

Bumblebee colonies produce larger foragers in complex landscapes

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Abstract

The negative effect of agricultural intensification on bumblebee populations is thought to partly be caused by loss of food plants, for example because of increased field size and concomitant loss of non-crop field borders and their nectar and pollen plants. Earlier studies have focused on how loss of foraging resources affects colony growth and thereby abundance of workers and sexual reproduction. By comparing bumblebees in agricultural landscapes of different complexity in Southern Sweden, we here demonstrate that also the adult size of bumblebee foragers is significantly related to the availability of foraging resources. This effect was independent of both species identity and foraging habitat type. This suggests a shortage of flower resources in landscapes of lower complexity, which may also affect the reproductive success of colonies negatively.

Zusammenfassung

Es wird angenommen, dass der negative Einfluss der landwirtschaftlichen Intensivierung auf Hummelpopulationen teilweise durch einen Verlust an Nahrungspflanzen hervorgerufen wird, beispielsweise wegen höherer Feldgrößen und dem damit verbundenen Verlust an Feldrändern und ihren Nektar- und Pollenpflanzen. Frühere Untersuchungen haben sich darauf konzentriert, wie der Verlust von Nahrungspflanzen das Koloniewachstum und damit Arbeiterabundanz und sexuelle Reproduktion beeinflusst. Indem wir Hummeln in südschwedischen Agrarlandschaften von unterschiedlicher Komplexität miteinander verglichen, zeigen wir, dass auch die Körpergröße von Hummelarbeiterinnen signifikant mit der Verfügbarkeit von Ressourcen verbunden ist. Dieser Effekt war unabhängig von der Artzugehörigkeit und dem Typ des Nahrungshabitats. Dies legt nahe, dass in Landschaften von geringer Komplexität ein Mangel an Blütenressourcen herrscht, der auch den reproduktiven Erfolg der Kolonien negativ beeinflussen könnte.

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Introduction

It is widely recognised that pollinating insects have been negatively affected by agricultural intensification, loss and fragmentation of natural and semi-natural habitats (Kearns,

Inouye, & Waser 1998; Biesmeijer et al. 2006; Potts et al. 2010). Several studies have focused on losses of bumblebees from regions with intensive agriculture (Kosior et al. 2007; Goulson, Lye, & Darvill 2008; Grixti, Wong, Cameron, & Favret 2009; Williams & Osborne 2009; Cameron et al. 2011). However, responses of bumblebees to landscape changes imposed by agriculture differ among studies and species, e.g. in the spatial scale of resource acquisition (Westphal, Steffan-Dewenter, & Tschardtke 2006; Goulson

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et al. 2010) and in the effects of mass flowering crops (MFCs) (Herrmann, Westphal, Moritz, & Steffan-Dewenter 2007; Knight et al. 2009; Westphal, Steffan-Dewenter, & Tscharnke 2009; Goulson et al. 2010). Also some species do remain common even in very simplified regions (Williams 1982; Goulson et al. 2008; Williams, Colla, & Xie 2009). These differences may reflect both species-specific responses and specific qualities of the study landscapes. Such variability of responses, together with the great importance of bumblebees as pollinators of crops and wild plants throughout much of the world (Goulson 2003; Cederberg, Pettersson, & Nilsson 2006; Winfree, Williams, Gaines, Ascher, & Kremen 2008), calls for continued research on the mechanisms underlying their responses to past and present landscape changes.

Bumblebees are social insects and the reproductive unit is only one queen per colony (Goulson 2003). This drastically reduces the effective population size in comparison to census counts of worker bees. Furthermore, bumblebees are central place foragers and their fitness depends on the distance between the nest and flower resources (Goulson 2003). Bumblebees therefore constitute both an important and interesting group to study in the light of the ongoing pollinator declines and intensification of agricultural landscapes.

