ORIGINAL PAPER

Drastic shifts in the Belgian bumblebee community over the last century

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Abstract

Bumblebees are undergoing strong declines in Europe caused by habitat loss and fragmentation, agricultural intensification, and climate change. Long-term records are necessary to estimate population trends precisely and to propose appropriate mitigation strategies. Based on an original database of 173,788 specimens from museum collections, scientific monitoring, and opportunistic citizen data from 1810 to 2016, we compared changes in species richness and area of occupancy of Belgian bumblebee species through three time-periods (1910–1930, 1970–1989, and 1990–2016). We also assessed if the observed trends are related to species-specific ecological traits and spatial scales (local, regional and national). Overall, species richness decreased over the last century in Belgium, but some regions retained relatively species-rich communities. A strong shift in community composition occurred. Three species remained among the "top five" in terms of species occurrence (area of occupancy) between the three time-periods (*B. pascuorum, B. lapidarius*, and *B. pratorum*), but several species that were once widespread declined drastically (*B. muscorum, B. humilis, B. ruderatus,* and *B. veteranus*), while a few species increased their distribution (e.g. *B. hypnorum* and *B. terrestris*). Habitat preferences significantly explained the observed trends, with declining species preferring open habitats and increasing species preferring wooded habitats.

Keywords *Bombus* · Species richness change · Area of occupancy · Habitat preference · Nesting strategy

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Introduction

Bumblebees (*Bombus*) are a diversified and common group of bee species found in temperate, alpine and arctic regions (Rasmont et al. 2015). They pollinate a wide diversity of crops and wild plant species (Ollerton et al. 2011). Many bumblebee species are undergoing a strong population decline in Western Europe and North America (Kosior et al. 2007; Goulson et al. 2010; Cameron et al. 2011; Nieto et al. 2014; Vray et al. 2019) caused by a shortage of floral resources, habitat loss and fragmentation, intensive use of agrochemicals and pesticides, with all three factors resulting primarily from the agricultural intensification seen during the second part of the twentieth century (Goulson et al. 2015). More recently, several studies have highlighted the contribution of climate change to bumblebee decline (Rasmont et al. 2015; Kerr et al. 2015). Among European bees, the genus *Bombus* includes the highest percentage of species with an extinction risk according to IUCN criteria (Nieto et al. 2014), but diverse communities can still be found in some areas (Iserbyt et al. 2015). Among the 68 species in Europe, 45.6% are decreasing, 29.4% are stable, and 13.2% show positive population trends and an expansion of their distribution (Nieto et al. 2014).

The variability in the response of different species to the same threats is predicted to be influenced by their ecological traits (Rasmont and Mersch 1988; Goulson et al. 2005; Bommarco et al. 2010; Williams et al. 2010; De Palma et al. 2015). Traits correlated with higher rates of species extinction are a narrow geographic distribution, slower reproductive rate, low population density, and ecological specialisation (Brook et al. 2008). Among European bumblebees, the severely declining species tend to be those with a low genetic diversity, a short flight season, a late emergence, a small number of habitat types, a long tongue, and/or a restricted dietary breadth associated with a narrow pollen diet or with flowers with long corolla such as Fabaceae, like *Bombus ruderatus*, *B. humilis* and *B. subterraneus* (Rasmont and Mersch 1988; Goulson and Darvill 2004; Goulson et al. 2005; Kleijn and Raemakers 2008; De Palma et al. 2015; Maebe et al. 2016). However, with regards to tongue length, results are less clear and some studies did not find any consistent pattern between bumblebee species decline at a national scale and this ecological trait (Williams 2005; Connop et al. 2010; Wood et al. 2019). Studies analysing bee population patterns in general, without setting apart bumblebees, could blur any results specific to bumblebees by lumping traits into categories corresponding to the diversity of all bee species (e.g. Aguirre-Gutiérrez et al. 2016). Therefore, taxon-specific multi-trait analyses are needed to identify traits that determine the species most at risk at national level, and design adequate mitigation strategies.

Here, we perform comparative analyses based on 100 years of records from Belgian bumblebee populations using an original specimen-level database compiled from museum collections, scientific monitoring, and opportunistic citizen data from the early nineteenth century to the present day. Belgium followed the typical pattern of agricultural intensification in Western Europe (Christians 1998), and its bumblebee fauna has been studied since the late nineteenth century (Ball 1914, 1920). The aim of this study was to quantify the shifts observed in bumblebee populations of Belgium, and to assess the link with species-specific ecological traits. We measured species richness changes at different spatial scales, as well as variations in their area of occupancy over three time periods (1910–1930, 1970–1989, and 1990–2016). We then assessed the possible association of these changes with species ecological traits.

Materials and methods

Study region

Belgium is a small and densely populated country (11,267,910 habitants in 2016 in 30,528 km², Belgian Federal government 2017) located in NW-Europe. Its temperate oceanic climate is characterised by relatively mild and rainy winters, and relatively cool and wet summers. Between 1990 and 2016, annual mean temperature was 10.2 °C, mean minimum temperature of the coldest month was 0.1 °C, mean maximum temperature of the warmest month was 22.5 °C, and mean annual precipitation was 878 mm (IRM 2017).

The altitude in Belgium does not exceed 700 m but, with the continental gradient, this explains a large part of the geographical East–West variability of environmental gradients in the country (Dufrene and Legendre 1991). Cropland (8504 km²) and urban areas with higher population density (6557 km²) are more associated with lower elevation areas in the northern and western part of the country, while woodland (6046 km²) and grassland (4796 km²) are associated with higher elevation areas in the south-east (Service Public Fédéral Belge 2019).

Two main biogeographic regions can be defined (called here Northern and Southern areas; see Dufrene and Legendre 1991) and are associated with different land use patterns and environmental changes during the last century, which can influence bumblebee population dynamic (see Annex A, Fig. S1).

To study bumblebee population trends, we analysed species richness change at different spatial scales: the whole country, biogeographic regions, and the finer spatial resolution of 10×10 km (corresponding to the UTM squares). The investigated area comprises 382 U.T.M. (Universal Transverse Mercator projection system) 10×10 km squares. This spatial resolution was the best compromise between the amount of data per grid cell and the low spatial resolution of the oldest data (corresponding to the resolution of 5×5 km grid cells).

