Table 1). Under the assumption of the importance of thistles for

- bumblebees, such regulations could impact bumblebee conservation through disruption of
- 92 male diet and ecology.
- Here, we assess the importance of thistles for bumblebee males across countries with
- 94 regulations against thistles by using field observations. We ultimately aim to evaluate the
- 95 potential consequences of regulations against thistles on bumblebee conservation.

Methods

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Plant systematics and definition of "Thistles"

- 98 We defined thistles as all species included in Cardueae (synonym: Cynareae); a monophyletic
- 99 worldwide tribe in the Asteraceae family. It contains 2400 species and 73 genera (Barres et al.
- 2013). For historic reasons, we followed the broad interpretation of Scrophulariaceae s.l. as
- used in Flora Europaea Vol. 3 (Tutin et al. 1972).

Database and description of the dataset

- We used opportunistic data consisting of 88 974 field observations of bumblebee (only
- observations of individuals feeding on flowers) which are recorded in the database *Banque de*
- 105 Données Fauniques de Gembloux et Mons (Rasmont & Iserbyt 2013, Rasmont et al. 2015).
- For each observation we looked at, (i) the plant species visited, (ii) the location, (iii) the date,
- and (iv) the visiting bumblebee species. All observations were performed in countries with a
- regulation against thistles (Table 1), with a proportion of 61% in France, 28% in Belgium,
- 109 11% in UK and 0.05% in the Netherlands. Observations were not fully distributed evenly
- across countries but were gathered in several regions (see the spatial distribution map in Fig.
- 111 1, created using ArcGIS 10 Esri software). Observations were carried out from 1878 to 2015
- and more than three-quarters (78%) were in summer (11% in June, 49% in July, and 18% in
- 113 August).

Assessing the importance of thistles for bumblebees

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We assessed the importance of thistles at *Bombus* generic and specific levels. 115 116 At the generic level, we compared for each caste the number of observations on flower at three plant taxonomic levels: between (i) plant families (n= 88 974 observations), (ii) 117 118 Asteraceae tribes (n= 15 746 observations) and (iii) Cardueae genera (n= 14 110 119 observations). Visit preferences between castes to different plant families were characterised using Correspondence Analysis (CA; 'FactoMineR' package) on the contingency table [34 120 plant families x 3 castes], only considering the plant families for which we had at least 50 121 122 observations (all castes combined). Moreover, since our data did not follow a normal distribution (Shapiro-Wilk test), differences in floral preferences between plant taxonomic 123 groups were examined with nonparametric tests (two-sample Wilcoxon sign-rank tests) for 124 each caste. All statistical analysis were done using R version 3.3.1 (R Development Core 125 Team 2016). 126 At the Bombus species level (20 567 queen observations, 15 007 male observations and 38 127 892 worker observations), we compared for each caste the relative number of observations on 128 the Cardueae tribe. 129 Thereafter, we assessed more specifically the consequences of national regulations against 130 thistles by comparing the number of individuals from each Bombus species feeding on the 131 four thistle species concerned by national regulations (n= 3016 observations): Carduus 132 crispus L., Cirsium arvense (L.) (Fig. 2a) Scop., Cirsium palustre (L.) Scop. (Fig. 2b), and 133 Cirsium vulgare (Savi) Ten (Tab. 1). 134

Results

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Bumblebees' floral preferences and importance of thistles

Our CA showed differences in floral visit preferences between castes (Fig. 3). The total inertia contained in the contingency table [34 plant families x 3 castes] was fully retained in two dimensions (respectively 79.93% for Axis 1 and 20.07% for Axis 2). The first dimension (Axis 1) was mainly defined by three plant families: Solanaceae (39.79%), Asteraceae (16.89%), and Brassicaceae (15.48%), and by two castes: queens (68.45%) and males (21.98%). The second dimension (Axis 2) was mainly explained by Fabaceae (28.59%), Asteraceae (26.81%) and Scrophulariaceae (11.36%), and for the castes by males (57.86%) and workers (38.14%). The global pattern presented by the CA showed that, among the five most visited plant families, Asteraceae was highly associated with male observations (Fig. 3). Focus on percentages of observations (Fig. 4a) and Wilcoxon sign-rank tests confirmed that males were significantly more observed on Asteraceae than on other families (41% of the 15 007 male observations; Wilcoxon sign-rank test, W = 1324400, p-value < 0.01). Queens were mainly observed on Solanaceae, Ericaceae, and Fabaceae families (respectively 20%, 19% and 14% of the 20 567 queen observations; only 7% on Asteraceae) and workers on Fabaceae, Asteraceae and Lamiaceae families (respectively 22%, 19% and 14% of the 38 892 worker observations). The surprisingly high percentage of queens recorded on Solanaceae is explained by observations of *Bombus terrestris* queens on *Salpichroa origanifolia* (Lam.) Baill. during September and October (4082 of the 4123 queens observations on Solanaceae). Among observations on Asteraceae, the Cardueae tribe was significantly more visited than other tribes by males (90% of the 5947 males observations, Wilcoxon sign-rank test, W = 84052, p-value < 0.001) and by workers (92% of the 7413 workers observations, Wilcoxon sign-rank test, W = 70105, p-value < 0.001), and recorded 79% of the 1446 queens (Fig. 4b). Among observations on Cardueae, 61% of the 1112 queens were observed on *Cirsium* spp., 22% on Centaurea spp. and 13% on Carduus spp. The 4722 male observations and the 6738

