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Impact of pollen resources drift on common bumblebees in NW Europe

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Abstract

Several bee species are experiencing significant population declines. As bees exclusively rely on pollen for development and survival, such declines could be partly related to changes in their host plant abundance and quality. Here, we investigate whether generalist bumblebee species, with stable population trends over the past years, adapted their diets in response to changes in the distribution and chemical quality of their pollen resources. We selected five common species of bumblebee in NW Europe for which we had a precise description of their pollen diet through two time periods (‘prior to 1950’ and ‘2004–2005’). For each species, we assessed whether the shift in their pollen diet was related with the changes in the suitable area of their pollen resources. Concurrently, we evaluated whether the chemical composition of pollen resources changed over time and experimentally tested the impact of new major pollen species on the development of *B. terrestris* microcolonies. Only one species (i.e. *B. lapidarius*) significantly included more pollen from resources whose suitable area expanded. This opportunist pattern could partly explain the expansion of *B. lapidarius* in Europe. Regarding the temporal variation in the chemical composition of the pollen diet, total and essential amino acid contents did not differ significantly between the two time periods while we found significant differences among plant species. This result is driven by the great diversity of resources used by bumblebee species in both periods. Our bioassay revealed that the shift to new major pollen resources allowed microcolonies to develop, bringing new evidence on the opportunist feature of bumblebee in their diets. Overall, this study shows that the response to pollen resource drift varies among closely related pollinators, and a species-rich plant community ensures generalist species to select a nutrient-rich pollen diet.

Keywords: bumblebee, diet performance, floral resources, food choices, land-use change, pollen

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Introduction

Pollen is bees’ major source of nutrients (Hügel, 1962; Day *et al.*, 1990; Roulston *et al.*, 2000). While some bee species are very specialized in their pollen sources, others are quite generalized. In response to the ongoing global environmental changes (e.g. loss and fragmentation of habitats, use of pesticides, climate change, modification of land management practices and/or non-native plant invasion) (Potts *et al.*, 2010; Winfree, 2010; Scheper *et al.*, 2014; Goulson *et al.*, 2015; Kerr *et al.*, 2015), such generalist species are potentially able to adapt their diet by integrating new valuable floral resources (Chittka & Schurkens, 2001; Kleijn & Raemakers, 2008). However, many species with generalist diets are in accentuated decline (Bommarco *et al.*, 2011; Nieto *et al.*, 2015). As the nutritive composition of

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pollen is highly variable (e.g. Roulston & Goodell, 2011), a shift in diet could substantially decrease the quality of the nutritional intake. Differences in the intake of sterols and amino acids have been proved to have an impact on bee development (i.e. hormone synthesis, lack of essential amino acids) and survival (De Groot, 1953; Rasmont *et al.*, 2005; Vanderplanck *et al.*, 2014b; Moerman *et al.*, 2015; Vaudo *et al.*, 2015). However, the role of pollen diet changes in pollinator conservation has been poorly investigated until now.

Here, we use data on the historical distribution and pollen quality of host plants foraged by five common bumblebee species in NW Europe (*B. hortorum*, *B. lapidarius*, *B. pascuorum*, *B. pratorum* and *B. terrestris*) during the 20th century to investigate whether common bumblebees share stability in the abundance and chemical quality of their resources. Three main questions are herein precisely addressed: (i) Is pollen diet shifting and is that shift related to changes in plant distribution? As bumblebee species are generalists and are able to incorporate expanding novel hosts, native or not, in their diet (e.g. *B. terrestris*, Chittka & Schurkens, 2001; Kleijn & Raemakers, 2008; Bommarco *et al.*, 2011); we expect that bumblebee species adapt their diets according to ecological opportunities (e.g. by including expanding alternative host plants). (ii) Is a shift in pollen diet associated with a shift in the chemical quality of pollen? As some studies suggested that bumblebees are able to detect and select plants according to the chemical composition of pollen (e.g. Hanley *et al.*, 2008), we hypothesize that a newly integrated resource will display similar nutritional content to those already used. (iii) How does changing to a different major source of pollen affect bumblebee colony development? We expect that bumblebee species' brood development will be maintained after such a change.

