



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

Sarah Vray, Thomas Lecocq, Stuart P.M. Roberts, Pierre Rasmont

► To cite this version:

Sarah Vray, Thomas Lecocq, Stuart P.M. Roberts, Pierre Rasmont. Endangered by laws: potential consequences of regulations against thistles on bumblebee conservation. *Annales de la Société Entomologique de France*, 2017, 53 (1), pp.33-41. 10.1080/00379271.2017.1304831 . hal-01972531

HAL Id: hal-01972531

<https://hal.univ-lorraine.fr/hal-01972531>

Submitted on 4 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.

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

Sarah Vray^{1,2*}, Thomas Lecocq^{1,3}, Stuart P.M. Roberts⁴, Pierre Rasmont¹

¹ *Laboratory of Zoology, Research institute of Biosciences, University of Mons, Place du Parc
20, B-7000, Mons, Belgium. E-mail: sarah.vray@umons.ac.be,
thomas.lecocq@umons.ac.be, pierre.rasmont@umons.ac.be. Phone: 0032.(0)65.37.34.35.*

² *Department of Geography, University of Namur, Rue de Bruxelles 61, B-5000 Namur,
Belgium. E-mail: sarah.vray@unamur.ac.be.*

³ *Research Unit Animal and Functionalities of Animal Products (URAFPA), University of
Lorraine – INRA, 2 Avenue de la Forêt de Haye, BP 172, F-54505, Vandoeuvre-lès-Nancy,
France. E-mail: thomas.lecocq@univ-lorraine.fr*

⁴ *Visiting Research Fellow, Reading University, Reading, RG6 6AR, UK*

*Corresponding author. E-mail: sarah.vray@umons.ac.be or sarah.vray@gmail.com. Tel:
+32(0)65/37.34.05

Running title: Regulations against thistles and bumblebee conservation.

Word count:

- Summary: 187 words
- Résumé : 220 words
- Main text: 2556 words
- Acknowledgements: 171 words
- References: 1069 words
- Table legend: 57 words
- Figure legends: 419 words

Number of tables: 2

Number of figures: 5

Number of references: 40

29 **Summary**

30 Many Bumblebee (*Bombus*) species are undergoing a strong decline in Europe due to,
31 amongst other things, a decrease of food resources. While leguminous plants (Fabaceae) are
32 considered to be one of the main pollen sources of bumblebees, thistles (Asteraceae tribe
33 Cardueae) have been suggested to be important for male diet. Yet, several European countries
34 apply strict regulations against thistles since they are considered to be one of the principal
35 weeds in agricultural landscapes. Such regulations could impact bumblebee conservation
36 through disruption of male diet and ecology. Here, we assess the male-depending importance
37 of thistles for bumblebee species based on field observations across countries where a legal
38 regulation against thistles is in effect. We ultimately aim to evaluate the potential
39 consequences of these regulations on bumblebee conservation. Our results confirm that most
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
42 likely a threat for bumblebees. Therefore, we advocate repealing the thistle removal acts to
43 make way for alternative thistle regulations which reconcile biodiversity conservation and
44 agricultural requirements.

45 **Résumé. Menacé par des lois : les conséquences potentielles des législations** 46 **d'échardonnage sur la conservation des bourdons.**

47 Les bourdons sont en régression en Europe, en partie à cause d'une diminution de leurs
48 ressources alimentaires. Alors que les légumineuses sont considérées comme étant une des
49 principales sources de pollen pour les bourdons, les chardons (Asteraceae, tribu des Cardueae)
50 ont été suggérés comme étant importants pour l'alimentation des mâles. Pourtant, plusieurs
51 pays européens appliquent des règles législatives strictes contre les chardons car ils sont
52 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, weed control legislation.

Introduction

Almost 90 percent of all flowering plant species are pollinated by animals (Ollerton et al. 2011). In cold and temperate regions of the Northern Hemisphere, the social species group of bumblebees (*Bombus* spp.) is the main pollinating agent (Heinrich 1979). However, many species are experiencing a strong population decline and range contraction fostered by landscape modifications and fragmentation, intensive use of agrochemicals, pathogen 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 developed to ensure bumblebee survival and to avoid a major disruption of pollination service. One strategy aims to mitigate the current qualitative and quantitative reduction in floral resources (e.g. Carvell et al. 2007; Kleijn & Raemakers 2008; Scheper et al. 2014) 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 bumblebee diet and ecology is therefore essential to plan efficient conservation management.