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worker observations were quite equitably distributed among the three genera (respectively 161 162 36% and 35% for Carduus, 30% and 32% for Centaurea, and 29% both for Cirsium; Fig. 4c). 163 Bumblebee species most observed on thistles 164 Regarding the bumblebee specific richness, a total of 43 species was recorded on Cardueae 165 (of the 45 species, all plant species included). For several species, more than half of recorded 166 visits were to this tribe. (Table 2, Fig. 5a). The largest numbers, in descending order were: 167 168 Bombus veteranus (95% of the observations), B. quadricolor (61%), B. mucidus (59%), B. mesomelas (56%) and B. norvegicus (52%; Fig. 5a). 169 Moreover, comparative analyses between castes show that many species have one or two 170 171 castes which are very often observed on Cardueae. Bombus veteranus males and workers were almost exclusively recorded on this tribe (respectively 98% and 96% of the 172 observations). Males of B. mucidus (87%), B. mesomelas (86%), B. confusus (85%), B. 173 mendax (81%), B. lapidarius (73%), B. quadricolor (70%) and B. sylvarum (70%) were also 174 175 commonly seen on Cardueae (Fig. 5a). Importance of the four thistle species included in the regulations 176 36 bumblebee species were observed on the four Cardueae species included in the regulations 177 178 (see Table S1 in Supporting Information), with the two most visited being Cirsium palustre and C. vulgare. The most frequently observed bumblebee species on these four plants were B. 179 180 norvegicus, B. distinguendus, B. campestris, B. quadricolor, B. soroeensis, B. bohemicus and B. sylvestris (respectively 19%, 17%, 16%, 15%, 12%, 11%, and 10% of the observations; 181 Fig. 5b). 16% of all the *B. norvegicus* specimens, 13% of all the *B. quadricolor* specimens 182

and 11% of all the B. soroeensis specimens were observed on the single species Cirsium

palustre, while 14% of all the *B. distinguendus* specimens and 10% of all the *B. campestris* were observed on *Cirsium vulgare*.

Discussion

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Importance of thistles for bumblebee males

We confirm at a larger geographic scale previous results (e.g. Carvell 2002; Carvell et al. 2006; Goulson et al. 2008) highlighting the large number of bumblebee male floral visits on Cardueae (mainly Carduus spp., Centaurea spp. and Cirsium spp). This strongly suggests an important role of Cardueae as a nectar resource during late summer when males perform their energy-consuming courtship behaviour (e.g. Croxton et al. 2002; Pywell et al. 2005; Goulson 2010). The lower number of workers and queens foraging on Cardueae could be explained by their need to collect pollen in addition to nectar for the colony development, unlike males which only feed on nectar. Yet, Asteraceae pollen is rarely found in queens and workers pollen loads (Goulson 2010), probably because it may represent a non-optimal diet for bumblebee colonies. This has recently been shown with the relative unsuitability of Cirsium pollen for the colony development of *B. terrestris* (Vanderplanck et al. 2016). It would have been of great interest to perform a comparison between time-periods of the importance of thistles in the foraging choice of bumblebees. However, our data set does not allow us to perform such a detailed study, because of the very different sampling efforts along time. Importance of Cardueae has also been pointed out for other insect pollinators (Vanbergen et al. 2014; Ricou et al. 2014). For instance, in the greenways and sown wildflower strips of Southern Sweden, Cirsium spp. and Centaurea spp. were the most visited plant species by eight bumblebee species, but also by 18 butterfly species (Haaland & Gyllin 2009). Cardueae are especially important in areas with intensive agriculture, where pollinators in general have a narrower spectrum and abundance of flowering plants (e.g. Cirsium species are a major

foraging source where other wildflower species are absent; Haaland & Gyllin 2009). Beside flower visiting insects, many phytophagous species are associated with Cardueae (Freese 1994) while thistle seeds provide food resource for some beetles, birds and rodents (McCallum & Kelly 1990).

