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ORIGINAL PAPER

Bumble bees show trait-dependent vulnerability to landscape simplification

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Abstract Agricultural intensification has resulted in large-scale loss of bee pollinators, but while some species have been negatively affected others seem to endure changed conditions. It has been suggested that certain morphological, ecological and life-history traits make some species more vulnerable to landscape changes. Information on which traits make species vulnerable and why may aid conservation of declining species. We performed a comprehensive analysis of how multiple traits related to diet breadth, movement and nesting habits moderate vulnerability of bumble bees to landscape simplification. We surveyed bumble bees in flower-rich non-crop habitats in either complex landscapes (with small crop fields bordered by non-crop habitats), or simple landscapes (with larger fields and therefore less non-crop habitats). We analysed if landscape type interacted with colony size, queen emergence date, colony life-cycle length, nesting habitat, thorax width, proboscis length or variability in thorax and proboscis, to explain bumble bee abundances. Workers and males of species with above-ground nests, small sized colonies and long colony cycle were relatively less abundant in simple compared to in complex landscapes. Simple landscapes hosted fewer males of late emerging species and species with highly variable proboscis length. This suggests that both nesting habitat and spatio-temporal availability of food resources act as ecological filters for bumble bees. Colony size correlated with nesting habitat and queen emergence when correcting for phylogenetic correlations, suggesting that landscape simplification acts through effects on combinations of traits. Our results have consequences for conservation by suggesting that declining bumble bee species can be supported by providing adequate nesting habitats and

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preferred plant species throughout the season and within short distance from nesting habitats, to allow utilisation also by species having colonies with few workers.

Keywords *Bombus* · Intra-specific variation · Life-history traits · Nesting habitat · Phenology · Phylogeny

Introduction

Bumble bees have experienced large-scale declines in response to agricultural intensification (e.g. Goulson et al. 2008a; Winfree 2010). However, while many species have declined some still remain common (Goulson et al. 2008a; Dupont et al. 2011; Bommarco et al. 2012; Kleijn et al. 2015). The reason for this is not well understood (Cariveau and Winfree 2015), but the decline of bumble bees in response to landscape changes have been proposed to vary depending on several morphological, ecological and life-history traits. Through loss of natural and semi-natural habitats and loss of food plants in those habitats (e.g. reviewed by Goulson et al. 2008a; Williams and Osborne 2009; Winfree 2010), landscape simplification not only decreases the amount of resources but also increases their spatio-temporal variability. This indicates that decline of bumble bees may be linked to an inability to efficiently exploit scattered resources. This inability may in turn be attributable to certain traits and the identification of those may aid conservation of declining species.

Based on previous studies, we propose that the following traits should lead to differences in the response of bumble bees to landscape simplifications. (1) *Thorax width* reflects flight capacity in bees (Greenleaf et al. 2007) and therefore indicate the distance from the nest bumble bee workers are able to forage (Westphal et al. 2006). Species with a smaller thorax, and thus shorter potential foraging ranges, may be less able to utilize the scattered resources in intensively farmed and simplified landscapes. We therefore expect such species to be less abundant in simple landscapes. (2) *Proboscis length* reflects diet, because it affects the foragers' capacity to access nectar in flowers of different morphologies. Species with long proboscis may be more sensitive to agricultural intensification because of a more narrow diet consisting of nectar from flowers with deeper corollas and a preference of pollen from the Fabaceae group (Goulson et al. 2008b; but see Connop et al. 2010; Kleijn and Raemakers 2008), whose availability has decreased with increasing agricultural intensification (Bommarco et al. 2012; Carvell et al. 2006; Stoate et al. 2001). We thus expect to find fewer individuals of species with long proboscis in simple landscapes. (3) *Variation in morphological traits* may be substantial (Goulson et al. 2002; Inoue and Yokoyama 2006; Peat et al. 2005). Such variation could reflect niche breadth, such that the foraging work force from a colony with higher phenotypic variability can exploit a broader niche. E.g. high variation in both proboscis length (Heinrich 1979, p. 29) and body size (Peat et al. 2005) within a colony may increase the number of flower morphologies efficiently handled per colony, which could be more advantageous in complex landscapes containing a higher species richness of flowering plants. In addition, variation in body size may increase niche breadth by affecting variation in correlated traits such as flight speed and the ability to transport nectar (Goulson et al. 2002) and foraging distance (Greenleaf et al. 2007). Such variation may be advantageous in complex landscapes where resources are well dispersed. In contrast, because larger areas are used for foraging by bumble bees in simpler landscapes (Jha and Kremen 2013), larger size

Table 1 The classifications of bumble bee species into trait-groups and the sample size of workers and males (excluding *Psithyrus* spp.)

Bombus species	Subgenus	N workers (S, C)	N males (S, C)	N *Psithyrus* species[d]	Queen emergence[b]	Colony cycle length[b]	Nesting habitat[b]	Colony size[b]	Pollen storage[b,c]	Thorax width, mm	*CV* × 100 thorax width	Proboscis length, mm (N sample)	*CV* × 100 proboscis length
B. luc./ter.[a]	*Bombus s.s.*	609 (347, 262)	809 (393, 416)	5/55	Early	Medium	Below	Large	Storers	4.61	9.76	6.99 (31)	10.18
B. soroeensis	*Kallobombus*	28 (6, 22)	5 (3, 2)	–	Late	Long	Below	Medium	Unclear	4.01	7.56	5.62 (29)	7.42
B. hortorum	*Megabombus*	156 (80, 76)	131 (69, 62)	–	Late	Short	Below	Medium	Pocket	4.47	11.62	10.55 (31)	16.87
B. lapidarius	*Melanobombus*	752 (477, 275)	323 (177, 146)	111	Early	Short	Below	Large	Storer	4.07	8.68	6.07 (31)	5.69
B. hypnorum	*Pyrobombus*	47 (20, 27)	22 (7, 15)	–	Early	Long	Above	Medium	–	4.12	10.39	5.73 (16)	6.00
B. pratorum	*Pyrobombus*	16 (5, 11)	14 (4, 10)	5	Early	Short	Above	Small	Storer	3.71	7.10	5.91 (12)	6.03
B. jonellus	*Pyrobombus*	1 (1, 0)	0	–	Late	Short	Above	Small	Storer	–	–	–	–
B. subterraneus	*Subterraneobombus*	42 (24, 18)	9 (8, 1)	–	Late	Short	Below	Medium	Pocket	4.78	12.96	8.60 (30)	12.03
B. muscorum	*Thoracobombus*	2 (1, 1)	1 (1, 0)	–	Late	Short	Above	Small	Pocket	–	–	–	–
B. pascourum	*Thoracobombus*	151 (40, 111)	38 (1, 37)	1	Early	Long	Above	Medium	Pocket	4.07	9.93	7.13 (30)	13.72
B. ruderarius	*Thoracobombus*	22 (8, 14)	8 (3, 5)	–	Late	Short	Above	Small	Pocket	4.69	10.28	6.90 (26)	8.84
B. sylvarum	*Thoracobombus*	240 (110, 130)	78 (11, 67)	–	Late	Long	Above	Small	Pocket	4.05	8.61	6.84 (20)	15.95

