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Plant-pollinator communities responsive to local and landscape level factors in grassland restorations.

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PLANT-POLLINATOR COMMUNITIES RESPONSIVE TO LOCAL AND LANDSCAPE LEVEL FACTORS IN GRASSLAND RESTORATIONS

By

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A Dissertation Approved on

November 12th, 2021

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DEDICATION

I dedicate this dissertation to Ashley.

For believing in me more than myself at times.

For your soft kindness and your sharp intelligence.

For your adventurous and excitable soul and your timeless beauty.

Without you, none of this work would have been possible.

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ABSTRACT

PLANT-POLLINATOR COMMUNITIES RESPONSIVE TO LOCAL AND LANDSCAPE LEVEL FACTORS IN GRASSLAND RESTORATIONS

Aaron N. Sexton

November 12, 2021

As humans continue to drive shifts in climate regimes and degrade ecosystems via greenhouse gas emissions and natural habitat destruction, other species are being pushed to the brink of extinction. In hopes to offset some of this degradation, habitat restoration attempts to restore ecosystem function to an improved state resembling intact, remnant values. This is an extremely difficult, but important, undertaking with many factors to consider at multiple spatial and temporal scales. The restoration and conservation of pollinator communities has garnered heightened attention because of the valuable ecosystem services they provide. Yet relatively little is known about how to best support these communities and more specifically, how ecological restoration influences them.

This dissertation investigates the local and landscape level factors of grassland restorations that influence plant-pollinator communities. Using a meta-analysis approach, I found that grassland restorations globally do a good job of improving pollinator communities. Importantly, I found that restorations are able to restore pollinator abundance and richness values to a near full recovery compared to those found in remnant grasslands. I followed this review with a field study investigating the influence that surrounding land use and local plant communities within restorations have on wild bee communities. I found that bees living in restorations with a greater proportion of native flowers laid more eggs on average, indicating a benefit at the local scale. At the landscape level, I found that bees in grassland restorations in areas with greater urban cover exhibited higher rates of offspring survival. Together, this meant the total number of bees surviving to adulthood in each site was greatest in urban grasslands with high proportions of native floral resources. My final study aimed to understand the local and landscape factors that influence floral phenology in grassland restorations, as plant-pollinator mismatches in phenology can cause reductions in pollinator diversity and abundance. Here I found earlier floral initiation and peak flowering date in urban grasslands compared to rural grasslands, setting up a potential phenological-mismatch with their pollinator communities. However, I also found that population-level floral duration was significantly extended in sites with higher species richness values. When broken down by season, I found summer species to benefit from urbanization, significantly extending their floral duration in urban sites, while spring and fall species contracted theirs. Additionally, spring species shifted their peak dates earlier in urban sites. Altogether these shifts led to what I have coined an “Urban Summer Spillage” effect whereby summer flowering species are spilling into the temporal niches of spring and fall species, potentially outcompeting them in urban areas where temperatures are consistently warmer.

These studies highlight the importance of grassland restorations for our native pollinator communities. I found that not only do grassland restorations support pollinator communities, but that increasing the floral quality of these restorations can in turn increase pollinator fitness, even in urban landscapes.

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INTRODUCTION

The rapid loss of biodiversity is one of the greatest threats to humankind in the 21st century. A recent UN Global Assessment Report on Biodiversity and Ecosystem Services estimated the abundances of native terrestrial species to have declined by at least 20% since their 1900 values (IPBES 2019). Among the most pronounced and concerning declines are those among native pollinators (Potts et al. 2010). In North America, this loss of native pollinators including butterflies, bumblebees (*Bombus sp*.), and thousands of solitary bee species is particularly concerning not only from an ecological perspective but also an economic and agricultural perspective as well (Kearns et al. 1998, Archer et al. 2014, Goulson et al. 2015). These pollinator declines can be attributed to several factors, including intensifying agricultural practices (increased pesticide usage, reduced diet diversity), introduction of invasive species (in particular the European Honeybee *Apis mellifera*), and habitat loss due to urbanization (Allen-Wardell et al. 1998, Whitehorn et al. 2012, Kopit and Pitts-Singer 2018). As natural areas are converted to human-dominated landscapes, pollinators face a perilous future. As such, the UN and other global bodies have deemed this decade, 2020-2030, the ‘International Decade of Habitat Restoration’, hoping to push local and national governmental bodies to expand and improve efforts to restore native ecosystems (Aronson et al. 2020).

Such restoration efforts are particularly critical in urban areas, which are rapidly expanding at a rate even faster than urban populations are rising. Current predictions estimate that total urban land cover will triple from 2000 to 2030 (Seto et al. 2012). The effects of urban expansion are manifold on biodiversity, directly via habitat loss and fragmentation, but also indirectly from factors such as altered nutrient cycling, increased pollution, increased surface temperatures, a reduction in native food resources, and changes in nesting substrates (McKinney 2002, Grimm et al. 2008, Faeth et al. 2011). As a result, a consistent suite of species tend to decrease in urban areas including amphibians, native trees and wildflowers, and birds (McKinney 2006). Pollinators, on the other hand, have highly nuanced responses to urbanization. Several recent studies have documented the impacts of urbanization on bee communities to be highly species-specific, dependent on life history traits and nesting substrate (Banaszak-Cibicka and Zmihorski 2012, Burdine and McCluney 2019, McCune et al. 2020). For example, Burdine and McCluney (2019) found bee community composition to be strongly associated with urbanization, with several species favoring rural areas, and others favoring urban areas. Additionally, Fitch et al. (2019) found that urbanization decreased solitary ground-nesting bee abundances but increased the abundance of solitary cavity-nesting bees. In fact, multiple studies across several systems have found solitary cavity-nesting bees to increase in urban areas (Cane et al. 2006; Banaszak-Cibicka and Zmihorski 2012; MacIvor and Packer 2016; McCune et al. 2020).

Improving our understanding of plant-pollinator responses to urbanization will allow us to build more effective habitat restorations in urban areas. While grassland restorations are often initiated as large-scale efforts in post-agricultural land, small-scale urban grassland restorations associated with small city parks or private landowners are becoming increasingly common (Yu et al. 2018, Dylewski et al. 2019). These efforts may serve as an extremely valuable tool for pollinator conservation yet receive an understated amount of research attention (Klaus 2013). Additionally, conventional ecological restoration research focuses heavily on the plant communities being restored, and not as much on the higher trophic levels such as pollinators. This dissertation sets out to identify the roles that grassland restorations play in supporting pollinator communities in and around urban areas.

STUDY SYSTEM

This dissertation consists of a quantitative literature review, or meta-analysis, (Ch. 2) and two field studies (Ch. 3 and 4) carried out in Louisville, KY (38.253° N, 85.759° W). The meta-analysis was conducted to understand how efficacious grassland restorations are in improving and conserving pollinator communities globally. The two field studies were designed to identify the local and landscape level factors that influence pollinators, and their floral resources. These studies were conducted in 19 grassland restoration in and around Louisville, along an urbanization gradient. Ch. 3 focuses primarily on the pollinator communities, chiefly wild bee demographic patterns, and Ch. 4 focuses on floral phenologies across these restoration sites.

ORGANIZATION OF DISSERTATION

In this dissertation I ask how local and landscape characteristics of grassland restorations influence plant and pollinator communities, specifically those in urban areas. I use a combination of meta-analysis and local field studies to answer these questions.

In chapter two of this dissertation, I examine the role restorations have played globally in restoring pollinator communities in previously degraded grasslands. I compiled data from dozens of publications across North America, Europe, and Asia by collecting data from supplemental and in-text tables and reaching out to authors directly. From each study I was able to standardize two key response variables: pollinator abundance and richness in grassland restorations compared to degraded grasslands, and in some cases, remnant grasslands. A central finding from these analyses was that grassland restorations significantly increase pollinator abundance and richness compared to degraded grasslands. Additionally, pollinator abundance and richness reached a near full recovery to values in remnant grasslands. Sub-analyses found that factors such as pollinator taxa, restoration age, and mode of land degradation all influenced pollinator recovery. Among the most consistent results were that older restorations (>10 years) showed the largest improvements in pollinator communities. These results indicate that grassland restoration can and should be used as a mode of supporting wild pollinator communities.

In chapter three I examine how urbanization and restoration quality interact to influence wild bee communities. Specifically, I surveyed solitary cavity-nesting bee nests in grassland restorations in and around Louisville, KY. I found that these bees benefited from urbanization, with higher larval survivability in urban grasslands compared to rural grasslands, possibly due to enemy release as their parasites and parasitoids decreased in a more fragmented urban landscape. Additionally, fecundity was higher in grasslands with a greater proportion of native forbs. Together, this meant the total number of bees surviving to adulthood in each site was greatest in urban grasslands with high proportions of native floral resources.

The fourth chapter of my dissertation examined the impacts that urbanization and restoration quality have on floral phenology. Understanding how these factors shift floral phenologies is crucial for pollinator conservation so that we can identify any potential phenological-mismatches between pollinators and their plant hosts, as has been documented in other systems (Memmott et al. 2007, Schenk et al. 2018, Zettlemoyer et al. 2019, Lee et al. 2020). Here, I surveyed forb communities bi-weekly in the same grassland restorations that were surveyed in chapter three. I found that urbanization caused earlier floral initiation and flowering peak dates across the entire forb community. When species were broken up by season of flowering (spring, summer, fall) I found that in urban areas spring species were advancing the most, while summer flowering species were significantly extending their floral duration, and fall species were contracting theirs. Together this led to an “urban summer spillage” effect where summer species were spilling into the temporal range of spring and fall species in urban grasslands. This effect was potentially fueled by Louisville’s particularly strong urban heat island (Stone et al. 2016). However, we did see that floral duration of a majority of species, regardless of seasonality, was significantly extended in grasslands with higher species richness. This suggests that the effects of urbanization on floral phenology advancement could be offset by increasing floral richness in grassland restorations.

The fifth and final chapter summarizes the main conclusions of my dissertation and presents ongoing and future research directions examining how restoration quality and urbanization interact to influence the persistence and stability of plant-pollinator interactions and communities. Specifically, I describe avenues of research to better address the potential mechanisms at play influencing the results from my field studies.

CHAPTER II

GRASSLAND RESTORATIONS IMPROVE POLLINATOR COMMUNITIES: A META-ANALYSIS[1]

SUMMARY

Natural grasslands are being destroyed at an alarming pace, but land managers are actively working to restore these habitats. Many of these efforts focus on restoring plant diversity but often do not consider responses of higher trophic levels such as pollinators, which provide crucial ecosystems services. We conducted a meta-analysis of 25 large-scale studies to examine the effects of grassland restorations on pollinator communities. Specifically, we compared pollinator communities in restored, degraded and remnant grasslands to determine if restorations improve pollinators from a degraded state and if they fully restore them to remnant values. We found that grassland restorations significantly improved both pollinator abundance and richness as compared to degraded grasslands. Additionally, pollinator abundance and richness did not significantly differ from remnant sites, indicating a near full recovery. Sub-analyses found that factors such as pollinator taxa, restoration age, and mode of land degradation all influenced the magnitude of recovery. In particular, lepidopteran abundance increased more than bee abundance in these restorations. Older restorations (>10 years) showed the strongest

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[1] Sexton, A.N., Emery, S.M. Grassland restorations improve pollinator communities: a meta-analysis. Journal of Insect Conservation 24, 719–726 (2020). https://doi.org/10.1007/s10841-020-00247-x

improvements in pollinator communities. This research highlights the importance of grassland restorations in supporting not only plant diversity but also pollinators.

INTRODUCTION

Native prairie and grassland habitats provide a wide diversity of ecosystem services, including the support of pollinator communities due to their high forb richness and abundance (Kearns, Inouye and Waser 1998, Ghazoul 2006). However, native grasslands have suffered widespread habitat destruction, often via conversion to agriculture, and in some regions have been reduced to just 0.1% of their historical cover (Samson and Knopf 1994, Moranz et al. 2012). Aside from managed species such as the European honeybee (Apis mellifera), native and wild pollinators cannot flourish without a diverse floral community both spatially and temporally (Ogilvie and Forrest 2017), and so the loss of native grasslands has been detrimental to pollinators as it has homogenized the landscape and reduced foraging and nesting resources. This landscape homogenization has especially negative consequences on rare species, dispersal limited species, and specialists (Baur 2014, Borschig 2013). Grassland restorations may enhance pollinator communities along with other ecosystem services, though few studies have focused on pollinator responses to large-scale grassland restoration efforts.

Historically, most land managers have focused on enhancing plant community diversity when implementing grassland restorations (Young 2000). This “plant-first” focus hopes to impact other trophic levels via food web interactions. Cascading effects from the plant community to higher trophic levels have been widely documented (Longcore 2003, Nemec and Bragg 2008, Molano-Flores 2009, Kaiser-Bunbury et al.

2017). For example, in studies by Nemec and Bragg (2008) and Molano-Fores (2009), herbivorous insects responded positively to grassland restoration, showing increased levels of seed herbivory and higher diversity levels in restored prairies. However, while grassland restoration efforts typically improve plant communities, it is still unclear whether such restorations are as successful in restoring pollinator communities, in part due to an inability to clearly define pollinator community restoration goals. For example, pollinator abundance and richness are two, sometimes contrasting, aspects of pollinator community diversity. Habitat type and restoration efforts may increase abundance of a single pollinator species but have differing effects on overall pollinator richness (Brown 1984). Efforts to increase Danaus plexippus (Monarch butterfly) abundance through creation of "Monarch Waystations" are examples of how restoration efforts may target one species and not an entire community. Further, pollinators may have taxon-specific responses to restoration efforts due to differing life histories, dispersal abilities, and nesting habits (Öckinger et al. 2018). For example, bees tend to respond to both local factors (e.g., habitat quality) and landscape factors (e.g., urbanization) while lepidopteran species are often more responsive to local factors (Sjodin, Bengtsson and Ekbom 2008, Munsch et al. 2019, Poniatowski et al. 2018, Williams et al. 2007, McCune et al. 2020, Carson et al. 2016, Renauld et al. 2016, Torne-Noguera et al. 2014). That being said, landscape level modifications will likely impact any species, especially at the level of the metapopulation and so it should not be discounted.

An additional consideration is the difficulty in defining restoration targets for pollinator communities. For plants, restoration targets are often defined based on historical records (Meine 1999). However, historical records are often lacking for pollinator communities, and so restoration targets are based on pollinator diversity in remnant grasslands (Bartomeus, 2019). Similar to plant community responses, a restoration may improve pollinator diversity, but not meet restoration targets when compared to remnant habitats. Finally, it is possible that degraded habitats may actually be better for pollinator communities, especially if they contain invasive plant species with abundant floral resources. For example, Emery and Doran (2013) found that an invasive forb, baby's breath (Gypsophila paniculata), significantly increased pollinator abundances in a sand dune grassland, and restoration efforts had little effect on pollinator communities.

Several technical aspects of grassland restoration efforts may further complicate responses of pollinator communities. Factors such as type of land degradation, restoration methods, or age of restoration can influence pollinator responses. For example, land degraded by an invasive plant species or animal grazing may have higher pollinator abundance and richness than one that was used for row-crop agriculture, as many solitary bees nest in the ground and are negatively impacted by tilling (Williams et al. 2010). Similarly, grassland restorations that involve multiple methods such as tilling or burning may negatively affect pollinators by killing larvae or adults. Finally, as with plant communities, it may take years or even decades for pollinators to colonize restored grassland patches and reach target diversity goals (Emery and Rudgers 2010).

We conducted a meta-analysis to assess the overall impact of grassland restorations on pollinator communities. Specifically, we asked:

1) Do grassland restorations improve pollinator communities compared to degraded sites?

2) Do these restorations restore the pollinator communities to remnant conditions?

We followed-up with sub-analyses to address specific aspects of pollinator community responses, namely: Do pollinator abundance and richness show differences in response to restoration efforts? Do pollinator taxa differ in their responses to restoration? Does the type of initial land degradation influence pollinator community responses? Do methods associated with restoration negatively affect pollinators? and Does length of time since restoration influence pollinator responses? We focused only on large-scale restoration efforts (>1 ha), as most pollinators are capable of relatively long-distance dispersal (Hill et al. 2011, Osborne et al. 1999). Additionally, large-scale restorations better reflect goals for land managers.

We hypothesized that pollinator communities would improve in grassland restorations but would fall short of remnant conditions, similar to the responses of many plant communities (Delaney, Jokela and Debinski 2015, Copeland et al. 2018). Additionally, we hypothesized that abundance would be more readily improved than richness, and that these responses would differ among taxa based on differences in floral resource preferences and dispersal abilities. We hypothesized that restorations of grasslands degraded by invasive species would improve pollinator communities more than those degraded by agriculture. We also hypothesized that restorations using multiple restoration methods would harm pollinators, by inadvertently killing off larval or adult populations with practices such as fire or tilling. Finally, we expected older restorations to have increased pollinator diversity compared to younger restorations.

MATERIALS AND METHODS

Literature search

To identify relevant studies, we conducted a search on Web of Science on April 12, 2019 using the following key terms “prairie restor* AND (pollinat* abundance OR pollinat* richness OR pollinat* diversity OR bee abundance OR butterfly abundance OR moth abundance)”, “savannah restor* AND pollinat*”, “prairie restor* AND bird pollinat*”, “meadow restor* AND pollinat*”, “grassland restor* and pollinat*. We also conducted haphazard searches in Google Scholar with similar keywords. In addition, we searched the reference lists of the papers selected to include studies not found by database searches. These searches yielded 416 papers.

Following these searches, we dropped studies that did not fit the scope of this meta-analysis. Studies that focused on land remediation of coal mines or quarries were not included, since land remediation practices and goals substantially differ from grassland restorations. We did not include small-scale studies that took place within a larger agricultural or urban context, such as wildflower strips or pollinator gardens. Studies that focused on floral resources within the plant community and did not measure pollinator responses directly were not included. We also dropped studies using small-scale experiments (plots only a few meters in size) as pollinator responses are only expected to occur at larger spatial scales. For all papers we identified the means and standard deviations or standard errors of the treatments. When these were not reported, we contacted the authors for this data. These restrictions resulted in 25 studies we could use in our meta-analysis (listed in Supplementary material S1).

Effect size calculations and data analyses

From the 25 studies, a total of 66 data points were obtained for analyses. To answer our two overarching questions, data points were first separated out into two large groups: 1) those that compared restorations to degraded sites, and 2) those that compared restorations to intact remnant sites. Some studies did both of these comparisons in their paper and so both data points were used. We further separated data points out by what metric of pollinator diversity they assessed: abundance or species richness. When studies compared restorations of different ages or at several time points, we chose those that were oldest and had been carried out for the longest time, similar to the methodology of previous studies e.g. Fleeger et al. 2018, Copeland et al. 2018.

To answer our secondary questions, we divided study results into smaller groups as available. Taxon-specific responses were analyzed for bees and lepidopterans. Studies that measured bee responses as a whole did not separate out A. mellifera responses, so we were unable to evaluate these responses at finer taxonomic scales. Studies varied widely in exactly how grasslands were degraded, but most studies fit into one of two general categories: degradation by invasive species or degradation by agriculture. To evaluate effects of methods associated with restoration practices, we separated studies into two groups: those that implemented one method (e.g., reintroduction of grazing), and those that used multiple methods (e.g., grazing and burning). Finally, to assess the effect of restoration age (time since initiation of efforts), we categorized studies as young (< 10 years) or old (>10 years).

To measure effect sizes across studies in this meta-analysis, we calculated Hedge’s d (Wasserman 1988) for each relevant study comparison. Hedge’s d takes into account the study’s sample size, variance and mean of each treatment. Effect sizes (d) along with the variation (v) for each study were calculated to assess restoration treatment significance using the R package metafor (Viechtbauer 2010). To compare effect size means across the different groups, we used randomized effect models carried out in R (Version 3.6.0), again, in metafor (Viechtbauer 2010). If a model was significant ($p<0.05$), we deemed the restoration to be different from the compared site (degraded or remnant grasslands respectively).

RESULTS

Both pollinator richness and abundance responded positively to grassland restorations when compared to degraded sites (“Full” analyses, Fig. 1; abundance: d = 1.31, p = 0.015; richness: d = 0.894, p = 0.045 respectively). When restorations were compared to remnant grasslands, pollinator communities were not significantly different, indicating that restorations were effective at restoring pollinators to target conditions (Fig. 2; abundance: d = –0.366, p = 0.167, richness: d = –¬¬0.411, p = 0.253).

Taxon responses: When the data points were separated by taxa, lepidopteran abundance in restorations was significantly improved compared to degraded sites (Fig. 1; d = 1.120, p = 0.047), though richness was not (Fig. 1; d = 1.455, p = 0.07). For bees, neither abundance nor richness were improved from degraded sites (Fig. 1; d = 0.925, p = 0.301; d = 1.541, p = 0.082).

When restorations were compared to remnants, bee abundance and richness did not differ (Fig. 2; abundance: d = –0.811, p = 0.06; richness: d = –0.322, p = 0.194). Lepidopterans showed similar responses (Fig. 2; abundance: d = –0.176, p = 0.767; richness: d = –0.874, p = 0.326).

Restoration age: There was a difference in response between young and old restorations (Fig. 1). Pollinator richness in older restorations (>10yrs) showed significant improvements compared to degraded sites (d = 2.35, p = 0.002). However, younger restorations did not show improvements from degraded sites (abundance: d = 0.922, p = 0.345; richness: d = 1.81, p = 0.202).When comparing young and old restorations to remnant grasslands, both old (Fig. 2; abundance: d = –0.33, p = 0.533; richness: d = 0.09, p = 0.86) and young restorations (Fig. 2; abundance: d = –0.32, p = 0.572; richness: d = –1.03, p = 0.189) do not differ significantly from remnants.

Land degradation history: There were no significant differences in responses of pollinators to restoration of agricultural lands compared to lands with invasive species (Fig. 1, Fig. 2).

Restoration methods: We only had enough studies to look at these effects for lepidopterans (n = 5; Bee or other taxa studies n=0). Lepidopteran abundance was influenced by restoration method, where restorations that implemented more than one method had a significant increase in abundance (Fig. 3; d = 1.0722, p = 0.003). However, richness was not affected by the number of methods used (Fig. 3; d = 0.09, p = 0.815).

DISCUSSION

Our results show that grassland restorations substantially improve pollinator community diversity, though factors such as pollinator taxon, land degradation history, and restoration age can influence these outcomes. In fact, seven of the studies used in this meta-analysis saw pollinator communities (abundance/richness) more than double in the restoration sites when compared to degraded sites (Griffin et al. 2017, Maccherini et al. 2009, Rutgers-Kelly and Richards 2013, Alison et al. 2017, Lettow et al. 2018, Skorka, Settele and Woyciechowski 2007, Helbing et al. 2015). However, a few studies did not see any improvement from degraded sites. For example Emery and Doran (2013) removed an invasive forb from their grassland sites, which left floral resources much lower than in invaded sites.

Notably, grassland restoration efforts did not just improve pollinator communities when compared to degraded habitats, but actually restored communities to match those found in target remnant sites. However, the mean effect sizes from most studies were negative, indicating a general trend that pollinator communities still can fall short of restoration goals, possibility due to needing more time or lack of key plant species. Interestingly, it is possible for restoration efforts to actually result in pollinator communities that are more diverse and abundant than remnant sites. For example, Ries, Debinski and Wieland (2001) actually found increased lepidopteran abundance and richness values in restoration sites as compared to remnant sites in roadside tallgrass prairies. This may be due to depressed pollinator communities in isolated remnant prairies that are no longer interconnected at a regional scale.