Potential consequences of regulations against thistles on bumblebee conservation

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The four thistle species concerned by regulations against thistles in Belgium, France, the Netherlands and UK (i.e. Carduus cripus, Cirsium arvense, Cirsium palustre and Cirsium vulgare, Table 1) are commonly visited by male bumblebees (Fig. 5b and Table S1 in Supporting information). The regulations could thus (i) greatly reduce the availability of food resources for, especially, bumblebee males during mating period and (ii), consequently, decrease the offspring production reinforcing the bumblebee decline through the population size decrease and the "extinction vortex" (Gilpin & Soulé 1986; Zayed & Packer 2005). Such a phenomenon is most likely in "Threatened" or "Near Threatened" (Cederberg et al. 2013) species commonly visiting thistle flowers (e.g. B. confusus, B. distinguendus, B. mucidus, B. veteranus; Rasmont et al. 2015). Moreover, thistle removal acts may affect several other plant species. Indeed, the correct identification of the species that are legislated against is not always easy for farmers and landowners. For the general public, "thistle" refers to all flowering plants characterized by leaves with sharp prickles on the margins. This usually implies that all thistles and thistle-like plants are wiped out leading to other Cardueae species decline (e.g. in Belgium, Cirsium dissectum, Cirsium tuberosum, Carduus nutans and Cirsium eriophorum; Crémer et al. 2008). Furthermore, many measures taken to eradicate thistles (e.g. repeated mowing, fertilize and lime to ensure the maintenance of an herbaceous cover, or herbicides) also affect non-Cardueae plants (e.g. Turner et al. 2007; Crémer et al. 2008; Andreasen & Andresen 2011), including Fabaceae, the main food resources for bumblebee females (Fig. 4a).

Guidelines for policy-makers and conservation organizations

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Because of the importance of thistles for bumblebee males (and also for other species ensuring the pollination ecosystem service) there is a premium on repealing the thistle removal acts but also on limiting Cardueae suppression in regions where thistle removal is not mandatory but is still carried out by most farmers (Bond & Grundy 2001; Turner et al. 2007; Melander et al. 2012). Moreover, bumblebees can act as umbrella species for the other organisms associated with thistle and thistle-like plants (butterflies, other bees and hoverflies). Despite the obvious benefit of minimising the removal of Cardueae for many pollinators, agricultural policy requires the control of thistles in order to maintain farmland productivity. Indeed, some thistles may weaken pasture and crops due to their allelopathy (i.e. releasing soluble inhibitors that discourage the growth of pasture grasses and legumes; Wardle et al. 1993), their highly effective seed dispersal and their clonal spreading ability (leading to large area monopolization; Kelemen et al. 2014). In grasslands, thistle control can be achieved by prevention techniques that maintain a large floral diversity (e.g. avoiding over-fertilizing, over- or under-grazing, and bare soils) coupled with more specific methods (e.g. alternating mowing and grazing). In crops, thistle control without the use of pesticides is possible by using crop rotation and stubble techniques (Andreasen & Andresen 2011; Nicholls & Altieri 2013). When such actions in croplands and grasslands are not possible, maintaining tolerable densities of thistles in fields could help to support pollinator populations (Nicholls & Altieri 2013). Moreover, thistle removal in other areas should not be promoted because they are very rarely a problem outside farmlands. Therefore, gardens can act as refuges for bees and bumblebees in urban environments and intensively managed farmlands, as already suggested by previous studies (e.g. Ahrné et al. 2009; Samnegård et al. 2011).

In summary, thistle removal regulations are obsolete because they are based on an old agricultural context, and methods of weed control have evolved since their establishment (Andreasen & Andresen 2011). These regulations should therefore be re-evaluated, taking into account the increasing consideration of biodiversity in agricultural landscapes (Nicholls & Altieri 2013) and particularly the high priority given to the wild pollinator conservation (IPBES 2016).