Several studies based on field observations have pointed out that leguminous plants (Fabaceae) are among the main pollen sources for bumblebees, especially for scarcer species (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 studies, floral preferences of other castes could be blurred. Yet, other caste requirements are thought to be different (Goulson 2010). For instance, some studies have suggested the importance of thistles (Asteraceae tribe Cardueae; Tree of Life Web Project 2009) for male 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 flowering, development and seed dispersal since they are considered to be noxious weeds in the agricultural landscape (Table 1). Under the assumption of the importance of thistles for

bumblebees, such regulations could impact bumblebee conservation through disruption of male diet and ecology.

Here, we assess the importance of thistles for bumblebee males across countries with regulations against thistles by using field observations. We ultimately aim to evaluate the potential consequences of regulations against thistles on bumblebee conservation.

Methods

Plant systematics and definition of "Thistles"

We defined thistles as all species included in Cardueae (synonym: Cynareae); a monophyletic 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 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, 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. 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 August).

114 *Assessing the importance of thistles for bumblebees*

115 We assessed the importance of thistles at *Bombus* generic and specific levels.

116 At the generic level, we compared for each caste the number of observations on flower at
117 three plant taxonomic levels: between (i) plant families (n= 88 974 observations), (ii)
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
120 using Correspondence Analysis (CA; ‘FactoMineR’ package) on the contingency table [34
121 plant families x 3 castes], only considering the plant families for which we had at least 50
122 observations (all castes combined). Moreover, since our data did not follow a normal
123 distribution (Shapiro-Wilk test), differences in floral preferences between plant taxonomic
124 groups were examined with nonparametric tests (two-sample Wilcoxon sign-rank tests) for
125 each caste. All statistical analysis were done using R version 3.3.1 (R Development Core
126 Team 2016).

127 At the *Bombus* species level (20 567 queen observations, 15 007 male observations and 38
128 892 worker observations), we compared for each caste the relative number of observations on
129 the Cardueae tribe.

130 Thereafter, we assessed more specifically the consequences of national regulations against
131 thistles by comparing the number of individuals from each *Bombus* species feeding on the
132 four thistle species concerned by national regulations (n= 3016 observations): *Carduus*
133 *crispus* L., *Cirsium arvense* (L.) (Fig. 2a) Scop., *Cirsium palustre* (L.) Scop. (Fig. 2b), and
134 *Cirsium vulgare* (Savi) Ten (Tab. 1).

135 **Results**

136 *Bumblebees’ floral preferences and importance of thistles*

137 Our CA showed differences in floral visit preferences between castes (Fig. 3). The total
 138 inertia contained in the contingency table [34 plant families x 3 castes] was fully retained in
 139 two dimensions (respectively 79.93% for Axis 1 and 20.07% for Axis 2). The first dimension
 140 (Axis 1) was mainly defined by three plant families: Solanaceae (39.79%), Asteraceae
 141 (16.89%), and Brassicaceae (15.48%), and by two castes: queens (68.45%) and males
 142 (21.98%). The second dimension (Axis 2) was mainly explained by Fabaceae (28.59%),
 143 Asteraceae (26.81%) and Scrophulariaceae (11.36%), and for the castes by males (57.86%)
 144 and workers (38.14%). The global pattern presented by the CA showed that, among the five
 145 most visited plant families, Asteraceae was highly associated with male observations (Fig. 3).
 146 Focus on percentages of observations (Fig. 4a) and Wilcoxon sign-rank tests confirmed that
 147 males were significantly more observed on Asteraceae than on other families (41% of the
 148 15 007 male observations; Wilcoxon sign-rank test, $W = 1324400$, $p\text{-value} < 0.01$). Queens
 149 were mainly observed on Solanaceae, Ericaceae, and Fabaceae families (respectively 20%,
 150 19% and 14% of the 20 567 queen observations; only 7% on Asteraceae) and workers on
 151 Fabaceae, Asteraceae and Lamiaceae families (respectively 22%, 19% and 14% of the 38 892
 152 worker observations). The surprisingly high percentage of queens recorded on Solanaceae is
 153 explained by observations of *Bombus terrestris* queens on *Salpichroa origanifolia* (Lam.)
 154 Baill. during September and October (4082 of the 4123 queens observations on Solanaceae).
 155 Among observations on Asteraceae, the Cardueae tribe was significantly more visited than
 156 other tribes by males (90% of the 5947 males observations, Wilcoxon sign-rank test, $W =$
 157 84052 , $p\text{-value} < 0.001$) and by workers (92% of the 7413 workers observations, Wilcoxon
 158 sign-rank test, $W = 70105$, $p\text{-value} < 0.001$), and recorded 79% of the 1446 queens (Fig. 4b).
 159 Among observations on Cardueae, 61% of the 1112 queens were observed on *Cirsium* spp.,
 160 22% on *Centaurea* spp. and 13% on *Carduus* spp. The 4722 male observations and the 6738

worker observations were quite equitably distributed among the three genera (respectively 36% and 35% for *Carduus*, 30% and 32% for *Centaurea*, and 29% both for *Cirsium*; Fig. 4c).