Table 1 continued

Bombus species	Subgenus	N workers (S, C)	N males (S, C)	N *Psithyrus* species[d]	Queen emergence[b]	Colony cycle length[b]	Nesting habitat[b]	Colony size[b]	Pollen storage[b,c]	Thorax width, mm	*CV* × 100 thorax width	Proboscis length, mm (N sample)	*CV* × 100 proboscis length
Total numbers		2042 (1106, 936)	1438 (677, 761)	177 (144, 33)									

Sample sizes from simple (S) and complex (C) landscapes are given within brackets, as are sample sizes for proboscis length measurements (N sample). *CV* = Coefficient of Variation

[a] Because of difficulties in determining workers of *Bombus* sensu stricto based on morphology we pooled this group. We did however find males of only *B. terrestris* (N = 785) and *B. lucorum* (N = 24), indicating that these species dominated the sample

[b] Classifications based on Benton (2006) and Löken (1973)

[c] Classification based on Sladen (1912)

[d] Former *Psithyrus* spp. were assigned to host species following Mossberg and Cederberg (2012): for *B. bohemicus B. lucorum*, for *B. vestalis B. terrestris*, for *B. rupestris B. lapidarius*, for *B. sylvestris B. pratorum*, and for *B. campestris B. pascuorum*

variation may reduce the proportion of workers that are able to reach forage resources, and thus reduce the ability for a colony to persist in such landscapes. Also between colony variation may be advantageous in complex landscapes, because it would allow different colonies to focus on and efficiently handle separate parts of a rich flora, both in terms of plant species and spatial extent. We therefore hypothesise to find fewer individuals from species with highly variable morphology in simple landscapes. (4) *Colony size* (i.e. the number of workers) reflects the spatial scale at which resources are utilized. Species with large colonies may be better at utilizing scattered and ephemeral resources in intensively farmed landscapes (Westphal et al. 2006; Rundlöf et al. 2008), because more workers mean that at least some workers per colony may locate and exploit ephemeral scattered resources. In contrast, when resources are scattered and variable as in simple landscapes, a small workforce may result in a high variance in food intake. Consequently we expect species with small colonies to be less abundant in simple landscapes. (5) *Phenology of queen emergence* will affect the critical temporal synchrony of colony development and flower resources (Memmott et al. 2007). Different strategies exist, from emergence early in spring to late at the start of summer (Benton 2006; Löken 1973). Agricultural intensification has resulted in an accentuated loss of late-season resources, which has been shown to affect late emerging species particularly negatively (Fitzpatrick et al. 2007). Furthermore, if suitable nesting sites are limited in simplified landscapes, late species can be expected to be competitively at a disadvantage compared to early species (Goulson et al. 2008a). We therefore expect that late-emerging species will be less abundant in simple landscapes. (6) *Colony cycle length,* i.e. the period from colony establishment until the departure of daughter queens, reflects the duration when resources need to be gathered to provision colony build up and reproduction. A long colony cycle may result in a prolonged period of vulnerability to resource limitations in simple landscapes, especially late in the season (Benton 2006; Williams et al. 2009), leading us to expect fewer individuals of such species in simple landscapes. Alternatively it could indicate a strategy of slow colony growth rate and gathering of the necessary resources for reproduction over an extended period, enabling persistence also in poor environments or environments where resource levels show high temporal variation. (7) Choice of *nesting habitat*, in particular the difference between below- and above-ground nests, may affect the ability to find suitable nest-sites spatially associated with foraging resources. Above-ground nesters generally nest in habitats with tussocks and tall withered grass (Benton 2006) and are therefore likely to be more sensitive to the loss of permanent (semi-) natural grasslands and linear habitats, associated with landscape simplification. Management of habitats may further affect vulnerability of trait groups differently, with above-ground nesters being sensitive to mowing of non-crop habitats (Fussell and Corbet 1992) and below-ground nesters sensitive to destruction by tillage (Roulston and Goodell 2010). We expect above-ground nesters to be less abundant in simple landscapes.

Here, we conduct the first comprehensive test of the effect of these traits on bumble bee vulnerability to landscape simplification. We analyse the impact of trait values (Table 1) on the differences of bumble bee (worker and male) abundances between simple and complex agricultural landscapes of southern Sweden. In this region bumble bee habitats are mainly semi-natural uncultivated areas in the form of non-crop field borders and grasslands. We focused on landscapes (complex vs. simple) defined by the amount of field borders they contained, because other semi-natural grasslands (e.g. pastures) are scarce, or almost non-existent, in simple landscapes. We consider abundance of workers as an indication of nest density and colony size, and number of males as a tentative proxy for reproductive output (cf. Pelletier and McNeil 2003). As outlined above, we hypothesise that the bumble bee species most vulnerable to landscape simplifications will be those with any one, or a combination, of the following trait characteristics: narrow thorax, long proboscis, large morphological variation and with small or medium sized, late founded and long lived colonies, that nest above ground. We discuss our results in relation to previously documented patterns of decline of *Bombus* species in southern Scandinavia from before 1950 until today (Dupont et al. 2011; Bommarco et al. 2012).

Materials and methods

Study design

The study was carried out in southernmost Sweden in the province of Skåne (Fig. 1), which is dominated by agriculture but with a large variation in land-use intensity and landscape complexity (Persson et al. 2010). Using ArcGis 9.2 (ESRI) we selected six simple and six complex non-overlapping circular landscapes (radius 2 km, hereafter called sites), based on digital information from the Integrated Administration and Control System (IACS, a yearly updated database on all registered farmland fields in Sweden from the Swedish Board of Agriculture). We defined simple sites as areas with large fields (mean >40 ha) and complex sites as areas with small fields (mean <15 ha), and both categories with less than 150 ha (i.e. 12 %) of permanent pastures (Fig. 1). I.e. the two categories differed in the amount and distribution of uncultivated field borders, which is an important bumble bee foraging habitat in intensively farmed landscapes (Banaszak 1992; Lagerlöf et al. 1992). Comparisons of land-use between landscape types (SAS Proc GLM, proportions arcsine-square-root transformed) showed that complex sites, as intended, had smaller fields than simple ones, but also differed in other correlated landscape variables (Table 2). Complex sites had a higher proportion of leys (perennial grass or grass/clover mixtures for silage and grazing), a lower proportion of annual crops, more forest (mainly small woodlots) and more permanent pasture, than did simple sites. Landscape types did not differ in the amount of oilseed rape, potentially an important early resource, nor did any site include red

