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The missing data in floral resource projects

‘Pollen: The missing data in floral resource projects’

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Abstract

Pollen is an important floral resource that has largely been ignored in favour of sampling nectar. Although nectar is an important source of carbohydrate, pollen provides the protein, sterols and lipids needed for many pollinator species. I quantified the floral longevity of 73 common UK farmland species and calculated their pollen production per 24 hours. Working on three farms in Somerset, the pollen productivity of each farm was measured between March and October. This was done by combining the floral longevity of each farmland plant species with published data on the farm's phenology and a combination of new and unpublished data on the total amount of pollen produced by each plant species. The mean floral longevity of the 73 plant species was 2.58 days ±1.4 SD, with a range of 1-8.1 days. The amount of pollen and nectar produced by plants is broadly correlated, although there are some outliers that do not follow this trend. Many of the weedy species such as *Taraxacum officinale* produce high quantities of pollen and nectar throughout the year, providing much needed floral resources for pollinators. Species like *Salix* spp. produce high quantities of pollen and nectar, however they only produce this for a short period of time, so overall their contribution to floral resources over the flowering season is small. Farmland pollen availability shows a strongly seasonal pattern, peaking in April, followed by a gap in June, before peaking again in July and August, then drops off rapidly. Two habitat types provide the highest quantities of pollen and nectar at the unit area level; hedgerows and woodland, however at the farm-scale, pasture provides the largest amount of pollen and nectar. This research expands on the poorly understood aspects of pollen availability and floral longevity of UK farmland species and is the first comprehensive database on daily pollen production of species.

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Author’s declaration

I declare that the work in this dissertation was carried out in accordance with the requirements of the University’s *Regulations and Code of Practice for Research Degree Programmes* and that it has not been submitted for any other academic award. Except where indicated by specific reference in the text, the work is the candidate's own work. Work done in collaboration with, or with the assistance of, others, is indicated as such. Any views expressed in the dissertation are those of the author.

Signed: ELLEN WRIGHT Date: 06/02/2023

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1.Introduction

1.1 Project aims and overviews

Pollinator decline is a concern for many scientists due to their importance in both wildflower and crop pollination (e.g., Goulson et al. 2008; Potts et a. 2010a; Ollerton et al. 2011; Powney et al. 2019). Roughly 9.5% of crops globally are predicted to be lost if pollinators disappeared (Gallia et al. 2009), leading to possibly negative changes to the human diet and further expansions of agricultural land to make-up for the loss of production (Smith et al. 2015; Potts et al. 2016). In the UK 71.7% of land is used for agricultural purposes (World Bank 2022) and much of this land is unavailable to pollinators. Agri-environmental Stewardship Schemes have been designed to provide financial incentives to farmers who manage their land in an environmentally friendly way (Natural England 2009). This scheme pays for conservation measures such as hedgerow planting and adding and flowering field margins, however there is little specific guidance on which flowers are beneficial to pollinators. This potentially leads to dietary gaps in some of the nutrients that they need (Carvell et al. 2007; Natural England 2009).

There are a small number of papers on nectar gaps and nectar supplies in the UK (e.g., Baude et al. 2016; Hicks et al. 2016; Timberlake et al. 2019; Tew et al. 2021; Barnsley et al. 2022), however, there is very little equivalent data on pollen gaps and supplies (Coffey & Breen 1997; Dicks et al. 2015; Hicks et al. 2016). This is due to the lack of data on both the amount of pollen per flower species and the longevity of flowers - thus how much pollen is produced per flower and for how long? The overall aim of my research is to quantify pollen availability using a combination of an unpublished dataset on the amount of pollen in common UK flowers collected by Mathilde Baude and collaborators, along with my own measurements of floral longevity. By combining these two datasets with a third dataset on the floral abundance on four Somerset farms from Timberlake et al. (2019), I will be able to calculate pollen availability at the farm scale.

In what follows, I will introduce the importance of pollinators, the evidence for pollinator decline, the impacts that anthropogenic drivers have on their populations, the nutritional

needs of pollinators and floral longevity. I end by stating the specific research objectives of this project.

1.2 The importance of pollinators

Pollinators provide vitally important ecosystem functions (pollination of wild plants) and services (pollinator of crops) to plants and humans respectively, and are a key component of global biodiversity. Insect pollinators pollinate a substantial amount of globally important crop species (~75%), including important crops such as fruits, seeds, nuts, coffee, cocoa, and oilseed rape (Klein et al. 2007; Gallai et al. 2009; Potts et al. 2016). This service is vitally important in maintaining our current rate of food production within the agricultural sector. Pollinators are also important for wildflowers, with <80% of the worlds wild species pollinated by insects (Burd 1994; Ashman et al. 2004; Potts et al. 2010b). The loss of pollinators could have considerable negative consequences for insect pollinated plants, possibly resulting in losses in floral diversity.

Pollinator-dependent crops are an important part of a balanced diet in humans, with many being the principal source of micronutrients, such as vitamin A and C, calcium, fluoride, and folic acid (Smith et al. 2015). The loss of these pollinator-dependent crops through pollinator loss could cause a substantial increase in preventable diseases (e.g., non-communicable diseases such as cancer and diabetes and malnutrition), potentially resulting in 1.42 million more deaths per year (Smith et al. 2015). The areas that would be most impacted by this would be low-income countries who already have a low consumption of Vitamin A and folic acid (Smith et al. 2015). Not only are pollinators vitally important in providing the world with food but they are also vital in pollinating plant used in medicines, biofuels, fibres, construction materials, musical instruments, arts, crafts, and recreation activities (Potts et al. 2016).

With 75% of all crops worldwide requiring pollination the decline in pollinator populations is worrisome (Klein et al. 2007; Potts et al. 2010a; Thomann et al. 2013). Moreover, our understanding of what affects pollinator species diversity, abundance, and community composition and how this effects seed and fruit yields is incomplete (Potts et al. 2010a). In 2005 the total world production value of crops used by humans was €1618 trillion with insect

pollinations contributing €153 billion to that total, ~9.5% of all crop species produced (Gallai et al. 2009), which has increased to an estimated global value of between US$195 billion to US$387 billion annually (Porto et al. 2020). Crops such as nuts, fruits, and coffee are most vulnerable to pollinator decline, while vegetables have the lowest vulnerability (Gallai et al. 2009; Potts et al. 2010a). Potts et al. (2010a) reported that different regions of the world had different groups of crops that are vulnerable to pollinator decline, for example in North America, nut production is most vulnerable while in central Asia fruit production is the most vulnerable. Although a loss of pollinators would not cause the whole agricultural sector to halt, it would cause significant issues for fruit, nut, and coffee production (Gallai et al. 2009), possibly resulting in price increases and/or availability decreases for consumers and loss of micronutrients in the diet (Smith et al. 2015). And while this estimation of €153 billion is a good starting point on how much pollinators are needed for crop production; the full extent of their impact is not well understood.

1.3 Evidence for declines in pollinators

Pollinator decline is believed to be occurring throughout the globe. The species with the most coverage are honeybees and bumblebees found within the US and Europe (Goulson 2003; Kosier et al 2007; van Engelsdorp et al. 2008; Goulson et al. 2008; Williams & Osborne 2009; Cameron et al. 2011; Potts et al. 2010b). There has been a clear decline in domestic honeybee populations, in the US honeybee stocks decreased by 59% between 1947-2005 and in Europe they decreased by 25% between 1985-2005 (NRC 2006; van Englesdorp et al. 2008; Potts et al. 2010a; Potts et al. 2010b). This decline in honeybee stock is problematic due to our dependency on them to pollinate food crops (Potts et al. 2010b). Although there have been regional losses in honeybee numbers, worldwide hive numbers have increased by 45% since 1961, however the amount of land used for crops has increased by ~300% resulting in a pollinator deficit (Aizen et al. 2009; Potts et al. 2010a).

Among wild bees, the most well documented group are the bumblebees (*Bombus* spp.) which have exhibited an ongoing decline in diversity in the UK. Out of 16 non-parasitic bumblebee species in the UK, six have declined substantially (*B. subterraneus* has become extinct), four may be in decline and six are stable or have increased (Goulson et al. 2008; Williams & Osborne 2009; Potts et al. 2010a). Data for other bee species within the UK is fragmented due to the lack of coordinated monitoring programmes, resulting in large knowledge gaps,

however a third of all wild pollinators in the UK have declined between 1980 and 2013 (Powney et al. 2019). This decline in bumblebee species has not only been seen in the UK, but other developed regions such as western Europe and North America (Goulson 2003; Kosior et al. 2007; Goulson et al. 2008; Cameron et al. 2010). A study conducted by Kosier et al (2007) studied 60 *Bombus* species found in 11 countries within Europe (Belgium, the Netherlands, Luzembourg, Denmark, Germany, Switzerland, Austria, Czech Republic, Slovakia, Hungary, and Poland) and identified that all countries contained species that were threatened with decline. Four species had gone extinct within the 11 countries (*B. armeniacus, B. cullumanus, B. serrisquama* and *B. sidemii*) between 1951-2000 (Konier et al. 2007). Similar declines have been seen across the US with species such as *B. occidentalis, B. penslyvanicus, B. affinis* and *B. terricola* experiencing widespread decline (Cameron et al., 2010).

Although there are widespread reports of declines in pollinator species worldwide, there are some species which remain somewhat unaffected by these drivers of decline (Goulson et al. 2008). These more common species tend to have broader foraging preferences, using non-native garden plants and crop monocultures in their diet (Goulson et al. 2002; Goulson et al. 2008). In Europe six species are widespread and common and are classed as generalist pollinators that adapt easily to altered environments (Goulson et al. 2002; Goulson et al. 2008). Species that have smaller geographic ranges, specific habitat associations or climate requirements are more likely to be affected by stressors such as habitat loss (Williams 2005; Goulson et al. 2008).

1.4 Anthropogenic drivers of pollinator decline.

There are many drivers of pollinator decline, both anthropogenic and natural, however anthropogenic drivers are most concerning. These drivers have considerable effect on pollinator populations with the most important drivers being land-use change; increasing pesticide use and environmental pollution; decreased resource diversity; alien species; spread of pathogens; and climate change (Hendrickx et al. 2007; Kosier et al. 2007; Vanbergen 2013; Goulson et al. 2015).

Habitat loss is widely considered the most important driver of bee decline. A quantitative review of 54 studies looking at the effects of different drivers on bees conducted by Winfree

et al. (2009), concluded that although all drivers play a small but significant role in bee decline, habitat loss/fragmentation was the most important driver. Widespread habitat loss and fragmentation has been seen throughout Europe and North America, usually due to increased urbanization and agricultural intensification (Williams & Osborne 2009; Vanbergen 2013; Goulson et al. 2015). This has resulted in large declines in flower-rich habitats such as grasslands which provide bees with a range of floral resources (Hendrickx et al., 2007; Goulson et al. 2015). An example of this is in the UK, where 97% of semi-natural grasslands were converted into farmland during the 20th century, causing major range contractions for many bee species, particularly long-tongued bumblebees (Fuller 1987; Bullock et al. 2011). The conversion of hedgerows, marginal grasslands and wetlands is driving further declines in pollinator abundance across the UK (Williams & Osborne 2009).

Agricultural intensification also causes an increase in other drivers such as pesticide, herbicide, and fertilizer use (Williams & Osborne 2009; Vanbergen 2013; Goulson et al. 2015). Although pesticides, herbicides and fertilizers use provide clear economic benefits to a farmer, their impact on bees is in direct conflict with these (LeBuhn & Luna 2021; Goulson et al. 2015). The use of herbicides is highly effective at reducing unwanted weeds in crop systems, but this results in reduced availability of diverse floral resource to pollinators, rendering farmland inhospitable and consisting largely of monocultures of food crops or grass (Morandin & Winston 2005; Goulson et al. 2010; Potts et al. 2010a; Goulson et al. 2015). Pesticides that are used in agriculture have been found within honeybee hives, with specific pesticides; neonicotinoids (thiamethoxam, imidacloprid and clothianidin) and organophosphates (phosmet and chlorpyrifos) posing the greatest risk to honeybees (Sanchez-Bayo & Goka 2014; Goulson et al. 2015). Neonicotinoid application on fields is strongly linked to bee decline more generally due to their neurotoxicity; they target the insect central nervous system resulting in decreased foraging efficiency, declining cognitive function, decreased colony fitness and death (Tomizawa & Casida 2005; Goulson 2013; Gill & Raine 2014; Goulson et al. 2015; Moffat et al. 2015; Pisa et al. 2015; Stanley & Raine 2016). The application of fertilizer is one of the most common causes of floral decline in the world (Tilman et al. 2001; Hautier et al. 2015; Villa-Galaviz et al. 2021). Only plant species that are adapted to living in nutrient rich soils can survive, causing an overabundance of perennial grasses within the borders of fields and grassland pastures on farmland (Phoenix et al. 2012; Harpole et al. 2016; Villa-Galaviz et al. 2016). This switch from diverse grasslands, with an

abundance of floral resources to a plant species poor environment, results in pollinators needing to travel longer distances to acquire the nutrients they need.

The introduction of alien plant species has allowed generalist pollinators to fill gaps in their nectar and pollen needs that cannot be filled by native floral resources (Stout & Morales 2009; Potts et al., 2010a). The continual decline in native habitats allow opportunistic alien species, such as *Impatiens glandulifera* to flourish, whilst also providing large quantities of pollen and nectar to native generalist pollinators (Stout & Morales 2009; Potts et al., 2010a). These introductions are a double-edged sword though, as increased alien species coverage will impact on native plant species, reducing their abundance and changing plant community composition (Stout & Morales 2009; Potts et al., 2010a). The changing community composition of habitats and subsequent decline in their native host plants may detrimentally affect specialist pollinators, as they may be unable to utilize invasive species (Stout & Morales 2009; Potts et al., 2010a).

