**Possible Titles:**

“Flower resource enhancements promote long-term species richness in an urban pollinator metacommunity.”

“Flower resource abundance and dietary specialization determine colonization and extinction dynamics in an urban pollinator metacommunity” – more broad and basic ecology focused

“Flowering trees and shrubs are more important than herbaceous meadow enhancements for urban pollinator conservation” – more specific and applied

**Abstract**

To mitigate widespread pollinator declines, improvements to urban landscapes are needed. While recent studies have identified that increasing the availability of flower resources in urban habitats leads to higher immediate measures of pollinator biodiversity, it is unclear whether these urban habitat enhancements translate into long-term pollinator community growth. Further, it remains unclear whether benefits of enhancements extend to more specialized pollinator species which may be of higher conservation concern. To compare the effectiveness of woody flowering plant enhancements and herbaceous reduced-mow meadow enhancements for long-term pollinator conservation, we conducted 334 wild bee and hoverfly surveys across a span of three years in eighteen urban parks located in Vancouver, Canada. We applied a Bayesian community occupancy model to these data that, while accounting for imperfect detection in the sampling process, allowed us to determine how interannual pollinator metacommunity dynamics respond to interactive effects of pollinator dietary specialization and the amount/type of flower resource enhancement each park. First, we found that relative to more generalized pollinator species, dietary specialists were less likely to occur initially and had low colonization rates, indicating habitat selection restrictions on where they may occur. Herbaceous meadow enhancements were associated with high initial occurrence rates, while woody flower enhancements particularly favoured colonization by specialist species through time. Using estimates for effects on metacommunity processes we projected that herbaceous meadow enhancements encourage stable high measures of species richness, while woody flower enhancements promote increasing species richness through time. The results of this study indicate that both enhancement types have positive impacts on urban pollinator biodiversity. However, perennial shrub and tree amendments (especially including native species) may be more effective than herbaceous reduced-mow meadow initiatives for long-term pollinator conservation.

***Introduction***

There is growing evidence that insect pollinators are facing global declines (Wagner etc). (). Urbanization may contribute to pollinator declines because inhospitable impervious surfaces that dominate urban landscapes can prohibit nesting opportunities () and reduce flowering plant food resources (). Other aspects of the urban environment such as urban pollution, urban warming, elevated disease and/or elevated competitive pressure from introduced pollinator species may further limit pollinator health and survival in urban landscapes (). Currently, the area of developed greenspace in an urban landscape is not associated with pollinator occurrence () suggesting that these habitats are not optimally designed for pollinator conservation. Improving developed urban greenspaces so that they promote stable pollinator populations could help to mitigate pollinator declines and sustain valuable pollination services in cities and towns.

Because flower resources provide food in the form of nectar and pollen, increasing the availability of flower resources in urban greenspaces should benefit pollinators. Many recent studies demonstrate a positive association between urban flower resources and urban pollinator biodiversity, for example, … some quick details about the specific refs (refs). However, these short-term increases in pollinator abundance and/or diversity could be misleading if flower resource enhancements simply congregate pollinators that were already present rather than increasing the number of pollinators in the landscape by improving survival and/or reproduction (Veddeler 2006). Flower resource enhancements could even act as ecological traps if these dense resource patches inordinately attract pollinators while simultaneously providing lower-quality resources () such as difficult to digest pollens from Asteraceae plants including common urban dandelion and daisy weeds ().

Tracking interannual pollinator metacommunity dynamics across a range of flower resource levels could clarify whether urban flower resource enhancements promote pollinator health. Long-term increases in occurrence may emerge if . . . This approach of tracking metacommunity dynamics has been used, for example, to show that flowering hedgerows promote long-term pollinator occurrence in the agricultural landscapes of central California (M’Gonigle 2015; Ponisio, 2019). Demonstrating that urban flower resource enhancements increase interannual pollinator occurrence would tell us that these land management investments not only elevate short term metrics of urban pollinator biodiversity, but ultimately that they translate into long-term pollinator conservation.

Different strategies may be used to increase flower resources in urban lands. To optimize urban pollinator conservation planning, it would be necessary to determine which enhancement strategies have the strongest impact on long-term pollinator occurrence. Explain meadows versus shrub/trees both in more detail

Species specialization – habitat selection and specialization/conservation concern connection.