Bumblebees dataset

We used a dataset consisting of 173,788 bumblebee specimens from 31 species in Belgium which were recorded in the database *Banque de DonnéesFauniques de Gembloux et Mons* (BDFGM; Rasmont et al. 2015), encompassing the period from 1810 to 2016. This database is a compilation of records from museum and university collections (mainly the University of Mons, the University of Liège-Gembloux Agro Bio Tech, and the Royal Belgian Institute of Natural Sciences), scientific monitoring and opportunistic citizen records from NGO initiatives (mainly the Belgian naturalist platforms www.observation.be from Natagora and www.waarnemingen.be from Natuurpunt) (see Annexe B, Table S1). The main originality of our dataset comes from the addition to the former database (used for example in Carvalheiro et al. 2013, 2019) of old Belgian records from the Hymenoptera collection of Ball (1914, 1920) stored at the Royal Belgian Institute of Natural Sciences (RBINS) in Brussels, which mainly covers the 1910–1930 period. We identified and encoded more than 60,000 bumblebee specimens from this collection. We assigned conventional geographical coordinates (corresponding to geographical coordinates of the village church) to these old records based on the locality mentioned on the label below the pinned specimen. Among the 31 species, three were deleted from the dataset because they were represented by less than 10 records: *Bombus cullumanus* (6 records, last one in 1918;

Rasmont 1982), *B. quadricolor* (2 records in 1943; Peeters et al. 1999), and *B. wurflenii* (3 records, last one in 1979; Debaille and Rasmont 1997).

As sampling effort and the amount of data differed greatly between years (Fig. S1), data was aggregated into time-periods (Annexe C, Fig. S2). On the basis of a Principal Coordinate Analysis (PCoA, "vegan" package of R software; Oksanen et al. 2011; see Annexe C, Fig. S3) and in order to maintain consistency with previous studies (e.g. Rasmont et al. 1993; Carvalheiro et al. 2013), we subdivided the dataset into three time-periods: (i) 1910–1930 (P1; 60,525 bumblebee records) which corresponds to the time before the use of agricultural moto-mechanisation and chemical fertilizers, occurring mainly from 1950 to 1970 (Mazoyer and Roudart 2006); (ii) 1970–1989 (P2; 23,862 bumblebee records) which corresponds to the beginning of the application of the Mansholt Plan, which led to a rapid intensification of Belgian agriculture (Christians 1998); and (iii) 1990–2016 (P3; 89,401 bumblebee records) with the establishment of agri-environmental schemes in Europe (AES), which allowed the integration of environmental concerns into the Common Agricultural Policy (CAP) and which became mandatory for EU Member States in 1992 (Kleijn and Sutherland 2003; Batáry et al. 2015).

Species ecological traits

We compiled data on species ecological traits from multiple sources: habitat preference, nesting strategy, tongue length and foraging preferences (BDFGM; Løken 1984; Goulson and Darvill 2004; von Hagen and Aichhorn 2014; see Annexe D, Table S2). Other factors can potentially have effects on the resilience of species, such as genetic diversity or phenology (e.g. emergence date, flight season duration), but due to a lack of data about these traits, we performed statistical analysis focusing on the four ecological traits explained below.

Habitat preference was defined according to three main types of habitat (Rasmont 1988; Goulson 2010): *open* for species living in open habitats (e.g. grasslands, pastures, field margins, heaths, gardens, urban parks), in contrast to *wood* for species living in forest habitats (e.g. deciduous or resinous forest, woodlot, grove), and *edge* for species living at the interface between forest and open lands (e.g. forest edge along a field, hedgerows).

Nesting strategy may be carder, renter, or inquiline. *Carder* species build their colony in above-ground nests using shredded plant material (e.g. moss and twigs of grass and bushes). *Renter* species nest in existing cavities either above or below the ground (e.g. abandoned micromammal nests). *Inquiline* species are Cuckoo bee species (i.e. social parasites species corresponding to the sub-genus *Psithyrus*) in which queens lay eggs in the nest of other species and do not produce workers (Løken 1984). Their reproductive success therefore depends on that of their host colony.

Tongue length can be a proxy to describe the morphological limitation to access to a reduced number of plant species (Brian 1957; Ranta and Lundberg 1980; Graham and Jones 1996). Using data provided by Goulson and Darvill (2004), we classified species into three categories: *short* (shorter than 8 mm), *medium* (between 8 and 9 mm) and *long* (longer than 9 mm) tongues. However, Belgian bumblebees are mainly short-tongued species (16 short-tongued species for a total of 28 species in P1 or 24 species in P3), and consequently presented little variability for this trait. A cross table of modalities between factors showed that the majority of combinations with tongue length were missing. We therefore selected habitat preference and nesting strategy, and rejected tongue length.

Using data from the BDFGM, we calculated a proxy of their degree of foraging preferences on their favourite plant family (i.e. Asteraceae, Ericaceae, Lamiaceae, Fabaceae, Onagraceae, Ranunculaceae, Rosaceae, Scrophulariaceae, or Solanaceae), as the ratio between the number of observed foraging specimens on their favourite plant family and the total number of observed foraging specimens. This index was calculated for queens and workers together separately from males due to differences in their foraging behaviour and their degree of preference (Vray et al. 2017).

Analyses of change in species richness

The greatest difficulty in comparing species assemblages between several time-periods is to 2013manage sampling bias (Carvalheiro et al. 2013; Isaac and Pocock 2015; Maes et al. 2015; van Strien et al. 2013). The number of species recorded in a sample is very sensitive to the number of sampled individuals (Gotelli and Colwell 2001), but historical data do not come from the same monitoring programmes, and by consequence, provide non-standardised sampling. They combine different methodologies with different sampling efforts in time and space. Estimates of variation in species richness based on historical records require a specific methodology that corrects for the effects of sampling effort (e.g. number of records per grid cell and time period), as well as bias associated with collectors, such as preference for rare species, greater attraction of volunteer recorders for places especially rich in biodiversity, under-representation of singletons due to efforts to capture differences due to sexual dimorphism (van Strien et al. 2013 Carvalheiro et al. 2013; Maes et al. 2015; Isaac and Pocock 2015).

For each of the three time-periods, we estimated the species richness for each 10×10 km UTM squares, following the method developed by Carvalheiro et al. (2013). This method allows comparison of species richness estimates among regions and between time-periods with unequal sampling effort and with potential oversampling of rare species (singletons, doubletons) which may bias richness estimates. For each selected cell, we obtained estimates of richness based on species accumulation curves using combination of both extrapolation and interpolation (i.e. extrapolation was only allowed up to three times the number of records of the least sampled period). To exclude low quality cells of the analyses, we only estimated richness change for cells with a ratio of records/number of species higher than 1.5 in each of the two compared time periods, and that had more than 15 records per time period (for poor richness cells). Then, the richness change estimates at each location were log-transformed and analysed using weighted general linear models (GLMw), with the inverse of variance (bootstrapped to correct for under/over-representation of singletons) applied as weight, to obtain unbiased estimates of richness change for each geographical location. This approach, developed at the same spatial resolution than in our study (10×10 km UTM squares), has shown to be robust in various previous studies to estimate richness changes, without correlation with sampling effort change (Carvalheiro et al. 2013, 2019).