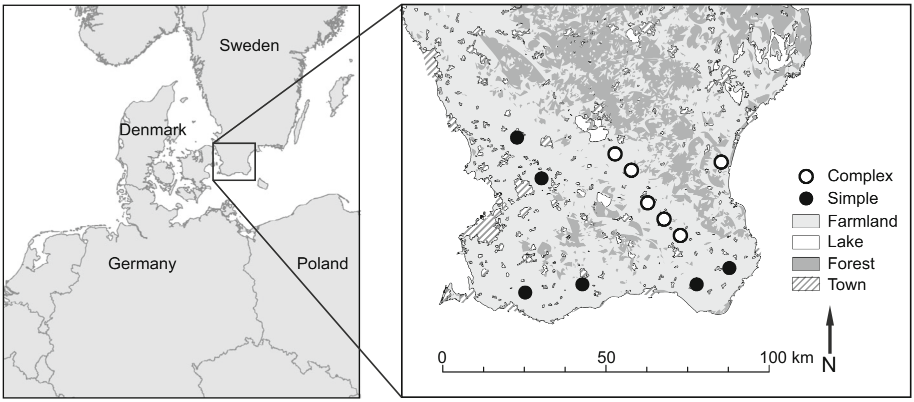

Fig. 1 The geographical position of complex and simple landscapes. *Circles* around landscape *symbols* delimit a 2 km radius within which 16 flower-rich sites (each 100 m^2) were selected for bumble bee sampling

Table 2 Field size and land-use in the two landscape types used for studies and results of tests for difference between landscape types (see 'Methods' section for details)

Variable	Landscape		F (1,10)	*P* value
	Complex (mean ± std)	Simple (mean ± std)		
Field size (ha)	5.54 ± 1.46	24.43 ± 3.56	144.76	<0.0010
Prop. forest	0.080 ± 0.062	0.010 ± 0.023	13.29	0.0045
Prop. farmland	0.80 ± 0.089	0.90 ± 0.028	7.66	0.020
Prop. pasture	0.068 ± 0.035	0.022 ± 0.021	7.42	0.024
Prop. leys	0.23 ± 0.081	0.050 ± 0.0062	44.02	<0.0010
Prop. annual crops	0.49 ± 0.10	0.82 ± 0.051	53.54	<0.0010
Prop. oilseed rape	0.047 ± 0.021	0.069 ± 0.037	1.40	0.26

Proportions are calculated as the area of the respective land use type per landscape (2 km radius). Farmland includes pastures, leys, annual crops and fallows

clover seed production fields, an important late flowering resource (Rundlöf et al. 2014). Sites were also selected so as not to include towns or villages, and only allowed for some small conglomerations of houses.

Selection of survey plots

We sampled bumble bees in 16 plots well dispersed within each of the twelve study sites. To gain sufficient number of bees for statistical tests of community trait composition we surveyed the two main pre-existing flower-rich habitat types available in the landscape, i.e. linear elements and small patches with semi-natural vegetation (12 plots) or gardens dominated by planted flowers (4 plots), henceforth referred to as habitat types. The semi-natural habitats consisted of a mixture of fallows, semi-natural grasslands and flower-rich borders of crop fields and leys, depending on what was available, and thus reflecting the habitat composition of the two types of sites (simple vs. complex). By focussing on flower-rich habitat, we do not necessarily reflect absolute abundances in the two landscape types, but we expected that our design would result in a representative sample of the bumble bee community in both types of landscapes (cf. Westphal et al. 2003; Heard et al. 2007). The selected 2 km radii sites were situated well within larger areas of the same landscape type. Regression analyses of five landscape variables (field size, proportion farmland, annual crops, leys and forest) calculated at both 2 and 3 km radius levels confirmed this; variables at the two spatial scales were highly correlated, all results $r > 0.92$. Thus, because plots close to the edge of a site share very similar characteristics to centrally placed plots, we do not expect bumble bees from sources of another landscape type than the focal one to confound the results.

Bumble bee and flower surveys

We sampled bumble bees (*Bombus* spp., including former *Psithyrus* spp.) on days with predominantly clear sky, temperatures >15 °C and without strong winds. All bumble bee workers and males found during a 10 min survey of 100 m^2 of each plot (semi-natural habitat or garden) were collected by hand netting and preserved in 70 % ethanol. Along field borders plots were linear (ca. 2 by 50 m), and in gardens 100 m^2-plots of flowering plants were identified and the shape thus depended on the garden design. We refrained from sampling queens in order to minimise any effects on the bumble bee populations. We carried out three survey rounds from Jun 25th to Aug 31st 2008, i.e. each site was visited three times. Bumble bees were determined to species and caste in the lab following Löken (1973), Prŷs-Jones and Corbet (1987) and Holmström (2007). Workers of species belonging to *Bombus* sensu stricto are not possible to separate based on morphological characters only (e.g. Williams et al. 2012b), while males can be separated based on genital morphology. We found males only of *B. lucorum* and *B. terrestris*, indicating that those two were dominating also among workers. Because those species are both morphologically similar and share categorical traits, they were combined in all analyses except for those regarding phylogenetic signals. Flowers were surveyed following each bumble bee survey, to be able to control for potential effects of flower abundance and species richness between the surveyed habitats in trait-based analyses. We counted only flower species known to be preferred by foraging bumble bees (Rundlöf et al. 2008; Persson and Smith 2013) and estimated the total number of inflorescences (sensu Williams and Kremen 2007).

Division into trait groups

Thorax width, the inter-tegular distance (ITD), of each collected bumble bee was measured using digital callipers (Table 1). Measures of proboscis length (glossa and prementum) were obtained from bumble bees sampled during a concurrent study in the same region with a similar design (Rundlöf et al. 2014) (Table 1). We calculated the percentage coefficient of variation ($CV = 100 \times \sigma/\mu$, where σ is standard deviation and μ is the mean value) of thorax width and proboscis length of each species with at least 12 workers sampled, thus leaving out *B. muscorum* and *B. jonellus* because of low sample sizes. Information on colony traits (categorical variables) was obtained from Scandinavian (Löken 1973) and British (Benton 2006) literature. Climatic differences, not only between these regions but also between northern and southern Scandinavia, may affect data on phenological traits so we combined these sources of information (see Table 1). For *B. terrestris* and *B. lucorum* Löken (1973) noted very late queen emergence, while Benton (2006) assigned them to the early group. Our personal experience is that an earlier start is the case in our study region (south Scandinavia), which is also backed up by Mossberg and Cederberg (2012). Colony cycle length was estimated from Löken's (1973) data on first dates of queen sightings and last sightings of workers. The life of the colony ends when workers stop activity, although new queens and males are still active. *B. jonellus* may have two generations per season in southern Sweden (Mossberg and Cederberg 2012) and southern Great Britain (Benton 2006). This is however not a trait we are investigating here. We are aware of that traits investigated here as categories, colony size, queen emergence, colony cycle length and nest habitat, are variable within a species (Benton 2006). However, there are few, if any, published estimations on variation in these traits and we therefore chose to rely on the estimation of mean trait values (and trait groups) made by others (Löken 1973; Benton 2006). Data on colony size may be less reliable than other trait data, because colonies are difficult to find and data therefore scarce. It also varies over season and depends on surrounding flower resources (Benton 2006). However, we believe that it is possible to make a coarse distinction between species generally forming large (ca. >200 workers), medium (ca. 100–200) or small (ca. <100) colonies.