Bumblebee species most observed on thistles

Regarding the bumblebee specific richness, a total of 43 species was recorded on Cardueae (of the 45 species, all plant species included). For several species, more than half of recorded visits were to this tribe. (Table 2, Fig. 5a). The largest numbers, in descending order were: *Bombus veteranus* (95% of the observations), *B. quadricolor* (61%), *B. mucidus* (59%), *B. mesomelas* (56%) and *B. norvegicus* (52%; Fig. 5a).

Moreover, comparative analyses between castes show that many species have one or two 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 observations). Males of *B. mucidus* (87%), *B. mesomelas* (86%), *B. confusus* (85%), *B. mendax* (81%), *B. lapidarius* (73%), *B. quadricolor* (70%) and *B. sylvarum* (70%) were also commonly seen on Cardueae (Fig. 5a).

Importance of the four thistle species included in the regulations

36 bumblebee species were observed on the four Cardueae species included in the regulations (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. 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; Fig. 5b). 16% of all the *B. norvegicus* specimens, 13% of all the *B. quadricolor* specimens 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

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

208 foraging source where other wildflower species are absent; Haaland & Gyllin 2009). Beside
209 flower visiting insects, many phytophagous species are associated with Cardueae (Freese
210 1994) while thistle seeds provide food resource for some beetles, birds and rodents
211 (McCallum & Kelly 1990).

212 ***Potential consequences of regulations against thistles on bumblebee conservation***

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

233 *Guidelines for policy-makers and conservation organizations*

234 Because of the importance of thistles for bumblebee males (and also for other species
235 ensuring the pollination ecosystem service) there is a premium on repealing the thistle
236 removal acts but also on limiting Cardueae suppression in regions where thistle removal is not
237 mandatory but is still carried out by most farmers (Bond & Grundy 2001; Turner et al. 2007;
238 Melander et al. 2012). Moreover, bumblebees can act as umbrella species for the other
239 organisms associated with thistle and thistle-like plants (butterflies, other bees and
240 hoverflies).

241 Despite the obvious benefit of minimising the removal of Cardueae for many pollinators,
242 agricultural policy requires the control of thistles in order to maintain farmland productivity.
243 Indeed, some thistles may weaken pasture and crops due to their allelopathy (i.e. releasing
244 soluble inhibitors that discourage the growth of pasture grasses and legumes; Wardle et al.
245 1993), their highly effective seed dispersal and their clonal spreading ability (leading to large
246 area monopolization; Kelemen et al. 2014). In grasslands, thistle control can be achieved by
247 prevention techniques that maintain a large floral diversity (e.g. avoiding over-fertilizing,
248 over- or under-grazing, and bare soils) coupled with more specific methods (e.g. alternating
249 mowing and grazing). In crops, thistle control without the use of pesticides is possible by
250 using crop rotation and stubble techniques (Andreasen & Andresen 2011; Nicholls & Altieri
251 2013). When such actions in croplands and grasslands are not possible, maintaining tolerable
252 densities of thistles in fields could help to support pollinator populations (Nicholls & Altieri
253 2013). Moreover, thistle removal in other areas should not be promoted because they are very
254 rarely a problem outside farmlands. Therefore, gardens can act as refuges for bees and
255 bumblebees in urban environments and intensively managed farmlands, as already suggested
256 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).

Acknowledgments

This research was supported by the Belgian Science Policy (project BR/132/A1/BELBEES). We acknowledge the committee and members of BWARS (the UK Bees, Wasps and Ants Recording Society) for access to their data holdings for UK. We also thank the numerous recorders who contributed to gather field observations in the four countries, especially R.G. Adam, R. Barone, C.J. Booth, P. Castle, C. Claessens, K. Colsell, P. Coppens, J.E. Crossley, B. Dawson, T. De Meulemeester, E. De Tré, E. Delattre, I. Demeuldre, K. Duncan, A. Durant, G. Else, P. Entwistle, J.F. Godeau, E. Grant, J. Hlusek, S. Iserbyt, A. Lachaud, G. Mahé, M. McDonald, B. Neill, G. Nisbet, S. Patiny, A. Pauly, R. Paxton, O. Ponchau, P. Sagot, M. Terzo, and M. Vandenberg. We also would like to thank all the persons that helped us collecting information about legislations against thistles across Western Europe: Y. J. Anagnostopoulos, D. Baldock, E. Budrys, I. Calabuig, L. Castro, M. Cornalba, M. Franzén, D. Goulson, R. Haveman, A. Jenic, D. Kleijn, M. Quaranta, H. P. Ravn, P. Sima, C. Vanappelghem, W. Vogt-Kaute, and P. Williams. We also thank J.-M. Michalowski for the use of his two photographs.

