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Article in *Basic and Applied Ecology* · March 2021

DOI: 10.1016/j.baae.2021.03.008

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Long-term data shows increasing dominance of *Bombus terrestris* with climate warming

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Received 21 October 2020; accepted 15 March 2021

Available online 16 March 2021

Abstract

While many bumblebee species decline due to climate and land-use changes, others cope well with contemporary conditions. One example is *Bombus terrestris*, which is common in intensively managed agricultural landscapes. During the 20th century its subgenus, which includes the *B. lucorum* complex (*B. lucorum*, *B. cryptarum* and *B. magnus*) came to dominate Scandinavian bumblebee communities, but the specific contribution of *B. terrestris* remains to be understood. Using historical data on males, we assessed how the relative abundances of *B. terrestris* and the *B. lucorum* complex changed over the past 150 years in southernmost Sweden. We tested if these changes differed between simplified and mixed landscapes and whether the relative abundance of *B. terrestris* was related to annual mean temperatures. Because floral availability has advanced as a response to climate change, we also tested if the activity period of males (estimated as catching date) has advanced and whether the advancement differs between taxa. The relative abundance of *B. terrestris* increased similarly in both landscapes, from 21% to 79% over the period, and this was largely explained by increasing temperature. Male activity period has advanced similarly in the two taxa, with 41 days between 1900 and 2015. Although the dominance of *B. terrestris* correlates clearly with annual mean temperature, it remains to disentangle why. It also remains to understand whether the success of *B. terrestris* occurs at the expense of other species or simply reflects that this species copes better with contemporary conditions.

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Keywords: Buff-tailed bumblebee; White-tailed bumblebee; Landscape complexity; Global change

Introduction

Bumblebee queens found their nest in spring, after emerging from diapause. In the beginning, the queen forages and provides the brood with pollen and nectar (Mossberg & Cederberg, 2012). A few weeks later, the first workers hatch and take over the responsibility for foraging and nest tending (Mossberg & Cederberg, 2012). After some time, the colony

shifts to producing males and new queens, i.e. sexually reproducing units. When the new queens have mated, they find a place to hibernate, whereas workers, males and old queens die before the winter (Mossberg & Cederberg, 2012).

Bumblebees are well-adapted to traditional agricultural landscapes where semi-natural habitats and extensively managed fields provide them with foraging and nesting resources throughout the season (Kells & Goulson, 2003; Smith et al., 2014). However, due to agricultural intensification and the conversion of semi-natural habitats to arable land, foraging and nesting habitats have become scarce

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(Ihse, 1995; Stoate et al., 2001), which is now threatening bumblebee populations (Benton, Vickery, & Wilson, 2003; Goulson, Nicholls, Botias, & Rotheray, 2015; Persson & Smith, 2013; Potts et al., 2016).

In recent years, an additional threat towards bumblebees has been noticed, namely climate change (Kerr et al., 2015; Soroye, Newbold, & Kerr, 2020). Climate change could affect bumblebees in various ways, for example by heat stress during summer heat waves and increased susceptibility to diseases due to milder winters (Rasmont & Iserbyt, 2012). In addition, drought and altered plant phenology can aggravate forage limitation (Ogilvie et al., 2017; Rasmont & Iserbyt, 2012). Summer heat waves and droughts usually occur by the end of summer, making species with early reproduction, i.e. production of new queens and males less sensitive to climate change than species with later reproduction (Rasmont & Iserbyt, 2012). Thus, a possible adaptation to climate change could be to advance the colony cycle and reproduction.

Species differ in their sensitivity to land-use and climate change. Generalist species, which easily adapt to new conditions, are in general less sensitive than specialist species (Clavel, Julliard, & Devictor, 2011). The buff-tailed bumblebee (*Bombus terrestris*) is a highly adaptive super-generalist (Mossberg & Cederberg, 2012) and can be found in strongly modified environments, such as urban areas (Hart, Maebé, Brown, Smaghe, & Ings, 2020) and contemporary agricultural landscapes (Walther-Hellwig & Frankl, 2000). During the past century, Scandinavian bumblebee communities have been increasingly dominated by the subgenus *Bombus* sensu stricto, consisting of *B. terrestris* and the *B. lucorum* complex (*B. lucorum*, *B. magnus* and *B. cryptarum*). Due to overlapping morphology, workers of these four species cannot be reliably distinguished without genetic methods and our understanding of their ecological differences is thus limited. Yet, known differences between species indicate that the increasing dominance of *Bombus* sensu stricto is not equally attributed to all four species. For example, *B. terrestris* has a wider ecological niche than the *B. lucorum* complex (Rasmont & Iserbyt, 2010–2014) and could thus be expected to be less sensitive to land-use and climate changes (Clavel et al., 2011). *B. terrestris*, is associated with open habitat (Svensson, Lagerlöf, & Svensson, 2000) and tends to be common in simplified agricultural landscapes (i.e. landscapes dominated by arable fields), where most other bumblebee species are less successful (Rollin et al., 2020). There are many potential reasons for this, for example that it has a large thorax-width and colony size, allowing it to utilize resources from distant patches (Persson, Rundlöf, Clough, & Smith, 2015; Walther-Hellwig & Frankl, 2000; Westphal, Steffan-Dewenter, & Tschardtke, 2006), which is beneficial in a highly fragmented landscape (Smith et al., 2014). The three species of the *B. lucorum* complex have smaller thorax-width and colony sizes and are instead associated with edge habitats in forest-dominated landscapes (Løken, 1973; Mossberg & Cederberg, 2012; Svensson et al., 2000).