The effect of large-scale landscape intensification and simplification on bumblebee populations is considered to in part act via loss of food plants (Benton, Vickery, & Wilson 2003; Carvell et al. 2006). The ability of a bumblebee colony to attain sufficient resources for reproduction depends on several aspects of the individual worker and the colony. The foraging range, which is positively (non-linearly) related to forager body size of bees in general (Greenleaf, Williams, Winfree, & Kremen 2007) and possibly also positively correlated with colony size in bumblebees (Westphal et al. 2006), may affect the ability to utilise fragmented resources. The size of workers may also affect the rate of energy influx to the colony since larger foragers have been found to be more efficient nectar foragers in *Bombus terrestris* (Goulson et al. 2002; Spaethe & Weidenmueller 2002), and this could also be so for other species. Larger foragers may also carry out a larger proportion of pollen collection (Brian 1952), although this was not confirmed in a later study (Goulson et al. 2002). A larger colony is presumably better able to meticulously scan for and utilise resources in the surrounding, compared to a colony of fewer workers. Larger foragers and colonies may thus increase the ability to cope with a high variation in food plant availability, which is significant for structurally simplified agricultural landscapes. There are inter-specific differences in mean size of workers and size of the worker caste (Löken 1973; Benton 2006), and this has also been suggested as a cause behind differences in population responses to land-use intensification and habitat fragmentation (Westphal et al. 2006; Rundlöf, Nilsson, & Smith 2008).

The size of adult worker bees is determined by the amount of food they are fed as larvae (Schmid-Hempel & Schmid-Hempel 1998; Goulson 2003). The number of sexual offspring produced by a colony is related to the amount of food

that the colony can harvest to build up a large worker caste in order to maintain the high rates of provisioning needed, especially during queen development (Goulson 2003). Smaller and fewer workers and fewer males in response to food shortage has been demonstrated in a lab environment (Schmid-Hempel & Schmid-Hempel 1998). In a field study competition from managed honeybees, *Apis mellifera*, resulted in decreased mean body size of co-occurring bumblebees (Goulson & Sparrow 2009). Smaller foragers may in turn result in a decreased influx of food, further reducing the size and number of the work force and adding to the already hampered performance of the colony. Quite plausibly this also affects the reproductive output negatively. One way of identifying landscapes where resource are in short supply could be to compare the size of worker bees. This would also allow for detection of inter-specific differences in ability of resource acquisition depending on the surrounding landscape.

Our aim was to investigate if the amount and spatial segregation of flower-rich non-crop habitats (i.e. a component of landscape structure), affects the mean size of bumblebee workers. Resources within a distance of 250 m up to 3000 m have been shown to affect bumblebee densities and this indicates an ability to forage within this distance from the colony (Westphal et al. 2006; Knight et al. 2009). Studies using other techniques have come to similar conclusions (Walther-Hellwig & Frankl 2000; Darvill, Knight, & Goulson 2004; Knight et al. 2005, 2009; Osborne et al. 2008). We therefore performed our study in contrasting landscapes where resources were separated by different mean distances, i.e. landscapes with differently sized agricultural fields. This variation in field size will inevitably also affect the amount of resources potentially found in field borders, since it affects the perimeter to area ratio. Based on the reasoning above we hypothesise to find smaller workers in landscapes of simplified structure. We also hypothesise to find differences between species in the response to landscape structure. If commonness reflects a high ability of a species to adapt to contemporary farmland and utilise its resources, then still common species may not respond to landscape simplifications by producing smaller workers. At least not to the same extent as more vulnerable species would.

Methods

Landscape selection

The study was carried out in southernmost Sweden in the province of Skåne (approximately 56°N, 13°30'E, Fig. 1). This region is dominated by agriculture but also shows a large variation in land-use intensity and landscape complexity (Persson, Olsson, Rundlöf, & Smith 2010). We used digital information from the Integrated Administration and Control System (IACS), a yearly updated database on all registered farmland fields in Sweden (Swedish Board of Agriculture), to select two classes of landscapes. Because we