Differences in pollinator taxa

Bees and lepidopterans represent the most important and common pollinator taxa in grasslands (Allen-Wardell et al. 1998, Archer et al. 2014). However, differences arise in how the two taxa respond to grassland restorations. For lepidopterans particularly, abundances rather than richness showed improvements in restorations. This may be because specific host plants of rarer lepidopteran species may not be included in a seed mix, or may be more difficult to support in restorations. Additionally, landscape factors may play a role, as butterfly specialists suffer the most from decreased habitat connectivity (Bruckmann, Krauss and Steffan-Dewenter 2010). Finally it is possible that land managers may give extra attention to the success of particular flagship species, which may increase overall abundance of the focus species while having marginal effects on species richness.

The lack of clear improvements in bee communities may be due to the fact that A. mellifera were lumped together with native bees in most of these studies. A. mellifera does not rely on native grasslands for habitat, and tends to be a dominant species when it is present. Several studies have shown that A. mellifera can have negative effects on the wild bee community (Walther-Hellwig et al. 2006, Herbertsson et al. 2016, Graystock, Goulson and Hughes 2014, Lindstrom et al. 2016). Even if restoration efforts improve habitat for native bees, the presence of A. mellifera may swamp out any benefits.

Additionally, many bee species, both solitary and social, are ground nesting (USDA, 2007). This nesting behavior may also drive the overall lack of response, as many restoration methods involve soil disturbances. However, single disturbance events are often beneficial as they can create open soil for ground dwelling species (Williams et al. 2010). This role of life history influencing where pollinators can nest and survive has already been documented in urban areas, where ground nesting bees are found in low numbers, but cavity nesters thrive (Fitch et al. 2019). As bees are the most important pollinators for most crop and wild species (Hanley et al. 2015, Allen-Wardell et al. 1998), more documentation and planning may be warranted when implementing grassland restorations.

Importance of time

The time subanalysis showed that it often takes 10 or more years for pollinator communities to be restored. This may be due to the fact that plant and soil communities often take several years to be fully restored. For example, soil nutrients or microbiota may be dramatically altered by agriculture or invasive species, and take decades to restore. McKee, Brye and Wood (2019) found that in a chronosequence of prairie restorations, almost all measures of soil health, including organic matter, bulk density, carbon, and nitrogen increased with time since restoration. Similarly, Scott and Morgan (2012) found the plant community in old fields took between 20–40 years to reach levels similar to those of uncultivated fields. During this time exotic species were slowly replaced with native cultivars and richness values were restored to remnant values. Additionally, it may take years for pollinators to disperse into a new restoration. For example, most Midwestern US prairie restorations are surrounded by agricultural land and therefore are habitat islands that can be difficult to recolonize, especially by those that are dispersal limited. (Samson and Knopf 1994). Öckinger et al. (2018) found that solitary bees were less likely to colonize a restoration than bumblebees and hoverflies and across all species, colonization was dependent on habitat connectivity.

Land degradation history

Degradation and land use history had minimal effects on the ability to restore pollinator communities. This is somewhat surprising as we expected agriculture to have particularly detrimental effects on pollinator communities due to regular tillage (Williams et al. 2010), and so be harder to restore. However, widespread usage of chemical herbicides to manage invasive plants could have strong deleterious non-target effects on pollinators (Motta, Raymann and Moran 2018, Balbuena et al. 2015), which may partially explain this lack of land use difference. Our findings are supported by at least one other study, which showed that agricultural history was not a good predictor of wild bees in pine savannah restorations (Odanaka et al. 2019).

Restoration methods

While we were only able to address this question for lepidopterans, we did find that restorations using multiple methods increased lepidopteran abundance, but not richness, compared to those that used only single restoration methods. We expected that multiple restoration methods might decrease pollinator diversity due to increased disturbance, which does not seem to be the case for lepidopterans. Instead, multiple methods may increase heterogeneity of habitat for pollinators (Glenn, Collins and Gibson 1992), increasing pollinator diversity. Only a handful of studies have addressed how management methods affect pollinator restoration though, and much more work is needed. Very little is known about how grazing, fire, tilling, and other restoration methods might interact to affect pollinator nesting and other behaviors. For example, Öckinger et al. (2018) found that pollinator richness was actually lower in restorations, possibly due to the reintroduction of grazers, which has been shown to have variable effects on pollinator communities (DeBano et al. 2016, Elwell, Griswold and Elle 2016, Hartnett, Hickman and Walter 1996). Several studies have shown that the net effects from grazers is highly dependent on the density, with low intensity grazing showing positive effects for pollinators (Sjodin et al. 2008, Albrecht et al. 2007).

Conclusions

Altogether, this meta-analysis shows that grassland restorations are important for pollinator conservation. These results are particularly relevant because they include large-scale studies that differ in land use history, location, and age but still show significant improvements in pollinator diversity and abundance. A clear difference arises between old and young restorations, indicating that practitioners should not expect a full recovery in the first few years.

If the funds are available, we cautiously suggest that employing two or more restoration methods may be useful, at least for lepidopterans. Restorations using more than one method saw significant increases in pollinator abundances compared to those using only one method. This finding is independent of the type of method used. For example, while we were not able to address whether fire was better than grazing or mowing, we can conclude that any combination of two methods was better than only one. However, there is a lack of research on how bees may respond to multiple restoration methods.

It is somewhat worrisome that bees showed weaker and more variable responses to restoration activities than lepidopterans. This may be because A. mellifera presence confounded responses of native bees in these studies. Native bees are vital pollinators for many grassland plant species and are often at the center of pollinator interaction networks (Hansen 2018; Forup and Memmott 2005). Historically, little focus has been given to nesting resources for native bees in restorations, but these should be considered as much as the floral resources if restorations are to support a robust native bee community.

Finally, while grassland restorations clearly improve pollinator communities, the d values for restorations compared to remnant grasslands were consistently negative, indicating that pollinator communities still fall short from being fully restored. In a simple vote count of results that compared restorations to remnant communities, about half of all studies found that pollinator communities were not fully restored. This highlights the need to not just restore degraded grasslands, but also protect remnant grasslands for pollinator conservation. Ideally, land managers could strive to connect the remaining fragmented remnant grasslands with corridors of restored grasslands or increase the size of remnant patches with adjacent restorations.

Figure Legends

Figure 1: Meta-analysis results for pollinator communities in grassland restorations compared to those in degraded grasslands. Effect size means and 95% CIs are depicted for each comparison. Abundance values are in blue circles and richness values are in red triangles. Values greater than zero (dashed line) indicate increases in pollinator measures compared to degraded sites. Sub-analysis groupings shown to the left (e.g. Bees) and samples sizes for each grouping are in parentheses. Statistically significant differences between restored and degraded sites at $p<0.05$ level indicated with an asterisk (*).

Figure 2: Meta-analysis results for pollinator communities in grassland restorations compared to those in remnant grasslands. Effect size means and 95% CIs are depicted for each comparison. Abundance values are in blue circles and richness values are in red triangles. Values less than zero (dashed line) indicate decreases in pollinator measures compared to remnant sites. Sub-analysis groupings shown to the left (e.g. Bees) and samples sizes for each grouping are in parentheses. No comparisons were statistically significant at the $p<0.05$ level.

Figure 3: Meta-analysis results for lepidopteran communities in grassland restorations using one or multiple restoration methods. Effect size means and 95% CIs are depicted for each comparison. Abundance values are in blue circles and richness values are in red triangles. Values greater than zero (dashed line) indicate increases in lepidopteran measures for restorations using multiple methods compared to single methods. Samples

sizes for each grouping are in parentheses. Statistically significant differences between single and multiple methodologies at p<0.01 level indicated with asterisks (**).

Figure 1

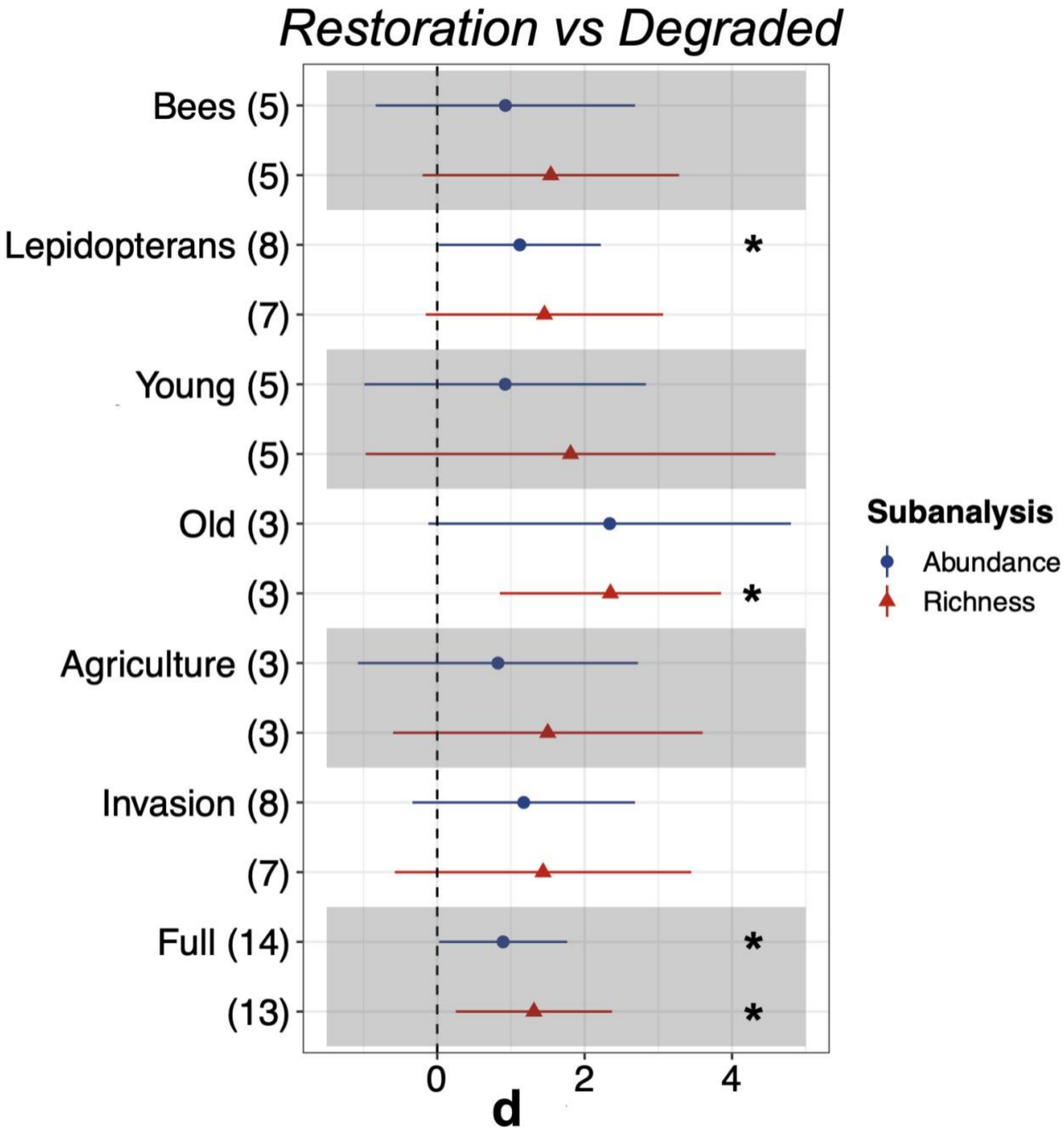
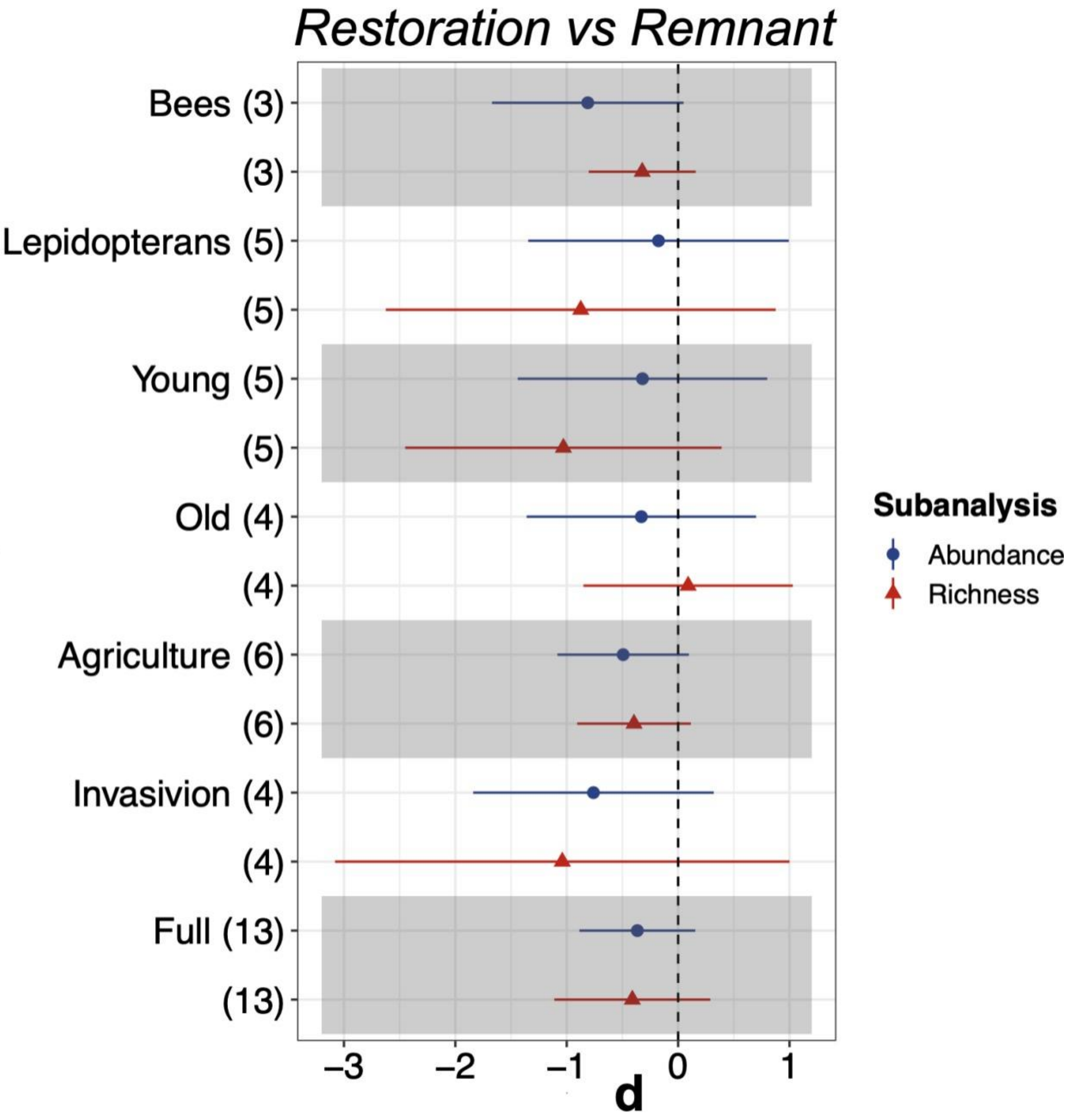


Figure 2


Restoration vs Remnant
Bees (3)
(3)
Lepidopterans (5)
(5)
Young (5)
(5)
Old (4)
(4)
Agriculture (6)
(6)
Invasivion (4)
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Full (13)
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−3
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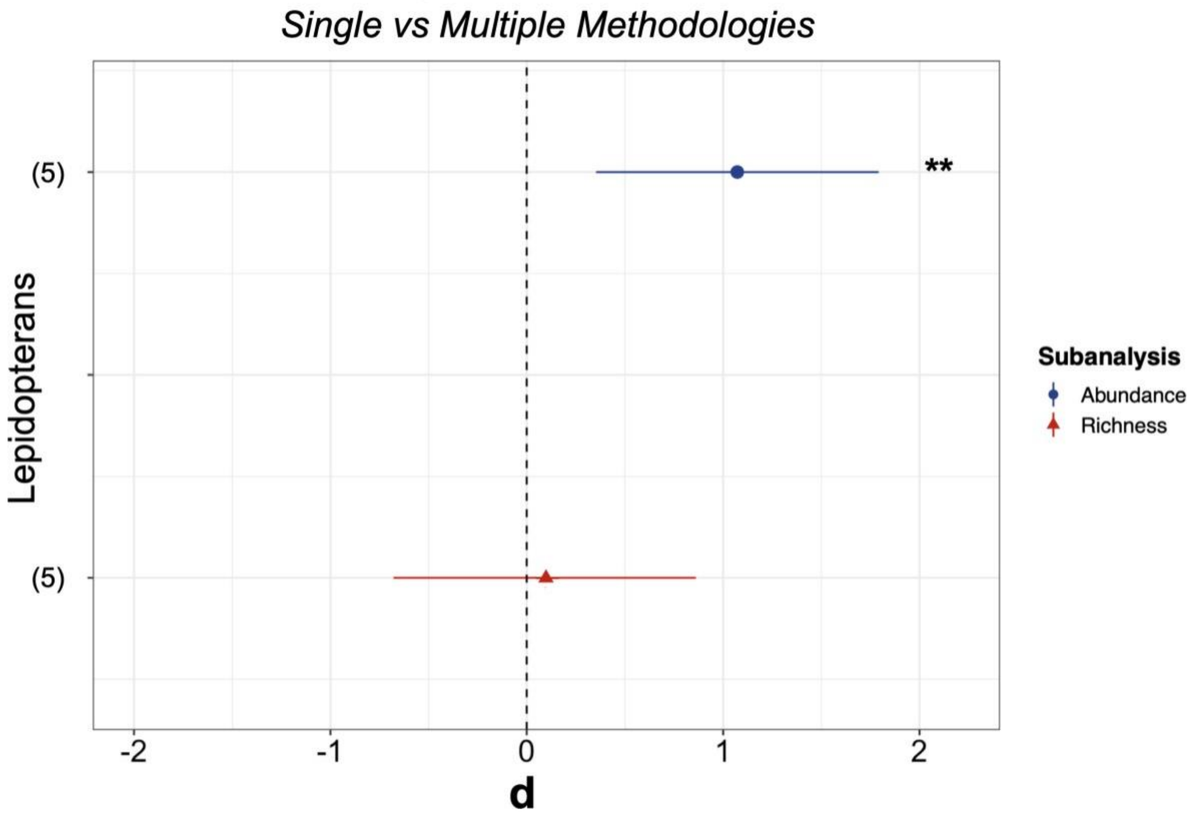
Subanalysis
Abundance
Richness

Figure 3


Single vs Multiple Methodologies
(5)
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Lepidopterans
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Subanalysis
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Richness
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CHAPTER III

REPRODUCTIVE PATTERNS OF SOLITARY CAVITY-NESTING BEES RESPONSIVE TO BOTH LOCAL AND LANDSCAPE FACTORS[1].

SUMMARY

Understanding how local and landscape-level factors influence species abundances and distributions is crucial for conservation and restoration efforts. Effects of urbanization are often negative at a landscape level, but some taxa such as solitary cavity-nesting bees perform better in urban areas, due to increases in food, nesting, and habitat resources at the local level. In this study, we ask how local and landscape factors across an urbanization gradient influence three demographic aspects of reproduction for solitary-nesting bees: fecundity, brood survivorship, and total adults to emerge in the spring. In 2018-2019, we surveyed solitary cavity-nesting bees active in 18 grassland restoration sites across the city of Louisville, Kentucky, USA using constructed nest boxes. We found that bee larvae had increased survivorship in urban areas as compared to surrounding rural areas, possibly due to decreased nest parasitism. Additionally, we found bee fecundity to increase with the proportion of native flowers in the surrounding floral community. These results indicate that urbanization can benefit some groups of solitary bees when paired with local grassland restoration efforts. This highlights the

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[1] Sexton, A.N., Benton, S., Browning, A.C. et al. Reproductive patterns of solitary cavity-nesting bees responsive to both local and landscape factors. Urban Ecosystems (2021). https://doi.org/10.1007/s11252-021-01116-4

importance of native plants and natural areas in the urban matrix to support pollinator communities.

INTRODUCTION

Urban areas are expanding at a rapid pace globally, and are projected to triple in size from 2000 to 2030 (United Nations 2014). This expansion can have dramatic impacts on ecosystems in several ways, including altered nutrient cycling, habitat loss and fragmentation, and subsequent species decline or extirpation (McKinney 2002, Grimm et al. 2008). While the effects of urbanization and associated land use shifts are often harmful for biodiversity, the impacts are species-specific and can be positive. Some taxa benefit from increases in novel food, nesting and habitat resources in the urban realm that can lead to increases in reproductive output and survivability (Kowarik, 2011). For example, many grassland specialists, such as the burrowing owl, *Athene cunicularia*, have higher population densities and improved demographic patterns in urban areas as compared to rural counterparts (Rebolo-Ifran et al. 2017). In the case of *A. cunicularia*, this improvement is a result of decreased predation in urban areas. Important functional groups such as pollinators show varying responses to urbanization; Persson et al. (2020) found bees to increase in urban areas, while hoverflies dramatically decreased along the same urbanization gradient. Gaining a better understanding of which species improve and which decline in urban areas is vitally important for the preservation of biodiversity.

Bees are an exceptionally important taxon that have garnered attention in the academic and public realms as recent research has brought their declines to attention

(Kearns et al. 1998, Scherer et al. 2020). Among the central drivers of this decline is land use change and habitat loss from a range of sources including agriculture and urbanization (Seto et al. 2012, Renauld et al. 2016). However, recent research has shown that urbanization does not always negatively impact bee species. Several studies have documented an increase of bees in urban areas (e.g., Wilson and Jamieson 2019), but the effects of urbanization on bees are dependent on several factors, such as species sociality, nesting substrate, and diet breadth, leading several studies to declare both “winners and losers” of urbanization. (Banaszak-Cibicka and Zmihorski 2012). For example, Wilson and Jamieson (2019) found that urbanization increased bee diversity, with an increase in solitary cavity-nesting bees, but a decrease in social bees. Burdine and McCluney (2019) found bee community composition to be strongly associated with urbanization, with several species favoring rural areas, and one species favoring urban areas. Similarly, McCune et al. (2020) found that urbanization had a negative impact on 34 wild bee species, but a positive impact on 12 species of wild bees. In many instances these species-specific responses are related to life history traits such as nesting habits. Fitch et al. (2019) found that urbanization decreased ground nesting bee abundance but increased the abundance of cavity-nesting bees. In fact, multiple studies across several systems have found solitary cavity-nesting bees to increase in urban areas (Cane et al. 2006, Banaszak-Cibicka and Zmihorski 2012, MacIvor and Packer 2016, McCune et al. 2020). Several hypotheses have been proposed to explain their increase in urban areas, including increased nesting substrate availability, shifts in floral resources, and enemy release. Urban areas have an increase in cavity-nesting substrates, including anthropogenic sources such as brick buildings and fence posts. There is also a likely decrease in ground nesting substrate as impervious surface increases in urban areas. This leads to a possible decrease in ground nesting bees, who are likely competitors with cavity-nesters for floral resources (Hudewenz and Klein 2013).

Additionally, the quantity and quality of local habitat patches often shifts in urban areas. Many ornamental urban trees serve as important pollen and nectar resources for bees (Somme et al. 2016). Urban parks can also provide islands of floral resources for bees and other pollinators (Dylewski et al. 2019, McFrederick and LeBuhn 2006, Baldock et al. 2019). Bee populations often increase with native floral richness, while nest establishment increases with floral abundance (Palladini and Maron 2014, Minckley et al. 1994, Williams and Kremen 2007, Zurbuchen et al. 2010a). Additionally, plant community composition, especially the presence of non-native plants, can influence bee populations. Palladini and Maron (2014) found that solitary cavity-nesting bee nest establishment rates were lower in sites dominated by non-native forbs, and Bruckman and Campbell (2014) found the introduction of a non-native forb decreased pollination visits from native wild bees and increased visits from non-native bees such as *Apis mellifera*, indicating changes to the bee community. Egerer et al. (2020) found that in urban gardens and nurseries, sites with a greater proportion of native plants have higher levels of wild bee abundances and richness. These findings suggest that management activities, such as maintaining natural areas with abundant native floral resources, may be able to counteract some effects of landscape-level land-use change (Lerman et al. 2018).