We estimated the mean change in species richness between each time-period at the three spatial scales defined before: local (10×10 km grid cells), regional (biogeographic areas) and for the whole country. We also estimated richness changes within each ecological group of bumblebees (i.e. according to their habitat preferences and nesting strategy) at the regional scale and for the whole country.

All analyses described above were made in R (R Development Core Team 2018) using scripts written by Luisa G. Carvalheiro, Petr Keil and Tom van Dooren for R (R Core

team). Scripts and the detailed method are available at https://github.com/lgcarvalheiro/richness.change. We mapped indicators for each time period using QGIS 3.6 software (QGIS Development Team 2019).

Analyses of change in area of occupancy

We estimated variations in species distributions between periods (P1 vs. P2 and P2 vs. P3) using the IUCN A2c index, especially the Area of Occupancy (AOO). This parameter represents the area of suitable habitat currently occupied by the taxon, excluding cases of vagrancy (IUCN 2019). In some cases, (e.g., irreplaceable nesting sites, crucial feeding sites) the area of occupancy is the smallest area essential at any stage to the survival of existing populations, and in many cases AOO can be a useful proxy for population size, because there is generally a positive correlation between AOO and population size (IUCN 2019). The area of occupancy (AOO) was adapted and used for the creation of the Red List of bees in Belgium and Europe (Nieto et al. 2014; Drossart et al. 2018). It corresponds to the ratio of the total number of populations of the species between time-periods (square UTM 10 × 10 km; Annexe E, Fig. S4), weighted by the ratio of sampling effort between periods. This index is calibrated to study species trends at the regional scale and is particularly adapted to a small country like Belgium, as well as their biogeographic regions, with historical database and has a real meaning in terms of prioritizing the implementation of actions in the field.

We assessed changes in the area of occupancy of bumblebees' species within each biogeographical region (Northern and Southern) and at the scale of the whole country. Then we assessed the relationship between species distribution trends across time periods and species ecological traits using linear models (LM). Values of change in AOO were log-transformed and analysed for the country and within biogeographic regions, as a function of habitat preference, nesting strategy, and index of foraging preferences on plant family. We ensured that the residuals' normality and independence requirements were satisfied. The models were computed using the restricted maximum likelihood method in R version 3.4.2 (R Development Core Team 2018).

Results

Change in species richness

At the country scale, a total of 28 species were recorded before 1930 (excluding *B. cullumanus*, *B. quadricolor* and *B. wurflenii*). The species richness fell to 26 species between 1930 and 1990, and to 24 species in the recent period despite the increase in sampling for the whole country (60,525 specimens recorded in P1, 23,862 in P2 and 89,401 in P3, see Table S1). *Bombus confusus* and *B. pomorum* disappeared from Belgium between P1 and P2 (last observation in 1957 and 1947, respectively) and *B. distinguendus* and *B. subterraneus* between P2 and P3 (last observation in 1971 and 1982, respectively). Three of them were already rare in the past (*B. subterraneus*, *B. pomorum*, and *B. confusus*). *Bombus distinguendus* was on the contrary relatively abundant before 1930, and drastically decreased then disappeared in P3 (Fig. S4).

Spatial patterns of changes in species richness were strongly similar between time-periods. Bumblebee richness declined significantly through time and at each spatial scale (Table 1). Due to the strong variation in sampling effort through time (Fig. 1), we

Table 1 Species richness change between P1 (1910–1930) and P2 (1970–1989) and between P2 and P3 (1990–2016) at different spatial scales

| Period	Scale	Number of cells	Nb cells SIGN decline	Nb cells SIGN increase	Estimated change (‰.)	log ratio	SE log ratio	Z-test change	P-value Change
P1 vs P2	10 × 10 km	48	22	6	− 18.079	− 0.0867	0.067	− 2.973	0.003
	Northern area	34	12	4	− 19.535	− 0.094	0.076	− 2.876	0.004
	Southern area	14	5	0	− 17.082	− 0.081	0.097	− 1.940	0.05
	Country	1	–	–	− 7.038	− 0.032	0.004	− 19.768	< 0.001
P2 vs P3	10 × 10 km	144	63	7	− 18.731	− 0.090	0.027	− 7.636	< 0.001
	Northern area	82	32	8	− 14.293	− 0.067	0.035	− 4.447	< 0.001
	Southern area	62	28	3	− 21.342	− 0.104	0.042	− 5.755	< 0.001
	Country	1	–	–	− 8.381	− 0.038	0.009	− 9.793	< 0.001

Nb cells SIGN corresponds to the number of cells with a significant decline/increase in species richness