References

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:

281 <http://dx.plos.org/10.1371/journal.pone.0005574>

282 Andreassen C, Andresen LC. 2011. Managing farmland flora to promote biodiversity in
 283 Europe. CAB Reviews: Perspectives in Agriculture, Veterinary Science, Nutrition and
 284 Natural Resources. 6:1-11.

285 Barres L, Sanmartín I, Anderson CL, Susanna A, Buerki S, Galbany-Casals M, Vilatersana R.
 286 2013. Reconstructing the evolution and biogeographic history of tribe Cardueae
 287 (Compositae). American Journal of Botany. 100:867–82.

288 Bond W, Grundy AC. 2001. Non-chemical weed management in organic farming systems.
 289 Weed Research. 41:383–405.

290 Carvell C. 2002. Habitat use and conservation of bumblebees (*Bombus* spp.) under different
 291 grassland management regimes. Biological Conservation. 103:33–49.

292 Carvell C, Meek WR, Pywell RF, Goulson D, Nowakowski M. 2007. Comparing the efficacy
 293 of agri-environment schemes to enhance bumble bee abundance and diversity on arable
 294 field margins. Journal of Applied Ecology. 44:29–40.

295 Carvell C, Roy DB, Smart SM, Pywell RF, Preston CD, Goulson D. 2006. Declines in forage
 296 availability for bumblebees at a national scale. Biological Conservation. 132:481–489.

297 Cederberg B, Michez D, Nieto A, Radchenko V, Rasmont P, Roberts S. 2013. *Bombus*. IUCN
 298 Red List of Threatened Species. Version 2013.2,1. [Internet]. Available from:
 299 www.iucnredlist.org

300 Crémer S, Knoden D, Stilmant D, Luxen P. 2008. Le contrôle des populations indésirables de
 301 rumex, chardons et orties dans les prairies permanentes. In: Delbeuck C, editor. Les
 302 Livrets de l'Agriculture. Vol. 17. Namur: Ministère de la Région Wallonne, Direction
 303 générale de l'Agriculture; p. 86.

304 Croxton PJ, Carvell C, Mountford JO, Sparks TH. 2002. A comparison of green lanes and

305 field margins as bumblebee habitat in an arable landscape. *Biological Conservation*.
306 107:365–374.

307 Freese G. 1994. The insect complexes associated with the stems of seven thistle species.
308 *Entomologia generalis*. 19:191–207.

309 Gilpin ME, Soulé ME. 1986. Minimum viable populations: processes of species extinction.
310 In: Soulé ME, editor. *Conservation biology: The Science of Scarcity and Diversity*.
311 Sunderland, MA: Sinauer Associates; p. 19–34.

312 Goulson D. 2010. *Bumblebees: behaviour, ecology, and conservation*. Oxford: Oxford
313 University Press. 2nd ed. 330pp.

314 Goulson D, Hanley ME, Darvill B, Ellis JS, Knight ME. 2005. Causes of rarity in
315 bumblebees. *Biological Conservation*. 122:1–8.

316 Goulson D, Lye GC, Darvill B. 2008. Diet breadth, coexistence and rarity in bumblebees.
317 *Biodiversity and Conservation*. 17:3269–3288.

318 Haaland C, Gyllin M. 2009. Butterflies and bumblebees in greenways and sown wildflower
319 strips in southern Sweden. *Journal of Insect Conservation* 14:125–132.

320 Heinrich B. 1979. *Bumblebee economics*. Cambridge, London: Harvard University Press.
321 288pp.

322 IPBES (Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services),
323 Potts SG, Imperatriz-Fonseca VL, Ngo HT, Biesmeijer JC, Breeze DT, Dicks L V.,
324 Garibaldi LA, Hill R, Settele J, et al. 2016. Summary for policymakers of the assessment
325 report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem
326 Services on pollinators, pollination and food production. Secretariat of the
327 Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services.
328 Bonn, Germany. 28pp.