Pollen limitation stuff. Explain in more detail (including why urban pollination is important) and link to other studies to set up expectations. Possibly cite claire’s framework of pollinator exporter versus concentrator hypotheses.

~~Intro to the methods. Additionally, studies with low-temporal replication that compare abundance and diversity across point-count surveys may not be able to disentangle the effects of the environment or species traits on detection versus ecology (). For example, simultaneous effects of flower resource enhancements on the detectability of pollinators may confound estimates for the effects of flower resource enhancements on the actual number of individuals or species that are present (). Alternatively, specialized or rare species may be more difficult to detect thereby causing us to underestimate where and when they occur (). Maybe some allusion to similar studies in agricultural landscapes (poinisio and mgonigle).~~

With the explicit goal of creating improved habitat for pollinators and other forms of wildlife, the city of Vancouver (Vancouver, Canada) initiated a large-scale reduced mow meadow program in a subset of its urban parks beginning in 2020. This experimental management program resulted in parks with a spectrum of different herbaceous flower resource levels. We surveyed plant and pollinator communities for multiple years in parks with the reduced mow management as well as in similar parks that did not receive the experimental management to test the effect of annual average herbaceous flower abundance of a site on pollinator metacommunity dynamics. Simultaneously, we collected data on the tree and shrub flower resource availability within each park site, allowing us to compare the effect size of increasing annual average tree and shrub flower resources against the effects of increasing herbaceous flower resources. We anticipated that both resource sources would increase pollinator colonization and persistence. By examining the effects on system dynamics (not simply comparing snaphsot estimates of abundance or diversity of pollinators) we aimed to project the trajectory of pollinator communities in sites with different types and levels of flower resource enhancement. With this work we aimed to identify whether enhancement strategies that are most effective for long-term pollinator conservation so that we could inform future management decisions both within our city and more broadly. By incorproating information about pollinator diet breadth we aimed to both understand how generalizable species traits impact the way that pollinator species navigate the spatial and temporal landscape in a human dominated system and moreover whether the recommended conservation management strategies benefit species of highest conservation concern.

**2. Methods**

***2.1. Data collection***

***2.1.1 Site selection***

We selected eighteen parks for multi-year monitoring. Half of the parks (nine parks) received a reduced mowing management regime, where traditionally intensively managed lawn space was left unmowed (or mowed only one to two times) from April – August of each year. No-mow areas constitute a portion (~0.75 – 2 hectare areas for the sites we selected) of the larger area of each park. These herbaceous flower enhancements were initiated in 2020 by the City of Vancouver (Vancouver, BC) with the explicit goal of creating semi-natural habitat that supports urban wildlife – including pollinators. These areas were also seeded with a mix blend of wildflower species (list species in supplement). The other nine parks were mowed ~biweekly during the spring and summer season. The management manipulations resulted in a gradation of variation in flowering plant resources that was subsequently surveyed and quantified and provided an opportunity to test the effects of a continuous range of herbaceous plant flower resources – from what we expected to be generally low in the biweekly mowed and unseeded sites along a continuum to the least mowed and most effectively seeded sites.

To isolate the impacts of park specific flower resources on pollinators we standardized our sites to limit the impacts of other potential confounds. We limited the influence of landscape context on by selecting park sites within low-medium density neighborhoods with low variation in the amount of impervious surface cover or tree cover within 1km radius of the central survey point of each park (supplement). We chose parks of approximately similar size with the total park space ranging from \_ to \_, with one park that was larger (Queen Elizabeth park) (supplements). Parks that received a reduced mowing treatment did not have significantly different proportion of impervious surface or tree cover in the surrounding landscape and were not on average larger than the parks that were mowed biweekly (supplement). We randomized our site selection with respect to mowing management from the east to west side of the city (supplement) to reduce potential confound of consequences of socieoeconomic status which may be spatially correlated and may mediate the quality of resources or management invested in a park or surrounding neighborhood greenspace (cite). To ensure intra-annual site independence we chose sites that were at least 1km distance from the nearest site (the upper end of a typical wild bee foraging ranges) (supplement). Overall, these controls reduced variation between park sites outside of flowers in lawn/meadow space and/or the curated trees and shrubs within the park space. Maybe put together a landscape style figure that shows some of these things?