The mean richness change estimated within the *Northern* and *Southern* areas, was calculated from the estimate richness change at each 10 × 10 km square included in the area
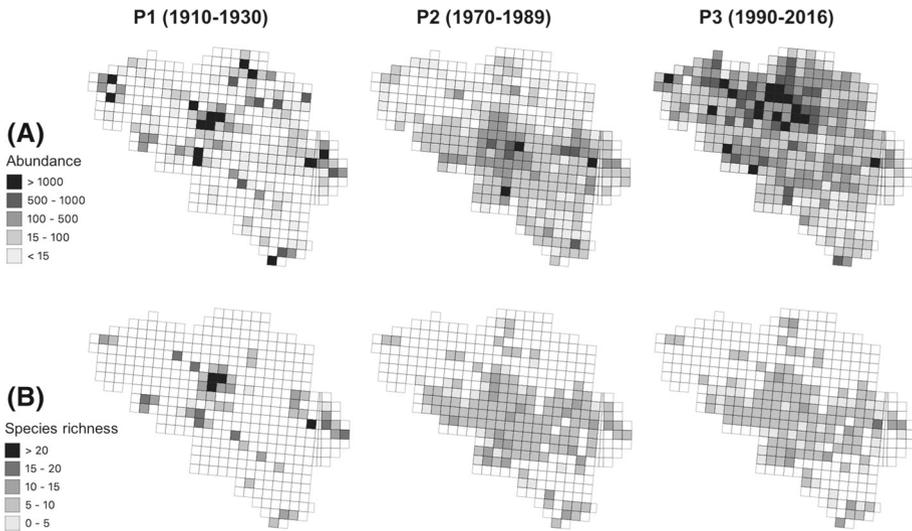
Fig. 1 Spatial distribution of the abundance of specimens (total records) (**a**) and estimated species richness (**b**) at the scale of Belgium for each time-period. Black squares correspond to 10×10 km UTM squares. Estimated species richness was calculated using both Interpolation and extrapolation method. We excluded cells with low quality (i.e. cells with less than 15 records per period and with a sampling effort higher that 20% of the maximum number of species found per cell)
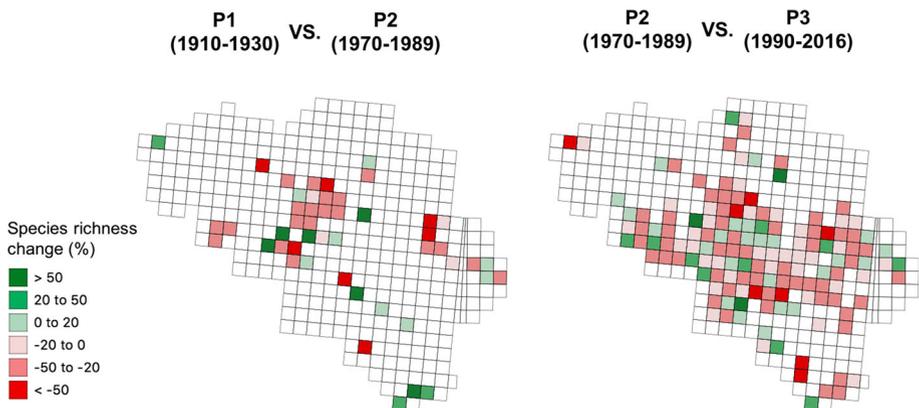
calculated species richness change using the method combining interpolation and extrapolation. However, regardless of the method used (interpolation, extrapolation and combination of interpolation and extrapolation), we found similar patterns of species richness change by time-period and spatial scale (Local at 10×10 km, region and entire country) (Fig. 2).
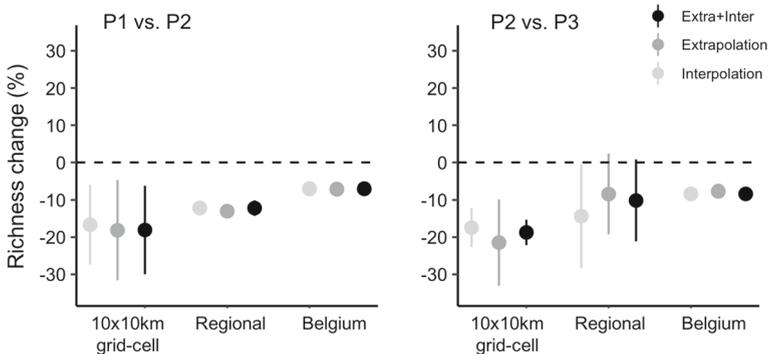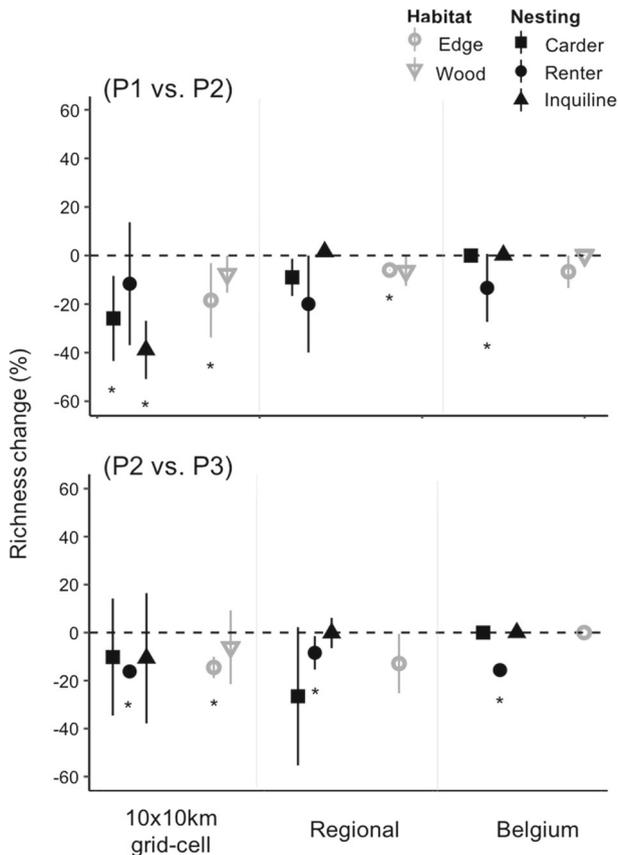

Fig. 2 Change of species richness (estimated weighted mean (in %) ± 95% confidence intervals) between P1 (1910–1930) and P2 (1970–1989) and between P2 and P3 (1990–2016) at different spatial scales (*regional* corresponds to biogeographic areas), using three different methods of calculation: interpolation, extrapolation and combining interpolation and extrapolation ("*Extra + Inter*"; i.e. extrapolation was only allowed up to three times the number of records of the least sampled period). Dotted line corresponds to no change in species richness (0%)

Among the sampled 10 × 10 km grid-cells, some locations show higher species richness than others depending on the time-period, while other locations show a high value over the three time-periods (Fig. 1). The sampled grid-cells showing the highest species richness before 1930 are around Brussels and in eastern Belgium, and after 1970 in southern-eastern Belgium. Through time, some cells showed a significant increase of richness at 10 × 10 km scale, but the majority of analysed cells (with an observation number meeting the selection criteria, both in the pre- and post-period) showed a significant decline tendency (Table 1, Fig. 3). Values of estimated richness change (corrected according to sampling effort) between periods for each 10 × 10 km grid cells are provided in Tables S3 and S4 (respectively, between P1–P2 and P2–P3). At the regional scale, even if both of the biogeographic areas showed a significant decline in species richness between all time-periods, decline in the Southern area was higher between P2 and P3 than between P1 and P2, and was more important than in the northern region, where the decline was lower in P2–P3 (− 14%) than in P1–P2 (− 19%) (Table 1).