Finally, solitary cavity-nesting bees may benefit from enemy release in urban habitat patches. Solitary cavity-nesting bee nests have relatively high rates of brood parasitism, or cleptoparasitism. Recent studies have recorded brood parasitism rates as high as 56% (Spear et al. 2016). The impacts of this parasitism can vary, dependent on both local and landscape level factors such as land management, nest density, and plant community composition (Groulx and Forrest 2018, Palladini and Maron 2014). Albrecht et al. (2007a) found that rates of brood parasitism in solitary cavity-nesting bees were higher in natural restored meadows than in intensively managed ones, indicating landscape-level factors can influence brood parasitism. This may be in part due to increased habitat fragmentation and isolation, which make it more difficult to maintain higher trophic levels such as parasites (Lawton et al. 1994, Davies et al. 2000, Albrecht et al. 2007b). As such, in urban environments where habitat patches tend to be more isolated or in areas where the landscape is simple and dominated by one land use type (agriculture, hay, lawn, etc.) parasites may be more negatively affected than herbivores, with cascading benefits to pollinators. However, local floral resources may also influence rates of parasitism. For example, Spear et al. (2016) found that Asteraceae specialist bees had significantly lower rates of brood parasitism, and that parasitic wasps (*Sapyga* sp.) were unable to develop to maturity on a strictly Asteraceae diet.

It is still unclear how these different factors operating at both local and landscape scales can interact to influence solitary cavity-nesting bees. In particular, it is important to understand how urbanization affects different aspects of bee fecundity, or offspring production, which is critical for maintaining viable bee populations. While several studies have found changes in community composition and species abundances along urbanization gradients, fewer have investigated how demographic patterns change along this gradient. Solitary cavity-nesting bees provide a unique system to study demographic patterns because trap nests can be easily established and opened to quantify demographic patterns such as fecundity and survivorship.

Here we ask how local and landscape level factors across an urbanization gradient influence three demographic aspects of reproduction for solitary, cavity-nesting bees: fecundity, brood survivorship, and total adults to emerge in the spring. We hypothesized that we would see an increase in solitary cavity-nesting bees in more urban areas, as has been found in several other studies (Cane et al. 2006, Hamblin et al. 2017, Wilson and Jamieson 2019, Banaszak-Cibicka and Zmihorski 2012, McCune et al. 2020, Fitch et al. 2019). Specifically, we hypothesized that fecundity would be most strongly influenced by local floral resources, with native plant abundance being a strong predictor of fecundity, as shown in Palladini and Maron (2014) and Minckley et al. (1994). We also hypothesized that larger habitat patches would facilitate increases in fecundity due to increases in floral resource availability. However, we predicted that brood survivorship would be more strongly influenced by urbanization, and as such we would see an increase in survivorship along an urbanization gradient. This would possibly be due to a decrease in brood parasites in the urban core, as other studies have found decreases in parasitism in urban areas (Rebolo-Ifran et al. 2017, Werner et al. 2020, Burks and Philpott 2017, da Rocha et al. 2020).

MATERIALS AND METHODS

Study system

In 2018-2019, we surveyed solitary cavity-nesting bees active in 18 grassland restoration sites across the city of Louisville, Kentucky, USA (38.253° N, 85.759° W)

(Fig. 1A). Average annual precipitation for Louisville is 115 cm, with summertime temperatures between 25 - 35°C, and the growing season typically lasting from April through October. Louisville's metro population is roughly 1.3 million, and the urban core is one of the strongest heat islands in the USA, with average high temperatures reaching 3-5°C warmer than the surrounding rural areas (Debbage and Shepherd 2015). Study sites were restorations that have been purposefully maintained as grasslands (via mowing, burning, etc.) that have all been managed for the last 2-15 years by five independent parks organizations and ranged in sizes from 0.5 -16 ha, with an average size of 4.22 ha. There was no correlation between size and urbanization ($r = 0.23$, $p=0.34$) nor urbanization and non-native plants ($r = -0.43$, $p = 0.13$), nor size and floral richness/abundance ($r = 0.38$, $p = 0.30$ and $r = 0.42$, $p = 0.16$ respectively) as other studies focused on urbanization and pollinators have found (McIntyre, 2000), which allowed us to look at the combined effects of these factors on bees.

Nest boxes

In early April of 2018 and 2019, solitary cavity-nesting bee nest boxes were placed in all study sites. One nest per site was established each year (one in 2018 and a new one in 2019). In 2018 we surveyed 17 sites, and we surveyed 13 sites in 2019. In 2019 one site was added (first year of grassland management) and five were dropped because of drastic shifts in site maintenance (shift to lawn). Nests consisted of two 5cm x 10cm x 20cm blocks of pine wood screwed together and attached to a 1.5m U-frame fence post. In each nest eight holes were drilled, two each with diameters of 1.27cm, 0.95cm, 0.63cm, and 0.55cm, making eight cavities per nest, which could accommodate bees of different sizes (Fig. 1B). All nest boxes were set up facing southeast, roughly in the middle of each grassland restoration site. Cotton rags soaked in motor oil were wrapped around the fence posts to block ant and spider colonization. Nest boxes were collected in December of 2018 and 2019. We extracted and opened each nest and counted total, living, and dead larval offspring per nest. Solitary bees compromise a majority of the native bees in North America (Kearns et al. 1998).

Landscape factors

We characterized three main landscape factors that could influence solitary cavity-nesting bee reproduction: restoration (site) size, urbanization, and habitat complexity. To measure urbanization and habitat complexity, surrounding land cover was selected in a 1.5 km radii buffer zone around each nest box using ArcMap 10.6. A radius of 1.5 km was selected, as this encompasses the average flight range for a larger solitary bee (Zurbuchen et al. 2010b). Land cover values for each buffer zone were determined using data from the 2011 National Land Cover Database (Jin et al. 2013). Land classes from this dataset included developed land (Open, Low, Medium, and High combined into a single measure) as well as 11 classes of vegetative cover (Deciduous Forest, Coniferous Forest, Agriculture, etc.), for a total of 12 types (listed in Appendix S1). Habitat complexity within each 1.5 km buffer zone was quantified by calculating Shannon’s diversity index (H’) based on the land usage data. We conducted a principal component analysis (PCA) to create a single composite measure of urbanization based on the 12 classes of land usage (loading scores in Appendix S2). PC1 explained 74% of the variation in land usage, and the variable loading scores on the first principal component (PC1) indicated an urbanization gradient. PC1 has high positive values for Developed Land, and strongly negative values for Forested Land (Appendix S2). For further analyses, PC1 scores were used as the measure of landscape-scale urbanization. Habitat patch size was also measured in 2019 in ArcMap 10.6, by drawing polygons around patch edges using aerial imagery (LOJIC Metro 2016 3-inch Map).

Local floral surveys

From April through October each year, bi-weekly floral surveys were conducted at each study site. 20 m transects were established in each cardinal direction radiating out from the nest box. Along each transect, four 2 x 2 m sampling subplots was established where floral surveys were conducted. At each subplot, all flowering heads were identified to species and counted. Counts from the 16 subplots were summed to one value per species per site per survey. The same number of sites were surveyed for floral communities as in the bee nest establishments (17 in 2018 and 13 in 2019). Each site received 13 surveys per year, for a total of 390 floral surveys. From these surveys we recorded average floral density and species richness per site per survey. Species were also grouped by whether they were native or non-native (Jones 2005) in order to calculate % native cover.

Data analysis

We had three bee reproduction response variables: fecundity (total eggs per nest), survivorship (% living eggs/larvae per nest), and emerging adults (total individuals living to spring per nest). For sites with two years of data collection, values were averaged across both years for one value per site. This was done because our experimental unit was the site and none of our landscape variables (urbanization, size and landscape complexity) changed across years. In order to maintain high sample sizes and include data from all 18 sites in a single analysis, we averaged bee and floral data across both years for sites with two year of data. Additionally, floral abundance and richness values were consistent across years at each site. (Abundance r = 0.830, Diversity r = 0.640). Another approach could have been to analyze each year separately, but we did not do this in order to maximize sample sizes for our statistical model. Each response was analyzed using multi-model inference as outlined in Burnham and Anderson (2004). In this approach, key predictor variables were identified by comparing all possible combinations of predictors using the coefficients from each model. The summed model weights ($\sum wi$) across all possible models give a measure of importance for each variable. $\sum wi$ ranges from 0 to 1, with higher values indicating that the predictor is more likely to be a part of the well-supported models (by AIC score). Variables that do not occur in well-supported models are shrinkage-adjusted toward zero. The best model is then selected based on the average coefficients (those significantly different from 0).

Each model (for fecundity, survivorship and emerging adults) began with six predictor variables; three landscape and three local. The landscape predictor variables were urbanization (PC1), restoration (site) size, and habitat complexity (land H’). The local predictor variables were floral density, floral richness and percent native floral community. Once model averaging indicated the variables that were most important and what the best fit model was (determined using the “dredge” function in the MuMIn package (Barton 2012)), we ran linear regressions to visualize these relationships. All statistical analyses were performed in R software, version 3.4.1 (R Development Core Team 2019). Figures were built using the ggplot package (Kahle and Wickham 2013), data were organized using the dplyr package (Wickham et al. 2020), model inference was performed with the MuMIn package (Bartoń 2012), and the package relaimpo (Grömping 2006).

RESULTS

124 forb species were recorded in 2018 and 86 in 2019, 64 of which were native species, with 114,773 flowering heads in 2018 and 68,621 in 2019 for a total of 183,394 flowering heads counted across all surveys. A total of 108 nest cavities were dissected in 2018 (average of 6.00 cavities per site) and 68 cavities in 2019 (average of 5.67 cavities per site) for a total of 176 cavities across both years. Average fecundity per cavity was 7.05, with an average survivability rate of 63.5% and an average of 5.01 emerging adults per cavity. Bees could not be identified to species as a majority of individuals were still in larval form during nest dissection. However, once the surviving individuals reached adulthood, a subset were identified to morphospecies and the predominant genera were *Megachile* and *Osmia*. In five nests *Xylocopa sp*. bees drilled holes into the side of the nests but were not included in data analyses as they are different taxa from the focus taxa of this study. The *Xylocopa* nests did not interfere with the pre-existing cavity nests. In almost all nests with dead bee larvae we found *Trogoderma sp.* beetles. These beetles have been considered predator/parasites of solitary bees and wasps in natural history reports, but other researchers consider them as secondary scavengers that invade the nest following death by some other cause (Forrest 2019 personal communication, Staab 2019 personal communication). Therefore, we cannot say for certain whether these beetles caused the bee death or simply colonized the nests postmortem.

Fecundity

The best model for predicting bee fecundity included one predictor variable: percent native flowers ($F_{1,17} = 5.034$, $p = 0.038$, $R^2 = 0.183$, Fig. 2, 3). Fecundity was significantly higher in sites where native flowers made up a higher percentage of the forb community. Model average coefficients for percent native flowers were significantly different from zero (Estimate: 0.505, LCL: 0.037, UCL: 0.974, $p = 0.035$). Model average coefficients for all response variables are reported in the Supplemental Information (Appendix S3).

Survivorship

The best model for predicting survivorship included one predictor variable: urbanization ($F_{1,17} = 6.066$, $p = 0.025$, $R^2 = 0.212$, Fig. 2, 4). Larval survivorship was significantly higher in urban sites, with ~75% survivorship in urban sites and ~30% survivorship in rural sites. Model average coefficients for urbanization were significantly different from zero (Estimate: 0.519, LCL: 0.055, UCL: 0.983, $p = 0.029$).

Emerging Adults

The best model for predicting total emerging adults included two predictor variables: percent native and urbanization ($F_{2,16} = 4.216$, $p = 0.034$, $R^2 = 0.263$, Fig. 5). Sites that were both urban and had high native forb cover had the greatest number of emerging adults, while rural sites with high non-native forb cover had the lowest number of emerging adults. Model average coefficients for percent native were significantly different from zero (Estimate: 0.491, LCL: 0.013, UCL: 0.967, $p = 0.043$, partial $R^2 = 0.211$, Fig. 2) and marginally significant for urbanization (Estimate: 0.417, LCL: -0.063, UCL: 0.898, $p = 0.088$, partial $R^2 = 0.134$, Fig. 2).

DISCUSSION

This study confirms previous findings that solitary cavity-nesting bees increase in urban areas, and we are able to provide some insight into the reproductive parameters that contribute to these patterns. We found that solitary cavity-nesting bees are not laying more eggs in urban areas but are instead exhibiting higher rates of brood survivorship. This improvement in reproductive success likely leads to more robust populations and, in concert with other factors such as increased nesting substrate, explains why these pollinators are increasing in urban areas. Additionally, this study shows that land usage was not the only factor that determined bee success; the quality of the local flower community significantly improved demographic patterns of solitary cavity-nesting bees.

One possible explanation for the increase in brood survivorship in urban areas could be a reduction in cleptoparasitism. As mentioned above, cleptoparasitism of solitary cavity-nesting bees is a significant source of mortality, with documented rates of parasitism over 50% in the field in previous studies (Spear et al. 2016). A meaningful reduction of parasitism in urban areas could partially explain the increased survival rates in urban areas we found here. Several recently published studies found pollinators' natural enemies tend to decrease in urban areas. For example, Corcos et al. (2019) sampled predators and parasitoids of flower visitors (Ampulicidae, Sphecidae, Crabronidae and Tachinidae) in Rome and found that at multiple spatial scales (local, landscape and sub-regional) urbanization led to decreases in these natural enemies. Additionally, Burks and Philpott (2017) found that at the local scale, increases in urban cover led to a decrease in parasitoid wasp richness. Enemy release commonly occurring in urban areas may occur because urban habitat patches tend to be more isolated, which more negatively affects higher trophic levels. In isolated habitat patches, higher trophic levels, like parasites, are more susceptible to population crashes and extirpation (Hess 1996, McCallum and Dobson 2002). As such, it is possible that enemy release is a common phenomenon in urban areas which would have positive effects on host/prey species population demographics, including solitary cavity-nesting bees.

This study also shows that solitary cavity-nesting bee fecundity is higher in areas with a greater proportion of native floral resources in the area. These results support other studies which have found benefits of native plants for pollinators (e.g., (Palladini and Maron 2014). There may be several reasons for this positive relationship including phenology, nutrients, and pollinator specialization (Roulston and Cane 2000, Kriesell et al. 2017). Phenology of native flowers is possibly a driving factor in why we saw a positive effect of natives in this study. Non-native and invasive plants tend to be more phenologically plastic, and may shift flowering times from year to year, causing asychronicity with native pollinators (Liao et al. 2020). This is of particular importance in urban heat islands where the temperature gradient is particularly strong. Native plants are more consistent in their phenology and may therefore be a more reliable source of food for native pollinators (Ogilvie and Forrest 2017). Alternatively, it may be possible that a site with more plastic, non-native flowering species will allow for increased floral availability throughout the season and actually be beneficial in other systems. Additionally, some native plant species fill unique phenological niches. For example, diets of wild bees in Michigan consisted of 60-90% native pollen with a reliance on native pollen peaking in the fall, especially from *Solidago spp.* (Wood et al. 2018). *Solidago spp*. were very abundant in many of our sites as well and provided one of the only floral resources late in the season. Early season surveys in both years were dominated by smaller, and highly abundant weedy species such as *Valerianella sp., Ranunculus sardosa,* and *Trifolium repens.* Finally, female bees have been found to take shorter foraging trips in sites with more native flowers, which would likely increase the amount a female can provision per brood (Palladini and Maron 2014). Zurbuchen et al. (2010a) found that longer foraging distances negatively affect solitary cavity-nesting bee fecundity. While we did find this positive relationship between fecundity and native plants, we cannot say for certain what direct benefit, if any, these plants are providing the bees because we did not directly measure any potential mechanisms (e.g., nectar chemistry, foraging trip duration)

The lack of an effect of habitat patch size on bee fecundity or survivorship, is surprising given that several previous studies involving a wide variety of species have documented that an increase in patch sizes leads to an increase in bee fitness (Lawton et al. 1994, Fahrig 2003). For example, previous studies found that increases in garden size and green spaces in urban areas can have positive effects on flower visitors (Hennig and Ghazoul 2011). The lack of a relationship found in our study may be due to our focus on urban grassland restorations associated with city parks that were relatively large, where even the smallest site was larger than 0.5 ha. This is larger than patch sizes for a majority of other urban bee studies that were conducted in habitats like community gardens and parks (Burks and Philpott 2017, Burdine and McCluney 2019, Egerer et al. 2020, Persson et al. 2020). Patch size may be more important for bees utilizing very small community gardens or residential sites. This difference in study site type (large natural area vs small lawns) may also explain why we saw no relationship between urbanization and non-native plant species, as other studies have found (McIntyre, 2000). While urban lawns may harbor large amounts of non-native ornamental species, these larger natural areas that are managed as grassland habitats were purposefully maintained to keep out non-natives as much as possible.

While we did not specifically measure air or soil temperatures in our sites, we do not find evidence for negative effects of urbanization for bee reproduction. We expected that more urban sites may have negative effects on bees due to associated increased surface temperatures from the urban heat island. However, even in Louisville, Kentucky, which has one of the strongest urban heat islands in the United States, we showed that fecundity did not decrease in urban areas and survivability increased. These results may be in contrast to other work that has shown that solitary cavity-nesting bees exposed to experimental warming had decreased survivability and mass, and shifts in phenology (CaraDonna et al. 2018). However, it may be that our field sites were buffered from urban heating by being located in larger city parks, and that smaller sites such as residential gardens may be more susceptible to urban heat island effects, as shown in other systems (Cheung and Jim 2019). Additionally, it is important to note that the effects of urban heat islands in temperate cities such as Louisville, KY may not extrapolate to other cities in warmer or drier environments (Yu et al. 2018).

At the local scale, we did not see a benefit to bees from increased overall floral abundance or species richness. Several studies have found that at both local and landscape scales, floral diversity is an important factor in determining wild bee health (Ghazoul 2006, Hopwood 2008, Cusser and Goodell 2013, Torne-Noguera et al. 2014, McCune et al. 2020). Specifically, studies have shown that increases in floral diversity and abundance are associated with increases in bee abundance and diversity, as well as have positive impacts on bee health. The larger sizes of our study sites may explain the lack of effect of overall floral abundance, as floral resources were generally plentiful throughout the growing season. In smaller sites, such as community or residential gardens and yards, floral richness or abundance may play a more significant role, as other studies have found (Pardee and Philpott 2014, Wilson and Jamieson 2019). One caveat to this study is that we were unable to identify bee larvae to the species-level. Future work may be able to examine shifts in bee community composition due to certain species changes in frequency, fecundity and survivorship along an urbanization gradient, which would give us further insight into how urbanization affects solitary bee communities.

Conclusion

This study highlights the importance of maintained natural areas in urban ecosystems. We found significant increases in solitary cavity-nesting bee reproduction in urban grassland restorations as compared to those in rural areas. This trend follows what has been found in previous studies, but importantly here we were able to address potential demographic indices that lend to this increase. Increased brood survivorship, possibly due to enemy release, may explain why solitary cavity-nesting bees increase in urban areas. It should be noted that while we saw a positive effect of urbanization for these bees, this may not apply to other important taxa; many social and ground nesting bees are decreasing in urban areas, as are predatory and parasitic arthropods (Sivakoff et al. 2020, Faeth et al. 2011, Youngsteadt et al. 2015, Fitch et al. 2019). Importantly, these findings provide valuable evidence for land managers and restoration practitioners to support the idea that even small restorations that incorporate native plants can play a key role in sustaining native bee populations in urban areas.

Figure Legends

Figure 1. (A) Map of study sites. Sites are indicated by white triangles. Red indicates Developed Land as classified by the National Land Cover Database. (B) A trap nest established in the field.

Figure 2. Coefficients from model averaging. Greater coefficients indicate the predictor is present in better-supported models and indicates higher importance. Landscape level factors in brown and local level factors in green. Bars indicate +/- 1SE.

Figure 3. Linear regression comparing average brood survivorship rate and the urbanization index value (PC1 score, Appendix S2) for each site.

Figure 4. Linear regression comparing nest fecundity and the proportion of the floral community that was native for each site.

Figure 5. Combined effects of urbanization and native flowers on emerging adults.