Figure – site locations and pictures of site habitats – and woody perennial flower resources?

***2.1.2 Plant surveys***

We visited the 18 selected parks 6 times per year for 3 consecutive summers (2021, 2022, and 2023) to survey the plant and pollinator communities. The earliest survey in each year was conducted on \_, \_ and \_; the latest survey conducted on each year was on \_, \_ and \_. We conducted two different plant community surveys on each visit. First, we surveyed the herbaceous plant community in the reduced mow area or analogous lawn space (what the meadow would have looked like if not mowed) with the intention of quantifying the outcome of management on variable plant community trajectories that we suspected would be linked to pollinator community trajectories. We tagged a gps point in our first year of the study near the center point of a 1 hectare area of the park containing reduced meadow or an analogous lawn space. We then counted all ‘floral units’ in twenty 1m2 quadrats with quadrats placed every 3 metres in each of 4 axes of a cross (4 transects of 5 quadrats radiating out from the center point). In the case of species with tightly packed inflorescences (Asteraceae, Trifolium, Medicago, …) we counted each inflorescence as a floral unit, otherwise, we counted each flower as one floral unit (). Plants were identified using a regional taxonomic key () supplemented with the park management seeding guide (supplement). If the quadrat following the transect would be placed on a trail, impervious park structure, or under the crown of a tree, we moved to the other side of the obstacle, advanced an additional 1 metre along the transect and then placed the quadrat to continue the transect sampling design. We averaged the flower resource units across the six surveys within each year to get an annual site-specific estimate of herbaceous flower abundance.

We quantified the flower resources offered by shrubs and trees by conducting walking transects through the 1 hectare survey area. We counted all flower units on all trees and shrubs within the survey area using two surveyors to confirm that all trees and shrubs within the site were counted. For tall trees and shrubs that could not be counted directly, we counted the number of floral units on five inflorescences, took an average, and then multiplied by a visual estimate of the number of inflorescences on the tree or shrub. Plants were identified using a combination of a regional taxonomic key () and a city shrub and tree planting guide (). We again averaged the flower resource units across the six surveys within each year to get an annual site-specific estimate of woody plant flower abundance.

We collected pollinator interaction data (see below) and used this data in part to determine whether different plant species counted in our surveys were of potential pollinator value. We filtered out floral units from both the herbaceous flower and woody plant flower data sets if we detected fewer than 5 potential plant-pollinator interactions during the entirety of our study. For example, yellow clover was abundant across sites but has minute (~\_ mm) flowers that we observed insects interacting with a total of three occasions; ornamental *Prunus sp.* trees were also abundant across sites but we never detected an insect interacting with these plants. These suspected low-value plants were filtered out so that we could compare the effect of changes in the abundance of flowers that provide viable pollen and nectar resources.

Finally, we z-score standardized the annual average (log) abundance of herbaceous flower resources and the annual average (log) abundance of woody plant flower resources to transform our predictors into a measure of how many standard deviations above or below each park is in terms of its flower resources relative to the average park in the sample (Gelman). As such, the estimates for parameters taking on flower abundance data represent the association between a response variable (occurrence, colonization, persistence or detection) and an increase in one standard deviation of the predictor (Gelman).

***2.1.3 Pollinator surveys***

We conducted 20-minute pollinator surveys by walking a spiral transect of the 1 hectare survey area in each park, use a sweep net to capture all hoverflies and wild bees that we observed interacting with flowers. We focused on wild bees and hoverflies because… . We only collected pollinators interacting with flowers so that we could simultaneously gather information to later make inferences about species dietary specialization from our pollinator detection data. If we completed the spiral transect before the 20-minute time period ended, we returned to any patches within the 1 hectare survey area where pollinators were observed to be most abundant. The 20-minute timer was paused for vialling and labelling the insects once an insect was securely captured in the net. We also used the timer to limit surveying in one area of the plot (a patch of flowers within arms reach) to a maximum of 2 minutes even if there were remaining uncaptured pollinators within the arms reach patch. This allowed us to ensure that we had enough time to survey across as much of the entire 1 hectare survey area as possible to cover our search across fine scale heterogeneity in the types of plants and pollinators distributed within each hectare survey area.