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References

- 279 Ahrné K, Bengtsson J, Elmqvist T, Ahrne K. 2009. Bumble bees (*Bombus* spp) along a
- gradient of increasing urbanization. PLoS One [Internet] 4(5):e5574. Available from:

http://dx.plos.org/10.1371/journal.pone.0005574 281 Andreasen C, Andresen LC. 2011. Managing farmland flora to promote biodiversity in 282 Europe. CAB Reviews: Perspectives in Agriculture, Veterinary Science, Nutrition and 283 Natural Resources. 6:1-11. 284 285 Barres L, Sanmartín I, Anderson CL, Susanna A, Buerki S, Galbany-Casals M, Vilatersana R. 2013. Reconstructing the evolution and biogeographic history of tribe Cardueae 286 (Compositae). American Journal of Botany. 100:867-82. 287 Bond W, Grundy AC. 2001. Non-chemical weed management in organic farming systems. 288 Weed Research. 41:383-405. 289 290 Carvell C. 2002. Habitat use and conservation of bumblebees (*Bombus* spp.) under different grassland management regimes. Biological Conservation. 103:33–49. 291 292 Carvell C, Meek WR, Pywell RF, Goulson D, Nowakowski M. 2007. Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable 293 field margins. Journal of Applied Ecology. 44:29-40. 294 295 Carvell C, Roy DB, Smart SM, Pywell RF, Preston CD, Goulson D. 2006. Declines in forage availability for bumblebees at a national scale. Biological Conservation. 132:481–489. 296 Cederberg B, Michez D, Nieto A, Radchenko V, Rasmont P, Roberts S. 2013. Bombus. IUCN 297 Red List of Threatened Species. Version 2013.2,1. [Internet]. Available from: 298 www.iucnredlist.org 299 Crémer S, Knoden D, Stilmant D, Luxen P. 2008. Le contrôle des populations indésirables de 300 rumex, chardons et orties dans les prairies permanentes. In: Delbeuck C, editor. Les 301 Livrets de l'Agriculture. Vol. 17. Namur: Ministère de la Région Wallonne, Direction 302 générale de l'Agriculture; p. 86. 303 Croxton PJ, Carvell C, Mountford JO, Sparks TH. 2002. A comparison of green lanes and 304

- field margins as bumblebee habitat in an arable landscape. Biological Conservation.
- 306 107:365–374.
- Freese G. 1994. The insect complexes associated with the stems of seven thistle species.
- 308 Entomologia generalis. 19:191–207.
- Gilpin ME, Soulé ME. 1986. Minimum viable populations: processes of species extinction.
- In: Soulé ME, editor. Conservation biology: The Science of Scarcity and Diversity.
- Sunderland, MA: Sinauer Associates; p. 19–34.
- Goulson D. 2010. Bumblebees: behaviour, ecology, and conservation. Oxford: Oxford
- 313 University Press. 2nd ed. 330pp.
- Goulson D, Hanley ME, Darvill B, Ellis JS, Knight ME. 2005. Causes of rarity in
- bumblebees. Biological Conservation. 122:1–8.
- Goulson D, Lye GC, Darvill B. 2008. Diet breadth, coexistence and rarity in bumblebees.
- Biodiversity and Conservation. 17:3269–3288.
- Haaland C, Gyllin M. 2009. Butterflies and bumblebees in greenways and sown wildflower
- strips in southern Sweden. Journal of Insect Conservation 14:125–132.
- Heinrich B. 1979. Bumblebee economics. Cambridge, London: Harvard University Press.
- 321 288pp.
- 322 IPBES (Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services),
- Potts SG, Imperatriz-Fonseca VL, Ngo HT, Biesmeijer JC, Breeze DT, Dicks L V.,
- Garibaldi LA, Hill R, Settele J, et al. 2016. Summary for policymakers of the assessment
- report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem
- Services on pollinators, pollination and food production. Secretariat of the
- 327 Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services.
- Bonn, Germany. 28pp.

