Pollinator communities on a landscape complexity gradient in southern Sweden

Hanna Olsson
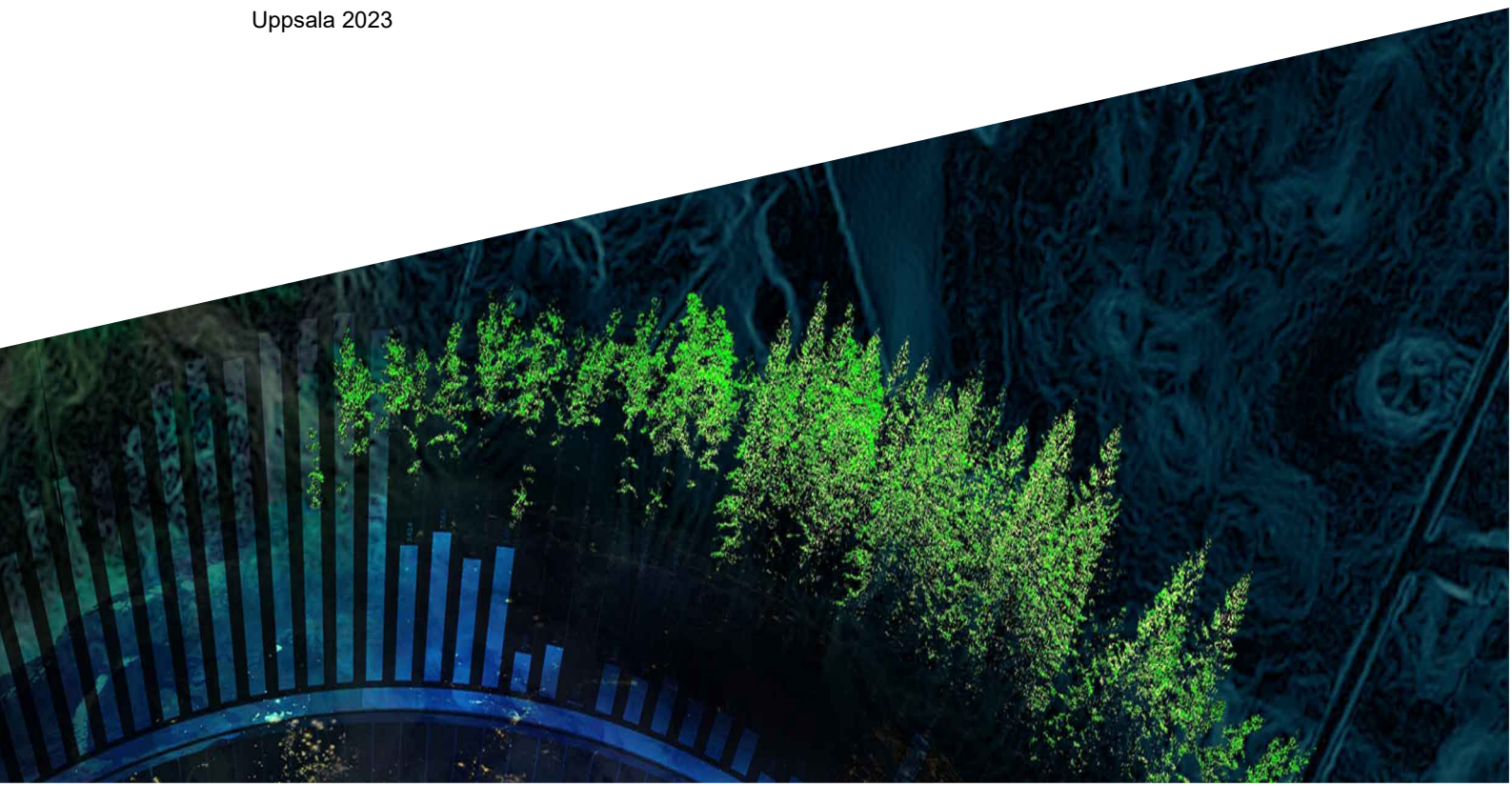
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Abstract

Investigating how pollinator populations are affected by land use changes is crucial for predicting their persistence in the landscape and thereby the persistence of the significant service they provide to crop production. Pollinator populations are subjected to multiple threats, particularly overall intensification of cropping systems and landscape simplification.

I investigated how landscape complexity affects pollinator and plant communities, and how pollinators interact with plant species across time. Rough pastures on a gradient of landscape complexity were assessed for ground cover of flowers and of vegetative ground cover of flowering plants, by estimation in 20 squares of one m^2 along two flower-rich transects of ten meters in each pasture. They were also sampled for pollinating insects by walking along the same transects and collecting them from flowers. The sites were spread out across Skåne in southern Sweden and sampled in early July, late July and early August of 2017.

Significant plant and floral shifts along the sampling period were observed. Floral resources decreased in late summer, potentially triggering population collapse of bumblebees. However, no effects of landscape complexity on plant and pollinator richness were observed. Similarly, I did not find relationships between landscape complexity and the percentage of bumblebees with long tongues (specialist bumblebees). However, there was a trend in higher proportion of female bumblebees, and a higher abundance of a red listed species (*Bombus muscorum*) in more complex landscapes.

My results show no clear relationships between landscape complexity and plant or pollinator richness. However, the positive trend between female bumblebees and landscape complexity suggest that collapse of bumblebee populations is delayed with more diversified floral resources. My results also show the importance of complex landscapes to maximize plant-pollinator interactions, while preserving red-listed species.

Populärvetenskaplig sammanfattning

Pollinatörer i jordbrukslandskapet är viktiga för pollinering av somliga grödor, då man vet att pollinering ger ökad fruktsättning och därmed en högre skörd. Det gäller särskilt sådana grödor som odlas för en varierad växtföljd samt för att producera proteinrika skördeprodukter. Våra vilda pollinatörer är utsatta för ett flertal hot, särskilt en allt intensivare växtodling samt ett allt mer homogent jordbrukslandskap. Denna utveckling gör att det blir allt mindre föda och färre boplatser, vilket negativt påverkar deras möjligheter att upprätthålla stabila populationer.