Through the globalisation of crop production, managed honeybees and bumblebees have been shipped around the world and are now present on every continent other than Antarctica (Stout & Morales 2009). High levels of overlap in plant use between native bee species and non-native *Apis mellifera* has been identified in the US, and between invasive *Bombus terrestris* and native *Bombus* species in Japan (Matsumura et al. 2004; Thomson 2006; Potts et al. 2010a). Introduced European bees have shown a preference for invasive European plant species in New Zealand, possibly resulting in an increase in abundance of these invasive species (Pearson & Braiden 1990). There is evidence of domestic honeybees displacing wild bumblebees from their foodplants and even whole areas if their hives are large enough (Walther-Hellwig et al 2006; Goulson et al. 2015). However, it is likely the bumblebees were already in decline due to other reasons such as habitat loss (Forup & Memmott 2005). But other than a handful of studies, the effect on introduced bee species on wild bee populations is not well understood or documented (Goulson 2003; Potts et al. 2010a). Although the consensus is that introduced pollinators can potentially have a seriously negative impact on native bee populations (Freitas et al. 2009; Williams & Osborne 2009), it remains possible that other factors have been the cause of observed decline.

One aspect of the introduction of non-native bee populations is the possibility for disease or pathogen transmission (Freitas et al. 2009; Stout & Morales 2009; Williams & Osborne 2009;

Potts et al. 2010; Vanbergen 2013; Goulson et al. 2015; LeBuhn & Luna 2021). Crossovers of 11 viruses from managed bees to wild bees have occurred, including black queen cell virus and chronic bee paralysis (Murray et al., 2019; LeBuhn & Luna 2021). In Brazil, captive honeybees have been carrying an infectious disease called European foulbrood which causes brood deformities and death and has been identified in 60% of native stingless bee populations (Teixeira et al., 2020; LeBuhn & Luna 2021). Allowing managed and wild hives to mix could result in more pathogen transmission rates between the two groups, resulting in possible widespread declines in populations.

Arguably one of the most prominent future drivers of pollinator decline is climate change. As the climate continues to change, plant and pollinator ranges will continue to shift in their distributions and phenologies (Fitter & Fitter 2002; Memmott et al. 2007; Vanbergen 2013; Goulson et al. 2015; Kudo & Cooper 2019). These range shifts could cause temporal and spatial mismatches between co-occurring plants and pollinators, impacting processes such as pollination (Memmott et al. 2007; Potts et al. 2010; Vanbergen 2013). Range shifts in response to climate change have been observed in montane bumblebees in Spain, where they have been shifting their lower altitudinal limit further uphill (Ploquin et al. 2013). Other impacts of climate change such as the increased abundance of extreme weather events (storms, floods, and drought), and the extinction of important flowering species will likely impact bee species worldwide (Goulson et al. 2015; LeBuhn & Luna 2021). Flowers grown under draught stress produce duller petals and higher levels of volatile compounds than plants under no stress, leading to a lower quality floral resource (LeBuhn & Luna 2021). Climate change has also altered the flowering phenology of species and countries. In the UK 16% of species flowered significantly earlier than expected with 3% flowering significantly later (Fitter & Fitter 2002). A study in Japan conducted on the species *Corydalis ambigua* found that the time of flowering became earlier if snowmelt and ambient surface temperatures increase at an earlier time of year, resulting in a phenological mismatch between the plant and bumblebees which pollinated it (Kudo & Cooper 2019). This mismatch resulted in a reduced seed-set for the plant, resulting in a small population in the following year (Kudo & Cooper 2019). This alteration in flowering phenology may impact pollinator species, resulting in large floral resource gaps when species need them the most. Although there is little evidence of the negative impact of climate change on pollinators, aside from shifts in their distribution, the expected increase in extreme weather events and temperature will likely play a role in further pollinator declines.

1.5 The nutritional needs of pollinators

Pollinators require two fundamental food resources from flowers: pollen and nectar. They rely heavily on a diversity of floral resources to obtain all the macro and micronutrients (i.e., amino acids, vitamins, minerals, proteins, and carbohydrates) that they require (Donkersley et al. 2014; Vaudo et al. 2015; Moerman et al. 2017; Woodard & Jha 2017). The quantity and blend of these nutrients vary greatly between different plant species (Donkersley et al. 2014; Moerman et al. 2017). Carbohydrates are obtained primarily from nectar and contain three main sugars, glucose, fructose, and sucrose (Percival 1961; Nicolson & Thornburg 2007; Vaudo et al. 2015). These three sugars vary in amount depending on the species of flower. Sugars are required for the development of bee larvae and for adult foraging and flight (Michener 2000; Brodschneider & Crailsheim 2010; Vaudo et al. 2015; Woodard & Jha 2017). The characteristics of nectar are relatively simple and consists of three variables: sugar composition, nectar volume and nectar concentration (Vaudo et al. 2015). Sugar composition refers to the amounts of glucose, fructose, and sucrose present within the nectar (Vaudo et al. 2015). Nectar volume varies greatly between species and families (Vaudo et al. 2015). This variation is proposed as an evolutionary trade-off between high volumes of nectar which are energetically costly and low volumes of nectar that do not attract pollinators (Harder & Cruzan 1990; Mu et al. 2014; Vaudo et al. 2015). The third characteristic is nectar concentration, which plays an important role in pollinator-plant visitation. The concentrations which bees prefer depends on the feeding apparatus length of the bee, honeybees are long-tongued bees and prefer a concentration of 30-50% while short-tongued bees prefer higher concentrations of 45-60% (Roubki & Buchmann 1984; Vaudo et al. 2015). Tongue length affects flower choice with pollinators with long feeding apparatuses being able to access flowers with long nectar tubes while species without this long apparatus cannot unless they rob the flower (Vaudo et al. 2015).

Pollen provides many important nutrients to pollinators. This includes protein, which is required by larvae for their metabolic growth. If in low supply during development this can lead to negative effects on adult bee physiology and performance (Brodschneider & Crailsheim 2010; Bukovinszky et al. 2017; Kämper et al. 2016; Woodard & Jha 2017; Filipiak 2019). The protein content of pollen differs considerably depending on the species, ranging from 2.5% - 62% dry weight (Buchmann 1986; Roulston & Cane 2000; Donkersley et al. 2014; Vaudo et al. 2015) requiring pollinators to forage for a variety of different plant

species. Although protein content differs, the most important amino acids to bumblebees and honeybees remain relatively similar across plant taxa (Roulston & Cane 2000; Weiner et al. 2010; Kämper et al. 2016). When specific amino acids are needed by the colony, bumblebees can discriminate among flowers with different pollen chemistry and preferentially forage on pollen with higher protein and amino acid content (Hanley et al. 2008; Leonhardt & Blüthgen 2012; Moerman et al. 2015; Ruedenauer et al. 2015; Somme et al. 2015; Kriesell et al. 2016; Moerman et al. 2017). Pollen is also a major component in beebread which is used by honeybee larvae during development (DeGrandi-Hoffman et al. 2013; Morais et al. 2013; Donkersley et al. 2014). The varying nutritional composition of beebread is mainly driven by the plant species that the honeybee has collected their pollen from (Donkersley et al. 2014). This indicates that even within hives there is variation in beebread composition (Donkersley et al. 2014). Pollen is also a bee's main lipid source, including fatty acids and sterols and its concentration ranges from 1% - 20% depending on the plant species (Roulston & Cane 2000). Lipids are needed for a variety of different physiological processes (e.g., egg production and wax production) and contribute to larval and adult health, larval development, and the ability of hives to overwinter successfully (Brodschneider & Crailsheim 2010; Vanderplanck et al. 2014; Vaudo et al. 2015). Sterols are the precursors of moulting hormones, making them an essential nutrient for larval development (Brodschneider & Crailsheim 2010; Vanderplanck et al. 2014; Vaudo et al. 2015) while linoleic acid (an essential fatty acid) is associated with higher worker production in honeybee colonies (Avni et al. 2014; Vaudo et al. 2015)

Many studies of bee nutrition have been conducted on honeybees and bumblebees and are not representative of most bee species (most of which are solitary, with many being oligolectic) (Roulston & Cane 2000; Brodscheider & Crainsheim 2010; Vaudo et al. 2015). With some bees specialising in one specific family or genus of plants, this suggests that different bee species have varying dietary requirements that are not represented by honey or bumble bees (Roulston & Cane 2000; Nicolson & Thornburg 2007; Behmer & Joern 2008; Vaudo et al. 2015). Although some studies exist (see Paoli et al. 2014; Stabler et al. 2015) very little is known about the specific nutrients needed for most bee species to remain healthy. There is also very little evidence of the nutritional needs of other insect pollinators such as moths, wasps, flies and beetles and what sort of nutrition they acquire from flowering plants.

The nutritional composition of pollen varies between different species, but all contain protein, nitrogen, amino acids, starch, sterols, and lipids (Roulson & Cane 2000). Many studies were conducted during the 1970s-1980s on pollen composition (Todd & Bretherick 1942; Bachmann 1986; Roulson et al 2000), while more recently large-scale studies have been conducted for specific areas or species (Hassan 2011). A recent study analysed the pollen chemistry of 219 different plant species using FT-Raman and FTIR spectroscopy to identify the chemical characteristics of the pollen (Kendel & Zimmermann 2020). Their study found that pollen chemistry differs within families and genera. Pollen chemical analyses requires large quantities of pollen and so is difficult to conduct, especially on small floral units (e.g. daisies; *Bellis perennis* and ragworts; *Senecio spp.)* resulting in large knowledge gaps (Roulston & Cane 2000).

Losses in floral diversity can lead to "hunger gaps" in the floral resources needed for pollinator nutrition (Timberlake et al. 2019). As habitat loss increases and agricultural intensification occurs, the number of flowering plants within an area will likely decrease. Baude *et al.* (2016) ranked UK habitats according to nectar production with calcareous grassland, broadleaved woodland, and neutral grassland ranked as the best and arable land regarded as the poorest. The problematic nature of farmland for floral resources is backed up by Timberlake *et al*'s (2019) study on four Somerset farms where *Bombus terrestris* hunger gaps were identified between March-April, June-July, and August-October. The hedgerows surrounding the arable fields were found to contain the greatest sugar per unit area, providing 9.4% of the total sugar whilst only covering 1% of the farm area (Timberlake et al. 2019). With nectar gaps being identified in the UK it is not unlikely that there will be pollen gaps too which may or may not correlate with the nectar gaps. If pollen gaps occur during times of pollinator reproduction, this may impact the larval development of bee species, both managed and native.

1.6 Floral longevity and why it's important in the context of pollinator dietary studies

Floral longevity plays a key role in plant reproduction as the length of time between a flower opening, the anthers dehiscing and then dying, will influence the total number of pollinator visitations that can occur (Primack 1985; Schoen & Ashman 1995; Ashman & Schoen 1996; Zhao et al. 2020). This will then affect the amount of pollen a flower can receive and the

amount of pollen it can release, ultimately affecting the plants overall fitness (Ashman & Schoen 1996). Plants with longer floral lifespans are often associated with infrequent pollinator visitation, while species who are visited more regularly may have shorter floral lifespans (Arroyo et al 1981; Weber & Goodwillie 2013; Zhao et al. 2020).

Floral development and maintenance requires a large investment of carbon, nutrients, and water, this creates an conflict for plants regarding whether they should maintain existing flowers for longer or create new flowers (Ashman & Schoen 1994; Ashman & Schoen 1996; Zhao et al. 2020). The trade-off ultimately depends on the species and how it can maximise its fitness at a minimum cost to the plant (Ashman & Schoen 1994; Ratcke 2003; Zhoa et al. 2020). There can be considerable variation in floral longevity between species and within species exposed to different environmental conditions (Primack 1985; Schoen & Ashman 1995; van Doorn 1997; Evanhoe & Galloway 2002; Zhoa et al. 2020). An example of between species variation is seen, for example in *Ipomoea purpurea* flowers which lasts a day, whilst others such as *Trillium grandiflorum* last 1-3 weeks and species in the Orchidaceae family can last between 1-2 months (Schoen & Ashman 1995). The effect of environmental conditions can change the length of flowering for some species, for example in the alpine plant *Oxalis compacta,* warmer temperatures reduced flowering length while cooler temperatures results in a normal flowering length (Arroyo et al. 2013). This variation in floral length suggests different resource allocations for maintain flowers and creating new flowers and may suggest that the one-day flowers may die even if they have not been pollinated. The longer-lived species such as the members of the Orchidaceae family wilt quickly after pollination, indicating pollination is their trigger for floral senescence (Ashman & Schoen 1996; van Doorn 1997; Abdala-Roberts et al. 2007). Senescence triggered by pollination does not occur in all species, and although it may influence floral longevity in some species it is unlikely to affect others (Ashman & Schoen 1996). The effect of pollination on floral longevity has been seen in *Campanula americana* where plants grown in absence of pollinators lasted 7-10 days compared to 3-5 days in the field where they were visited by pollinators (Evenhoe & Galloway 2002).

The evolution of floral longevity is believed to be an allocation strategy of resource to either create or maintain the floral unit, however it is not influenced by pollinator guilds, but rather habitat and the taxonomic class of the species (Primack 1985; Ashman & Schoen 1996). This would explain the different in floral longevity seen within the same species which were

subject to different environmental conditions (Primack 1985). The large diversity in floral longevity in different flowering plants also supports the idea that environmental conditions such as, water availability and air temperature influence this adaptation (Primack 1985; Ashman & Schoen 1996).

1.7 Objectives of this Thesis

There are four objectives to this thesis:

1. Measure the floral longevity of common farmland plant species, specifically the plant species recorded on the four Somerset farms in Timberlake et al. (2022).

2. Calculate the volume of pollen produced by individual plant species in a 24-hour period and compare this with 24-hour nectar production.

3. Quantify the phenology of pollen availability and compare it with the phenology of nectar availability.

4. Identify species and habitats that provide the largest proportion of pollen and nectar.

2. Materials & Methods

The underlying aim of this study was to quantify farmland pollen availability over the course of the pollinator flight season in order to identify important pollen-provisioning plant species and habitats and establish the phenology of pollen availability for pollinators. To do this the floral longevity of farmland plant species needs to be measured, as data on the amount of pollen produced per 24hrs is required. Working at replicate field sites around Somerset, in the west of England, I measured the floral longevity of a range of common farmland plants and combined this information with pollen production data (mostly from Baude et al. unpublished, augmented by my own measurements) to calculate pollen production values over a 24-hour period. These values were used in combination with farm-scale floral abundance estimates from three replicate Somerset farms, using the floral abundance data from Timberlake et al. (2019). Together, these data were used to calculate farmscale-level pollen availability throughout the pollinator flight season in a similar manner to that done with nectar availability (e.g., Timberlake et al 2019, Baude et al 2016). Thus, there were three different types of information that needed to be collected and merged: 1) the amount of pollen produced by individual flowers of each farmland plant species; 2) the floral longevity of each farmland plant species to enable the calculation of pollen production per 24-hour period; and 3) the floral abundance of each plant species throughout the year so that pollen values could be scaled up to the landscape-scale.

