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“The Impacts of a Rewilding Project on Pollinator Abundance and Diversity at a Local Scale”

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Abstract

The recent concerns regarding biodiversity loss have resulted in the emergence of new conservation management strategies, one of which is rewilding. Rewilding aims to restore ecosystem functionality with minimum human input. While rewilding does have potential to benefit both habitats and species, like most traditional conservation methods, it has many limitations. However, rewilding does present a unique opportunity to reshape abandoned landscapes and investigate how this impacts organisms and the interactions they have with their environment. A group of organisms not typically associated with rewilding are pollinators. The current decline in pollinator populations is strongly linked to habitat loss and fragmentation, and rewilding has the potential to improve pollinator abundance and diversity. This study aimed to assess the impacts a rewilding project has on pollinator populations at a local scale. Pan traps were set up in fields at Knepp Rewilding Estate and all pollinators captured were identified to species level. Transect walks were also conducted in individual fields to gather more information on pollinator numbers and diversity, and to observe pollinator behaviour. The results of this study suggest that year since agricultural abandonment has no significant effect on pollinators. However, the vegetation structure within fields does impact the pollinator groups recorded in this study. Overall, pollinators preferred areas of greater vegetation height deviation, and this trend was amplified when individual groups were analysed separately. Bumblebees and hoverflies preferred taller vegetation, whereas butterflies and moths were more frequently observed in open habitat. A major factor contributing to the distribution of pollinators was limited forage choice, although other factors not measured could also play a role. The results of this study, though broad, demonstrate the need for rewilding projects to maintain an element of habitat heterogeneity. Further research into this topic is necessary to provide a more extensive insight into how pollinators utilise different resources and how this influences their distribution. However, this study has shown that pollinators can benefit from rewilding, which has implications for both rewilding projects and future pollinator conservation.

Introduction

Biodiversity Loss

Over the last two centuries, increased human activity has resulted in a massive loss of biodiversity across the globe (Ehrlich & Wilson, 1991; Soulé, 1991; Geist & Lambin, 2002). Species extinction rates are currently 1000 times higher than background levels, and it is estimated that overall terrestrial biodiversity has declined by 25% between 1970 and 2000 alone (Pimm *et al*, 1995; Loh & Wackernagel, 2004). Biodiversity has inherent intrinsic values and plays a key role in the functioning of ecosystems (Jones *et al*, 1994; Cardinale *et al*, 2006; Power *et al*, 2006). As such, the reduction in species richness will have negative consequences for ecosystems in terms of stability and overall functionality. In an effort to preserve and limit the loss of existing biodiversity, several new conservation approaches have been introduced (Naeem *et al*, 1994). Rewilding is one of these proposed management strategies which has gained recent traction with scientists, governments and among the general public (Nogués-Bravo *et al*, 2016).

Rewilding

Rewilding is a relatively novel conservation approach which aims to restore land to its natural state by enhancing the functionality of the ecosystem (Sandom *et al*, 2012; Carver, 2016). It was proposed originally in 1998 as a universal means for conserving global biodiversity with minimum management through human activity (Soulé & Noss, 1998). The perceptions of rewilding are varied within the scientific community and public domain, and the exact definition is subject to interpretation. This lack of clarity is arguably both its greatest weakness and greatest asset. The precise approach to individual projects is flexible and therefore widely applicable, however its transparency also means it is open to criticism (Jørgensen, 2015).

The basis for all rewilding is the process of ecological succession. Succession is the change in the dynamics and structure of species communities within an ecosystem over time (Peet & Christensen, 1980). It begins with the establishment of pioneer species, for example lichens (Syers & Iskandar, 1973). Through a process of change and colonisation, a climax community, which is often closed canopy woodland, is reached and the ecosystem becomes stable (Walker & del Moral, 2003).

There are two types of rewilding; passive and active. Passive rewilding relies solely on the succession process. Whereas active rewilding involves the reintroduction of native keystone species, herbivores or predators. Active rewilding is a top-down approach that aims to re-establish self-regulating ecosystems, and the trophic cascades from these introduced species means that the impacts will begin at the top of food webs and travel towards the base (Estes *et al*, 2011).

Future Landscapes

The ‘final product’ of rewilded land is contested amongst conservationists. The climax community of undisturbed succession is typically closed canopy woodland (Conti & Fagarazzi, 2005), this does not however, mean that this will be the end result for all rewilding projects. The agricultural history of an area i.e. the degree of pesticide usage, duration of farming, and whether the land was used for crop or livestock production, may affect the results of a project. Rewilding is also not restricted to previously farmed land, and has been applied to other areas including disused military sites, wetland areas, and forested land previously used for timber production (Navarro & Pereira, 2015). All of this means that the final outcome of rewilded sites will not always be closed canopy woodland, and as such rewilded land is not exclusively beneficial for woodland species.

Concerning biodiversity, it is important to maintain some element of habitat heterogeneity. An area which has a more ecologically complex habitat will undoubtedly be more biodiverse than an area of one habitat type as organisms are able to fill more niches and exploit a greater abundance of resources (Bazzaz, 1975; Tews *et al*, 2004). Passive rewilding, or land abandonment without the introduction of any large herbivores, is likely to result in the formation of forest (Conti & Fagarazzi, 2005). However, in active rewilding sites where large herbivores have been introduced, grasses, saplings, and small shrubs will be consumed and subsequently an aspect of open grassland habitat will be retained, although this will be dependent on the stocking rate (Sunderland, 2002). Therefore, groups of organisms traditionally dependent on open meadow habitats, for example pollinators, can also gain from rewilding projects. The main aim of any rewilding project is to restore ecosystem functionality, and pollinators provide an extremely beneficial ecosystem function in the form of pollination.

Pollinators

Pollination is arguably one of the most valuable services provided by the ecosystem (Kearns *et al*, 1998; Dodd *et al*, 1999; Goulson, 2003). The sessile nature of angiosperms means that they rely on vectors for sexual reproduction, and it is estimated that 87% of plants are pollinated by animals (Ollerton *et al*, 2011). In both agricultural and wild contexts, plant-pollinator interactions are highly important to both the plants and the pollinators; pollinators are essential for many flowering plants to produce fruits and seeds, and pollinators are dependent on the foraging rewards provided by plants (Kearns *et al*, 1998). Plant-pollinator relationships are also thought to be a major driver in the diversification of multiple plant and animal groups (Dodd *et al*, 1999; Ollerton, 1999). While the value of this service is multifaceted, with the foundation of most food webs being dependent on the interaction, with reference to human requirements, the economic value of plant-pollinator interactions was estimated to be €153 billion in 2005 alone (Gallai *et al*, 2009).

In spite of their ecological and economic importance, pollinators are declining (Williams, 1982; Fitzpatrick *et al*, 2007; Ollerton *et al*, 2014). There are a number of factors responsible including disease and competition from non-natives, but the current reduction in pollinator populations is most strongly associated with the intensification of agriculture, which has led to habitat loss and fragmentation (Thomas *et al*, 2004). Approximately half of all farmland hedgerows have been removed in Britain since the 1940s (Robinson & Sutherland, 2002), and approximately 97% of original flower rich grassland has been lost to agriculture, with similar figures depicted across Europe (Howard *et al*, 2003). Research also suggests that pollinators with specific traits will be disproportionately affected; species reliant on particular habitats or diets are more likely to suffer losses (Biesmeijer *et al*, 2006). Important pollination services, for example sonication, could be impacted by this bias, and therefore the stability of pollination services could be reduced (Larsen *et al*, 2005).