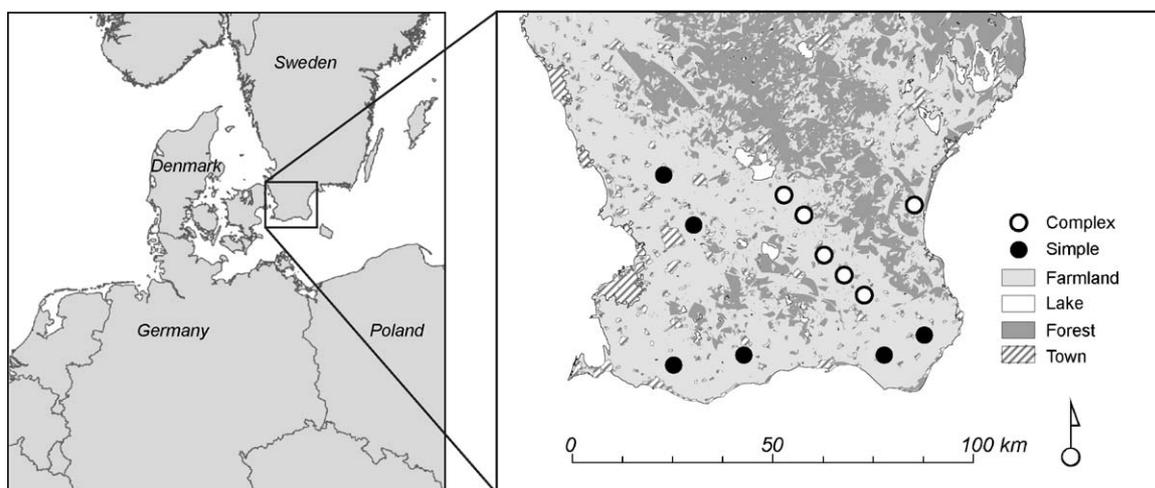


Fig. 1. The position of landscapes used for the study. Circles around landscape symbols delimit a 2 km radius. Complex landscapes (white circles) have smaller agricultural fields (mean < 15 ha) than do simple landscapes (black circles, mean > 40 ha).

were interested in the effect of the amount and distribution of non-crop field margins on bumblebees, we selected circular landscapes (radius 2 km) with either large (mean > 40 ha) or small (< 15 ha) fields, but with less than 200 ha of permanent pasture, which may affect bumblebees positively (Morandin, Winston, Abbott, & Franklin 2007; Öckinger & Smith 2007). It should be noted that according to our classification pastures are permanent, semi-natural grasslands used exclusively for grazing and may not be fertilized. In contrast, leys are rotational crops where grass mixed with clover (*Trifolium repens* or *T. pratense*) is cultivated for grazing, hay or silage production. Leys are typically included in the crop rotation and a field is used for ley at least two and sometimes up to more than five years in sequence. We also aimed at minimizing the amount of forest and larger woodlots within the landscapes. In IACS, fields are reported in units of “blocks”, which typically consist of one or several adjacent fields (i.e. without non-crop borders in between), surrounded by a border that can be identified on an aerial photograph. Data was processed in ArcGis 9.2 (ESRI) and six landscapes of each class were selected. Landscapes composed of large blocks of fields are hereafter called “simple” and those of small blocks are called “complex” (Fig. 1).

We used landscapes of 2 km radius since landscapes of this size should suffice to describe the landscape encountered by central-place foraging bumblebees. The circular landscapes were also well positioned within larger “simple” or “complex” regions (not shown). All circular landscapes are at least 3 km apart such that, regarding foraging bumblebees, we can consider them independent. However, because of the geography of our study region, simple and complex landscapes cannot be completely interspersed, potentially resulting in spatial auto-correlation (Fig. 1). We took account of this by maximizing interspersion, within the constraints of landscape variation and reasonable driving distances, and tested for spatial autocorrelation when analysing results.

Selection of survey sites

In order to allow statistical analyses of sufficient power we collected a dataset where we detected as many bumblebees from as many species as possible in each landscape. We did this by surveying only flower-rich habitats where bees may come to forage. From each circular landscape ($n = 12$) we therefore selected 4 gardens and 12 other flower-rich sites consisting of fallows, semi-natural habitats or flower rich borders of crop fields and leys during field visits, i.e. in total 16 survey sites per circular landscape (Table 2). In addition we placed 4 sets of pan-traps in each circular landscape (3 plastic cups, 6 cm deep, Ø 15 cm; one white, one blue, one yellow, sprayed with the corresponding fluorescent colour (Sparvar, Leuchtfarbe), filled with 50% propylene glycol) (Table 2). Pan-traps were placed directly on the ground and in order to avoid damage by agricultural activities they were placed within or bordering to one of the habitat types mentioned above. We aimed at an even spread of survey habitats and pan-traps over each circular landscape.

Bumblebee collection

All bumblebees found during a 10 min survey of 100 m² of each survey site were collected by hand netting and preserved in 70% ethanol. Sites were sampled 3 times, from 25 June to 31 August 2008. Pan-traps were emptied in connection with each survey round (Table 2). No queens were collected to avoid affecting population persistence, but we could not avoid accidental collection of some queens in the pan-traps. Bumblebees were determined to species and caste in the lab following Löken (1973), Prÿs-Jones and Corbet (1987) and Holmström (2007). The thorax width of each individual was measured using digital callipers.