Pollinators netted during the sampling effort were returned to the lab for under microscopy using taxonomic keys () and reference specimens from the UBC Spencer Entomological Collection. Voucher specimens were deposited in the UBC Spencer Entomological Collection and in the lab collection. For a select number of common species for which female individuals are readily identified by eye in the field (*Apis melifera*, *Bombus vosnesenskii, Bombus mixtus, Bombus flavifrons, Bombus nevadensis, Bombus melanopygus, Halictus rubicundus, Agapostemon texanus, Anthidium oblongatum* and *Melissodes microstictus*), we released the female pollinators from our cooler back into the park at the end of the survey period. This was intended to reduce unnecessary lethal sampling and to reduce interference with a separate simultaneous mark-recapture study conducted at these sites. If we were not confident about identifications, we kept the specimen for identification in the lab. We caught and released honey bees during our surveys but did not include them in any of our analyses because there numbers may be driven by the spatial locations of managed hives rather than the local or landscape habitat.

We quantified the diet specialization of each species using the plant interaction collected during our pollinator surveys. Following Ponisio and Mgonigle, we classified dietary specialization using the species-specific “Bluthgen’s d” metric. Bluthgen’s d characterizes the distribution of plant species that a pollinator interacts with relative to the availability of the plants. Pollinators that interact with many plant species approximately in proportion to the relative availability of those plant species are scored as most generalized (low d’), while pollinators that interact with very few plant species even though those plant species have low availability are scored as most specialized (high d’). Bluthgen’s d was calculated using the bipartite package which extracts the .. from a system wide network of interactions. We added interactions from other recent studies that have recorded plant-pollinator interactions for wild bees and/or flies in the Vancouver metro area (do and cite) to the interaction data set before calculating species d’, which allowed us to have a stronger characterization of the full range of choices and relative frequency of choices made by each species reducing the chance that the choices made in our more limited dataset were do to random chance rather than true preference. d’ scores which range between 0 and 1 were z-scored for standardization prior to our analysis to facilitate interpretation of coefficient parameter estimates.

***2.2 Statistical analyses***

We used multi-species dynamic occupancy models to estimate initial occurrence states (whether species were present or absent at each of our sites in the first year of the study) and how these occurrence states changed over the subsequent years of our study. Species that occurred at a site in a given year can either persist to the following year or experience local extinction. Species that do not occur at a site in a given year may occur in the following year if a colonization event takes place. Information about these dynamic processes can then be used to infer the composition and trajectory of pollinator communities at different time points under particular environmental suites. The hierarchical model structure that we used explicitly incorporates uncertainty in the detection process into the estimation of these ecological parameters. Because we aimed to understand process patterns for the overall pollinator community, rather than for individual pollinator species, we used a model structure with an additional hierarchical layer that linked species-specific parameter estimates assuming that the processes for each species come from common distributions with community mean and variance features that we estimated. Linking species-specific parameters in this way allowed us to include data for species that were seldom occurred (rare species that we were particularly interested in tracking) and thus would otherwise be difficult to track.

For species *i*, we let *Zijk* represent its true occupancy state (presence or absence) at site *j* in year *k*. We assumed that the occupancy of species *i* at site *j* in year *k* is the outcome of a Bernoulli random variable *Zijk ~ Bernoulli(PSIijk)*. In the initial year of the study we treated PSIijk as an probability of occurring given all prior history of the site and community, where PSIijk = PSI\_1ijk. Because a species occurrence in subsequent years is dependent on the occurrence state in the previous year as well as a colonization/persistence process, we for all years after the initial year of the study we assumed that PSIijk = PSIijk-1 \* PHIijk + GAMMAijk \* (1 - PSIijk-1). This induces a temporal lag where if the species is inferred to be more likely present in year k-1 (PSIijk-1 approaches 1) then we estimate the likelihood of inferred presence/absence in year *k* given a value of a proposed value of PHIijk. If the species is inferred to be more likely absent in year *k*-1 (PSIijk-1 approaches 0) then we estimate the likelihood of inferred presence/absence given a value of a proposed value of GAMMAijk.