Compared to the *B. lucorum* complex, *B. terrestris* has a shorter queen winter diapause (Rasmont & Iserbyt, 2010–2014), and in recent years, there have even been observations of winter-active *B. terrestris* in southern UK, possibly due to climate warming and all-year-round provision of pollen resources in cities (Hart et al., 2020; Stelzer, Chittka, Carlton, & Ings, 2010). In Sweden, where *B. terrestris* still needs a winter diapause, the spring queens are usually observed a few weeks earlier than those of *B. lucorum*, whereas the males often hatch a few weeks later in summer, possibly because it takes longer time to build up the large colonies of *B. terrestris* (Cederberg, pers. comm.). The queens of *B. cryptarum* are observed simultaneously with those of *B. lucorum*, whereas *B. magnus* has a later queen emergence and a later density peak of workers and males, likely reflecting a specialization on late-flowering heathland species (Scriven, Whitehorn, Goulson, & Tinsley, 2016).

Despite large distributional overlaps, the *B. lucorum* complex and in particular *B. cryptarum*, has a substantially more northern range boundary and occurs at higher elevations than *B. terrestris* (Geue & Thomassen, 2020; Løken, 1973; Rasmont & Iserbyt, 2010–2014). However, during the past half-century, *B. terrestris* has expanded its geographic range northwards, possibly due to climate warming and trading with the species (Martinet et al., 2015). To conclude, as *B. terrestris* seems to be well adapted to both climate and land-use changes that have occurred during the past century, we hypothesized that the increasing relative abundance of *Bombus* sensu stricto (Bommarco, Lundin, Smith, & Rundlöf, 2012) has been driven mainly by *B. terrestris*.

Using specimens from the entomological collections at Lund University, we assessed how the relative abundance of *B. terrestris* compared to the *B. lucorum* complex has changed over time and with mean annual temperature, as an estimate of climate warming. As we expected that increasing landscape simplification, i.e. increasing dominance of arable fields, would benefit the relative abundance of *B. terrestris*, we tested if the changes over time depended on landscape simplification. We also assessed whether a potential shift among species could be explained by differences in the ability to adapt the colony cycle to earlier forage availability and spring arrival by comparing phenology shifts in the two taxa.

Materials and methods

Data collection

We used historical data from the entomological collections of the Biological Museum at Lund University (<https://doi.org/10.15468/dahk2a>) and assumed that the relative numbers of collected individuals per species reflected their relative abundances in the field (Bartomeus et al., 2013; Mathiasson & Rehan, 2019). The specimens had been collected with both random and targeted sampling, but according to the staff at the museum, there had been no targeted

sampling focusing particularly on any of the species in this study. Four previous employees at the museum had collected more than 80% of the specimens and all of them had sampled both *B. terrestris* and the *B. lucorum* complex. The samples that we used were already determined to the species level, but not to caste, which was done within this study. Workers were not considered, since workers of these species cannot be reliably distinguished from each other without genetic methods (Williams et al., 2012). Four species of the subgenus *Bombus* sensu stricto (*B. terrestris*, *B. lucorum*, *B. cryptarum* and *B. magnus*) are native to the region (Cederberg, pers. comm.). Two of these, *B. cryptarum* and *B. magnus*, were considered varieties of *B. lucorum* during parts of the study period and the division into true species has not yet been accepted by all authors (Rasmont & Iserbyt, 2010–2014). We thus expected that specimens noted as *B. lucorum* included *B. cryptarum* and *B. magnus*, and therefore pooled the few specimens identified as the latter two (one and seven males, respectively, and no queens) with *B. lucorum*.

We collected data on when and where the specimens had been caught from the information on their labels. Specimens with insufficient information were discarded. We only included specimens collected in Scania, the southernmost county of Sweden. This decision was made because (1) *B. terrestris* is known to expand northwards, and by limiting the area, we reduced the risk of accidentally including recently colonized areas where the relative abundance of *B. terrestris* of necessity increases during the colonization, (2) we expected to obtain more robust results by doing this, because most of the specimens at the museum had been collected in Scania, and (3) site information on the labels is sometimes limited, difficult to interpret, and thus requires geographic knowledge about the region and collectors, which we have specifically for Scania.