2.1 Choosing the plants to sample.

The species selected to be studied were chosen from Timberlake et al. (2019) species list which contains 216 species from three Somerset farms. The three farms were Birches Farm (51°25′19.04″N, 2°40′49.93″W), Eastwood Farm (51°29′41.71″N, 2°60′56.74″W) and Elmtree Farm (51°21′58.04″N, 2°85′44.36″W) and they contained varying proportions of pasture, and arable fields, hedgerows, field margins and woodlands (Table S1). To keep the workload manageable, the species which contributed 95% of the floral units across all three farms were identified, resulting in a list of 75 plant species to sample (see Supp info, Table 2). One species was dropped as only female plants are found in the UK (*Fallopia japonica*) and one other species were dropped due to insufficient sample sizes in the field.

2.2 Study sites for measuring floral longevity.

Floral longevity was measured between August-October 2021 and March - June 2022 at 24 field sites located within an 8 km radius of Bristol, UK. The sites were chosen as they provided a wide range of habitats including pasture, field margins, hedgerows, arable fields, woodlands, public green space, and private gardens, and therefore a wide range of plant species (Figure 1). All the target plant species could be found in at least one of these 24 field sites.

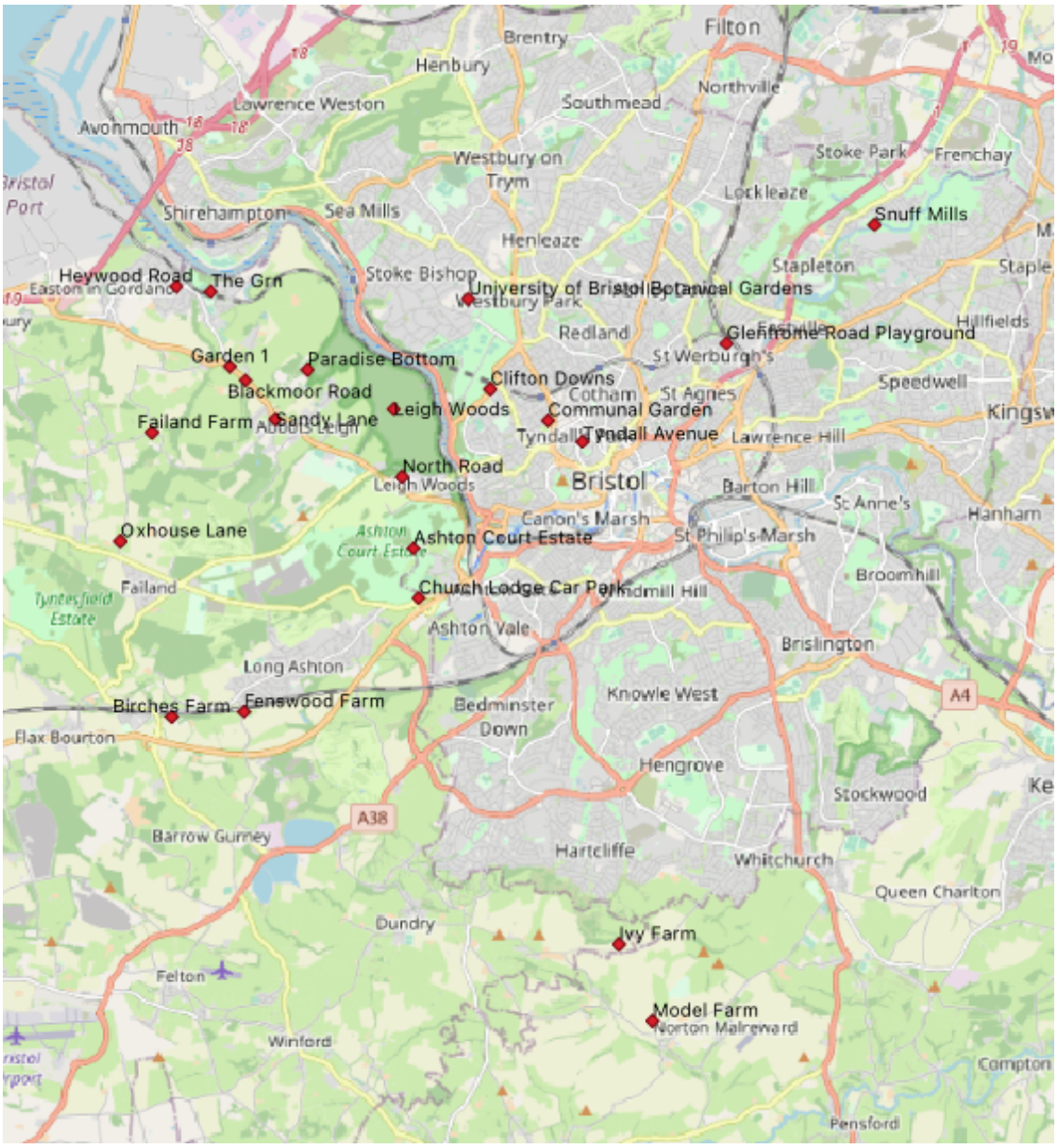

Figure 1:Study site locations used to sample the floral longevity and pollen; all study sites were within an 8km radius of Bristol.

2.3 Collecting the pollen volume data

Of the 70 common farmland plant species to record in our study, 60 had existing pollen volume values from Baude et al. (unpublished data) and ten were lacking this data (see supp info, Table 3). For these 10 species, I collected samples of their flowers from two different field sites in order to calculate pollen volume per flower. The following sections detail how pollen was collected and measured in this study.

2.3.1 Collecting plant material

For each of the 10 target species, flowers were collected from the field whilst unopened and transported to the laboratory and placed in water. I collected at least 10 stalks with flowers attached in case some didn't open. Any flowers that had already opened were removed. Depending on the species, and the stage of the bud at time of collection, dehiscing of the anthers takes 24-72 hours.

2.3.2 Collecting newly dehisced anthers

Flowers were checked regularly with a magnifying glass to ascertain whether their anthers had dehisced. Once this had occurred, the anthers from at least 5 different flowers were collected using scissors, taking care not to lose any pollen when cutting; these were placed in an Eppendorf microtube containing 0.5mL of 70% ethanol and stored in a freezer at -20C. For each target species, ~15 anthers were collected in total, depending on the species. Approximately 8 replicate Eppendorf tubes (each from a separate flower, and from two separate field sites) were collected for each species and each tube contained a median of 15 anthers (range = 8-26).

2.3.3 Pollen extraction

Pollen was extracted from anthers by sonicating the suspended anthers for 10 minutes in their Eppendorf tubes. This mixture was then vortexed for 20 seconds and the liquid collected using a micropipette, leaving other floral matter behind (stigmas, petals etc). The resulting pollen suspension was then pipetted into a separate labelled Eppendorf microtube. To the

remaining floral matter, 200µl of ethanol was added, and this was vortexed for 20 seconds to rinse off any remaining pollen. This liquid phase was then micropipetted into the second labelled Eppendorf microtube containing the pollen suspension. I then took one of the anthers from the original Eppendorf tube and examined it with the binocular magnifier to see if any pollen remained attached. If any pollen was still present, I would repeat a second and even a third rinse and keep a record of each of these steps.

These tubes containing pollen suspension were centrifuged for 5 minutes at 3000 rpm (with a progressive stop) to create a pollen pellet. The supernatant was removed from the surface using a micropipette, leaving only the pollen pellet. The Eppendorf tube containing the pollen pellet was then placed in an oven at 60C for between 30-90 minutes to dry off any remaining ethanol.

2.3.4 Counting the extracted pollen

The tubes containing the dry pollen pellets were resuspended in between 60 and 300 µl of 70% ethanol. The volume of ethanol depended upon the size of the pellet - the smallest pollen pellets required only 60µl, whilst larger pellets required 300µl; the volume added was recorded for each tube. The pollen pellet was then vortexed in order to resuspend it in the ethanol. A haemocytometer was used to count the pollen grains. Depending on the type of Fuch-Rosenthal grid that's used, between 20-50µl of the pollen suspension was pipetted between the counting cell and the slides, holding the micropipette at a 45° angle to the slide. The pollen grains were counted using a hand-held using a light microscope until a total of 200 grains were counted; the aim being to find out how many squares are needed to reach exactly 200 pollen grains.

2.3.5 Measuring the volume of a single pollen grain

The pollen grain's size was measured using their polar and equatorial axis. This allowed the volume of one pollen grain to be calculated using the formula $V = \frac{a}{2} \times \frac{b}{2} \times \frac{c}{2} \times \frac{4}{3}\pi$.
Five pollen grains were measured in each of the c. 8 replicates, giving a total of ~40 pollen grains measured per species over the two field sites.

2.3.6 Calculating the pollen quantity

To find the pollen grain concentration of each sample I first calculated the suspension volume of all small grid squares covered by pollen grains by multiplying the number of small grid squares by the volume of squares (the volume of the hemocytometer is engraved on it). Then I calculated the concentration of pollen grains in the counting volume by dividing the number of pollen grains counted by the suspension volume (the volume of ethanol the pollen had been suspended in). Once I had found the concentration of pollen grains, I calculated the initial quantity of pollen found in the first tube by multiplying the concentration of pollen grains by the initial suspension volume (before any of the suspension was taken out for counting). This quantity of pollen grains was divided by the number of stamens collected from the sample to obtain the number of pollen grains per stamen. The data on pollen grain volume and pollen quantity are combined, as described below (section 2.5) in order to calculate the volume of pollen per plant species.

2.4 Record the floral longevity of common farmland plant species (Objective 1)

For each of the 70 species, I recorded the floral longevity of c. 20 individual flowers from two different sites. The flowers were identified while in bud, marked and tagged prior to opening. If the flower was a composite head containing many individual flowers (e.g., a daisy), I would mark individual flowers on multiple flower heads.

Figure 2: Ranunculus repens labelled for monitoring.

After marking the flowers, return visits were made to the flower five days a week (Mon-Wed and Fri-Sat) to monitor its progress. If the flower appeared to be open, it would be inspected to identify if the anthers had dehisced (Figure 2). I would then return to the flower each day to check on the anthers and the state of the flower to ascertain the point at which the flower either dies or drops its anthers. Floral longevity was calculated as the number of days from the anthers dehiscing to point at which the flower dies, or the anthers drop off. Some species were very challenging to sample due to their small flower size. For example, many of the Asteraceae family have very small flowers in composite heads which had to be individually marked and monitored (Figure 3).

Figure 3: An Asteraceae flower (lesser burdock, Arctium minus) with the individual flowers marked with an orange marker pen.

2.4.1 Floral longevity analysis

The mean floral longevity was calculated for each species, along with its standard deviation. To test whether floral longevity was conserved within plant families, a one-way ANOVA was used to test for significant differences between families in their floral longevity. All statistical analyses were performed using R Version 4.2.1 (R Core Team 2022).

2.5 Calculate the volume of pollen produced by individual plant species in a 24-hour period and compare this with 24-hour nectar production (Objective 2).

The volume of pollen produced by individual plant species in a 24-hour period was calculated by dividing the total pollen volume per floral unit (from Baude et al., unpublished and my own pollen measurements), by the mean floral longevity of the species (measured in days). This gave a *per unit time* measure for pollen which is comparable to the daily nectar production values listed in Baude *et al.* 2016. To establish whether there is a relationship between the nectar and pollen production of the 70 farmland plant species recorded in this study, I correlated the daily nectar values (from Baude et al. 2016) against the daily pollen values calculated in this study. A general linear model (GLM) was used to test this correlation and the analysis was repeated at the floral unit and individual flower level to check whether the relationship differed depending on how a flower is defined. We define a 'floral unit' as one or multiple flowers that can be visited by insects without flying (Carvalheiro et al. 2008); for example, a composite flower head of daisy, *Bellis perennis*.

2.6 Quantify the phenology of pollen availability and compare it with the phenology of nectar availability (Objective 3).

To scale my measures of pollen volume per floral unit up to the farmscale and establish the phenology of farmland pollen availability, I multiplied my floral unit pollen values for each species by the number of floral units of that species recorded in a fixed area of farmland throughout the flowering season (data from Timberlake *et al.* 2019). Timberlake et al. (2019) recorded the abundance of floral units every week from March-October 2017 on three medium-sized (142-213 ha) mixed farms in Somerset, West England, UK (Birches Farm, Elmtree Farm and Eastwood Manor Farm). In each semi-natural habitat on the three farms (permanent pasture, semi-natural woodland, hedgerows, and field margins) floral abundance was estimated from 30 individual m^2 quadrats spaced equally along 6 randomly placed transects (5 quadrats per transect). This provided an estimate of the number of floral units of each species at each time point per m^2 of each habitat type. Floral abundance values per metre squared were then multiplied by the area of each habitat within a $1km^2$ area of the farm to provide an estimate of each species' floral abundance at a landscape level.

The floral abundance estimates were multiplied by daily nectar (from Baude et al. 2016) and pollen production values (from the methods outlined above) to calculate the mass of sugar and the volume of pollen produced by each plant species at the landscape level. To compare the phenology of nectar availability with that of pollen availability, we summed the total pollen and the total nectar produced by all species at a given sampling point and plotted the total quantity of both these resources on two graphs. We also plotted the total number of floral units at each sampling point on a third graph, for comparison. For each of these three measures of floral resources (nectar, pollen, and floral units), a generalised additive model (GAM) in the R package mgcv (Wood 2011), was used to model a smooth, non-linear trend in the resource over time. A thin-plate regression spline was used to model day of the year, with the degree of smoothing selected using the default generalised cross-validation method (Wood 2011).

2.7 Identify species and habitats that provide the largest proportion of pollen and nectar (Objective 4).

In addition to modelling nectar and pollen availability at the whole farm scale (Objective 3), I also modelled these resources at the individual plant species and at the habitat level, using the same GAM approach as outlined in Section 2.6. This enabled us to estimate pollen and nectar values for each plant species and each habitat on any day of the year. For each plant species and habitat, we summed these pollen and nectar values over the period March-October, to calculate total annual pollen/nectar productivity and identify species and habitats providing the majority of floral resources on farmland. The nectar and pollen production of different habitats were compared using a one-way ANOVA, whilst a stacked area graph was used to demonstrate the shifting importance of different plant species through the year.