Materials and methods

Effect of change in plant distribution on pollen foraging

To determine whether bumblebees change their pollen diet according to the plant availability, we considered the five commonest bumblebee species in NW Europe (Belgium, Netherlands and United Kingdom): *Bombus hortorum*, *B. lapidarius*, *B. pascuorum*, *B. pratorum* and *B. terrestris* (Nieto *et al.*, 2015). Their pollen diets were described in the Netherlands and the United Kingdom for the beginning of the 20th century (prior to 1950, i.e. past diet) and 2004–2005 (i.e. recent diet) (Kleijn & Raemakers, 2008). Plant species that constituted at least 2% of the past or recent diet were selected for the analyses leading to a total of 45 plant species/taxa belonging to 20 different families (Appendix S1). Species distribution models (SDMs) were used to estimate the suitable area for each plant species in two 20-year time periods that roughly matched the dates for which we had information on pollen diet: from 1950 to 1969 (period 1) and from 1990 to 2009 (period 2), using data on plant species occurrences as well as several climate and land-use variables likely to affect the plant survival and distribution. Unfortunately, due to data limitations, we were not able to run SDMs for a period of time prior to 1950, but we assumed that suitable areas for periods 1 and 2 were representative for the time periods 'prior to 1950' and '2004–2005'.

Data on plant species occurrences were obtained from the UK National Biodiversity Network (2015), from Florabank (Van Landuyt *et al.*, 2012), Landelijke Vegetatie Databank (http://www.synbiosys.alterra.nl/natura2000/googlemapslvd.aspx) and the NDFF FLORON database (http://www.floron.nl/publicaties). Distribution data were not available for some taxa, leaving us with a total of 38 plant taxa for which more than 3000 species presence records distributed across the study area were available (see Appendix S1). For climate, maximum, minimum and average values of temperature and precipitation per grid cell were obtained from the project 'Climate EU: historical and projected climate data for Europe' (Hamann *et al.*, 2013). Climatic data were extracted at the same resolution as the species distribution data (1 × 1 km grid cells) and then used to calculate the 19 bioclimatic variables as described in Hijmans *et al.* (2005). To avoid collinearity between predictors, from the 19 bioclimatic variables originally available, we only selected the ones with absolute Pearson correlation coefficients equal or smaller than 0.70, which also aids avoiding potential model overfitting (Dormann *et al.* 2013). When two variables were highly correlated between each other, we selected the one less correlated to others and thought to be more ecological important for the modelled species. After correlation analyses of all bioclimatic variables, we selected seven temperature-related variables (all in °C) and two precipitation-related variables (all in mm): mean diurnal temperature range, isothermality, temperature seasonality, mean temperature of wettest quarter, mean temperature of driest quarter, mean temperature of warmest quarter, mean temperature of coldest quarter, precipitation seasonality and precipitation of wettest quarter. Land-use data were obtained from the HILDA project (Fuchs *et al.*, 2015) and contained information on six land-use/cover classes: settlements, cropland, forest, grassland, other land and water. Based on these maps, we calculated for each 1 × 1 km grid cell and time period a total of four land-use metrics that characterize aspects of landscape and habitat structure (Tscharntke *et al.*, 2012): percentage of each land-use class (for the six classes), number of land-use classes, total edge density (m/ha) and average patch area (ha). All calculations of land-use metrics were carried out in R (http://cran.r-project.org) with the 'SDMTools' package (VanDerWal *et al.*, 2014).

Whenever diet information on plant taxa contained multiple species, we assumed the *Bombus* species visited all species equally and modelled data for all congruent plant species with available data. To build the SDMs for both time periods here analysed, we used the selected climatic variables and the calculated land-use metrics mentioned above. When constructing the SDMs, we carried out an ensemble model approach with four different modelling algorithms: generalized linear models, maximum entropy with MaxEnt (Phillips & Dudík, 2008), random forest and generalized boosted models. For each algorithm, we did five model repetitions based on a random selection of 80% of the data points whereas the remaining 20% were used for model testing. The ensemble models were generated using the averages of the model predictions weighed by their model performance scores computed by the area under the curve (AUC) values of the receiver-operating characteristic (Hanley & McNeil, 1982). This ensemble model approach can account for the variation within and between algorithm variations in model results, resulting in more robust predictions (Thuiller, 2004; Aguirre-Gutiérrez *et al.*, 2013).

The SDMs were then used to estimate the relative change in suitable area across time periods (area in period 2 divided by the area in period 1) by converting ensemble suitability maps into binary maps (presence–absence) using the threshold that maximizes the sensitivity and specificity of the model (Jiménez-Valverde & Lobo, 2007). For each floral resource, different species were used for the SDMs (see Appendix S2 for the detailed list of species used for each plant taxa). All species distribution and range change analyses were carried out in the R platform (http://cran.r-project.org) with the 'biomod2' package (Thuiller *et al.*, 2015).