For males, we obtained data for 1254 *B. terrestris*, 758 *B. lucorum*, seven *B. magnus* and one *B. cryptarum*, collected during 61 individual years over a period of 145 years (1871–2015, see Appendix A: Tables 1 and 2). We obtained data for 304 *B. terrestris* queens and 66 queens of *B. lucorum* (see Appendix A: Table 3), which we considered too few to test how relative abundance and phenology had shifted across the period. We therefore based the analyses on males only.

Land-use and temperature data

To characterize the agricultural landscape in which each individual was caught, we use the so-called large production areas (Swedish: stora produktionsområden), defined by the Swedish Board of Agriculture (Fig. 1). The production areas (eight categories covering Sweden), are based on the large-scale conditions for farming, including soils, topography and climate (Statistics Sweden, 2014), and can thus be used as a proxy for general agricultural intensity and landscape heterogeneity. Three categories are represented in Scania:

the southern plains, characterized by a simplified landscape structure dominated by arable fields (hereafter: simplified landscapes), the mixed landscapes, and the forested mixed landscapes. These production areas can also be used as an estimate of land-use change, because during the second half of the 20th century, land-use transformations in these categories have developed in two opposite directions; in the simplified landscapes, arable land has continued to expand, while in the mixed landscapes, agriculture has been abandoned and replaced by forest (Ihse, 1995). Because only few bumblebees were obtained from the forested mixed landscapes (67 *B. terrestris* and 52 *B. lucorum*), we pooled this category with the mixed landscapes. We used ArcMap (ESRI) to overlay a shape-file of production areas with the geographic coordinates of each specimen's sampling location, as determined from its label. For each of the years when individuals had been collected, we obtained data on Swedish mean annual temperatures (°C) from the Swedish Meteorological and Hydrological Institute (SMHI, 2020; see Appendix A: Table 2).

Statistical analyses

We used R version 4.0.2 (R Core Team, 2020) for the statistical analyses.

To analyze how the relative abundance of the taxa had changed across the study period, we aggregated the number of collected males per year, taxon (*B. terrestris* or the *B. lucorum* complex) and production area (simplified or mixed) (see Appendix A: Table 2). We analyzed the relative shift with a generalized linear model, specifying a binomial distribution with a logit link. This function allowed us to compare the relative abundance of the two taxa, while also correcting for the higher uncertainty during years with few collected individuals compared to years with many collected individuals (Zuur, Leno, Walker, Saveliev, & Smith, 2009). As response variable, we specified the number of males for each taxon. As fixed factors we specified year and production area (simplified or mixed landscapes), together with their interaction. Because model residuals were overdispersed, we changed the distribution to quasibinomial, thus adding an overdispersion parameter to the variation of the response variable (Zuur et al., 2009). Using a similar model, we tested how the relative abundance of *B. terrestris* correlated with mean annual temperature, production area and the interaction between these two variables. For both models, we estimated p-values using a likelihood ratio test and removed the non-significant interaction in order to interpret the main effects. We calculated R squared with the package *rsq* (Zhang, 2020).

To estimate how the absolute numbers of *B. terrestris* and the *B. lucorum* complex changed over time, we combined the estimates obtained from models of relative change over time with published data on the development of the bumblebee communities between the 1930s and 2000s in Danish