329 Kelemen A, Török P, Valkó O, Deák B, Migléc T, Tóth K, Ölvedi T, Tóthmérész B. 2014.
 330 Sustaining recovered grasslands is not likely without proper management: vegetation
 331 changes after cessation of mowing. *Biodiversity and Conservation*. 23:741–751.

332 Kleijn D, Raemakers I. 2008. A retrospective analysis of pollen host plant use by stable and
 333 declining bumble bee species. *Ecology*. 89:1811–1823.

334 McCallum K, Kelly D. 1990. Pre- and post-dispersal predation of nodding thistle seeds by
 335 birds and rodents. In: *Proceedings of the Forty-Third New Zealand Weed and Pest*
 336 *Control Conference*. Proceedings; Pacific Park Hotel, Dunedin on 14-16 August 1990.
 337 pp. 216–219.

338 Melander B, Holst N, Rasmussen IA, Hansen PK. 2012. Direct control of perennial weeds
 339 between crops – Implications for organic farming. *Crop Protection*. 40:36–42.

340 Nicholls CI, Altieri MA. 2013. Plant biodiversity enhances bees and other insect pollinators in
 341 agroecosystems. A review. *Agronomy for Sustainable Development*. 33:257–274.

342 Ollerton J, Winfree R, Tarrant S. 2011. How many flowering plants are pollinated by
 343 animals? *Oikos*. 120:321–326.

344 Persson AS, Smith HG. 2013. Seasonal persistence of bumblebee populations is affected by
 345 landscape context. *Agriculture, Ecosystems & Environment*. 165:201–209.

346 Pywell RF, Warman EA, Carvell C, Sparks TH, Dicks LV, Bennett D, Wright A, Critchley
 347 CNR, Sherwood A. 2005. Providing foraging resources for bumblebees in intensively
 348 farmed landscapes. *Biological Conservation*. 121:479–494.

349 R Development Core Team. 2016. R: A Language and Environment for Statistical
 350 Computing. Team RDC, editor. R Foundation for Statistical Computing, Vienna, Austria.
 351 Available from: <http://www.r-project.org>

352 Rasmont P, Iserbyt S. 2013. Atlas of the European Bees: genus *Bombus*. 3d Edition. STEP

353 Project, Atlas Hymenoptera, Mons, Gembloux. Available from:
 354 <http://www.zoologie.umh.ac.be//hymenoptera/page.asp?ID=169>.

355 Rasmont P, Franzén M, Lecocq T, Harpke A, Roberts SPM, Biesmeijer JC, Castro L,
 356 Cederberg B, Dvorák L, Fitzpatrick Ú, et al. 2015. Climatic Risk and Distribution Atlas
 357 of European Bumblebees. *Biorisk* 10 (Special Issue):246pp.

358 Rasmont P, Mersch P. 1988. First estimation of faunistic drift by bumblebees of Belgium,
 359 (Hymenoptera: Apidae). *Annales de la Societe Royale Zoologique de Belgique*. 118:141–
 360 147.

361 Ricou C, Schneller C, Amiaud B, Plantureux S, Bockstaller C. 2014. A vegetation-based
 362 indicator to assess the pollination value of field margin flora. *Ecological Indicators*.
 363 45:320–331.

364 Rundlöf M, Persson AS, Smith HG, Bommarco R. 2014. Late-season mass-flowering red
 365 clover increases bumble bee queen and male densities. *Biological Conservation*.
 366 172:138–145.

367 Samnegård U, Persson AS, Smith HG. 2011. Gardens benefit bees and enhance pollination in
 368 intensively managed farmland. *Biological Conservation*. 144:2602–2606.

369 Scheper J, Reemer M, van Kats R, Ozinga WA, van der Linden GTJ, Schaminée JHJ, Siepel
 370 H, Kleijn D. 2014. Museum specimens reveal loss of pollen host plants as key factor
 371 driving wild bee decline in The Netherlands. *Proceedings of the National Academy of*
 372 *Sciences*. 111: 17552–17557.