Statistical methods

The sum of bumble bees per plot found during three surveys were used for further calculations and statistical analyses. For continuous variables (thorax and proboscis) we calculated the community-weighted mean (CWM) of the trait-values per plot: CWM = $\sum_{i=1}^{n} p_i x_i$, where p_i is the relative abundance of species i in a specific transect and x_i is the trait value of species i (Ricotta and Moretti 2011). CWM-values were log-transformed to reach normality. Statistical analyses were carried out in SAS 9.3 for Windows (SAS Institute Inc.). Workers and males were analysed separately and all models of males were run with and without males of parasitic species (former *Psithyrus*). In all the mixed models described below, local abundance and richness of plant species flowering at the time of each survey (log transformed) were included as covariates. Those factors were correlated ($r = 0.68$, $P < 0.0010$), but below the threshold ($r = 0.70$) regarded to pose any problems of collinearity (Dormann et al. 2013). Habitat type (garden or semi-natural) was included as a fixed factor to account for habitat effects not controlled for by flower abundance and richness, e.g. that gardens have an exotic flora and may provide different micro-climate compared to more open habitats. Random structures were used to account for the dependency of observations within a site and allow for random variation in the effect of habitat type between sites, i.e. random factors were site and the interaction term habitat type × site. Fixed effects were tested using F-tests with the degrees of freedom estimated with the Kenward-Roger (KR) method. We used Moran's I (SAS Proc Variogram) to test for spatial auto-correlation of the residuals from each model using the standardized centre coordinates of each site as location.

To check for general effects of landscape type on bumble bee abundance, i.e. irrespective of traits, we fitted a generalised linear mixed model (SAS Proc Glimmix, Poisson distribution, log-link function) without a trait division of bumble bees. Response variable was N bumble bees (workers or males) per transect and fixed effects were landscape type, habitat type and their interaction.

We tested for differences in (log) CWM of thorax and proboscis between landscape types using linear mixed models (SAS Proc Mixed), with fixed effects landscape type and habitat type, and their interaction. If the interaction was non-significant (at $P < 0.05$) it was excluded and only the component factors and covariates were retained. Analyses were weighted by the (log) number of bumble bees (workers or males) found in each plot, so as not to give disproportionate weight to data points of low sample sizes. Homoscedasticity of residuals were examined with Levene's test (using SAS Proc GLM). The one case of heterogenic variance found (worker *CV* proboscis length) was accounted for in the model by fitting a variance structure assuming different residual spread per landscape type (SAS random statement option Group = landscape type). Approximate normality of residuals were confirmed by examining residual diagnostic plots. Models were run with and without including former *Psithyrus* males, as well as with and without *B. pratorum* and *B. hypnorum* because of low sample sizes ($N < 20$) of morphological trait measurements for those species (for *B. hypnorum* only regarding proboscis measurements).

To analyse if categorical trait composition differed between landscape types bumble bee abundances per plot and trait group were analysed using generalised linear mixed models (SAS Proc Glimmix, Poisson dist., log-link function). Because data was over-dispersed we used a Quasi-Poisson distribution (SAS random residual). Fixed factors were landscape type, habitat type, trait, and the two-way interactions trait × landscape type and trait × habitat type. To account for the additional dependency of observations of different trait groups within sites and habitat types, the basic random structure was extended to also include trait(site), and trait(habitat type × site). In some cases estimations of random factors were (non-significantly) negative. We then used the Nobound option, allowing negative random factors, because the KR method otherwise produce inflated degrees of freedom.

To aid interpretations of trait effects on bumble bee abundances, we analysed if the traits used as predictors were interrelated. We used Pearson correlations (SAS Proc Corr) for continuous traits. For class variables different tests were used depending on the number of trait classes (2 × 2 classes: Fisher Exact test, 2 × 3: Cochran-Armitage test for trend, 3 × 3: Jonckheere–Terpstra test; all SAS Proc Freq). To check for interrelation between continuous and categorical variables we used General Linear Models (SAS Proc GLM), with the continuous variable as dependent and the categorical variable as fixed effect. To further evaluate the confidence with which community responses can be assigned to single traits or to different life history strategies composed of several traits, and to dismiss the possibility that such traits combinations co-occur simply by descent, we investigated the evidence for phylogenetic signals in traits (ESM).

The abundance of Fabaceae flowers in survey plots were analysed with a Linear Mixed Model (SAS Proc Mixed, Normal dist.). Because there were no Fabaceae in any garden the analysis was run with semi-natural plots only. Response variable was log(N flowers + 1) and fixed factor landscape type. Random factors were site and plot (site).

Results

We sampled in total 2042 workers and 1438 male bumble bees of 13 social species (Table 1). The most numerous were *B. lucorum/terrestris* (609 workers and 809 males, of which 785 *B. terrestris* males and 24 *B. lucorum* males) and *B. lapidarius* (754 workers, 322 males). We also sampled 177 former *Psithyrus* spp. males. In total, 1106 workers, 674 males and 144 parasitic males were collected in the 6 simple sites, while 936 workers, 752 males and 33 parasitic males were collected in the 6 complex sites. Males of parasitic bumble bees were assigned to their host species for analyses. Species that may have more than one host were assigned to the main host according to Mossberg and Cederberg (2012), (Table 1).

General effects on total abundance

In the basic model (modelling bumble bee abundance irrespective of trait), there were no significant landscape effects: non-significant interactions between landscape type × habitat (workers $F_{1,11.3} = 0.26$, $P = 0.62$; males (incl. former *Psithyrus*): $F_{1,11.9} = 0.53$, $P = 0.48$), and no significant difference in abundance between landscape types (workers: $F_{1,8.9} = 0.53$, $P = 0.49$; males: $F_{1,9.4} = 0.42$, $P = 0.53$). There was no significant effect of habitat type on worker abundance ($F_{1,25.7} = 0.30$, $P = 0.59$), while males were more abundant in gardens than in semi-natural habitats ($F_{1,26.9} = 26.28$, $P < 0.0001$). The results were qualitatively the same when excluding former *Psithyrus* males. We found no evidence of spatial auto-correlation in the model residuals (all $P > 0.23$).