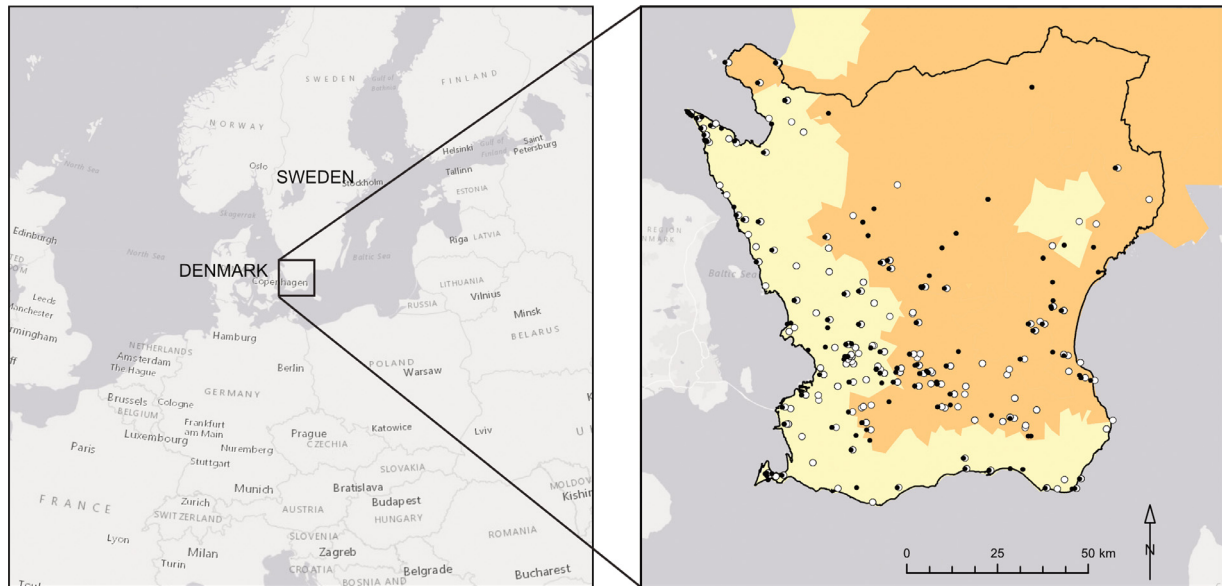


Fig. 1. Map showing the southern plains, which are characterized by a simplified agricultural landscape (beige/light grey), and the mixed/mixed forested landscapes (orange/dark grey) in the county Scania (within the black line), where specimens of the *B. lucorum* complex (filled circles) and *B. terrestris* (open circles) were collected. Note that most circles represent multiple specimens and that dots have been shifted slightly (east west) to improve readability. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

red clover fields (Dupont, Damgaard, & Simonsen, 2011). We considered Denmark a proper choice due to geographical proximity to our study region, Scania (Fig. 1). Similar data have been published for Sweden (Bommarco et al., 2012) but did not consider population changes in absolute numbers and would therefore not be useful here. Assuming that the relative change within the subgenus has been similar in Denmark and Scania, we calculated absolute changes by multiplying the absolute abundance of the subgenus in Danish red clover fields during the periods 1930–1934 and 2008–2009 with the estimated relative abundance of *B. terrestris* in Scania during the same periods (calculated from the mean year for each period, i.e. 1932 and 2008.5). Because the relative abundance of *B. terrestris* was strongly associated with mean annual temperatures, we additionally estimated absolute numbers using the mean temperature for each of the two periods (1930–1934 and 2008–2009, respectively) instead of year.

To analyze how the phenology of males from the two taxa changed across the study period, we specified a linear model, with collection date as response variable (see Appendix A: Table 4). Information on collection date was lacking for 218 individuals (see Appendix A: Table 1), which we excluded from the analysis. As a first attempt, we analyzed data at its highest resolution, using year as a random factor to account for non-independence among samples from the same year. However, because of non-normally distributed residuals, we instead used the mean collection date per year and taxon, without any random factors. As fixed factors we specified year, taxon, and the interaction between them

(Year $\times$ Taxon), to test if the advancement had occurred at a similar rate in the two taxa. To account for non-linear effects of climate warming and the possibility of any such effect differing between the taxa, we added the quadratic term of year and its interaction with taxon (Year $\times$ Taxon²). We estimated *p*-values using *F*-tests and removed non-significant interactions and the (non-significant) quadratic term of year to enable interpretation of the main term effects.

Results

After removing the non-significant interaction between production area and year ($F(1,82) = 0.0003$, $p = 0.99$), the analysis showed that *B. terrestris* was more associated with simplified landscapes than the *B. lucorum* complex ($F(1,83) = 12.67$, $p < 0.001$, Fig. 2). We also observed that the relative abundance of *B. terrestris* had increased strongly over time ($F(1,83) = 21.84$, $p < 0.001$, Fig. 2, $R^2 = 0.27$), from 21% to 79% between 1871 and 2015. Using data from Danish red clover fields (Dupont et al., 2011) we estimated that this shift corresponds to a 600% density increase in *B. terrestris* between 1932 and 2008, and a 50% density increase of the *B. lucorum* complex. When using the mean temperatures to estimate abundance, we detected a 400% density increase in *B. terrestris* and a 100% increase of the *B. lucorum* complex during the same period.

We observed a strong positive correlation between increasing relative abundance of *B. terrestris* and mean annual temperature ($F(1,83) = 45.87$, $p < 0.001$, $R^2 = 0.42$,