Jag har tittat på hur landskapskomplexitet, i form av andel markyta i ett landskap som utgörs av annat än jordbruksmark, påverkar samhällen av pollinatörer och blommande växter i naturbetesmarker runtom i Skåne. Jag har även tittat på hur samhällen av pollinatörer och blommande växter ser ut över tid. Den övervägande delen av pollinatörerna som hittades i naturbetesmarkerna var humlor (80 %), följt av tambin (10 %) och övriga bin (10 %). Vilda pollinatörer utgjorde alltså 90 % av de pollinatörer som påträffades i naturbetesmarkerna.

Jag kunde konstatera att mängden blommor, och därmed tillgång av nektar och pollen, i naturbetesmarkerna var hög under hela juli, för att sedan sjunka markant till början av augusti. Jag kunde även se att andelen manliga humlor gick upp i början av augusti, och eftersom humlesamhällen kollapsar i slutet av varje sommar och endast då producerar manliga humlor, kan det vara ett tecken på samhällskollaps. Det skulle kunna vara så att brist på blommor bidrar till att humlesamhällen kollapsar redan i början av augusti.

Jag såg inga samband mellan landskapskomplexitet och antal arter av vare sig pollinatörer eller blommande växter. Inte heller mellan landskapskomplexitet och långtungade pollinatörer (vilka anses mera specialiserade än korttungade pollinatörer). Däremot såg jag tecken på färre manliga humlor i komplexa landskap, och det skulle kunna vara så att en jämnare tillgång på blommor över säsongen i komplexa landskap bidrar till att fördröja humlornas årliga samhällskollaps. Jag hittade även en rödlistad humleart i mer komplexa landskap.

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1. Introduction

Increasing demands for agricultural products to sustain human population growth have led to an increase in the intensification of agricultural cropping systems (Bommarco et al., 2013), resulting in an increasing trend of landscapes with fewer, more similar crops in shorter rotations (Bennett et al., 2012). Current literature shows that the aim to increase yields by means of intensification is not always a possible way forward, and in some cases, yields may even decrease in intensively managed cropping systems (Bennet et al., 2012). In addition, the simplification of landscapes resulting from agricultural intensification threatens several ecosystem services and functions that, in turn, feed back on crop production, such as pollination and pest management (Dainese et al., 2019). One way to alleviate these trade-offs can be to maintain diversified landscapes, which has been shown to enhance several ecosystem services without compromising crop yields (Tamburini et al., 2020). Despite the increasing recognition of the negative impacts of agricultural intensification on key ecological services, we still lack a better understanding of these impacts at different scales, how they relate to below- and above-ground communities of organisms that provide these services, and ultimately how this affects crop productivity (Bommarco et al., 2013). Pollinators are a key group to understand effects of crop management on biodiversity because they determine human well-being and contribute to food security and maintenance of biodiversity (Potts et al., 2016; Dainese et al., 2019). For example, pollinator density has been directly linked to higher crop yields of winter oilseed rape (Lindström et al., 2015). However, a drastic decrease in pollinator populations has been reported worldwide (Potts et al., 2010) which can impact ecosystem function (Bennet et al., 2012).

Overall, simplification of agricultural landscapes have shown to negatively impact pollinators (Öckinger et al., 2006; Le Féon et al., 2010; Connelly et al., 2015; Aguilera et al., 2020). Degradation of semi-natural habitats is another threat to pollinator populations (Steffan-Dewenter & Westphal, 2008). Thus, several studies have shown the importance of preserving semi-natural grasslands of flower-rich grassland patches (Öckinger & Smith, 2007; Le Féon et al., 2010; Holland et al., 2017) or hedgerows (Garratt et al., 2017) to enhance pollinator populations. This is probably because these habitats provide food resources and habitats for reproduction of pollinator populations (Öckinger & Smith, 2007). For

example, the lack of fertilizers or intensive management in semi-natural grasslands promote high species and functional diversity of both plants and insects, but also promotes steady production of flower resource along the growing season. By contrast, some of the agricultural crops can produce massive amounts of flowers, and thereby nectar and pollen, to pollinators (Westphal et al., 2003; Holzschuch et al., 2016). However, the observed increases in pollinator populations in crops producing mass flowering during a limited time (Westphal et al., 2003) are not always accompanied by increases in sexual reproduction (Westphal et al., 2009). Thus, increases of pollinators in simple landscapes due to mass flowering plants do not necessarily imply more sustained populations across time (Persson & Smith, 2013). Instead, pollinator populations in simple landscapes may be better supported with late-flowering crops (Persson & Smith, 2013; Rundlöf et al., 2014) and semi-natural areas (Öckinger & Smith, 2007; Le Féon et al., 2010, Holland et al., 2017). Thus, ensuring a higher diversity of flowering plants and a higher landscape complexity should benefit pollinator communities, but this remains to be explored.

Several indicators can be employed to assess whether stressors affect populations in a given landscape. For example, richness or diversity indices together with the presence of certain traits among the studied species or population may indicate whether stressors are simplifying both populations and the resources (i.e. plants) which these populations depend upon. In bumblebees, a good example is tongue length, a trait that influences which plant species that the bumblebee can interact with. This trait can thereby help indicate the floral diversity in a given landscape. Particularly, pollinators with long tongues are specialized in obtaining nectar from longer plant spurs (Whittall & Hodges, 2007). In addition, tongue length is also an indicator of the presence of specialist versus generalist bumblebees, since species with short tongues are able to feed on many flowers (Miller-Struttmann et al., 2015). Due to the bumblebee life cycle, in which the colony collapses each year, coinciding with the hatching of males, the relative abundance of males to females is an indicator of colony collapse (Zayed et al., 2004). Thus, measures of pollinator abundances together with tongue traits and sexual stages in bumblebee populations are useful to assess their stability, complexity and persistence.

