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# An assessment of historical and contemporary diet breadth in polylectic *Andrena* bee species

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ABSTRACT

The loss of key forage plants and a narrow pollen diet have both been implicated in the decline of wild bees over the past 70 years. These ideas have been studied extensively in recent years in bumblebees (*Bombus* spp.), but have rarely been investigated in other bee groups, due in part to a lack of detailed ecological data for many species of wild bee. Chambers (1968) extensively documented pollen preferences in bees from the genus *Andrena* collected in Bedfordshire, UK, during the 1940s, before the period of rapid agricultural intensification following the Second World War. This extensive dataset allows for the importance of diet breadth in modifying the response of bees to environmental change to be investigated in a common and widespread but understudied genus of bees. We compared the pollen preferences of a suite of *Andrena* species collected in the 1941–1949 period with a similar suite of *Andrena* species collected between 1985 and 2016. Relative diet breadth was consistent across studied species between the historical and contemporary period. However, dietary composition changed with a shift away from Rosaceae and towards Brassicaceae. The reduction in the collection of Rosaceae pollen was more pronounced in spring-flying than summer-flying *Andrena*, which may be due to a reduction in the length and quality of hedgerow habitats and hence spring-flowering woody Rosaceae present in the countryside, and an increase in the availability of the mass-flowering crop oilseed rape (*Brassica napus*). Both historical and contemporary diet breadth were significant positive predictors of how frequently *Andrena* species are encountered on contemporary farmland, with those species with a relatively wider diet present on the majority of farms. These findings support the idea that inherent differences in diet breadth mediate the ability of bee species to respond to changes in resource availability resulting from agricultural intensification. A more detailed understanding of species-level characteristics can help improve our understanding of why seemingly similar species respond very differently to environmental change.

## 1. Introduction

Access to food resources is the most important limiting factor for wild bee populations on farmland (Roulston and Goodell, 2011), and the loss of key forage plants has been extensively linked with declines in wild bee populations (Goulson et al., 2005; Biesmeijer et al., 2006; Kleijn and Raemakers, 2008; Scheper et al., 2014; Ollerton et al., 2014). This principle has been most extensively studied in bumblebees (*Bombus* spp.), with an over-dependence for pollen on a narrow range of grassland plants suggested as a key factor behind their decline in Europe (Rasmont, 1988; Goulson et al., 2005). This was explicitly tested by Kleijn and Raemakers (2008) who used microscopic analysis of the pollen loads present on bee specimens from museums to quantify bee diets prior to their subsequent post-World War II decline. Bumblebee species that declined over this period were found to collect pollen from one-third of the number of plant genera compared with those species that remained common and widespread.

However, still relatively little is known about the species composition of pollen collected by wild bees, even for large, abundant and charismatic species such as bumblebees (Kleijn and Raemakers, 2008). Whilst the general ecological niche and pollen preferences of many central and northern European bee species are reasonably well known (Westrich, 1989; Müller, 1996), their specific and relative pollen preferences at the plant genus or species level are poorly understood except in the few cases where recent genus-level investigations and revisions have been conducted (e.g. Müller, 1996; Müller and Kuhlmann, 2008; Sedivy et al., 2008). As shown by these studies, the use of microscopic analysis of pollen loads is a powerful tool that allows for the explicit quantification of bee species' pollen preferences and for the direct comparison of diet breadth between species. Much of the analysis into

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species level sensitivity to agricultural intensification has been conducted at the generalist/specialist level (Bommarco et al., 2010; De Palma et al., 2015). As a categorical analysis, this does not capture the variation present within groups of generalist species, such as species that collect pollen from many different plant species (polylectic species), and consequently may not fully explain patterns of range contraction or expansion that have occurred in response to environmental change.

*Andrena* is a large genus of bees with around 1450 described species (Gusenleitner and Schwarz, 2002) which is found predominantly in temperate Holarctic environments. Most species fly in the spring, though bivoltine and univoltine summer and autumn phenologies are known and the genus displays very wide variation in pollen preferences, from polylecty sensu strictu to narrow oligolecty (Westrich, 1989; Larkin et al., 2008; Amiet et al., 2010, see Supplementary Table S1 for lecty definitions). Chambers (1968) published an account of pollen preferences in 31 species of British *Andrena* from specimens collected between 1941 and 1949 in Bedfordshire, England, listing all pollen types detected and concluding that there was little evidence of oligolecty in the studied *Andrena* species. Definitions and categories of host range have since been refined and explicitly quantified, allowing for a more consistent use of terms to be applied (Cane and Sipes, 2006; Müller and Kuhlmann, 2008). Whilst not published, Chambers did record the relative proportion of the different pollen types detected, allowing for a comparison of both the type and relative quantities of pollen species in *Andrena* pollen diets between this historical and contemporary time period.