For each plant species, we calculated the shifts of its importance in the pollen diet as the ratio between its contribution in the past and in the recent diets. Afterwards we used the general linear models to test how changes in bumblebee pollen foraging patterns were related to changes of plants' suitable area. To evaluate such relationship for each bumblebee species, the model included the interaction between change in plants' suitable area and bumblebee species ID. Data were log-transformed to fulfil parametric assumptions. Post hoc asymptotic t-tests comparing the means and variances of two levels to the pooled variance across all levels were run using the function glht of the R package 'multcomp' to evaluate effects per species. All data analyses and figures were performed in R 3.2.2 (R Core team, 2015).

Effect of shifts in pollen diet on diet chemical quality

For each plant species, pollen was removed from fresh anthers using a tuning fork and collected on a glass plate. We were able to collect enough pollen from 25 plant species (Appendix S1) representing more than 85% of the total diet of the five bumblebee species. Pollen samples were lyophilized for 24 h and stored at −20 °C until chemical analyses.

Amino acid content was assessed based on 3–5 mg of floral pollen (dry weight) according to the protocol detailed in Vanderplanck *et al.* (2014a). We were able to sample 25 plant species (Appendix S1). Total amino acid extracts were analysed using an ion exchange chromatograph and norleucine as internal standard for further amino acid quantification. Sterol content was extracted and purified from 15 mg of lyophilized pollen samples from 18 plant species according to Vanderplanck *et al.* (2011) (Appendix S1). Sterolic extracts were analysed by gas chromatography coupled to a flame ionization detector (GC-FID) using betulin as internal standard for sterol quantification.

We tested whether total amino acid (TAA), total essential amino acids (EAA) and total sterol contents varied between the different plant species, using analysis of variance followed by Tukey tests (i.e. pairwise comparisons). We also tested whether the overall mean amino acid (i.e. TAA, EAA) and sterol content per plant species varied between the past and recent diets using t-tests. Assumptions (i.e. normality and homoscedasticity) were tested before performing statistics. Nonparametric equivalents were used when violation occurred (namely Wilcoxon–Mann–Whitney, Kruskal–Wallis followed by LSD post hoc tests and Wilcoxon rank tests). Moreover, we also tested the similarity in sterol and amino acid profiles (i.e. concentration of each element) between the past and recent diets using PERMANOVAS (permutational multivariate analysis of variance) and multiple pairwise comparisons (Bonferroni's adjustment) based on Bray–Curtis distances and 999 permutations ('adonis' command, R-package vegan, Oksanen *et al.*, 2013). Prior to PERMANOVA, the multivariate homogeneity of within-group covariance matrices was verified using the 'betadisper' function implementing Marti Anderson's testing methods. Differences in diet composition were visually assessed on UPGMA clusters using the Bray–Curtis dissimilarity index. We assessed the uncertainty in hierarchical cluster analysis with *P*-values calculated via multiscale bootstrap resampling (R-package pvclust, Suzuki & Shimodaira, 2006). All analyses were conducted in R version 3.0.2 (R Core Team, 2013).

Effect of pollen diet shift on colony development

To test the effect of changes in pollen diet on colony development, we used a total of 40 queenless microcolonies of *Bombus terrestris* fed on one of four different monofloral diets: two with species that, according to Kleijn & Raemakers (2008), are species that only recently became dominant in the diet of the five bumblebee species (*Rubus* sp. and *Trifolium repens)* and two control diets (see details below). The effect of the nutritive value of pollen diets on the development of microcolonies reared under laboratory conditions was shown to be a good method to estimate of queen-right colony development (Tasei & Aupinel, 2008a). Because it is difficult to rear wild bumblebee species, it was impossible to study the impact of diet shift for all five bumblebee species. *Bombus terrestris* was selected as a model because it is domesticated and easy-to-rear species. Colonies were provided by the company Biobest bvba (Westerlo, Belgium). For each diet, we used 10 queenless microcolonies composed of five 2-day-old workers reared in plastic boxes (8 × 16 × 16 cm).