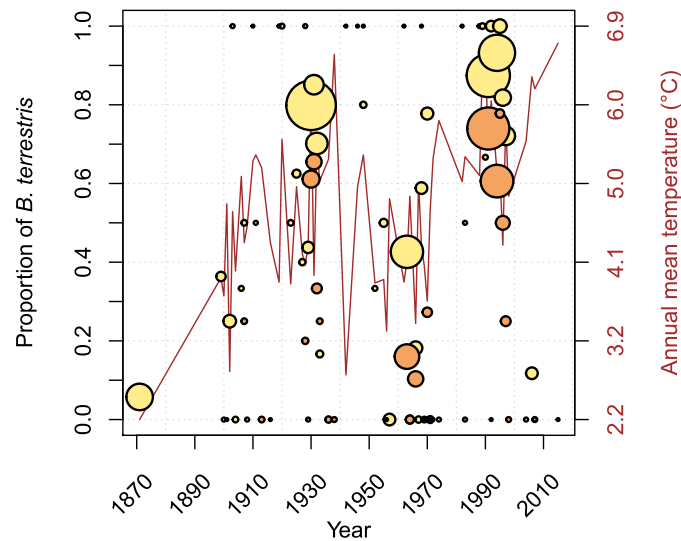


Fig. 2. The relative abundance of *B. terrestris* changed equally in the simplified (beige/light grey circles) and the mixed landscapes (orange/dark grey circles) over the study period and was highly correlated with mean annual temperature (°C) in Sweden (red/black line) for the years when bumblebees were collected. The area of the circles is proportional to the number of collected individuals for a particular year. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Fig. 2), which was equally strong in the two production areas, as shown by the non-significant interaction between production area and annual mean temperature ($F(1,82) = 0.02$, $p = 0.90$). *Bombus terrestris* was again more associated with simplified landscapes than the *B. lucorum* complex ($F(1,83) = 7.55$, $p = 0.007$).

Males of *B. terrestris* were on average collected 9.8 days later than males of the *B. lucorum* complex ($F(1,86) = 18.33$, $p < 0.001$, Fig. 3). The collection date had advanced with 0.36 days per year during the study period ($F(1,86) = 91.58$, $p < 0.001$), corresponding to 41 days since

1900. This change was similar for the two taxa (year $\times$ taxa: $F(1,84) = 0.67$, $p = 0.42$, Fig. 3). We found no evidence for accelerated advancement in either of the two taxa (year² $\times$ taxa: $F(1,83) = 1.33$, $p = 0.25$, year²: $F(1,85) = 1.47$, $p = 0.23$).

Discussion

We show that *B. terrestris* has become strongly dominating within its subgenus across the study period, from constituting only a fifth of the collected individuals in the late 1800s, to around 80% in 2015. This suggests that the previously observed increase in *Bombus sensu stricto* in Scandinavian red clover fields (Bommarco et al., 2012; Dupont et al., 2011) is driven primarily by *B. terrestris*. The remarkable variation in relative abundance among years was largely explained by mean annual temperature ($R^2 = 0.42$ for temperature, compared to $R^2 = 0.27$ for year) and was similar in the two production areas despite their contrasting land-use development. While the exact mechanism remains to be revealed, this suggests that climate warming is the main driver of the observed change. Climate warming generally has a negative impact on bumblebees (Soroye et al., 2020). However, when estimating densities by combining our estimates with data from Danish red clover fields (Dupont et al., 2011), we rather observe a density increase in both *B. terrestris* and the *B. lucorum* complex since the 1930s, albeit much more pronounced in *B. terrestris*. Although this result should be carefully interpreted, due to potential differences between the two regions and inherent differences between the studies (e.g. focus on workers and queens versus males), a potential explanation for the

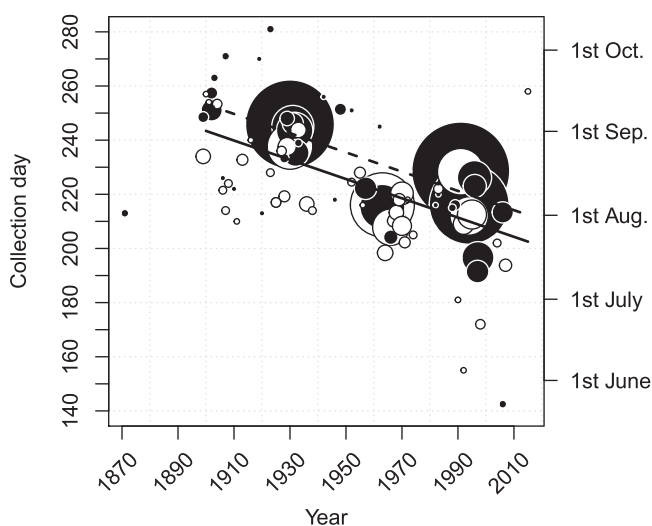


Fig. 3. The mean collection day changed over the study period for both *B. terrestris* (open circles and solid line) and the *B. lucorum* complex (filled circles and dashed line). The area of the circles is proportional to the number of collected individuals.

observed pattern is that the region is near the northern distribution limit for *B. terrestris* and parts of the *B. lucorum* complex and that previous temperatures were unfavorably cold, especially for *B. terrestris*, which has the most southerly distribution (Rasmont & Iserbyt, 2010–2014). In a warmer region, the population development could be expected to differ, which might explain why Rollin et al. (2020) find that *B. lucorum* has become scarcer in Belgium since around 1980, while *B. terrestris* has increased.