373 Tree of Life Web Project. 2009. Cardueae Cass.. Thistles. Version 11 January 2009. Tree Life
 374 Web Project [Internet]. Available from: <http://tolweb.org/Cardueae/104543/2009.01.11>

375 Turner RJ, Davies G, Moore H, Grundy AC, Mead A. 2007. Organic weed management: A
 376 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]. Available 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

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

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

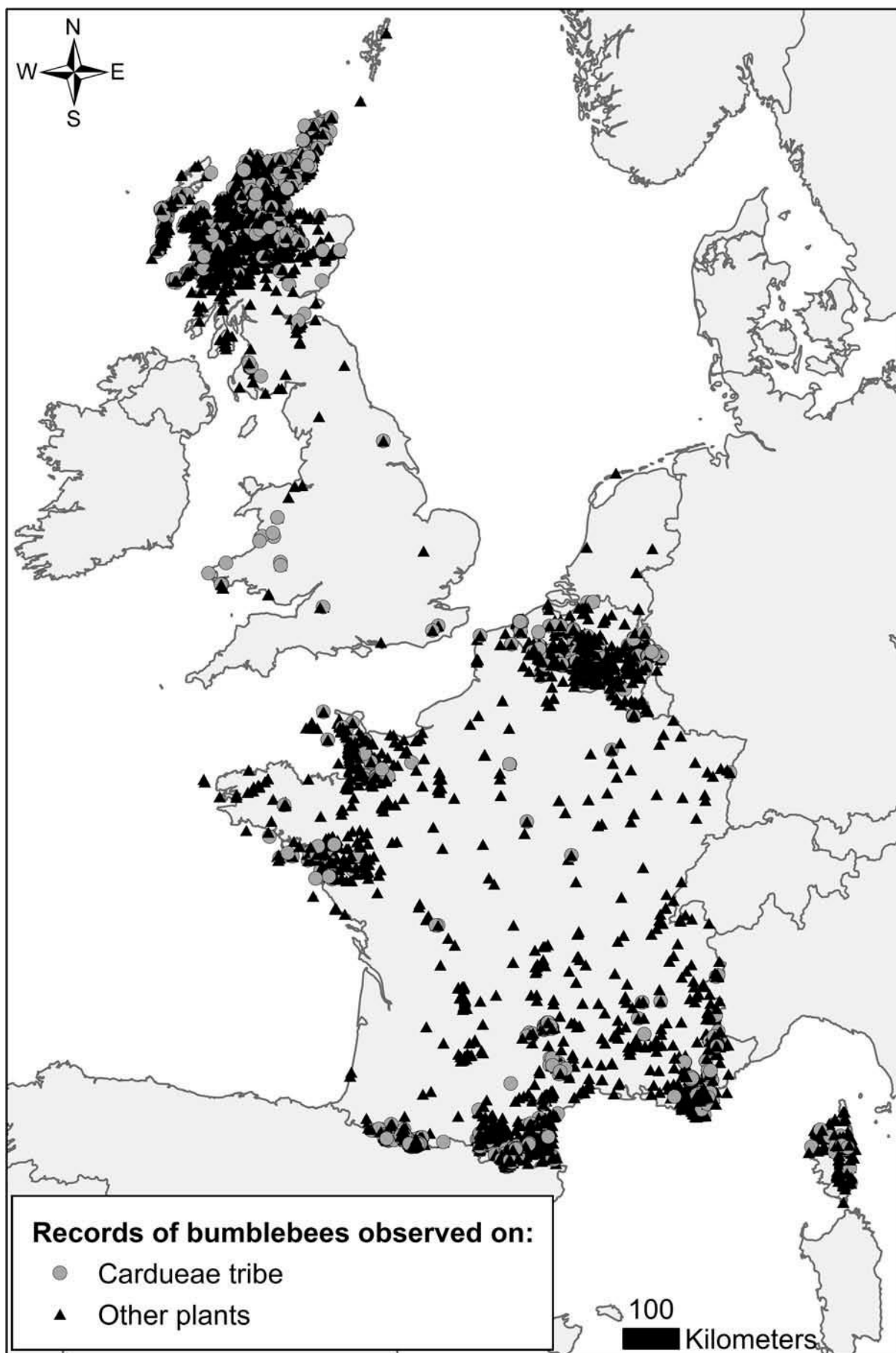
395
396

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.