At all time-periods, the most affected group at the largest scales (regional and whole country) was the *renter* bumblebees (nesting in existing cavities either on or below the ground) with a significant richness decline (Fig. 4). On the contrary, at the local scale (10 × 10 km grid-cells) before 1990 (between P1 and P2), the richness of *carder* (nest in above-ground nests) and *inquiline* (social parasites species) bumblebees fell significantly, while only renter species showed a significant richness change between P2 and P3 (after 1990). Due to the poor representation of open land species in our database, we could not calculate estimated richness change for this group. The richness of edge species (living at the interface between forest and open lands) declined significantly at the local scale (10 × 10 km) for both time-periods and at the regional scale before 1990.

Fig. 3 Spatial distribution of estimate species richness change (in%) between P1 and P2, and P2 and P3. Squares correspond to 10 × 10 km UTM squares. Richness changes were calculated using the weighted value (based on the inverse of the variance) and both interpolation and extrapolation method (i.e. extrapolation was only allowed up to three times the number of records of the least sampled period). We only selected cells with records in both the pre-period and post-periods and, with a minimum of 15 records for each period and a sampling effort higher that 20% of the maximum number of species found per cell per period

Fig. 4 Species richness change (estimated weighted mean (in %) ± 95% confidence intervals) between P1 (1910–1930) and P2 (1970–1989) and between P2 and P3 (1990–2016) at the different spatial scales (*regional* corresponds to biogeographic areas) and according to habitat preferences and nesting strategy of bumblebee species. Richness changes were calculated using combined interpolation and extrapolation method. Stars (*) below the points indicate a significant richness change. Horizontal dotted line corresponds to no change in species richness (0%). Carder: nest in above-ground using shredded plant material; Renter: nest in existing cavities either on or below the ground; Inquiline: social parasites species; Wood: species living in forest habitats; Edge: species living at the interface between forest and open lands; *Open* habitat group does not appear due to an insufficient number of cells to the calculation

Change in areas of occupancy

The trends observed in area of occupancy between P1 and P2 showed that 16 species drastically regressed (including 2 extinct species), three were stable, and nine expanded (Table 2, see also Annex E for maps of bumblebee species rank by period). Between P2 and P3, 2 other species disappeared and 11 others drastically declined. Nine species present the same trend in the two time-periods comparisons. Seven were always decreasing (until the extinction of *B. distinguendus* and *B. subterraneus*), *B. hortorum* remained stable and only *B. lapidarius* was always expanding.

The most geographically restricted species in P1 were *B. norvegicus*, *B. pomorum* and *B. confusus*. Among them, two went extinct (*B. pomorum* and *B. confusus*) in P2, while *B.*

Table 2 Trends based on the ratio of species Area of Occupancy (AOO) between time-periods, estimated using the A2c IUCN index method between P1 (1910–1930) and P2 (1970–1989), P2 and P3 (1990–2016), and between P1 and P3

Taxon	Number UTM P1	Number UTM P2	Number UTM P3	A2c_AOO (P1 vs P2)		A2c_AOO (P2 vs P3)		A2c_AOO (P1 vs P3)	
B. barbutellus	48	10	4	− 88.10	CR	− 69.67	EN	− 96.39	CR
B. bohemicus	26	69	58	51.65	(+)	− 36.26	VU	− 3.33	(=)
B. campestris	50	38	126	− 56.57	EN	151.45	(+)	9.20	(=)
B. confusus	17	0	0	− 100	EX	/	/	− 100	EX
B. cryptarum	38	63	40	− 5.26	(=)	− 51.85	EN	− 54.38	EN
B. distinguendus	51	2	0	− 97.76	CR	− 100	EX	− 100	EX
B. hortorum	85	173	241	16.30	(=)	5.64	(=)	22.86	(+)
B. humilis	31	8	7	− 85.25	CR	− 33.65	VU	− 90.21	CR
B. hypnorum	35	165	253	169.39	(+)	16.28	(=)	213.24	(+)
B. jonellus	27	6	39	− 87.30	CR	392.92	(+)	− 37.41	VU
B. lapidarius	75	167	308	27.24	(+)	39.86	(+)	77.95	(+)
B. lucorum	46	152	91	88.82	(+)	− 54.60	EN	− 14.27	(=)
B. magnus	35	5	25	− 91.84	CR	279.17	(+)	− 69.05	EN
B. muscorum	44	5	2	− 93.51	CR	− 69.67	EN	− 98.03	CR
B. norvegicus	4	17	15	142.86	(+)	− 33.09	VU	62.50	(+)
B. pascuorum	98	240	332	39.94	(+)	4.90	(=)	46.80	(+)
B. pomorum	12	0	0	− 100	EX			− 100	EX
B. pratorum	75	220	287	67.62	(+)	− 1.07	(=)	65.82	(+)
B. ruderarius	51	91	45	1.96	(=)	− 62.50	EN	− 61.76	EN
B. ruderatus	51	3	6	− 96.64	CR	51.67	(+)	− 94.90	CR
B. rupestris	46	11	55	− 86.33	CR	279.17	(+)	− 48.19	VU
B. soroeensis	20	24	33	− 31.43	VU	4.27	(=)	− 28.50	NT
B. subterraneus	30	8	0	− 84.76	CR	− 100	EX	− 100	EX
B. sylvarum	38	16	10	− 75.94	EN	− 52.60	EN	− 88.60	CR
B. sylvestris	35	100	92	63.26	(+)	− 30.23	VU	13.91	(=)
B. terrestris	53	174	208	87.60	(+)	− 9.35	(=)	70.06	(+)
B. vestalis	28	26	59	− 46.94	VU	72.08	(+)	− 8.69	(=)
B. veteranus	46	19	6	− 76.40	EN	− 76.05	EN	− 94.35	CR

Red List category adapted for Belgium scale are *EX (Extinct)*: A2c = − 100%; *CR (Critically Endangered)*: A2c < − 80%; *EN (Endangered)*: − 80% < A2c < − 50%; *VU (Vulnerable)*: − 50% < A2c < − 30%. If the ratio is < − 20%, it reveals species defined as Near Threatened (NT) that would be at the limit of the threshold of 30% with significant decline trends. (=) and (+) represent respectively stable (− 20% < A2c < 20%) and positive significant trends (A2c > 20%). UTM_1, 2 and 3 correspond to the number of 10 × 10 km cells with positive occurrence of the species at P1, P2 and P3, respectively

norvegicus generally increased on the whole century. The four more widespread species before 1930 were, by descending order, *B. pascuorum*, *B. hortorum*, *B. lapidarius*, and *B. pratorum*. These species remain among the most widespread ones in the recent period and increased their area of occupancy, even if only *B. lapidarius* was still increasing after 1990, while the three other species showed a stabilisation of their area of occupancy (Table 2). Species showed non-constant trends over time: some were increasing (*B. bohemicus, B. lucorum, B. norvegicus, or B. sylvestris*) or stable (*B. cryptarum, B. ruderarius*) between P1 and P2 but decreasing between P2 and P3, and others show a regression between P1 and P2 followed by an expansion between P2 and P3 (*B. campestris, B. jonellus, B. magnus, B. ruderatus, B. rupestris* and *B. vestalis*).