Strong shift in male activity period

Climate change can have various effects on bumblebees, for example through summer heat waves causing drought and forage deficiency. Species that fulfill their life cycle in late summer are particularly sensitive to such aspects of climate change (Rasmont & Iserbyt, 2012). One way for bumblebees to adapt to climate warming is to adjust the timing of the colony cycle, including sexual reproduction, to the temporal shifts in floral resources (Ogilvie et al., 2017). Therefore, intraspecific variation in this ability could explain why some species are more sensitive to climate warming. Our results on the shifts of the male activity period indicate that *B. terrestris* and the *B. lucorum* complex have adapted equally well in this respect, with an advancement of 41 days from 1900 to 2015. We therefore suggest that it is not a faster advancement in colony development and reproduction that drives the increasing dominance of *B. terrestris*. Instead, it is possible that *B. terrestris*, which has a slightly more southerly distribution (Kerr et al., 2015; Rasmont & Iserbyt, 2010–2014) and is associated with lower altitudes (Geue et al., 2020; Kerr et al., 2015) than the *B. lucorum* complex, is better adapted to climate warming in other aspects. These could be for example higher tolerance to heat stress, lower susceptibility to fungal diseases (Rasmont & Iserbyt, 2012), or that the larger body size of *B. terrestris* (Goulson & Sparrow, 2008) allows it to forage over larger areas (Westphal et al., 2006) making this species particularly good at compensating for local lack of flowers during periods of drought.

Dominance of *B. terrestris* in simplified landscapes

As we expected, the dominance of *B. terrestris* was more pronounced in simplified landscapes dominated by large arable fields, verifying this species' ability to cope with contemporary agricultural landscapes. However, surprisingly, the dominance of *B. terrestris* increased similarly on the plains and in the mixed landscapes. This occurred despite the fact that during the second half of the study period, the simplification of agricultural landscapes mainly occurred on the plains, whereas agricultural land was partly abandoned and forested in the mixed landscapes (Ihse, 1995). We

expected that the substitution of agricultural land for forest would have a positive effect on the relative abundance of the *B. lucorum* complex because of its association with edge habitats in forested landscapes (Løken, 1973; Mossberg & Cederberg, 2012), but found no evidence for this. However, we cannot rule out that a weak effect of land-use change is masked by the more prominent effect of climate warming, or that a lack of effect is a result of our rather crude land-use estimates and the non-standardized sampling method of museum specimens.

Does the success of *B. terrestris* occur at the expense of other species?

When taxa with similar niches coexist, as is often the case for *B. terrestris* and *B. lucorum* (Geue et al., 2020), as well as the species within the *B. lucorum* complex (Waters, Darvill, Lye, & Goulson, 2011), competition for resources can result in the exclusion of the least competitive one (Hardin, 1960). However, despite large overlaps in nesting substrate and foraging plants, these taxa have continuously coexisted over a large geographic area (Mossberg & Cederberg, 2012; Rasmont & Iserbyt, 2010–2014). The reason for this is likely that they are specialized in different habitats, altitudes and temperatures, partly separating their distributions and interactions at local scales (Geue et al., 2020; Scriven et al., 2016). For example, in the southeastern part of their common distribution, *B. terrestris* is more common in lowlands and open habitats, whereas *B. lucorum* is often dominating in forested landscapes and at high altitudes (Geue et al., 2020). As temperatures continue to rise, we expect *B. terrestris* to expand its territory to higher altitudes and latitudes, likely including places where species from the *B. lucorum* complex have previously dominated. This becomes particularly interesting given that there are not only differences in activity temperature between *B. terrestris* and the *B. lucorum* complex (Kerr et al., 2015; Rasmont & Iserbyt, 2010–2014), but also among the species within the *B. lucorum* complex (Scriven et al., 2016; Waters et al., 2011). For example, *B. cryptarum* generally occurs at higher elevations and latitudes than the other two species (Rasmont & Iserbyt, 2010–2014) and when co-occurring, *B. cryptarum* and *B. magnus* are active in colder weather than *B. lucorum* (Scriven et al., 2016). *B. cryptarum* has in fact been found by some observers to completely supplant *B. lucorum* north of the Arctic Circle (Rasmont & Iserbyt, 2010–2014). While bumblebees seem to easily adapt locally to cold temperatures, adaptations to warmer temperatures seem to be much more constrained (Pimsler et al., 2020), possibly making *B. cryptarum* particularly sensitive to climate warming. These differences suggest that the population changes of the three species within the *B. lucorum* complex vary, which highlights the need for more research regarding their ecological dissimilarities and population changes. It also raises the

question of whether or not a continued success and northward expansion of *B. terrestris*, and possibly *B. lucorum*, would occur at the expense of other bumblebee taxa, such as *B. cryptarum*.

While tackling climate change would be the obvious, albeit extremely challenging, solution to conserve bumblebee diversity (Kerr et al., 2015; Soroye et al., 2020), indirect effects of climate change, such as reduced forage resources (Ogilvie et al., 2017; Rasmont & Iserbyt, 2012) and changed competitive advantages, can possibly be mitigated by the provision of additional resources (c.f. Herbertsson, Lindström, Rundlöf, Bommarco, & Smith, 2016). In order to take appropriate actions to conserve bumblebees it is therefore important to disentangle the components behind the effect of climate warming on bumblebee communities.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Author contributions

AP and LH formulated the initial idea. RK and SB collected data with help from KJ and RB. LH analyzed the data with input from AP. AP made Fig. 1. LH made Fig. 2 and 3. LH wrote the manuscript with help from all authors.