Using a logit transformation to bound PSI1, PHI and GAMMA between 0 and 1, we then modeled linear scale effects of species identity and habitat on the probability of initial occurrence and on the probability of annual state transitions (persistence or colonization) as:

as:

1. LOGIT( PSI\_1ijk ) = PSI\_1 [i] + PSI\_1\_1 \* d’[i] + PSI\_1\_2 \* woody flower abundance[j,k] + PSI\_1\_3 \* herbaceous flower abundance[j,k] + PSI\_1\_4 \* d’[i] \* woody flower abundance[j,k] + PSI\_1\_5 \* d’[i] \* herbaceous flower abundance[j,k];
2. LOGIT ( PHIijk )= PHI\_0[i] + PHI\_1 \* d’[i] + PHI\_2 \* woody flower abundance[j,k] + PHI\_3 \* herbaceous flower abundance[j,k] + PHI\_4 \* d’[i] \* woody flower abundance[j,k] + PHI\_5 \* d’[i] \* herbaceous flower abundance[j,k];
3. LOGIT( GAMMAijk ) = GAMMA\_0[i] + GAMMA\_1 \* d’[i] + GAMMA\_2 \* woody flower abundance[j,k] + GAMMA\_3 \* herbaceous flower abundance[j,k] + GAMMA \_4 \* d’[i] \* woody flower abundance[j,k] + GAMMA\_5 \* d’[i] \* herbaceous flower abundance[j,k];

Here, PSI\_1\_0, PHI\_0 and GAMMA\_0 represent global intercepts in initial occurrence, persistence and colonization respectively. PSI\_1\_0\_SPECIES[i], PHI\_0\_SPECIES[i] and GAMMA\_0\_SPECIES[i] represent species-specific effects on each of these processes, with each assumed to be the outcome of a normally distributed random variable: PSI\_1\_0\_SPECIES[i] ~ NORMAL(0, sigma\_ PSI\_1\_0\_SPECIES), PHI\_0\_SPECIES[i] ~ NORMAL(0, sigma\_ PHI \_0\_SPECIES) and GAMMA\_0\_SPECIES[i] ~ NORMAL(0, sigma\_ GAMMA\_0\_SPECIES).

Slope parameters 1 represent effects of species-specialization (d’). Negative values of parameters 1 would indicate that more specialized species are less likely to have occurred initially, and less likely to persist or colonize through time. Slope parameters 2 represent effects of annual mean site-specific woody flower abundance, while slope parameters 3 represent effects of annual mean site-specific herbaceous flower abundance. Positive values of parameters 2 and 3 would indicate that increasing strength of either flower abundance sources increases the odds that a species occurred initially or persists or colonizes through time. Slope parameters 4 and 5 represent interactions between species-specialization and woody flower and herbaceous flower abundances, respectively. Positive values for the interaction parameters would indicate that rates of initial occurrence, persistence and colonization for specialist species are more positively affected by stronger woody flowering plant or herbaceous flowering plant enhancements relative to the rates for more generalist species.

To estimate and account for uncertainty in the true occupancy states, *Zijk*, we then assumed that detection of a species at a site in each year on the *l*th visit, *Vijkl*, was the outcome of a Bernoulli random variable: *Vijkl ~* BERNOULLI(*Zijk \* pijkl*). We modelled heterogeneity in detection rate (the probability of observing a species given that it is present) on a linear scale using a logit-link function:

1. LOGIT( pijkl ) = p0[i] + p1 \* degree[i] + p2[i] \* date[j,k,l] + p3[i] \* (date[j,k,l])^2 + p4 \* survey flower abundance [j,k,l]

Where p0 represents a global detection intercept with normally distributed species-specific variation: p0\_species[i] ~ NORMAL(0, sigma\_species\_p0). We used p1 to estimate and explain part of the variation in detection rates potentially due to species degree, where positive values of p1 would indicate that species that have a high degree (make connections with many different plant species) are generally easier to detect. Many pollinators have shorter flight seasons that do not span the entire summer and therefore detectability should vary throughout the summer according to each species unique phenology. By including date[j,k,l] and date[j,k,l]^2 in the model, the detection probability was able to vary around a species-specific peak (p2) with a species-specific decay (p3). Positive values of p2 indicate that a species phenology peaks later than the average survey date. More negative values of p3 would indicate that a species has a very short phenology window (rapid decay in detectability around it’s peak), while values of p3 closer to zero would indicate that a species has a relatively wide phenology (no decay in detectability over the course of the spring/summer season). Slope parameter p4 represents an effect of survey specific flower abundance, accounting for the average deviation between woody flower resources and herbaceous flower resources on a given site visit. Positive values of p4 would indicate that species are more likely to be detected on a visit when more flowers are in bloom. Including survey specific flower resource covariate here allowed us to control for a potential confound between effects of flower resources on occurrence versus simultaneous effects of flower resources on the ease of netting a species in the survey area.