Since there is a general lack of detailed knowledge as to the pollen preferences of solitary bees, revisiting the work of Chambers through access to his original data offers an opportunity to explore how diet breadth affects species occurrence in a genus of bees other than the comparatively well-studied *Bombus*. Given the documented population decline in bumblebees with relatively narrow diets, we hypothesise that i) relative to other *Andrena* species, diet breadth has been consistent over the past 70 years but that ii) rather than widening their diets, species with narrow diets will instead be less widespread on agricultural land in the present day than species with broad diets. We analysed historical and contemporary pollen diet data aiming to better understand aspects of pollen choice in wild bees and to develop more effective conservation strategies for this genus of bees through the provision of high-resolution dietary information.

## 2. Methods

### 2.1. Bee sample collection

Chambers (1968) presented data on 1173 pollen loads from 31 species from Bedfordshire, England (Fig. 1) between 1941 and 1949. The distribution of these loads was unequal however, with 13 species represented by fewer than 10 loads. The specific quantities of each pollen type from each pollen load were not presented in his original publication; this information was extracted from his personal notebooks and digitised. Excluding oligolectic species ($n = 7$) and those species with small sample sizes of fewer than five analysed pollen loads (an additional $n = 3$), data was available for 1064 pollen loads from 21 species, representing a high proportion of the data for these selected species that was published in his 1968 manuscript (99.0% $n = 1075$). By definition, oligolectic bees are substantially restricted in their diets and so these species were excluded from further analysis.

In the present day, 561 *Andrena* specimens with pollen loads representing 26 species were obtained from the personal collections of the authors and other members of the Bees, Wasps and Ants Recording Society (BWARS) of the United Kingdom (see Acknowledgements). Specimens were freely collected over central and southern England, Wales and the Channel Islands (Fig. 1) between 1985 and 2016. Because the latter geographic area exceeds the area searched by

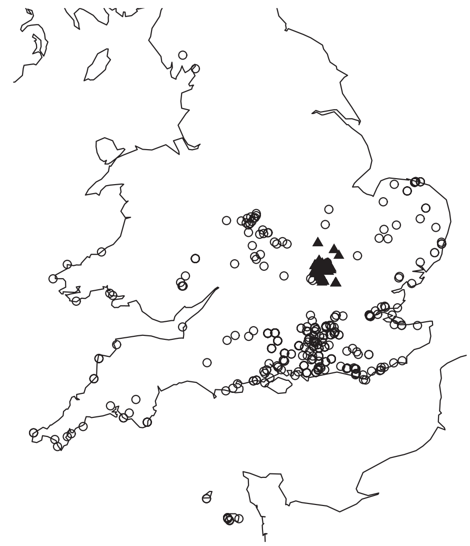

**Fig. 1.** Map of *Andrena* specimen sampling locations in England, Wales and the Channel Islands. The 1941–1949 Chambers' (1968) sampling locations are marked by closed triangles and the 1985–2016 contemporary sampling locations are marked by open circles.

Chambers, no attempt was made to test whether diet breadth has increased or decreased in absolute terms across polylectic *Andrena* species over this time period. A wider contemporary diet may be simply because a different range of plant species are available in these geographically different areas independent of agricultural intensification. The Bedfordshire sites originally surveyed by Chambers should be revisited and resampled for this analysis to be conducted more accurately. In addition, whilst the contemporary samples were collected over a longer period than for the Chambers dataset, the majority of the samples (76.1%) were collected between 2008 and 2016 (Supplementary Fig. S1), the same length as the nine year collecting period of Chambers. The longer contemporary sampling period is not expected to significantly affect the results since the whole of the 1985–2016 collecting period post-dates the greatest period of agricultural intensification in Britain (Robinson and Sutherland, 2002; Ollerton et al., 2014).

An up to date Red List for British bees is not available, with the most recent assessment produced 30 years ago (Shirt, 1987). Additionally, this rarity classification was based in part on absolute occurrence rather than population stability per se. As such it is not a good metric for considering the current conservation status of the British species and how steeply they may have declined. A new assessment based on up to date BWARS data is ongoing (M. Edwards pers. comm.) but is also currently unavailable. However, 19 farms were extensively surveyed for aculeates between 2013 and 2015 across the south-east of England (Hampshire and West Sussex, Wood et al., 2016) and the relative frequency with which each species was found on a farm-by-farm basis was used as an indication of how widespread each species is in the contemporary southern English countryside.

### 2.2. Pollen identification and diet characterisation

The scopal pollen load of bee specimens was analysed by light microscopy using the method outlined by Westrich and Schmidt (1986) and modified as follows: before removing pollen from the scopae, the total load was visually estimated relative to a full load for that species, ranging from 8/8 (full load) to 1/8 (one eighth load). The pollen grains were removed from the scopae using a clean entomological pin and transferred to a drop of water on a microscope slide. Pollen that was not clearly held in the scopae was not sampled as this may have become attached to other parts of the body during nectar visits to non-host plant flowers. The slide was gently heated to allow grains to absorb water and achieve their maximum size and to evaporate excess water. Molten