Acknowledgement

We would like to thank B. Cederberg for answering numerous questions about the Swedish populations of the subgenus *Bombus* sensu stricto, T. Pedersen, J. Henriksson, I. Karlsson and C. Winter for information about when Sweden started to import bumblebees, and H. Smith for statistical advice. Formas funded AP (grant number: 2014-01313) and LH (grant number: 2018-01466).

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.baae.2021.03.008.

References

- Bartomeus, I., Ascher, J. S., Gibbs, J., Danforth, B. N., Wagner, D. L., Hedtke, S. M., et al. (2013). Historical changes in northeastern US bee pollinators related to shared ecological traits. *Proceedings of the National Academy of Sciences of the United States of America*, 110, 4656–4660.
- Benton, T. G., Vickery, J. A., & Wilson, J. D. (2003). Farmland biodiversity: Is habitat heterogeneity the key? *Trends in Ecology & Evolution*, 18, 182–188.
- Bommarco, R., Lundin, O., Smith, H. G., & Rundlöf, M. (2012). Drastic historic shifts in bumble-bee community composition in Sweden. *Proceedings of the Royal Society B: Biological Sciences*, 279, 309–315.
- Clavel, J., Julliard, R., & Devictor, V. (2011). Worldwide decline of specialist species: Toward a global functional homogenization? *Frontiers in Ecology and the Environment*, 9, 222–228.
- R Core Team. (2020). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Dupont, Y. L., Damgaard, C., & Simonsen, V. (2011). Quantitative historical change in bumblebee (*Bombus* spp.) assemblages of red clover fields. *PLoS One*, 6, e25172.
- Geue, J. C., & Thomassen, H. A. (2020). Unraveling the habitat preferences of two closely related bumble bee species in Eastern Europe. *Ecology and Evolution*, 10, 4773–4790.
- Goulson, D., Nicholls, E., Botias, C., & Rotheray, E. L. (2015). Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science*, 347.
- Goulson, D., & Sparrow, K. (2008). Evidence for competition between honeybees and bumblebees; effects on bumblebee worker size. *Journal of Insect Conservation*, 13, 177–181.
- Hardin, G. (1960). The competitive exclusion principle. *Science*, 131, 1292–1297.
- Hart, A. F., Maebe, K., Brown, G., Smagghe, G., & Ings, T. (2020). Winter activity unrelated to introgression in British bumblebee *Bombus terrestris* audax. *Apidologie*.
- Herbertsson, L., Lindström, S. A. M., Rundlöf, M., Bommarco, R., & Smith, H. G. (2016). Competition between managed honeybees and wild bumblebees depends on landscape context. *Basic and Applied Ecology*, 17, 609–616.
- Ihse, M. (1995). Swedish agricultural landscapes—patterns and changes during the last 50 years, studied by aerial photos. *Landscape and Urban Planning*, 31, 21–37.
- Kells, A. R., & Goulson, D. (2003). Preferred nesting sites of bumblebee queens (Hymenoptera: Apidae) in agroecosystems in the UK. *Biological Conservation*, 109, 165–174.
- Kerr, J. T., Pindar, A., Galpern, P., Packer, L., Potts, S. G., Roberts, S. M., et al. (2015). Climate change impacts on bumblebees converge across continents. *Science*, 349, 177–180.
- Løken, A. (1973). Studies on Scandinavian bumble bees (Hymenoptera, Apidae). *Norwegian Journal of Entomology*, 20, 1–218.
- Martinet, B., Rasmont, P., Cederberg, B., Evrard, D., Ødegaard, F., Paukkunen, J., et al. (2015). Forward to the north: Two Euro-Mediterranean bumblebee species now cross the Arctic Circle. *Annales de la Société entomologique de France (N.S.)*, 51, 303–309.
- Mathiasson, M. E., & Rehan, S. M. (2019). Status changes in the wild bees of north-eastern North America over 125 years revealed through museum specimens. *Insect Conservation and Diversity*, 12, 278–288.
- Mossberg, B., & Cederberg, B. (2012). *Humlor i Sverige: 40 arter att älska och förundras över*. Stockholm, Sverige: Bonnier Fakta.