Figure 1

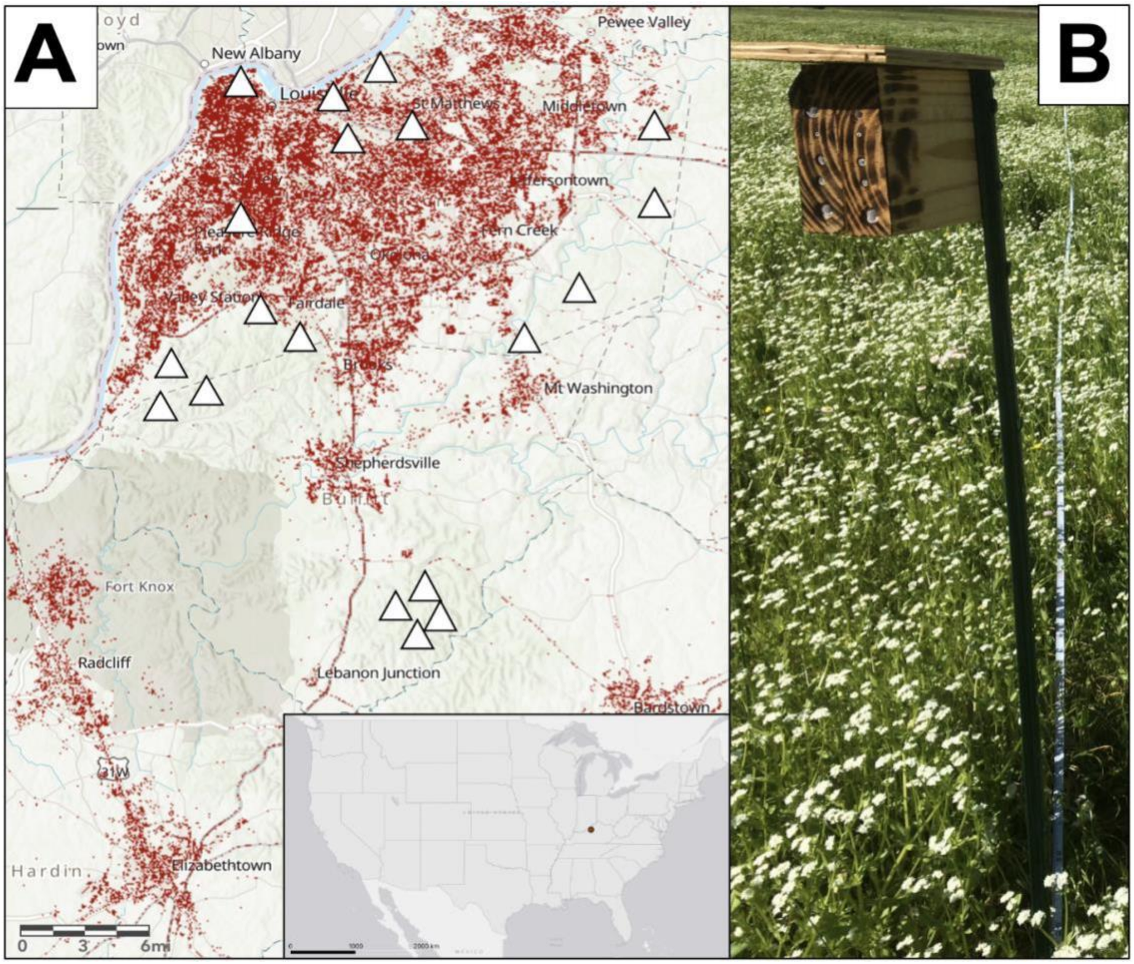
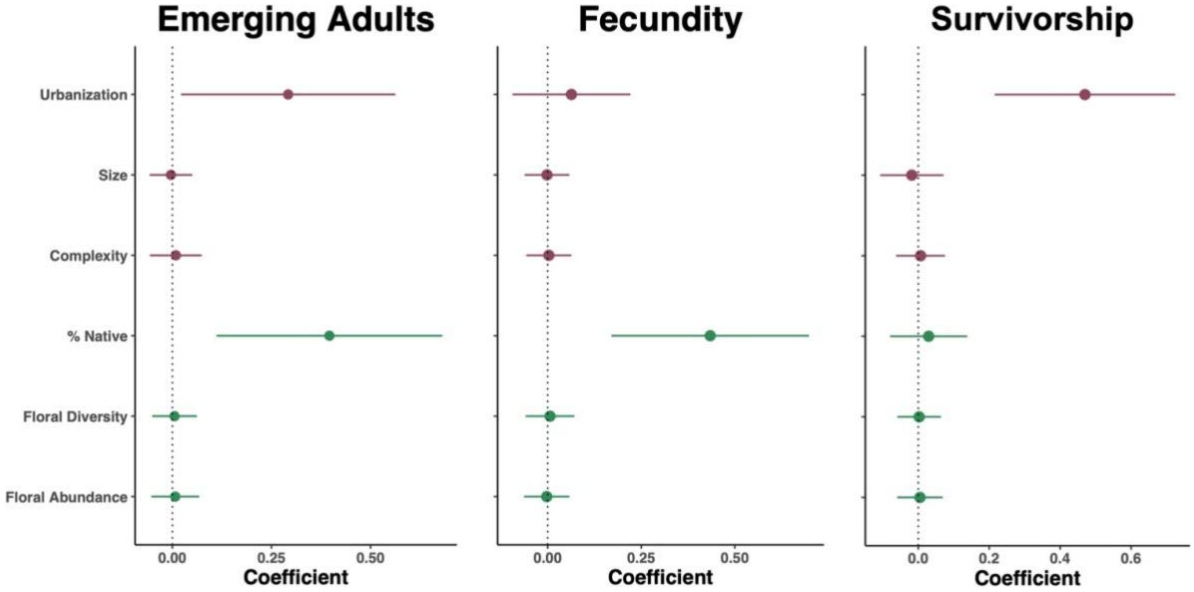

A
New Albany
Louisville
Pewee Valley
St Matthews
Middletown
Jeffersontown
Fern Creek
Pleasure Ridge Park
Okolona
Valley Station
Fairdale
Brooks
Mt Washington
Shepherdsville
Bullitt
Fort Knox
Radcliff
Lebanon Junction
Bardstown
31W
Hardin
Elizabethtown
0
3
6mi
B

Figure 2



Emerging Adults
Fecundity
Survivorship
Urbanization
Size
Complexity
% Native
Floral Diversity
Floral Abundance
0.00
0.25
0.50
Coefficient
0.00
0.25
0.50
Coefficient
0.0
0.2
0.4
0.6
Coefficient

Figure 3

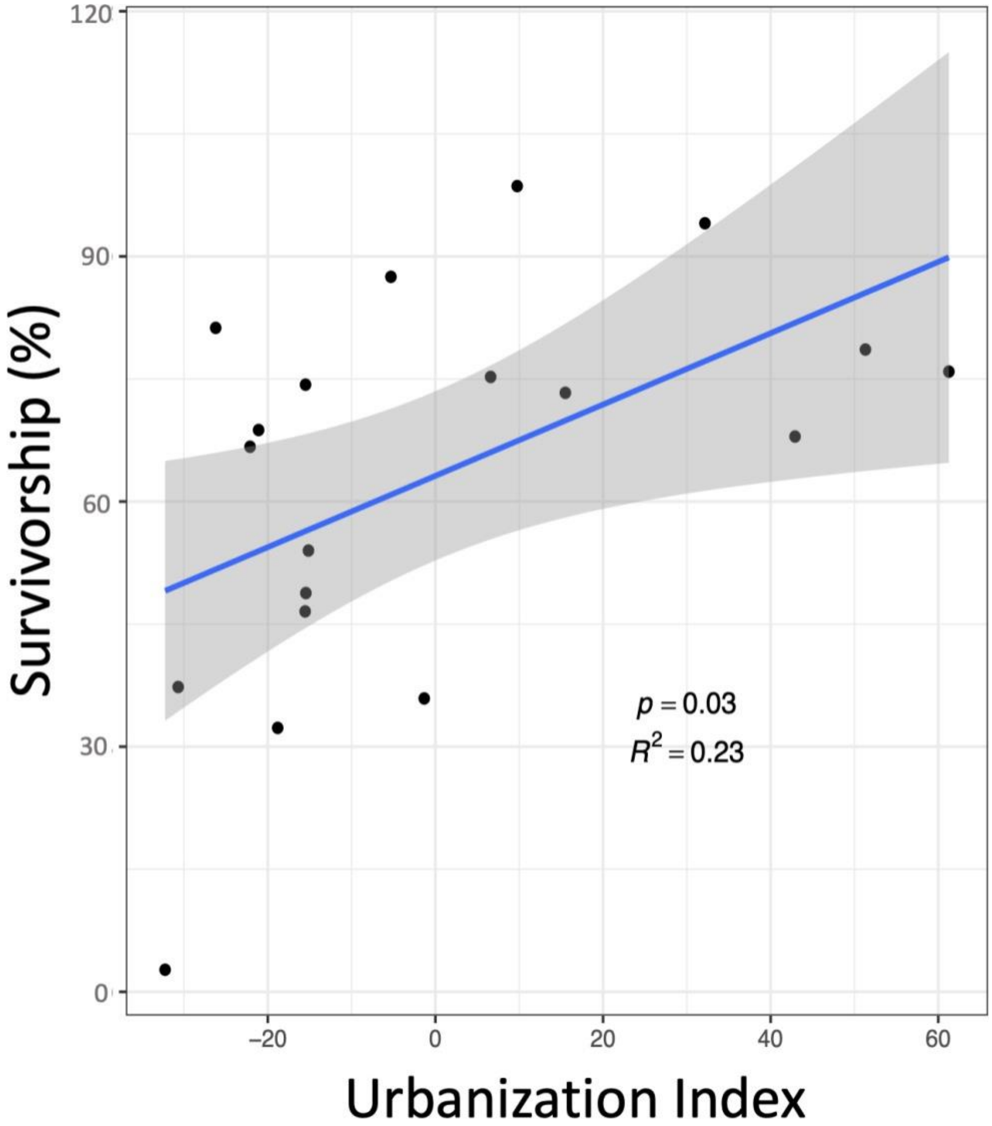

Survivorship (%)
120
90
60
30
0
−20
0
20
40
60
Urbanization Index
$p = 0.03$
$R^2 = 0.23$

Figure 4

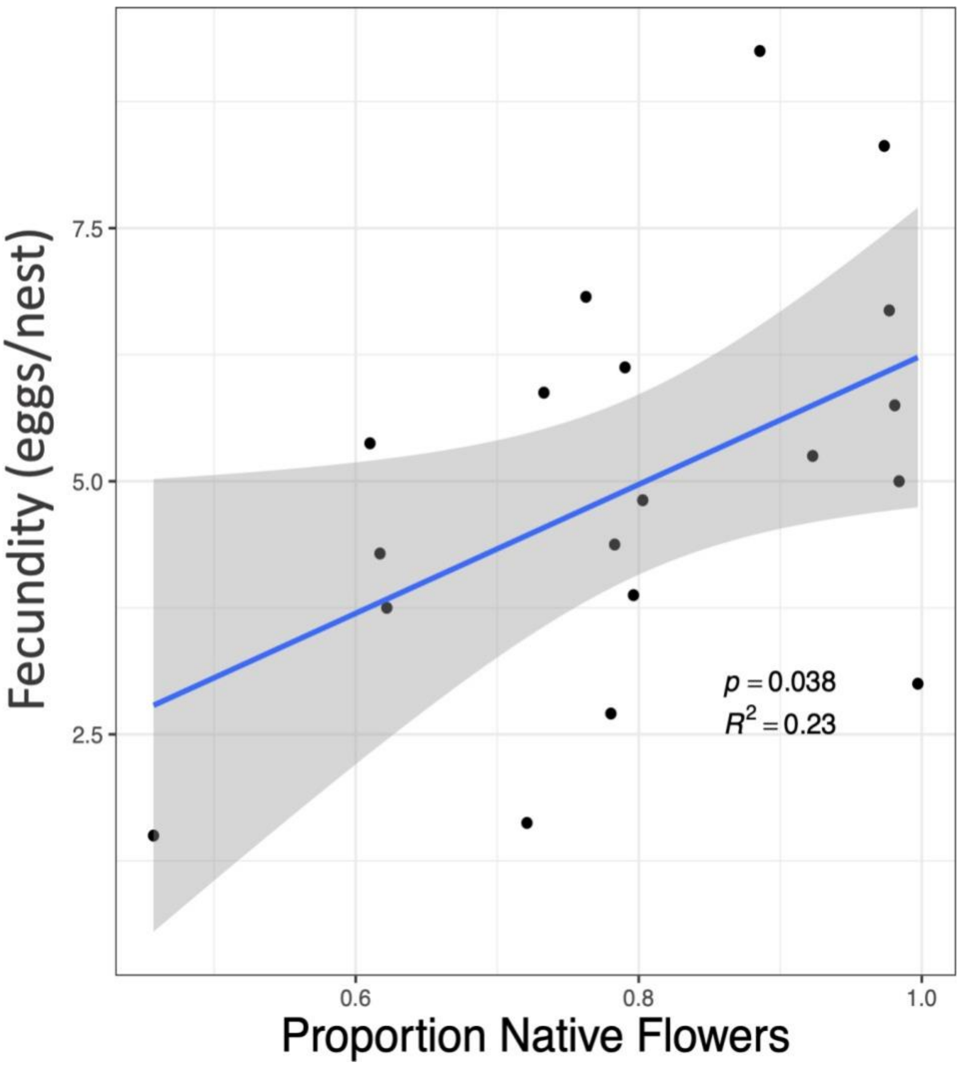
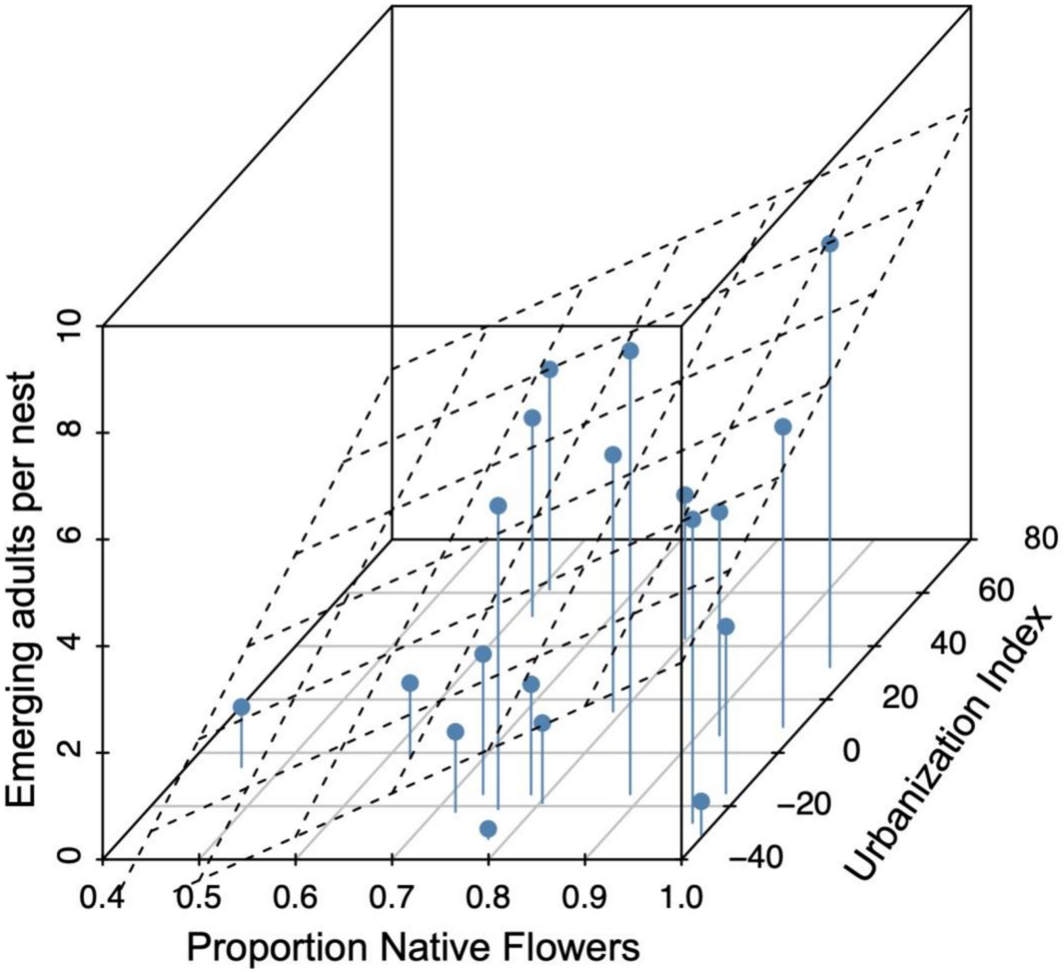

Fecundity (eggs/nest)
7.5
5.0
2.5
0.6
0.8
1.0
Proportion Native Flowers
$p = 0.038$
$R^2 = 0.23$

Figure 5



Emerging adults per nest
0
2
4
6
8
10
0.4
0.5
0.6
0.7
0.8
0.9
1.0
Proportion Native Flowers
−40
−20
0
20
40
60
80
Urbanization Index

CHAPTER IV

URBANIZATION AND PLANT DIVERSITY INFLUENCE DIFFERENT ASPECTS OF FLORAL PHENOLOGY

SUMMARY

Plant and animal phenologies can shift as global temperatures rise and landscapes become human dominated. In urban areas, where surface temperatures can reach 5-6°C warmer than in surrounding rural areas, phenologies are expected to shift significantly. However, small high-quality habitat patches within urban areas can hold diverse communities of plants and animals and may have the potential to offset some of the detrimental effects of urbanization. In this study, we examined how floral phenology— the onset, duration, and distribution of floral events— shifted in small grassland restorations across an urbanization gradient in Louisville, Kentucky, a city with one of the most severe urban heat islands in the US. In addition to urbanization, we examined how habitat patch size, plant richness, and soil water-holding capacity influenced floral phenology. Our objectives were to understand 1) how urbanization influences floral phenology 2) if high-quality local habitats could influence or offset some effects of urbanization, and 3) if species responses varied across seasons. We found that average first date of flowering and peak abundance date occurred 1-2 weeks earlier in urban compared to rural areas. However, we found that floral duration was longest in sites with high plant richness, regardless of urbanization. We also found that summer-flowering

species increased their floral duration in urban areas while spring and fall-flowering species did not. In fact, spring and fall species shortened their flowering duration in urban areas and spring species experienced earlier peak dates in urban areas. These differences in seasonal responses lead to an “urban summer spillage” effect where urbanization causes summer-flowering species to move into the temporal niche of spring and fall species. Such shifts in floral phenology due to urbanization have implications for pollinator communities, and it is encouraging that increasing plant richness at a local scale may help counteract larger-scale environmental changes. These findings highlight the importance of understanding not only how urbanization influences floral phenology, but how we can manage habitats in urban areas to support robust plant and animal communities.

INTRODUCTION

Urban areas are expanding and intensifying globally as more of the human population moves into cities (Seto et al. 2012). This urban expansion and fragmentation of the natural landscape can lead to dramatic abiotic changes, local extinctions, reduction in plant and animal genetic diversity, introduction of alien species, and disruptions to species interactions (Radeloff et al. 2005, Johnson and Munshi-South 2017). Among the most pronounced and consistent abiotic changes in urban environments is an increase in surface temperatures, often termed the ‘urban heat island’ (Arnfield 2003, Debbage and Shepherd 2015). Urban surface temperatures can often reach daytime highs and nighttime lows 3-7° C warmer than those of the surrounding rural areas. This urban heat island effect can have profound impacts on species inhabiting urban environments.

Elevated temperatures associated with urbanization can cause direct physiological harm to species, reducing reproductive capacity, survivability and growth (Sivakoff et al. 2021, Beck and Heinsohn 2006). In addition to direct stress, elevated urban temperatures can also cause drastic phenological shifts, with a potential cascade of negative effects (Fisogni et al. 2020, Zipper et al. 2016). Several studies have documented earlier flowering in urban habitats for a range of plants including forbs, shrubs and trees (Li et al. 2017, Fisogni et al. 2020, Zipper et al. 2016, Ruan et al. 2019). These phenological shifts can cause disruptions in important species interactions, such as between plants and their pollinators. For example, Fisogni et al (2020) found urbanization to drive earlier flowering in spring plants, but found no change in pollinator emergence, potentially leading to a detrimental phenological mismatch.

Several studies in both urban and natural settings have documented stronger responses to elevated temperatures in spring-flowering species compared to those that flower in summer or fall (Neil and Wu 2006, Ding et al. 2020), including in a large review of nearly 400 British flora (Fitter and Fitter, 2002). There are several possible explanations for why spring species may respond so strongly to temperature changes. Spring-flowering species may be at heightened risk for phenological mismatches with pollinators, and so may be more plastic in their responses to temperatures to avoid reduced seed set (Kudo et al. 2004, Kudo and Ida 2013). Spring species also experience heightened costs from a mistimed emergence from frost damage or die off, something summer and fall species are largely not at risk of. These intensified costs may lead to increased selective pressure on spring species phenologies, making them more responsive to changes in the abiotic environment than summer or fall species.

Fortunately, local site characteristics related to habitat quality have the potential to offset some of the deleterious effects of urbanization on plant phenology. Urban parks and other islands of natural vegetation can reduce local temperatures by reducing impervious surface cover (Norton et al. 2015, Cheung and Jim 2019). Edaphic factors, such as soil moisture, can directly affect plant phenology as well. For example, researchers found a strong correlation between decreased moisture availability and delayed floral phenology in Mediterranean shrublands (Peñuelas et al. 2004). Additionally, the plant neighborhood, or community composition, may influence floral phenology as well. Grassland plants in higher diversity systems have increased drought resistance and decreased pest damage (Tillman and Downing 1994). In these diverse systems plants may be able to reallocate resources away from defense and towards reproduction, and therefor shift their floral duration, peak date or initiation.

Our study set out to understand how urbanization and habitat quality interact to influence floral phenology. Specifically, we ask 1) Are landscape-level characteristics of urbanization associated with shifts in plant community floral phenology? 2) Can local site quality factors offset some of these shifts in phenology? And finally, 3) Are species' responses to urbanization consistent across seasons? We predicted that we would see plants flowering earlier and for shorter periods in urban habitats and smaller habitats compared to the surrounding rural habitats. We also predicted that increases in local site quality could reduce effects of urbanization. Finally, we hypothesized that while many species may shift their phenologies in response to urbanization, the change would be greatest for spring-flowering species. To our knowledge, this is one of the first studies to address how both local and landscape factors associated with urbanization can impact multiple aspects of floral phenology at the community level.

MATERIALS AND METHODS

Study system

In 2018 and 2019, we conducted floral surveys in small grassland restorations in and around the city of Louisville, Kentucky, United States (38.253° N, 85.759° W). Annual precipitation in Louisville was 170cm in 2018 and 116cm in 2019 (NWS Louisville weather station, NOAA), with summertime temperatures between 25 - 35°C, and a growing season typically lasting from April through October. Louisville's metro population is roughly 1.3 million, and the urban core is one of the strongest heat islands in the USA, with average warm season high temperatures and cool season low temperatures 3-7° C warmer than the surrounding rural areas (Stone et al. 2019). We surveyed 17 sites in 2018 and 13 in 2019, all of which had been actively managed as native grasslands (Fig. 1; Site descriptions and site Latitudes and Longitudes in Appendix S1). Restorations ranged in age from 1-15 years old, with an average size of 4.22 ha (0.5-15 ha range). Management tactics included annual mowing, burning, and/or targeted removal of woody and invasive plant species. We removed five sites from sampling in 2019 because of changes in site management, and in 2019 we added one new restoration site. There was no correlation between site size and urbanization (measurement details below; $r = 0.23$, $p=0.34$), nor urbanization and plant richness ($r = -0.43$, $p = 0.13$), nor site size and floral richness/abundance ($r = 0.38$, $p = 0.30$ and $r = 0.42$, $p = 0.16$ respectively), as other studies focused on urbanization and pollinators have found (McIntyre 2000), which allowed us to look at the combined effects of these factors on floral phenology.

Phenological data collection

From April – October of 2018 and 2019 we surveyed the floral community every other week at each site, for a total of 13 surveys per site per year, 390 surveys across the entire study. For surveys, we randomly selected a location in the middle of each grassland site and marked this location with a cavity-nesting bee nest (used for a concurrent study, see Sexton et al. 2021). From this point, we ran four 20 m transects radiating out in each cardinal direction. Along each transect, four 2 x 2 m sampling subplots were spaced every 5 m, and all inflorescences were identified to species and counted during each survey. Floral species richness was aggregated across all subplots in each survey at each site, and then these values were averaged to give one whole-season metric of floral richness per site. To quantify different aspects of community floral phenology, counts from the 16 subplots were summed to give one value per species per site per survey. We calculated four metrics of floral phenology for each species in each site: relative floral initiation date, relative floral duration, relative peak flowering date, and flowering schedule shape. These measures allow for a more nuanced understanding of phenology compared to just using floral initiation date (Austen et al. 2014, Inouye et al. 2019). At the end of each field season, we also categorized plant species by whether they were spring (first appearance in surveys 1-4), summer (first appearance in surveys 5-9) or fall (first appearance in surveys 10-13) flowering to calculate season-specific phenology metrics.

We calculated relative floral initiation date by subtracting the flower initiation date at a specific site by the average initiation date across all sites for a given species. This measure provides insight on whether species tend to flower earlier or later at specific sites compared to the region as a whole. The same was done for duration, where we subtracted the duration (# of surveys present) of a given species at a given site by the average duration for that species, and for peak flowering date. Flowering schedule shape is a multivariate measure that incorporates the distribution of flowering for each species across time and is among the most complete characterization of phenology of a population or community (Austen et al. 2013, Inouye et al. 2019). Multivariate visualization of how floral distributions change from site to site allow us to interpret changes in flowering schedule shape across our local and landscape predictor values. For these metrics we excluded all species that only occurred at one or two sites, as our research question was focused on how species change from site to site across an urbanization gradient. From this restriction, we used 63 species for phenological analysis of the 124 species recorded in the field in 2018 and 48 out of the 64 species in 2019.

Soil sampling

We used water holding capacity as an indicator of soil quality as it is highly correlated with organic matter, and also addresses local water budgets, both of which are important to plant development (Cohudhri and Singh 1987, Mujdeci et al. 2017). In June of 2018 (and 2019 for the one new site), we collected soil cores from each site to quantify water holding capacity following standard methods (Williams 1979). In brief, 10 soil cores (2cm diam x 15cm depth) were haphazardly taken from each site and homogenized. We then brought the soils back to the lab and let them air dry in open plastic bags. Once dried, we weighed dry samples; then water was pulled through 100g of soil via vacuum pressure. We then calculated water holding capacity by comparing each sample's dry weight to its weight after water collection.