Table 1. Data on differences in land-use and land cover between the two landscape classes studied.

Variable	Complex (mean \pm std)	Simple (mean \pm std)	$F(1,10)$	P
Field size (ha)	9.49 \pm 2.82	53.11 \pm 8.71	136.19	<0.0001
Prop. farmland	0.81 \pm 0.085	0.90 \pm 0.026	7.61	0.020
Prop. pasture	0.090 \pm 0.044	0.022 \pm 0.031	11.24	0.0073
Prop. leys	0.28 \pm 0.094	0.054 \pm 0.0072	53.16	<0.0001
Prop. annual crop	0.61 \pm 0.12	0.91 \pm 0.036	41.87	<0.0001
Prop. forest	0.080 \pm 0.062	0.010 \pm 0.023	6.57	0.028

Statistics

Statistical analyses were carried out in SAS 9.2 for Windows (SAS Institute Inc., Cary, NC) using General Linear Models (SAS proc GLM) and Linear Mixed Models (SAS Proc Mixed). Where proportions were used to describe land-use they were arcsin-square-root transformed before statistical testing to normalise data and avoid the variance to be associated with the mean. Land-use data were analysed with GLMs at the level of each landscape, with landscape class as the explaining factor. For the bumblebee data analyses were made at the level of an individual bumblebee. Since workers from the same landscape are not independent estimates of the effect of landscape structure and even may be sisters (Darvill et al. 2004), we used a Mixed Model (SAS Proc Mixed) and accounted for non-independence at the landscape level via the random structure. We used individual thorax width as the response variable and landscape class, species and habitat type as fixed factors. We assigned landscape, landscape \times habitat type and landscape \times species as random factors. Degrees of freedom were estimated using the Kenward–Rogers method. We used the Nobound option since covariance estimation of one random factor was non-significantly negative and the Kenward–Rogers method otherwise gives inflated denominator degrees of freedom. To account for possible effects of differences in sampling date between landscapes we also ran the model including date of each sample. Date alone did however not have a significant effect, nor did it interact with landscape class and we therefore dropped it from the model. We tested for spatial auto-correlation by including a spherical spatial covariance structure. However, this covariance was not significant ($z=0.58$, $P=0.28$) and inclusion of it did not affect results qualitatively and was therefore not included. We present model least square means (lsm) while standard error means (sem) were calculated from data aggregated at the level they were tested at, using SAS Proc Means.

Results

Landscapes

Because landscapes were selected based on mean block size, complex landscapes necessarily had significantly

smaller fields. Landscapes also differed because of correlated differences in other landscape variables. Complex landscapes had a higher proportion of leys and consequently, less annual crop area than simple landscapes (Table 1). Although we aimed to only select landscapes with little permanent pasture and forest, complex landscapes contained slightly but significantly more pasture and forest than did simple ones.

Bumblebees

In total 2033 foraging worker bees from 11 species were collected and included in the analysis. The most common species were *B. lapidarius* (754 individuals), *B. terrestris* (563), *B. sylvarum* (239), *B. hortorum* (156) and *B. pascourum* (151). In simple landscapes only 5 individuals of *B. pratorum* were sampled and from only 2 landscapes, we therefore also ran the model excluding *B. pratorum*. However this only changed the results marginally and in favour of larger bees in complex landscapes. We therefore only present the results based on all species.

We found that foraging worker bees were significantly larger, on average 2%, in complex compared to simple landscapes (lsm \pm sem (mm) complex 4.28 \pm 0.059, simple 4.19 \pm 0.049, effect size 1.61; $F_{1,9.7}=6.60$, $P=0.019$, Fig. 2). Species, naturally, differed in size ($F_{10,96.7}=40.04$, $P<0.0001$, Fig. 2). There were also significant differences in size of workers caught foraging in different habitat types ($F_{4,28.2}=3.67$, $P=0.016$). Workers caught in gardens and adjacent to leys were larger (4.29 \pm 0.022 and 4.31 \pm 0.026 respectively) than those caught in or adjacent to pasture (4.18 \pm 0.037), crop fields (4.23 \pm 0.017) and fallow

Table 2. Sampling set-up of the study: two landscape classes, complex and simple, of 6 circular landscapes each were sampled according to this set-up.