- Ogilvie, J. E., Griffin, S. R., Gezon, Z. J., Inouye, B. D., Underwood, N., Inouye, D. W., et al. (2017). Interannual bumble bee abundance is driven by indirect climate effects on floral resource phenology. *Ecology Letters*, 20, 1507–1515.
- Persson, A., Rundlöf, M., Clough, Y., & Smith, H. (2015). Bumble bees show trait-dependent vulnerability to landscape simplification. *Biodiversity and Conservation*, 1–21.
- Persson, A. S., & Smith, H. G. (2013). Seasonal persistence of bumblebee populations is affected by landscape context. *Agriculture Ecosystems and Environment*, 165, 201–209.
- Pimsler, M. L., Oyen, K. J., Herndon, J. D., Jackson, J. M., Strange, J. P., Dillon, M. E., et al. (2020). Biogeographic parallels in thermal tolerance and gene expression variation under temperature stress in a widespread bumble bee. *Scientific Reports*, 10, 17063.
- Potts, S. G., Imperatriz-Fonseca, V., Ngo, H. T., Aizen, M. A., Biesmeijer, J. C., Breeze, T. D., et al. (2016). Safeguarding pollinators and their values to human well-being. *Nature*, 540, 220–229.
- Rasmont, P., & Iserbyt, S. (2010). *Atlas of the European bees: Genus bombus*. -2014, (3rd ed.). Mons, Gembloux: STEP Project, Atlas Hymenoptera. <http://www.atlashymenoptera.net/page.aspx?ID=169>.
- Rasmont, P., & Iserbyt, S. (2012). The Bumblebees Scarcity Syndrome: Are heat waves leading to local extinctions of bumblebees (Hymenoptera: Apidae: *Bombus*)? *Annales de la Société entomologique de France (N.S.)*, 48, 275–280.
- Rollin, O., Vray, S., Dendoncker, N., Michez, D., Dufrêne, M., & Rasmont, P. (2020). Drastic shifts in the Belgian bumblebee community over the last century. *Biodiversity and Conservation*, 29, 2553–2573.
- Scriven, J. J., Whitehorn, P. R., Goulson, D., & Tinsley, M. C. (2016). Niche partitioning in a sympatric cryptic species complex. *Ecology and Evolution*, 6, 1328–1339.
- SMHI, Swedish Meteorological and Hydrological Institute (2020). <https://www.smhi.se/klimat/klimatet-da-och-nu/klimatindikatorer/klimatindikator-temperatur-1.2430>. Accessed 21st October 2020.
- Smith, H. G., Birkhofer, K., Clough, Y., Ekroos, J., Olsson, O., & Rundlöf, M. (2014). Beyond dispersal: The role of animal movement in modern agricultural landscapes. L.-A. Hansson, & S. Åkesson, *Animal movement across scales* L.-A. Hansson, & S. Åkesson. (pp. 51–70). Oxford University Press.
- Soroye, P., Newbold, T., & Kerr, J. (2020). Climate change contributes to widespread declines among bumble bees across continents. *Science*, 367, 685–688.
- Statistics Sweden. (2014). Bilaga 2, Områdesindelningar i lantbruksstatistiken. *Jordbruksstatistisk årsbok 2014 [Yearbook of agriculture statistics 2014]* (pp. 1–392). Sweden: Statistics Sweden, Agriculture Statistics Unit Örebro.
- Stelzer, R. J., Chittka, L., Carlton, M., & Ings, T. C. (2010). Winter active bumblebees (*Bombus terrestris*) achieve high foraging rates in urban Britain. *PLoS One*, 5, e9559.
- Stoate, C., Boatman, N. D., Borralho, R. J., Carvalho, C. R., Snoo, G. R., & Eden, P. (2001). Ecological impacts of arable intensification in Europe. *Journal of Environmental Management*, 63, 337–365.
- Svensson, B., Lagerlöf, J., & Svensson, B. G. (2000). Habitat preferences of nest-seeking bumble bees (Hymenoptera: Apidae) in an agricultural landscape. *Agriculture, Ecosystems & Environment*, 77, 247–255.
- Walther-Hellwig, K., & Frankl, R. (2000). Foraging habitats and foraging distances of bumblebees, *Bombus* spp. (Hym., Apidae), in an agricultural landscape. *Journal of Applied Entomology*, 124, 299–306.
- Waters, J., Darvill, B., Lye, G. C., & Goulson, D. (2011). Niche differentiation of a cryptic bumblebee complex in the Western Isles of Scotland. *Insect Conservation and Diversity*, 4, 46–52.
- Westphal, C., Steffan-Dewenter, I., & Tschamntke, T. (2006). Bumblebees experience landscapes at different spatial scales: Possible implications for coexistence. *Oecologia*, 149, 289–300.
- Williams, P. H., Brown, M. J. F., Carolan, J. C., An, J., Goulson, D., Aytekin, A. M., et al. (2012). Unveiling cryptic species of the bumblebee subgenus *Bombus* s. str. worldwide with COI barcodes (Hymenoptera: Apidae). *Systematics and Biodiversity*, 10, 21–56.
- Zhang, D. (2020). *rsq: R-Squared and related measures*. R package version 2.0. <https://CRAN.R-project.org/package=rsq>.
- Zuur, A., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. New York: Springer.

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