3. Results

A total of 1316 measurements of floral longevity were recorded from 73 species in the 24 sites (Table S2). Between 2-20 measurements were recorded per species from two separate field sites (average 18 samples per species). The recorded species were from 23 different families, with Asteraceae making up the highest number of these (n=13). These floral longevity measurements were used alongside data collected by Mathilde Baude on pollen volume (Baude *et al*. unpublished), my own measurements of pollen volume and the floral counts from three Somerset farms collected by Timberlake et al. 2019, to address the following four objectives.

3.1 Calculate the average floral longevity (from dehiscing to death) per plant species and test whether this differs between families (Objective 1)

The mean and medium values for the floral longevity of the 72 plant species were 2.580 days ±1.400 SD and 2.280 days respectively, with a range of 1-16 days (Table S3). Only two species flowered for more than 8 days on average (Figure 4); these were *Brassica napus (*8.25days ±1.446 SD*)* and *Hyacinthoides non-scripta* (8.15days ±1.864 SD). Several species had a floral longevity of only one day; these *were Convolvulus arvensis, Cirsium vulgare, Galium mollugo, Calystegia sepium, Sorbus* aucuparia and *Stellaria media.* Some species were highly variable in their floral longevity, for example *Achillea millifolium* (5.75 days ±4.387 SD) and *Primula vulgaris* (5.85 days ±3.066 SD), though most species were consistent in their longevity with variation ranging from ±0 SD to ±1.965 SD (Supp. Table 3).

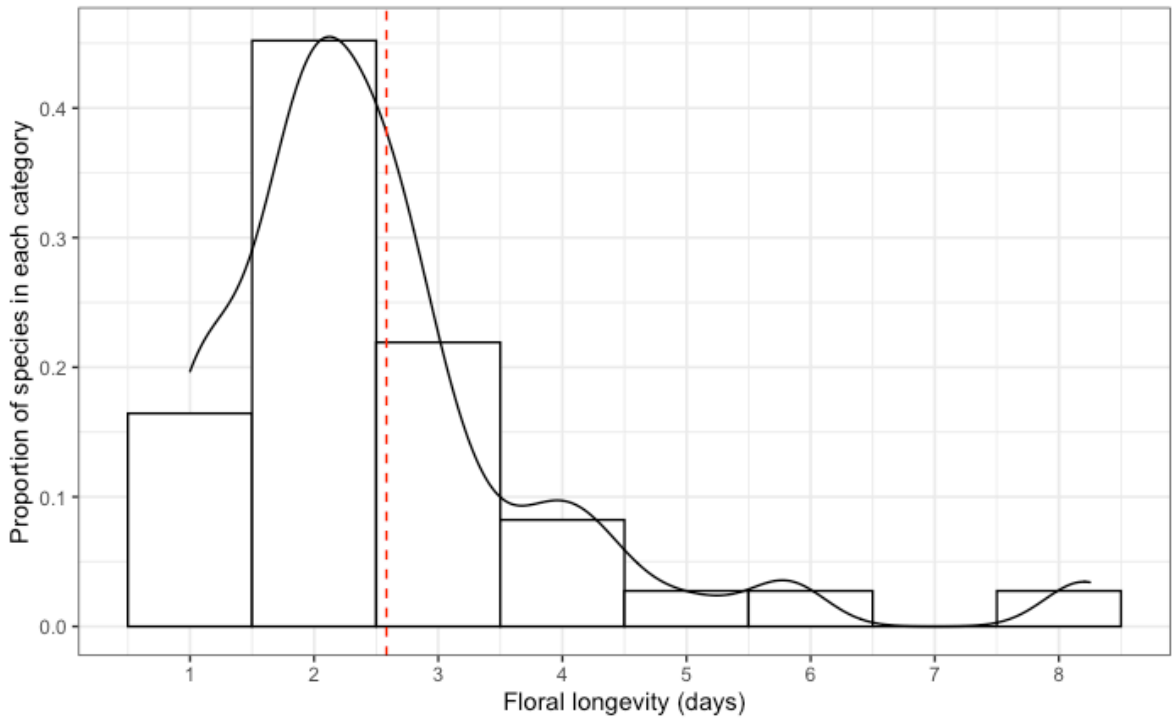

Figure 4: The proportion of species with a given floral longevity (measured in days). Each bin is one day plus half a day on either side, e.g., 1=0.5-1.5, 2=1.5-2.5 etc.

was limited variation in floral longevity between plant families and this was not found to be significant using an ANOVA (*F=1.333, df=9, p=0.248*) (Figure 5). This excluded the 18 families from which only one species was sampled. Amongst all 28 families sampled, Asparagaceae had the highest floral longevity (8.16 days ±0 SD, n=1), however, this only comprised one species. Of the families comprising more than one species, Ranunculaceae had the highest recorded floral longevity at 3.95 days (±1.376 SD, n=4). The families with the lowest recorded floral longevity were Convolvulaceae (1 day ±0 SD, n=2) and Plantaginaceae (1.05days ±0SD, n=1). The family with the highest number of recorded species was Asteraceae (n=13), and within this family *Cirsium arvense* and *Senecio jacobaea* had the highest floral longevity (2.7 days ±0.732 SD and 2.7 days ±0.923 SD respectively). In contrast, *Cirsium vulgaris* had the lowest floral longevity at 1 day ±0 SD. The Convolvulaceae family had the lowest variability in its floral longevity, with all individual flowers from both sampled species showing a longevity value of 1 day. In contrast, the Brassicaceae family showed the highest variation amongst families (±2.829 SD, n=5), ranging from floral longevity values of 1.5 days±1.055SD (*Cardamine flexuosa*) to 8.25 days ±1.446 SD (*Brassica napus).*

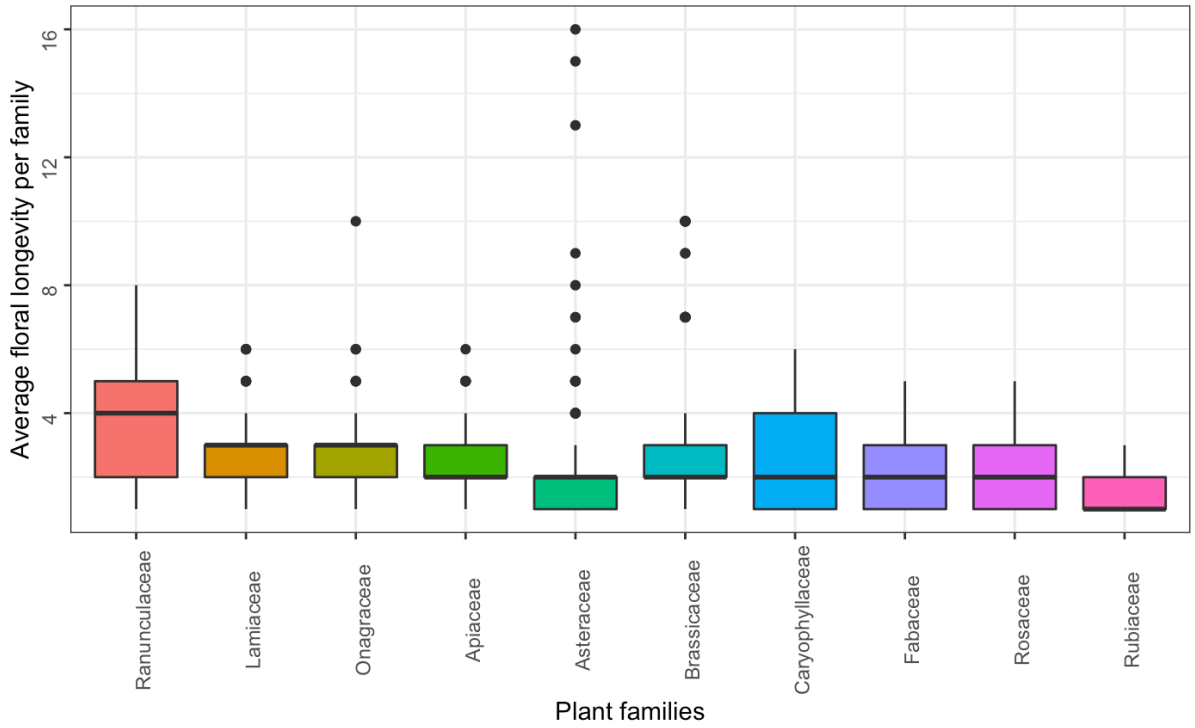

Figure 5: Floral longevity of each family sampled shown as box and whisker plots. The black points show any outliers within each family.

3.2 Calculate the volume of pollen produced by individual plant species in a 24-hour period and compare this with 24-hour nectar production (Objective 2)

The linear model showed a significant positive correlation between pollen and nectar availability per species per floral unit in a 24-hour period ($F=35.33$, $df=70$, $p<0.001$, adjusted R-squared=0.326*),* indicating that on average species that produce large quantities of pollen also produce large quantities of nectar (Figure 6). While there is a general positive relationship between pollen and nectar availability, there are nevertheless some notable outliers in the data. For example, *Salix* spp produced more pollen than expected based on its nectar production, whilst *Myosotis arvensis* and *Allium ursinum* produced much lower pollen volumes than expected based on their nectar values. Three species produced no nectar, but still produced pollen: *Filipendula ulmaria*, *Corylus avellana* and *Tripleurospermum inodorum*.

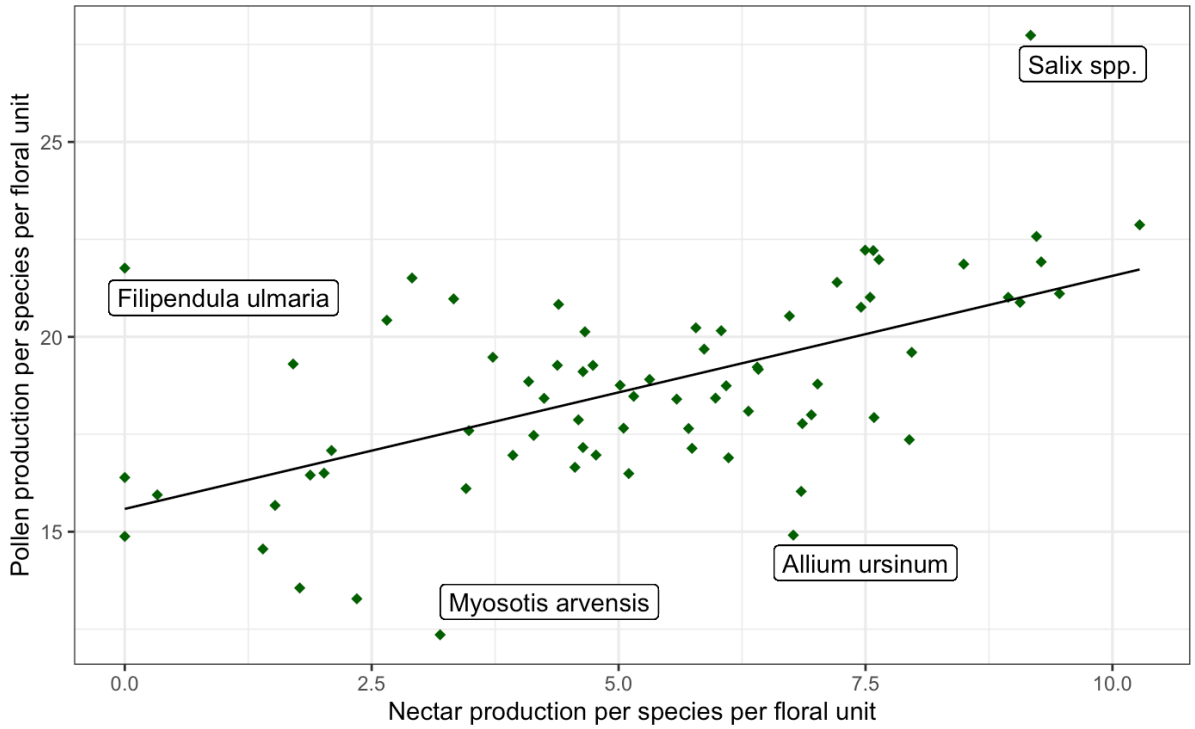

Figure 6: The relationship between pollen and nectar production, per plant species, per floral unit; outliers are identified by name.

In addition to testing the nectar: pollen relationship at the floral unit level, I also tested the relationship at the individual flower level, to check whether the relationship was affected by species whose floral units comprise multiple individual flowers (e.g., *Bellis perennis* contains c. 95 flowers per floral unit, whilst *Rubus fruticosus* has only one flower per floral unit). As expected, species with multiple flowers per floral unit (e.g., Asteraceae, umbellifers and Salix) decrease in pollen and nectar quantities compared to species with single flowers, and this changed the pollen: nectar relationship slightly. The flower-level data showed a weaker correlation between nectar and pollen availability (*F=18.730, df=70, p*<0.001, *adjusted R-squared=0.199*) in comparison to the floral unit data, however the correlation remains significant (Figure 7). The outlier species remain similar to those in the floral unit-based plot, though *Calystegia sepium,* with its large individual flowers, becomes more of an outlier.