Kelemen A, Török P, Valkó O, Deák B, Miglécz T, Tóth K, Ölvedi T, Tóthmérész B. 2014. 329 Sustaining recovered grasslands is not likely without proper management: vegetation 330 changes after cessation of mowing. Biodiversity and Conservation. 23:741–751. 331 Kleijn D, Raemakers I. 2008. A retrospective analysis of pollen host plant use by stable and 332 declining bumble bee species. Ecology. 89:1811–1823. 333 McCallum K, Kelly D. 1990. Pre- and post-dispersal predation of nodding thistle seeds by 334 birds and rodents. In: Proceedings of the Forty-Third New Zealand Weed and Pest 335 336 Control Conference. Proceedings; Pacific Park Hotel, Dunedin on 14-16 August 1990. pp. 216–219. 337 Melander B, Holst N, Rasmussen IA, Hansen PK. 2012. Direct control of perennial weeds 338 between crops – Implications for organic farming. Crop Protection. 40:36–42. 339 Nicholls CI, Altieri MA. 2013. Plant biodiversity enhances bees and other insect pollinators in 340 agroecosystems. A review. Agronomy for Sustainable Development. 33:257–274. 341 Ollerton J, Winfree R, Tarrant S. 2011. How many flowering plants are pollinated by 342 animals? Oikos. 120:321-326. 343 Persson AS, Smith HG. 2013. Seasonal persistence of bumblebee populations is affected by 344 landscape context. Agriculture, Ecosystems & Environment. 165:201–209. 345 Pywell RF, Warman EA, Carvell C, Sparks TH, Dicks LV, Bennett D, Wright A, Critchley 346 CNR, Sherwood A. 2005. Providing foraging resources for bumblebees in intensively 347 farmed landscapes. Biological Conservation. 121:479–494. 348 R Development Core Team. 2016. R: A Language and Environment for Statistical 349 350 Computing. Team RDC, editor. R Foundation for Statistical Computing, Vienna, Austria. Available from: http://www.r-project.org 351 Rasmont P, Iserbyt S. 2013. Atlas of the European Bees: genus Bombus. 3d Edition. STEP 352

Project, Atlas Hymenoptera, Mons, Gembloux. Available from: 353 http://www.zoologie.umh.ac.be//hymenoptera/page.asp?ID=169. 354 355 Rasmont P, Franzén M, Lecocq T, Harpke A, Roberts SPM, Biesmeijer JC, Castro L, Cederberg B, Dvorák L, Fitzpatrick Ú, et al. 2015. Climatic Risk and Distribution Atlas 356 of European Bumblebees. Biorisk 10 (Special Issue):246pp. 357 Rasmont P, Mersch P. 1988. First estimation of faunistic drift by bumblebees of Belgium, 358 (Hymenoptera: Apidae). Annales de la Societe Royale Zoologique de Belgique. 118:141-359 360 147. Ricou C, Schneller C, Amiaud B, Plantureux S, Bockstaller C. 2014. A vegetation-based 361 indicator to assess the pollination value of field margin flora. Ecological Indicators. 362 45:320-331. 363 364 Rundlöf M, Persson AS, Smith HG, Bommarco R. 2014. Late-season mass-flowering red clover increases bumble bee queen and male densities. Biological Conservation. 365 172:138-145. 366 Samnegård U, Persson AS, Smith HG. 2011. Gardens benefit bees and enhance pollination in 367 368 intensively managed farmland. Biological Conservation. 144:2602–2606. Scheper J, Reemer M, van Kats R, Ozinga WA, van der Linden GTJ, Schaminée JHJ, Siepel 369 370 H, Kleijn D. 2014. Museum specimens reveal loss of pollen host plants as key factor driving wild bee decline in The Netherlands. Proceedings of the National Academy of 371 Sciences. 111: 17552-17557. 372 Tree of Life Web Project. 2009. Cardueae Cass.. Thistles. Version 11 January 2009. Tree Life 373 Web Project [Internet]. Available from: http://tolweb.org/Cardueae/104543/2009.01.11 374 Turner RJ, Davies G, Moore H, Grundy AC, Mead A. 2007. Organic weed management: A 375

review of the current UK farmer perspective. Crop Protection. 26:377–382.

377	Tutin TG, Heywood VH, Burges NA, Moore DM, Valentine DH, Walters SM, Webb DA.
378	1972. Flora Europaea: Volume 3: Diapensiaceae to Myoporaceae. Cambridge:
379	Cambridge University Press. 415pp.
380	Vanbergen AJ, Woodcock BA, Gray A, Grant F, Telford A, Lambdon P, Chapman DS,
381	Pywell RF, Heard MS, Cavers S. 2014. Grazing alters insect visitation networks and
382	plant mating systems. Functional Ecology. 28:178–189.
383	Vanderplanck M, Decleves S, Roger N, Decroo C, Caulier G, Glauser G, Gerbaux P, Lognay
384	G, Richel A, Escaravage N, Michez D. 2016. Is non-host pollen suitable for generalist
385	bumblebees? Insect Science [Internet]. Avalaible from:
386	http://onlinelibrary.wiley.com/doi/10.1111/1744-7917.12410/full
387	Wardle DA, Nicholson KS, Rahman A. 1993. Influence of plant age on the allelopathic
388	potential of nodding thistle (Carduus nutans L.) against pasture grasses and legumes.
389	Weed Research. 33:69–78.
390	Zayed A, Packer L. 2005. Complementary sex determination substantially increases
391	extinction proneness of haplodiploid populations. Proceedings of the National Academy
392	of Sciences of the United States of America. 102:10742-6.
393	