Landscape Measures

We quantified two landscape factors that may influence floral phenology in our system: habitat size and urbanization, following methodology used in Sexton et al. (2021). We used ArcMap 10.6 to measure habitat size by drawing polygons around site edges using aerial imagery (LOJIC Metro 2016 3-inch Map). To measure urbanization, a 1.5 km radius buffer zone around the center points of each of our sites was selected, and surrounding land cover values for each buffer zone were determined using data from the 2011 National Land Cover Database (Jin et al. 2013). Land classes from this dataset included developed land (Open, Low, Medium, and High combined into a single category) as well as 11 classes of vegetative cover (Deciduous Forest, Coniferous Forest, Agriculture, etc.), for a total of 12 types (listed in Appendix S1). We conducted a principal component analysis (PCA) to create a single composite measure of urbanization based on the 12 classes of land usage (loading scores in Appendix S2). PC1 explained 74% of the variation in land usage, and the variable loading scores on the first principal component (PC1) indicated an urbanization gradient. PC1 has high positive values for Developed Land, and strongly negative values for Forested Land (Appendix S2). For further analyses, PC1 scores were used as the measure of landscape-scale urbanization.

Statistical analyses

To address how univariate floral phenology metrics responded to local and landscape level factors we used multi-model inference, or AIC model averaging, as outlined in Burnham and Anderson (2004). In this approach, key predictor variables were identified by comparing all possible combinations of predictors using the coefficients from each model. The summed model weights range from 0 to 1, with higher values indicating that the predictor is more likely to be a part of the well-supported models (by AIC score).

We also separated each of our univariate phenology responses (relative floral initiation, duration, peak) by season of flowering (spring, summer, fall) and sampling year (2018, 2019), and ran each model with four predictor variables: urbanization, size, floral community diversity and soil water holding capacity. Once model averaging indicated the variables that were most important to each response, and what the best fit model was (determined using the "dredge" function in the MuMIn package [Barton 2002]), we ran linear regressions to visualize these relationships. All statistical analyses were performed in R software, version 3.4.1 (R Development Core Team 2019). Model estimates and their standard errors are reported for best fit models in the results.

To examine differences in flowering schedule shape, we used a Permutational Multivariate Analysis of Variance (PERMANOVA) using the "Adonis" function in the "vegan" R package (Oksanen et al. 2016), using Bray-Curtis distances to assess dissimilarity in schedule shape. Our explanatory variables in this analysis were urbanization, size, diversity, water holding capacity and seasonality of flowering (spring, summer, fall). Response variables were the population floral abundance from each survey week the species was present, giving the full species flowering distribution in a given site. If we found significant differences in the PERMANOVA we conducted a test of within group variation using a Permutational Analysis of Multivariate Dispersions

(PERMDISP). The PERMDISP allowed us to determine if significant differences in the PERMANOVA were due to differences in group dispersion or differences in ordination space. To visualize these results, we created nonmetric multidimensional scaling (NMDS) plots for each year (2018 and 2019).

RESULTS

We recorded 124 forb species in 2018 and 86 in 2019, with 114,773 inflorescences in 2018 and 68,621 in 2019 for a total of 183,394 inflorescences counted across all 390 surveys. Average floral richness peaked in late-September in 2018 and peaked in mid-July in 2019.

Urbanization

Urbanization was not a significant predictor of any measure of floral phenology in 2018 when species were not separated by season of flowering (Fig. 2), but in 2019 urbanization did influence overall relative floral initiation, with plants flowering roughly two weeks earlier in urban compared to rural areas. (Fig. 2, Fig. 3, Model Estimate = -0.0051, SE = 0.0022, p = 0.01). Urbanization also predicted peak flowering date in 2019, again pushing the peak date up two weeks in urban areas (Fig 2, Fig. 3, Model Estimate = -0.0040, SE = 0.0018, p = 0.03). Urbanization did not have a significant overall effect on floral duration. (Fig. 2, Model Estimate = 0.0053, SE = 0.0036, p = 0.13)

Site Quality

In both 2018 and 2019 floral community richness best predicted floral duration, with species flowering roughly two weeks longer in diverse sites than in sites with low floral diversity (Fig. 2, Fig. 3; 2018 – Model Estimate = 0.1754, SE = 0.0342, p < 0.001;

2019 – Model Estimate = 0.2250, SE = 0.0635, $p < 0.001$). We saw no effect of soil water holding capacity or site size in either the full dataset or when species were separated by season of flowering for both years.

Seasonality

The impact that urbanization and floral richness have on floral phenology became more nuanced when species were separated by season of flowering. In both 2018 and 2019, summer-flowering species significantly extended their floral duration in urban areas (Fig 2; 2018 – Model Estimate = 0.0171, SE = 0.0075, p = 0.02; 2019 – Model Estimate = 0.0150, SE = 0.0058, p = 0.01). Additionally, in 2018 spring-flowering species shortened their duration in urban areas (Model Estimate = -0.0130, SE = 0.0053, p = 0.01), and in 2019 fall-flowering species shortened theirs in urban areas as well (Model Estimate = -0.0094, SE = 0.0047, p = 0.050). Spring-flowering species were largely responsible for the shift to earlier peak flowering in urban areas seen in the full data set (Model Estimate = -0.0066, SE = 0.0027, p = 0.01).

In both 2018 and 2019, the PERMANOVA indicated that differences in flowering schedule shape among species was largely due to season of flowering (Fig. 4: 2018 – $F_{2,198} = 3.705$, p = 0.005; 2019 – $F_{2,186} = 9.000$, p = 0.001). Summer-flowering species had a unique schedule shape with flowering more normally distributed throughout the season, while spring and fall species had schedule shapes similar to each other with peaks skewed towards earlier dates, followed by subsequent declines (Fig. 4). In 2019 the PERMANOVA and PERMDISP indicated that summer-flowering species had the most distinct distribution and had the greatest within-group dispersion ($F_{2,186} = 3.392$, p = 0.036), meaning their distribution shape was the most variable of all seasons, but also the most different from spring and fall distributions. In 2018, the PERMANOVA indicated that summer species had a unique distribution, but the PERMDISP indicated all species had equal within-group dispersion ($F_{2,196} = 0.560$, $p = 0.572$). In 2019, urbanization and seasonality interacted to influence schedule shape (Fig. 4 $F_{2,186} = 2.679$, $p = 0.029$). While spring and fall species' schedule shape was not significantly influenced by urbanization, urbanization increased the proportion of summer species that exhibited a normally distributed schedule shape, as opposed to the peak-crash shape common to spring and fall flowering species.

DISCUSSION

Urbanization effects on phenology

In both 2018 and 2019 we saw strong effects of urbanization on multiple parameters of phenology, including floral initiation, peak date, duration, and flowering schedule shape. Across all species, urbanization caused earlier initiation and peak flowering date, likely as a result of the urban heat island effect. Louisville's strong urban heat island can regularly increase temperatures up to 6°C, which is greater than the temperature shifts examined in many other studies, which simulate climate-related warming by manipulating temperatures by just 3-4°C (Stone et al. 2019). Pronounced shifts in floral phenology as a result of climate warming have been well documented in recent years, especially in montane/alpine systems (Inouye 2008). Research on how urbanization influences floral phenology is less extensive, but consistent trends are beginning to emerge, at least at the landscape scale. In a 2020 study conducted in France, researchers found floral phenology to advance roughly four weeks earlier in urban areas

(Fisogni et al. 2020), though pollinator phenology did not advance. Several remote sensing studies have also documented earlier ‘green-up’ as well as expanded summer growth in urban areas compared to surrounding rural areas, indicating a change in plant phenophases (Dallimer et al. 2016, Yuan et al. 2020, Li et al. 2017b). A recent study using data from a community-science photograph database (iNaturalist) found extended floral duration across multiple plant functional groups in urban areas, with stronger effects for woody perennials than herbaceous species (Li et al. 2021). Our study complements this landscape-level work by demonstrating that floral phenologies of individual species in plant communities are similarly responding to urbanization. These consistent effects on floral phenology can have profound effects on urban ecosystems beyond the pollinator mismatches mentioned above. Urban and rural sub-populations may diverge enough temporally that they could become functionally separated, leading to a fragmenting of meta-populations. Previous studies have already documented stark differences in genomic compositions of urban and rural plant populations (Wandeler et al. 2003, Partecke and Gwinner 2007, Harris et al. 2013, Johnson and Munshi-South 2017). Additionally, as our study and others have shown, not all species will shift their phenologies equally in response to temperature changes, causing some species to struggle in urban areas as they expand and intensify, and as global temperatures continue to rise (Neil and Wu 2006, Liancourt et al. 2012, CaraDonna et al. 2014, Zettlemoyer et al. 2019).

It is worth noting that the observed effects of urbanization on floral phenology were less consistent in 2018 than 2019, possibly due to differences in climate between the two years. There was a significant drought in the summer and fall of 2019, with precipitation from July through October (summer and fall in our system) less than 33% of precipitation levels in 2018 during that same period (PRISM, 2004). Additionally, floral abundance peaked in 2018 in mid-September and in mid-July in 2019, pointing to a loss of fall floral production in 2019. Drought, extreme heat, and other aspects of global climate change may exacerbate effects of urbanization in the future (Yu and Zhai, 2020). Finally, while we were unable to directly measure temperatures at our sites (due to lost/damaged data loggers) we are confident our urban sites were significantly warmer than our rural sites. Previous studies focused on Louisville specifically and nation-wide studies have demonstrated that Louisville's urban heat island is among the most pronounced in the US, with temperatures 3-6°C warmer than surrounding rural areas (Stone et al. 2019, Matson et al. 1978, McLean et al. 2005, Chakraborty et al. 2020).

Seasonal variation in phenological responses

Summer-flowering species exhibited the most positive response to urbanization, extending their flowering duration in urban areas while spring and fall species shortened theirs. Additionally, in 2019 we saw spring species shifting their flowering peak earlier in urban areas. These phenological shifts indicate an "Urban Summer Spillage" effect, where summer-flowering species move into the temporal niche of spring and fall-flowering species in urban areas (visualized in Fig. 5). This urban summer spillage may be of concern, as it may increase competition for pollinators, nutrients, and moisture, which could lead to reductions in late-spring and early-fall ephemerals in urban areas. Additionally, specialization in plant-pollinator networks tend to be highest in the spring and when resources are scarcer (CaraDonna and Waser 2020, Souza et al. 2018). As more generalists are introduced into what were previously spring communities, specialist interactions may face heightened strain in urban areas. Finally, urban summer spillage may also contribute to homogenization of floral communities in urban areas, similar to what has been observed in other urban areas where distant urban plant and animal communities are more similar to each other than they are to the surrounding rural plant and animal communities (McKinney 2006, Groffman et al. 2014, Johnson and Munshi-South 2017).

Local site factors influence phenology

While our work shows that urbanization has significant impacts on floral phenology, we also found evidence that local site characteristics can directly influence phenology as well. Plants flowering in richer plant communities exhibited extended periods of floral duration compared to populations of the same species in low richness communities. Several other studies have documenting increased plant performance in high diversity grassland communities. For example, more diverse grassland communities have been found to be more drought resilient, produce increased biomass, and have more resistance to invasion than low-diversity communities (Tilman and Downing 1994, Isbell et al. 2015, Kreyling et al. 2017, Hahl et al. 2020). It is possible that in more diverse grassland communities, plants may experience reduced stressors and may be able to invest more heavily in reproduction, thereby increasing floral duration.

It is also possible that site diversity is not directly affecting phenology but is instead an indicator of disturbance regimes or habitat quality. While we were unable to obtain detailed management records of our sites, discussions with land managers indicated that sites with greater diversity consistently received greater management attention in the form of burning or mowing, which may alter phenological patterns. Mola and Williams (2018) found that floral phenology was lengthened in grasslands that had been recently burned, leading to increases in floral abundances in summer months. Consistent management may influence phenologies directly, or potentially indirectly by reducing hyper-competitive species, thereby increasing diversity and phenologies.

Changes in soil microbial communities associated with increased plant diversity may also be responsible for phenological shifts. For example, Hahl et al. (2020) found that soil microbial communities originating from plant monocultures caused plants to shift their investment to defense-related traits, and away from growth and reproduction. Other greenhouse and field studies have shown that rhizospheric organisms can have significant influences on floral phenology (Wagner et al. 2014, Forey et al. 2015, Lu et al. 2018). For example, arbuscular mycorrhizal communities have the ability to increase total floral production, as well as floral rewards, such as nectar and flower size (Barber and Gorden 2015). Abiotic soil factors such as soil nutrients and structure may also influence floral phenologies. Cleland et al. (2006) found that soil nitrogen additions advanced forb floral phenology, while delaying the flowering of grasses. Future studies investigating how feedbacks between plant community diversity, soil microbial communities, and soil nutrients can influence plant reproductive traits such as floral phenology would certainly be warranted.

An alternative explanation for extended floral duration in high-diversity sites could be increased competition for pollinators. Once pollinated, flowers will senesce, so if pollinators are abundant and frequently visiting, flowers will senesce earlier leading to shortened individual floral duration. A greenhouse experiment found floral longevity of *Mimulus guttatus* to be positively associated with neighborhood plant diversity (Arceo-

Gomez and Ashman 2014). Plants in higher diversity neighborhoods also experienced lower pollinator visitation rates and higher heterospecific pollen transfer. In a field experiment, Trunschke and Stocklin (2017) found that bagging flowers could increase their longevity, indicating that lack of pollination can increase floral duration. While our study looked at population-level floral duration and not individual level floral longevity as the two above-mentioned studies did, it is possible the same mechanisms are lengthening floral durations at a larger scale.

Surprisingly, our study found no evidence that habitat patch size influences floral phenology or modulates effects of urbanization. We expected that larger sites would be more buffered from heat island effects, as several studies have shown that even minimal vegetation increases, as much as 10-50% within 20m radii, can reduce surface temperatures by as much as 0.4-1.0°C in urban parks (Coutts & Harris 2013, Cheung and Jim 2019). Instead, we found significant effects of urbanization even in our relatively large patches of natural grasslands averaging 4 ha in size. While increasing site size may help reduce effects of urbanization on very small habitat patches such as community gardens and residential lawns, large parks seem no more resistant to urbanization effects than small parks in our study, indicating that local management decisions alone cannot counteract landscape level effects of urbanization.

Conclusion

Floral phenology is a multi-faceted phenomenon, and here we show that different aspects of floral phenology, including floral initiation, peak, duration, and schedule shape, can shift independent of one another in response to environmental changes. Floral phenology is responsive to local factors, such as community richness, as well as landscape-level factors like urbanization. Importantly, we showed that species differed in their responses to urbanization, in part based on their seasonality. We documented an urban summer spillage phenomenon by which summer-flowering species extend their duration, while spring and fall shrink theirs and move peak flowering dates away from summer species in urban areas. Over several years this could lead to the dominance of summer species and the increased homogenization of urban natural areas. However, we may be able to offset some of these negative effects by maintaining diverse local communities within urban ecosystems.

Figure Legends

Figure 1. Map of study sites. Sites surveyed in 2018 and 2019 are indicated by white triangles, those surveyed only in 2018 are indicated by circles, and 2019 only sites by diamonds. Red indicates Developed Land as classified by the National Land Cover Database.

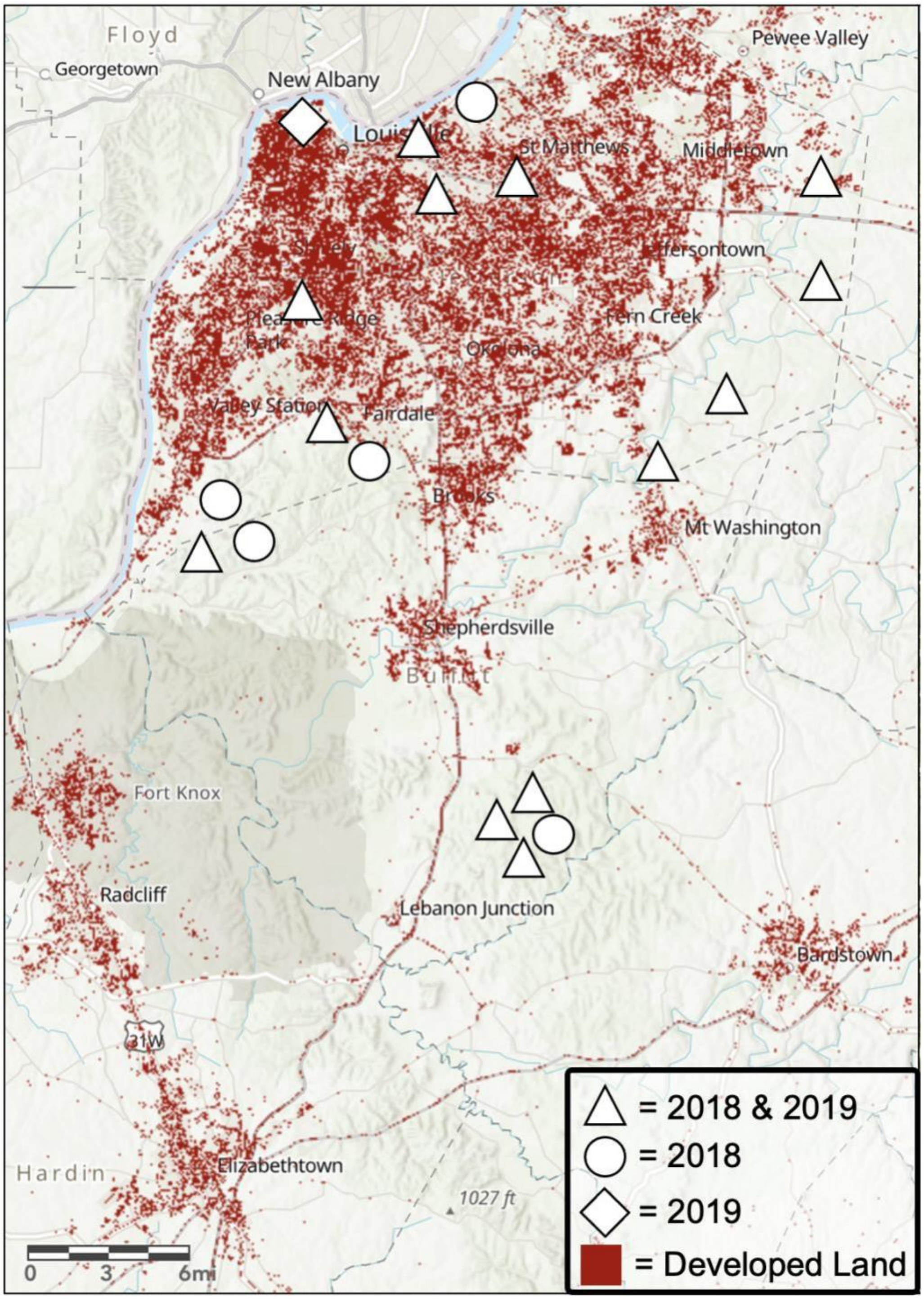
Figure 2. Coefficients from model averaging. Greater coefficients indicate the predictor is present in better-supported models and indicates higher importance. Size of the estimate point indicates model significance. Duration values are sea green, Initiation values are orange and Peak values are purple. Bars indicate +/- 1SE.

Figure 3. Linear regressions showing how the three major phenological time points (A- initiation, B- peak and C- duration) responded to local and landscape level factors.

Figure 4. NMDS visualizing how flowering schedule shape varies across species and sites (A-2018, B- 2019). Each point represents the schedule shape of one species at one site used in this analysis. In both 2018 and 2019, summer species had a significantly different schedule shape compared to spring and fall via a PERMANOVA analysis. Color of points denotes if a species is spring, summer or fall flowering. In 2019 seasonality had a significant interaction with urbanization, so points sizes indicate if the site is urban, suburban or rural. To visualize how schedule shape changes in ordination space we plotted a select handful of species' schedule shapes surrounding the 2019 NMDS.

Figure 5. Hypothetical distributions visualizing how urbanization's impact on floral phenologies can lead to summer species encroaching on spring and fall temporal niches.