Survey sites per circular landscape ($n=12$)	Sampling methods
Twelve non-crop habitats (100 m ²)	Hand-netting (10 min), 3 times
Four domestic gardens (100 m ²)	Hand-netting (10 min), 3 times
Four sets of pan-traps in non-crop habitats	Left in field for 3 periods of 16.4 \pm 4.3 days

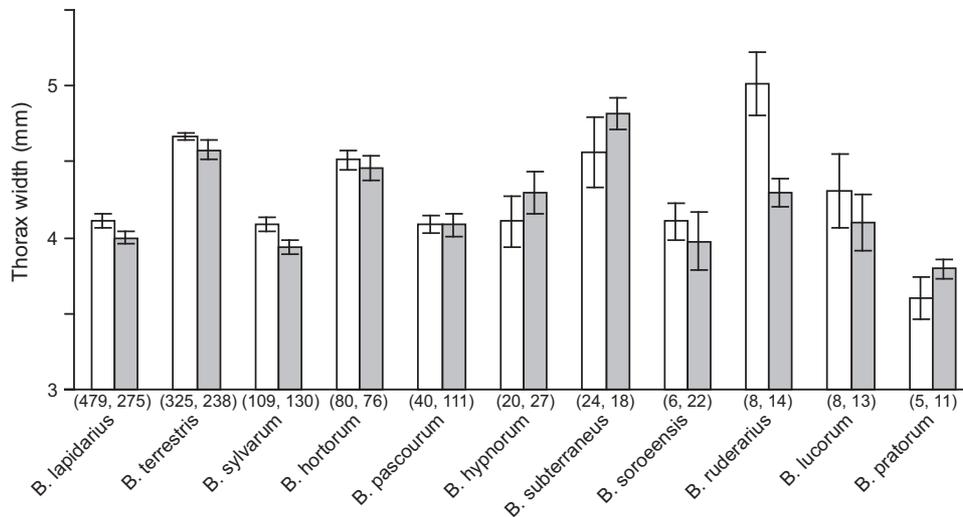


Fig. 2. Mean thorax width (mm) \pm sem of bumblebee species collected in complex (white bars) and simple landscapes (grey bars). Sample sizes are given for complex and simple landscapes separately within brackets under each species' bar. Individuals caught in complex landscapes were significantly larger than those caught in simple ones and mean size differed between species.

(4.18 ± 0.027). We did not find any significant interactions between landscape class and either species or habitat type, indicating that the pattern of difference between landscapes was general.

Discussion

Bumblebee foragers were larger in more complex landscapes, independent of species identity. Hence, the five most common species, which have been considered to be able to cope with intensively managed, simple landscapes (Kosior et al. 2007; Goulson et al. 2008), were similarly negatively affected by the simplified landscape structure. This effect on forager size could be caused by food availability, as modified by the presence of non-crop field borders, leys, pastures and forest edges, affecting the growth of larvae and thus the adult size of bumblebee workers. Production of smaller individuals and fewer sexuals in response to low food availability has been documented for *B. terrestris* in a lab environment (Schmid-Hempel & Schmid-Hempel 1998). Smaller bumblebee workers of several species have also been found when they are sympatric with managed honeybees, *Apis mellifera*, which was suggested to indicate competition for food (Goulson & Sparrow 2009). Alternatively, it has been suggested that production of smaller workers is an adaptive response to starvation, since smaller bumblebees survive longer during low colony nectar intake rates (Couvillon & Dornhaus 2010). This could mean that colonies in simple landscapes adjust to food scarcity by producing more, smaller and hardier workers rather than fewer, larger and more energy demanding ones. As we do not have information on landscape specific colony sizes we can unfortunately not evaluate this hypothesis. However, it still implies that the colonies sampled in simple landscapes experience a shortage of resources.