Table 1. National regulations requiring the control of thistles in the European Union

Countries	Period	Species concerned	Regulation's name / source
Belgium	1987 - present	Carduus crispus	"Arrêté royal du 19 novembre 1987
		Cirsium arvense	relatif à la lutte contre les organismes
		Cirsium palustre	nuisibles aux végétaux et aux produits
		Cirsium vulgare	végétaux."
			(Crémer et al. 2008)
France	1994 - present	Cirsium arvense	"Article L383 du Code Civil"; and
			subsequent local legislations (i.e.
			" arrêtés préfectoraux/municipaux")
Netherlands (only	1950 - present	Varies per province,	Local legislations (i.e.
provinces Friesland,		usually:	"Distelverordening
Utrecht, Noord-Holland,		Cirsium arvense	(bestrijdingsplicht)" and "Algemene
Zeeland, Zuid-Holland,		Cirsium palustre	Plaatselijke Verordening (APV)")
and Noord-Brabant)		Cirsium vulgare	-
United Kingdom	1959 - present	Cirsium arvense	"Weeds Act 1959"
_	•	Cirsium vulgare	

Table 2. Total number of specimens recorded on all plant species and number of specimens recorded on a plant species of the Cardueae tribe.Q = queen; M = male; W = worker; U = unknown. Bombus sp. are Bombus unspecified specimens in the database.

Bombus species All Bombus species	0			pecimens		Number of specimens observed on a Cardueae				
All Bombus species	_	M	W	U	Total	Q	M	W	U	Total
	20567	15007	38892	14509	88974	1145	5334	6851	783	14113
Bombus sp.	38	53	185	152	428	2	9	72	9	92
B. alpinus (L.)	4	3	11	3	21	-	-	-	-	-
B. argillaceus (Scopoli)	12	23	89	1	125	-	2	25	-	27
B. barbutellus (Kirby)	26	118	-	2	146	4	25	-	-	29
B. bohemicus Seild	249	1164	-	25	1438	20	546	-	8	574
B. brodmannicus Vogt	36	-	29	2	67	-	-	1	-	1
B. campestris (Panzer)	31	164	-	2	197	7	74	-	-	81
B. confusus Schenk	21	81	92	-	194	3	69	18	-	90
B. cryptarum (Fabricius)	528	98	235	1	862	2	56	16	-	74
B. cullumanus (Kirby)	14	7	34	-	55	3	1	15	-	19
B. distinguendus Morawitz	226	77	265	1564	2132	30	34	70	556	690
B. flavidus Eversmann	5	122	-	1	128	4	45	-	1	50
B. gerstaeckeri Morawitz	239	55	112	3	409	-	-	-	-	-
B. hortorum (L.)	1051	661	1573	1357	4642	31	103	144	30	308
B. humilis Illiger	306	148	1300	1	1755	10	77	263	_	350
B. hypnorum (L.)	90	88	274	100	552	4	21	18	4	47
B. jonellus (Kirby)	766	104	319	334	1523	16	16	13	2	47
B. lapidarius (L.)	1056	1237	3204	477	5974	115	907	905	24	1951
B. lucorum (L.)	1939	1722	3270	284	7215	31	219	215	17	482
B. magnus Vogt	431	72	263	76	842	19	_	20	13	52
B. mendax Gerstaecker	44	42	359	1	446	4	34	22	_	60
B. mesomelas Gerstaecker	121	121	1058	17	1317	30	104	608	2	744
B. mocsaryi Kriechbaumer	4	_	13	_	17	2	_	13	_	15
B. monticola Smith	179	566	2357	213	3315	2	72	58	_	132
B. mucidus Gerstaecker	33	47	182	2	264	3	41	113	_	157
B. muscorum (L.)	204	81	239	70	594	27	44	101	20	192
B. norvegicus (Sparre Schneider)	2	73	_	_	75	1	38	_	_	39
B. pascuorum (Scopoli)	2695	984	4611	2343	10633	320	266	468	33	1087
B. perezi (Schulthess-Rechberg)	3	114	-		117	-	30	-	-	30
B. pereziellus (Skorikov)	19	6	32	_	57	_	-	1	_	1
B. pomorum (Panzer)	41	16	119	_	176	12	8	56	_	76
B. pratorum (L.)	886	718	1432	216	3252	7	105	131	17	260
B. pyrenaeus Pérez	33	162	833	12	1040	4	82	114	1	201
B. quadricolor (Lepeletier)	31	90	-	1	122	11	63	_	_	74
B. ruderarius (Müller)	450	628	1608	24	2710	22	297	303	7	629
B. ruderatus (Fabricius)	309	513	981	2	1805	4	36	33	-	73
B. rupestris (Fabricius)	79	166	-	6	251	16	92	-	1	109
B. sichelii Radoszkowski	40	75	940	14	1069	7	14	196	2	219
B. soroeensis (Fabricius)	729	445	3671	65	4910	93	157	1321	4	1575
B. subterraneus (L.)	94	155	385	1	635	4	60	50	-	114
B. sylvarum (L.)	220	146	2400	20	2786	25	102	522	8	657
B. sylvestris (Lepeletier)	118	306	-	27	451	15	140	-	4	159
B. terrestris (L.)	6876	2447	4628	7052	21003	212	448	235	18	913
B. vestalis (Fourcroy)	45	109	-020	20	174	1	44	-	2	47
B. veteranus (Fabricius)	69	848	705	-	1622	22	833	678	-	1533
B. wurflenii Radoszkowski	175	151	1074	28	1428	-	20	32	1	53