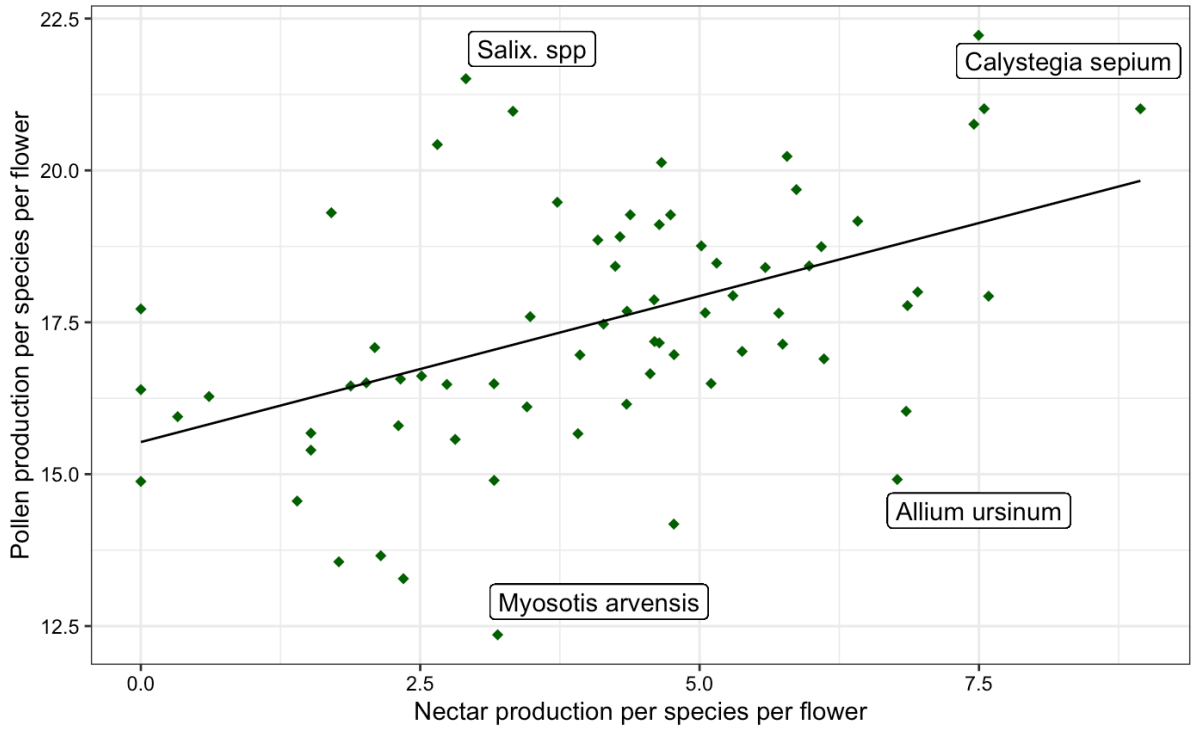

Figure 7: The relationship between pollen and nectar production, per plant species, per individual flower; outliers are identified by name.

3.3 Quantify the phenology of farmland pollen availability and compare it with the phenology of nectar availability (Objective 3)

Farmland pollen availability shows a strongly seasonal pattern with a large spring flowering peaking on 21st April, followed by a gap during June which is at its lowest on the 22nd June, which is followed by a an increase in pollen, peaking on 10th July. August sees a further increase in pollen production, peaking on the 11th August, followed by another smaller peak on the 2nd September. After the late summer peak pollen production drops off rapidly and does not increase again till April (Figure 8c).

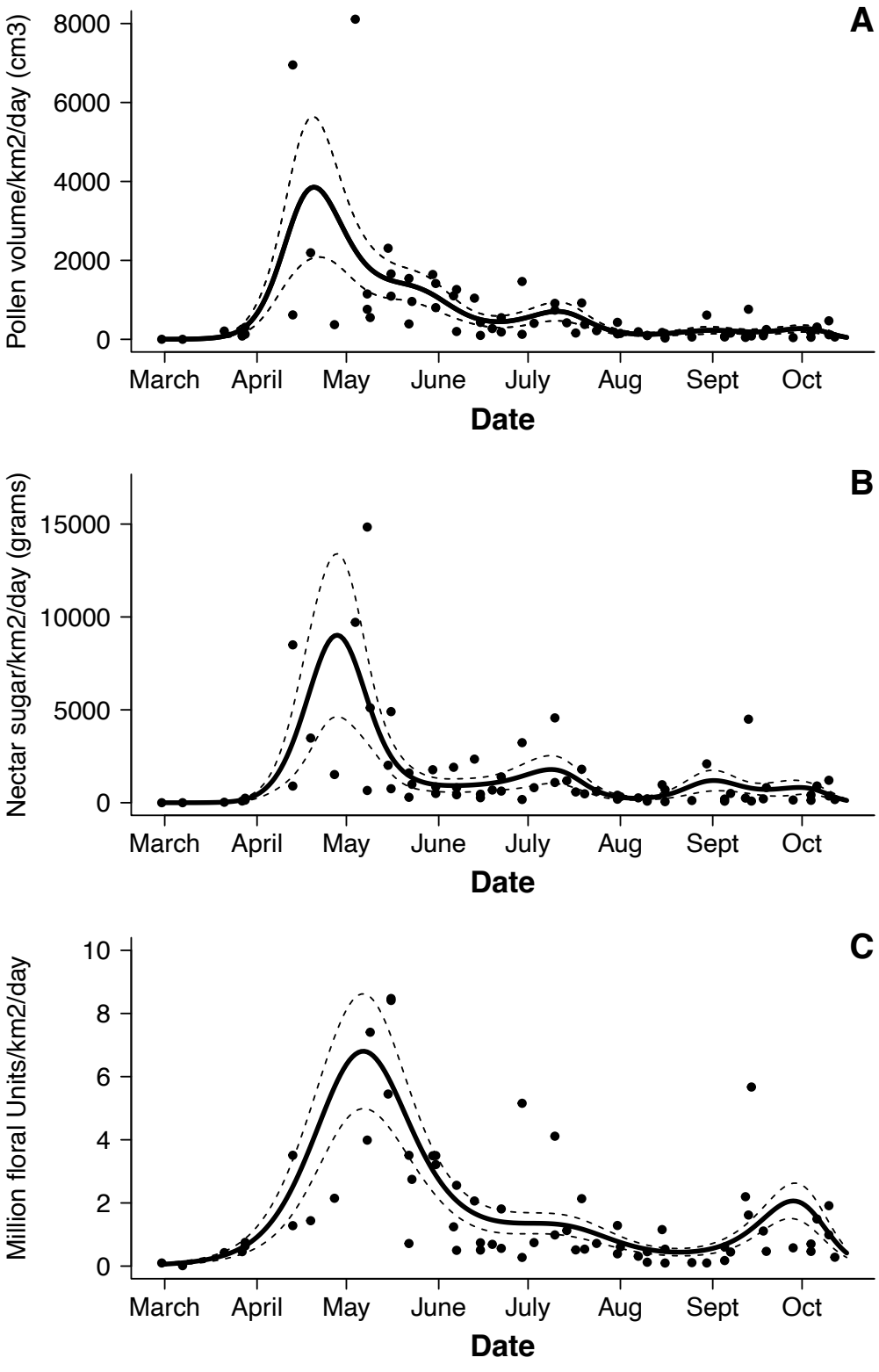

Figure 8: The phenology of three different measures of farmland floral resources: a) pollen volume; b) nectar sugar and c) abundance of floral units, at a whole-farm scale throughout the flowering season. Points represent individual sampling events on the three study farms (Birches, Eastwood and Elmtree) and the data from all three farms are smoothed with a Generalized Additive Model (±SE; dashed lines).

The phenological pattern of pollen and nectar supply are remarkably similar, however the timing of the peaks and troughs differed slightly, whilst the floral abundance differs greatly (Table 1). There respected spring peak occurred relatively close together (pollen:21st April, nectar: 29th April), whilst floral abundance peaked on 8th May, however during the June gap pollen production did not show such a steep decrease, compared to nectar which decreased rapidly till the 7th June and pollen being the 22nd June (Figure 8b & c). The floral abundance showed no specific June gap or summer peak in its phenology. The late summer peak (generated mainly by the flowering of *H. helix*) is also less pronounced for pollen than for nectar, although the peaks do occur within a few days of one another (pollen: 10th July, nectar: 12th July). The same can be said for the summer gap where nectar is slightly earlier, but only by three days, whilst the floral abundance drops much later (22nd August). The late summer peak of nectar and pollen occurs on the same day (2nd September), whilst again, the floral abundance peaks much later (29th September) and rapidly drops of at the end of October.

Table 1: The responsive peaks and troughs for each floral resource measured and the floral abundance.

Floral resource peak or trough	Date for pollen	Date for nectar	Date for floral abundance
Spring peak	21 April	29 April	8 May
'June gap'	22 June	07 June	N/A
Summer peak	10 July	12 July	N/A
Summer gap	11 August	07 August	22 August
Late summer peak	02 September	02 September	29 September

3.4 Identify species and habitats that provide the largest proportion of pollen and nectar (Objective 4)

The species that provided the highest proportion of pollen and nectar per farm differed greatly through the year. Pollen production was dominated by *Ranunculus ficaria* (46%) and *Prunus spinosa* (36%) in March (Figure 9). This was quickly taken over by *Centaurea nigra* (49%) and *Taraxacum officinale* (21%) in April. *C. nigra* continued to produce the largest amount of pollen in May (28%), alongside *Ranunculus repens* (15%), *Cerastium fontanum*

(13%) and *Crataegus monogyna* (13%) respectively. June and July saw a large increase in *Rubus fruticosus* and *Filipendula ulmaria* pollen production, until August where *Heracleum sphondylium* (18%), *Calystegia sepium* (14%) and *Hedera helix* (14%) pollen is more common. The end of August sees the increased availability of *Hedera helix* pollen which dominates till November where *Geranium robertianum* (13%), *Lamium purpureum* (36%) and *Veronica persica* (50%) appear. April and May contained the largest number of different species providing pollen on Birches farm, whilst September and October had low numbers of species. *Rubus fruticosus* consistently produces high quantities of pollen through June-August, whilst *Hedera helix* made up the largest proportion from August onwards. In contrast, nectar production on Birches farm was dominated by *Prunus spinosa* (79%) during March, *Centaurea nigra* (41%) and allium ursinum (40%) during April, *Rubus fruticosus, Trifolium repens* and *Heracleum sphondylium* throughout the summer (May, June, July) and *Hedera helix* and *Cirsium arvense* from August-September (Figure 9).

Eastwood farm contained many of the same species as Birches Farm, however it contained fewer species that contributed a high percentage to the monthly pollen and nectar supply (Figure 10). Pollen production in March was dominated by *Taraxacum officinale* (62%) and *Bellis perennis* (28%), April saw a large increase in the number of species available to pollinators. July's species richness decreased somewhat and was dominated by *Filipendula ulmaria* (53%) which only produces pollen. During August, *Filipendula ulmaria* was replaced by *Hedera helix* and *Ranunculus repens*, whilst October and November were mainly made up of *Hedera helix* and *Taraxacum officinale*. The distribution of nectar and pollen differs during the summer, however during spring and autumn they were relatively similar. *Taraxacum officinale* provided most of the nectar and pollen for March and April which was replaced by *Allium ursinum* for nectar during May (84%). In summer species such as *Trifolium repens, Rubus fruticosus* and *Cirsium arvense* become common, however after August *Hedera helix* and *Taraxacum officinale* dominated nectar production.

The final field site, Elmtree farm, was dominated by *Salix* spp during March, which contributed 97% of the total pollen available at this time (Figure 11). *Salix* spp rapidly decreased, with *Crateaegus monogyna* and *Anthriscus sylvestris* taking over in May. June saw Rubus fruticosus, *Ranunculus repens* and *Heracleum sphondylium* pollen contribution increasing through untill August when *Hedera helix* starts to appear. *Stellaria media* also increases its pollen availability in November (83%). The nectar supply in March mainly

consisted of *Prunus spinosa* (64%) and *Taraxacum officinale* (23%). Between May and August *Heracleum sphondylium, Cirsium arvense* and *Rubus fruticosus* provided the majority of nectar. September saw *Hedera helix* and *Cirsium arvense* becoming the major suppliers, whilst November included *Stellaria media*.

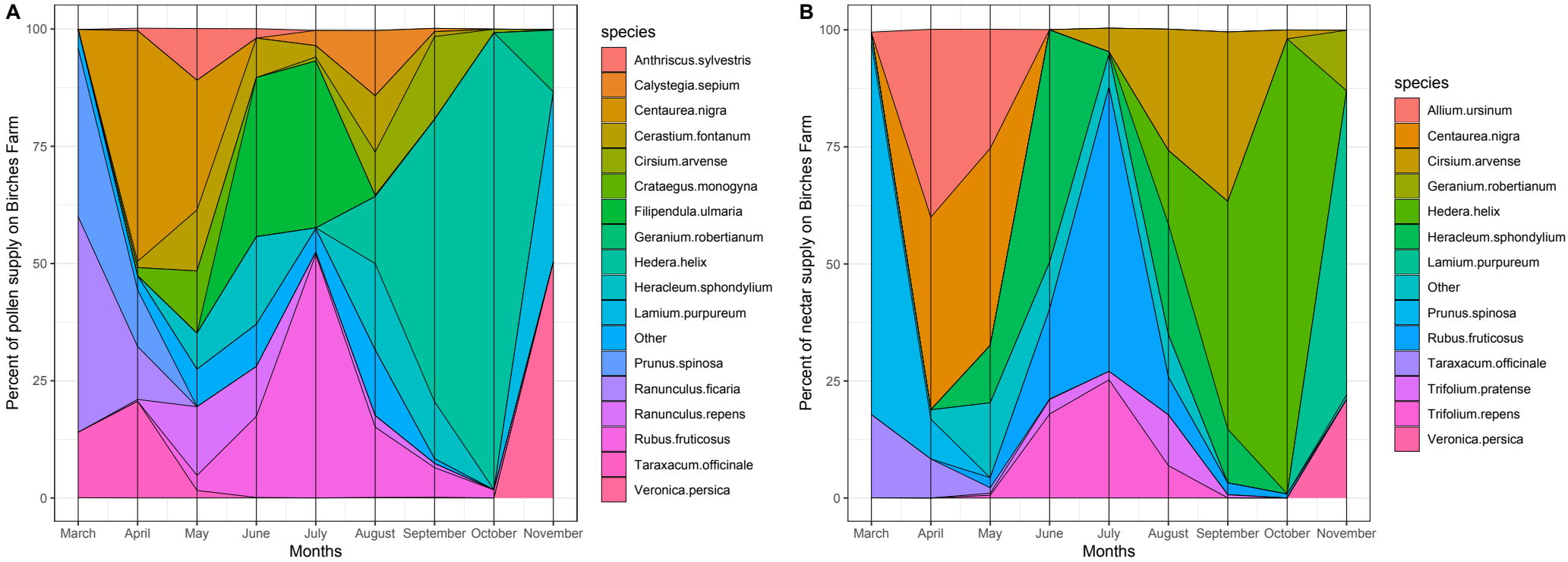

Figure 9: The monthly pollen and nectar availability on Birches farm during the flowering season. All individual species within this plot have nectar and pollen values of 10% or over during any given month. Any species below that was classified in the 'other' category.