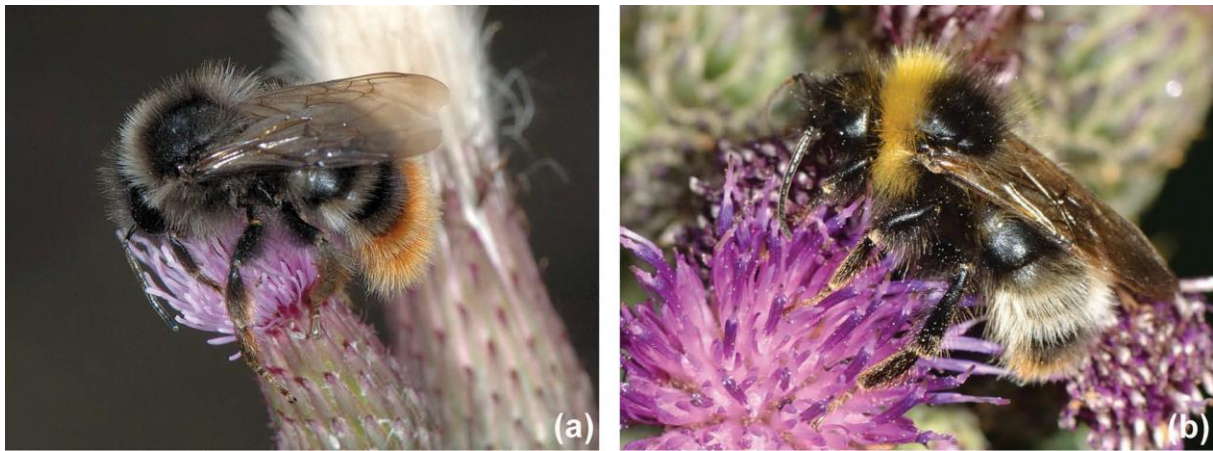
<i>Bombus</i> species	Total number of specimens					Number of specimens observed on a Cardueae				
	Q	M	W	U	Total	Q	M	W	U	Total
All <i>Bombus</i> species	20567	15007	38892	14509	88974	1145	5334	6851	783	14113
<i>Bombus</i> sp.	38	53	185	152	428	2	9	72	9	92
<i>B. alpinus</i> (L.)	4	3	11	3	21	-	-	-	-	-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

402 **Figures**
403
404

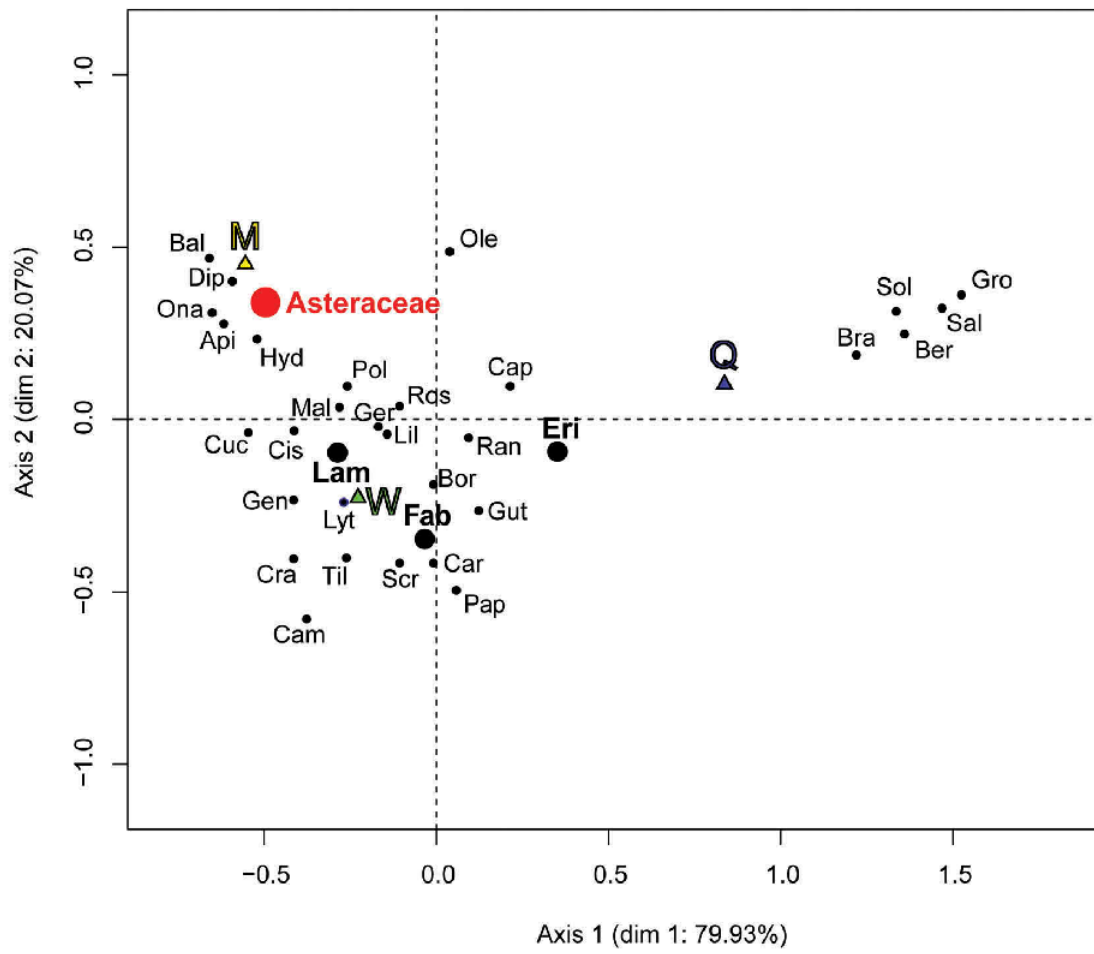
405 **Figure 1.** Spatial distribution of the bumblebee observations feeding on flower in the four
406 countries concerned by thistles regulations (Belgium, France, The Netherlands, and UK).