We used a hierarchical community model that links together species-specific parameters by assuming that they come from a shared distribution. Specifically, we treated the values for PSI1\_0, PHI0, GAMMA0, p0, p2 and p3 were each drawn from normal distributions defined by community mean and community variance parameters that we also estimated: X[i] ~ NORMAL( MU, SIGMA ).

We fit the model to our three years of detection data using a Bayesian statistical framework with models written in the probabilistic programming language STAN (), implemented from R using the “rstan” package (). Following best practices we tested the effectiveness of our custom models using a simulation-based approach (supplements). We used weakly-informative priors to discourage HMC simulations from searching for unrealistic parameter values (i.e., rates of occurrence or detection approaching positive or negative infinity). We ran our model for a length of 10,000 HMC simulations, discarding the first 5,000 simulations as warmup. To ensure that chains were adequately mixed and that possible parameter spaces were efficiently explored we confirmed that Ruben-Gelman Rhat values were below 1.05 for all parameters, that our model did not encounter any divergent transitions after the warmup period and that the effective samples sizes were \_. We assessed goodness of fit of our model using a visual posterior predictive check: at each step in the HMC run, we simulated the total number of detections across all visits for each species given the parameter estimates proposed by our model; after fitting the model we compared the true number of detections in our dataset and confirmed that this number fell within the lower and upper 95% quantiles of detections predicted by our model (supplement). R and STAN code as well as all of our data are available online (see data availability). We consider that we have weak certainty that an unknown parameter has a positive or negative effect if the 50% Bayesian Credible Interval (BCI) did not overlap with zero; we consider that we have strong certainty that an unknown parameter has a positive or negative effect if the 95% Bayesian Credible Interval (BCI) did not overlap with zero.

Finally, we used the estimates for the effects of woody flower abundance and herbaceous flower abundance to project long-term species richness trends. … by simulating from the posterior distribution produced by our model. Assuming the same stochastic ecological processes proposed by our model we summed the number of species occurring after we simulated occurrence as binomial trial with probability PSIijk, where the expected value PSIijk is determined by randomly drawing an iteration of the HMC and pulling the parameter values proposed at that step of the iteration. By repeating this random draw procedure and simulation we propagated uncertainty from our model estimates into uncertainty about the species richness at each potential site. We did this for sites along a proposed continuum of herbaceous flower abundances while holding woody flower abundance constant, and vice versa, to observe how the effects of these park management aspects on species-specific dynamics scale up to community outcomes.

**Results**

**Figure 1: Site map**

**Figure 2: Diet specialization histogram with pollinators**

**Figure 3: Metacommunity dynamics with respect to herb and woody – community averages in column 1 and diet breakdown in column 2.**

**Figure 4: Species richness with respect to herb (A) woody (B) and binary meadow for average woody (C).**

**Figure 5: Pollen limitation outcome**

A collage of different colored lines

Description automatically generated

**A close-up of a graph

Description automatically generated**

A close-up of a flower

Description automatically generated**Figure X:** When stigmatic surfaces were receptive (A), we supplemented a load of fresh conspecific pollen on one flower for each *Clarkia amoena* plant our study (B). We compared the seed set of the fruit capsule from the pollen supplemented flower against the seed set for a fruit capsule developing from a paired flower on the same plant that developed under ambient pollination conditions. Comparison flowers that produced fewer than 50% of seeds relative to the pollen supplemented flower on the same plant were scored as pollen limited. We then tested the association between flower abundance and the probability of pollen limitation (C). Dark and light grey uncertainty bands indicate 50% BCI and 95% BCI’s. Jittered points show the pollen limitation outcomes for the 175 plants from the 11 sites included in the experiment.

**Discussion**

Big ideas

Ending with application implications.

**References**