Honeybees (*Apis mellifera*) are predominant in literature concerning pollinator declines (Potts *et al*, 2010). In spite of losses regionally, honeybee populations are increasing on a global scale; since 1961 the number of managed hives is estimated to have increased by 45% (Aizen & Harder, 2009). There are still concerns regarding honeybee populations however, as the quantity of crops dependent on them are increasing at a rapid rate which cannot be sustained by current honeybee numbers (Aizen & Harder, 2009). Despite their environmental and commercial value, wild pollinator declines have been poorly documented (Ghazoul, 2005). An exception to this are the butterflies, which have been the subject of coordinated recording

initiatives for decades, and so their decline has been substantially monitored (Settele *et al*, 2008; Lewis & Senior, 2011). Butterfly declines across Europe are severe; in 1840 the Bavarian Reserve, Germany, had 117 species of butterfly present, but only 71 in 2013 (Habel *et al*, 2016). Many species of bees, which are responsible for most pollination services provided by animals, have also shown similar reductions in numbers (Buchmann & Nabhan, 1996; Klein *et al*, 2007; Cameron *et al*, 2010; Ellis *et al*, 2015). Of all bee species, bumblebees (*Bombus* sp.) have been the most frequently monitored (Goulson *et al*, 2008). In Britain, six species of bumblebee (not including those belonging to the subgenus *Psithyrus*) have shown considerable declines (Williams & Osborne, 2009). Data for other bee species is fragmentary due to an absence of recording schemes (Potts *et al*, 2010). Studies suggest that other groups of pollinating insects are exhibiting equivalent, if not more pronounced, trends (Thomas, 2005).

Rewilding and Pollinators

Thus far, literature concerning rewilding has focussed primarily on the conservation of mammal and bird species. The quantity of land previously used for agriculture in Europe that has been abandoned, and is set to be abandoned, is considerably large (MacDonald *et al*, 2000). Therefore rewilding does provide a much needed conservation approach for animals with extensive habitat ranges, for example *Canis lupus* and *Lynx lynx*, which are not compatible with traditionally small nature reserves or the fragmented landscape of Western Europe (Fritts & Carbyn, 1995). However, the majority of biodiversity is smaller and functions at lesser spatial scales, and in order for rewilding to be considered a viable conservation tool it must be suitable for all kinds of biodiversity, not just a select few species.

Despite accounting for the majority of biodiversity and providing valuable ecosystem functions, insects are vastly under-represented in conservation research (Clark & May 2002; Cardoso *et al*, 2011). The literature surrounding rewilding reflects this, with only a few studies concerning insects, and an even lesser amount focussing on the impacts of rewilding on pollinators (Merckx, 2015).

Mata *et al* (2016) produced a report which detailed species that should be targeted for rewilding projects in Melbourne. Insect species made up 29% of all priority organisms, and this included pollinator species such as *Amegilla* sp., which were selected because of their contribution to the pollination of many native plant species. Other pollinators suggested

included *Heteronympha merope*, as they are easily recognisable by the public and an indicator of climate change. A paper produced by Merckx (2015) highlighted the potential benefits and caveats of rewilding on moth and butterfly species. It is proposed that rewilding can be a useful conservation tool for Lepidoptera, but in order for it to be effective, a degree of habitat heterogeneity must be maintained. Merckx concludes that a completely passive rewilding approach, whereby a climax community will dominate the entire landscape, will have limited outcomes not just for Lepidoptera, but for other pollinator species also.

Knepp Rewilding Estate

Currently, the most extensive survey which attempts to quantify the effects of rewilding on pollinators is the 2005 baseline study at Knepp Rewilding Estate in West Sussex (Greenaway, 2005). The estate covers approximately 3500 acres and over the past two decades has transformed from an agricultural farm into a lowland rewilded landscape. The project is ongoing, and the core goal is to monitor and record how the vegetation structure and overall biodiversity has changed since moving away from agricultural practices. The land at Knepp was subject to increasingly intensively farming following the Second World War. The success of traditional agriculture was limited however due to the heavy clay soil, and competition from more successful farms resulted in little profit being made. After the visible results from the restoration of the Repton Park in the estate in 2001, the owner, Charles Burrell, decided to rewild the entire estate. A selection of herbivores including Tamworth pigs, Exmoor ponies, and English longhorn cattle were introduced onto the southern block of the estate to aid in restoring ecosystem functionality and provide the top-down maintenance that is typical of active rewilding projects. Introducing large mammals would also prevent the establishment of dense woodland that is typical of passive rewilding projects (Marren, 2016). The results of the project thus far have demonstrated its conservation success, and it is recognised for its nationally scarce species such as *Streptopelia turtur* and *Apatura iris* (Tree, 2017).

The survey at Knepp recorded over 1000 species of flora and fauna, and while this is an impressive quantity, the invertebrates are likely to be underestimated due to the time frame of the survey. Three species of Syrphidae were recorded over the course of a single day, one of which, *Pipiza lugubris*, is of notable conservation importance. Butterflies were monitored using transects, and 13 species were recorded over a 15-hour period. The survey of

Hymenoptera revealed very little; 12 bee species from four different genus' (*Andrena*, *Bombus*, *Lasioglossum*, and *Nomada*) were recorded in pitfall traps. There are likely to be much more species present at Knepp however, as pitfall traps are not an effective method of monitoring bees.

Knepp Estate provides a unique opportunity to investigate the impacts of rewilding on pollinator diversity and abundance with reference to succession. Fields were taken out of agricultural production at different times, and the vegetation structure is likely to reflect this. The presence of large herbivores also means that areas of open grassland will be prevalent throughout the site, and this could prove important for pollinators.

Hypotheses

The main aim of this study was to assess the impacts a rewilding project can have on pollinator populations at a local scale. There were three hypotheses:

- (i) Fields which were taken out of agricultural production most recently would have a greater abundance and diversity of pollinators present than fields which were taken out of production earlier.
- (ii) Fields which were taken out of agricultural production most recently would have less developed vegetation i.e. more open habitat.
- (iii) A greater abundance and diversity of pollinators would be observed in fields where the vegetation was in the earlier stages of succession.

Methods

Data was collected between May 15th and June 15th 2018 at Knepp Rewilding Estate in West Sussex. The estate is divided into three blocks by roads, and this project focused on the southern block only (Fig. 1). The southern block was further divided into three sections, with each section corresponding to an experimental repeat. Within each section, five fields were selected at random using a random number generator; four were representative of different years taken out of agricultural production from years 2002, 2003, 2004, and 2005. The fifth field was permanent pasture, which is maintained by Knepp Estate and mown every three years. The permanent pasture fields acted as the control.