Landscape effects on community-weighted means of morphological traits

CWM of *CV* proboscis length based on male abundance was lower in simple landscapes and there was a non-significant tendency for the same pattern for workers (Table 3; Fig. 2). Neither CWM of proboscis length, thorax width, nor *CV* thorax width differed between landscapes for either workers or males (Table 3). CWM thorax, *CV* thorax and worker CWM proboscis length were higher in gardens (Table 3). The results were qualitatively the same when excluding former *Psithyrus* males in all cases but for *CV* proboscis, where the landscape effect turned marginally non-significant ($F_{1,8.4} = 4.98$, $P = 0.055$), while the habitat effect turned significant ($F_{1,18.4} = 5.91$, $P = 0.026$) with a higher CWM found in gardens. Results were qualitatively the same when removing the weight (bumble bee abundance per plot; results not shown). Result were also qualitatively the same when excluding *B. pratorum* and *B. hypnorum*, although there was a significant interaction between landscape and habitat type ($F_{1,10.1} = 6.18$, $P = 0.032$) in the model of CWM *CV* proboscis length. The interaction was caused by a higher CWM *CV* proboscis length in complex landscapes, but only when comparing semi-natural habitats (as shown by simple main effect, SAS option Slice: $\mathrm{F}_{1,16.4} = 17.46$, $P = 0.0007$). CWM *CV* proboscis length was also higher in gardens than in semi-natural habitats, but only in simple landscapes (simple main effects: $\mathrm{F}_{1,16.5} = 10.74$, $P = 0.0046$). We found no evidence of spatial autocorrelation in any of the models (all $P > 0.15$).

Interacting effects of landscape and categorical traits

Colony size, nesting habitat and colony cycle length all significantly interacted with landscape type to explain the bumble bee abundances for both workers and males (Table 4). Results were qualitatively the same when former *Psithyrus* males were excluded. For queen emergence there was a significant landscape × trait interaction for males, but only when including former *Psithyrus* males. To illustrate how the composition of trait groups differ between landscape types we plot the model predicted $\log_{10}$ difference in

Table 3 Results of landscape and habitat effects on community weighted mean values (CWM) of individual based traits analysed with mixed models (see 'Methods' section for details)

Trait analysed	Caste	Landscape effect		Habitat effect	
		F_{df}	*P*-value	F_{df}	*P*-value
Thorax width CWM	Workers	$0.02_{1,11.3}$	0.89	$19.57_{1,26.0}$	**<0.0010**
	Males	$0.79_{1,10.8}$	0.39	$15.70_{1,24.6}$	**<0.0010**
CV Thorax CWM	Workers	$1.87_{1,10.5}$	0.20	$27.55_{1,22.4}$	**<0.0010**
	Males	$0.12_{1,9.6}$	0.73	$8.12_{1,19.3}$	**0.010**
Proboscis length CWM	Workers	$0.79_{1,8.9}$	0.40	$10.62_{1,16.6}$	**0.0047**
	Males	$0.48_{1,9.3}$	0.50	$4.28_{1,17.2}$	0.054
CV Proboscis CWM	Workers	$3.76_{1,9.3}$	0.083	$3.21_{1,15.3}$	0.093
	Males	$10.19_{1,9.0}$	**0.011**	$3.53_{1,18.3}$	0.076

Significant results are typed in bold. Workers and males were analysed separately. Models were based on CWM trait-values per plot within a site and weighted by the sample size in each plot. Results for males include former *Psithyrus* spp. *CV* = Coefficient of Variation

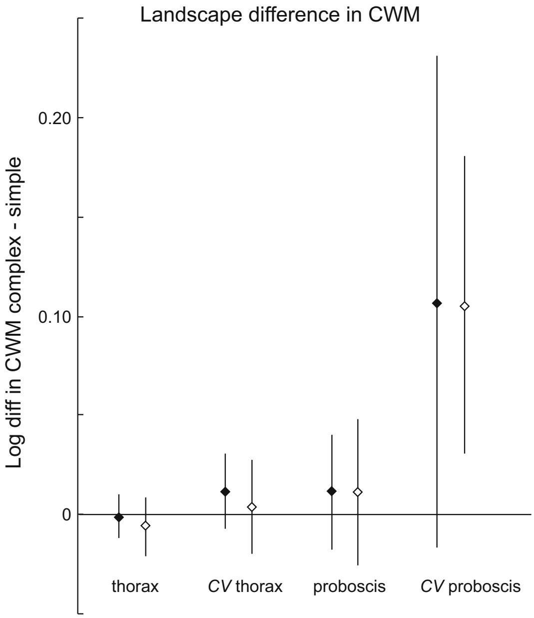

Fig. 2 Landscape effects on community-weighted mean (CWM) values of continuous traits, modelled for workers (*closed symbol*) and males (*open symbol*) separately. *Graphs* show the log difference between complex and simple landscapes in model estimated least square mean values. *Error bars* show model estimated 95 % CI. Values > 0 mean that abundance of a trait group is higher in complex landscapes compared to simple ones, while values < 0 mean the opposite. Only *CV* proboscis length CWM for males differed significantly between landscape types. For results of tests of difference between landscape types see Table 3

Table 4 Results from models analysing effects of the interactions trait × landscape type and trait × habitat type, on bumble bee abundance per trait group

Trait analysed	Caste	Landscape × trait		Habitat × trait	
		F_{df}	*P*-value	F_{df}	*P*-value
Colony size	Workers	$4.52_{2,20.60}$	**0.024**	$11.40_{2,18.81}$	**<0.0010**
	Males	$17.21_{2,43.99}$	**0.0020**	$4.04_{2,51.51}$	**0.023**
Queen emergence	Workers	$1.43_{1,7.14}$	0.27	$1.52_{1,12.11}$	0.24
	Males	$4.87_{1,14.77}$	**0.044**	$0.25_{1,18.54}$	0.62
Col. cycle length	Workers	$4.20_{2,17.30}$	**0.033**	$9.27_{2,19.69}$	**0.0015**
	Males	$8.84_{2,30.52}$	**<0.0010**	$16.71_{2,25.63}$	**<0.0010**
Nesting habitat	Workers	$7.75_{1,8.69}$	**0.022**	$0.07_{1,12.42}$	0.79
	Males	$17.01_{1,34.58}$	**<0.0010**	$13.55_{1,17.38}$	**0.0018**

Workers and males were modelled separately with generalised linear mixed models (see 'Methods' section for details). Results for males include parasitic species (former *Psithyrus*). Significant results are typed in bold

abundance between complex and simple landscapes (Fig. 3). The relative abundance of workers and males from the groups forming small and medium sized colonies was lower in simple than in complex landscapes, while the group forming large colonies showed the opposite pattern (Fig. 3a). With respect to queen emergence, the relative abundance of males of the late emerging group was lower in simple compared to complex landscapes, while the early group showed the opposite pattern (Fig. 3b). The relative abundances of workers and males from the group with a long colony cycle were lower in simple than in