According to Kleijn & Raemakers (2008), three pollen resources were significantly newly dominant in the recent diet of the five bumblebees: *Lotus corniculatus*, *Rubus* sp. and *Trifolium repens*. To prepare the monofloral pollen diets, we collected pollen loads from honeybee hives with pollen traps in areas where the selected plant species were abundant. As the honeybee is a generalist species, we carefully sorted pollen pellets based on colour after microscopic examination to obtain monofloral diets. We collected enough pollen (~300 g) from *Rubus* sp. and *Trifolium repens* but not from *Lotus corniculatus* to perform the bioassays. According to previous study, we additionally used *Cistus* and *Salix* diets as negative and positive controls, respectively (Tasei & Aupinel, 2008b). Pollen loads were purchased from the companies 'Ruchers de Lorraine' for *Salix* and from 'Pollenergie France' for *Cistus.* Sorted pollen loads were then mixed with inverted sugar syrup (BIOGLUC, Biobest) (83% and 17% w/w for *Cistus*, *Rubus* and *Trifolium* diets and 78% and 22% for *Salix* diet) to obtain consistent monofloral candies stored at −20 °C. Differences in pollen/syrup mass ratio resulted from different texture of pollen load (i.e. drier in *Salix*). We assumed that it did not affect food intake as the food was provided *ad libitum*.

The 40 microcolonies were fed *ad libitum* with sugar syrup (BIOGLUC®, Biobest) and pollen candies in a dark room at 29–30 °C and 65% relative humidity during a 19-day period. New pollen candy was provided every 2 days, while the previous one was removed and weighed. Several parameters were used to estimate bumblebee performance (adapted from Tasei & Aupinel, 2008b): (i) mass and number of eggs, (ii) mass and number of non-isolated larvae, (iii) mass and number of isolated larvae, (iv) mass and number of pupae, (v) number of ejected larvae, (vi) total pollen collection (i.e. mass of pollen consumed and stored) and (vii) total syrup collection. All weighed parameters (i.e. brood, pollen or syrup) were standardized by the total weight of the five workers of the microcolony to avoid potential effect of worker activities related to their size (i.e. consumption and brood care). We calculated pollen efficacy as mass of total offspring divided by total pollen collection. We additionally considered the fat body content of workers as an indicator of individual condition (Korner & Schmid-Hempel, 2005). The abdominal fat body content was measured following the method of Ellers (1996). The dissected abdomens of workers were dried at 70 °C during 3 days, weighed and placed in 2 ml of diethyl ether for 24H. After rinsing twice with diethyl ether, they were placed 7 days at 70 °C and weighed. Mass difference between the two weights was used as parameter standardized by the initial weight.

The performance on the different diets was compared based on aforementioned nine features using analysis of variance followed by Tukey tests. Nonparametric equivalents were used when assumptions were not met.

Results

Drift in the distribution of bumblebee host plants

Half of the plant taxa used by the five *Bombus* species expanded their suitable area (Appendix S1). For the taxa with range expansions, the average increase was 19.7% (SD 20). The species from the genera *Pulmonaria*, *Rhododendron* and *Rubus* showed the highest range expansions. The remaining plant taxa showed average contractions of their suitable area of 13.3% (SD 10.6). The species with the greatest losses in modelled range were *Stachys* spp. and the *Lotus* spp. Except for *B. hortorum*, plant species whose suitable areas expanded tended to become more frequent in the bumblebee diet, while plant species whose suitable areas contracted tended to become less frequent with significant positive effect only for *B. lapidarius* (Fig. 1).

Pollen chemical composition of old and novel hosts

Total and essential amino acid concentrations were significantly different among the plant species (TAA, H = 69.63, df = 24, $P < 0.001$; EAA, H = 70.32, df = 24, $P < 0.001$) with *Malus pumila* displaying significantly lower concentration than *Borago officinalis*, *Chelidonium majus* and *Symphytum officinale* (Appendix S4). However, all species contained the full spectrum of essential amino acids. Although PERMANOVA detected a significant difference in amino acid profiles ($F_{24,57} = 15.81$, $P < 0.001$), pairwise comparisons did not define discrete groups of plants. Statistical tests did not detect significant difference in total and essential amino acid concentrations between the pollen hosts of the two time periods (TAA, $t = -0.94$, df = 114, $P = 0.351$; EAA, $t = -1.01$, df = 114, $P = 0.313$) as well as in amino acid profiles ($F_{1,114} = 1.48$, $P = 0.191$) as illustrated by UPGMA cluster (i.e. no species cluster based on time period) (Fig. 2).