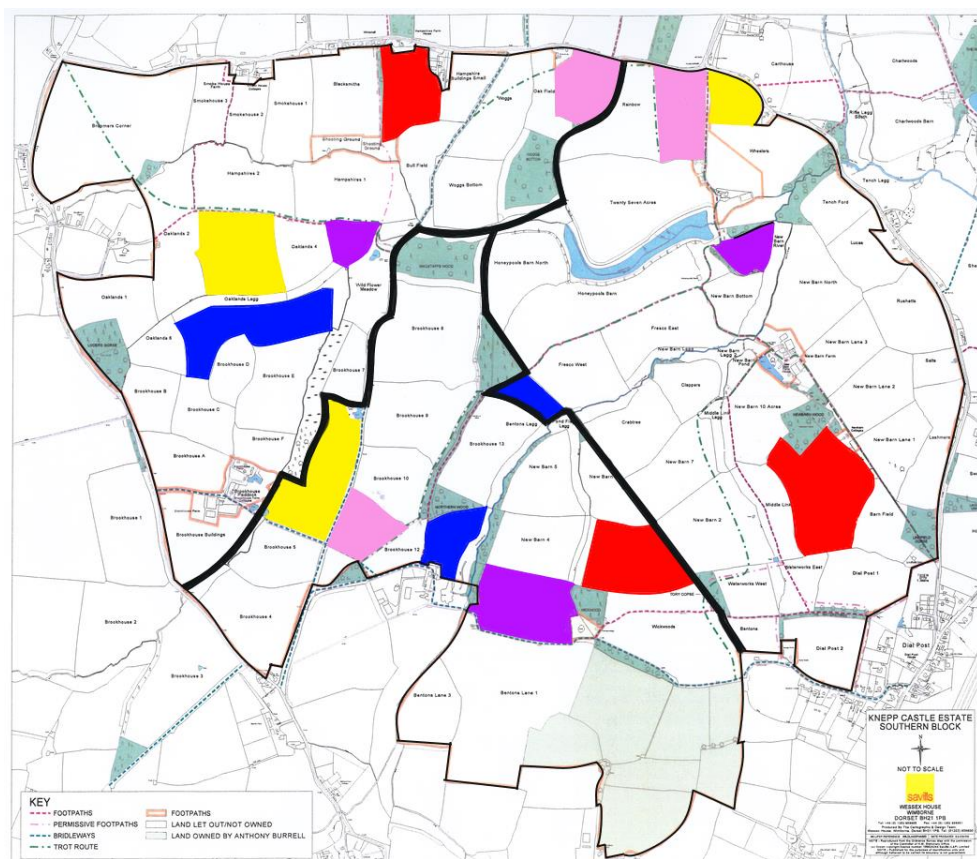


Figure 1: The southern block of the Knepp Rewilding Estate. The thick black lines dividing the site in three indicate where the block was split, with each section corresponding to a week's data collection. The highlighted fields represent the field selected for survey and each colour signifies a different year taken out of agricultural production; red are the fields taken out of production in 2005, yellow are fields from 2004, pink are 2003, blue are 2002, and purple shows permanent pasture.

Week 1

NVC Data Collection

National Vegetation Classification (NVC) surveys were carried out in all 15 fields over the course of the first seven days. The NVCs covered four levels; ground, field, shrub and tree. For both the ground and field layer a quadrat measuring 0.5m x 0.5m was placed randomly in the field five times. The scrub layer was assessed using a 30m measuring tape and measuring a 5m x 5m quadrat. The plant species within the quadrat boundaries were identified and given a score using the Domin scale, which ranges from 1 (a single plant covering less than 10% of the quadrat area) to 10 (the plant covers 100% of the quadrat area). A digital photograph was also taken of each quadrat. All fields were bordered by trees, and so the tree layer was measured by randomly selecting a 25m stretch of tree line and identifying all the tree species. Again, each species was given a score using the Domin scale. Opportunistic sightings were made also by conducting a 10 minute search period, whereby any individuals not found in quadrats were recorded. All NVC data was quantified using Modular Analysis of Vegetation Information System (MAVIS).

Drone Mapping

All field sites were mapped using a drone (Mavic Pro). A central point was taken of each field and a 20m buffer was applied to select the area for mapping. The drone was then flown at 78m which produced a picture of the area with a resolution of 2cm per pixel. DroneDeploy software was used to generate structure from motion, and calculated the standard deviation of vegetation height within the selected area.

Weeks 2 - 4

Pan Trapping



Figure 2: An aerial view of the pan trap set-up. Traps were placed on top of a crate which raised them up from the ground level. 4 colours were used; pink, white, yellow, blue.

Four pan traps measuring 18cm in diameter and coloured white, red, yellow, and blue were set up as close to the centre of each field as possible (Fig. 2). The traps were raised off of the ground using a black crate (35cm x 45cm x 22cm) which was secured into the ground using pegs. Clear traps were cable tied to the crate base, and the coloured pan traps were secured into them using unscented adhesive.

Every morning between 9am and 11am the traps were filled approximately two thirds full of water and a few drops of unscented dishwashing liquid (Greenscents) were added also. Every evening between 6pm and 8pm the contents of the traps were emptied into separate sealed plastic bags. The samples were taken back to a temporary laboratory setup at Knepp, and sorted through. Every individual was identified to order level, and any honeybees, bumblebees, solitary bees, wasps, butterflies, moths and hoverflies were removed from the liquid, pinned using forceps, labelled, and then mounted onto a polystyrene base. Once dry, a microscope and identification guides (Waring & Townsend, 2014; Ball & Morris, 2015; Falk,

2015; Lewington, 2015) were used to identify the samples to species level. Traps were setup in each section of the southern block for six days, and on the seventh the traps were removed from the fields.

Transect Sampling

Transect surveys were conducted in each of the five fields for seven days between 10am and 3pm. Beginning as close to the centre of the field as possible, a distance of 100m was walked at a steady pace. The direction of walking was determined by generating a random number between 0 and 360 and following that direction using a compass. If an unpassable obstacle was encountered, the observer would make a 90 degree turn to the left and continue walking. Whilst walking, a note was made of any bee, butterfly, hoverfly, moth or wasp seen within a 2 meter distance to the left or right of the observer on the ground and 2m above the observers head for flying insects. Individuals were classified as far down as possible by the observer in the field. As well as their presence, their behaviour (flying, foraging, resting, mating etc.) was recorded. If foraging, the forage plant would also be recorded. This was done in each of the three sections of the southern block.

Statistical Analysis

All data were analysed in R (version 3.3.2) using linear models with a normal distribution (package: base). The normality of the distribution of all variables was calculated using a Lilliefors test (package: nortest), and the output of this determined whether a parametric or non-parametric test was undertaken. The Simpson's Diversity Index (D) of pollinators observed on transects was calculated for each of the years taken out of production (Simpson, 1949), and these were compared using a one-way ANOVA (package: car). The effect of year taken out of production on the standard deviation of vegetation height was determined using a Kruskal-Wallis test (package: car).

Linear regressions were used to examine the relationship between the standard deviation of vegetation height and the frequency of pollinators (packages: car, mblm). As well as overall abundance, each of the seven pollinator groups was also tested individually: Apini, Bombini, Heterocera, Rhopalocera, Syrphidae, Vespidae, and the solitary bee species. All solitary bee species observed on transects (*Andrena*, *Halictus*, *Hylaeus*, *Lasioglossum*, and *Osmia*) were

combined into a single group to provide the statistical power to analyse the data. All graphs were produced in the ggplot2 package.

Results

A total of 3359 individuals were caught in pan traps over the three week period. Of this, 45 were organisms this study aimed to concentrate on (Apini, Bombini, Heterocera, Rhopalocera, Syrphidae, Vespidae, and solitary bees). The remaining individuals belonged to Aranea (1%), Coleoptera (5%), Diptera (excluding Syrphidae species) (43%), Hemiptera (49%), and Hymenoptera (<0.5%). 786 pollinators were observed on transect walks and these were categorised into seven groups: Apini (n = 374), Bombini (n = 116), Heterocera (n = 79), Rhopalocera (n = 82), Syrphidae (n = 89), Vespidae (n = 17), and the solitary bees (n = 29).

NVC

All 15 fields had unique NVC classifications, encompassing seven different habitat types (Appendix A). The most prevalent habitat was *Lolium perenne-Trifolium repens leys*, occurring in five fields from three different groups (2003, 2004, and pasture). The second most common habitat type also occurred in three field groups and was *Lolium perenne repens leys*. The only group of fields to have consistent habitat types across all three fields were those taken out of production in 2003.

Pan Traps

All 45 individuals caught in the pan traps are listed in Appendix B. The species caught most frequently was *Symmorphus gracilis* which was found in four of the five field categories (n = 15). Pasture fields showed the greatest diversity of pollinators present with 9 species caught, and both 2002 and 2003 fields had the lowest diversity (n = 4). Pasture fields also had the greatest abundance of individuals caught (n = 19), whereas 2003 only had 4 individuals.