Figure 1



Floyd
Georgetown
New Albany
Louisville
Pewee Valley
St Matthews
Middletown
Shively
Jeffersontown
Jefferson
Pleasure Ridge Park
Fern Creek
Okolona
Valley Station
Fairdale
Brooks
Mt Washington
Shepherdsville
Bullitt
Fort Knox
Radcliff
Lebanon Junction
Bardstown
31W
Hardin
Elizabethtown
1027 ft
0
3
6mi
△ = 2018 & 2019
○ = 2018
◇ = 2019
■ = Developed Land

Figure 2

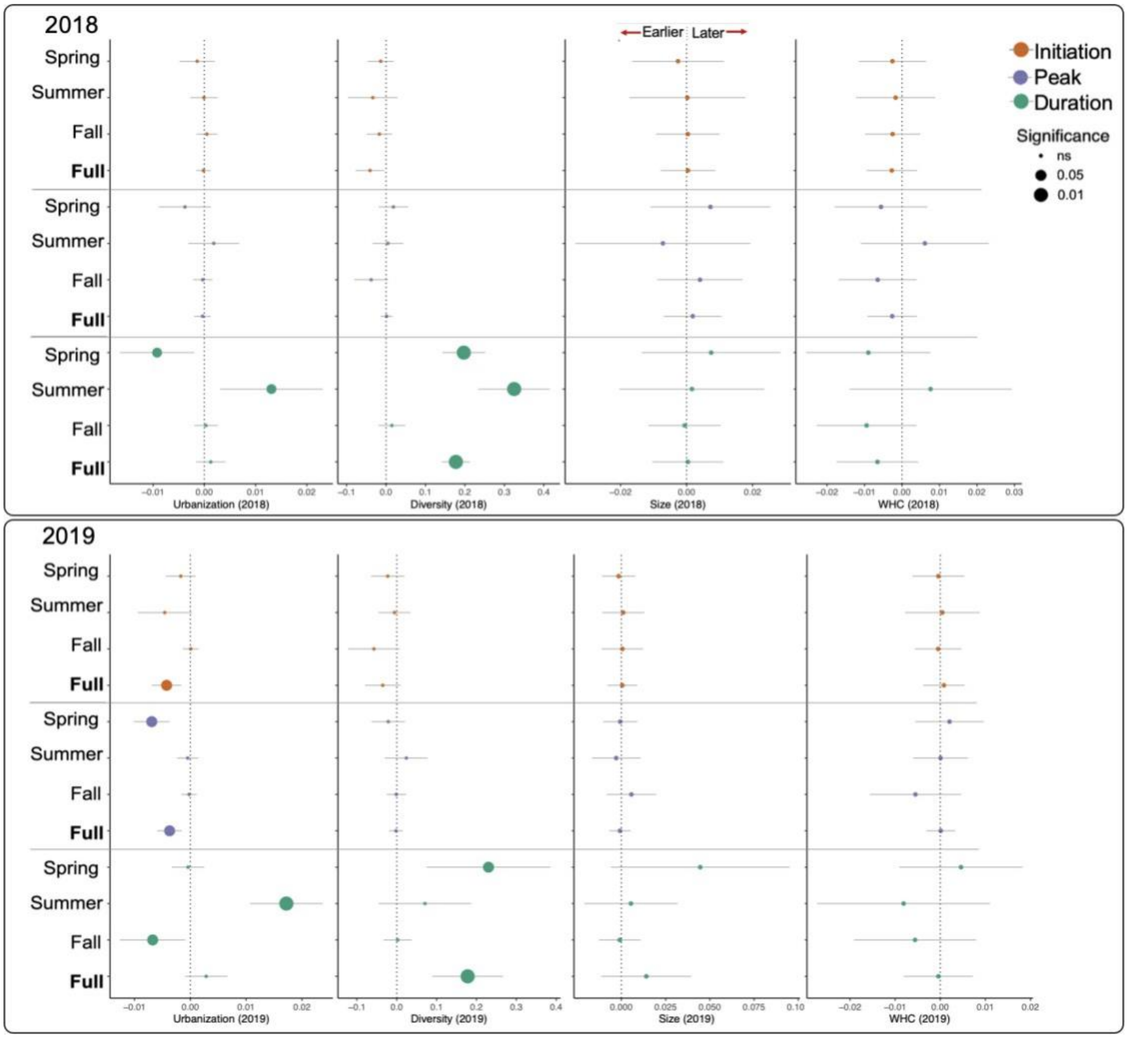

2018
2019
Earlier
Later
Spring
Summer
Fall
Full
Initiation
Peak
Duration
Significance
ns
0.05
0.01
Urbanization (2018)
Diversity (2018)
Size (2018)
WHC (2018)
Urbanization (2019)
Diversity (2019)
Size (2019)
WHC (2019)

Figure 3

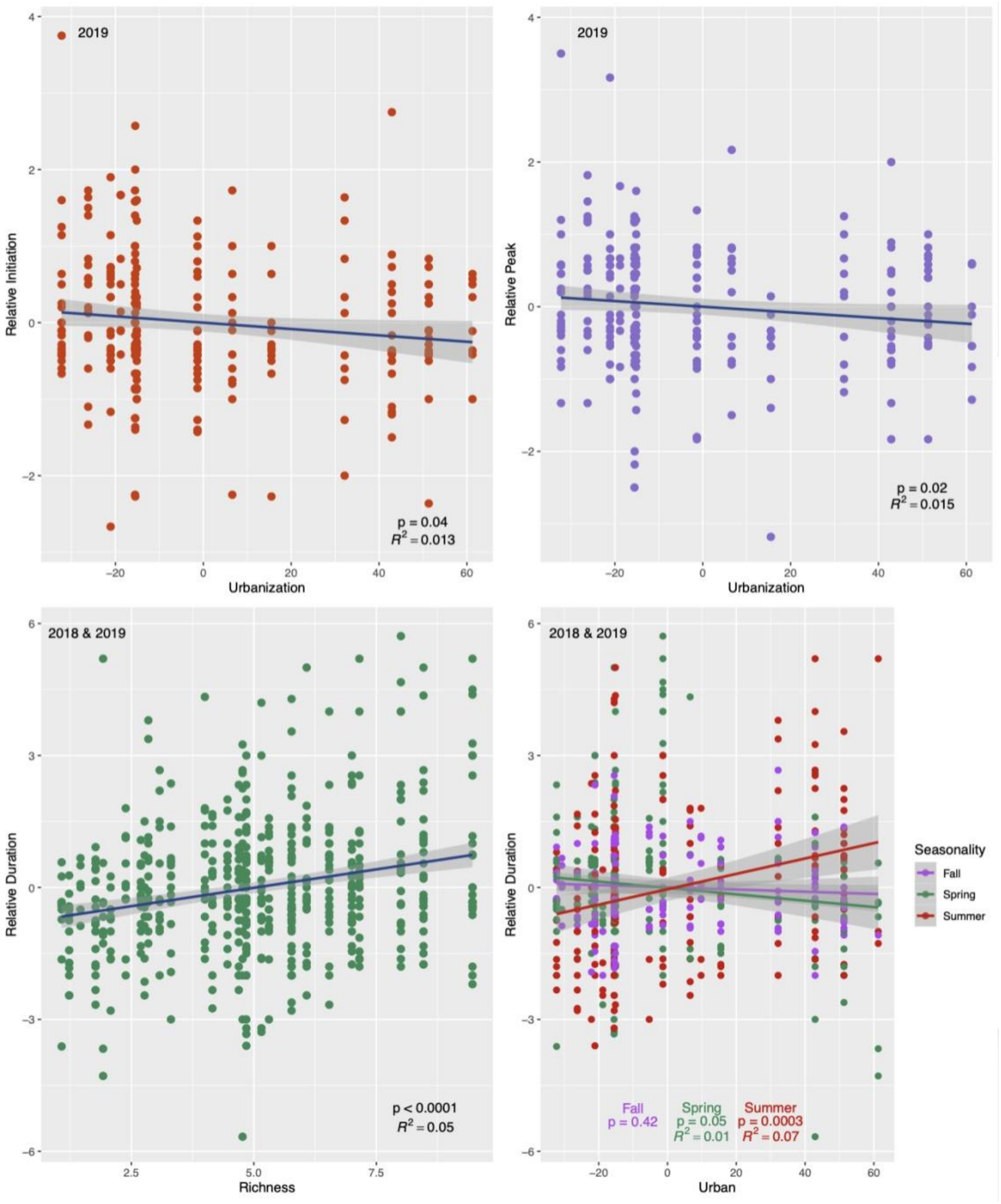

2019
Relative Initiation
Urbanization
p = 0.04
$R^2 = 0.013$
2019
Relative Peak
Urbanization
p = 0.02
$R^2 = 0.015$
2018 & 2019
Relative Duration
Richness
p < 0.0001
$R^2 = 0.05$
2018 & 2019
Relative Duration
Urban
Seasonality
Fall
Spring
Summer
Fall
p = 0.42
Spring
p = 0.05
$R^2 = 0.01$
Summer
p = 0.0003
$R^2 = 0.07$

Figure 4

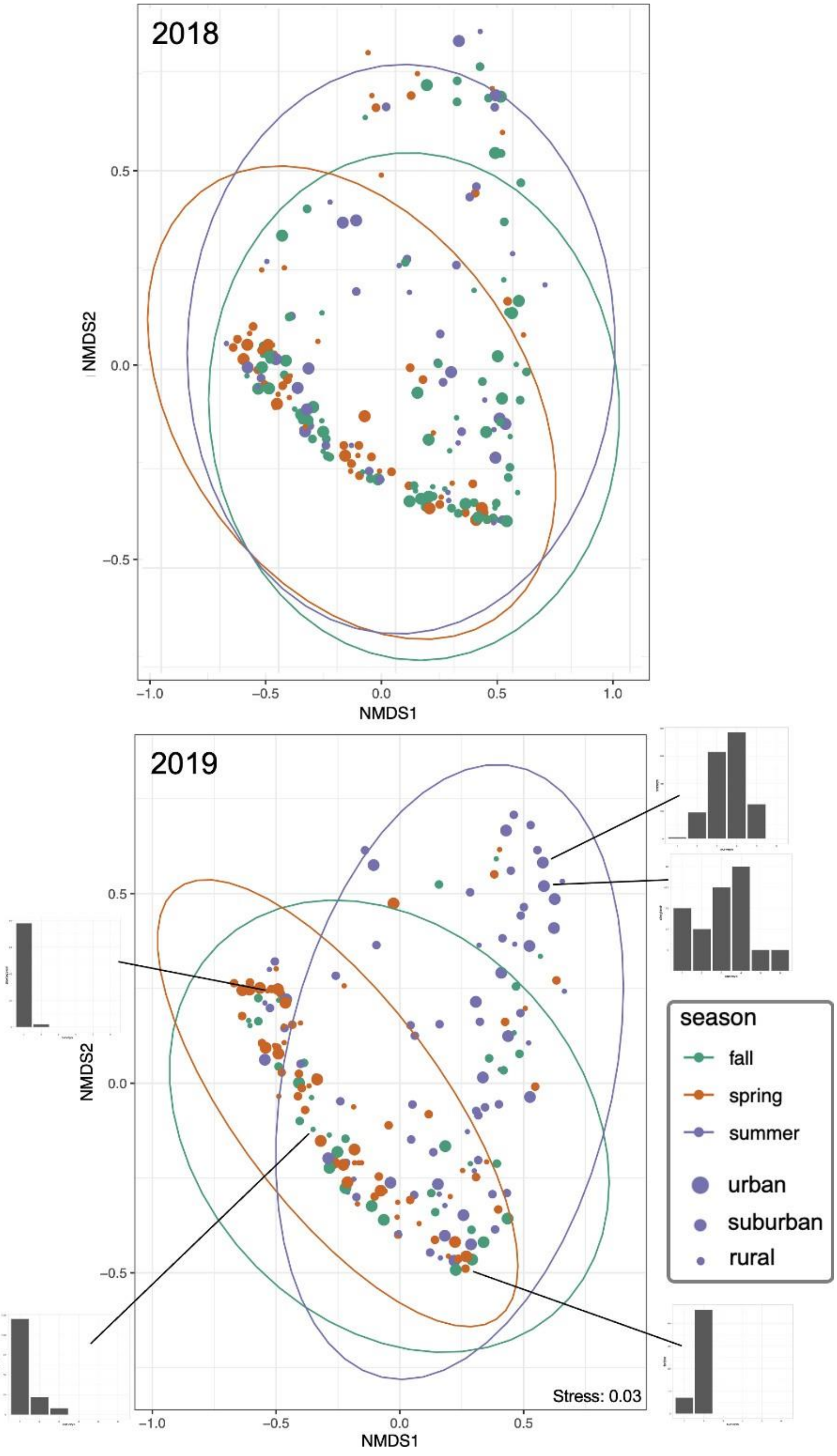
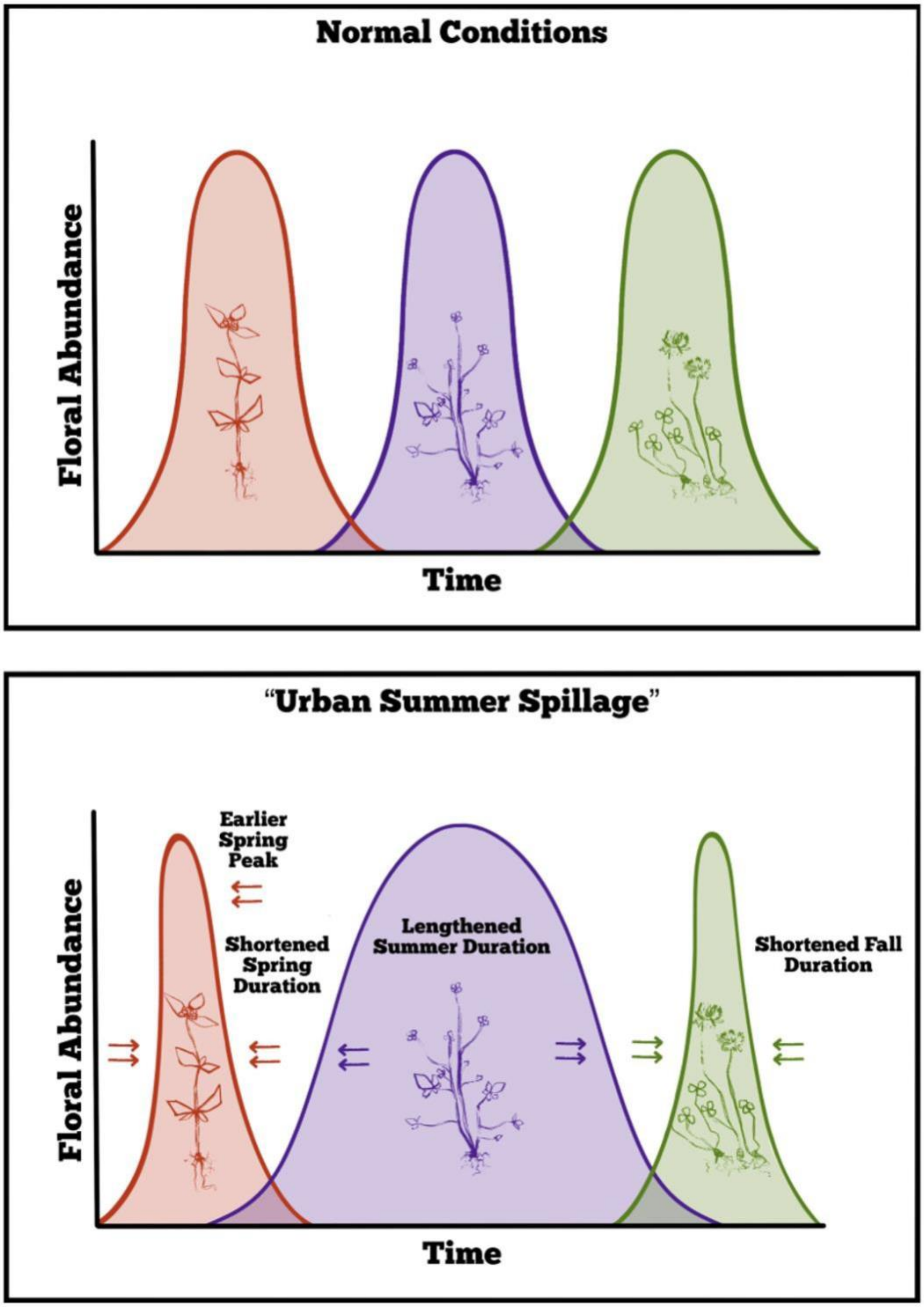

2018
NMDS2
0.5
0.0
−0.5
−1.0
−0.5
0.0
0.5
1.0
NMDS1
2019
NMDS2
0.5
0.0
−0.5
−1.0
−0.5
0.0
0.5
NMDS1
Stress: 0.03
season
fall
spring
summer
urban
suburban
rural

Figure 5


Normal Conditions
Floral Abundance
Time
"Urban Summer Spillage"
Earlier Spring Peak
Shortened Spring Duration
Lengthened Summer Duration
Shortened Fall Duration
Floral Abundance
Time

CHAPTER V:

SUMMARY AND FUTURE DIRECTIONS

SUMMARY

This dissertation demonstrates that grassland restorations are a powerful tool in the fight against rapid pollinator declines. Important to this though, I found that the quality and location of these restorations are a vital factor. High quality restorations with rich native forb communities and consistent management are better able to support diverse pollinator communities. Additionally, I found strong evidence that urban land usage around these restorations can influence both plants and pollinator communities existing within.

In chapter two I showed that globally, grassland restorations not only improve pollinator abundance and richness compared to degraded grasslands, but they may even fully restore communities to their remnant values. This is a valuable finding because although grassland habitats host an extremely high proportion of pollinator diversity, grassland restoration practices historically focus solely on the plant communities and not higher trophic levels, such as pollinators. The findings in this dissertation lends support to the theory “A rising tide lifts all ships” whereby a restoration focused on plant communities can also benefit higher trophic levels, such as pollinators. However, there is evidence that not all restorations are equal, and I found that older restorations supported higher pollinator abundance and richness than younger ones. Additionally, I found that restorations that applied multiple restoration tactics, (e.g., burning AND mowing), supported more pollinators than those that applied just one. Finally, I also saw butterflies to benefit more from restoration than bees, an interesting finding that deserves further investigation.

In chapters three and four I showed that the local and landscape-level parameters of a restoration are important determinants of how the plant and pollinator communities fare. At the landscape level, urbanization can have positive impacts for some species – increasing bee fecundity and lengthening summer flowering periods. However, it can have a negative effect for others –spring and fall forb species showing shortened flowering periods. Locally though, I consistently found that restoration quality—increased species richness and native species—had positive impacts on both the floral and pollinator communities. In bee communities I found increased fecundity in restorations with a higher proportion of native plants. This indicates a benefit from these native plants for the bee community, possibly through increased nutrient profiles, reduced foraging times, reduction of parasites, or other mechanisms that I was not able to identify. In the forb community, I saw lengthened flowering periods in restorations with high richness, which has the potential to offset some of the negative impacts of urbanization. This may also alleviate phenological mismatches between plants and their pollinators as temperatures continue to rise both locally, as a result of land use change, and globally, as a result of climate change.

FUTURE DIRECTIONS

While I was able to show that changes in land usage can impact pollinators and their floral resources in a number of ways, further work is warranted to understand how these shifts interact with each other and across trophic levels. A prime example of this is my research focused on floral phenology. While I found urbanization to have pronounced impacts on the initiation and peak date of floral phenology, I was not able to address how urbanization influenced wild bee phenologies.

As mentioned above, the advancement of floral phenologies has the potential to separate forbs and their pollinators temporally, with serious consequences. However, without knowing how wild bee phenologies shift in response to urbanization, I cannot confidently say what the ecological consequences are of these observed floral phenology shifts. It is entirely possible that bees will shift their phenologies in concert with forbs and therefore dampen the negative impacts on the system. Alternatively, bees may not be able to shift their phenologies in the same direction, or same magnitude, or at all, as their plant host species. In a recent study conducted in France, researchers found floral phenology to advance roughly four weeks earlier in urban areas, as we found in our system, though they found no change in pollinator phenology (Fisogni et al. 2020). Additionally, Forrest & Thomson (2011) conducted a field study on solitary cavity-nesting bees in the Rocky Mountains, US, and found similar asynchrony developing between plants and pollinators as a result of climatic warming. They found that while the bees' phenologies were tied to temperature thresholds, like plants, they were more constrained and were not able to shift their phenologies as much as their host plant species were. These results do not bode well for insects living in the urban heat island, however further research could help us better understand these shifting phenologies. With continued research, we could better understand the basic science driving these shifts, as well as how to mitigate these effects, like our finding that increased floral richness can extend floral duration, offsetting the mismatch potential in urban areas. Further research investigating solitary cavity-nesting bee phenologies along an urbanization gradient would build well off this research. New trap nests have been developed since I started this dissertation that allows researchers to observe nest construction throughout the season via plexiglass siding (https://www.youtube.com/watch?v=zqqLL4S0bDs&t=300s). These nests would be particularly valuable in allowing researchers to observe when females are constructing nests and if there are significant phenological shifts along an urbanization gradient, and if these shifts align with my observed floral phenology shifts.

My finding of extended population-level floral duration in high richness sites is among the most interesting findings of the fourth chapter, yet it is not yet fully explained. Several possible explanations for this phenomenon exist, yet they require further investigation. One possible explanation for the extended floral duration could be a result of increased competition for pollinators. In high richness systems, pollinators may be saturated with food choices, and as a result, individual flowers may go longer without being visited by a pollinator. In a low diversity system with fewer floral resources, pollinators will quickly visit a higher percentage of the flowers, resulting in faster floral senescing, and decreased population-level floral duration. Plants in higher diversity neighborhoods have been documented to experience decreased visitation rates and a higher proportion of heterospecific pollen (Arceo-Gomez and Ashman 2014). A 2017 field study found that bagging flowers could increase their longevity, indicating that lack of pollination can increase floral duration (Trunschke and Stocklin 2017). In a similar vein, a population lengthening its floral duration may be a form of bet-hedging to ensure cross-pollination. Ecological theory states that as community diversity increases, population stability decreases, due to increased competition (Thibaut and Connolly 2013). In a high diversity system, an individual plant likely does not have as many conspecific neighbors, and so it may stretch out its flowering time to ensure that its floral period is more likely to overlap with one of its conspecific neighbors. For example, several references have documented flowering plants in the tropics, where plants are rare and spread out, to have relatively long flowering periods of at least 22 days (Gentry 1976). However, one tropical tree, *Handroanthus guayacan*, is known to produce a “big bang” flowering event characterized by extreme synchrony within and among individuals and they have an abnormally short flowering period of roughly 3-4 days (Chen et al. 2018; Newstrom et al. 1994; Numata et al. 2013; Sakai et al. 2006). In a monoculture, or a system where one plant clearly dominates, species may be more likely to synchronize their reproductive period to an extreme degree, thus decreasing their reproductive time period. Similar to the tropical example above where trees synchronize in the span of days, this also plays out in masting systems common in temperate trees such as conifers and oaks, that synchronize their reproductive events at annual patterns.

Several interesting experiments could be developed to further test the influence pollinators have on population-level floral duration. One such experiment could directly test the hypothesis that reduced diversity may allow plants to more readily synchronize their phenologies and therefore decrease the population’s flowering period. Forbs could be grown in pots of one of two community diversity treatments: a monoculture, grown in a pot with several other conspecifics, or a high diversity pot with the same plant density, but increased species richness. Pots would then be bagged so that each pot is an enclosed air system and the only plant-to-plant communication is within one pot. If increased diversity is lengthening population-level floral duration, then we would expect the same plant species to flower for longer periods of time in the diversity pots compared to the monoculture pots. If this is a result of plants synchronizing their phenologies to ensure greater cross-pollination, then we wouldn't expect to see major differences in individual plant phenologies between treatments, but instead greater intraspecific variation between the start date and end date of each individual in a given species in the high diversity pots. This greater variation would lead to an observed increase in population-level floral duration in high diversity systems. However if extended floral duration in high diversity systems is the result of some other phenomenon, we would expect each individual to flower for longer periods, thereby extending the population's duration. The relationship between community diversity and intraspecific variation has long been debated (Westerband et al. 2021). Diversity may decrease intraspecific variation via increased competition for resources, leading to a 'niche packing' effect and strong selection against overlapping traits (Violle et al., 2012). Conversely, in habitats of increased diversity, landscape heterogeneity is likely to persist, which would lead to increased variation from individual to individual within a population. In a monoculture, it is likely that there is a more equal distribution of shade, nutrients, and soil moisture, which would decrease the variation in plant traits such as leaf nitrogen, specific leaf area, and possible phenology. While there is evidence for both negative and positive relationships, I argue that our observational study may add evidence to the argument that increased diversity can increase intraspecific variation. Further experiments like the one proposed above may further clarify this argument.

Finally, extended floral phenologies in high diversity systems may be a result of a positive feedback loop, whereby diversity begets diversity and facilitation is a central player. In a high diversity plant community, the C:N ratios, lignin composition and trace minerals of plant litter is more varied than in a monoculture, which will allow a wider range of fungi, bacteria, and archaea to persist in the soils (van der Heijden et al. 1998, Eskelinen et al. 2009, Schnitzer et al. 2011). This increased microbial diversity may lead to increased plant fitness and productivity as plant-soil partnerships increase. For example, Hahl et al. (2020) found that plants grown in soil microbial communities originating from plant monocultures caused plants to shift their investment to defense-related traits, and away from growth and reproduction. Other greenhouse and field studies have shown that rhizospheric organisms can have significant influences on floral phenology (Wagner et al. 2014, Forey et al. 2015, Lu et al. 2018). For example, arbuscular mycorrhizal communities can increase total floral production and floral rewards such as nectar and flower size (Barber and Gorden 2015). These increases in floral production almost certainly have the potential to increase population-level floral duration.

To address this hypothesis, I have already begun a greenhouse experiment investigating the influence soil microbial communities have on floral phenologies. In 2020, I collected soils from six sites that were surveyed in chapter four – three high plant diversity sites (with long floral duration) and three low plant diversity sites (with shorter relative floral duration). I then isolated the bacterial and fungal communities from these soils, and in a factorial design, added them to plants grown in sterile potting soil. Plants received one of the six site treatments (effectively one of two diversity treatments – high or low diversity), and then within these treatments, one of three microbial treatments – all microbes, bacteria only, or sterile. I expect to see increased biomass, floral production and duration in high diversity and full microbe treatments compared to low diversity treatments. This research will serve not only as basic science by understanding the role that facilitation plays in diversity-ecosystem-function, but also in an applied service, as it will inform stakeholders and land managers how to build the most robust and stable grassland restorations, a central goal this dissertation set out to answer.