In this study, I assessed the effect of landscape complexity on pollinator diversity, plant-pollinator interactions and other indicators (i.e. tongue length and abundance of males). I also studied the temporal variation of pollinator diversity along the summer months and how this relates to variation in floral resources. Plant, floral and pollinator data were obtained from rough pastures in Skåne (southern Sweden), which were surrounded by landscapes with varying complexity. Richness was calculated and used as diversity index. I also assessed main pollinator traits

(i.e. tongue length) related to resource specialization, and the abundance of male bumblebees at different times. I hypothesize that i) higher landscape complexity will promote pollinator diversity, and that ii) in more complex landscapes there will be a higher abundance of less common pollinator species, iii) a set of pollinator species with different traits (i.e. short and long tongues) and iv) a later appearance of male bumblebees.

2. Material and methods

2.1 Study site

The study was performed in Skåne (southern Sweden) during the summer of 2017. ArcMap (version 10.3.1) was used to find rough pastures varying in the proportion of landscape complexity in a 1-kilometer radius surrounding it. In total, 17 pastures with surroundings were selected ranging from 1% to 99% in their cover of semi-natural habitat. Sampling of plants and pollinators was performed during three times of the summer of 2017 (early July, late July and early August).

2.2 Sampling

Sampling was conducted along two 100 meter long transects in each rough pasture. These transects were placed at least 5 meters away from the pasture border and were attempted to cover the small-scale variability in topography, vegetation types and other features that could exist within the pasture. Therefore, transects were allowed to be irregular but always keeping a minimum distance of 10 meters between each part of the transect. Additionally, transects were placed in the most flowering rich part of the pasture to maximize possibility to encounter pollinator-plant interactions. Therefore, transects might have changed during the different sampling visits.

2.3 Plant communities

The identity and abundance of all flowering plant species were recorded in all the sites at each visit. Ten 1 m^2 plots were placed at regular intervals along each transect (a total of 20 plots per pasture). A species list was recorded in each plot, and the vegetative ground cover of each species was estimated according to a semi-logarithmic scale (Table 1). Average ground cover per site (%) and sampling time was estimated by summing up the cover of all plants at the site and dividing by number of squares (Table 1).

Table 1. Classes used to estimate ground cover of flowering plant species. This criterion was used for all the present plant species.

Estimated ground cover of flowering plant species	Median
<1 %	0,5 %
1 – 5 %	3 %
5 – 12,5 %	8,75 %
12,5 – 25 %	18,75 %
25 – 50 %	37,5 %
>50 %	75 %

2.4 Floral resources

Floral abundance by area was measured by selecting two 1 x 10 meter strips in each transect (i.e. four strips per site), and estimated by quantifying the number of flower units and the average size of a flower unit in each transect (independently of plant species identity).

2.5 Pollinator-plant-interactions

Sampling of pollinator-plant interactions was performed by walking along the transects described in section 2.2 for 10 active minutes, recording all pollinators visiting a flower within 1 meter of each side of the transect. These pollinators were collected for species identification and the visited plant species was identified.

2.6 Pollinator identification

Pollinators were collected in vials with ethyl acetate and kept at -18 degrees Celsius until identification. Identification was made to species level for bumblebees (which accounted for 85% of the captured individuals) except for *Bombus lucorum*, *Bombus terrestris* and *Bombus soroeensis* which were grouped together as *"B. lucorum* group". *Apis mellifera* (which accounted for 10% of the captured individuals) was identified to species level as well, while the rest of the pollinators (5% of captured individuals) were classified as "other bees". Identification was

based mainly on the books Humlor i Sverige (Mossberg & Cederberg 2012) and Bumblebees (Benton 2006).

2.7 Data analysis

Linear regressions were used to identify relations between changes in pollinator and plant communities and landscape variables. Pollinator richness and abundances were calculated from the visitation data, which means that only pollinators found to have an interaction with a plant were included. Flower richness was calculated as the number of flowering plant species, and flower abundance was calculated as flower resource abundance (see above). Linear regressions were performed between landscape complexity (as reflected by percentage of semi-natural habitat) and plant richness, average floral area, pollinator richness and number of pollinator-plant interactions. ANOVAs were then used to test seasonal differences in the measured parameters. Data was checked for normality and homocedasticity and data was log transformed if assumptions were not met. To check for normality, data was plotted against theoretical quantiles from a normal distribution (QQ plots), and Shapiro-Wilk test was performed to test for significance. Homocedasticity was checked by plotting the residuals against fitted values. Data was considered heterocedastic when residual plots showed funnel type shape. Tukey HSD was used to test differences between seasons. P-values lower than 0.05 were considered significant. Analyses were done using R 3.6.1, package vegan 2.5.