Transects

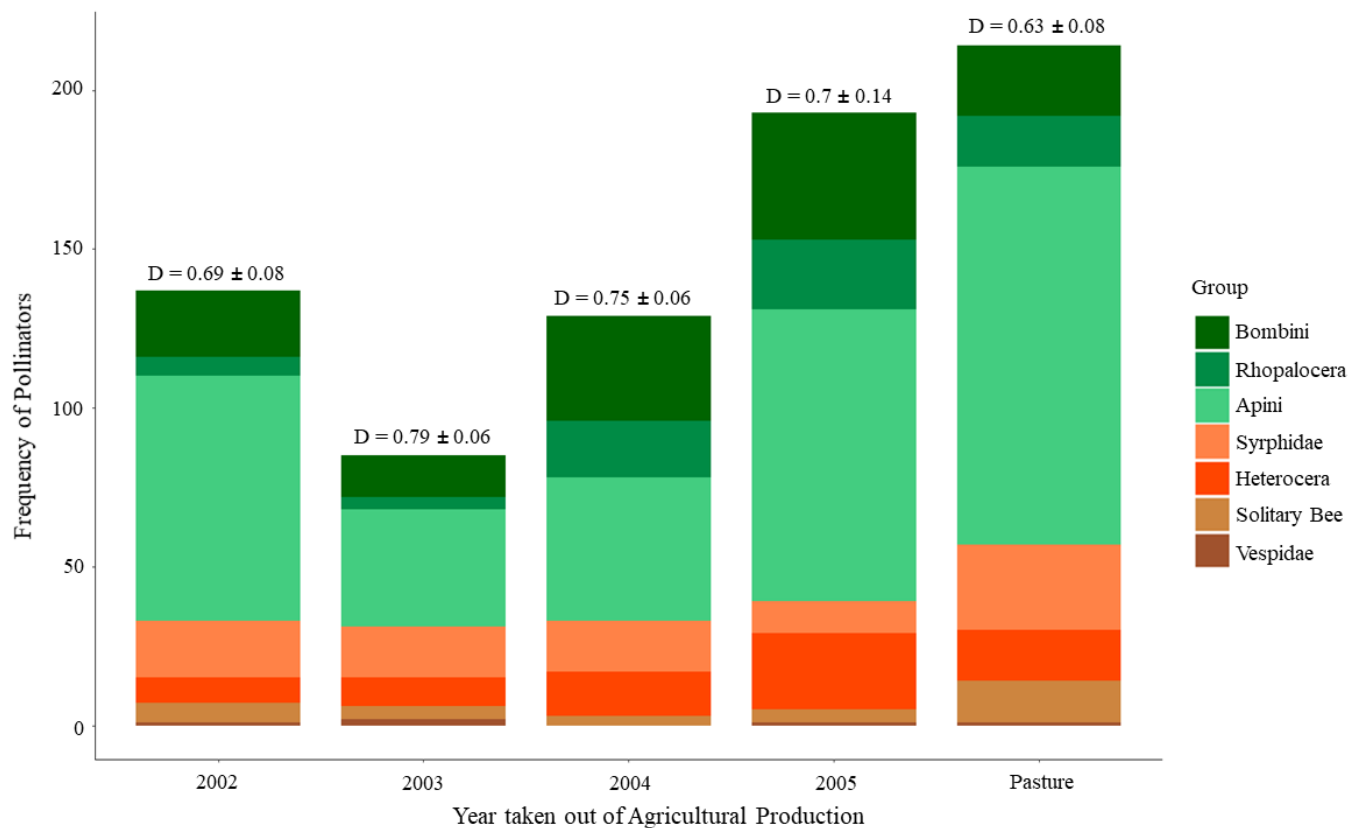


Figure 3: The frequency of pollinators observed on transects in each field category. The Simpson's Diversity Index (D) is stated along with the associated standard error. A Simpson's Diversity Index of 0 signifies no diversity, and 1 shows a high diversity.

Overall pasture fields had the greatest abundance of pollinators ($n = 214$), and fields in the 2003 category had the least ($n = 85$). Honeybees (Apini) were the most abundant group in all field categories accounting for 56% of all individuals in 2002 fields, 44% in 2003, 35% in 2004, 48% in 2005, and 56% in pasture fields. Vespidae were the least observed group in all field categories, and no individuals of Vespidae were seen in 2004 fields. Fields taken out of agricultural production in 2003 had the greatest overall diversity ($D = 0.79 \pm 0.06$), and pasture fields had the lowest ($D = 0.63 \pm 0.08$). 2002 fields had a Simpson's diversity index of 0.69 ± 0.08 , fields from the 2004 category had a diversity of 0.75 ± 0.06 , and 2005 fields had a diversity of 0.7 ± 0.14 . There was no significant variation in the diversity of each field category (ANOVA: $F = 0.12$, $n = 15$, $p = 0.88$; Fig. 3).

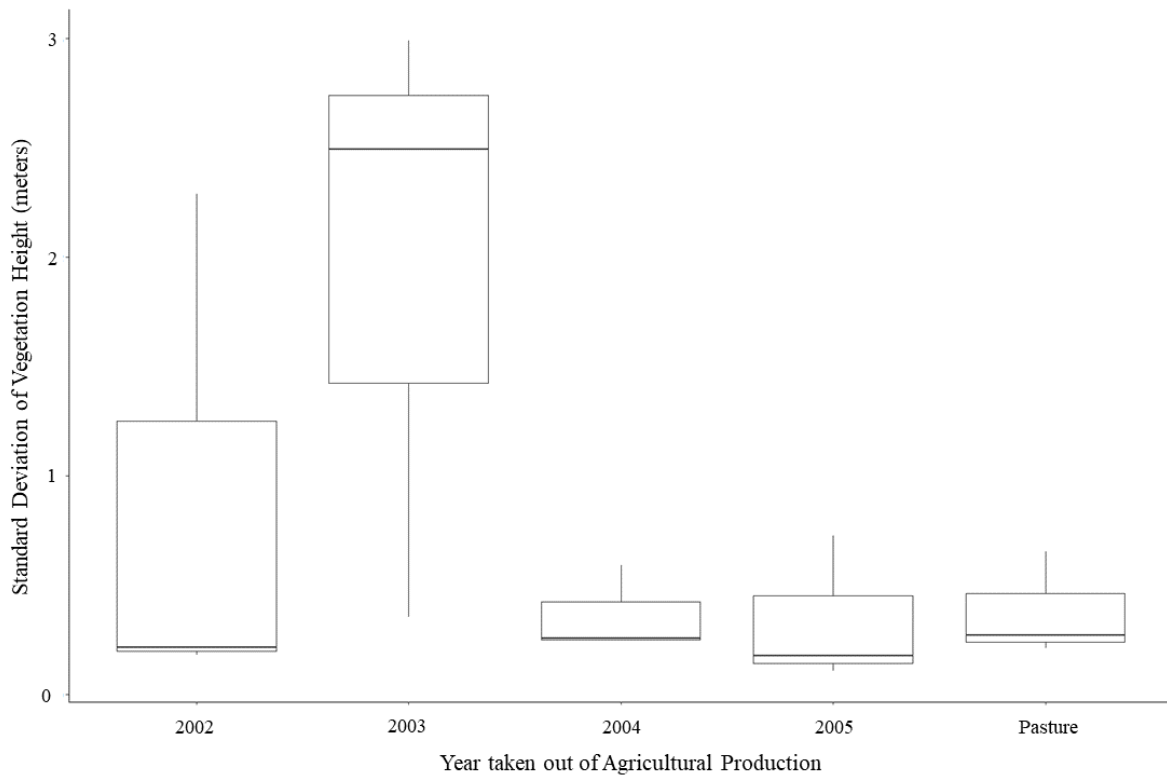


Figure 4: The standard deviation of vegetation height (in metres) of each field category. The boxes depict the median and interquartile range, and the whiskers indicate the maximum and minimum values. A standard deviation of vegetation height of 0 indicates an area of vegetation consistent in height, and a value of 3m would show that vegetation present within the site varied 3m in height between the tallest and shortest vegetation.