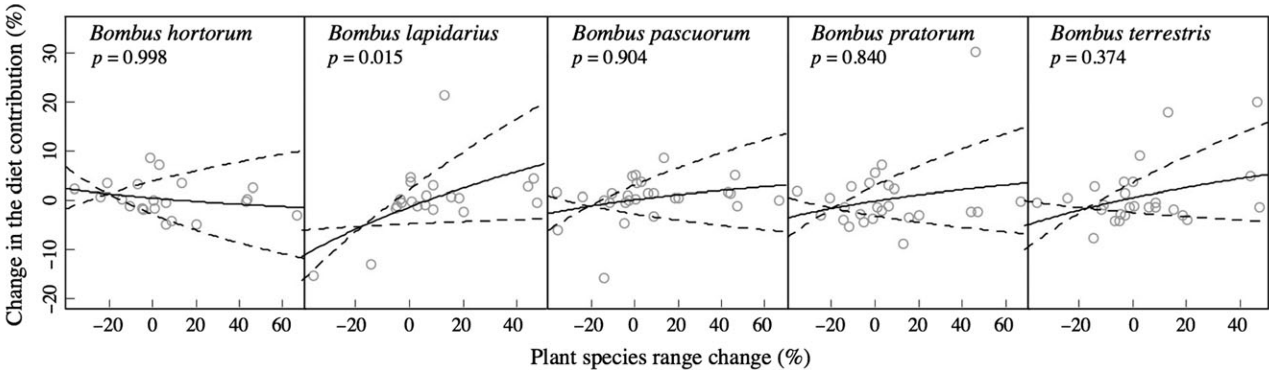
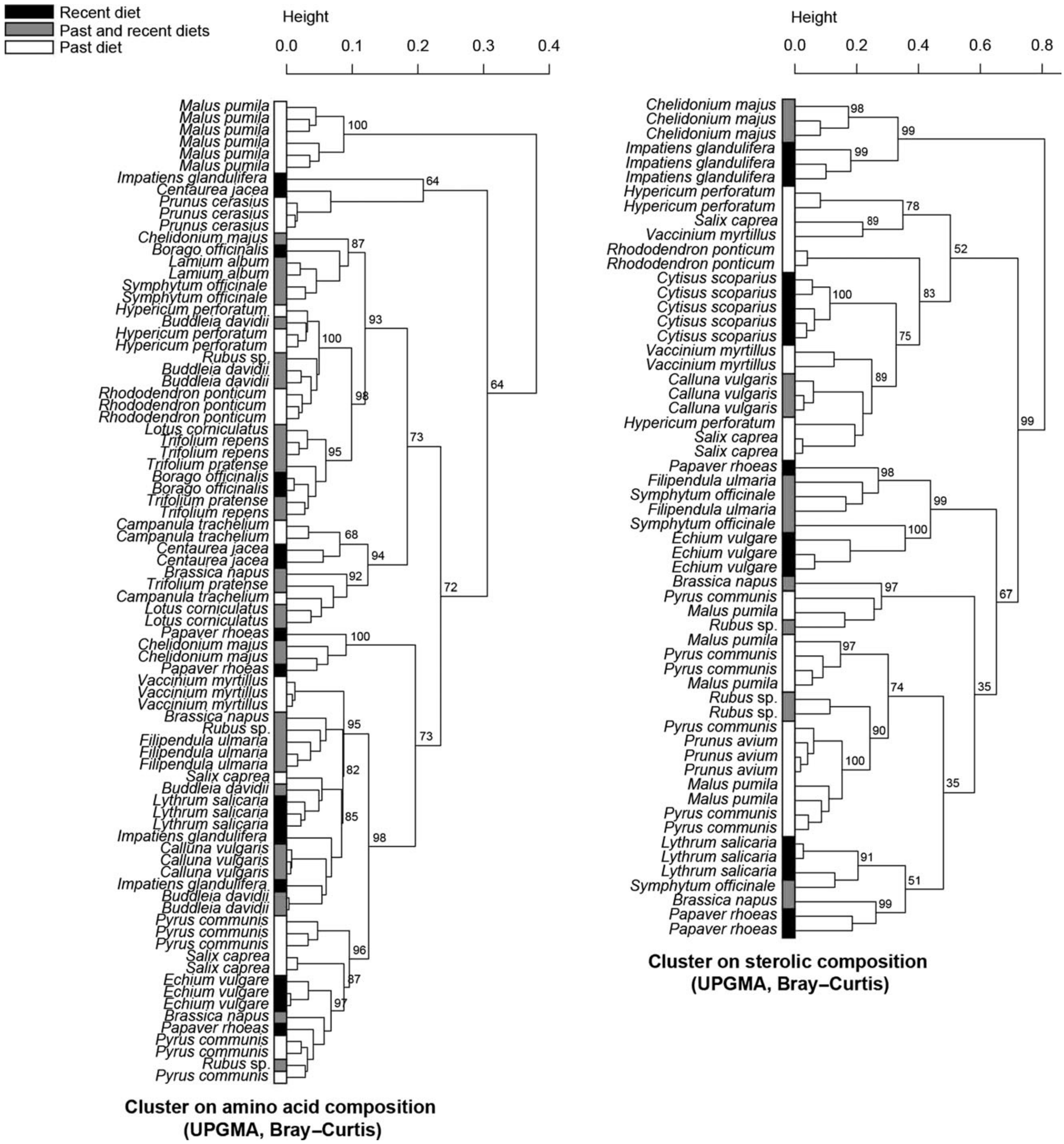