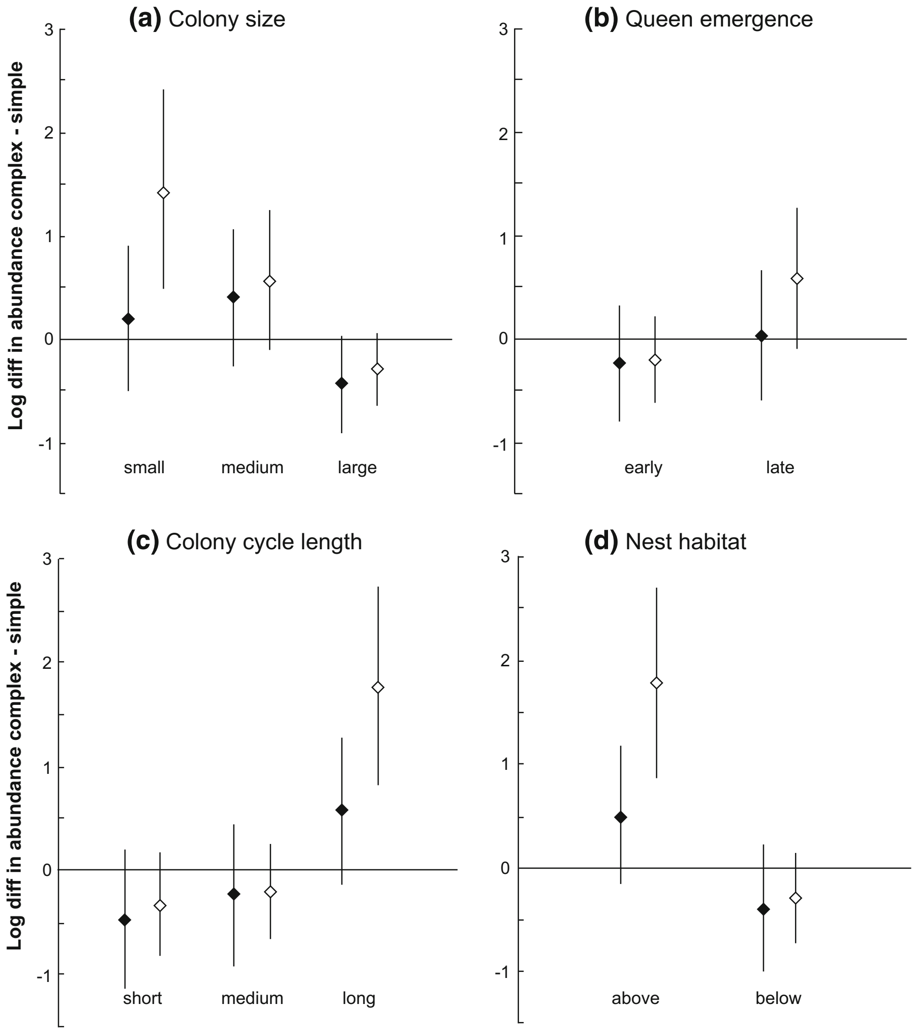

Fig. 3 Landscape effects on abundances of workers (*closed symbol*) and males (*open symbol*) depending on categorical traits: **a** colony size, **b** queen emergence time, **c** colony cycle length, **d** nesting habitat. *Graphs* show the $\log_{10}$ difference in model estimated least square mean abundances between complex and simple landscapes. *Error bars* show model estimated 95 % CI. Values > 0 mean that abundance of a specific trait group is higher in complex landscapes compared to simple ones, while values < 0 mean the opposite. Landscape effects, manifested in the form of significant interactions between trait and landscape type, were detected for all traits except worker queen emergence time (Table 4), because the relative abundance of trait groups differed between landscape types

complex landscapes, while he groups with short or medium colony cycles showed the opposite pattern (Fig. 3c). The relative abundance of workers and males of the above-ground nesting group were lower in simple landscapes, while the opposite was the case for below-ground nesters (Fig. 3d). Although the patterns were similar between the castes, the analyses of males resulted in clearer patterns, where the groups with small colonies, long colony life-cycles and above ground nests were significantly less common in simple compared to complex landscapes, i.e. where 95 % confidence intervals do not overlap zero (Fig. 3). There was no evidence of spatial auto-correlation in any of the model residuals (all $P > 0.080$).

Trait correlations and phylogenetic signals

Coefficients of variations (*CV*) of both thorax width and proboscis length were positively related to the means of the respective traits (thorax width: $r_{10} = 0.81$, $P = 0.0043$; proboscis length: $r_{10} = 0.77$, $P = 0.0092$). There were also non-significant tendencies for thorax width to be related to proboscis length ($r_{10} = 0.58$, $P = 0.062$), and for *CV* thorax width to be related to proboscis length ($r_{10} = 0.58$, $P = 0.077$). None of the four morphological traits were significantly related to any of the categorical traits (all $P > 0.15$). Colony size was significantly related to nesting habitat ($Z_{12} = -2.00$, $P = 0.046$), with below-ground nesting species having larger colonies than above ground nesters, and non-significantly related to queen emergence ($Z_{12} = 1.83$, $P = 0.068$), with early species creating larger colonies than later ones. No other correlations of categorical traits were significant (all $P > 0.31$).

The 13 species studied here represent seven different subgenera and are well distributed across the *Bombus* phylogenetic tree (Table 1, Cameron et al. 2007). Three of the subgenera were represented by two or more species. There were fewer estimated state changes than expected along the phylogenetic tree, resulting in a significant phylogenetic signal for nesting habitat (randomization-based $P = 0.019$) and for colony size ($Z_{13} = -2.22$, $P = 0.0030$). The phylogenetic signal was not found to be significantly stronger than expected under a Brownian motion model of trait evolution for any of the continuous traits or their *CV*, nor for queen emergence time or colony cycle length (ESM, Table A). We built a phylogenetic generalised least squares model for colony size, with nesting habitat and emergence time as fixed explanatory variables and a phylogenetic correlation structure (Pagel's λ). Both fixed variables were highly significant ($P < 0.0010$). The phylogenetic correlation was not significant when either nesting habitat together with emergence time, or only nesting habitat were included as explanatory variables, as suggested by a likelihood-test comparing the model with and without the phylogenetic correlation (both variables included: Likelihood-Ratio < 0.0010, $P = 0.98$, $\lambda = -0.0090$; only nesting habitat included: Likelihood-Ratio $= 0.80$, $P = 0.37$, $\lambda = 0.75$). When including just emergence time among the explanatory terms, the model comparison suggested that a phylogenetic correlation structure contributed significantly to the model (Likelihood-Ratio $= 6.86$, $P = 0.0090$, $\lambda = 1.60$).