The average standard deviation of vegetation height for fields taken out of agricultural production in 2002 was $0.89 \pm 0.69\text{m}$, 2004 had an average of $0.36 \pm 0.11\text{m}$, and the average for pasture fields was $0.38 \pm 0.14\text{m}$. Fields in the 2003 group had the greatest average height ($1.94 \pm 0.8\text{m}$) and 2005 had the smallest ($0.34 \pm 0.19\text{m}$). The standard deviation of vegetation height showed no significant difference between fields (Kruskal-Wallis: $\chi^2 = 4.8$, $n = 15$, $p = 0.31$; Fig. 4).

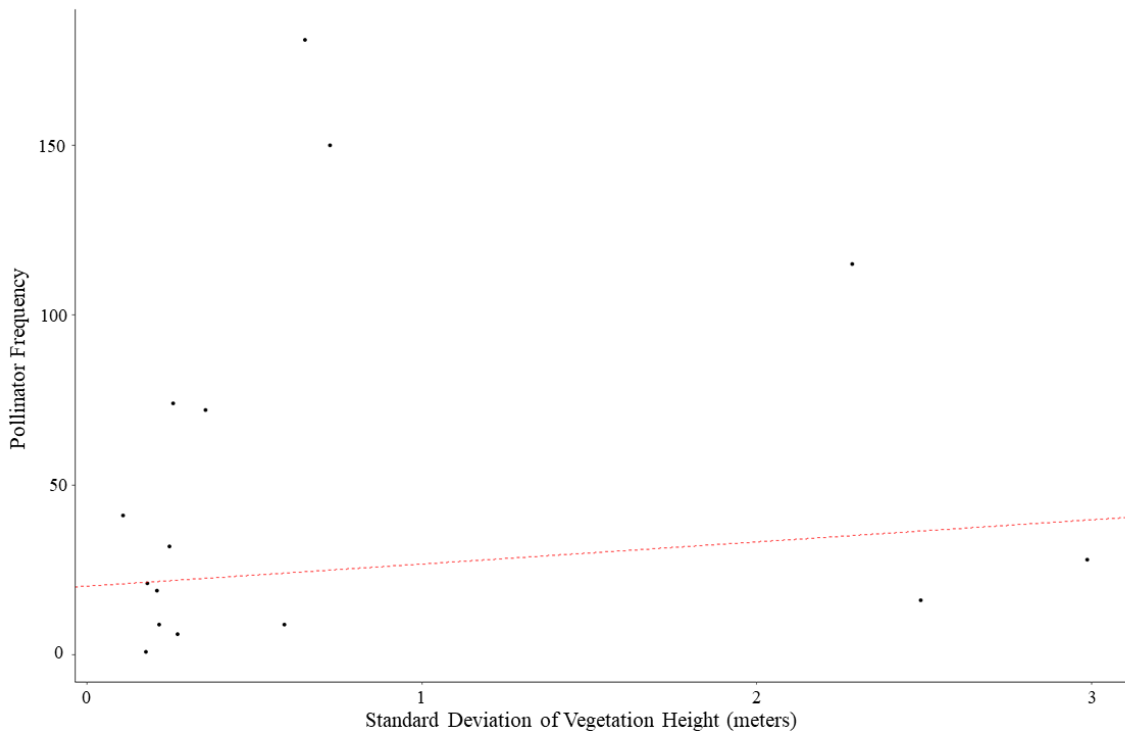


Figure 5: The standard deviation of vegetation height (in meters) against the frequency of pollinators observed on transects. A standard deviation of vegetation height of 0 indicates an area of vegetation consistent in height, and a value of 3m would show that vegetation present within the site varied 3m in height between the tallest and shortest vegetation.

There was a positive correlation between the standard deviation of vegetation height and the total abundance of pollinators seen on transects ($R^2 = 0.15$, $n = 796$, $p = 0.03$; Fig. 5). Only 1 pollinator was seen at a vegetation height of 0.17m, and the pollinator frequency peaks at a vegetation deviation of 0.65m ($n = 181$). At the highest vegetation height deviation (2.99m) 28 pollinators were observed, and 41 individuals were seen at the lowest vegetation height deviation (0.11m).

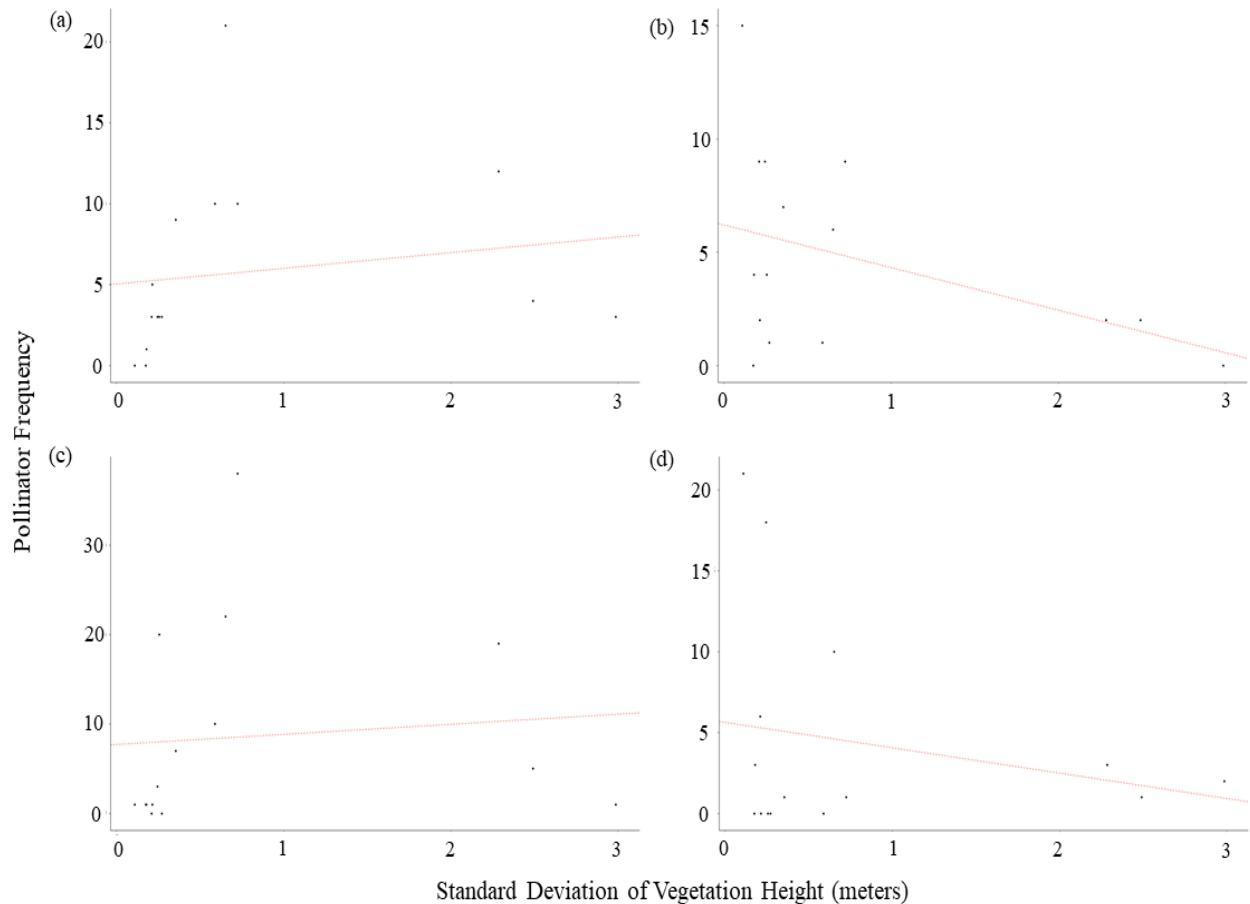


Figure 6: The standard deviation of vegetation height (in meters) against the frequency of **(a)** Syrphidae, **(b)** Heterocera, **(c)** Bombini, and **(d)** Rhopalocera. All organisms were seen on transect walks. A standard deviation of vegetation height of 0 indicates an area of vegetation consistent in height, and a value of 3m would show that vegetation present within the site varied 3m in height between the tallest and shortest vegetation.