Fig. 1 Effect of changes in the suitable area of the floral resource species on the relative contribution to the diet of several bumblebee species. Lines represent the fitted values ±95% Confidence Interval (see Appendix S2 for model details).



Cluster on amino acid composition (UPGMA, Bray–Curtis)

Cluster on sterolic composition (UPGMA, Bray–Curtis)

Fig. 2 UPGMA cluster based on Bray–Curtis dissimilarity index based on amino acid composition (left) or sterolic composition (right); colour refers to the presence of the floral species in the diet of the 5 *Bombus* species before 1950 (white), after 1950 (black) or both (grey). The values near nodes are multiscale bootstrap resampling, and only values of main groups are shown.

Overall, sterol contents are significantly different among the plant species included in bumblebee diet (H = 45.89, df = 17, $P < 0.001$) with *Echium vulgare* displaying a significantly lower concentration than *Malus pumila* and *Pyrus communis* (Appendix S5). Overall, no significant difference was detected in terms of sterol profiles between past and recent diets ($F_{1,73} = 2.16$, $P = 0.079$, Fig. 2), but a significant difference was detected in sterol profiles between the different plant species ($F_{17,40} = 13.28$, $P < 0.001$). Moreover, plants foraged before 1950 had a higher median sterol concentration than those foraged in the later time period, 2004–2005 (W = 0.90, $P < 0.001$).

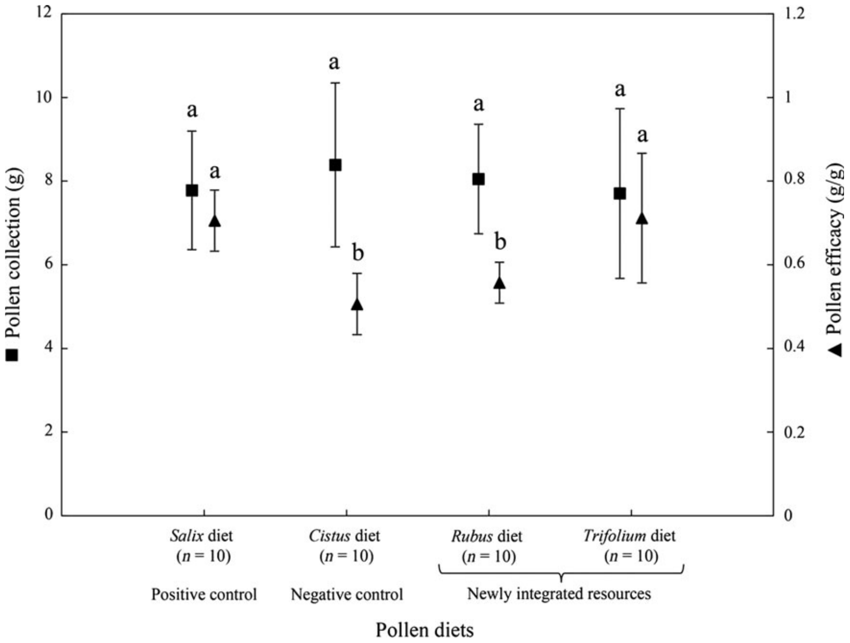


Fig. 3 Pollen collection and pollen efficacy (offspring mass divided by pollen collection) for microcolonies fed on different diets (mean ±SD). Groups differing significantly from each other in post hoc test are marked with different letters, shared letters indicating non-significant difference.