Access to Fabaceae in plots and landscapes

Semi-natural plots in complex sites contained more Fabaceae flowers compared to plots in simple sites ($F_{1,10} = 5.88$, $P = 0.036$; least square mean ± SEM (log-values) complex sites: 4.1 ± 0.3; simple sites: 3.1 ± 0.3). This was partly a result of the higher representation of ley borders among the semi-natural plots in complex sites, and when excluding those plots the landscape effect was non-significant ($\mathrm{F}_{1,10.7} = 4.19$, $P = 0.066$; complex sites: 3.8 ± 0.4; simple: 2.6 ± 0.4). As shown in the analyses of land use ley fields were indeed more common in complex sites (Table 2).

Discussion

We demonstrate that several key life-history traits affect bumble bee vulnerability to landscape simplification caused by agricultural intensification. This is manifested as significant interactions between those traits and landscape type in explaining numbers of workers and males observed. We also found an effect of queen emergence time on abundance of males (Table 4). We thus detected a lower relative abundance of individuals of species with traits we hypothesized *à priori* to indicate susceptibility to disturbance and inability to exploit scattered resources: small sized colonies, using above-ground nest sites, with a long colony life-cycle and late queen emergence (males only). In contrast, individuals of species forming large colonies, nesting below-ground, with a short reproductive cycle and emerging early (males only), were equally or relatively more abundant in simple landscapes (Fig. 3). While categorical trait × landscape interactions were significant for both males and workers (except for queen emergence), the effects were more pronounced for male abundances (Fig. 3). This indicates that the effects of landscape simplification are manifested to a higher degree in reproductive output, possibly because of a strong relation to colony level energy status, which should be related to a combination of the number of foragers and the surrounding flower resources. These results thus support earlier studies of traits causing bee species vulnerability to habitat disturbance and landscape simplification (e.g. colony size: Rundlöf et al. 2008, nesting habitat: Williams et al. 2010, queen emergence: Goulson et al. 2005; Fitzpatrick et al. 2007; Williams et al. 2009). Although colony cycle length has been suggested to be of importance (Benton 2006; Williams et al. 2009), it has to our knowledge not previously been confirmed by empirical analyses. In contrast to most previous trait-based studies, we employed a landscape design (complex vs. simple farmland landscapes) in combination with sampling in naturally occurring foraging habitats, (but see Rundlöf et al. 2008). We can therefore draw conclusions specifically related to effects of landscape simplifications caused by agriculture. In addition, our analyses of several traits, together with between-trait correlations, enable a comprehensive discussion of both separate and combinations of traits.

Effects of trait combinations in relation to landscape changes

We found indications that trait correlations could result from co-adaptation of traits related to seasonal foraging strategies. Closely related species were more similar in terms of colony size and nesting habitat (see also the association between subgenera and traits, Table 1), but we could show with phylogenetic generalised least squares models that colony size was related to nesting site and emergence time also when accounting for potential underlying phylogenetic correlation of all 13 species. Therefore, rather than having an effect through any one single trait, landscape simplification may affect species via combinations of traits, e.g. disfavouring the "smaller colony, late and above-ground" strategy, especially in combination with a long reproductive cycle.

Mid and late season flowering habitats (e.g. meadows, legume-based fodder crops, non-cropped habitats) have largely been lost from contemporary farmland (Stoate et al. 2001; Carvell et al. 2006; Fitzpatrick et al. 2007; Goulson et al. 2008a; Bommarco et al. 2012) and lack of such resources may limit bumble bee populations (Rundlöf et al. 2014). Substantially lower abundances of flower resources in simple compared to complex landscapes were documented in our study region, especially during mid/late season (Persson and Smith 2013). Early resources, in this region mainly solitary trees and shrubs, may still suffice for colony establishment of early species. Winter-sown oilseed rape (OSR) may further add resources during this period. Since it would take a large work force already by mid-May to efficiently localize and exploit such abundant but ephemeral resources (Westphal et al. 2006), large scale farming of OSR could provide the basis for survival and reproduction of large colonies with an early and short life-cycle, but not for species with the opposite traits. In addition, simple landscapes likely offer only short flushes of resources, be it early or late, while complex landscapes offer a more continuous supply. The former would benefit species with a short reproductive cycle, while the latter is necessary to allow species with long cycles to reproduce and persist. It may thus not only be a decrease in forage *per se* but the spatial and temporal match (or mismatch) between colony phenology, foraging ranges and resources that explain contemporary pattern of bumble bee abundance, with a few relatively successful species but many more facing serious declines.

Irrespective of the correlation between nest site with colony size and possibly queen emergence, the relative abundance of above-ground nesters was lower in simple than in complex landscapes. A likely cause is the landscape wide loss of preferred nesting habitats of this group; tussocks of tall and withered grass (e.g. Fussell and Corbet 1992), in concordance with the general loss of permanent grasslands and linear non-crop habitats (Banaszak 1992). Management regimes (e.g. summer cutting) of remaining field borders and road verges cause disturbance or destruction of nests, which further increase vulnerability of this group (Williams and Osborne 2009; Roulston and Goodell 2010).

Effects of morphological traits

The CWM of *CV* proboscis length was lower in simple landscapes for males. We cannot know to what extent the measured *CV* of morphological traits is caused by variation within or between colonies, however both levels of variation may be favourable in complex landscapes. High variation in proboscis length *within* a colony potentially allows it to efficiently handle and exploit flowers of varying morphologies. This may be beneficial in complex landscapes with a diverse flora. In contrast, and as indicated by our results, the same variation may be a disadvantage in landscapes containing a simplified flora. In such landscapes it is presumably more advantageous with a less variable workforce, which can efficiently utilise the few flowering species (including mass-flowering OSR), often with open flowers and shallow corollas. High proboscis length variation *between* colonies may be advantageous in complex landscapes because it could allow different colonies to focus on and efficiently handle separate parts of a rich flora, with the same drawbacks at stated above in simple landscapes. Species mean proboscis and its *CV* were positively related, and so the effect of proboscis length variation may include the effect of a diet of flowers with deeper corollas, such as Fabaceae. These were indeed less common in simple landscapes, partly as a result of less clover leys and thus fewer ley borders where clover was left to flower.