3. Results

3.1 Plant communities

In total 56 flowering plant species were found at all sites during all three sampling times. The richness ranged from 4.7 ± 0.2 to 11 ± 1.2 at the different sites, from 6.8 ± 0.6 to 7.8 ± 0.5 at the different sampling times, and did not significantly vary between sampling times (P = 0.372, dF= 48). *T. repens* was the most abundant flowering plant species (23% $\pm$ 2.8), followed by *S. gramina* (14% $\pm$ 2.7) and *T. medium* (12% $\pm$ 1.1). Several plant species flowered across the three sampling times, while some less common species flowered at one or two sampling times (Figure 1). Early August showed more shifts in plant communities, while early and late July resembled each other more (Figure 1). However, plant cover of flowering plants varied across sampling times (P < 0.001 dF=48), with late July having the highest plant cover (38% $\pm$ 5) and early August the lowest (8% $\pm$ 3) (Figure 2, left). The increase in plant cover in late July was mainly due to peaks in flowering of the most common plant species.
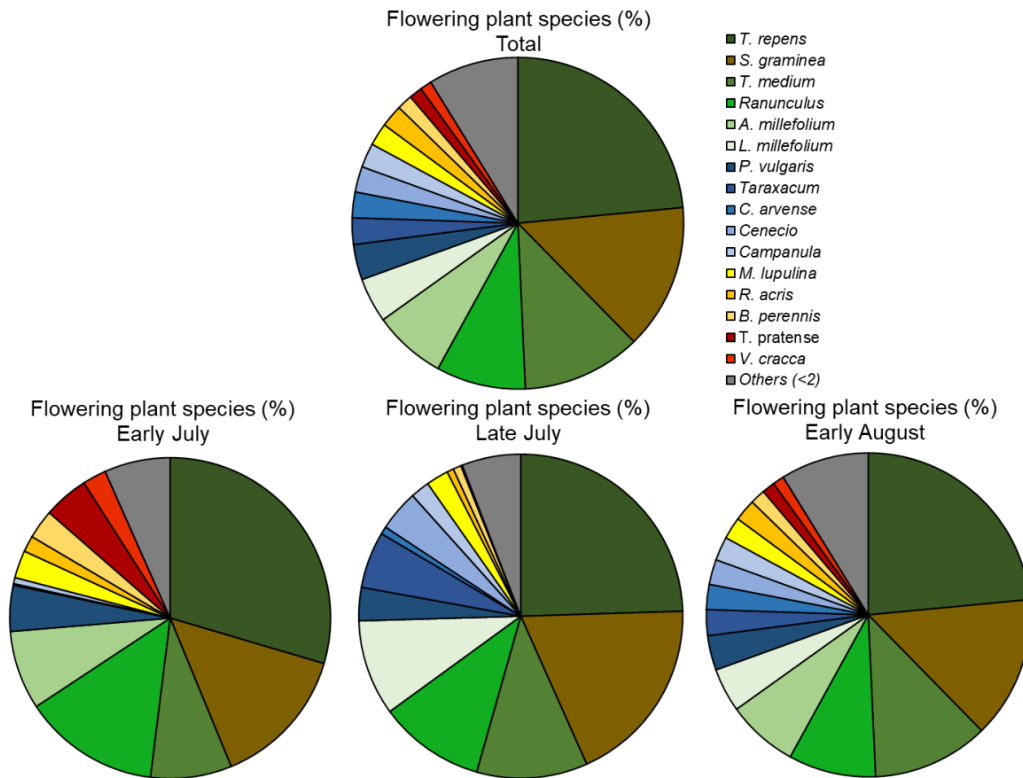
Figure 1. Flowering plant species at all the sites in early July, late July and early August and at all sampling times.
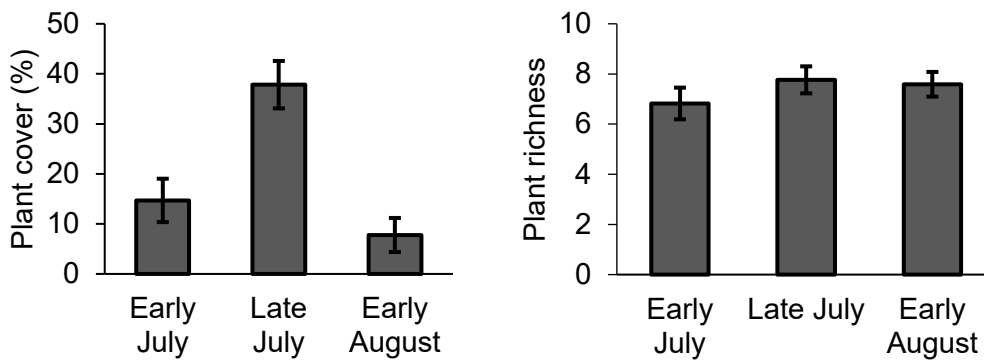

Figure 2. Changes in plant cover (left) and plant richness (right) at the three sampling times. Error bars indicate standard error.

There were no relationships between observed average plant richness in the pastures (i.e. averaged values of the three sampling times) and the degree of complexity in the surrounding landscape (P = 0.720, dF= 15, Figure 3, left) nor pasture size (P = 0.634, dF= 15, Figure 3, right).
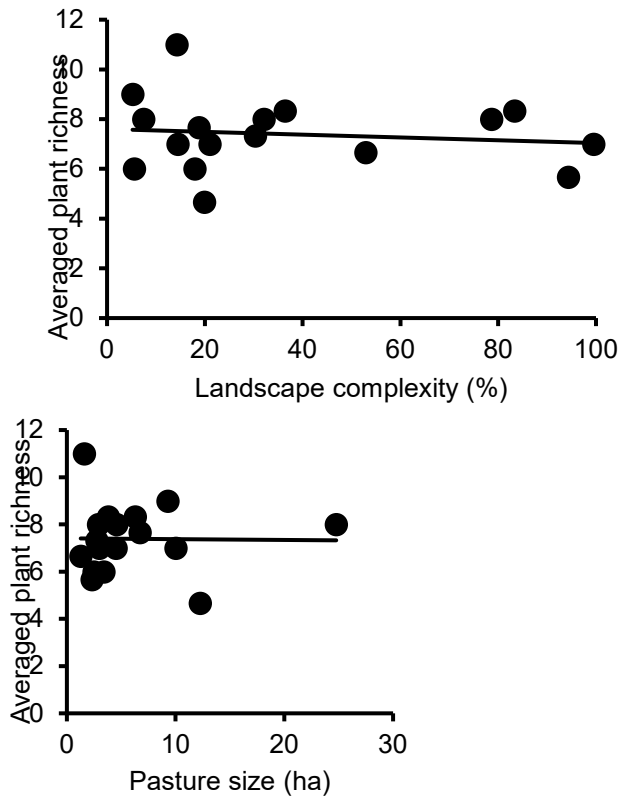
Figure 3. Linear regression of averaged plant richness with landscape complexity (left) and with pasture size (right).