Bumblebee performance on new pollen resources

When evaluating effects of changes in pollen resources in microcolonies of *B. terrestris*, no significant difference was detected in pollen collection ($F_{3,36} = 0.33$, $P = 0.806$) between the two diets tested. However, the pollen diet provided to the microcolonies appeared to affect syrup collection ($F_{3,36} = 37.51$, $P < 0.001$) as workers in microcolonies fed with *Trifolium* pollen collected significantly more syrup than others (post hoc tests, $P < 0.001$). No significant difference was detected for total brood mass ($H = 6.29$, df = 3, $P = 0.098$), but we observed a trend of higher offspring production for *Trifolium* and *Salix* diets compared with *Rubus* and *Cistus* diets (Appendix S6). These higher levels of productions are reflected in the pollen efficacy, which was significantly higher for *Trifolium* and *Salix* diets than for *Rubus* and *Cistus* diets ($H = 21.49$, df = 3, $P < 0.001$) (Fig. 3). With regard to each brood stage, no significant difference was detected for the total mass of non-isolated larvae ($F_{3,36} = 2.17$, $P = 0.109$), isolated larvae ($H = 7.09$, df = 3, $P = 0.070$) and pupae ($H = 0.35$, df = 3, $P = 0.951$), while egg mass was significantly higher for *Salix* diet than other ones ($F_{3,36} = 3.59$, $P = 0.023$). Considering numbers, eggs were more abundant for *Salix* than for *Rubus* and *Trifolium* diets ($F_{3,36} = 4.79$, $P = 0.007$). No significant difference was detected for non-isolated larvae ($F_{3,36} = 2.66$, $P = 0.063$) or pupae ($H = 0.922$, df = 3, $P = 0.820$). Microcolonies fed on the *Salix* diet displayed a significantly higher number of isolated larvae than those fed on *Rubus* and *Trifolium* diets ($F_{3,36} = 4.76$, $P = 0.007$). These differences are also reflected in total offspring number (i.e. non-isolated larvae, isolated larvae and pupae) ($F_{3,36} = 7.51$, $P < 0.001$) with *Cistus* and *Salix* diets displaying a higher offspring production than *Trifolium* and *Rubus* diets. Mean larval mass (i.e. non-isolated and isolated) was higher for broods developed on *Trifolium* and *Rubus* diets than for those fed with *Cistus* ($F_{3,36} = 4.72$, $P = 0.007$). Moreover, percentage of ejected larvae was higher in microcolonies fed with the *Trifolium* diet than for those fed with the *Rubus* diet ($F_{3,36} = 4.76$, $P = 0.009$) and intermediate for microcolonies fed with *Cistus* and *Salix* pollen. Workers were not affected by the diet as no significant difference was detected in their total abdominal fat body content ($H = 2.08$, df = 3, $P = 0.56$).

Discussion

Relation between drift in plant distribution and pollen diet shift

As far as we know, the role of resources shifts in the accentuated bumblebee decline or stability has been poorly investigated in the context of ongoing global environmental changes. However, there is some evidence that bumblebees adapt their diet by incorporating novel hosts through time and space (e.g. Inoue *et al.*, 2008; Kleijn & Raemakers, 2008; Bommarco *et al.*, 2011; Harmon-Threatt & Kremen, 2015). Our results clearly show that four of five *Bombus* species studied tended to forage on pollen resources of expanding plants, even if this tendency was only significant for one species (*B. lapidarius*). The variability in the ability to incorporate a novel resource could be explained morphologically, particularly, by the tongue length (Goulson & Darvill, 2004). Short-tongued species such as *B. lapidarius* may be described in this context as ecological opportunists as they have clearly integrated novel hosts with expanding areas (i.e. *Trifolium repens*). This probably accounts for the recent increase of *B. terrestris* and *B. lapidarius*, both short-tongued bees, in a bumblebee community as it was shown in Sweden (Bommarco *et al.*, 2011). In contrast to floral species with short corolla tubes, those with long tubes are not expanding but they are still maintained in the diet of *B. hortorum* (i.e. *Trifolium pratense*) as it was shown in the southern United Kingdom where this species was specialized almost entirely on *T. pratense* (Goulson & Darvill, 2004). This long-corolla species maintenance regardless of plant potential expansions could be explained by the greater harvesting efficacy of *B. hortorum* on this floral morphology compared to that of other bumblebee species (Inouye, 1980).