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



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



428

429

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.

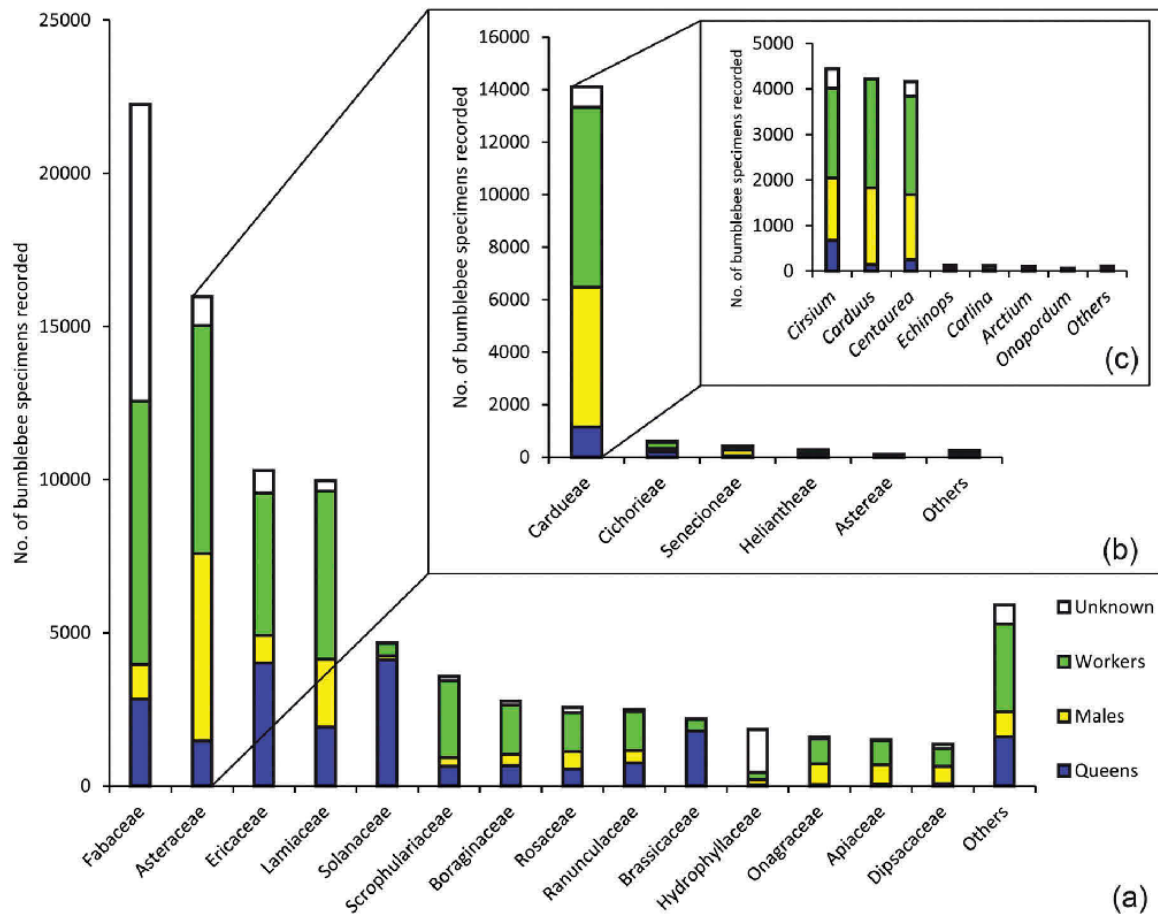


Figure 5. Proportion of bumblebee specimens observed on (a) Cardueae and (b) the four thistle species concerned by the regulations (number on Cardueae = 14 113 specimens; number on the four species = 3016 specimens; total number = 88 974 specimens). Only species with a percentage higher than (a) 25%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