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APPENDIX I

SUPPLEMENTAL DATA FROM CHAPTER II

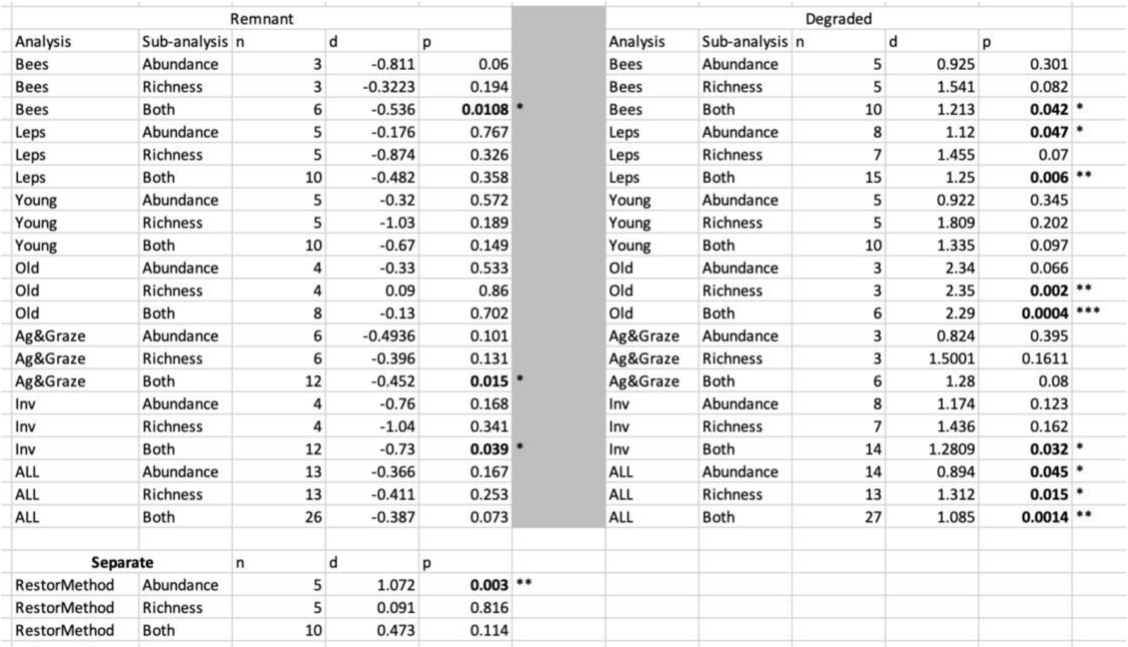
Appendix Table 1: Individual Study Values

This table outlines all the studies used in the analyses and the data points used from each study. The majority of studies fell into one of two groups, whether restoration values were being compared to a remnant grassland (Restoration vs Remnant) or the restoration values were being compared to a degraded grassland (Restoration vs Degraded). Within those groups data points were further grouped by whether they recorded pollinator abundance or richness values (Variable column). The columns Taxa, Age and Degradation pertain to the sub analyses conducted in our meta-analysis. Taxa refers to the taxonomy of the pollinators collected in each study (Bees, Lepidopteran or All flower visitors). Age of sites were split into two groups; Old (>10 years since restoration began) or Young (<10 years since restoration began). The following columns refer to the statistics of each study; sample size, averages, standard deviation, Hedges d, and variation. The "Restoration Methodology" sub analysis refers to a separate sub set of papers that did not compare restorations to remnant or degraded grasslands, but instead between restorations that used different restoration methodologies. The comparison of interest in our meta-analysis was between restoration that applied one restoration methodology versus those that applied multiple methods.

Study_ID	Authors	Variable	Treatment vs Control	Taxa	Age	Degradation	n1	n2	m1	m2	sd1	sd2	d	v
1	Griffin et al. (2017)	SR	Restored vs Degraded	Bee	Old	Agriculture	12	3	28.5000	12.3000	5.4689	4.1633	3.8832	0.9193
1	Griffin et al. (2017)	SR	Restored vs Remnant	Bee	Old	Agriculture	12	3	28.5000	33.0000	5.4689	3.0000	-0.8710	0.4420
1	Griffin et al. (2017)	Abundance	Restored vs Degraded	Bee	Old	Agriculture	12	3	119.0833	34.0000	35.5770	5.5678	2.5941	0.6410
1	Griffin et al. (2017)	Abundance	Restored vs Remnant	Bee	Old	Agriculture	12	3	119.0833	188.6667	35.5770	59.6518	-1.7297	0.5164
2	Summerville (2008)	SR	Restored vs Remnant	Lepidopteran	Young	Agriculture	3	5	70.4000	69.6000	23.9000	15.5000	0.0427	0.5334
2	Summerville (2008)	Abundance	Restored vs Remnant	Lepidopteran	Young	Agriculture	3	5	318.0000	260.0000	121.3000	119.7000	0.4824	0.5479
3	Helbing et al. (2015)	Abundance	Restored vs Degraded	Lepidopteran	Variable (not used in age subanalysis)	Invasion	5	5	16.4720	0.6460	13.8580	0.9580	1.6112	0.5298
4	Yamaura et al. (2012)	SR	Restored vs Degraded	Bee	Variable (not used in age subanalysis)	Other (not used in degradation subanalysis)	5	4	65.0000	57.0000	11.0000	10.0000	0.7559	0.4817
4	Yamaura et al. (2012)	Abundance	Restored vs Degraded	Bee	Variable (not used in age subanalysis)	Other (not used in degradation subanalysis)	5	4	464.0000	480.0000	171.0000	177.0000	-0.0922	0.4505
5	Maccherini et al. (2009)	SR	Restored vs Remnant	Lepidopteran	Young	Invasion	12	16	20.0000	29.8000	1.2200	2.9500	-4.1228	0.4494
5	Maccherini et al. (2009)	Abundance	Restored vs Remnant	Lepidopteran	Young	Invasion	12	16	44.4000	66.8000	7.2700	11.2300	-2.2968	0.2400
5	Maccherini et al. (2009)	SR	Restored vs Degraded	Lepidopteran	Young	Invasion	12	5	20.0000	10.2000	1.2200	1.9200	6.8040	1.6449
5	Maccherini et al. (2009)	Abundance	Restored vs Degraded	Lepidopteran	Young	Invasion	12	5	44.4000	22.6000	7.2700	7.5700	2.9655	0.5420
6	Skorka et al. (2007)	SR	Restored vs Degraded	Lepidopteran	Old	Invasion	3	6	20.3330	11.6700	1.1550	4.9970	2.1465	0.7562
6	Skorka et al. (2007)	Abundance	Restored vs Degraded	Lepidopteran	Old	Invasion	3	6	87.0000	25.0000	10.8170	13.9140	4.7314	1.7437
7	Ockinger et al. (2006)	SR	Restored vs Degraded	Lepidopteran	Young	Invasion	12	12	9.3000	11.2000	1.3000	1.5000	-0.4082	0.1701
7	Ockinger et al. (2006)	Abundance	Restored vs Degraded	Lepidopteran	Young	Invasion	12	12	101.0000	216.0000	21.0000	12.0000	-0.6984	0.1769
8	Poyry et al. (2004)	SR	Restored vs Degraded	Lepidopteran	Variable (not used in age subanalysis)	Invasion	6	6	22.4000	33.3000	4.7000	7.8000	-0.7570	0.3572
8	Poyry et al. (2004)	Abundance	Restored vs Degraded	Lepidopteran	Variable (not used in age subanalysis)	Invasion	6	6	126.0000	306.0000	73.8000	141.8000	-0.7133	0.3545
9	Rutgers-Kelly & Richards (2013)	SR	Restored vs Degraded	Lepidopteran	Old	Other (not used in degradation subanalysis)	4	3	58.5000	47.0000	11.3284	6.2450	1.1951	0.6853
9	Rutgers-Kelly & Richards (2013)	Abundance	Restored vs Degraded	Lepidopteran	Old	Other (not used in degradation subanalysis)	4	3	1435.7500	1269.3300	1065.4490	590.1820	0.1837	0.5857
10	Shuey et al. (2016)	SR	Restored vs Remnant	Lepidopteran	Old	Agriculture	4	4	16.8300	17.5000	4.1670	0.7070	-0.2242	0.5031
10	Shuey et al. (2016)	Abundance	Restored vs Remnant	Lepidopteran	Old	Agriculture	4	4	126.3330	105.0000	57.7920	21.2130	0.4901	0.5150
11	Ries et al. (2001)	Abundance	Restored vs Remnant	Lepidopteran	Young	Other (not used in degradation subanalysis)	4	8	3.2500	1.7500	0.3400	0.5100	1.2776	0.4430
11	Ries et al. (2001)	SR	Restored vs Remnant	Lepidopteran	Young	Other (not used in degradation subanalysis)	4	8	2.3100	1.6100	0.2000	0.2700	1.1630	0.4269
12	Shepard & Debinski (2005)	SR	Restored vs Remnant	Lepidopteran	Variable (not used in age subanalysis)	Agriculture	12	12	6.0000	9.1300	0.7900	0.7900	-1.1946	0.1964
12	Shepard & Debinski (2005)	Abundance	Restored vs Remnant	Lepidopteran	Variable (not used in age subanalysis)	Agriculture	12	12	11.7300	13.4800	2.6600	2.6600	-0.1984	0.1675
13	Denning & Foster (2017)	Abundance	Restored vs Remnant	All flower visitors (not used in taxa subanalysis)	Variable (not used in age subanalysis)	Agriculture	5	5	543.8333	683.2000	236.0727	156.5669	-0.6958	0.4242
13	Denning & Foster (2017)	SR	Restored vs Remnant	All flower visitors (not used in taxa subanalysis)	Variable (not used in age subanalysis)	Agriculture	5	5	98.0000	93.6000	12.8647	11.4368	0.3615	0.4065
14	Alison et al. (2017)	Abundance	Restored vs Degraded	Lepidopteran	Variable (not used in age subanalysis)	Agriculture	32	32	107.7030	49.1720	71.0210	39.7750	1.0169	0.0706
14	Alison et al. (2017)	SR	Restored vs Degraded	Lepidopteran	Variable (not used in age subanalysis)	Agriculture	32	32	18.7190	12.6250	6.1340	5.2370	1.0685	0.0714
15	Smith & Cherry (2014)	Abundance	Restored vs Degraded	Lepidopteran	Variable (not used in age subanalysis)	Other (not used in degradation subanalysis)	46	10	6.9700	2.8000	0.4900	0.6000	1.3498	0.1380
15	Smith & Cherry (2014)	SR	Restored vs Degraded	Lepidopteran	Variable (not used in age subanalysis)	Other (not used in degradation subanalysis)	46	10	2.7000	1.3800	0.1400	0.2500	1.4500	0.1405
16	Forup & Memmot (2005)	Abundance	Restored vs Remnant	All flower visitors (not used in taxa subanalysis)	Old	Other (not used in degradation subanalysis)	2	2	89.0000	83.0000	24.0416	25.4558	0.2423	1.0073
16	Forup & Memmot (2005)	SR	Restored vs Remnant	All flower visitors (not used in taxa subanalysis)	Old	Other (not used in degradation subanalysis)	2	2	40.5000	30.5000	17.6777	9.1924	0.7098	1.0630
17	Forup et al. (2008)	Abundance	Restored vs Remnant	All flower visitors (not used in taxa subanalysis)	Old	Invasion	4	4	344.7500	362.2500	132.1044	120.3170	-0.1385	0.5012
17	Forup et al. (2008)	SR	Restored vs Remnant	All flower visitors (not used in taxa subanalysis)	Old	Invasion	4	4	40.5000	32.0000	9.2916	4.9666	1.1410	0.5814
18	Tarrant et al. (2013)	Abundance	Restored vs Remnant	All flower visitors (not used in taxa subanalysis)	Variable (not used in age subanalysis)	Other (not used in degradation subanalysis)	9	9	12.8890	12.5600	9.2660	4.1600	0.0458	0.2223
18	Tarrant et al. (2013)	SR	Restored vs Remnant	All flower visitors (not used in taxa subanalysis)	Variable (not used in age subanalysis)	Other (not used in degradation subanalysis)	9	9	8.3330	11.5000	5.0250	6.2900	-0.5563	0.2308
19	Winsa et al. (2017)	Abundance	Restored vs Degraded	Bee	Young	Invasion	18	10	31.3890	37.9000	20.1730	40.6920	-0.2247	0.1565
19	Winsa et al. (2017)	Abundance	Restored vs Remnant	Bee	Young	Invasion	18	10	31.3890	33.1000	20.1730	16.3320	-0.0904	0.1557
19	Winsa et al. (2017)	SR	Restored vs Degraded	Bee	Young	Invasion	18	10	15.0560	15.5000	6.4210	10.1680	-0.0561	0.1556
19	Winsa et al. (2017)	SR	Restored vs Remnant	Bee	Young	Invasion	18	10	15.0560	17.3000	6.4210	6.7790	-0.3424	0.1576
20	Emery & Doran (2013)	SR	Restored vs Degraded	All flower visitors (not used in taxa subanalysis)	Young	Invasion	5	4	0.8300	1.2500	0.7500	0.9600	-0.4962	0.4637
20	Emery & Doran (2013)	SR	Restored vs Remnant	All flower visitors (not used in taxa subanalysis)	Young	Invasion	5	5	0.8300	1.8000	0.7500	1.4800	-0.8268	0.4342
20	Emery & Doran (2013)	Abundance	Restored vs Degraded	All flower visitors (not used in taxa subanalysis)	Young	Invasion	5	4	1.0000	2.5000	1.5500	2.0800	-0.8350	0.4887
20	Emery & Doran (2013)	Abundance	Restored vs Remnant	All flower visitors (not used in taxa subanalysis)	Young	Invasion	5	5	1.0000	1.6000	1.5500	1.3400	-0.4086	0.4086
21	Tonietto et al. (2017)	Abundance	Restored vs Degraded	Bee	Variable (not used in age subanalysis)	Agriculture	25	10	105.2400	149.3000	46.7000	60.0800	-0.8717	0.1509
21	Tonietto et al. (2017)	SR	Restored vs Degraded	Bee	Variable (not used in age subanalysis)	Agriculture	25	10	0.8800	0.8790	0.0800	0.0280	0.0200	0.1400
21	Tonietto et al. (2017)	Abundance	Restored vs Remnant	Bee	Variable (not used in age subanalysis)	Agriculture	25	11	105.2400	151.0000	46.7000	44.9600	-0.9940	0.1450
21	Tonietto et al. (2017)	SR	Restored vs Remnant	Bee	Variable (not used in age subanalysis)	Agriculture	25	11	0.8800	0.8900	0.0800	0.0390	-0.1430	0.1310
22	Lettow et al. (2018)	Abundance	Restored vs Degraded	Bee	Young	Invasion	5	5	54.0000	31.0000	8.0000	1.0000	4.0350	1.2140
22	Lettow et al. (2018)	SR	Restored vs Degraded	Bee	Young	Invasion	5	5	21.0000	12.0000	3.0000	1.0000	4.0250	1.2100
Only used in Restoration Methodology Subanalysis														
23	Vogel et al. (2007)	SR	Burn vs Burn & Graze	Lepidopteran	Old	Agriculture	26	27	8.6400	8.5300	1.4800	1.1900	0.0821	0.0756
23	Vogel et al. (2007)	SR	Graze vs Burn & Graze	Lepidopteran	Old	Agriculture	16	27	7.4400	8.5300	1.7800	1.1900	-0.7600	0.1063
23	Vogel et al. (2007)	Abundance	Burn vs Burn & Graze	Lepidopteran	Old	Agriculture	26	27	20.1700	31.4800	6.2800	7.2500	-1.6652	0.1017
23	Vogel et al. (2007)	Abundance	Graze vs Burn & Graze	Lepidopteran	Old	Agriculture	16	27	27.7800	31.4800	5.6700	7.2500	-0.5510	0.1031
24	Moranz et al. (2014)	Abundance	Burn and Graze vs Burn	Lepidopteran	Young	Agriculture	4	4	134.7500	117.2500	43.2400	56.1000	0.3494	0.5076
24	Moranz et al. (2014)	SR	Burn and Graze vs Burn	Lepidopteran	Young	Invasion	4	4	13.5000	14.7500	1.7300	2.8700	-0.5275	0.5174
25	Bendel et al. (2018)	Abundance	Season Long Graze vs Patch Burn Graze	Lepidopteran	Old	Invasion	2	2	12297.0000	29289.5000	5494.2200	6159.6100	-2.9114	2.0595
25	Bendel et al. (2018)	SR	Season Long Graze vs Patch Burn Graze	Lepidopteran	Old	Invasion	2	2	31.5000	30.5000	0.7100	4.9500	0.2828	1.0100
25	Bendel et al. (2018)	Abundance	Rotational Graze vs Patch Burn Graze	Lepidopteran	Old	Invasion	2	2	23981.0000	29289.5000	4584.8800	6159.6100	-0.9777	1.1195
25	Bendel et al. (2018)	SR	Rotational Graze vs Patch Burn Graze	Lepidopteran	Old	Invasion	2	2	41.0000	30.5000	8.4900	4.9500	3.2855	2.3494

Appendix Table 2: Model Outputs

The Model Outputs table shows the statistics for the Random Effects models used for the meta-analysis, using the data points in the previous table. (n) refers to the sample size, d refers to the random effects model estimate, and p refers to the p value (significance) for the model. Statistically significant analyses (p<0.05) are indicated in bold. The Separate analysis table refers to the restoration methodology sub analysis described in the previous table.



		Remnant							Degraded			
Analysis	Sub-analysis	n	d	p			Analysis	Sub-analysis	n	d	p	
Bees	Abundance	3	-0.811	0.06			Bees	Abundance	5	0.925	0.301	
Bees	Richness	3	-0.3223	0.194			Bees	Richness	5	1.541	0.082	
Bees	Both	6	-0.536	**0.0108**	*		Bees	Both	10	1.213	**0.042**	*
Leps	Abundance	5	-0.176	0.767			Leps	Abundance	8	1.12	**0.047**	*
Leps	Richness	5	-0.874	0.326			Leps	Richness	7	1.455	0.07	
Leps	Both	10	-0.482	0.358			Leps	Both	15	1.25	**0.006**	**
Young	Abundance	5	-0.32	0.572			Young	Abundance	5	0.922	0.345	
Young	Richness	5	-1.03	0.189			Young	Richness	5	1.809	0.202	
Young	Both	10	-0.67	0.149			Young	Both	10	1.335	0.097	
Old	Abundance	4	-0.33	0.533			Old	Abundance	3	2.34	0.066	
Old	Richness	4	0.09	0.86			Old	Richness	3	2.35	**0.002**	**
Old	Both	8	-0.13	0.702			Old	Both	6	2.29	**0.0004**	***
Ag&Graze	Abundance	6	-0.4936	0.101			Ag&Graze	Abundance	3	0.824	0.395	
Ag&Graze	Richness	6	-0.396	0.131			Ag&Graze	Richness	3	1.5001	0.1611	
Ag&Graze	Both	12	-0.452	**0.015**	*		Ag&Graze	Both	6	1.28	0.08	
Inv	Abundance	4	-0.76	0.168			Inv	Abundance	8	1.174	0.123	
Inv	Richness	4	-1.04	0.341			Inv	Richness	7	1.436	0.162	
Inv	Both	12	-0.73	**0.039**	*		Inv	Both	14	1.2809	**0.032**	*
ALL	Abundance	13	-0.366	0.167			ALL	Abundance	14	0.894	**0.045**	*
ALL	Richness	13	-0.411	0.253			ALL	Richness	13	1.312	**0.015**	*
ALL	Both	26	-0.387	0.073			ALL	Both	27	1.085	**0.0014**	**

Separate		n	d	p	
RestorMethod	Abundance	5	1.072	**0.003**	**
RestorMethod	Richness	5	0.091	0.816	
RestorMethod	Both	10	0.473	0.114	

APPENDIX II:
SUPPLEMENTAL DATA FROM CHAPTER III:

Appendix II Table 1: Site land usage

Plot	Open_Water	Developmental	Barren	Deciduous_Forest	Evergreen_Forest	Mixed_Forest	Shrub	Grassland	Pasture	Agriculture
Cherokee	0.267789	61.476664	0	33.843407	4.182606	0.102015	0	0	0	0
Seneca	0	67.460475	0	27.455727	4.548	0	0	0	0	0
Beckley Cree	1	28	0	48	1	0	1	1	17	2
Allee Wetlar	0.179	6.284232	0	56.4306	1.6826	0	0	11.3575	11.5742	11.7272
SkyDome	0.1782	4.13794	0	55.271199	9.4856	0.84033	0	13.5982	5.6532	9.371
Lowland Plai	0	14.1691	0	42.839	11.532	1.0958	0	5.109	15.9913	7.1228
Entrance Pra	3.0596	5.4813	0.2167	61.7925	8.1208	0.0637	0.45895	1.17287	17.33809	1.109
Research Bld	3.326	9.7234	0.2166	62.75	4.9955	0.0637	0.395	1.0959	13.4701	2.434
By Lake	2.1553	4.6294	0	66.4838	9.5906	0	0.0637	0.8162	14.5644	0.7397
Rear Prairie	2.8797	3.8735	0	73.5346	6.6258	0	0.369	0.99388	10.334	0.4587
Scotts Gap	0.1275	1.5552	0	78.7453	0.0637	0	0	3.672	15.058	0
HQ	0.369	13.3405	0.204	44.9796	0	0	0	0.0892	35.5504	0
Foxrun Rd	0.42	12.294	0	76.595745	5.848	0.089	0	1.5798	3.11	0
Grace Nurse	0.50968	17.2519	0	73.7385	4.2686	0	0	1.58	2.561	0
Hingckly	0.3699	2.9722	0.204	79.2294	0	0	0	7.91	8.3057	0