With regard to the differences in trends according to species ecological traits, between P1 and P2 same patterns were observed at the regional scale (Northern and Southern areas) and for the whole country (Fig. 5). Species living in open lands (e.g. croplands and grasslands) showed a strong decrease in their area of occupancy while species living in wooded habitats showed stable or positive trends. Between P2 (1970–1989) and P3 (1990–2016), difference between species living in open or wood lands at the whole country could be mainly due to trends observed in the Northern area (Fig. 5d, e). Indeed, in the Northern area species living in open habitats showed a higher regression of their area of occupancy than species living in wooded habitat or edges (as observed at the Belgium scale), whereas trends were not significant in the Southern area. Moreover, after 1990 (between P2 and P3), species showed a significant trend according to nesting preferences only in the Northern area. We observed a high regression in the area of occupancy of carder species (i.e. nesting in above-ground nests), while no significant difference was observed between bumblebee groups in the Southern area. We did not find significantly different bumblebee distribution trends depending on the foraging preferences, regardless of time-period and spatial scale.

Discussion

Changes in Belgian bumblebee communities and comparison with European trends

We showed that Belgian bumblebee communities strongly declined in their species richness, and that numerous species decreased in terms of distribution since the last century, particularly between 1930 and 1990. Species richness decreased from 28 to 24 species, with the disappearance of *B. confusus*, *B. distinguendus*, *B. pomorum*, and *B. subterraneus* (Table S1). Furthermore, the species richness decreased continually across all time-periods (Table 1). This decline in richness was generalised at the country scale with an estimated negative change of − 7%, but also showed strong variations at the smallest scales. Estimates change were around − 18% and − 12%, respectively at the 10 × 10 km grid-cell and regional scale (Table 1). We observed some exceptions where communities remain relatively rich and the richness increased (Fig. 3). The decrease in species richness occurred along a significant change in the area of occupancy of bumblebee species (Table 2). A large part of species once widespread dramatically decreased between 1930 and 1990 (i.e. 15 on the 28 species present in P1) but some others increased their distribution and became very widespread in Belgium (e.g. *B. pascuorum*, *B. pratorum*, *B. terrestris*).

Previous Belgian studies based on abundance trends have estimated that, among the 28 species, 14 to 19 species were in regression during the last century (Rasmont and Mersch 1988; Rasmont et al. 1993). Similar trends were observed in other countries, such as the UK and Ireland (Edwards and Williams 2004; Williams 2005; Fitzpatrick et al. 2007), Poland (Kosior et al. 2008), Hungary (Sárospataki et al. 2005), and Denmark (Dupont et al. 2011). At the European scale, four species recorded from Belgium are categorised as "vulnerable" by the IUCN (Nieto et al. 2014; Rasmont et al. 2015; Table S2): *B. confusus*, *B. distinguendus*, *B. pomorum* and *B. muscorum*. *Bombus distinguendus* is also "near threatened" in Sweden and "critically endangered" in Denmark (Dupont et al. 2011; Bommarco et al. 2012). Three species (*B. confusus*, *B. distinguendus* and *B. pomorum*)
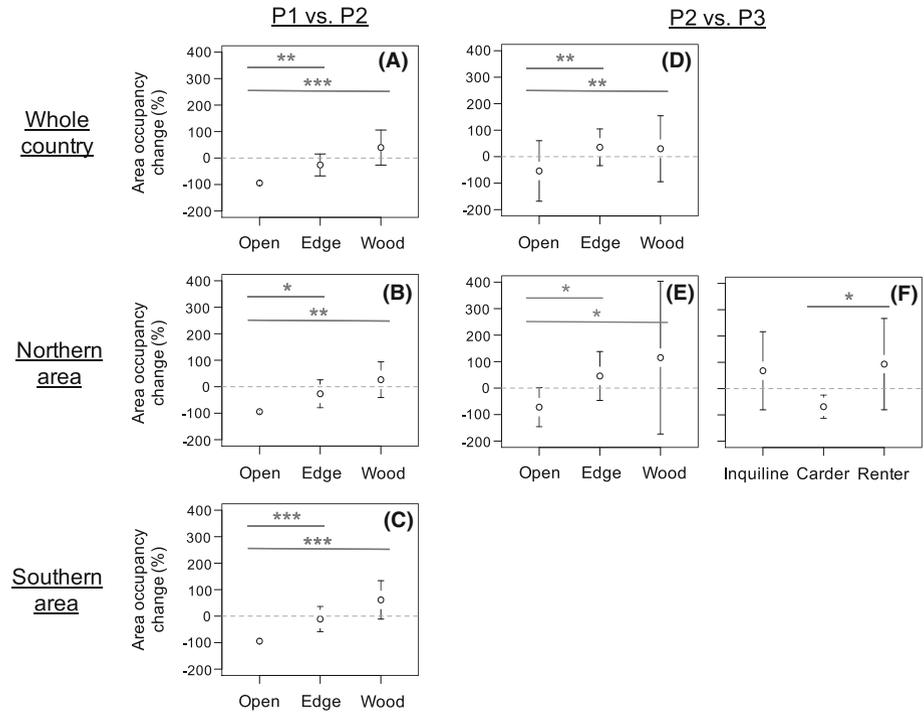
Fig. 5 Change (mean (in %) ± 95% confidence intervals) in area occupancy of the bumblebee species (from the reduction in area of occupancy index A2c_AOO—of the IUCN Red List) according to significant ecological traits in models: habitat preference (**a–e**) and nesting strategy (**f**), between P1 (1910–1930) and P2 (1970–1989) (**a–c**) and between P2 and P3 (1990–2016) (**d–f**) at the whole country (**a, d**) and regional scale (Northern (**b, e, f**) and Southern (**c**) areas. Horizontal lines with stars indicate significant difference between two ecological groups (*0.05 > p-value > 0.01; **0.01 > p-value > 0.001; ***0.001 > p-value). Grey dotted line in each graph represent no change (= 0%) in the area of occupancy. Nesting strategy: *Carder*: nest in above-ground nests using shredded plant material; *Renter*: nest in existing cavities either on or below the ground; *Inquiline*: social parasites species. Habitat preferences: *Wood*: species living in forest habitats; *Edge*: species living at the interface between forest and open lands; *Open*: species living in open habitat

disappeared in Belgium and *B. muscorum* decreased drastically from 1,398 observations in 1910–1930 to only five observations in 1990–2016.