Of the seven pollinator groups observed on transects, four had statistically significant results (Fig. 6). The frequency of Syrphidae had an overall positive relationship with standard deviation of vegetation height ($R^2 = 0.36$, $n = 89$, $p = 0.02$; Fig. 6a). The greatest number of Syrphidae is seen at a vegetation height deviation of 0.65m ($n = 21$), and the lowest frequency is at 0.17m with no individuals observed. Heterocera had a significant negative relationship with standard deviation of vegetation height ($R^2 = 0.27$, $n = 79$, $p < 0.01$; Fig. 6b). The frequency of Heterocera was greatest at a vegetation height deviation of 0.12m ($n = 15$), and lowest at 0.17m ($n = 0$). The abundance of Bombini also had a positive correlation with standard deviation of vegetation height ($R^2 = 0.12$, $n = 116$, $p < 0.01$; Fig. 6c). Bombini abundance was highest at 0.73m vegetation height deviation ($n = 36$), and no individuals were seen at vegetation height deviations of at 0.21m, 0.27m and 2.5m. The

frequency of Rhopalocera had an overall negative correlation with standard deviation of vegetation height ($R^2 = 0.48$, $n = 82$, $p = 0.03$; Fig. 6d). No Rhopalocera were observed at five sites (standard deviation of vegetation heights 0.17m, 0.21m, 0.26m, 0.27m, and 0.59m), and the greatest abundance was seen at a vegetation height deviation of 0.12m ($n = 21$).

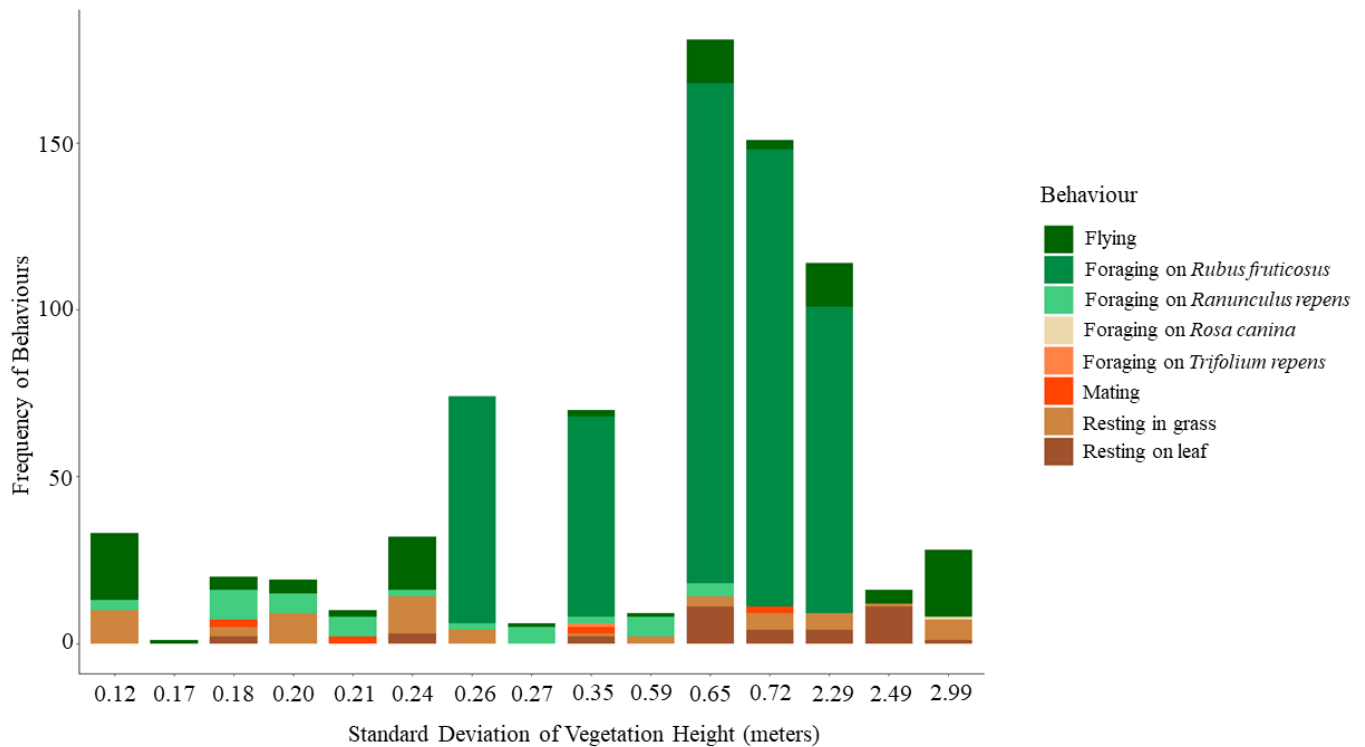


Figure 7: The behaviours of pollinators observed on transects against the standard deviation of vegetation height (in meters). A standard deviation of vegetation height of 0 indicates an area of vegetation consistent in height, and a value of 3m would show that vegetation present within the site varied 3m in height between the tallest and shortest vegetation. The 15 bars represent the 15 fields surveyed in this study.

Foraging on *R. fruticosus* accounted for 64% for all behaviours observed on transects ($n = 507$) and occurred in five fields ranging in vegetation height deviation from 0.26m to 2.29m. Foraging on *Rosa canina* and *Trifolium repens* were the least observed behaviours ($n = 1$) and were only observed in fields where the vegetation height deviation was 2.99m and 0.35m respectively. Fields with a vegetation height deviation of 0.35m had the greatest variety of behaviours with only one behaviour (sonication) not being present. Flying was observed in all fields except one, where the vegetation height deviation was 0.26m.

Discussion

Year and Vegetation

The overall abundance and diversity of pollinators observed on transects was not influenced by the year in which fields were taken out of agricultural production (Fig. 3). This suggests that the time since agricultural abandonment has little impact on whether pollinators will choose to inhabit an area or not. Although it is expected that organisms which have been negatively affected by agriculture would be more abundant in fields that had been removed from agricultural practices for longer, the lack of relationship could be explained by the vegetation structure of the fields.

Figure 4 shows the relationship between the standard deviation of vegetation height and year taken out of agricultural production. Despite 2003 appearing to have a greater vegetation height overall, this was insignificant, and there was no statistical difference in vegetation height deviation between different years. The fields surveyed at Knepp Estate were taken out of agricultural production only one year apart. A single year does not provide a sufficient amount of time for vegetation to establish and grow, which could account for the lack of significant difference between field categories. With regards to the apparent higher vegetation deviation in the 2003 fields, one of the fields in this category had a centre point which was located on the edge of a woodland running through the field. The presence of the woodland could account for the greater vegetation height observed in this category.

Vegetation and Pollinators

The frequency of pollinators increased with vegetation height, with more pollinators being present in areas with a greater variation of vegetation heights (Fig. 5). This suggests that pollinators prefer habitats which vary in structure, i.e. a greater degree of habitat heterogeneity. Numerous studies have described positive relationships between insect biodiversity and habitat heterogeneity (Atauri & Lucio 2001; Baz & Garcia-Boyer, 1995; Murdoch *et al.*, 1972; Southwood *et al.*, 1979), and this study demonstrates this phenomenon also. Though the overall relationship was positive, the abundance of pollinators peaks at a standard deviation of vegetation height around 0.65m, and then it declines. This peak, and the general higher abundance of pollinators surrounding this vegetation height deviation, correlates with the presence of *Rubus fruticosus* bushes (Fig. 7). Recorder observations

revealed that during data collection *R. fruticosus* was the most prevalent plant in flower, and therefore likely to be the primary food source for pollinators throughout the duration of the project.