3.2 Floral resources

Floral cover changed significantly across the sampling period (P < 0.001, dF=48), but differences were only significantly different between the two first sampling times and early August (P < 0.001 for both, Figure 4, left). Floral cover ranged from 0.19 ± 0.02 m²/m² (early July) to 0.02 ± 0.005 m²/m² (early August), with an average floral cover of 0.13 m²/m². However, there were no relationships between average floral cover and the percentage of landscape complexity (P = 0.789, dF = 15, Figure 4, right).

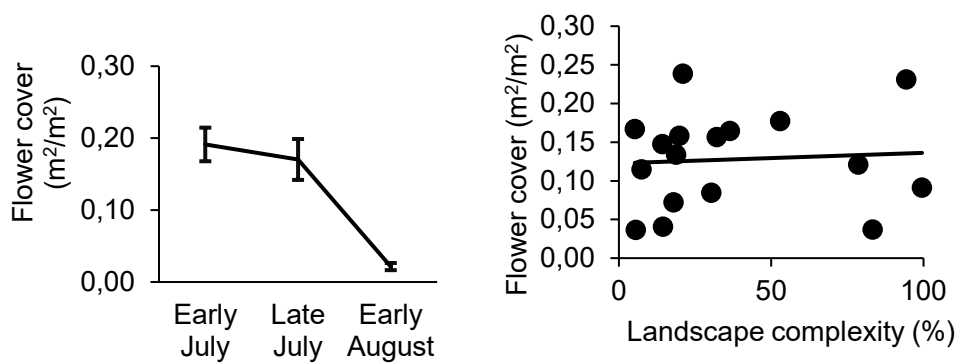*Figure 4. Changes in floral cover across the sampling period (left) and relationships between floral cover and percentage of landscape complexity (right). Error bars indicate standard error.*

3.3 Pollinator communities

Pollinator communities were dominated by species belonging to the genus *Bombus* (Figure 5). Overall, *B. lucorum* group was the most abundant species (24%), followed by *B. lapidarius* (20%), *B. pascuorum* (11%), *A. mellifera* (10%) and *B. ruderarius* (9%). The abundance of some of the pollinator species changed across the sampling period. For example, *B. lucorum* group and *B. pascuorum* were more dominant in early August that in July, while some species only were observed in early August (*B. humilis*) or declined from July to August (*A. mellifera*, *B. ruderarius*). Interestingly, during early August some pollinator species increased in abundance compared to early July (*B. humilis*, *B. jonellus*, *B. pratorum*) .

Number of pollinators
Total

- ■ B.lucorum.group
- ■ B.lapidarius
- ■ B.ruderarius
- ■ B.pascuorum
- □ A.mellifera
- □ B.hortorum
- ■ B.subterraneus
- ■ B.muscorum
- □ B.pratorum
- □ B.jonellus
- □ B.humilis
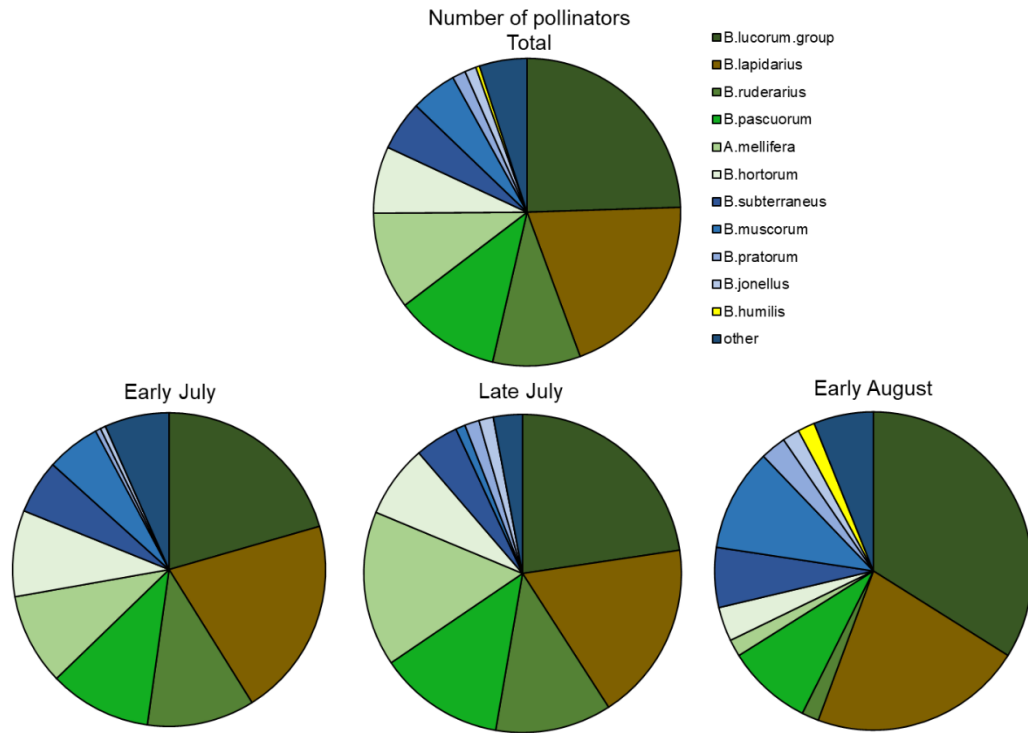- ■ other

Early July

Late July

Early August

Figure 5. Averaged pollinator communities (top) and pollinator communities observed in early July (bottom left), late July (bottom center) and early August (bottom right).