403 **Figures**

Figure 1. Spatial distribution of the bumblebee observations feeding on flower in the four countries concerned by thistles regulations (Belgium, France, The Netherlands, and UK).

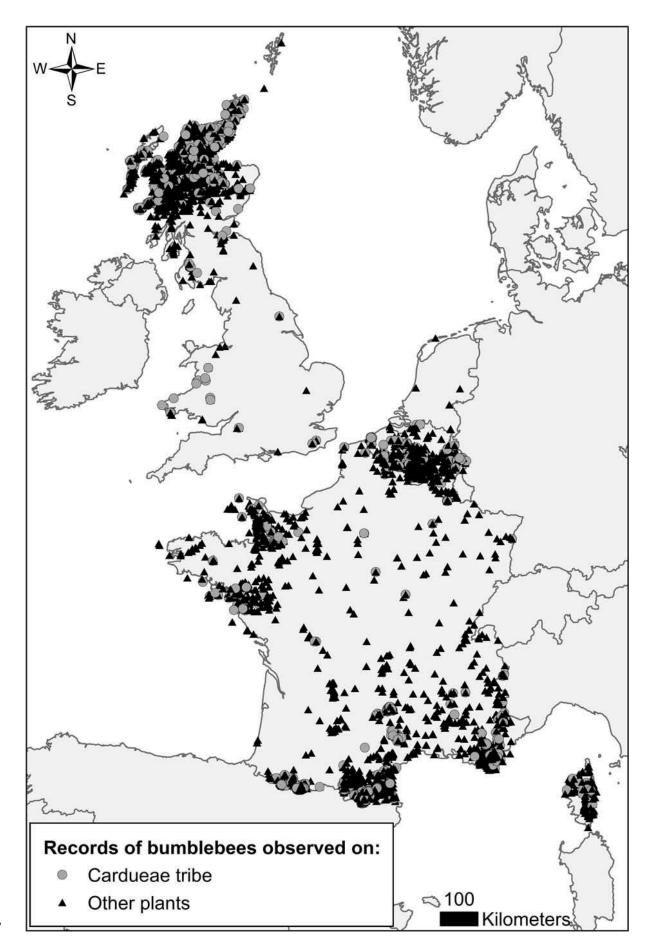


Figure 2. (a) *Bombus rupestris* male on *Cirsium arvense*, and (b) *Bombus sylvestris* male on *Cirsium palustre* (Photos: J.-M. Michalowski).