All other species present in Belgium are categorised as "least concern" at the European scale (Nieto et al. 2014; Rasmont et al. 2015, Table S2), and their European population trends are broadly similar to those observed in Belgium. The eight species with a decreasing trend in Europe also have a regressing trend in Belgium in terms of their area of occupancy (*B. barbutellus, B. humilis, B. ruderarius, B. ruderatus, B. sylvarum, B. veteranus*) or have even disappeared (*B. subterraneus*). Among the six species with an increasing trend in Europe, five present a clear expending trend in Belgium across the last century (*B. hypnorum, B. lapidarius, B. pascuorum B. pratorum* and *B. terrestris*). *Bombus hypnorum*, a common bumblebee species in continental Europe, is a perfect example of successful colonisation in all northern Europe and showed the strongest increase in its area of occupancy between P1 and P3. It also increased in Denmark (Dupont et al. 2011) and Hungary (Sárospataki et al. 2005) and has completely colonised the UK over the past two

decades, after a first record in 2001 (Goulson and Williams 2001; Benton 2006; Rasmont et al. 2015; Bees Wasps and Ants Recording Society 2019). *Bombus terrestris* had a global tendency to increase since 1930, even if we have observed a stabilisation between 1970 and 1990 (Table 2). On the contrary, its cuckoo species, *B. vestalis,* showed a clear regression in Belgium before 1990 (Table 2). *Bombus hortorum* significantly increased its distribution in Belgium, while it slightly decreased in Denmark (Dupont et al. 2011), Britain (Williams 2005; Fitzpatrick et al. 2007), and Sweden (Bommarco et al. 2012). Finally, *B. norvegicus*, one of the seven species with a stable trend at the European scale, had a general increase of its area of occupancy, even if its distribution significantly regressed in Belgium since 1990. Overall, we can conclude that the trend of Belgian bumblebee populations is similar to other countries in NW Europe, but seems to be worse than the mean European trends at the continental scale.

A contraction of the area of occupancy could be an indicator of a risk of extinction debt, i.e. the future extinction of species due to events (e.g. habitat destruction) that occurred in the past (Tilman et al. 1994; Kuussaari et al. 2009). This time-delayed but deterministic extinction can also affect dominant species (Tilman et al. 1994). The phenomenon of extinction debt has already been suggested for pollinators in south-eastern Sweden (Bommarco et al. 2014) and the Netherlands (Aguirre-Gutiérrez et al. 2015), where historical modifications of landscape better explain current species distribution and the recent changes in species richness than current landscape. Therefore, even if several species persist today, sometimes in very few local populations (e.g. *B. barbutellus, B. humilis, B. muscorum, B. ruderatus, B. sylvarum, B. veteranus*), they could still become extinct due to past drivers that weakened their populations, even if these impacts have ceased or slowed down today, as shown by the IUCN index classification (Table 2).

Relation between species ecological traits and population changes

We found that before 1990, regardless of spatial scale, species living in open habitats were more prone to decline than species preferring forests (both in term of richness change and contraction of area of occupancy), as found in previous studies (Rasmont and Mersch 1988). These habitats correspond to agricultural landscapes (e.g. crop areas, temporal and permanent grasslands) which suffered from stronger modifications than wooded areas, due to the intensification of agricultural practices with the beginning of the agricultural revolution (Rasmont and Mersch 1988; Goulson et al. 2005; Kosior et al. 2007; Williams and Osborne 2009). This trend was still observed at the 10×10 km resolution after 1990 (between P2 and P3). Renter species (i.e. ground nesting species) strongly depend on these open habitats for their nesting resources and we observed that it was the bumblebees group most affected by reduction in their richness at the country and regional scales.

The area of forests increased in Belgium over the last 150 years by 25% (Société Royale Forestière de Belgique 2018), which can explain the positive or stable trends for species living in these habitats. However, they mainly occur in the Southern area (around 2000 km^2 in the Northern area, compared to 6500 km^2 in the Southern area; see Fig. S1). Some locations in the northern and central parts of Belgium were characterised by a strong reduction of ligneous hedgerows, particularly urbanisation and the beginning of the application of the Mansholt Plan in 1970 promoting the rapid intensification of agricultural areas (Christians 1998). In accordance with these land use changes at the local scale, we showed that the richness of carder species (i.e. nest in above-ground nests, using hollow stems, tree cavities for example or shredded plant material) decreased the most at the

10 × 10 km resolution before 1990 (between P1 and P2, Fig. 4). This negative impact on carder species continued after 1990, with a sharp reduction in their area of occupancy in the Northern area (Fig. 5e). We also have showed that the *renter* bumblebees (nesting in existing cavities either on or below the ground) had a significant richness decline between P2 and P3, regardless the spatial scale, while between P1 and P2 this decline was significant only at the whole country (Fig. 4). This strongest decline after 1970 could be also explained by the strong intensification of agricultural practices, promoting by the Mansholt Plan in 1970. These changes were associated to low perennial habitat ratio, higher use of inputs and strong ground disturbance with deep and frequent ploughing, reducing nesting opportunities for renter bees in the landscapes.

The Northern area is also characterised by strong urbanisation. While settlements areas stayed constant during each time period in the Southern area (around 1050 km^2, i.e. 7.7% of the region), around 1600 km^2 were urbanised between P1 and P2 in the Northern area (i.e. 7% of the region), for a total area of settlement of 5800 km^2 in P3 (Fig. S1). That could partly explain the increasing trends of bumblebee species living in these habitats (e.g. *Bombus hypnorum*). Crowther et al. (2014) showed that the density of *B. hypnorum* is positively correlated with the extent of urban areas. This species nests frequently near human settlements, preferring building its nest above ground, often using old inhabited bird boxes (Benton 2006; Bees Wasps and Ants Recording Society 2019).