R. fruticosus is a perennial, deciduous shrub found in a wide variety of habitats across the UK. It can grow up to three metres in height and the woody stems of the plant bear thorns to deter herbivory. The flowers are white or pale pink with five petals and multiple stamens, and flowering begins in early spring and can last through to late summer (Zia-Ul-Haq *et al*, 2014). Plants can produce hundreds of individual flower heads, each containing a plentiful supply of nectar and pollen (Percival, 1946). The flowers of *R. fruticosus* have a very open structure with easy access to both the nectar and pollen, therefore organisms do not require any specialised mouth parts to obtain the foraging reward of the plant (Verma *et al*, 2014). The open access to flower heads combined with the high quality foraging reward means that *R. fruticosus* is visited by the majority of pollinator groups (Zia-Ul-Haq *et al*, 2014).

While the relationship between pollinator abundance and vegetation height deviation was positive overall, it is important to note that it only applies from mid-May until mid-June when data was collected, and that during this time frame the foraging choice of pollinators was restricted to mainly *R. fruticosus*. Further research is required to confirm or refute these findings, as the relationship is highly likely to change throughout the season as different plants begin to flower.

Syrphidae

Syrphidae species were found more frequently in areas where the vegetation height deviation was greater (Fig. 6a). This relationship mirrors the overall pollinator abundance (Fig. 5), with a peak around 0.65m and then a decline. Again, this relationship is likely explained by the presence of *R. fruticosus*, which provides a rich nectar and pollen source for the adult hoverflies.

The most common species of Syrphidae was *Helophilus pendulus*, accounting for 78% of all Syrphidae caught in the pan traps (Appendix B). This is a fairly common UK species and the larvae feed on wet, decaying organic matter. As a result of this, *H. pendulus* is often found near ponds or cattle manure (Sommaggio, 1999). During the summer months when temperatures increase, cattle are known to seek out areas of shade to stay cool (Blackshaw & Blackshaw, 1994). Taller vegetation, i.e. trees, will provide cattle with shelter from the sun

and so this is where cattle will congregate during the day. This will in turn result in manure being deposited in close proximity to taller vegetation, and therefore more individuals of *H. pendulus* may be found in these areas.

An important factor to consider when investigating Syrphidae species is moisture. All Syrphidae have 3 larval stages which are maggot-like, but unlike other Diptera larvae, Syrphidae have tails. In contrast to the homogenous feeding habits of the adults, the larvae of Syrphidae have an array of feeding practices including saprophages, mycophages, and phytophages (Sommaggio, 1999). Knepp Estate does have both large and small water bodies on site, however this was not measured during this study. Future studies into the distribution of Syrphidae species at Knepp should take into account the presence or absence of water and its proximity to the study site.

Heterocera

Heterocera did not follow the overall pollinator relationship with vegetation height deviation (Fig. 5), and instead exhibited a negative correlation. Moths occurred more frequently in areas of consistent vegetation height (Fig. 6b). In this study, fields which had a low standard deviation of vegetation height are representative of open grassland fields as opposed to low deviations that would be observed in other vegetation heights which are fairly consistent, for example fields of only woodland or scrub. This is owing to there being no fields surveyed in this study which were comprised of only woodland or scrubland habitat.

Heterocera are a hugely biodiverse taxon with over 2500 species in the UK encompassing 19 different lepidopteron families (Fox *et al*, 2011). The ecology of individual moth species is highly varied also, with different species preferring different habitat types.

In the context of this study, two moth species were found in the pan traps, *Autographa gamma* and *Tyria jacobaeae* (Appendix B). Both of these moth species rely on consistently open vegetation. *A. gamma* is a migratory moth in the UK which migrates south to the Mediterranean basin during the winter months (Heath & Emmet, 1983). The adult moths are generalists and feed on nectar from plants including *Centaurea scabiosa* and *Cirsium arvense*, which excrete an odour attractive to the moths (Plepys *et al*, 2002). The females lay their eggs on low-lying herbaceous plants, such as *Trifolium* sp. and *Rumex* sp., which the caterpillars consume (Chinery, 1995).

T. jacobaeae on the other hand is a specialist moth species which has a strong association with its food plant, *Senecio jacobaeae*. Adult moths emerge in the spring and lay clusters of eggs on the underside of the basal leaves, which the young caterpillars consume once hatched. As the caterpillars develop they move towards the inflorescences of the plant and consume the flower buds (Dempster, 1982). Plants used for both adult and larval feeding of *A. gamma* and *T. jacobaeae* are found in areas of open vegetation. Therefore the greater abundance of Heterocera in more consistent vegetation heights i.e. open grassland, can be explained by the species found in the pan traps.

Bombini

As the standard deviation of vegetation height increased, as did the abundance of bumblebees observed on transects (Fig. 6d). Again, around 0.73m the frequency of bumblebees was at its greatest before decreasing. As with Syrphidae species, the flowering of *R. fruticosus* is likely responsible for this trend, and therefore it is inclined to change as the season progresses.

Another alternative explanation for this relationship could be nesting behaviour. Bumblebees often utilise disused small mammal burrows for their nests (Sladen, 1913). While not all bumblebee species nest in this way, for example *Bombus hypnorum* prefers to nest in above-ground cavities like holes in trees or walls (Benton, 2006), the only bumblebee species found in the pan traps, *Bombus terrestris* (Appendix B), does (Sladen, 1913). Nests located in close proximity to *R. fruticosus* could benefit from the plant in two major ways; (1) the dense structure of *R. fruticosus* bushes can provide shelter from the sun, preventing overheating of the nest (Jones & Oldroyd, 2006), and (2) the woody stems of *R. fruticosus*, along with their spinescence, could provide protection from potential predators (Richards, 1978).

A common large mammal predator of bumblebee nests is *Meles meles*, which locate nest sites and excavate the entire brood and comb for consumption (Alford, 1975; Pease, 1898; Sladen, 1913). Bees and wasps have been estimated to account for 6.5% of *M. meles* diet throughout the summer months (Cleary *et al*, 2009). A study by Goulson *et al* (2017) found that large mammals were most frequently responsible for the destruction of bumblebee nests, accounting for 5.5% of all occurrences. *M. meles* are present at Knepp Rewilding Estate, and so shelter from *R. fruticosus* could minimise the likelihood of an attack on the nest. No nests were observed in the field, however the relationship between bumblebee nesting behaviour and *R. fruticosus* with regards to predation could be investigated in the future.

Rhopalocera

Fig. 6d shows the relationship between the standard deviation of vegetation height and the frequency of butterflies. Just like the moths (Fig. 6b), butterflies are found in greater abundance in vegetation which is consistent in height, like open meadow habitat.

There are currently 59 species of butterfly in the UK, all of which interact with their environment in a different way. Butterflies typically prefer open habitat, where they feed, await mates and lay eggs (Ford, 1945). The negative correlation between butterfly abundance and vegetation height in this study can be explained by the butterflies caught in the pan traps. Two species of butterflies were caught in the pan traps, *Ochlodes sylvanus* and *Maniola jurtina* (Appendix B).

O. sylvanus is a common UK species belonging to the family Hesperidae. It is predominantly found in open grassy habitats, such as meadows, road verges, and hedgerows. The males of this species often rest in prominent, sunny positions awaiting a passing female. The females lay their eggs in tall grasses, such as *Dactylis glomerata*, *Molinia caerulea*, and *Brachypodium sylvaticum*, and the caterpillars feed on these grasses (Chinery, 1995). *M. jurtina* is another common UK species that prefers open grassland habitat. The caterpillars feed on a wide range of grasses including *Agrostis* sp. and *Poa* sp. The adult butterflies are generalists and will feed on nectar from multiple plant species including *Erica* spp. and *Scabiosa* spp. (Chinery, 1995). Both species of Rhopalocera inhabit areas where there is an open vegetation structure, and this could account for the relationship observed in this study.