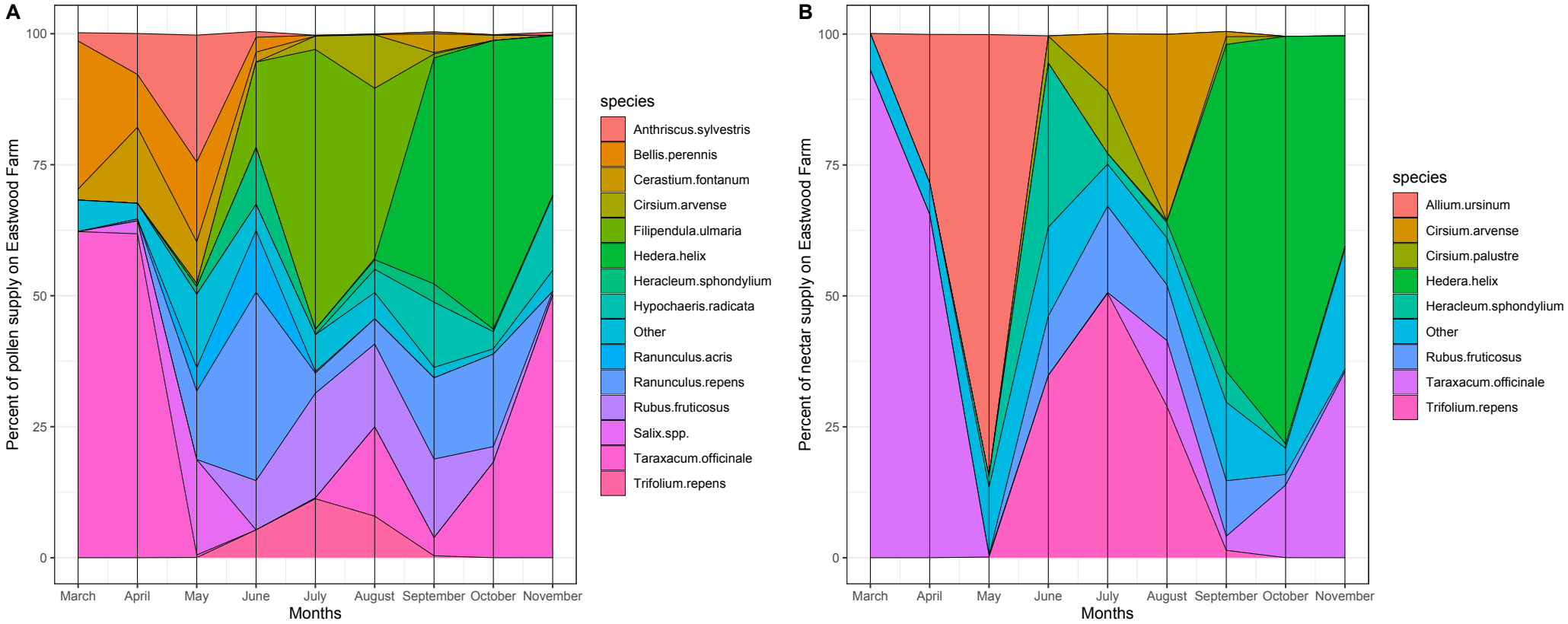

Figure 10: The monthly pollen and nectar availability on Eastwood farm during the flowering season. All individual species within this plot have nectar and pollen values of 10% or over during any given month. Any species below that was classified in the 'other' category.

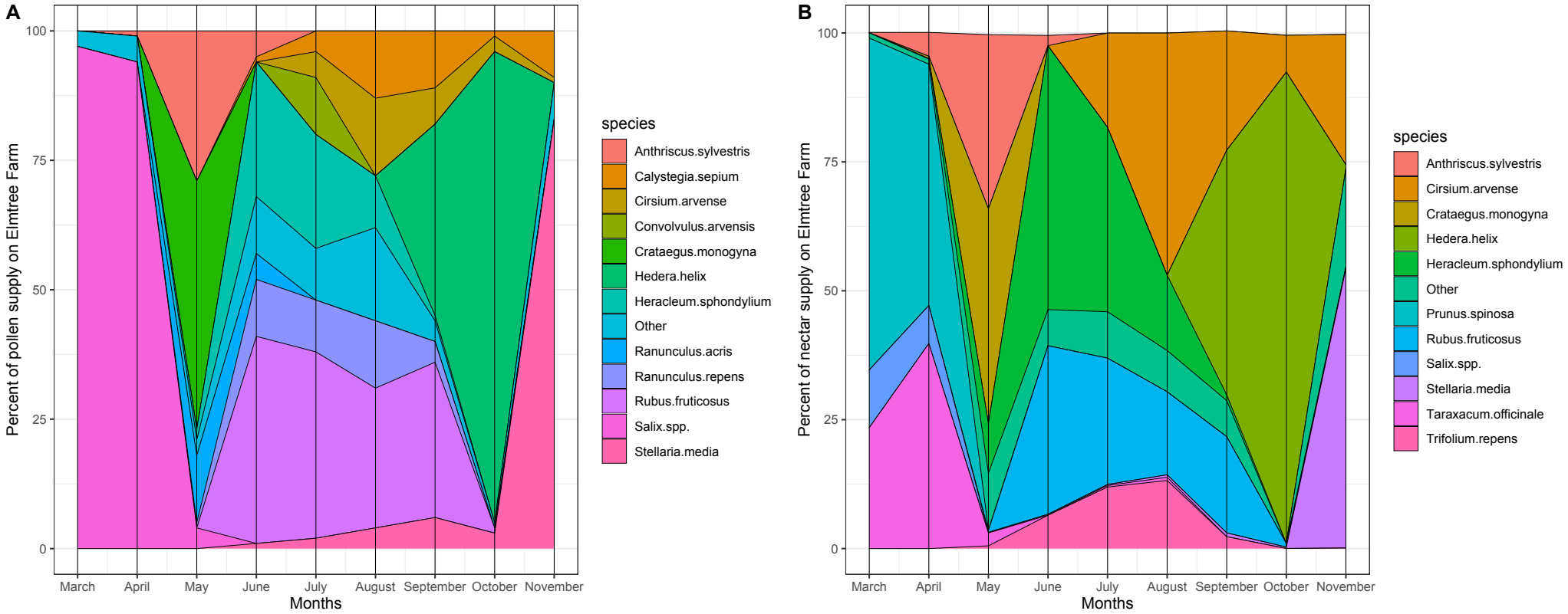

Figure 11: The monthly pollen and nectar availability on Elmtree Farm during the flowering season. All individual species within this plot have nectar and pollen values of 10% or over during any given month. Any species below that was classified in the 'other' category.

The four habitats on the three farms (hedge, pasture, margin and woodland), differed considerably in their pollen and nectar production. There is a significant difference in the volume of pollen available per m^2 from the four different habitat types (*F=122.5, df=992, p=2x10^{-16}*). Hedgerows were the most productive habitat for pollen, followed by field margins and woodland; pasture has the lowest value of the four habitats (Figure 12). However, when corrected for the amount for area of each habitat takes up on the farms (Supp Table…) pasture becomes the dominant habitat for pollen production (*F=122.5, df=992, p=2x10^{-16};* Figure 13). This effect is seen as while pasture produces very low volumes of pollen, it is the most common habitat on the farms, for example on Birches farm, pasture makes up 50% of the farm, in comparison to 5% hedgerow, 1% margins and 5% woodland. Similar patterns are seen in the nectar production per m^2, of different habitats; hedgerow and woodland produce the highest volume of nectar per m^2 (*F=51.57, df=992, p=2x10^{-16}*; Figure 14). When corrected for the area each habitat takes up, there is a significant difference between the habitats (*F=80.89, df=992, p=2x10^{-16}*). Pasture again produces the highest volumes of nectar at the landscape-scale, with woodland following closely behind (Figure 15).

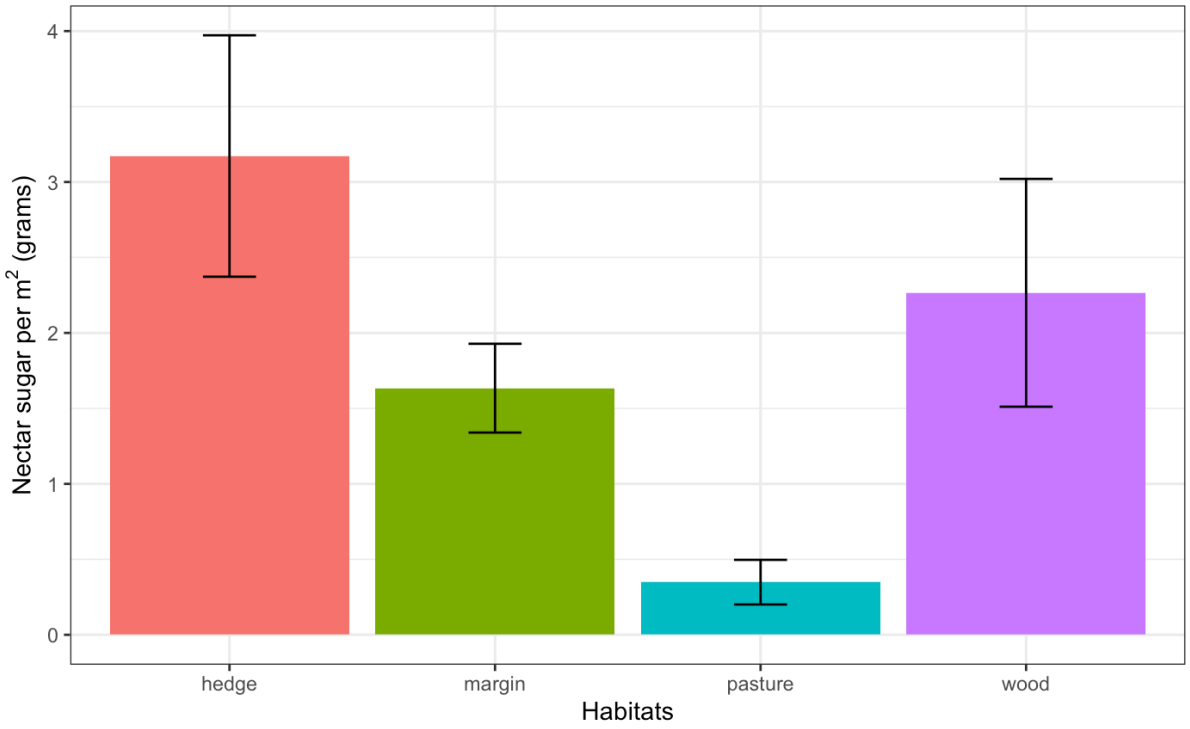

Figure 12: The volume of pollen produced per m2 of the four habitat types found on the three farms, over a year. Values for each habitat type is expressed as a yearly mean of the three study farms (Birches, Eastwood and Elmtree) ±SE.

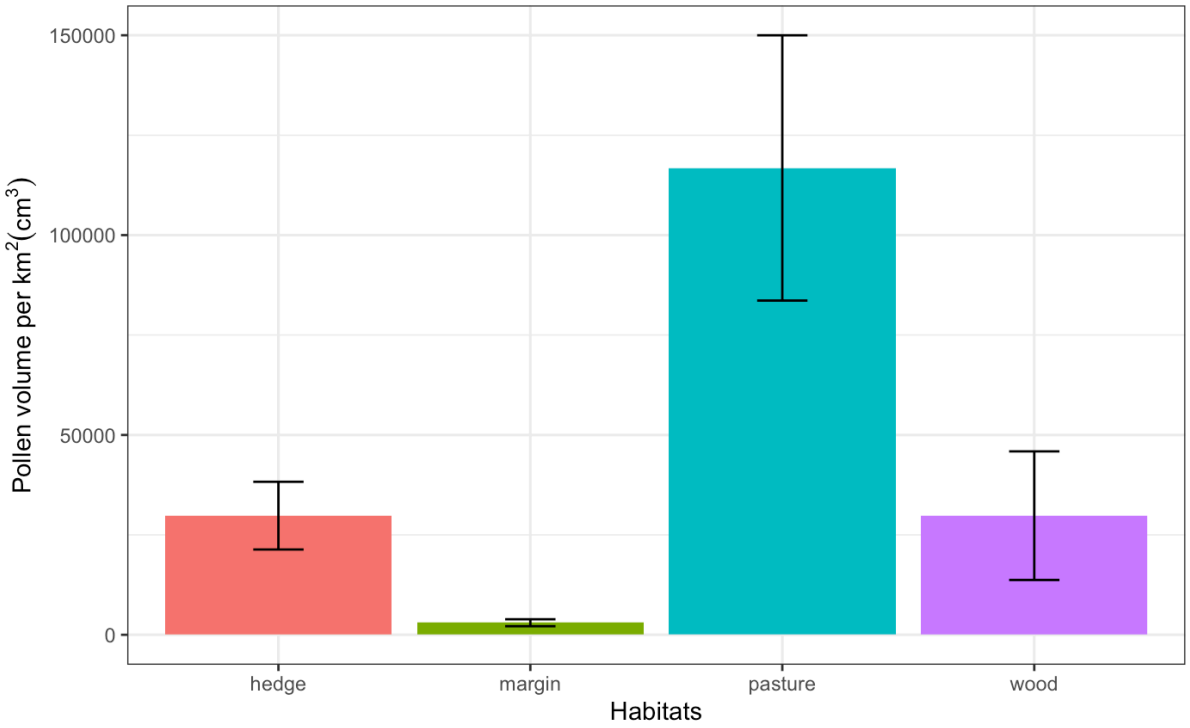

Figure 13: The volume of pollen produced per km2 of the four habitat types found on the three farms, over a year. Values for each habitat type is expressed as a yearly mean of the three study farms (Birches, Eastwood and Elmtree) ±SE.