Pollinator richness did not change significantly throughout the sampling period (P = 0.720, dF= 48), paralleling the trends in plant richness. Despite a negative trend, there was no relationship between averaged pollinator richness and landscape complexity (P = 0.341, dF= 15, Figure 6, left). Despite an increased trend, there was no correlation between averaged pollinator richness and plant richness (P = 0.520, dF= 15, figure 6, right).
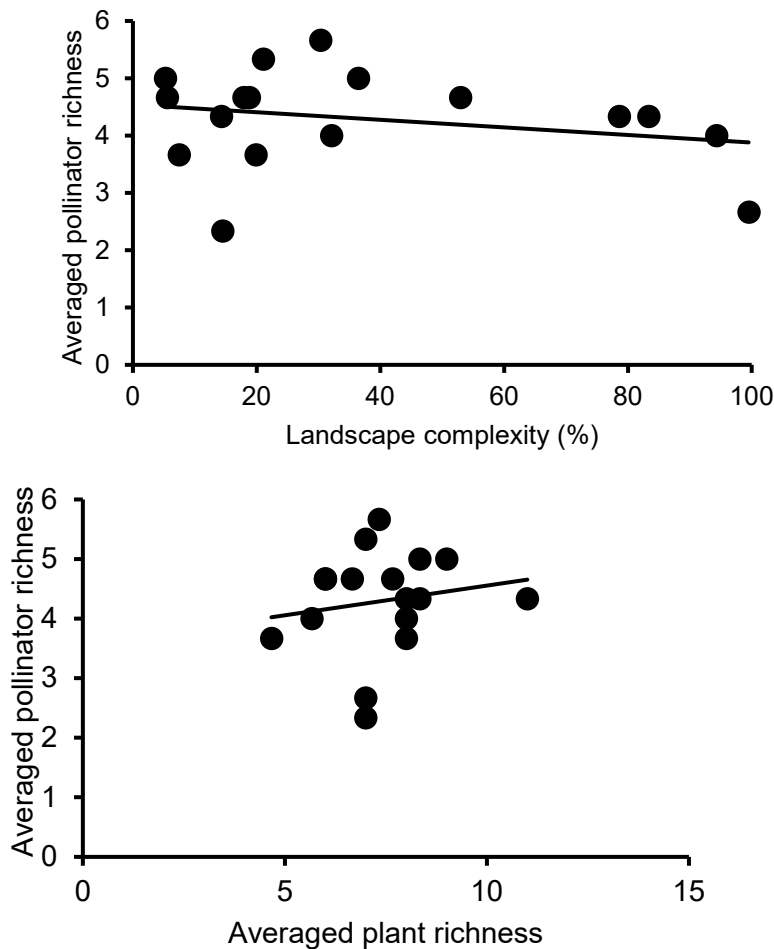
Figure 6. Relationships between pollinator richness and landscape complexity (top), and between pollinator richness and plant richness (bottom).

3.4 Patterns of pollinator traits and sexual reproduction across a landscape complexity gradient

There were no relationships between the abundance of bumblebees with long tongues and the landscape complexity ($P = 0.942$, dF= 15, Figure 7). There were, however, overall higher abundances of bumblebees with short tongues than with long tongues ($P < 0.001$, dF= 15). There was also a clear decrease in the percentage of female bumblebees during early August ($P = 0.002$, dF= 48, Figure 8, left). There was a positive trend between the abundance of female bumblebees and the percentage of landscape complexity, although this was marginally significant ($P= 0.086$, dF= 15, Figure 8, right). When analyzed separately by sampling period, these trend was observed for late July and early august, although again these relationships were not significant ($P>0.05$).
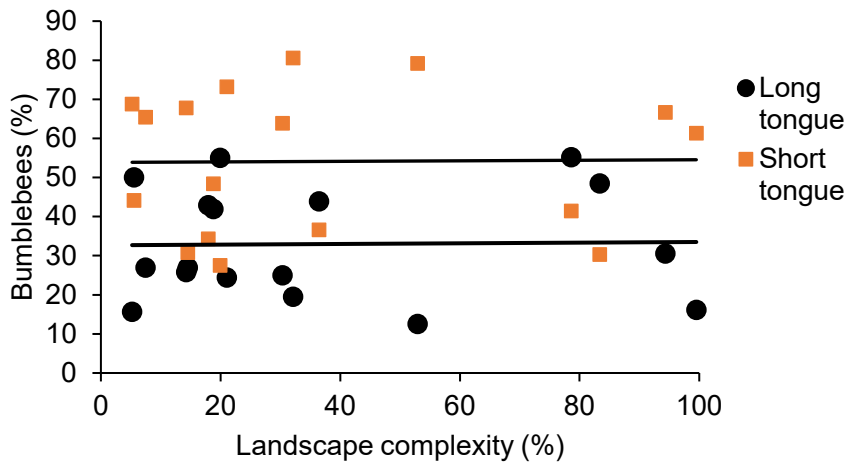
Figure 7. Relationships between the relative abundance of bumblebees with long and short tongues and the landscape complexity.
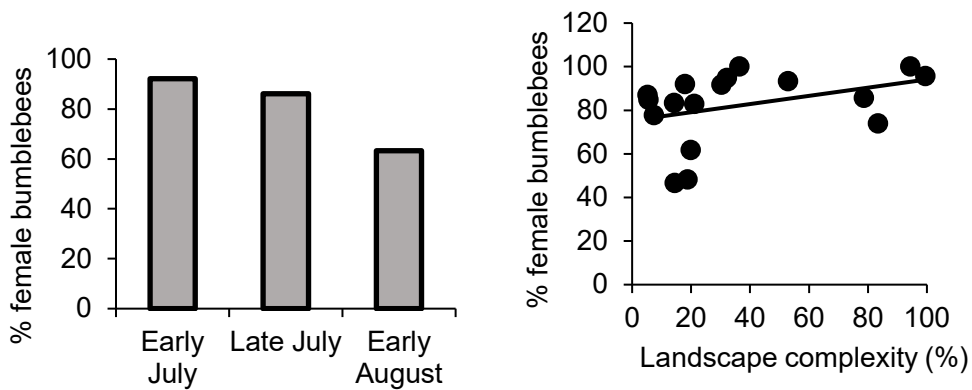
Figure 8. Changes in relative abundances of female bumblebees across the sampling period (left) and relationships between the percentage of female bumblebees and the landscape complexity (right).