Non-significant Groups

Apini, Vespidae, and solitary bees had no significant relationship with the standard deviation of vegetation height. Honeybees were the most frequently seen species on transects (n = 374), yet they showed no relationship with vegetation height deviation. The communication capabilities of honeybees combined with their ability to forage greater distances from the hive could be a reason as to why they did not have a correlation with vegetation height deviation. A study by Beekman & Ratnieks (2000) illustrated the great distances honeybees can travel to find flowers. Honeybees are unique in that if they do locate a good quality patch far away from the hive, they can inform other workers using a waggle dance (Karaboga, 2005). Due to the limited forage choice at Knepp Estate during data collection, it is highly

likely that honeybees were travelling off-site in order to find better forage, and so their presence was limited to fields containing *R. fruticosus*.

Vespidae were observed the least frequently of all groups on transects (n = 17). The Vespids are a large group of organisms, with species encompassing a vast range of different ecological niches (Jandt & Toth, 2015). Despite being a diverse group, in this study the Vespids were characterised by a single species, *Symmorphus gracilis* (Appendix B). *S. gracilis* is a species of potter wasp which nests in pre-existing cavities in plants, wood and human structures (Guichard, 1972). The lack of significant relationship between the Vespids and vegetation height deviation could be because the group was only represented by one species, and therefore all individuals will occupy the same habitat type.

A potential reason as to why the solitary bees showed no significant relationship could be due to the wide diversity of species compiled into this category. Species from five genus' (*Andrena*, *Halictus*, *Hylaeus*, *Lasioglossum*, and *Osmia*) were collated together to provide sufficient statistical power to analyse the data. While there is a wider diversity of moth species than solitary bee species in the UK, in this study only two species of moth were caught in the pan traps compared to nine species of solitary bees. Also, hoverflies have a similar species richness to solitary bees in the Britain, but again only four species were identified in this study. Solitary bees caught in this study are hugely varied in morphology and ecology, exhibiting a multitude of various feeding preferences and nesting behaviours. For example, *Osmia* sp. are long-tongued species and are able to access the foraging rewards of a wider selection of flowers than shorter-tongue bee species, such as *Andrena* sp. or *Lasioglossum* sp. (Falk, 2015). The social structure of solitary bees also varies; *Hylaeus* sp. are not cleptoparastic or eusocial, however some species of the genus *Halictus* are sub-social or primitively eusocial (Pesenko, 2004). Numerous species of solitary bee were seen both on transects and in pan traps (Appendix B), and this could explain the lack of pattern between solitary bees and vegetation height deviation.

Conclusion

The duration of time since agricultural abandonment appears to have little impact on pollinator abundance or diversity, rather it is the vegetation structure that influences what pollinator groups will be present and in what numbers. The overall trend suggests that pollinators prefer habitats which have a greater variance in vegetation height i.e. a greater degree of habitat heterogeneity, and when analysed as individual groups, this relationship was amplified. Different pollinators had varying inclinations for different habitat types, with some favouring open spaces and others preferring taller vegetation.

While this study was relatively broad, and encompassed a vast array of pollinator groups, it is evident from the results that rewilding projects seeking to increase the biodiversity of an area should maintain some element of habitat heterogeneity. Having multiple successional stages present across a site will result in a greater diversity of organisms inhabiting the area.

Whether this involves introducing large herbivores and predators, or increasing human management will depend on a multitude of factors, for example the location of a project.

With regards to increasing human management, the success of a rewilding project should not be determined by how passively managed it is, but by the overall functionality of the ecosystem and the outcomes of the project.

Concerning conservation management, whether rewilding or a hands-on approach is preferable will be largely dependent on the goals and desired outcomes of individual projects. Projects looking to target specific species or habitats will more likely benefit from traditional conservation practices, and those looking to restore ecosystem functionality may benefit more from rewilding.

Further research is necessary to investigate other variables not assessed in this project which could affect the distribution of pollinator groups, such as proximity to water and nesting behaviours. Although this study showed no relationship between year since abandonment and vegetation structure, as fields were only taken out a year apart there could still be a link, and future research is needed to investigate this potential relationship further. Also, collecting data at different points during the active foraging period of pollinators and across multiple years is necessary to determine if the results from this study are representative of entire seasons or as a consequence of limited forage choice. Nevertheless, this study has provided a

comprehensive and much needed assessment of pollinator population dynamics at a local scale in the context of a rewilding project.

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Appendix

Appendix A

The National Vegetation Classification (NVC) data from all 15 fields surveyed as described by the Modular Analysis of Vegetation Information System (MAVIS).

Year taken out of Production	Field Name	NVC Classification	Habitat
2005	Hampshire Big	MG7A 34.59	<i>Lolium perenne repens leys</i>
	New Barn 1	OV26 28.74	<i>Epilobium hirsutum</i> community
	New Barn 3	MG7A 32.31	<i>Lolium perenne repens leys</i>
2004	Brookhouse 6	MG7B 39.75	<i>Lolium perenne-Poa trivialis leys</i>
	Oaklands 3	MG7A 38.13	<i>Lolium perenne repens leys</i>
	Pound Corner	MG7A 28.57	<i>Lolium perenne-Trifolium repens leys</i>
2003	Brookhouse 11	MG7A 44.22	<i>Lolium perenne-Trifolium repens leys</i>
	Hammer	MG7A 25.05	<i>Lolium perenne-Trifolium repens leys</i>
	Honeypools	MG7A 37.95	<i>Lolium perenne-Trifolium repens leys</i>
2002	Benton's Place	OV21 44.74	<i>Poa annua-Plantago major</i> community
	Keens	MG11a 33.29	<i>Lolium perenne</i> subcommunity
	Oaklands 5	MG7A 33.39	<i>Lolium perenne repens leys</i>
Pasture	East of Hammer	OV21 34.21	<i>Poa annua-Plantago major</i> community
	Pond Field	MG7A 37.11	<i>Lolium perenne-Trifolium repens leys</i>
	Wildflower	MG9 38.02	<i>Holcus lanatus-Deschampsia cespitosa</i> grassland

Appendix B

All individuals caught in the pan traps over the three week period. Organisms are grouped by the year in which fields were taken out of production.

Year taken out of Production	Species	Abundance
2005	<i>Apis mellifera</i>	1
	<i>Bombus terrestris</i>	1
	<i>Maniola jurtina</i>	1
	<i>Helophilus pendulus</i>	1
	<i>Symmorphus gracilis</i>	4
2004	<i>Eristalis tenax</i>	1
	<i>Helophilus pendulus</i>	2
	<i>Helophilus triittatus</i>	1
	<i>Lasioglossum villosulum</i>	2
	<i>Osmia bicornis</i>	1
	<i>Symmorphus gracilis</i>	1
2003	<i>Andrena haemorrhoa</i>	1
	<i>Helophilus pendulus</i>	1
	<i>Hoplitis claiensis</i>	1
	<i>Lasioglossum morio</i>	1
2002	<i>Andrena bicolor</i>	1
	<i>Bombus terrestris</i>	1
	<i>Helophilus pendulus</i>	3
Pasture	<i>Symmorphus gracilis</i>	1
	<i>Autographa gamma</i>	1
	<i>Halictus rubicundus</i>	1
	<i>Hylaeus communis</i>	1
	<i>Lasioglossum malactunum</i>	1
	<i>Lasioglossum villosulum</i>	1
	<i>Ochlodes Sylvanus</i>	2
	<i>Syricta pipiens</i>	1
	<i>Tyria jacobaeae</i>	2
	<i>Symmorphus gracilis</i>	9