The richness of parasitic species (i.e. inquilines, commonly called "cuckoo bees") showed a strong decline only at the 10 × 10 km resolution before 1990, with an estimate change of − 39% (Fig. 4), probably due to the beginning of massive agricultural intensification in the 1950's through the whole country. During this same period, four of the seven cuckoo bumblebees also showed a significant decrease of their area of occupancy (*B. barbutellus*, *B. campestris*, *B. rupestris* and *B. vestalis*) and only *B. sylvestris* significantly extended through the country (Table 2). Cuckoo bees depend on their host species for their reproduction and are therefore vulnerable to changes in their host abundance and distribution, making them more prone to decline. Generally, parasitic species followed the main trend of their host during the last century (between P1 and P3), with the slight difference that they showed a stable trend in their area of occupancy when their host had an increasing distribution (Table 2). However, as in other studies (e.g. Kosior et al. 2008), we showed that some species do not follow the same trends than their hosts. *Bombus barbutellus* and *B. rupestris* have a decreasing area whereas their host species, *B. hortorum* and *B. lapidarius*, remain among the most abundant and widespread bumblebee species at the national scale (Table 2). This could suggest that other causes than their host population trends could act on cuckoo species vulnerability, such as their climatic niche breadth (generally smaller than that of their host; Rasmont et al. 2015) or the availability of their floral resources (mainly thistles, Vray et al. 2017).

Foraging preferences did not explain differences in species trends during either the first or second part of the century, while previous studies explained the regression of some bumblebee species by the drastic reduction of leguminous crops, and especially clover crops (i.e. *Trifolium* spp.; Rasmont and Mersch 1988; Goulson and Darvill 2004; Goulson et al. 2005; Carvell et al. 2006; Bommarco et al. 2012). However, other studies indicated that floral preferences may not be enough to explain complex interactions between ecological traits and environmental factors that may be associated with higher susceptibility of bumblebee declines (Williams and Osborne 2009; Connop et al. 2010). In Belgium, the area covered by forage leguminous crops decreased from 164,000 hectares before 1910 to 45,000 in 1950, 13,000 in 1970, 2300 in 1990 and only 3000 hectares in 2014 (Rasmont and Mersch 1988; Belgian Federal government 2017). Others studies have also shown the

importance of Asteraceae, especially thistles (e.g. *Carduus* spp. and *Cirsium* spp.) for male diet of some bumblebee species (Carvell et al. 2007; Vray et al. 2017; see Annexe D). Foraging preferences could impact the local bumblebee richness via the diversity and availability of local floral resources. We can hypothesize that the spatial resolution of 10 × 10 km was too coarse to study this ecological trait on bumblebee populations and could show a null result as a result of a smoothing effect on the variability.

Difference in dynamic of land use change and bumblebee trends

Our analyses showed similar trends in species richness change between P1 and P2 and between P2 and P3, with the same level of estimated changes (in%) for a same spatial scale (Table 1). However, we observed a reduced number of species with a contraction of their area of occupancy between P2 (1970–1989) and P3 (1990–2016), compared to the trends between P1 (1910–1930) and P2 (Table 2). We also show differences between periods regarding the relation between ecological traits of bumblebee species and their population trends. These differences between P1–P2 and P2–P3 could result from the different dynamic of change in land use before and after the 1980's, and which are also pronounced between the two main geographic areas. Most of changes in land use in the Southern area occurred between P2 and P3 with an important increase of both open crop lands and forest areas, to the detriment of grasslands (see Fig. S1). These could explain the strong species decline in the Southern area without differential response among species according to their ecological niches and traits (e.g. open vs woodland habitat).

Between P1 and P2, agriculture fundamentally changed with the beginning of massive agricultural intensification in the 1950s (and the Mansholt Plan in the 1970s), characterised by changes in crop rotations (simpler and faster), landscape homogenisation, mechanisation of practices, and use of chemical inputs (fertilizers and pesticides) (Robinson and Sutherland 2002; Baessler and Klotz 2006). All these new practices led to the transformation of a traditional countryside comprising small mixed crops with hedges and trees, toward intensive and homogeneous landscapes, with large monocultures, intensive pastures and grasslands cut regularly for silage (Christians 1998; Mazoyer and Roudart 2006). This simplification of agricultural landscapes reduced nest sites availability for bumblebees as well as the composition and the spatial and temporal availability of floral resources (Goulson et al. 2015). The implementation of conservation measures that have become more widespread across Belgium during recent decades could also partly explain the lower variations in the area of occupancy of species between P2 and P3 than between P1 and P2 (Carvalheiro et al. 2013). Indeed, measures such as sowing bee-friendly plants on arable field margins appear to be favourable to bumblebees and bees, at least to the very generalist species (Croxton et al. 2002; Carvell et al. 2004; Pywell et al. 2006). The composition of flower mixes sown should take into account the various preferences of each caste and a continuous bloom until late in the season, with, for example a high proportion of Fabaceae (especially *Trifolium* spp.) for queens and workers of a numerous species and Asteraceae (especially *Carduus* spp., *Cirsium* spp., and *Centaurea* spp.) for males (Carvell et al. 2007; Vray et al. 2017). In this way, some legislation should still be reviewed, such as the ones requiring the destruction of thistles (i.e. *Carduus* and *Cirsium* spp.; Vray et al. 2017). In addition to the improvement of floral resource availability and diversity, nesting sites could be provided by withered grass and tussocks found in banks, field margins, hedgerows and edges between open and wooded habitat for example (Svensson et al. 2000; Croxton et al. 2002; Kells and Goulson 2003).

Conclusions and recommendations

Based on an original data set of 173,716 specimens at the Belgian scale throughout one century, we found a high proportion of species declining, analysing both richness changes and species range size during the last century in Belgium. The three dominant species remain the same across time-periods and even increase their dominance, leading to community homogenisation in most Belgian regions. Some species that were once very widespread are drastically declining, while some others are increasing, leading to major shifts in community composition. Our study showed that historical data from various unstandardized sampling protocols can be combined to study changes in bumblebee community patterns at large spatial and temporal scale, using appropriate statistical methods. Some groups of bumblebees seem to be more sensitive to decline, depending on landscape changes and environmental intensification.

However, future research will need to improve; first, the management of sampling bias to assess species dominance and abundance. Second, the estimation of reciprocal roles of the various factors of decline in the observed trends at different spatial scales have to be improve to consider local drivers of bumblebee community patterns (i.e. local quality and quantity of floral and nesting resources). Third, the impact of climate change also needs to be considered in studies over large temporal extents, due to their direct and indirect impacts (e.g. composition and abundance of plant community, asynchrony between phenology of plant resources and associated pollinator species) on bumblebee communities. Very few studies investigate the several drivers of bumblebee decline in the same analysis (but see Goulson et al. 2015; Aguirre-Gutiérrez et al. 2016), despite the fact that they are highly likely to act in synergy (Brook et al. 2008; Tylianakis et al. 2008; Potts et al. 2010; Schweiger et al. 2010; Casey et al. 2015; Schleuning et al. 2016).

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