3.5 Red-listed pollinators

One species in the dataset, *Bombus muscorum*, is included in the European Red List of Bees, and classified as Vulnerable. This species was observed at all three sampling times, but particularly in early August, with twelve individuals observed at the 17 sites. Interestingly, there was a strong positive correlation between the relative abundance of this species and the percentage of landscape complexity surrounding the site (P = 0.006, dF= 15, Figure 9).
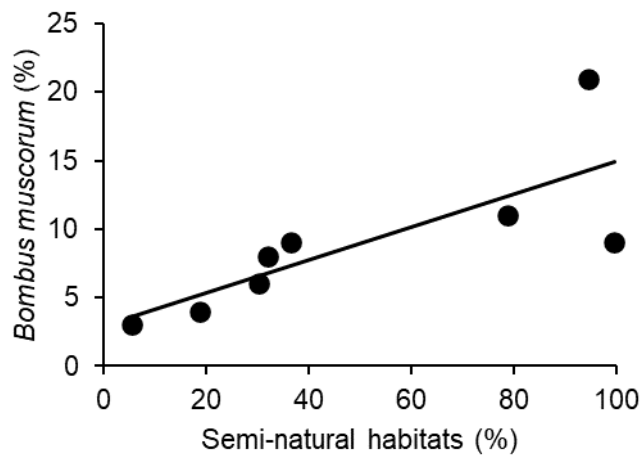
Figure 9. Percentage of Bombus muscorum by landscape complexity.

4. Discussion

In this study, I investigated how landscape complexity affects pollinator and plant communities and their interactions, by assessing both communities in a gradient of sites with distinct landscape complexities during three sampling times. I observed important plant and floral changes across the sampling period, especially in late summer. Contrary to what I hypothesized, there were no effects of landscape complexity on plant and pollinator richness nor on the abundance of species with long tongues. However, I observed interesting trends of both higher female abundance and relative abundance of a red-listed species, *B. muscourum*, at sites in more complex landscapes, according to my hypothesis.

No relationship between landscape complexity and pollinator richness

I did not observe a relationship between pollinator diversity and the landscape complexity. It is possible that pollinator populations in the sites with low landscape complexity were supported by habitats located at different spatial scales than the one measured here. It is possible that other landscape elements such as hedgerows contribute to supporting bumblebee populations in landscapes with very low complexity (Garratt et al., 2017), for example by providing valuable floral resources (Öckinger & Smith et al., 2007). It is not very likely that mass flowering crops in fields surrounding the study sites affected pollinator abundance or richness at the sites, since the most common of these crops *(Brassica napus)* would not be flowering during the sampling period.

Sustained floral resources with time support distinct pollinator communities

Despite a decrease in floral abundance during early August which paralleled decreases in pollinator-plant interactions, it is worth to highlight that still during this period there were a few pollinator species that increased in abundance. These were the three least common *Bombus* species. This highlights the importance of late-flowering crops or vegetation to support pollinator communities (Persson & Smith, 2013, Rundlöf et al., 2014). Thus, a diversified plant community in these land patches may support pollinators by ensuring floral cover sustained over time.

Landscape complexity does not influence tongue traits in bumblebee populations

Surprisingly, there were no relationships between the percentage of bumblebees with long tongues and landscape complexity. This is contrary to my hypothesis but

match the previous results of lack of plant richness changes across a landscape complexity gradient. In this study, I expected a richer plant community as landscape complexity increases, and that this would match with increasing abundances of pollinators with long tongues. Instead, a less complex landscape would simplify plant communities, which could promote pollinators that feed on many floral species, such as generalist pollinators with short tongues (Miller-Struttmann et al., 2015). The floral resources produced in these landscapes could be of a type that can feed both pollinators with long and short tongues, such as the long spured *T. repens*. Whether other landscape elements provide these resources is unknown, but even in the studied patches this may be the case.

Indicators of population collapse early August relate to landscape complexity

Despite the lack of effects of landscape complexity on tongue length, I observed indicators of population collapse in bumblebees in early August. During this time, the percentage of females decreased from 83% to 63%. A decrease in the relative abundance of females (i.e. increases in relative abundances of males) have been shown to indicate collapse of bumblebee populations (Zayed et al., 2004). Thus, my findings indicate that colony collapse potentially starts in early August in some populations. In addition, I observed a tendency of higher relative abundances of males with lower landscape complexity, suggesting that pollinators inhabiting simpler landscapes might be more affected by declining food resources or other stressors, despite harboring similar plant and pollinator diversities. As would be expected, the increase in the relative abundance of males coincides with the decreased floral availability observed during early August, highlighting again the importance of late flowering plants to sustain pollinator colonies over time. Despite the potential of mass flowering crops in providing massive amounts of food to pollinators, boosting their populations as previously observed (Westphal et al., 2003), the lack of reliable food sources sustained over time may induce these to a fast collapse, potentially affecting their sexual reproduction (Westphal et al., 2009). Thus, these results have implications for how landscape complexity affect population stability over time.

5. Conclusions

In this study I investigated relationships between landscape complexity and several population indicators for pollinators. My results show that there are no relationships between landscape complexity and pollinator attributes such as richness, percentage of female bumblebees or tongue length. However, I did find a relationship between landscape complexity and abundance of *Bombus muscourum*, a bumblebee species with conservational interest. New studies should extend the sampling time towards autumn, to see if we can confirm the trend of earlier colony collapse of bumblebees in simpler landscapes.