Relation between shifts in pollen diet and diet chemical quality

No difference in the amino acid profiles (total and essential) and concentrations has been revealed between the past and recent diets of the five common bumblebees in NW Europe. The chemical quality of pollen resources seems therefore quite stable at global scale (i.e. within the community of entomophilous plants), which corroborates a previous study that evaluated changes of chemical quality (i.e. amino acid content) of different plant communities (i.e. exotic vs. native species and collected vs. noncollected species) from the same area (Harmon-Threatt & Kremen, 2015). However, this stability is mainly linked to high diversity of pollen resources (Roulston *et al.*, 2000). According to our results, the host plant pollen show a continuum in their chemical composition in both amino acid and sterol profiles. It seems that bumblebees take advantages of these diverse resources by mixing different elements to constitute an optimal diet (Eckhardt *et al.*, 2014). Many field data have confirmed that bumblebees do not forage randomly (Leonhardt & Blüthgen, 2012; Somme *et al.*, 2014; Harmon-Threatt & Kremen, 2015). However, a depauperate plant community could be composed of 'extreme' elements of the continuum, leading to a potential unbalanced diet. For example, *Calluna vulgaris* is a poor resource in terms of sterols because this pollen shows high concentration of δ7-sterols, potential toxic sterols (Behmer & Nes, 2003) and low concentration in sterols positively associated with bee development (e.g. 24-methylenecholesterol and β-sitosterol) (Rasmont *et al.*, 2005; Vanderplanck *et al.*, 2014b). Moreover, even if the general sterol profile is similar between past and recent diets, the total sterol content is lower in the recent diet which could cause physiological problems (e.g. moulting, ovaries development) and lead to an increase in pollen collection by bumblebees. An evaluation of mean amino acid and sterol intakes taking in consideration the contribution of each plant species to the diet of bumblebees could reveal changes in diet chemical composition.

Effect of novel host pollen on bumblebee performance

B. terrestris displayed good performance on its newly integrated pollen resources with similar pollen and syrup intakes. This invariability in resource collection has been already described for *B. terrestris* (Vanderplanck *et al.*, 2014b) and honeybees (Pernal & Currie, 2002). However, bioassays revealed that a *Trifolium* diet is more efficient, in terms of brood mass produced by the amount of collected pollen (i.e. pollen efficacy), than a *Rubus* diet, which probably results from the higher amino acid content of the *Trifolium* pollen (Vanderplanck *et al.*, 2014b). Considering the brood composition, microcolonies reared on *Cistus* (negative control) and *Salix* (positive control) diets produced numerous small larvae whereas those fed on *Trifolium* and *Rubus* diets produced less numerous but larger larvae. This could constitute an ecological advantage because larger larvae exhibit higher immunocompetence (Vogelweith *et al.*, 2013), larger workers can be better foragers (Spaethe & Weidenmuller, 2002) and larger queens have greater hibernation survival and reproductive success (Beekman *et al.*, 1998). In addition, the size of nursing workers influences both the number of emerging workers and egg cells (Cnaani & Hefetz, 1994).

We observed that low amino acid concentration in diet affects the larval mass but not adult fat body mass. This could be explained by the fact that larvae and adults have different nutritional requirements. Despite the lack of studies comparing adult and larval physiologies in bumblebees, it is known that the requirement for amino acids is 250 times higher for larvae than for adults (Stabler *et al.*, 2015).

Given the great diversity within the genus *Bombus*, and the particular plasticity of *B. terrestris* in its pollen diet (Kleijn & Raemakers, 2008; Leonhardt & Blüthgen, 2012), caution has to be used in interpreting our results on bumblebee performance on novel host pollen. Further studies are needed on other species such as *B. lapidarius* and *B. hortorum* that are both impacted by plant distribution drifts but in a different way. Nevertheless, our study clearly shows that responses to these distribution drifts can vary among bumblebees displaying the same ecology, highlighting the need to consider a large number of species in detailed studies to design mitigation strategies. A good understanding of species adaptability is clearly necessary to be able to predict how changes in ecological networks, including those resulting from global change, could affect the species stability and then the species biodiversity in ecosystems.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. List of the 45 plant taxa/species selected for this study and associated analyses.
Appendix S2. Detailed list of species used for SDMs.
Appendix S3. Contribution of each floral resource in past and recent diets of which of the 5 studied bumble bee species, and relative range change of their suitable environment.
Appendix S4. Amino acid analyses (25 species).
Appendix S5. Sterol analyses (18 species).
Appendix S6. Bumblebee fitness parameters for each diet.