We found no landscape effect on CWM of worker thorax width or thorax *CV*. Although thorax width is assumed to correlate with bee foraging ranges (Westphal et al. 2006; Greenleaf et al. 2007), the variation in thorax width between the *Bombus* species studied here is low (range 3.71–4.78 mm) compared to that in a broader study relating bee thorax width to flight range (1 to >5 mm, Greenleaf et al. 2007). It is therefore possible that the interspecific variation was too low to mediate any landscape effects. Interestingly it has been shown that several *Bombus* species (*B. terrestris*: Osborne et al. 2008, *B. pascuorum*: Goulson et al. 2010; Carvell et al. 2012, *B. lapidarius*: Carvell et al. 2012, *B. vosnesenskii*:

Jha and Kremen 2013) adjust their foraging ranges depending on the surrounding resource distribution and diversity. This may indicate that, at the spatial scales of resource distribution studied here, flight capacity itself (via its proxy thorax width) may not limit resource acquisition by bumble bees.

Comparison to general trends in *Bombus*

We can relate our results to two recent studies comparing bumble bee abundance and community composition in red clover fields in southern Scandinavia before 1950 with present day data (Dupont et al. 2011: absolute changes in abundance; Bommarco et al. 2012: relative changes). The five species reported as declining (*B. sylvarum, B. hortorum, B. ruderarius, B. distinguendus, B. muscorum*) exhibit between two and four of the four categorical traits we suggest to cause vulnerability to landscape simplification. *B. hortorum* and *B. sylvarum* also exhibit the highest variation in proboscis length of the species in our study, while such data is missing for *B. distinguendus*. The four stable species (*B. subterraneus, B. hypnorum, B. pascuorum, B. pratorum*) have two or three of these traits, while the two increasing species (*B. terrestris, B. lapidarius*) do not have any such trait. Thus, our results fairly well predicted declining versus stable or increasing species.

Potential caveats

We are aware of the difficulties of separating workers from species within the subgenus *Bombus* sensu stricto (including *B. cryptarum, B. lucorum, B. magnus* and *B. terrestris*) based on morphological characters (e.g. Williams et al. 2012b). Males are however easier to determine. We only found males of *B. terrestris* and *B. lucorum*, which indicate that those species dominated the sample also for workers. Because only traits related to individual morphology (thorax and proboscis) differ between *B. terrestris* and *B. lucorum*, and because *B. terrestris* likely dominates the group (as indicated by the males sampled) we feel confident that results would be qualitatively unaffected if we were to group these individuals differently.

The weak but significant correlations between three traits (significant between colony size and nesting habitat, non-significant tendency between colony size and queen emergence) may lead to one trait partly driving the apparent landscape effect detected in the other. For example, if colonies of early emerging queens benefit from early mass-flowering crops in simple landscapes, this may result in apparent landscape-dependency of nesting habitat and colony size, without an underlying causation. However, as previously discussed, trait correlations may also be a result of co-adaptation related to seasonal foraging strategies. An additional trait may merit further investigation: larval feeding regime (Sladen 1912), i.e. if pollen is stored separate from brood cells and each larvae is fed individually (pollen storers) or if pollen is placed in pockets adjacent to each brood cell from which larvae feed themselves and compete for food (pocket-makers) (Table 1). The latter has been suggested to be common for declining species (Benton 2006). We did not include this trait because published information is lacking for both *B. soroeensis* and *B. hypnorum* and because feeding regime has also been suggested to affect worker size variation (Benton 2006), which we already investigate here.

Because the abundance of some species was low, we performed analyses based on trait groups or CWM trait values rather than species. While a possible drawback is that common species dominate the response, an advantage is that it is possible to include trait attributes of rare species, instead of having to disregard them altogether. Because the number of individuals of some species is small, so is the sample size for morphological traits of those species. This could affect the accuracy in the estimated mean and variation of traits. We therefore analysed landscape effect on morphological traits both with and without species with less than 20 sampled individuals, with the same qualitative results. The relatively small number of species in the communities studied increases the risk that the effects of landscape simplifications detected for the traits, some of which exhibit phylogenetic signals, could be caused by unexamined confounding traits shared by related species, e.g. larval feeding regime. Our focus on testing explicit hypotheses specified *à priori* reduces this problem, but the extension of the present analysis to an international, preferably intercontinental, data set, including a wider phylogenetic sample of species is desirable (see e.g. Williams et al. 2009).

A higher abundance of workers could mean either more colonies, larger colonies or both. Genetic methods can be employed to more accurately estimate landscape wide colony densities (e.g. Carvell et al. 2012), but was not possible to employ on our data set including 13 species. Plasticity in colony size is indeed a trait, which could potentially promote persistence through periods of variable forage availability. However, abundances of workers and males should still relate to amount of forage available and the colony level ability to extract those resources (Williams et al. 2012a), which is in turn regulated by traits related to foraging and seasonality. We therefore believe that this type of field data can inform on important landscape scale effects on bumblebee populations. It may be questioned to what degree male abundance is related to colony reproduction, because factors other than the colony nutrient status and worker number may affect the switch from worker production into either production of queens or males, or both (Duchateau et al. 2003). It has been suggested that queen hibernation time and nutritional status after overwintering effect queen vs. male production, where longer hibernation means a lower status because of depleted energy reserves, leading to an early switch and predominantly male progeny (Duchateau et al. 2003). This indicates that our analyses are conservative, because hibernation period is likely similar between landscapes types while late season flower resources are especially scarce in simple landscapes (Persson and Smith 2013). This likely leads to decreased energy intake by new queens in simple landscapes and a lower nutrient status when emerging and nesting the coming season, and thus an increased male relative to queen production (Duchateau et al. 2003). Our results of fewer males from species with certain traits in simple landscapes may therefore be a conservative measurement of reproductive success, and indicate that the difference regarding daughter queen production is actually even more accentuated in benefit of complex landscapes.

Complex landscapes were somewhat clustered (Fig. 1), because landscape type is related to soil type, resulting in more productive agriculture and concomitant landscape simplification to the west and south (Persson et al. 2010). However, we did not detect any spatial auto-correlation affecting the results. It is thus unlikely that our results are caused by distributional patterns rather than by responses to landscape quality.

Conclusions

We found that colony size, nesting habitat, colony cycle duration, variation in proboscis length and possibly also queen emergence time affected bumble bee vulnerability to landscape simplifications caused by contemporary agricultural practices. Three of the traits (colony size, nest habitat and possibly queen emergence time) were interrelated and may have evolved together, resulting in alternative life-history strategies, which have rendered some species unsuccessful in coping with landscape simplifications. We suggest that species with colonies of few workers, late emerging queens, above-ground nests, long reproductive cycle and variable proboscis length have a reduced chance of reproducing in simplified landscapes. Any remedy to the on-going loss of bumble bees must therefore include actions to increase the fit of resources to those groups, both at the level of the individual worker and of the colony. Establishing flower-rich field margins may not have an effect on bumble bee populations if they do not also contain flowers of the required morphology and phenology, if the spatial scale of implementation does not allow for smaller colonies to find and utilise them, or if the flowering season is too restricted. Introducing more landscape complexity into agricultural regions therefore seems a promising general intervention to aid declining bumble bee species.

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