It should be noted that because we decided to include each individual forager in the analysis (with species as a fixed factor), rather than, for example using a mean value per species and landscape, abundant species affect the result more than do rare ones. There are pros and cons of the two alternative ways of analysis. Either common species will affect the analysis more than rare species or data from the substantially fewer individuals of rare species will have an un-proportionally large effect on the results. We believe that our approach is the more robust one because the size differences of the rarer species will be less precisely estimated, but we are at the same time aware of its limitations in accounting for the rarer species. There may be some concerns regarding spatial auto-correlation, since landscapes cannot be perfectly interspersed given the overall structure of landscape variation. We argue that the landscapes were separated enough to be independent considering the foraging ranges of bumblebees (e.g. Knight et al. 2005; Osborne et al. 2008; Wolf & Moritz 2008), but close enough to allow gene-flow preventing local adaptations (Kraus, Wolf, & Moritz 2009; Lepais et al. 2010). However, although the result was unaffected when accounting for spatial auto-correlation, it is clear that a correlative study cannot ascertain which aspects of landscape variation are causing the differences in the size of workers. In real landscapes characteristics are inevitably linked (Persson et al. 2010). For example, although our design attempted to maximize differences in farmland complexity, there is a small but significant difference between the landscapes in the amount of forest. However, given that we focused on maximizing the difference in farmland complexity while minimizing variation in amount of pasture and forest, we believe that the cause for variation in worker size should primarily be sought in landscape complexity or in factors closely linked to farmland complexity.

Landscape complexity is the mix of habitat types within an area, i.e. the number of land-use classes, their distribution and configuration (Turner, Gardner, & O'Neill 2001; Vepsäläinen 2007). Field size contributes directly to the degree of complexity (Vepsäläinen 2007) and in the current experimental design we studied bumblebees in landscapes of contrasting complexity, based on size of agricultural fields. Because of correlated differences in land-use, including the amount of flower-rich habitats (e.g. field margins, leys and possibly forest edges) (Persson et al. 2010), flower resources were both fewer and farther apart in simple compared to in complex landscapes. Therefore food shortage for bumblebees will also be coupled with longer foraging trips and we can thus not separate effects of forage abundance and foraging distance on the size of foragers. However, a lab study (Schmid-Hempel & Schmid-Hempel 1998) found no effect on worker size under a regime of ample food supplied with large temporal variations. Bumblebees also evolved in the temperate and alpine regions of the world (Hines 2008), which are characterised by large variations in food supply due to flowering phenology of plants and frequent changes in weather conditions, resulting in periods of several days when foraging may not be possible (Couvillon & Dornhaus 2010). This could imply an ability to cope also in structurally simple landscapes, despite long foraging distances and large temporal forage resource variation (e.g. in the form of MFCs), if these resources are sufficient to compensate for temporary food shortages, throughout the colony life cycle. Given this, the detection of smaller foragers in simplified landscapes therefore suggests that the shortage of forage in itself, rather than that the spatial separation of resources is the cause behind the detected size differences. However, the increased foraging distance most likely adds to the hardships of colonies in simplified landscapes.

Because smaller workers are less efficient in gathering nectar (Goulson et al. 2002; Spaethe & Weidenmueller 2002), the whole colony could be expected to suffer from lowered energy input and end up in a downward spiral, further decreasing the size and efficiency of its potential work force and therefore also its production of queens and males. Interestingly, other studies have suggested that mass flowering crops (MFCs) early in the season may boost bumblebee worker numbers but not reproduction (Herrmann et al. 2007; Westphal et al. 2009). In the region studied here, oilseed rape is widely grown. It is thus possible that colonies have been initiated and grown large in response to oilseed rape early in the season. However, in simple landscapes these colonies would later compete for the few available resources in non-crop habitats and, as a consequence, be unable to keep up the size of their workers.

It is known that bumblebees prefer to forage on flowers which fit their morphology (Peat, Tucker, & Goulson 2005), such that a smaller worker would presumably chose smaller flower heads than larger ones would. Accordingly, the mean size of foragers differed between habitat types, most probably reflecting differences the flora of these habitats. If this line of reasoning is transferred to a landscape perspective, an

alternative explanation to our results may be that the flower compositions of simple and complex landscapes differ such that smaller bees are more efficient foragers of simple landscapes, while larger bees work better in complex landscapes. In this case, smaller foragers would be a colony level plastic response to the available flora. Data from a previous study in the same region show indeed that the proportion of annual to perennial flowers is higher in simple compared to in complex landscapes (Persson & Smith unpublished data), indicating that simple landscape contain more of open and easily accessible flowers. However, the total amount of flower resources was also substantially lower in simple landscapes (Persson & Smith unpublished data) and it is therefore unlikely that the smaller size of workers detected here is solely due to flower morphology.

In summary the results presented here indicate that simple landscapes with a shortage of food are indeed hampering body size of foraging workers and thereby possibly colony development of several bumblebee species. It is therefore urgent to increase the amount of suitable resource flowers for bees especially in simplified landscapes, e.g. by recreating and properly managing non-crop habitats.

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