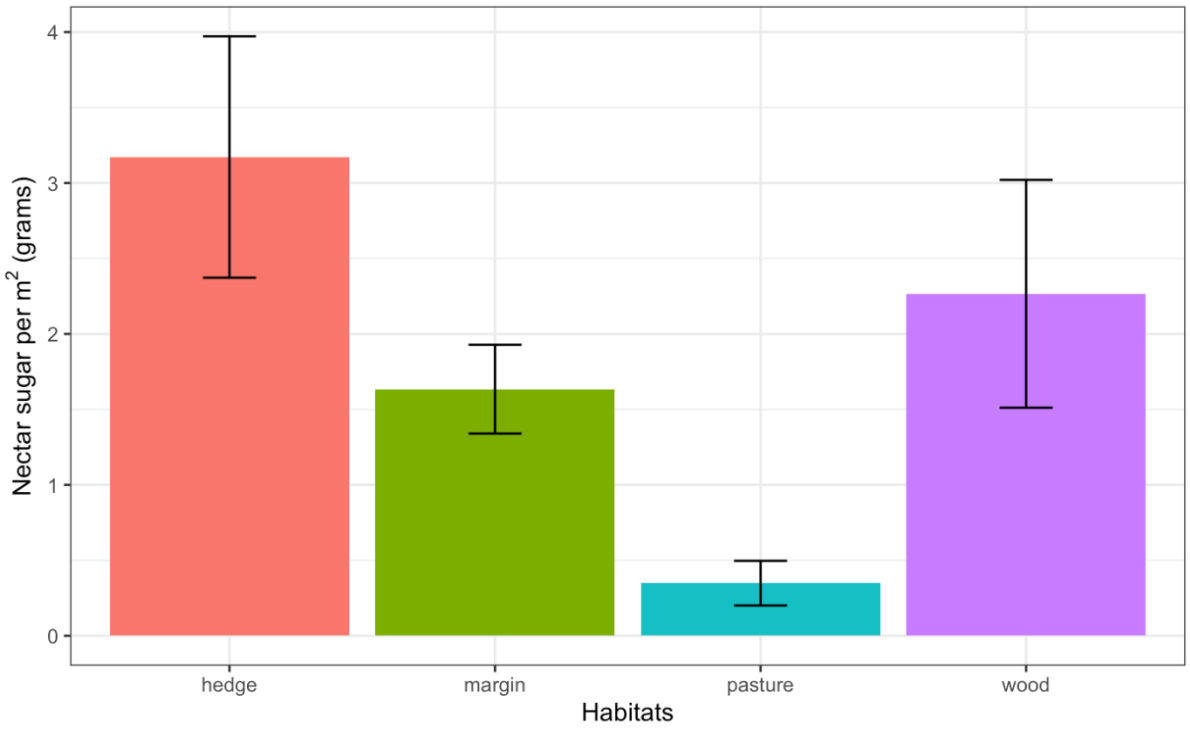

Figure 14: The grams of nectar sugar produced per m2 of the four habitat types found on the three farms, over a year. Values for each habitat type is expressed as a yearly mean of the three study farms (Birches, Eastwood and Elmtree) ±SE.

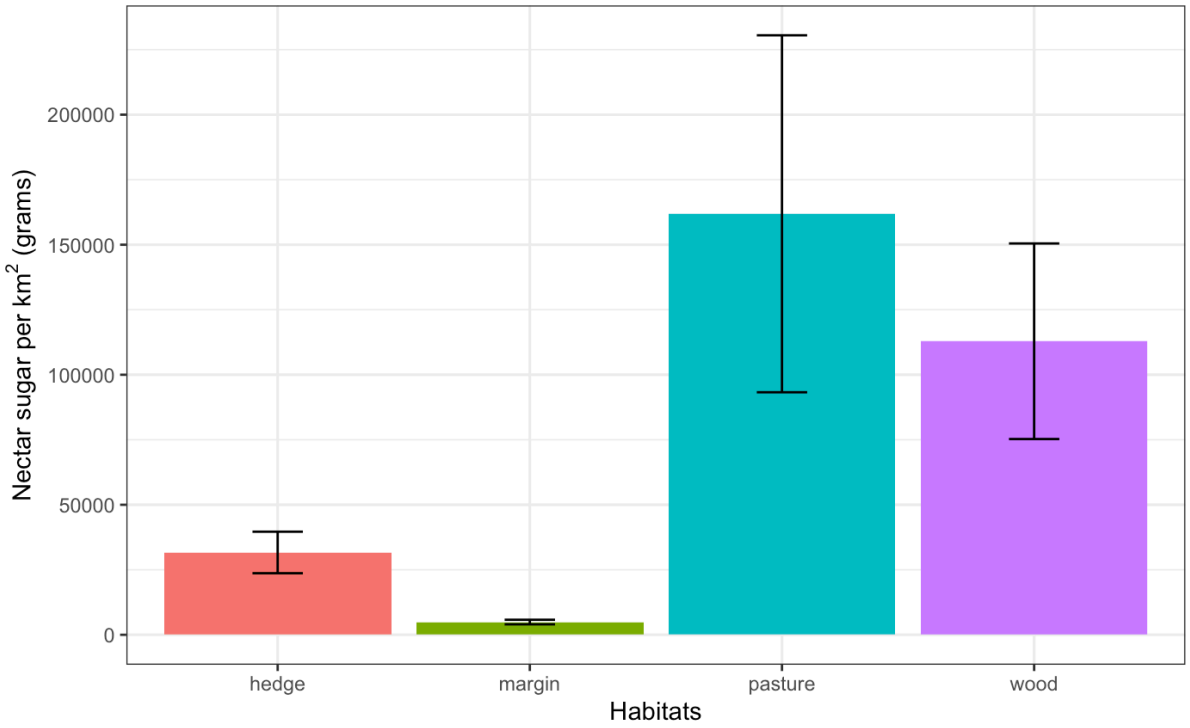

Figure 15: The grams of nectar sugar produced per km2 of the four habitat types found on the three farms, over a year. Values for each habitat type is expressed as a yearly mean of the three study farms (Birches, Eastwood and Elmtree) ±SE.

4. Discussion

In this study, I record the floral longevity of common farmland plant species and combine this information with pollen production data and floral abundance data to characterise and quantify pollen availability at the whole-farm scale for the first time. The results show that most plant species produce pollen for between 1 and 4 days, with some lasting as long at 8.5 days. Daily pollen production of individual plant species was significantly correlated with daily nectar production, though there were some notable outliers such as *Myosostis arvense* and *Filipendula ulmaria*. Scaling up pollen production to the landscape level, I show that the farmland pollen supply is dominated by just a few species, with *Hedera helix, Taraxacum officinale* and *Rubus fruticosus* being the most important contributors. Pollen production differed significantly amongst habitats and through the year, with supply peaking in late April and early July and with far less available before April and after August. The phenology of pollen production showed a broadly similar trend to nectar production, though the June gap in pollen production was much less prominent compared to nectar. In general, landscape-level pollen and nectar availability are relatively good proxies for one another, although the most important species involved in supplying these two resources do differ somewhat. In what follows, I will consider the limitations of the study, put my results into the context of previous research in this field, consider any recommendations for management and outline some future research directions.

4.1 Limitations to research

There are five main limitations to my research. Firstly, the study is relatively limited in its geographical scope, with all floral phenology data coming from three farms in the west of England. This was necessary due to the highly labour-intensive nature of phenology surveys whereby sites need to be visited weekly. The three farms were shown to be representative of farmland in the west of England (Timberlake *et al.* 2019) but it nevertheless limits my ability to extrapolate results to other regions of the country. Secondly, the phenology work is based on one year's floral counts, therefore, there is no measure of year-to-year variation in flowering, which may occur due to variation in weather conditions and farm management. The general patterns and dominant species are likely to be broadly conserved from year

however (Timberlake *et al.* 2019). Thirdly, I didn't measure the floral longevity and pollen production of all the species on the farm due to the time constraints of my masters, however I did sample all the species collectively contributing 95% of floral units on the farms. Fourth, this study collected data on the *quantity* of pollen only and not the *quality*. Using the pollen quantity data may not give the correct interpretation of pollinator needs as pollen varies substantially between species in its nutritional value. Data on the nutritional content of pollen is currently limited for whole plant communities, though could be easily combined with my data in the future, when it became available. The final limitation of the method used in this thesis to collect the floral longevity data; is how long it takes to collect the data. Thus, each flower must be monitored for its whole flowering period which involves multiple daily visits to multiple sites. This presents a to extending this study to the rest of the British flora, and thereby to other regions, though citizen science approaches may offer a more achievable alternative. In the future, it may be possible to set up an app or website and to use a citizen science approach. This would also provide information on the latitudinal differences in flowering times in the UK, as well as enabling the general public to be involved in a scientific project.

4.2 Floral Longevity

While there is very little floral longevity data for the UK, there are some studies from the rest of the world. For example, Song et al. (2022) collates information from over 416 papers, many of which studied the floral longevity of species in Asia and the Americas. Many of these studies do not include any pollen data however, making it impossible to calculate daily pollen production, as done here. My study provides novel data on the floral longevity of 73 common farmland plant species in the UK, thus filling an important knowledge gap. In terms of floral resources for pollinators, pollen has been largely ignored in favour of nectar, due to the relative ease of extraction and quantification. Pollen production has very rarely been quantified at the landscape scale, representing a major gap in our understanding of food resources for pollinators. Pollen is a vital aspect of pollinator nutrition, and this new dataset can be used to advance research into this area.

4.3 Important weed species

The most important plant species on the three farms are those species which flower for long periods of time and provide high quantities of pollen throughout their flowering period. These species are typical weedy species that are often removed from managed habitats, these include, *Taraxacum officinale* and *Rubus fruticosus*. These two species flower for over four months of the year and provide the highest overall amount of pollen for pollinator species over the field season. It is well known that weedy species are important for pollinators, however these species are usually removed from sites. Species such as *T. officinale, Tripleurospermum inodorum* and *Convolvulus arvensis* have all been found to attract many different species of wild bee (Nichols et al. 2019) and each are described as a weed. Bee species such as *Bombus lapidaries* and *Andrena dorsata* are often found on *T. officinale* whilst *C. arvensis* was visited by six solitary bee species, including *Chelostoma campanularum* and *Halictus tumulorum* (Nichols et al. 2019). It should be noted however, that some plant species on the farms may produce pollen that is either of such low quality or so inaccessible that it is not of use to many pollinators. For example, some species within the Ranunculaceae family have toxic pollen, such as *Ranunculus acris,* even though it produces lots of pollen (Roulston & Cane 2000; Nichols et al. 2019). Likewise, some plant species with long corollas, such as Trifolium spp. may have pollen which is inaccessible to short-tongued pollinators. Such species could change the overall phenology of pollen availability if they are unavailable to most pollinators.

Mass flowering crops such as *Brassica napus* (Oilseed rape) were not present on the study farms, though they would likely change the phenology of pollen supply. The additional value of resources such as these is questionable however, given that they tend to flower during periods of peak pollen and nectar production and the quality of their floral resources is considered low (Ryder et al. 2021). Thus Ryder el al (2021) state that *B. napus* pollen contains low levels of essential amino acids and thus reduces effective larvae rearing in *Bombus terrestris* colonies. This research adds to the evidence of the negative aspects of monofloral and poor nutrient diets for pollinators. Similar effects have occurred when *Apis melliferi* and *Bombus terrestris* were feed a diet of pure maize pollen, which lacked the important amino acid histidine (Hass et al. 2019; Höcherl et al. 2012). Our study showed that ~50% of pollen was produced by just four plant species, suggesting that monotonous diets

may be a problem even in landscapes without mass flowering crops. Given that ~70% of the UK is comprised of agricultural land (GOV 2022), it is important that pollinators are able to obtain a sufficiently diverse diet on farmland alone.

4.4 Contribution of different habitats to pollen production

Similar to the nectar production data reported by Timberlake et al. (2019), my data shows that that even though hedgerows produce the highest quantity of pollen per unit area, their contribution to land-scape level floral resource production is much lower. Likewise, pasture has the highest land-scape level production of pollen, due to its large percentage area of the three farms. More generally, farmland pasture covers ~40% of UK land (GOV 2015), and with the intensification of agricultural management increasing, pasture is becoming less florally diverse (Woodcock et al. 2014). This reduction in floral diversity and abundance has negatively impacted the abundance of pollinators (Wratten et al., 2012; Jönsson et al., 2015).

Creating more diverse pasture with more weedy species such as *T. officianale, Convolvulus arvensis* and *Salix* spp. could substantially increase pollen availability to pollinators (Nicholls & Altieri 2012). Management strategies implemented by the UK Government for improving pollinator resources mainly focus on creating field margins planted with wildflowers and reduced mowing (Natural England 2012; DAERA 2022). Although these areas do provide floral rich habitats, which have been found to improve pollinator abundance (Haaland et al. 2011; Jönsson et al. 2015), they represent a very small percentage of most farmland habitats. Out of the three study farms within this study, only Birches and Elmtree had field margins, and they only took up 1% of the land on both the farms. The same can be said for hedgerows, as they provide high quantities of pollen and nectar, and have been found to support higher bee richness (Dicks et al. 2015; Sardiñas & Kremen 2015), however they also make up a small percentage of the farms studied (Birches: 5%, Eastwood: 4%, Elmtree: 4%). Focusing on improving pollinator resources in more abundant habitat types such as pasture, may increase the abundance of pollinators within farmland landscapes (EIPWALES 2021, Orford et al. 2016). Overall though, both the improvement of existing habitats such as pasture and further development of floral rich field margins and hedgerows are key ways to improve pollinator resource availability on farms.

4.5 Pollinator nutritional requirements

The nutritional requirements of pollinators are known to differ among species (Cane et al. 2016, Cane 2016, Vaudo et al. 2016b, Ahrenfeldt et al. 2019), however the specific nutrients required by pollinators (e.g., amount of protein, lipids, amino acids etc.) is not well understood. It is known that pollen is the main source of protein for bees and thus is an important aspect of their diet (Nicolson 2021). Pollen is particularly important for the reproduction and development of bees as these processes require high quantities of protein and lipid (Cane et al 2016). Worker bees from *Bombus terrestris* and *Bombus impatiens*, are able to vary the protein:lipid ratio in their diets, indicating that these species are able to select foods that provide them with the correct ratio of these two nutrients (Vaudo et al. 2016a). This behaviour has also been recorded in *Osmia bicornis* (Ahrenfeldt et al 2019).