Figure 3. Correspondence Analysis factor map obtained from the contingency table of the three 412 413 castes (triangles) and the 34 plant families for which we had more than 50 observations (points). Bigger points are the four plant families with more than 9000 observations, Asteraceae being 414 the most visited family with 15 015 observations. M = males (14 874 obs.); Q = queens (20 326 415 obs.); W = workers (38 579 obs.); Api = Apiaceae (1493 obs.); Bal = Balsaminaceae (52 obs.); 416 417 Ber = Berberidaceae (74 obs.); Bor = Boraginaceae (2642 obs.); Bra = Brassicaceae (2163 obs.); 418 Cam = Campanulaceae (747 obs.); Cap = Caprifoliaceae (74 obs.); Car = Caryophyllaceae (114 obs.); Cis = Cistaceae (184 obs.); Cra = Crassulaceae (113 obs.); Cuc = Cucurbitaceae (320 419 obs.); Dip = Dipsacaceae (1223 obs.); Eri = Ericaceae (9570 obs.); Fab = Fabaceae (12 556 420 421 **obs.**); Gen = Gentianaceae (436 obs.); Ger = Geraniaceae (227 obs.); Gro = Grossulariaceae (485 obs.); Gut = Guttiferae (176 obs.); Hyd = Hydrophyllaceae (443 obs.); Lam = Lamiaceae 422 (9624 obs.); Lil = Liliaceae (618 obs.); Lyt = Lythraceae (142 obs.); Mal = Malvaceae (121 423 424 obs.); Ole = Oleaceae (64 obs.); Ona = Onagraceae (1533 obs.); Pap = Papaveraceae (149 obs.); Pol = Polygonaceae (52 obs.); Ran = Ranunculaceae (2430 obs.); Ros = Rosaceae (2386 obs.); 425 Sal = Salicaceae (359 obs.); Scr = Scrophulariaceae (3434 obs.); Sol = Solanaceae (4643 obs.); 426 Til = Tiliaceae (117 obs.). 427

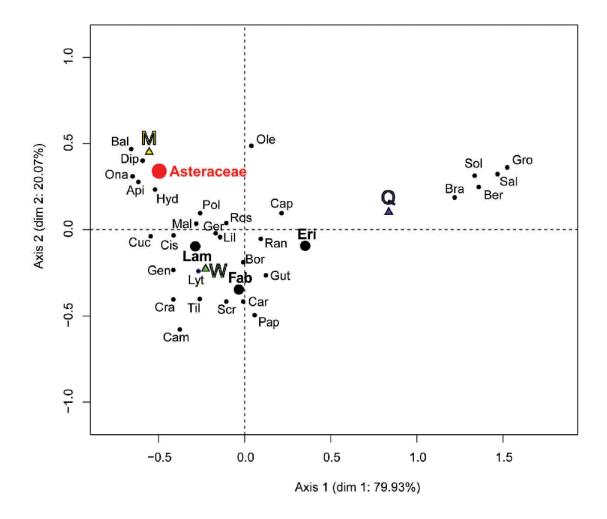


Figure 4. Number of bumblebee specimens recorded to different (a) plant families (all bumblebee species combined; $N = 88\,974$ specimens), (b) tribes of the Asteraceae family (all bumblebee species combined; $N = 15\,746$ specimens), and (c) genera of the Cardueae tribe (all bumblebee species combined; $N = 13\,353$ specimens). "Others" are (a) 79 plant families with less than 800 observations each totalling 5912 observations, (b) 10 tribes of Asteraceae with less than 70 observations each totalling 240 observations, and (c) 8 genera of Cardueae with less than 40 observations each totalling 100 observations.

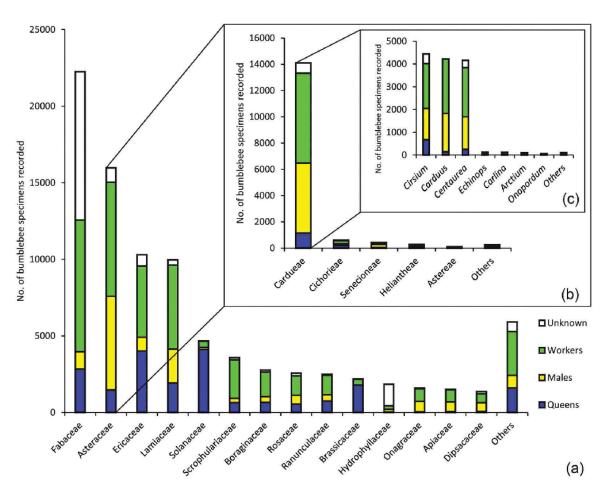


Figure 5. Proportion of bumblebee specimens observed on (a) Cardueae and (b) the four thistle species concerned by the regulations (number on Cardueae = 14 113 specimens; number on the four species = 3016 specimens; total number = 88 974 specimens). Only species with a percentage higher than (a) 25% and (b) 3% (for all castes combined) are presented.