Appendix II Table 2: PCA loading scores

PCA Importance of Components	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10
Standard deviation	28.4591	11.7193	9.18654	6.25053	3.53604	1.21832	0.53019	0.22232	0.17415	0.11889
Proportion of Variation	0.7464	0.1266	0.07777	0.03601	0.01152	0.00137	0.00026	0.00005	0.00003	0.00001
Cumulative Proportion	0.7464	0.873	0.95075	0.98676	0.99828	0.99965	0.99991	0.99996	0.99998	1
Plot	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10
Cherokee	42.91025	-15.317367	-3.8228474	-1.1654685	-1.4180273	0.3636734	-0.1169276	-0.0902272	0.00815992	-0.1039406
Seneca	51.308361	-14.959726	-6.1443108	-1.866039	-1.7821827	0.69913125	-0.3052535	-0.2312265	-0.1791634	0.22909923
Beckley Creek	6.586791	-0.1438697	-9.4012193	4.0968034	2.1638003	-1.5658925	-1.3209778	0.48939582	0.04223995	-0.0494588
Allee Wetlands	-15.149239	4.9923846	-4.8010661	-10.995242	7.1366798	-2.6459756	0.13198473	-0.3401122	-0.2079209	0.03214149
SkyDome	-15.495134	4.8624493	-1.39252	-17.000281	0.4947194	2.06717946	0.13982991	0.27908577	-0.0154205	-0.162963
Lowland Plain	-1.33498	9.5425797	-11.887322	-8.4597158	-5.193518	-0.2384659	-0.0074221	-0.059484	0.45058908	0.15500994
Entrance Prairie	-18.820962	5.0041645	-3.6290374	2.2437557	-4.3416849	0.06469306	-0.6562379	0.01135804	-0.2204869	0.0156262
Research Bldg	-15.543983	1.2838031	-0.8024096	1.8378292	-1.3756262	-1.3300829	0.75171328	0.34428333	-0.1174532	0.08857779
By Lake	-22.116167	1.4066465	-0.9338305	1.6478904	-5.8161571	0.11735815	-0.3478567	-0.3462434	-0.1744611	-0.2400714
Rear Prairie	-26.215637	-3.1352916	4.6532535	2.3815999	-3.0948452	-0.4419576	0.29079419	0.18536329	-0.1458258	0.10277341
Scotts Gap	-32.253651	-4.9422221	1.558515	5.8053691	4.0239635	0.2326977	-0.4058138	-0.2411052	0.24989818	-0.0828898
HQ	-5.307737	14.6077184	-22.624936	11.3763415	2.3648755	1.33475036	0.88317938	-0.0722785	-0.0281252	-0.0174841
Foxrun Rd	-21.09743	-12.891394	8.5747712	0.7964127	-2.1498391	-0.2720031	0.42702695	0.0117733	0.07765318	-0.0031874
Grace Nursery	-15.457442	-13.972986	8.0387522	1.2418464	-0.7127592	-0.3993735	0.52309321	0.03030252	0.04813625	-0.0148802
Hingckly	-30.694128	-7.8516039	6.0901117	0.7794989	5.7673763	2.67425595	-0.4496818	0.03962173	-0.0414535	0.17105511
The Swamp	9.753534	19.2169677	16.4051184	1.732104	-1.4984312	-0.0897351	-0.1071481	-0.0917089	0.01283889	0.05984205
Thurman Hutchins	15.503425	13.7859003	11.669332	3.4126001	1.1879465	-0.4866951	-0.1879551	-0.13503	0.20254131	0.01584845
Iriquois	32.159273	-18.268875	-0.5251881	1.5760015	2.2943899	-0.6981438	0.50736344	0.07266606	0.15350784	-0.1225125
Portland	61.264857	16.7807206	8.9748329	0.5586936	1.9493196	0.61458568	0.2502893	0.14356599	-0.1152542	-0.0725859
Land_Class	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8		
Open_Water	0.15619479	0.5689528	0.67307841	0.25411057	0.04850006	-0.0483501	-0.0412456	-0.1842806		
Developmental	0.7491001	-0.5071488	-0.0252797	0.20601908	0.05572378	-0.0354047	-0.0539141	-0.188455		
Barren	-0.0001952	0.00306117	-0.000774	0.00515819	0.00280008	0.02417694	0.02846459	0.09845813		
Deciduous_Forest	-0.6214573	-0.5538751	0.30885615	0.27505633	0.05861687	-0.0783154	-0.0221642	-0.1817127		
Evergreen_Forest	-0.0342275	0.015016	-0.0339017	-0.2913716	-0.8574647	0.12259625	-0.1195995	-0.2127303		
Mixed_Forest	-0.0007913	0.00629821	-0.0074177	-0.0324246	-0.0265901	0.05036488	0.02185694	0.18010685		
Shrub	-0.001322	0.00064421	-0.0064027	0.00972108	-0.0083739	-0.0829861	-0.2450812	0.76091865		
Grassland	-0.0600884	0.02773539	-0.0365313	-0.5021789	0.4657694	0.53921937	-0.2922491	-0.2124992		
Pasture	-0.1502666	0.32324662	-0.6543382	0.50475677	0.06010178	-0.0325546	-0.1734418	-0.2327671		
Agriculture	-0.027869	0.07284034	-0.1167559	-0.4707368	0.18563305	-0.7399709	0.22556078	-0.1558609		
Woody_Wetland	-0.0100727	0.03815803	-0.0799052	0.05040768	0.00786636	0.3545115	0.86503839	0.09981209		
Herbaceous_Wetland	0.0005414	0.00456688	-0.0133626	-0.0126901	0.00102435	-0.0136087	0.06770047	-0.3122987		

Appendix II Table 3: AIC Model Averaging Outputs

Emerging Adults	Model-averaged coefficients						
	(conditional averages)						
		Estimate	SE	AdjustedSE	z	p	
	(Intercept)	-7.86E-17	2.14E-01	2.32E-01	0	1	
	native	4.91E-01	2.26E-01	2.43E-01	2.016	**0.0438**	*
	urban	4.17E-01	2.27E-01	2.45E-01	1.703	**0.0886**	.
	complexity	7.43E-02	2.55E-01	2.75E-01	0.271	0.7867	
	abundance	1.51E-01	2.60E-01	2.80E-01	0.539	0.5898	
	diversity	4.68E-02	2.55E-01	2.74E-01	0.171	0.8645	
	size	-1.41E-01	2.56E-01	2.76E-01	0.51	0.6098	
	Confidence Intervals						
		2.50%	97.50%				
	(Intercept)	-0.4536461	0.4536461				
	native	**0.01369273**	**0.9674493**				
	urban	**-0.0629997**	**0.8978892**				
	complexity	-0.463916	0.6125138				
	abundance	-0.3972638	0.6987567				
	diversity	-0.4908123	0.5844103				
	size	-0.6808809	0.3995355				
	lm(formula = alive ~ native + urban + 1, data = livebee)						
	Coefficients:						
	Estimate Std. Error t value Pr(>|t|)						
	(Intercept) -1.537e-16 1.969e-01 0.000 1.0000						
	native 5.277e-01 2.104e-01 2.508 0.0233 *						
	urban 4.410e-01 2.104e-01 2.096 0.0523 .						
	Residual standard error: 0.8583 on 16 degrees of freedom						
	Multiple R-squared: 0.3452,Adjusted R-squared: 0.2633						
	F-statistic: 4.217 on 2 and 16 DF, p-value: 0.03382						
Fecundity	Model-averaged coefficients						
	Conditional averages						
		Estimate	SE	AdjustedSE	z	p	
	(Intercept)	-1.16E-16	2.15E-01	2.32E-01	0	1	
	native	5.05E-01	2.22E-01	2.39E-01	2.113	**0.0346**	
	urban	2.83E-01	2.31E-01	2.49E-01	1.134	0.2568	*
	abundance	1.05E-01	2.77E-01	2.98E-01	0.351	0.7254	
	complexity	7.73E-02	2.44E-01	2.64E-01	0.293	0.7696	
	diversity	-1.02E-01	2.81E-01	3.02E-01	0.338	0.7357	
	size	-2.12E-03	2.43E-01	2.62E-01	0.008	0.9936	
	Confidence Intervals						
		2.50%	97.50%				
	(Intercept)	-0.4550615	0.4550615				
	native	**0.03651871**	**0.9743757**				
	urban	-0.2058177	0.7708715				
	abundance	-0.4790014	0.688177				
	complexity	-0.4399216	0.5945327				
	diversity	-0.6927069	0.4891504				
	size	-0.5160757	0.5118454				
	lm(formula = fecundity ~ native + 1, data = fecbee)						
	Coefficients:						
	Estimate Std. Error t value Pr(>|t|)						
	(Intercept) -1.332e-16 2.074e-01 0.000 1.0000						
	native 4.780e-01 2.130e-01 2.244 0.0385 *						
	Residual standard error: 0.9038 on 17 degrees of freedom						
	Multiple R-squared: 0.228		Adjusted R-squared: 0.1831				
	F-statistic: 5.034 on 1 and 17 DF, p-value: 0.03847						
Survivability	Model-averaged coefficients						
	Conditional averages						
		Estimate	SE	AdjustedSE	z	p	
	(Intercept)	-2.60E-16	2.11E-01	2.28E-01	0	1	
	urban	5.19E-01	2.19E-01	2.37E-01	2.191	**0.0285**	*
	native	2.00E-01	2.28E-01	2.46E-01	0.813	0.4164	
	size	-2.56E-01	2.59E-01	2.77E-01	0.924	0.3557	
	complexity	8.30E-02	2.72E-01	2.91E-01	0.285	0.7758	
	abundance	1.37E-01	2.75E-01	2.95E-01	0.466	0.6411	
	diversity	4.20E-02	2.46E-01	2.66E-01	0.158	0.8746	
	Confidence Intervals						
		2.50%	97.50%				
	(Intercept)	-0.4466201	0.4466201				
	urban	**0.05463335**	**0.9828839**				
	native	-0.2823555	0.6823906				
	size	-0.7998642	0.287498				
	complexity	-0.4882057	0.6541751				
	abundance	-0.4400524	0.7146548				
	diversity	-0.479183	0.5630907				
	lm(formula = survivability ~ urban + 1, data = survbee)						
	Coefficients:						
	Estimate Std. Error t value Pr(>|t|)						
	(Intercept) -2.624e-16 2.027e-01 0.000 1.0000						
	urban 5.128e-01 2.082e-01 2.463 0.0247 *						
	Residual standard error: 0.8834 on 17 degrees of freedom						
	Multiple R-squared: 0.263		Adjusted R-squared: 0.2196				
	F-statistic: 6.066 on 1 and 17 DF, p-value: 0.02475						

Appendix II Table 4 Plant species list:

Scientific Name	Common Name	Native Status	2018	2019
Achillea millefolium	Yarrow	Y	Y	Y
Agalinis tenuifolia	Pink 5star	Y	Y	Y
Ageratina altissima	Snakeweed	Y	Y	Y
Ageratina aromatica	White snakeroot	Y	Y	Y
Agrimonia parviflora	Long skinny yellow	Y	Y	Y
Agrimonia parviflora	Southern Agrimony	N	Y	N
Anemone sp.	Anemone	Y	Y	N
Antennaria sp.	Antenaria	Y	Y	N
Apiaceae spp. 1	UkCarrot 2	N	Y	N
Apiaceae spp. 2	Small carrot	N	Y	N
Apocynum cannabinum	Dogbane	Y	Y	Y
Apocynum sp.	yellow Dogbane	N	Y	Y
Asclepias syriaca	Purple milkweed	Y	Y	Y
Asclepias tuberosa	Orange Milkweed	Y	Y	Y
Asclepias tuberosa	Pink milkweed	Y	Y	Y
Asclepias viridis	Green Milkweed	Y	Y	Y
Asteraceae spp.1	Whory Daisy	Y	Y	Y
Bidens aristosa	Bidens	Y	Y	Y
Bidens sp.	Beggars tick	Y	Y	N
Brassica sp. 1	White Brassica	N	N	Y
Brassica sp. 2	Yellow Mustard	N	Y	N
Calystegia sepium	White Morning Glory	Y	Y	Y
Chamaecrista fasciculata	Yellow Patridge Pea	Y	Y	Y
Chrysanthemum leucanthemum	White Daisy (Regular Daisy)	N	Y	Y
Cirsium arvense	Teasel	N	Y	Y
Cirsium sp. 2	Purple Thistle	Y	Y	Y
Commelina communis	Dayflower	N	Y	N
Conoclinium coelestinum	Mistflower	Y	Y	Y
Coreopsis sp.	Tick trefoil	Y	Y	Y
Coronilla varia	Crown Vetch	N	Y	Y
Creeping mint?	Ground Ivy	N	Y	N
Daucus carota	White carrot	N	Y	Y
Echinacea paradoxa	Yellow Sundrop	Y	Y	Y
Echinacea purpurea	Purple Coneflower	Y	Y	Y
Eclipta prostrata	False Daisy	Y	Y	N
Erigeron philadelphicus	Lazy Daisy	Y	Y	Y

Erynigium yuccifolium	Green Thistle	Y	Y	Y
Eupatorium perfoliatum	Boneset	Y	Y	Y
Eupatorium sp.	Yellow Snakeroot	Y	Y	N
Fragaria virginiana	Strawberry	Y	Y	Y
Galium aparine	Bedstraw	Y	Y	Y
Gentianopsis crinita	Purple Petites	Y	Y	N
Geranium columbinum	Geranium	N	Y	Y
Geum canadense	Avens	Y	Y	N
Helenium amarum	Autumn Sneezeweed	N	N	Y
Helianthus maximilianii	Maximilian sunflower	N	Y	Y
Heracleum lanatum	Yellow Cow Parsnip	Y	Y	Y
Houstonia caerula	Bluets	Y	Y	Y
Hypericum adpressum	St J Wort	Y	Y	Y
Hypericum densiflorum	StJWortShrub	Y	Y	Y
Hypoxis hirsuta	Yellow star	Y	Y	N
Impatiens capensis	Jewelweed	Y	Y	Y
Lamiaceae spp.1	Creeping Purple Mint	N	N	Y
Lamiaceae spp.2	PinkMint	N	N	Y
Lamium amplexicaula	Dead Nettle	N	Y	Y
Lamium purpureum	-	N	N	Y
Lespedeza virgincana	Slender Bush Cover	Y	Y	N
Lobelia inlfata	Lobelia	Y	N	Y
Lonicera maackii	Honeysuckle	N	Y	Y
Ludwigia sp	Willow Primrose	Y	Y	N
Lycopus sp.	Cutleaf water horehound	Y	Y	N
Mimulus alatus	Mimulus	Y	Y	Y
Monarda fistulosa	Bee Balm	Y	Y	Y
Oenothera biennis	Evening Primrose	Y	Y	N
Ornithogalum umbellatum	St Bethlaham	N	Y	Y
Oxalis corniculata	Wood sorrel	N	Y	Y
Passiflora incarnata	Passionflower	Y	Y	N
Penstemon digitalis	White Trumpets (foxglove)	Y	Y	Y
Penstemon sp.	Pink Cup	Y	Y	Y
Perilla frutescens	Beefsteak mint	N	Y	N
Persicaria glabra	Pinknotweed	Y	Y	Y
Persicaria minor	White Pinknotweed	Y	Y	Y
Phlox maculata	Phlox	N	N	Y
Phyla lanceolata	FrogFruit	Y	Y	Y
Prunella vulgaris	Self Heal	Y	Y	Y

Ranunculus ficaria	Buttercup	N	Y	Y
Rorippa palustris	Yellow Cress	Y	Y	Y
Rorippa sylvestris	New Yellow Cress	N	Y	N
Rosa multiflora	-	N	N	Y
Rubus allegheniesis	Blackberry	Y	Y	Y
Rudbeckia hirta	Black Eyed Susan	Y	Y	Y
Rudbeckia triloba	Smaller shruby BES	N	Y	Y
Ruellia caroliniensis	Wild petunia	Y	Y	Y
Ruellia caroliniensis	Ruellia Stalks	Y	Y	N
Sabatia angularis	Sabatia	Y	N	Y
Salvia lyrata	Liarleaf Sage	N	Y	Y
Senecio vulgaris	Senecio (Ragwort)	N	Y	Y
Silphium integrifolium	Silphium	Y	Y	Y
Solanum carolinense	Vibrate Stamens	Y	Y	Y
Solidago sp.	Goldenrod	Y	Y	Y
Solidago sp. 2	Skinny Goldenrod	Y	Y	Y
Spiranthes odorata	Frilly Orchid	N	N	Y
Spiranthes vernalis	Spring ladies'-tresses	Y	Y	Y
Stellaria media	Chickweed	N	Y	Y
Stellaria sp.	Purple Chickweed	N	Y	Y
Symphyotrichum novae-angliae	Fall Aster	Y	Y	N
Symphyotrichum sp.	Heath Aster	Y	Y	Y
Taraxacum officinale	Dandelion	N	Y	Y
Tradescantia virginiana	Spiderwort	Y	Y	Y
Tragopogon dubius	Yellow Goatsbeard	N	Y	Y
Trifolium campestre	Yellow Clover	N	Y	Y
Trifolium pratense	Purple Clover	N	Y	Y
Trifolium repens	White clover	N	Y	Y
Valerianella radiata	Cornsalad	Y	Y	Y
Verbascum blatteria	Moth Mullein	N	Y	N
Verbena sp.	Vervain	Y	Y	N
Verbesina alternifolia	Yellow Coneflower	N	Y	Y
Veronia gigantea	Ironweed	Y	Y	Y
Veronica arvensis	Little Blue Mint	N	Y	Y
Veronica arvensis	Veronica	N	Y	N
Viola sororia	Violet	Y	Y	Y

CURRICULUM VITAE

Aaron N. Sexton
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EDUCATION

2017-pres.	Ph.D. University of Louisville, Department of Biology (Ecology track) Advisor: Dr. Sarah Emery Dissertation Title: "*Plant-pollinator communities responsive to both local and landscape level factors in grassland restorations*"
2013-17	B.A. University of Denver, Ecology & Biodiversity Advisor: Dr. Robin Tinghitella

PROFESSIONAL EXPERIENCE

2020	Adjunct Faculty, Spalding University
2018-pres.	Educational Consultant, Idlewild Insectarium. Developer and instructor for a series of educational courses open to the public at an urban insectarium. Work includes lectures and workshops covering a variety of entomological topics for ages 13+, depending on the course.
2013-17	Research Technician, University of Denver. Responsibilities: data collection, insect rearing, manuscript and proposal writing.
2016	Research Technician, Bonanza Creek LTER Alaska. Part of a team working with the LTER, USFS and Alaska DNR to collect data in the field and implementing a large-scale field study.

PUBLICATIONS

Sexton, A. N., Benton S. F., and Emery, S. M. 2021. Urbanization and plant diversity influence different parameters of floral phenology. (*in peer-review, manuscript available upon request*)

Sexton, A. N., Benton S. F., Browning, A. B., and Emery S. M. 2020. Reproductive patterns of solitary cavity-nesting bees responsive to both local and landscape factors. *Urban Ecosystems*. https://doi.org/10.1007/s11252-021-01116-4

Sexton, A. N. and S. M. Emery. 2020. Grassland restorations improve pollinator communities: a meta-analysis. *Journal of Insect Conservation*. https://doi.org/10.1007/s10841-020-00247-x

Jenck, C. S., W. R. Lehto, B. T. Ketterman, L. F. Sloan, **A. N. Sexton**, and R. M. Tinghitella. 2019. Phenotypic divergence among threespine stickleback that differ in nuptial coloration. *Ecology & Evolution*. https://doi.org/10.1002/ece3.6105

GRANTS AND AWARDS

2017-21	University of Louisville, Graduate Fellowship, $44,000
2021	Cornett Entomological Research Grant, $500
2021	Furnish Teaching Award, Top Graduate Student Teacher in U of L Biology Dept.
2020	Joan Ehrenfeld Award (*Top Student Presentation in Urban Ecology at ESA*)
2020	Kentucky Native Plant Society, $500
2020	Beechmont Garden Club, $1,000
2019	University of Louisville Graduate School of Arts & Sciences, $248
2019	National Science Foundation, Graduate Research Fellowship, Honorable Mention
2018	Kentucky Academy of Sciences, Marcia Botany Fund, $1,565
2018	Kentucky Natural History Society, $800
2018	University of Louisville College of Arts & Sciences, $500
2018	University of Louisville Biology Graduate Student Association, $175
2018	University of Louisville Graduate School of Arts & Sciences, $250
2016	University of Denver, Dean's Scholarship, $500
2015-16	University of Denver, H&B Agnew Scholarship, $500 (*Two-time awardee*)

PROFESSIONAL PRESENTATIONS

2020	Sexton, A.N., Emery, S.M., Benton, S., Browning, A., *Urbanization and native plants: How local and landscape level factors influence solitary bee communities*. Ecological Society of America Annual Meeting
2020	Sexton, A.N., Garces, K.R., *Urbanization influences floral reproductive output but not floral phenology*. Graduate Network of Arts & Sciences Symposium
2019	Sexton, A.N., Emery, S.M., *Floral phenology influenced by soil moisture, not urbanization*. Kentucky Academy of Sciences
2019	Sexton, A.N., *How urban areas are influencing plant-pollinator interactions*. Graduate Student Council Research Conference
2019	Sexton, A.N., Emery, S.M., Benton, S., *Floral phenology influenced by soil moisture, not urbanization*. Ecological Society of America
2018	Sexton, A.N., Emery, S.M., *Can urban prairie restorations support stable solitary bee communities?* Graduate Network of Arts & Sciences Symposium

TEACHING EXPERIENCE

Instructor-of-Record

2019-20	Environmental Biology (BIOL 263), University of Louisville

Instructor of record for both lecture and lab. (24 Students)
Instruction was face-to-face in 2019 and hybrid in 2020. Responsibilities: course design, lecturing, assessment & lab management

2020 Environmental Science (ENVS-101), Spalding University
Instructor of record for Environmental Science. (12 students)
Adjunct Faculty. taught online because of COVID-19. Responsibilities: course design, lecturing & assessment

Teaching Assistant

2021 Diversity of Life (BIOL 242), University of Louisville
Teaching the recitation section of Diversity of Life (40 students)
Responsibilities: lecturing, lab management & assessments

2020-21 Quantitative Biology (BIOL 244), University of Louisville
Teaching the lab section of Quantitative Biology (60 students)
Responsibilities: lecturing, lab management & assessment.

2017-18 Laboratory for Biology: Current Issues and Applications (BIOL 104), University of Louisville. Teaching lab section (80 students/semester)
Responsibilities: lecturing, lab management & assessment. Lab design in 2018.

Undergraduate Research Supervision and Mentoring

2020-pres Ally Michels – Guided on floral phenology data collection and storage, plant watering, root and shoot biomass collection.
Project title: *Effects of soil microbes on above and belowground biomass on Chamaecrista fasciculata.*

2020 Marissa Huber – Guided on pollinator observations, floral phenology counts, biomass data collection and general data formatting and storage.
Project title: *Effects of urbanization and pollinator limitation on Chamaecrista fasciculata*

2019-20 Adam Browning – Guided on floral phenology data collection, pollen storage and identification and general data formatting and storage. Guided on grant writing.
Project title: *Can bee pollen usage protect solitary bees against parasitism?*
Received two grants during mentorship totaling $3,500

2018-pres Lisa Heng (High School and Undergraduate) – Guided on field work, data collection, arthropod identification. Project title: *How doe1s land management affect tick abundances in urban parks?* 2nd place Regional & State Science Fair

2018 Kristen Ehringer – Guided on pollen storage and identification

2018-19	Sarah Fosnight – Guided on floral phenology data collection, plant biomass processing and method development. Awarded Summer Research Opportunity grant ($3,000)
2018-19	Heather Griffith – Guided on field work, soil processing and experimental design
2016-17	Tutor, University of Denver (Ecology courses and labs)

COMMUNITY ENGAGEMENT

2021	“*Other Pollinators*” invited talk, Yew Dell Botanical Gardens
2021	FirstBuild Video Series, Bee expert, “*Prototyping A Solitary Bee Bath House For Home Conservation, Gardening, And Pollination*”
2021	Kentucky Conservations Conversations, Radio interview
2021	Jefferson County Master Gardener Conference, invited speaker. “*Whats the buzz? Natural history, ecology and maintenance of solitary bees”*
2020	Forward Radio, Interview
2020-21	Lead Organizer, University of Louisville Biology Dept. Fall Seminar Series
2020	Kentucky Master Gardener Conference, invited speaker: “*Whats the buzz? Natural history, ecology and maintenance of solitary bees”*
2020	Beer with a Scientist, invited speaker & organizer: *Urbanization and native plants: impacts on solitary bee communities*
2019-20	TriBeta Association, Entering Graduate School Panel, Panelist
2018-20	Kentucky Science Center STEMinar Series, invited speaker: *Urbanization and native plants: impacts on solitary bee communities*
2018-20	Manual High School, Science Fair Judge
2019	WCHQ Community Spotlight, Interview
2019	Louisville Metro Parks Department, Safety event teaching students about plants and insects in the parks
2019	Chance Elementary, Earth Day Event, invited speaker discussing pollinators
2019	Manual High School, Mentor for STEM research and careers
2018-19	Central High School, advisor for science fair project
2018-20	Moore Middle School, Day of Science event. Students visiting the University of Louisville, engaging them in the scientific process, plants, seed dispersal and experimentation

MEMBERSHIPS

Ecological Society of America

University of Louisville Biology Graduate Student Association

President 2020-2021

Outreach Chair 2019-20

Kentucky Academy of Science

Kentucky Society of Natural History
Louisville Science Policy and Outreach Group

SKILLS

Plant rearing in field, greenhouse and climate-controlled settings
Uni- and multi-variate data analyses
Extensive knowledge of plant ecology
Experimental and observational research
Fluent in R, QGIS, ArcMAP and Microsoft
Effective presentation skills
Documentation, scientific and report writing
Building and maintaining collaborations
Training, mentoring and leading team members