The decline in floral diversity within farmland landscapes may result in reduced reproduction rates of solitary bee species due to the low quantity of pollen available to them and the lack of understanding of their dietary needs. Some studies have identified some issues with *B. terrestris* diet (Stabler et al. 2015; Archer et al. 2021), however the impacts of different quantities of amino acids and other important nutrients remains unclear. Studies have shown that when a *B. terrestris* colony is deficient in pollen, they do not specifically forage for protein rich flower species but increase the number of workers foraging for pollen (Kämper et al 2016). *Bombus impatiens* has been reported to assess the protein:lipid ratio in pollen and forage for specific plant species (Vaudo et al 2016a) which suggests that there may be specific plant species that are more important than others for some pollinators. This importance will be based on the plant's phenology of floral resources, as well as it's resource chemistry and the accessibility of its flowers. My data on the quantity and phenology of pollen production through the year can be used to infer which plant species are likely to be favourable to different pollinators at different times of year. Looking forward, if combined with data on the nutritional composition of pollen, this data could be used to quantify the phenology of nutrient availability, rather than just the raw quantities produced. This would enable us to design more targeted and nutritionally sensitive conservation interventions for pollinators.

4.6 Climate change shifting phenology impacts

Plants in the UK are flowering a month earlier on average than they did 40 years ago (Büntgen et al 2022). This could negatively impact pollinators which require pollen at times of year when few species are flowering, as there is minimal redundancy in the system at these times. For example, in my study *Salix* flowered during February and March and produced large quantities of pollen. If the flowering of *Salix* shifted forward to January/February, there may not be sufficient resources available for bee species to feed their broods during their emergence time in March. There are very few studies on the negative impacts of climate change on pollinators, however Burkle et al. (2013) investigated the impacts of climate change on pollinators. They identified temporal mismatches and species extinctions occurring across the globe, indicating that climate change is already having a detrimental impact on pollinators (Burkle et al. 2013). Similar findings were identified by Kudo & Ida (2013), where phenological mismatch resulted in reduced seed production in their focal plant species. In many other parts of the world, pollinators currently appear to be keeping pace with shifting plant phenologies (Forrest 2015), though this may not remain the case in the future, especially as climate warming accelerates. With detailed data on the phenology of pollen and nectar availability, we are in a much better position to predict and mitigate changes in resource availability for pollinators due to climate change.

4.7 Do we need floral longevity data – what has it added to our knowledge of floral resources?

There are a relatively small number of floral longevity studies available (Song et al. 2022), and very few of them contain information on pollen. Moreover, many of these studies only look at one species, or a small group of species within a habitat (Andersson 2000, Aizen 2005, Bie 2018). By measuring the longevity of a community of species as done here (at least for the species that produced 95% of the floral units), I could use this data in combination with pollen data and floral abundance data to investigate daily pollen production over an entire field season. In short, having floral longevity data provides a means to ask some interesting questions about the availability of floral resources across time and space.

Nectar and pollen are broadly correlated in the data presented here, which while often assumed to be the case, hasn't previously been proven. This may not be the case in all habitat

types as within this study, several species were outliers to the general trend, including *Myosotis arvensis, Galium aparine, Galium odoratum* and *Allium ursinum*. Although my data enables us – for the first time - to accurately quantify pollen production at the landscape scale, the nutrient content of pollen remains largely unknown. While there is some information published on specific nutrients contained within pollen, for example by Todd & Bretherick (1942), Roulston & Cane (2000) and Vaudo et al. (2020), these studies focus on a small subset of taxa and do not provide an overall picture of the pollen nutrients available to foraging pollinators. Many of the studies also look at pollen collected by bees, which is mixed with nectar and bee secretions and so does not give an accurate estimation of its nutrient content (Kostić et al 2015, Taha 2015, Li et al 2018).

In the data presented in this thesis, there was no association between floral longevity and plant taxonomy. However, this study wasn't set up to measure this (this would have involved getting approximately equal number of samples from a broad range of families) and there were low samples sizes from some of the plant families. That said, there were some trends, for example, all replicates of both Convolvulaceae species had a floral longevity of exactly 1 day, and many of the other families had low standard deviation within the samples e.g., Fabaceae and Rubiaceae. A recent review using data from published floral longevity studies, reported a significant association between species of the same family and their floral longevity (Song et al 2022); this may have been shown to be the case here, if more species per family were sampled in this study.

4.8 Future directions

The literature on pollen nutrients is sparce, with no available data for the vast majority of species. Adding nutrient data to the pollen production values I have reported will enable ecologists to identify particularly plant species with both a high quantity and quality of floral resources. Combining this information with phenology data, as I have done in this study would also enable us to identify periods of the year when specific nutrients may be lacking for pollinators; these could be useful targets for management interventions. While there is no publicly available data on these topics, this is an area of considerable interest and there is ongoing work in this field (e.g. the NERC funded project running at Kew Gardens "Are sterols landscapes limiting nutrients for wild bees in the UK") which bodes well looking forward.

Identifying the specific nutritional needs of pollinators is also important, for example, the dietary needs of bees, flies, beetles, and other pollinators may differ. The nutritional needs of honeybees are beginning to be understood (e.g., Bonoan et al. 2019, Tsuruda et al. 2021), however there are major gaps remaining in our knowledge. For example, what nutrients are required at different stages of colony development and which specific micronutrients are required for optimal growth. The nutritional needs of non-bee pollinators are far less well understood (Jones & Rader 2022). While it's unlikely that conservation schemes would focus on the nutritional needs of a particular pollinator species (unless perhaps it was one of particular concern), some rules of thumb on what pollinators require in general would be very useful.

Although this dataset does address the floral longevity and pollen quantities of the most common UK species, it does not include species from other habitat types such as wetlands, heathlands, and upland grazing areas. These areas will likely have different phenologies and be dominated by different species. Collecting floral longevity data for habitats other than farmland would improve our overall understanding of the availability of pollen and nectar in different habitat types. Moreover, this would eventually enable a landscape level approach to assessing the availability of floral resources; something that would be useful given that most pollinators are mobile and not restricted to a particular habitat. Indeed, some studies are starting to use automated methods in combination with aerial imagery for quantifying resources (e.g., Barnsley et al. 2022), and it may soon be possible to quantify floral resources at much larger spatial scales.

4.9 Conclusion

In summary, quantifying floral longevity for a community of plants made it possible to calculate the productivity of pollen on replicate farms, this providing a first picture of the amount of pollen available to pollinators over an entire field season. Pollen production has been largely ignored in comparison to nectar production, largely because it's a much more complicated commodity to measure. Looking forward though, this approach (especially in combination with measures of pollen nutritive value and information on the nutrients that pollinators need) will likely provide new tools for conserving pollinators and the pollination services they provide.

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Supplementary Information

Table S1: Cover of each major habitat type found on the three study farms (Birches, Eastwood and Elmtree) and the total area of each farm in km2. Data from Timberlake et al. (2019).

Habitat type	Percentage of total farm area		
	Birches	Eastwood	Elmtree
Pasture	50%	73%	63%
Woodland	10%	7%	0%
Field margin	1%	0%	1%
Hedgerow	5%	4%	4%
Arable field	30%	7%	19%
Other (incl. rough ground)	4%	10%	13%
Total area (km^2)	1.42	2.13	1.82

Table S2: The 70 plant species sampled at the 24 field sites. The number of samples completed for each species and the number of field sites used. Each flower was sampled at the floral unit level. Species for which no existing pollen information was available are marked in the table; these are the species which were sampled for pollen in my study.

Species	Number of sites used	Total samples conducted	Pollen information
Acer.campestre	1	2	Yes
Achillea.millefolium	3	20	Yes
Ajuga.reptans	3	19	Yes
Allium.ursinum	2	19	No
Angelica.sylvestris	3	20	Yes
Anthriscus.sylvestris	2	19	Yes
Arctium.minus	2	6	Yes
Barbarea.vulgaris	2	16	No
Bellis.perennis	2	19	Yes
Brassica.napus	2	20	Yes
Calystegia.sepium	2	18	Yes
Capsella.bursa.pastoris	2	18	Yes
Cardamine.flexuosa	2	18	Yes
Cardamine.pratensis	2	20	Yes
Centaurea.nigra	2	20	Yes
Cerastium.fontanum	2	20	Yes
Chamerion.angustifolium	2	8	Yes
Circaea.lutetiana	2	20	Yes

Cirsium.arvense	2	20	Yes
Cirsium.palustre	2	20	Yes
Cirsium.vulgare	1	10	Yes
Clematis.vitalba	2	17	Yes
Convolvulus.arvensis	3	20	Yes
Cornus.sanguinea	2	18	Yes
Corylus.avellana	2	17	Yes
Crataegus.monogyna	2	18	Yes
Crepis.capillaris	2	18	Yes
Epilobium.hirsutum	3	15	Yes
Filipendula.ulmaria	2	12	Yes
Galium.aparine	2	19	Yes
Galium.mollugo	2	19	Yes
Galium.odoratum	2	19	No
Geranium.robertianum	3	17	No
Glechoma.hederacea	2	18	Yes
Hedera.helix	2	19	Yes
Heracleum.sphondylium	5	20	Yes
Hyacinthoides.non.scripta	2	19	Yes
Hypochaeris.radicata	3	16	Yes
Ilex.aquifolium	3	19	No
Impatiens.glandulifera	3	20	Yes
Lamium.album	2	18	Yes
Lamium.galeobdolon	2	19	Yes
Lamium.purpureum	2	19	Yes
Lathyrus.pratensis	3	20	Yes
Lonicera.periclylum	2	20	Yes
Lotus.corniculatus	3	19	Yes
Myosotis.arvensis	2	20	Yes
Polygonum.aviculare	2	17	Yes
Primula.vulgaris	4	20	Yes
Prunus.spinosa	2	20	Yes
Ranunculus.acris	3	18	Yes
Ranunculus.ficaria/ Ficaria verna	2	20	Yes
Ranunculus.repens	4	20	Yes
Rosa.canina	2	19	Yes
Rubus.fruticosus	3	20	Yes
Salix spp.	2	20	No
Sambucus.nigra	2	18	Yes
Senecio.jacobea	3	20	Yes
Silene.dioica	4	18	Yes

Sonchus.oleraceus	2	18	Yes
Sorbus.aucuparia	2	13	Yes
Stachys.sylvatica	4	20	Yes
Stellaria.holostea	2	19	No
Stellaria.media	2	20	No
Symphytum.officinale	2	20	No
Tamus.communis	3	19	No
Taraxacum.officinale	3	20	Yes
Trifolium.pratense	2	17	Yes
Trifolium.repens	3	20	Yes
Tripleurospermum.inodorum	2	16	Yes
Veronica.persica	2	20	Yes
Vicia.sativa	2	20	Yes
Vicia.sepium	2	17	Yes

Table S3: The species sampled and their average floral longevity and their variations.

Target species on study farms:	Average days open	Variation days open
Acer.campestre	2	0
Achillea.millefolium	5.75	4.387482194
Ajuga.reptans	2.833333333	0.857492926
Allium.ursinum	3.842105263	0.374634325
Angelica.sylvestris	2.9	1.4832397
Anthriscus.sylvestris	2.222222222	0.427792632
Arctium.minus	1.333333333	0.516397779
Barbarea.vulgaris	2.5625	0.62915287
Bellis.perennis	2.10526316	0.315301768
Brassica.napus	8.25	1.446411167
Calystegia.sepium	1	0
Capsella.bursa.pastoris	1.611111111	0.501631326
Cardamine.flexuosa	1.5	1.05564155
Cardamine.pratensis	2.35	0.587142949
Centaurea.nigra	1.65	0.489360485
Cerastium.fontanum	1.75	0.85069631
Chamerion.angustifolium	2.125	0.640869944
Circaea.lutetiana	3.8	1.96281216
Cirsium.arvense	2.7	0.7326951
Cirsium.palustre	1.6	0.50262469
Cirsium.vulgare	1	0
Clematis.vitalba	5.05882353	0.96634545
Convolvulus.arvensis	1	0
Cornus.sanguinea	2.944444444	0.416176182

Corylus.avellana	1.94117647	0.24253563
Crataegus.monogyna	1.666666667	0.766964989
Crepis.capillaris	2	0
Epilobium.hirsutum	2.4	0.98561076
Filipendula.ulmaria	3.083333333	0.900336637
Galium.aparine	1.842105263	0.374634325
Galium.mollugo	1	0
Galium.odoratum	1.684210526	0.582392725
Geranium.robertianum	2.1875	0.655108134
Glechoma.hederacea	4.055555556	1.161754364
Hedera.helix	3.89473684	1.24252149
Heracleum.sphondylium	2.75	1.33278497
Hyacinthoides.non.scripta	8.157894737	1.863782233
Hypochaeris.radicata	2.6875	1.493039406
Ilex.aquifolium	2	0.666666667
Impatiens.glandulifera	2	0.64888568
Lamium.album	2.27777778	0.7519039
Lamium.galeobdolon	2.526315789	0.696692268
Lamium.purpureum	3.368421053	0.955133866
Lathyrus.pratensis	2.35	0.933302004
Lonicera.periclylum	2	0.917662935
Lotus.corniculatus	2.368421053	1.065130473
Myosotis.arvensis	3.25	0.5501196
Polygonum.aviculare	1.11764706	0.33210558
Primula.vulgaris	5.85	3.06551275
Prunus.spinosa	2.85	0.933302
Ranunculus.acris	4.555555556	1.381483526
Ranunculus.ficaria/ Ficaria verna	1.95	0.39403446
Ranunculus.repens	4.25	1.585294261
Rosa.canina	2.388888889	0.777544316
Rubus.fruticosus	2.15	1.039989878
Salix.spp	1.8	0.41039134
Sambucus.nigra	3.3	0.732695097
Senecio.jacobea	2.7	0.92338052
Silene.dioica	2.722222222	1.127493605
Sonchus.oleraceus	1.72222	0.66911316
Sorbus.aucuparia	1	0
Stachys.sylvatica	2.7	0.57124057
Stellaria.holostea	4.263157895	0.561951487
Stellaria.media	1	0
Symphytum.officinale	2.5	0.512989176

Tamus.communis	1.947368421	0.621260744
Taraxacum.officinale	1.15	0.489360485
Trifolium.pratense	2	1.060660172
Trifolium.repens	2.5	0.76088591
Tripleurospermum.inodorum	2	0.632455532
Veronica.persica	1.05	0.2236068
Vicia.sativa	1.25	0.444261658
Vicia.sepium	2.470588235	1.067570083