References

Aguilera G, Roslin T, Miller K, Tamburini G, Birkhofer K, Caballero-Lopez B, Lindström SA-M, Öckinger E, Rundlöf M, Rusch A, et al. (2020). Crop diversity benefits carabid and pollinator communities in landscapes with semi-natural habitats. *Journal of Applied Ecology* 57: 2170–2179.

Bennett AJ, Bending GD, Chandler D, Hilton S, Mills P. (2012). Meeting the demand for crop production: the challenge of yield decline in crops grown in short rotations. *Biological Reviews* 87: 52–71.

Benton, T. (2006). *Bumblebees*. First edition, HarperCollins Publishers.

Bommarco R, Kleijn D, Potts SG. (2013). Ecological intensification: harnessing ecosystem services for food security. *Trends in Ecology & Evolution* 28: 230–238.

Connelly H, Poveda K, Loeb G. (2015). Landscape simplification decreases wild bee pollination services to strawberry. *Agriculture, Ecosystems & Environment* 211: 51–56.

Dainese M, Martin EA, Aizen MA, Albrecht M, Bartomeus I, Bommarco R, Carvalheiro LG, Chaplin-Kramer R, Gagic V, Garibaldi LA, et al. (2019). A global synthesis reveals biodiversity-mediated benefits for crop production. *Science Advances 5*: eaax0121.

Diekötter T, Peter F, Jauker B, Wolters V, Jauker F. (2014). Mass-flowering crops increase richness of cavity-nesting bees and wasps in modern agro-ecosystems. *GCB Bioenergy* 6: 219–226.

Dupont YL, Padrón B, Olesen JM, Petanidou T. (2009). Spatio-temporal variation in the structure of pollination networks. *Oikos* 118: 1261–1269.

Le Féon V, Schermann-Legionnet A, Delettre Y, Aviron S, Billeter R, Bugter R, Hendrickx F, Burel F. (2010). Intensification of agriculture, landscape composition and wild bee communities: A large scale study in four European countries. *Agriculture, Ecosystems & Environment* 137: 143–150.

Ferreira PA, Boscolo D, Felipe Viana B. (2013). What do we know about the effects of landscape changes on plant-pollinator interaction networks? *Ecological Indicators* 31: 35–40.

Garratt MPD, Senapathi D, Coston DJ, Mortimer SR, Potts SG. (2017). The benefits of hedgerows for pollinators and natural enemies depends on hedge quality and landscape context. *Agriculture, Ecosystems & Environment* 247: 363–370.

Holland JM, Douma JC, Crowley L, James L, Kor L, Stevenson DRW, Smith BM. (2017). Semi-natural habitats support biological control, pollination and soil conservation in Europe. A review. *Agronomy for Sustainable Development* 2017 37:4 37: 1–23.

Holzschuh A, Dainese M, González-Varo JP, Mudri-Stojnić S, Riedinger V, Rundlöf M, Scheper J, Wickens JB, Wickens VJ, Bommarco R, et al. (2016). Mass-flowering crops dilute pollinator abundance in agricultural landscapes across Europe. *Ecology Letters* 19: 1228–1236.

Lindström SAM, Herbertsson L, Rundlöf M, Smith HG, Bommarco R. (2015). Large-scale pollination experiment demonstrates the importance of insect pollination in winter oilseed rape. *Oecologia* 2015 180:3 180: 759–769.

Miller-Struttmann NE, Geib JC, Franklin JD, Kevan PG, Holdo RM, Ebert-May D, Lynn AM, Kettenbach JA, Hedrick E, Galen C. (2015). Functional mismatch in a bumble bee pollination mutualism under climate change. *Science* 349: 1541–1544.

Mossberg, B. & Cederberg, B. (2012). Humlor i Sverige. Sjätte upplagan, Bonnier fakta.

Persson AS, Smith HG. (2013). Seasonal persistence of bumblebee populations is affected by landscape context.   165: 201–209.

Potts SG. (2010). Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution* 25: 345–353.

Potts SG, Imperatriz-Fonseca V, Ngo HT, Aizen MA, Biesmeijer JC, Breeze TD, Dicks L V., Garibaldi LA, Hill R, Settele J, et al. (2016). Safeguarding pollinators and their values to human well-being. *Nature* 2016 540:7632 540: 220–229.

Rundlöf M, Persson AS, Smith HG, Bommarco R. (2014). Late-season mass-flowering red clover increases bumble bee queen and male densities. *Biological Conservation* 172: 138–145.

Steffan-Dewenter I, Westphal C. (2008). The interplay of pollinator diversity, pollination services and landscape change. *Journal of Applied Ecology* 45: 737–741.

Tamburini G, Bommarco R, Wanger TC, Kremen C, Heijden MGA van der, Liebman M, Hallin S. (2020). Agricultural diversification promotes multiple ecosystem services without compromising yield. *Science* Advances 6: eaba1715.

Westphal C, Steffan-Dewenter I, Tscharntke T. (2003). Mass flowering crops enhance pollinator densities at a landscape scale. *Ecology Letters* 6: 961–965.

Westphal C, Steffan-Dewenter I, Tscharntke T. (2009). Mass flowering oilseed rape improves early colony growth but not sexual reproduction of bumblebees. *Journal of Applied Ecology* 46: 187–193.

Whittall JB, Hodges SA. (2007). Pollinator shifts drive increasingly long nectar spurs in columbine flowers. *Nature* 2007 447:7145 447: 706–709.

Zayed A, Roubik DW, Packer L. (2004). Use of diploid male frequency data as an indicator of pollinator decline. *Proceedings of the Royal Society of London.* Series B: Biological Sciences 271.

Öckinger E, Hammarstedt O, Nilsson SG, Smith HG. (2006). The relationship between local extinctions of grassland butterflies and increased soil nitrogen levels. *Biological Conservation* 128: 564–573.

Öckinger E, Smith HG. (2007). Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. *Journal of Applied Ecology* 44: 50–59.

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